

A review of the genus *Hydrocynus* Cuvier 1819 (Teleostei: Characiformes)

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Introduction

The genus *Hydrocynus* is a member of the Characidae (Order Characiformes) one of the largest families of freshwater fishes found in both Africa and the Neotropics. *Hydrocynus* is, however, endemic to Africa, (see p. 201 for details of distribution). As noted by Weitzman & Fink (1983: 340), the current classification of the characids is problematical. Roberts (1969: 443) divided the African Characidae into the sub-families Hydrocyninae, (to include only *Hydrocynus*) and Alestiinae (to include all remaining African characids). Géry (1977: 18) subsequently erected the family Alestidae to include Roberts's sub-families Hydrocyninae and Alestiinae and restricted the Characidae to include only Neotropical taxa. Géry's (1977) work was not based on a cladistic analysis of the Characidae (*sensu* Greenwood *et al.* 1966) and the characters he used to define the Alestidae appear to be a mixture of plesiomorphies and apomorphies. Vari (1979: 342) included Roberts's Hydrocyninae with the Alestiinae because the latter represented a non-monophyletic assemblage with some of its members being more closely related to *Hydrocynus* than to members of their own sub-family. The current classification of the characids is clearly unsatisfactory but pending further phylogenetic analysis the concept of the Characidae *sensu* Greenwood *et al.* (1966) is followed here.

Species of *Hydrocynus* are pike-like predators, commonly termed 'tigerfishes' for their prominent dentition and dark lateral stripes. The genus was first described by Cuvier (1819) and characterized by him as follows:

... par des dents peu nombreuses, longues, coniques, très-aiguës tranchantes par les bords, qui se croisent quand la bouche est fermée, et qui ne sont pas recouvertes par les levres. J'en trouve 7 à chaque intermaxillaire, ce qui fait en tout 14 pour la mâchoire supérieure, mais les trois dernières de chaque côté sont beaucoup plus petites que les autres; il n'y en a que 6 de chaque côté à la mâchoire inférieure, et ce sont les deux dernières qui sont petites. On compte donc 8 grandes dents à chaque machoire. La gueule n'est pas très fendue, et le maxillaire qui n'a pas de dents se recourbe transversalement sur la commissure. La langue et le palais sont lisses, et les os pharyngiens garnis de dents en velours.

With the exception of the teeth overlapping the jaws when the mouth is closed, these characters are applicable to all other members of the Characidae. Valenciennes (1849) added to this list, the presence of an adipose eye-lid, a feature found in other members of the Characidae, such as the African genus *Alestes*, in other characiforms for example the Neotropical families Curimatidae and Hemiodontidae and in unrelated teleosts, notably members of the Clupeidae and Mugilidae.

Boulenger (1907) redefined the genus *Hydrocynus* using the following principal characters: teeth in a single series; a moderately large maxilla which slips beneath the second infraorbital; an elongate body; a large supraorbital bone; a fontanelle present in juveniles, separating the frontals posteriorly and the parietals entirely; a large air-bladder with a posterior chamber about three times the length of the anterior chamber, and a strongly ossified skull. Again, with one exception (see below) these characters are applicable to other members of the Characidae.

Of those characters given by Cuvier (1819) and Boulenger (1907), only two are synapomorphic for species of the genus *Hydrocynus*; viz: moderately large maxilla which slips beneath the second infraorbital; uniserial teeth that overlap the opposing jaw. Roberts (1966, 1967 & 1969) remarked on certain features such as jaw and tooth structure, tooth replacement, posttemporal fossae and presence of an orbitosphenoid tube. On the basis of these characters, Roberts (1966: 215; 1967: 242; 1969: 443) postulated *Hydrocynus* to be related to the African characid genus *Alestes*. However, in the absence of any osteological definition of either *Hydrocynus* or *Alestes*, no evidence could be presented to either corroborate or refute Roberts's hypothesis of relationship between these genera.

There is also confusion concerning the validity of certain currently recognized species of *Hydrocynus*. Boulenger (1909) recognized five species solely on the basis of meristic characters for which there was overlap in the ranges. Boulenger (1901, 1907) commented that two of the recognized species of *Hydrocynus* were so alike that he hesitated to retain them as distinct species. Svensson (1933) also noted the close resemblance between some species; Johnels (1954) also found it very difficult to distinguish the species of *Hydrocynus* and concluded that the taxonomy of the genus was unsatisfactory. Nonetheless, all five species have continued to be recognized despite various authors' misgivings concerning their validity.

The aims of this paper are three-fold. Firstly, to define the genus on osteological characters; secondly to present an hypothesis of relationship to other characiforms by adopting a cladistic approach, and thirdly, to review the taxonomy of the contained species.

Note on the nomenclature

The application of the name *Hydrocynus* to the African tigerfishes has been a subject of controversy. Hasselquist (1757) described a taxon *Salmo dentex* from the Nile, which is now recognized as *Alestes dentex*. Forsskål (1775: 66) identified a Nilotic fish as *Salmo dentex* of Hasselquist. Unfortunately, this specimen is no longer extant (Klausewitz & Nielsen, 1965: 12) but the description and meristic data given by Forsskål are without doubt those of a tigerfish.

Lacepède (1803: 272–273) further confounded the issue as he regarded *S. dentex* of both Hasselquist and Forsskål to be synonyms of *Characinus dentex* (Geoffroy Saint Hilaire in Lacepède 1803). Geoffroy Saint Hilaire (1809) wrote at length of the differences between Hasselquist's *Salmo dentex* and the specimen identified as the same by Forsskål, although he did nothing to resolve the problem. In 1817, Cuvier introduced a new genus, *Hydrocynus* which included in a footnote Forsskål's *Salmo dentex* (non Hasselquist). In a later paper, Cuvier (1819: 353–357) gave Forsskål's *Salmo dentex* the name '*Hydrocyon forskahlii*' in an attempt to resolve the confusion that had arisen over the identity of this fish.

Rüppell (1829: 5) subsequently used the binomen *Hydrocyon dentex* for the tigerfish in question. However, Hasselquist's *S. dentex* is not available as the description precedes the starting point of zoological nomenclature (International Code of Zoological Nomenclature 1985: article 3). *Salmo dentex* (as of Forsskål) is not available as a senior synonym for *Hydrocynus forskahlii* under article 49 of the International Code of Zoological Nomenclature.

Materials

The osteology and soft anatomy were studied using ethanol preserved specimens, double stained alcian blue/alizarin red 'S' transparencies (following the procedure detailed by Dingerkus & Uhler, 1977), dry skeleton preparations, and radiographs.

Most of the material used in the preparation of this paper, is held in the British Museum (Natural History) (BMNH) collection, but additional specimens have been examined from the following institutions: Muséum National d'Histoire Naturelle, Paris (MNHN); Musée Royal de l'Afrique Centrale (MRAC); Institut Royal des Sciences Naturelles, Brussels (IRSN); Rijksmuseum van Natuurlijke Historie, Leiden (RMNH) and California Academy of Sciences (SU). A detailed list of the material examined is given in the species descriptions, and outgroup material examined is given in Appendix 1.

Note on the measurements

The standard length (SL) is measured from the tip of the snout, including premaxilla, to the region of the caudal peduncle approximating to the posterior margin of the hypural bones. Body depth is measured at the deepest part of the body anterior to the dorsal fin; head length is measured from the tip of the snout, including the premaxilla, to the posterior edge of the operculum; snout length is measured in the horizontal plane from the tip of the snout, including premaxilla, to the anterior margin of the eye. The interorbital width is measured as the greatest width of the frontals between the eyes. The 4th infraorbital is measured at the greatest width from the posterior margin of the eye to the posterior margin of this element. The depth of the premaxilla is measured in the mid-line from its junction with the supraethmoid to the base of the teeth. All measurements are made in millimetres and proportions are expressed as a percentage of the standard length.

The vertebrae are counted as abdominal (including the 4 Weberian elements) and caudal (including the first fused ural and preural centra).

Lateral line scale counts are taken from the first pore-bearing scale posterior to the supra-cleithrum to the origin of the caudal fin.

Abbreviations used in the figures

AA	anguloarticular	EPB	epibranchial
ABH	anterior basihyal	ES	extrascapular
AHY	anterohyal	EX	exoccipital
AO	antorbital	F	frontal
AP	premaxillary ascending process	FM	foramen magnum
BB	basibranchial	FR	fin rays
BO	basioccipital	H	hyomandibula
BSR	branchiostegal rays	HB	hypobranchial
C	claustrum	HP	hypural
CB	ceratobranchial	HS	hyomandibular spine
CE	centrum	HSP	haemal spine
CL	cleithrum	IC	intercalar
COR	coracoid	ICL	intercalarium
CSI	cavum sinus imparis	IH	interhyal
D	dentary	IO	infraorbital
DHY	dorsohyal	IOP	interoperculum
DR	distal radial	LE	lateral ethmoid
DSP	dermosphenotic	LP	lateral process of centrum 2
ECT	ectopterygoid	M	maxilla
END	endopterygoid	MC	mesocoracoid
EP	epioccipital	MET	metapterygoid

mm1F	maxillary-mandibular ligament facet	PTF	posttemporal fossa
MRP	median rostral process	PTS	pterosphenoid
N	nasal	PTT	posttemporal
NC	neural complex	PU	preural centrum
NSP	neural spine	PV	pelvic bone
OP	operculum	Q	quadrate
OS	orbitosphenoid	R	radial
P	palatine	RA	retroarticular
PA	parietal	S	scaphium
PB	pharyngobranchial	SC	supracleithrum
PBH	posterior basihyal	SCP	scapula
PC	postcleithrum	SO	supraoccipital
PC SB	posterior chamber of the swimbladder	SOP	suboperculum
PHY	posterohyal	SP	sphenotic
PLR	pleural rib	SP ST	sphenotic strut
PM	premaxilla	SU	supraethmoid
POP	preoperculum	SUO	supraorbital
PPLR	pleural rib articulating with postero-ventral surface of haemal spine	SYM	symplectic
PRO	prootic	TP	toothplate
PROX	proximal radial	TR	tripus
PS	parasphenoid	V	vomer
PT	pteric	VHY	ventrohyal

Osteology of the genus *Hydrocynus*

The description is based on *Hydrocynus forskahlii* Cuvier 1819, type species of the genus. The terminology of Weitzman (1962) is followed, with the following exceptions: vomer for prevomer and intercalar of opisthotic (Roberts, 1969); supraethmoid for ethmoid, and epioccipital for epiotic (Patterson, 1975); anguloarticular for articular, and retroarticular for angular (Nelson, 1973).

Kampf (1961) described the osteology and myology of *H. forskahlii* in a paper concerned with the comparative functional morphology of this species and *Gasterosteus aculeatus*, *Spinachia spinachia* and *Esox lucius*. I disagree with Kampf's identification and nomenclature of the cranial bones, those labelled prefrontal, prootic, epioccipital, ectethmoid and palatine by Kampf are identified here as supraethmoid, sphenotic, extrascapular, lateral ethmoid, and ectopterygoid respectively. In his figure 27 (p. 424) the bones labelled 'ectopterygoid' and 'endopterygoid' seem to be an endopterygoid that has fractured giving the appearance of two bones. Subsequent figures show this bone to be entire, and labelled as the 'ectopterygoid'.

Neurocranium

In dorsal view the *neurocranium* is tapered, being widest posteriorly.

The *supraethmoid* is a 'T'-shaped bone (Fig. 1A), its stem being slightly shorter than the broad lateral wings forming the cross-bar of the 'T'. The anterior border bears a median rostral process, with a shallow depression in the vertical mid-line. This depression accepts the ascending premaxillary processes while the lateral wings articulate with facets on the premaxillae (see pp. 171–172). The lateral supraethmoid wings are thick, blunt, transverse processes with a ventral curvature. A ligament connects the ventral portion of the lateral supraethmoid wing to the palatine (see p. 175). Each lateral supraethmoid wing rests laterally in the dorsomedial premaxillary facet and contacts the anterior tip of the ascending limb of the maxilla; the whole complex is tightly bound by connective tissue. Ventrally, the supraethmoid and vomer meet at a straight, transverse juncture. The *nasals* are rod-shaped and lie lateral to the supraethmoid.

The *vomer* is a rectangular bone with an elliptical, posteriorly directed process (Fig. 1C). Posterodorsally, the main part of this bone contacts the lateral ethmoid; the dorsal surface of the

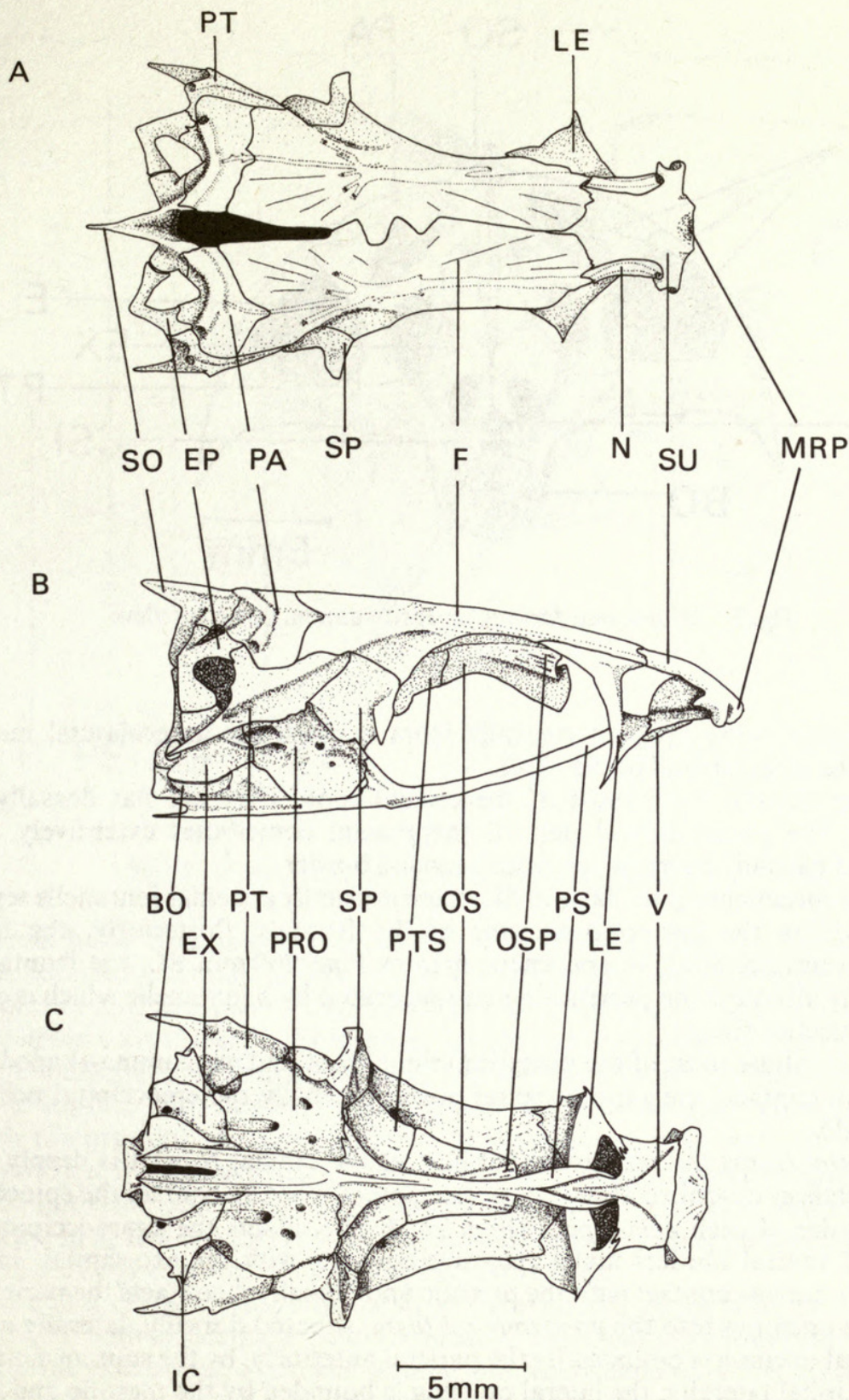


Fig. 1 *Hydrocynus forskahlii* neurocranium: A, dorsal view; B, right side, lateral view; C, ventral view.

posterior process contacts the parasphenoid. Ventrally, the vomer is formed into a 'V' shaped ridge (Fig. 1C), although the development of this ridge appears to be variable.

The *lateral ethmoid* lies beneath the anteroventral portion of the frontal. The paired lateral ethmoid elements contact the supraethmoid cartilage in the mid-line. Each bone has a medially situated foramen for the passage of the olfactory nerve. In some specimens larger than 400 mm SL a tubular ossification extends posteriorly from around the olfactory foramen and contacts the posterior part of the orbitosphenoid process.

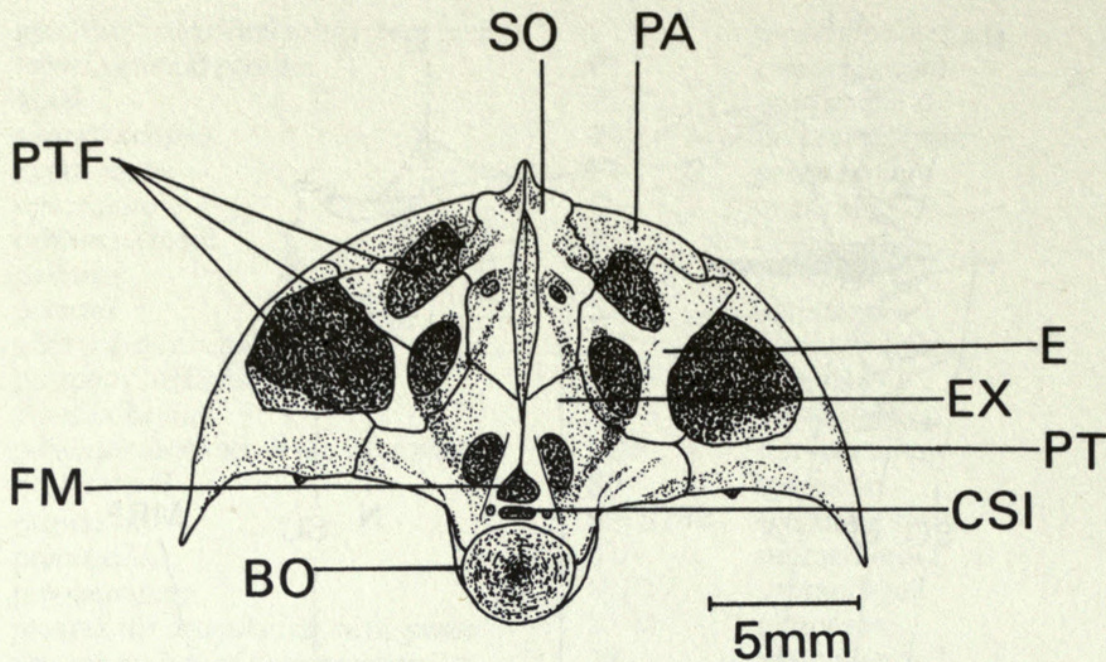


Fig. 2 *Hydrocynus forskahlii* neurocranium, posterior view.

The lateral ethmoid wing projects ventrally from beneath the anterolateral margin of the frontal, forming the anterior wall of the orbit.

The rectangular *frontals* form most of the cranial roof. They are flat dorsally with well-developed striae. The posterolateral part of the frontal contributes extensively to the long dilator fossa and partially overlaps the fossa's medial border.

In juveniles and specimens up to 300 mm SL, there is usually a medial fontanelle separating the parietals and dividing the posterior margins of the frontals. Posteriorly, the fontanelle is bordered by the supraoccipital. In specimens greater than 300 mm SL, the frontals abut one another posteriorly although the parietals remain separated by a fontanelle which is covered by a thick sheet of connective tissue.

The *parietals* contribute most of the posterior cranial roof and are comma-shaped bones (Fig. 1A). Each parietal contacts the supraoccipital posteromedially the epioccipital posteriorly and the pterotic laterally.

The *supraoccipital* forms the posteromedial part of the cranial roof; it is deeply sulcate and contacts the parietals as described above; its posterolateral borders contact the epioccipitals.

The medial border of each *epioccipital* (Figs 1A & 2) contacts the supraoccipital, while the ventromedial and ventral borders make extensive contacts with the exoccipital. Laterally, the epioccipital makes narrow contact with the pterotic and dorsally it contacts the parietal.

There are three openings into the *posttemporal fossa*, situated dorsally, laterally and medially (Fig. 2). The dorsal opening is bounded by the parietal anteriorly, by the supraoccipital medially, and by the epioccipital laterally; the lateral opening is bounded by the pterotic and epioccipital; the medial opening is contained entirely within the epioccipital.

The *exoccipitals* are irregular in shape (Fig. 2). Each contacts the supraoccipital dorsally and epioccipital dorsolaterally, the pterotic laterally, the basioccipital ventrally and the prootic anteroventrally. Medially, both exoccipitals contact each other dorsal and ventral to the foramen magnum and cavum sinus imparis. The intercalar (see below) lies ventral to the suture between the exoccipital and pterotic. The exoccipital is pierced posterolaterally by the large foramen for the tenth cranial (vagus) nerve. Together, the ventral part of the exoccipital and the dorsal part of the basioccipital form the small, slightly inflated lagenar capsule (Fig. 1B). In specimens up to 120 mm SL the capsule is greatly inflated, a characteristic of all characiforms (see Fink & Fink, 1981: 315). Species of *Hydrocynus*, however, attain a much larger size than most other characiforms, thus the apparently reduced inflation is a negatively allometric phenomenon.

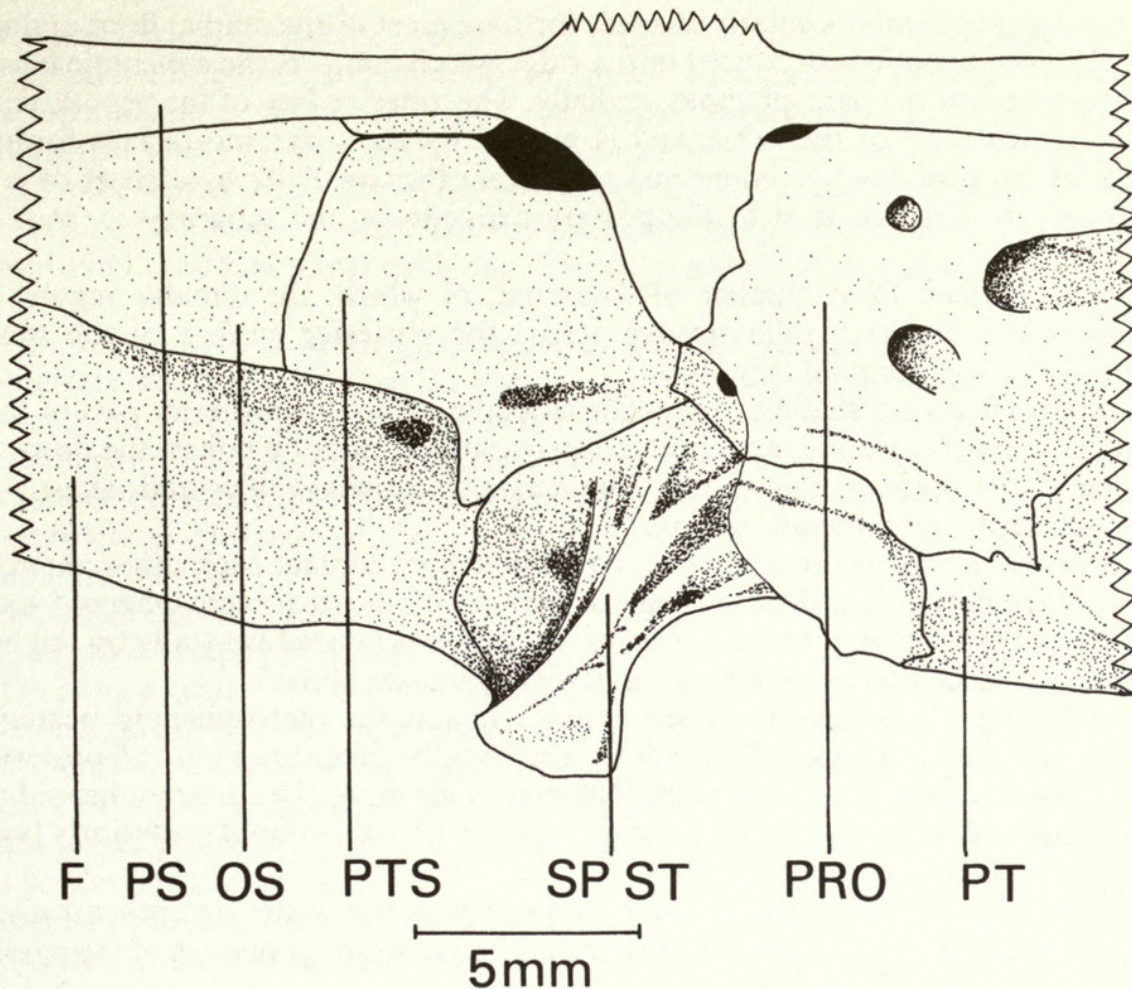


Fig. 3 *Hydrocynus forskahlii* orbito-otic region, ventral view.

The *intercalar* has a flask-shaped outline (Fig. 1C) and lies ventral to the suture between the pterotic and exoccipital, contacting the prootic anteriorly. The intercalar bears a short, thorn-like posterior process which is connected ligamentously to the posttemporal (see p. 179).

The *basioccipital* contributes to the lagenar capsule (see above) and is bordered by the prootics anteriorly; the parasphenoid ventromedially, and the exoccipitals dorsally (Fig. 1B & C). It is divided bilaterally into bony lamellae which contact the parasphenoid ventrally. These lamellae, together with the prootics and posterior part of the parasphenoid form the floor of the large posterior myodome. In specimens up to 600 mm SL the myodome opens ventrally through a deep notch in the posterior section of the parasphenoid (Fig. 1C). This ventral opening closes ontogenetically, in specimens above 600 mm SL, the notched parasphenoid is progressively less evident and in the largest specimens examined is just visible.

Each *pterotic* (Figs 1B & C) forms the posterolateral portion of the cranium and contacts on its side, the parietal and epioccipital posterodorsally, the frontal anterodorsally, the sphenotic anteriorly and the exoccipital, intercalar and prootic ventromedially. The posterolateral surface of the bone contributes to the dilatator fossa, which continues posteriorly as a groove. The pterotic has a long posteroventrally directed spiny process from which originate, anteriorly, the *levator operculi* muscle; ventrally it provides the site of origin for the *protractor pectoralis* muscle, and posterodorsally an insertion for part of the epaxial body musculature.

The ventrolateral surface of the pterotic is deeply indented by the hyomandibular fossa, which articulates with the posterodorsally situated hyomandibular facet.

The *sphenotic* contacts the frontal dorsally, and forms the anterior surface of the long, deep dilator fossa (Fig. 1b). The sphenotic spine forms the posterior margin of the orbit; ventrally it is expanded to form a short thick process (Fig. 1B) from which the *levator arcus palatini* muscle dilator fossa (Fig. 1B). The sphenotic spine forms the posterior margin of the orbit; ventrally it is bone (Fig. 3), the posteromedial edge of which contacts the sphenotic facet. The sphenotic facet articulates with the anterodorsal surface of the hyomandibula.

The *prootics* are large and irregularly shaped, forming most of the cranial floor and wall (Fig. 1C). Anteriorly, each prootic is produced into a ridge which contacts the sphenotic laterally and the ascending process of the parasphenoid medially. The anterior face of the prootic contributes to the posteroventral wall of the orbit, and is pierced by the trigemino-facialis foramen. The anterior faces of the prootics, are connected to one another medially by a sheet of connective tissue that forms the anterior roof to the posterior myodome and separates it from the optic nerve.

The prootic is pierced by a number of foramina, of which, the circular jugular foramen continues posteriorly as the jugular groove across the posterior surface of the prootic and anterior margin of the exoccipital (Fig. 1C).

The subtemporal fossa is a shallow depression extending from the posterior part of the prootic to the suture between the prootic, exoccipital, intercalar and pterotic bones, the deepest part of the fossa lying at the point of this suture. The *adductor hyomandibulae* and *adductor operculi* muscles originate from the subtemporal fossa.

The *pterosphenoid* bones are roughly hexagonal in shape, contact each other anteromedially and form part of the posterior wall of the orbit. Posteromedially, each pterosphenoid is separated from its partner by the foramen for the optic nerve, which is floored ventrally by the horizontal sheet of connective tissue that extends between the prootics (see above).

The *orbitosphenoid* is a rectangular bone which contacts the pterosphenoid posteriorly and frontal dorsally; a tubular process (Fig. 1B & C), encloses the olfactory bulb and posterior end of the olfactory nerve. In some large specimens (400 mm SL or more), the orbitosphenoid process is sutured to a similar tubular process that extends from the lateral ethmoid posteriorly (see p. 167). The olfactory nerve is thus entirely enclosed.

The *parasphenoid* is a stout, elongate bone that contacts the vomer anteroventrally, and the prootic and basioccipital posterolaterally (Fig. 1C). The ascending processes of the parasphenoid are convex where they meet the prootic.

Jaws

In lateral view, the *lower jaw* is elongate, roughly triangular and deepest posteriorly, where the dorsal surface is rather convex (Fig. 4). The *dentary* tapers anteriorly and is joined to its partner by an interlocking symphysial hinge (described by Eastman, 1917). The medial wall of the dentary contains a roofed over replacement tooth trench, that is pierced by large foramina

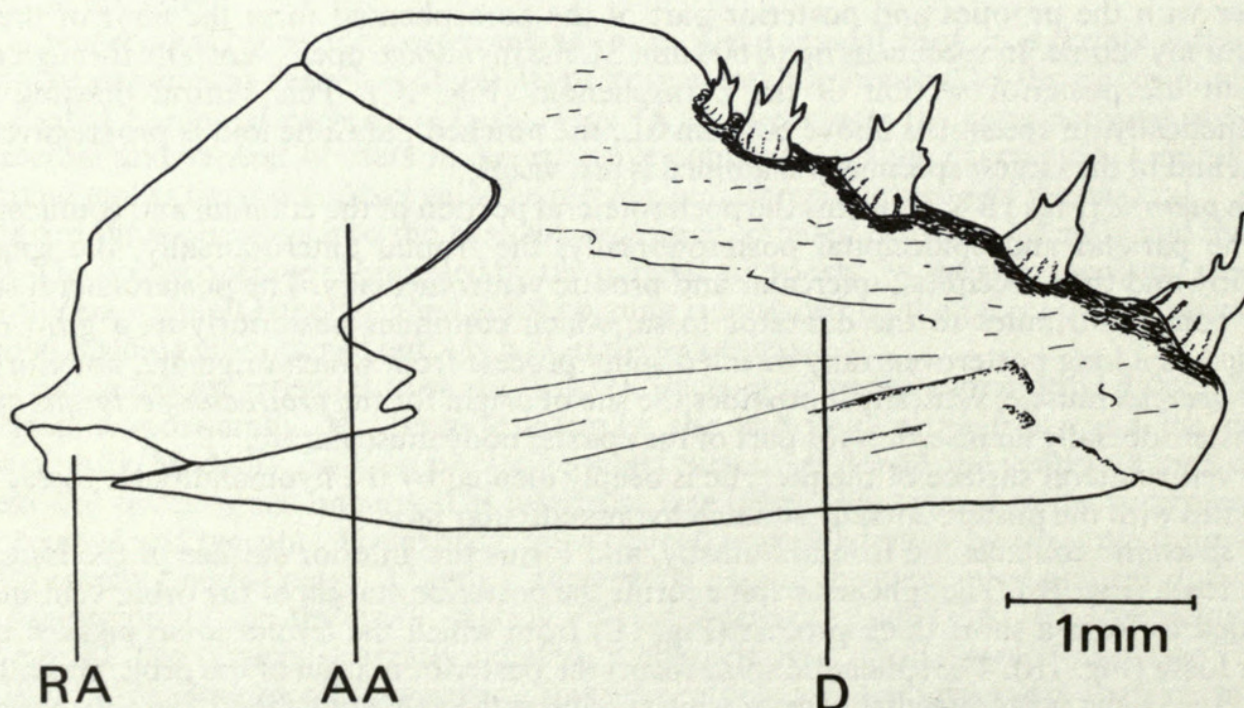


Fig. 4 *Hydrocynus forskahlii* lower jaw, right side, lateral view.

immediately above each replacement tooth (see Roberts, 1967: 233). The trench is referred to herein as 'replacement cavities' in preference to 'trench' because the individual replacement teeth are compartmentalized as opposed to being compressed together in an open trench, as in other African characids. There are five tooth replacement cavities, the anterior four each containing a single large tooth, whereas the fifth may contain one or two small, usually tricuspid teeth. The replacement teeth are directed posterodorsally with their tips just protruding above the rim of the replacement cavity. The functional teeth are widely and evenly spaced along the dorsal border of the dentary.

Posteriorly, the dentary is sutured to the *anguloarticular*, the latter having a diarthritic joint with the quadrate. Meckel's cartilage lies between a small posterior process on the anguloarticular and an anterior dentary process. The small triangular coronomeckelian bone lies dorsal to Meckel's cartilage on the anteromedial surface of the anguloarticular. The posteroventral edge of the anguloarticular is grooved to accommodate the small, wedge-shaped *retroarticular*.

The posterolateral surfaces of the dentary and anguloarticular are broadly recessed to accommodate the maxilla.

The *premaxillae* are elongate bones, each bearing 6 or 7 functional teeth, and are united anteromedially by a symphysial hinge. Unlike the halves of the lower jaw, the premaxillae do not interlock but have a syndesmotic connection. As in the dentary, the tooth replacement trench is roofed over and partitioned into usually five replacement cavities. The posterior cavity may contain two or more small, tricuspid replacement teeth; the other four cavities each contain a single large conical tooth. The replacement teeth are orientated posterodorsally within the cavities, with their tips just projecting beyond the rim. The functional teeth are widely and evenly spaced along the ventral border of the premaxilla.

The ascending process of the premaxilla is a short, square blade with a small dorsal notch (Fig. 5). Posteromedial to the ascending process there is an articular fossa, which articulates with the lateral border of the supraethmoid process. A second, dorsomedially situated facet accommodates the lateral supraethmoid wing. This coupling of the supraethmoid and premaxillae forms a condylar joint permitting a limited dorsoventral rotation of the upper jaw.

Distally, the premaxilla is very deep and its dorsomedial surface is grooved to accommodate the ascending limb of the maxilla. Posteroventrally, the premaxilla and maxilla are ankylosed, although they can be separated in specimens up to 100 mm SL.

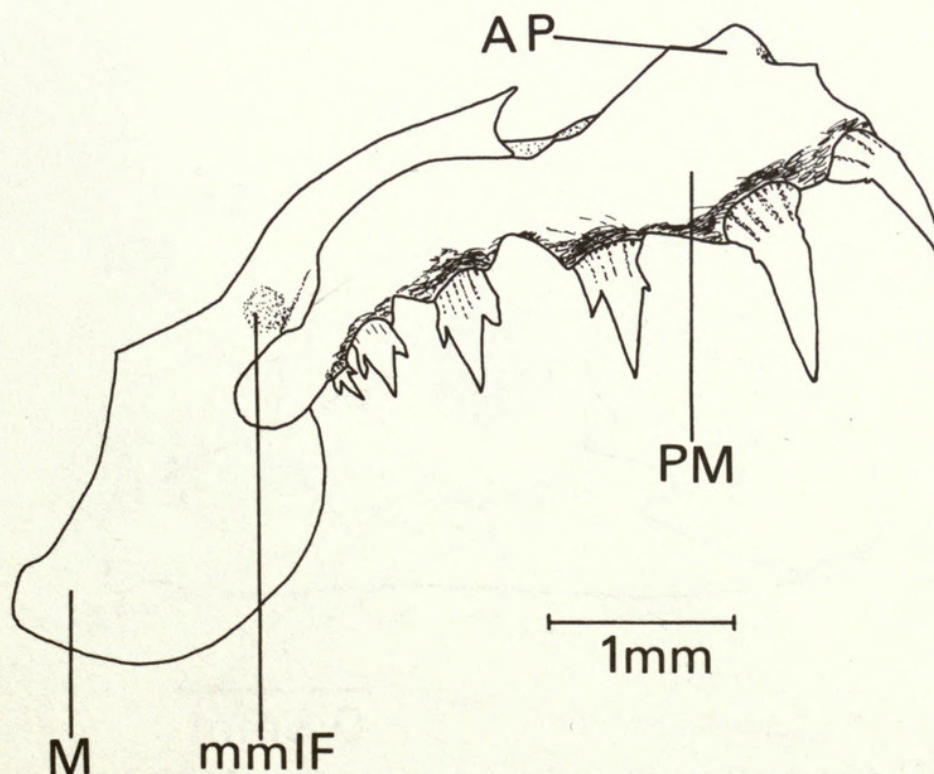


Fig. 5 *Hydrocynus forskahlii* upper jaw, right side, lateral view.

The *maxilla* is an edentulous, lamellar bone with an anteriorly curved, ascending process that rests on the premaxilla (see above; Fig. 5). The anterolateral face of the maxilla bears a small depression to which the maxillary-mandibular ligament is attached. Dorsomedially, the posterior margin of the maxilla has a small cup-shaped protuberance onto which insert some dorsomedial fibres of the *adductor mandibularis* muscle.

Teeth

The smallest alizarin/alcian blue stained specimens examined (16 mm, 22 mm, 23 mm and 25 mm SL (BMNH 1981.2.17: 2600–2609)) display a transition from a conical to tricuspid dentition. The 16 mm SL specimen is heterodont, with 14 upper and 8 lower jaw teeth, of which 2 on either side of the upper jaw and a single tooth on the lower jaw are tricuspid. The remaining teeth are all conical in the upper jaw and right dentary (Fig. 6), but are bicuspid in the left dentary. The conical juvenile teeth are simple, uniserial, translucent and, in the upper jaw they contact one another, thus closely resembling the conical dentition of the dwarf characid, *Lepidarchus adonis*.

This 16 mm specimen has 8 upper and 6 lower tricuspid replacement teeth, which lie medial to the functional dentition. Each tricuspid replacement tooth can be separated into three conical elements, thus suggesting that such teeth are formed by the fusion of 'juvenile' conical elements (see also p. 187).

The 22 mm SL specimen retains a conical tooth on each side of the upper jaw, which closely contacts the anterior second tricuspid tooth; all other functional and replacement teeth are tricuspid. Diastemata separate the functional teeth.

The 23 and 25 mm SL specimens have a functional and replacement dentition of 12 upper and 8 lower tricuspid teeth. A specimen of 40 mm SL has conical teeth anteriorly in both jaws but

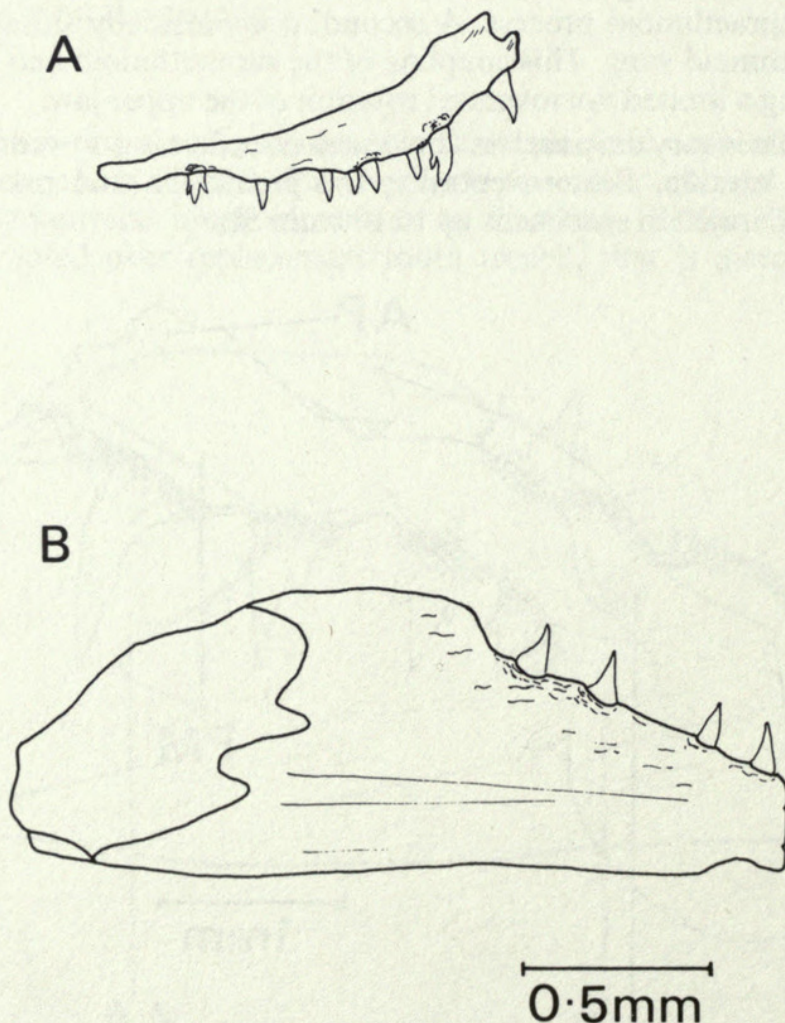


Fig. 6 *Hydrocynus forskahlii* 16 mm SL specimen: A, premaxilla, right side, lateral view; B, lower jaw, right side, lateral view.

each tooth has lateral cusps in the form of very small, nipple-like protuberances. The posterior teeth of this specimen are all tricuspid with well-developed lateral cusps.

In specimens larger than 50 mm SL the lateral cusps on the anterior teeth are difficult to detect but the teeth at the posterior margin of each jaw are always tricuspid (see also p. 187).

The attachment of the teeth to the jaw is type 1 (*sensu* Fink, 1981), that is they are completely ankylosed to the bone.

Circumorbital series

The *antorbital* is a small ovate bone tightly bound by connective tissue to the anteroventral margin of the supraorbital and the posterodorsal margin of the first infraorbital.

The *first infraorbital*, or lachrymal, is a triangular bone that lies lateral to the posterior third of the premaxilla. Dorsally it contacts the antorbital (see above), and ventrally the second infraorbital. The laterosensory canal runs through the orbital margin of the circumorbitals.

The *second infraorbital* is very large and covers the posteroventral surface of the upper and posterodorsal surface of the lower jaws, and lying lateral to the posterior surface of the maxilla (Fig. 7). Ventromedially, the second infraorbital is secured to the posterior margin of the anguloarticular by a sheet of connective tissue which also covers the maxillary-mandibular ligament. Posteriorly, the second infraorbital contacts the third infraorbital.

The *third infraorbital* is extensive, covering most of the cheek musculature. The *fourth* and *fifth infraorbitals* are also large but, unlike the others, are rectangular. The fifth infraorbital contacts the sphenotic spine anteromedially.

The *dermosphenotic* (sixth infraorbital) is ovoid, posterodorsally curved, and contacts the frontal dorsally, where that bone is indented by the dilatator fossa. The dermosphenotic covers the posterior part of the *dilatator operculi* muscle. The laterosensory canal bifurcates in the dermosphenotic; the anterior branch is continuous with the supraorbital canal, the posterior branch contacts the parietal canal and the ventral branch communicates with the canal of the 5th infraorbital.

The *supraorbital* is an elongate bone that lies anterior to the dermosphenotic. It has extensive contact with the lateral margin of the frontal and contacts the antorbital anteriorly (see above).

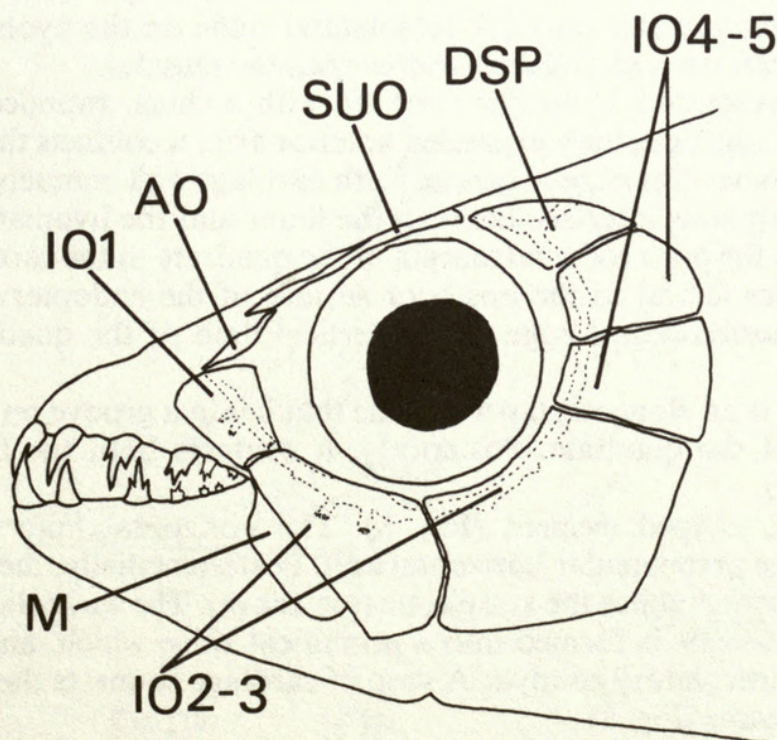


Fig. 7 *Hydrocynus forskahlii* circumorbital series, left side.

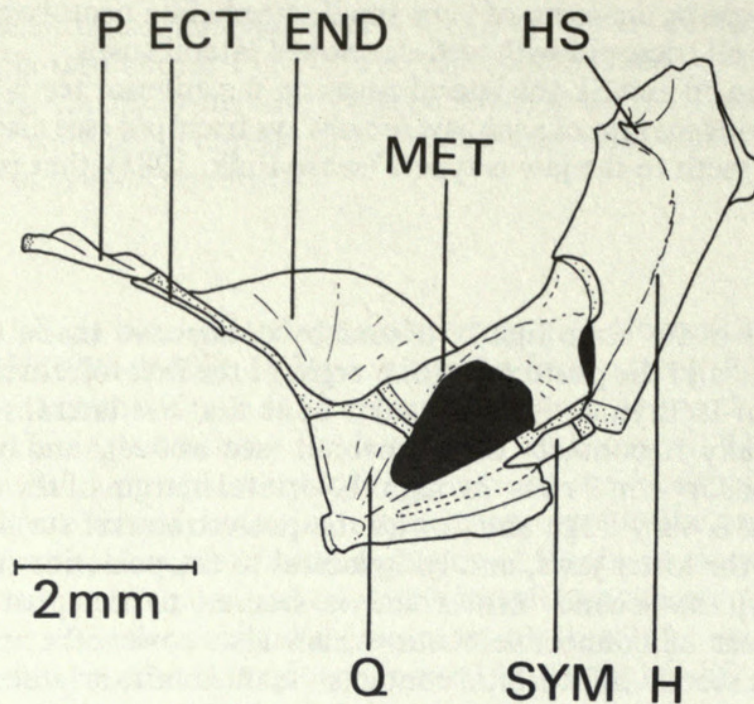


Fig. 8 *Hydrocynus forskahlii* hyopalatine arch, left side, lateral view. Stippling represents cartilage.

Hyopalatine arch

The *hyomandibula* is roughly rectangular in outline, with a strong posterodorsally inclined shaft (Fig. 8). It has a long dorsal condylar articulation with the cranium, and posteriorly, a condylar articulation with the operculum. There are two points of contact between the hyomandibula and metapterygoid (Fig. 8). The anterior edge contacts the short posterior arm of the metapterygoid, and the anteroventral surface of the shaft contacts the posteroventral angle of the metapterygoid. An elongate and narrow, near crescentic foramen separates the hyomandibula and metapterygoid between these points of contact (Fig. 8). The posterodorsal edge of the hyomandibular shaft is deeply grooved to accommodate the anterodorsal edge of the ascending arm of the preoperculum. Ventrally, the hyomandibular shaft lies medial to the preoperculum.

There is a distinct anterolaterally directed dorsolateral spine on the hyomandibula (Fig. 8), which separates the *dilatator operculi* and *levator arcus palatini* muscles.

The *metapterygoid* is axe-shaped in outline (Fig. 8), with a short, rounded posterior arm, a broad ventral arm and a long, anteriorly expanded anterior arm; it contacts the hyomandibula in two places (see above). Its ventral edge is capped with cartilage and contacts the margin of the symplectic and the cartilaginous interface between the latter and the hyomandibula (Fig. 8). A strip of cartilage connects the posterodorsal margin of the quadrate to the cartilage of the ventral arm. The anterior arm lies lateral to the posterior surface of the endopterygoid (Fig. 8), and anteriorly contacts the posterodorsal edge of the vertical limb of the quadrate at a cartilage interface.

The *symplectic* (Fig. 8) is an elongate, tapered bone that lies in a groove on the medial surface of the horizontal limb of the quadrate. Posteriorly, it contacts both the hyomandibula and metapterygoid (see above).

The *quadrate* is an 'L'-shaped element (Fig. 8). The horizontal limb lies lateral to the anterodorsal surface of the preopercular horizontal arm. Posteromedially, there is a deep groove in the quadrate which accommodates the symplectic (see above). The ventrolateral surface of the horizontal limb of the quadrate is formed into a prominent ridge which, anteriorly, forms the lateral facet of the stout articulatory condyle. A strip of cartilage connects the anterodorsal edge of the quadrate to the palatine (Fig. 8).

The *metapterygoid-quadrate fenestra* is ovate and bordered by the metapterygoid and quadrate. The fenestra is filled by a sheet of connective tissue.

The *endopterygoid* is a fan-shaped bone. Its borders lie medial to the metapterygoid, quadrate and to the cartilaginous strip connecting the quadrate and palatine (Fig. 8). A sheet of connective tissue joins the dorsal edge of the endopterygoid to the ventral border of the parasphenoid.

The *ectopterygoid* is a small, edentulous and thin disc, which lies on the anteroventral margin of the palatoquadrate arch (Fig. 8). Anteriorly, it contacts, and is ligamentously joined to, the posteroventral edge of the palatine. The ectopterygoid and palatine are tightly bound by connective tissue.

The *palatine* is an approximately rectangular block of bone, its cartilaginous head articulating with the lateral facet on the lateral wing of the supraethmoid (see p. 166). The palatine head is also ligamentously secured to the supraethmoid and to the ventral surface of the vomer.

Opercular series

The *operculum* is roughly triangular, with an anteromedially situated condyle for articulation with the hyomandibula. Its ventral surface lies lateral to the suboperculum, whereas the anterior margin lies medial to the vertical limb of the preoperculum. Anteroventrally, the operculum contacts and is slightly overlapped by the interoperculum.

The *preoperculum* is crescentic, with a well-developed lateral sensory canal in both the vertical and horizontal arms (Fig. 9). The anterodorsal surface of the horizontal arm lies medial to the quadrate. A short ligament connects the anteroventral tip of the horizontal arm to the retroarticular. Ventrally, the horizontal preopercular arm lies lateral to the interoperculum.

The vertical arm of the preoperculum lies lateral to the hyomandibular shaft anteriorly, and to the operculum posteriorly.

The *interoperculum* is a long, anteriorly tapered bone (Fig. 9). The dorsal margin has two slight protuberances which contact the preoperculum posteriorly and the ventral surface of the quadrate anteriorly. Posteriorly the interoperculum lies lateral to the anterior edge of the suboperculum. Medially, the interoperculum is held in place by a connective tissue sheet which surrounds the opercular series.

The *suboperculum* is a long posteriorly tapered bone, with a small anterodorsal process (Fig. 9). The posterior and ventral edges of the suboperculum are poorly ossified.

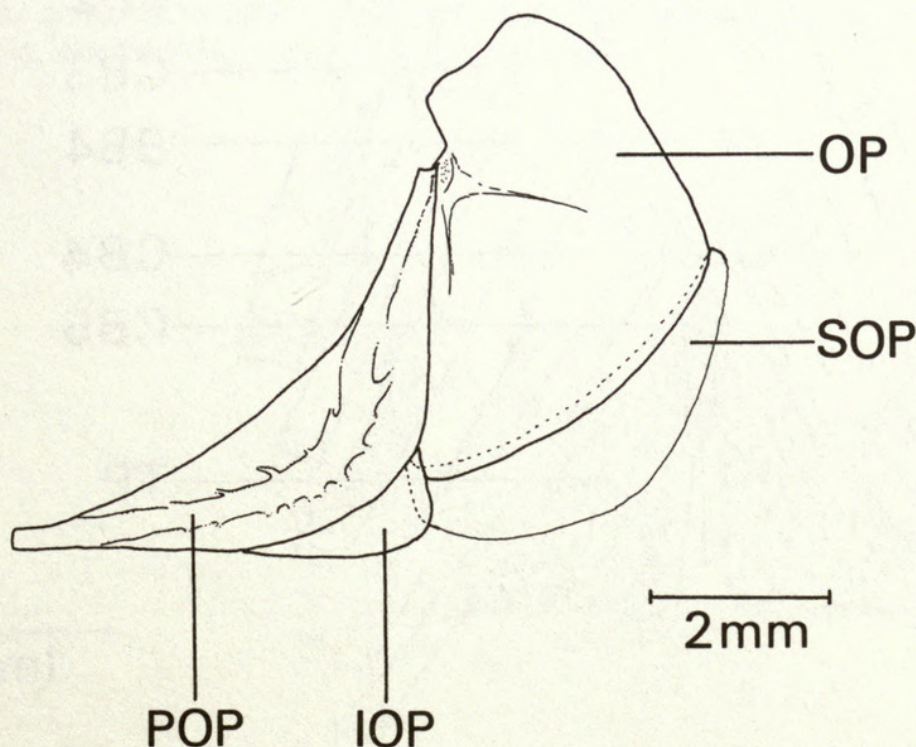


Fig. 9 *Hydrocynus forskahlii* opercular series, left side, lateral view.

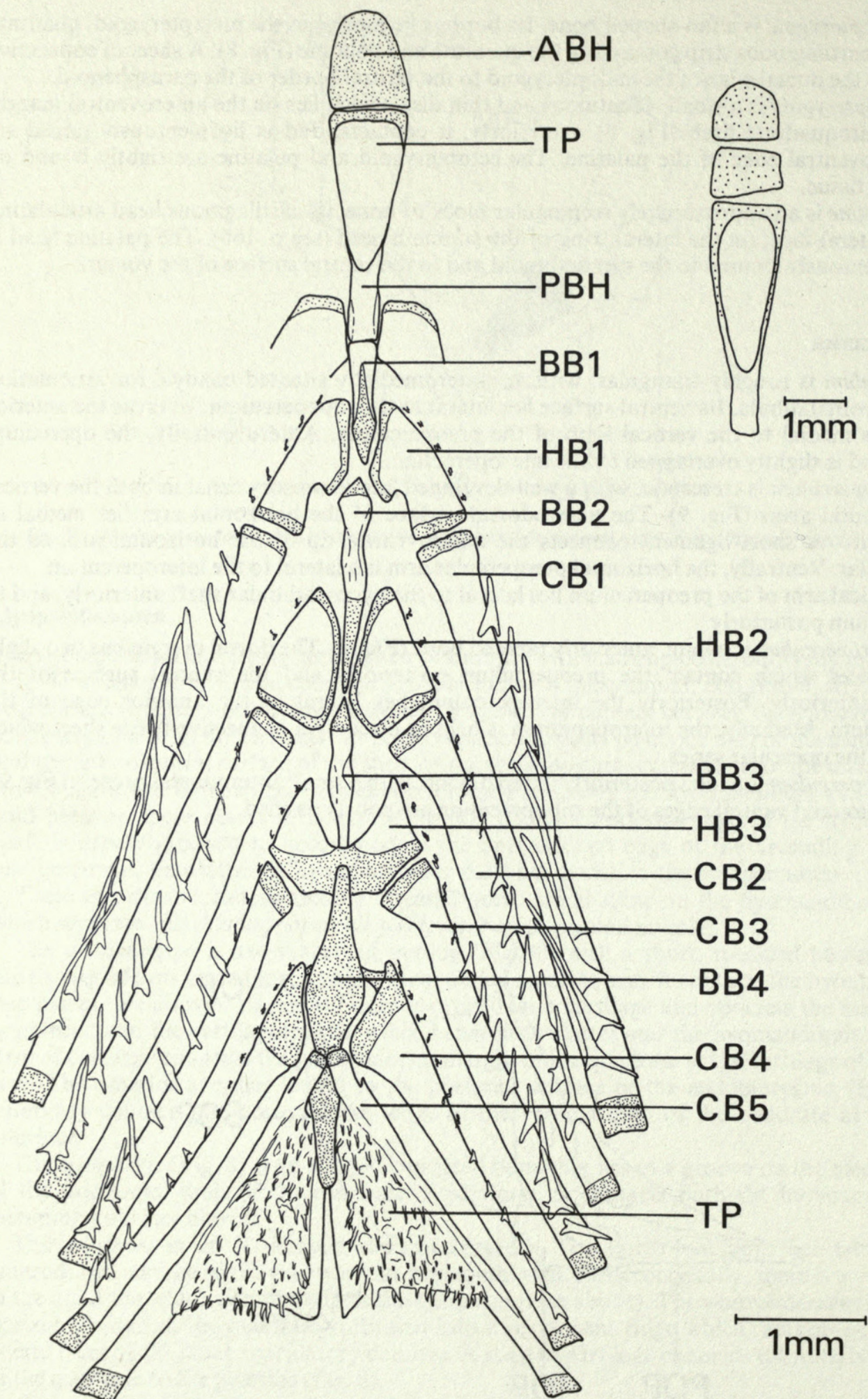


Fig. 10 *Hydrocynus forskahlii* lower gill arch, dorsal view. Stippling represents cartilage.

Fig. 11 Upper right: *Hydrocynus goliath* fragmented basihyal, dorsal view.

Hyoid and branchial arches

The *basihyal* is fragmented; anteriorly a dome-shaped cartilage bloc articulates with the larger, partially ossified posterior section of this element (Fig. 10). In some specimens larger than 100 mm SL the anterior basihyal element is represented by two cartilage blocs; the anterior one is dome-shaped and articulates with a second and square cartilage bloc which, in turn, articulates with the larger posterior section (Fig. 11). The posterior element is connected to the anterior cartilage bloc(s) by dense connective tissue. A ligament connects the dorsolateral surface of the ventrohyal to the connective tissue of the posterior basihyal element and anterior cartilaginous element or elements.

The posterior section of the basihyal is spatulate, ossified posteriorly but cartilaginous anteriorly (Fig. 10); its anterodorsal surface lies below a large elongate, ovoid edentulous tooth-plate (Fig. 10). Posteriorly, this section of the basihyal articulates laterally with both the first basibranchial and with each dorsohyal.

The *dorsohyal* (Fig. 12) is an axe-shaped bone, which articulates anteromedially with the posterior basihyal element, just anterior to the articulation between the latter and the first basibranchial. The dorsohyal is surrounded by connective tissue which also connects this element to the posterior, ossified section of the basihyal. Posteriorly, the dorsohyal contacts the anterohyal at a cartilage interface. The dorsohyal contacts the ventrohyal anteroventrally.

The *ventrohyal* (Fig. 12) is rectangular, with a prominent anteroventral process. The anterior surface of the process is connected by a short, strong ligament to an anterolateral facet on the urohyal. The ventrohyal contacts both the dorsohyal anterodorsally and the anterohyal posteriorly at a cartilage interface.

The *anterohyal* (Fig. 12) is waisted in lateral view, with a finger-like process anterodorsally that lies between the dorso- and ventrohyals. A blood vessel enters the anterohyal posteriorly, passes through a dorsolateral canal and emerges anteriorly at the ventromedial surface of the finger-like process.

The *posterohyal* is quadrilateral; its ventral surface capped with cartilage which is continuous anteriorly with the cartilage interface between the postero- and anterohyals. The blood vessel associated with the anterohyal (see above) passes medial to the posterodorsal surface of the posterohyal, enters the large foramen which pierces the posterohyal dorsally, to run across the lateral surface of this bone and the cartilage interface before entering the anterohyal canal.

The *interhyal* is a short, rod of bone with a lateral cartilaginous cap, it articulates with the medial face of the posterohyal and is connected *via* a short ligament to the cartilage interface of the hyomandibula, symplectic and metapterygoid laterally.

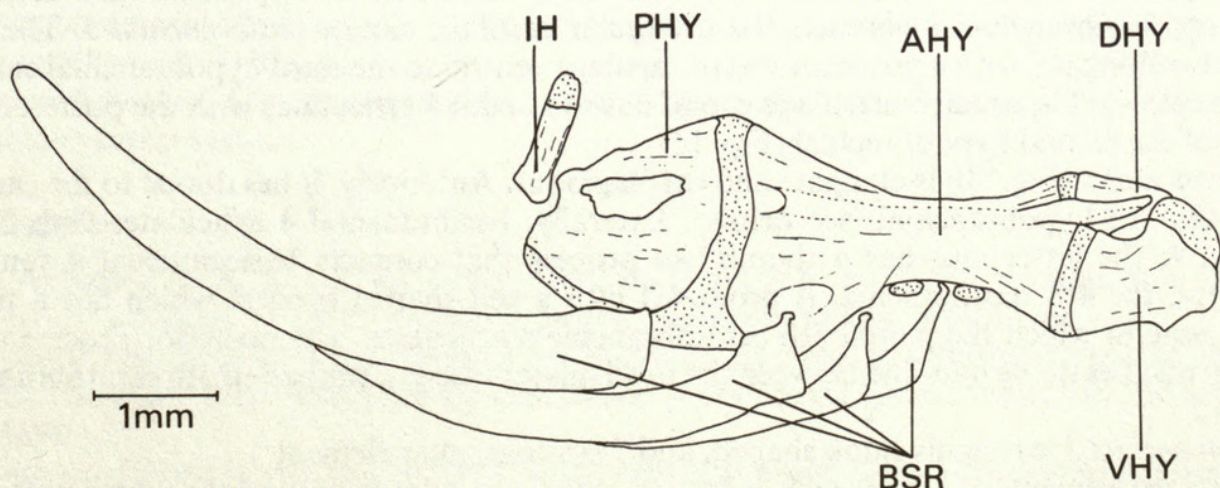


Fig. 12 *Hydrocynus forskahlii* hyoid arch right side; lateral view; basihyal not included.

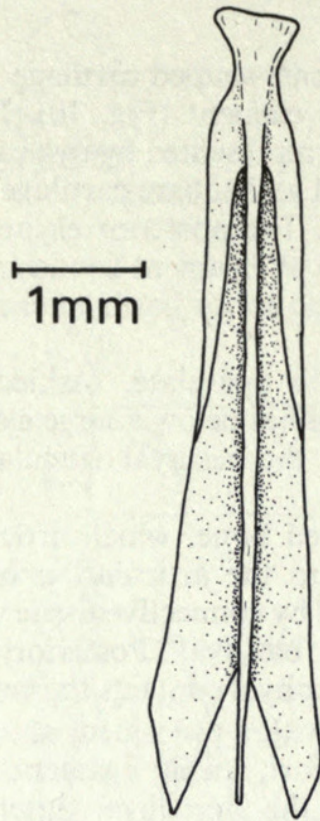


Fig. 13 *Hydrocynus forskahlii* urohyal, dorsal view.

The *urohyal* is elongate, club-shaped and is trifurcate posteriorly (Fig. 13). Its anterior surface is formed into two facets which are ligamentously connected to the anteroventral processes of the ventrohyals (see above, p. 177).

The *first branchiostegal ray* articulates with the ventral surface of the anterohyal cartilage blocs which contact that element.

The *second branchiostegal ray* articulates with the posteroventral surface of the anterohyal.

The *third branchiostegal ray* articulates in a lateral fossa on the posterolateral surface of the anterohyal.

The *fourth branchiostegal ray* articulates with the anteroventral surface of the posterohyal.

Basibranchial 1 (Fig. 10) is peg-shaped, articulating with the basihyal anteriorly; with each first hypobranchial laterally; there is no apparent contact between the first and second basibranchials. Posteriorly, the bone has an arrow-shaped cartilage cap.

Basibranchial 2 is elongate with a triangular cartilaginous cap anteriorly and a rod of cartilage posteriorly, with whose posterolateral surfaces the second pair of hypobranchials articulate. Posteriorly, basibranchial 2 contacts the triangular cartilage cap of *basibranchial 3*. The latter bone is also elongate, with a posterior rod of cartilage ventral to the third hypobranchial cartilage bloc (see below). The anterior cartilage cap of basibranchial 3 articulates with the posteromedial surfaces of the second hypobranchial (Fig. 10).

Basibranchial 4 (Fig. 10) is elongate and cartilaginous. Anteriorly, it lies dorsal to the cartilage bloc of the 3rd hypobranchial (see below). Laterally, basibranchial 4 articulates with ceratobranchial 4; the latter also has a thumb-like process that contacts basibranchial 4 ventrally. Posteriorly, the 4th basibranchial is produced into a rod-shaped process which has a pair of dorsal fossae in which the paired 5th ceratobranchials articulate. The posterior process of this basibranchial lies in the mid-line between the tooth plates fused to the paired 5th ceratobranchials (Fig. 10).

Hypobranchial 1 is roughly hook shaped, and 2 is a triangular element.

The ossified elements of *hypobranchial 3* are roughly triangular in outline and joined posteriorly by a large 'W'-shaped cartilage bloc, which is sandwiched between the posterior cartilage elements of basibranchial 3 ventrally and the anterior part of basibranchial 4 dorsally (Fig. 10).

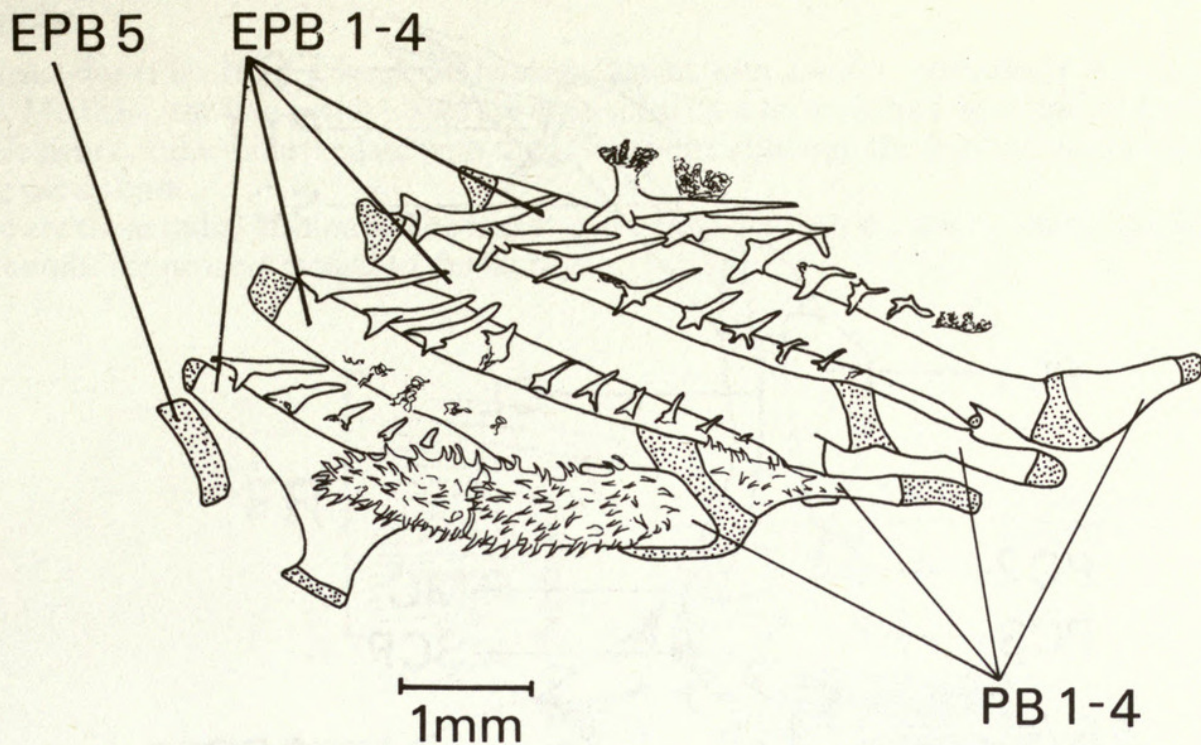


Fig. 14 *Hydrocynus forskahlii* upper gill arch, ventral view.

Ceratobranchials 1–5 are all similar, rod-shaped elements. Ceratobranchials 1–3 articulate anteriorly with their respective hypobranchials, but ceratobranchials 4 and 5 both articulate with basibranchial 4. Anteriorly, ceratobranchial 4 has a large cartilage cap, with an anteroventrally directed thumb-like process that contacts the ventral surface of basibranchial 4 (see above, p. 178).

Epibranchials 1–3 are rod-shaped (Fig. 14). The first has a short uncinat process which articulates with a ventral process on pharyngobranchial 2. Epibranchial 2 has a short antero-ventral uncinat process that articulates with a ventral process on pharyngobranchial 3. Epibranchial 3 articulates with the posterior edge of pharyngobranchial 2, the anterior edge of pharyngobranchial 3 and through an uncinat process with the ventral surface of the cranium.

Epibranchial 4 is a triangular-shaped bone, and *epibranchial* 5 (Fig. 14), is a short, cartilaginous rod.

Pharyngobranchial 1 is cone-shaped; it contacts the ascending arm of the parasphenoid dorsally and epibranchial 1 posteriorly.

Pharyngobranchial 2 is a rod-like bone with a small oval plate bearing a few small conical teeth fused to its surface ventrally.

Pharyngobranchial 3 is triangular; fused onto its ventral surface there is a triangular toothplate bearing small conical teeth.

Pharyngobranchial 4 is rectangular, with two large tooth plates bearing small conical teeth fused to the ventral surface.

Pectoral girdle

The *extrascapula* (Fig. 15) is an ovate bone that contacts both the parietal and pterotic. Posteriorly, it overlaps the posttemporal laterally. The sensory canal is bifurcate.

The *posttemporal* (Fig. 15) is triangular; dorsally, its apex lies posterior to the parietal. Medially, there is a short and thick process which is connected ligamentously to the intercalar (see p. 169).

The *supracleithrum* is an elongate bone with short and broad dorsal process which lies across the posteromedial surface of the posttemporal (Fig. 15). Ventromedially, and immediately posterior to the apex of the ascending limb of the cleithrum, the supracleithrum is connected to the basioccipital by Baudelot's ligament.

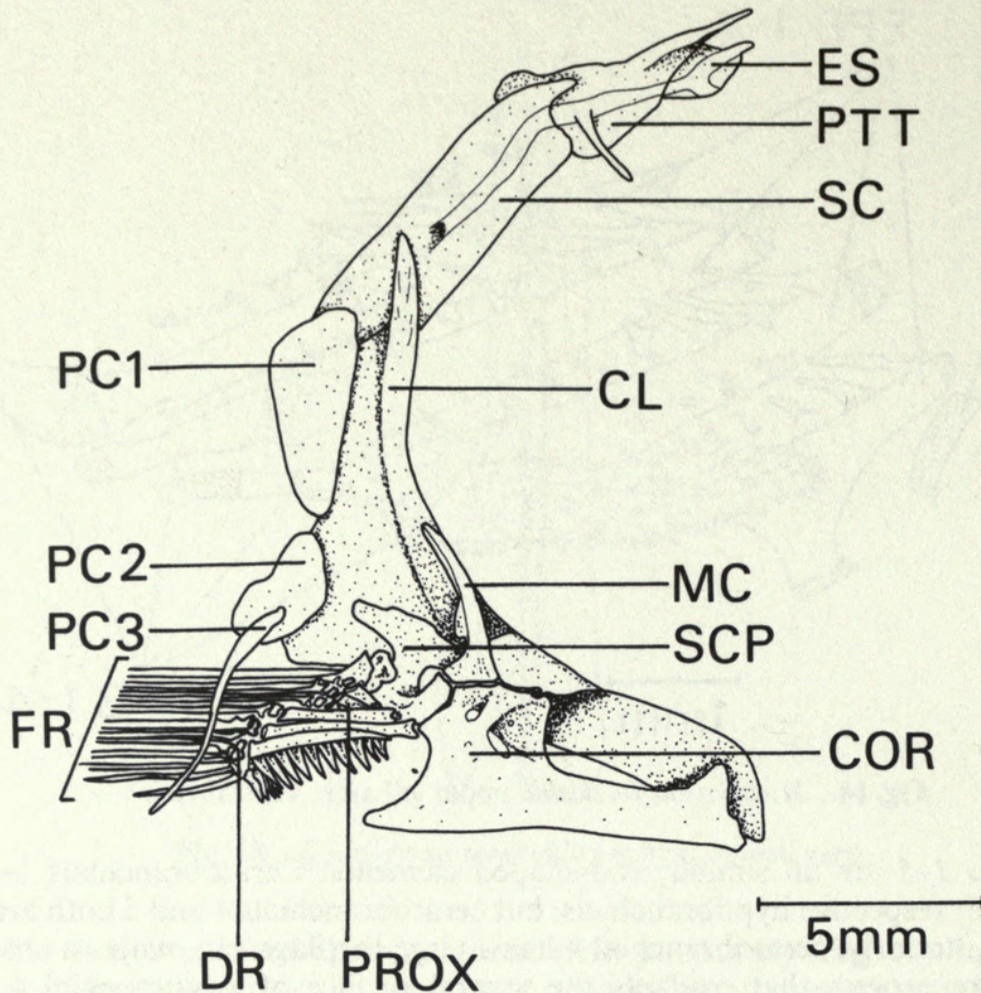


Fig. 15 *Hydrocynus forskahlii* left pectoral girdle, medial view.

The *cleithrum* (Fig. 15) is an 'L'-shaped element. The ascending limb contacts the medial surface of the supracleithrum dorsally and the anterolateral surfaces of postcleithra 1 and 2 posteriorly (see below).

The horizontal limb has a posteromedial shelf-like process with synchondritic connection to the scapula. The posteromedial edge of this shelf-like process has a hook-shaped extension which interlocks with the anterodorsal edge of the dorsal coracoid process (Fig. 15). Anteromedially, the horizontal limb of the cleithrum contacts the apices of the coracoid and the opposing cleithrum.

Postcleithrum 1 is ovate, *postcleithrum 2* is a small palette-shaped element the greater part of which lies medial to the posteroventral surface of the cleithrum, *postcleithrum 3* is a long, rod-shaped bone that contacts the medial surface of postcleithrum 2.

The *scapula* (Fig. 15) has an irregular, near anvil-shaped outline and surrounds a large scapular foramen, the anterior border of which is very narrow. A short, dorsally directed scapular process contacts the mesocoracoid. Posterodorsally, two of the proximal pectoral fin radials articulate directly with the scapula.

The *mesocoracoid* (Fig. 15) is triangular with a long, dorsal process, the ventral part of which spans the scapular foramen.

The *coracoid* is shaped like a jack plane (Fig. 15). Posterodorsally it contacts the mesocoracoid and scapula, and a thick band of connective tissue joins it to the 3rd and 4th proximal radials.

There are four *proximal radials*. The first articulates posteriorly with the first three distal radials, whereas, the others each articulate posteriorly with a single distal radial. The 1st and 2nd proximal radial contact each other laterally and articulate anteriorly with the scapula. The 3rd and 4th proximal radial are tightly bound by connective tissue to the coracoid (see above).

There are six hour-glass shaped *distal radials*. The 3rd bifurcates posteriorly, and the 6th is cartilaginous.

Pelvic girdle

The *pelvic bone* (Fig. 16) is a large triangular element with a short, posteriorly directed, ischiac process. Medially, the two pelvic bones are connected by a short, broad ligament. Posteriorly, the radial elements of the fin articulate with the pelvic bone although the first ray articulates directly with the pelvic bone.

There are three radial elements. The first two are anvil-shaped, the third comma-shaped, with a short, thumb-like process medial to the fin rays.

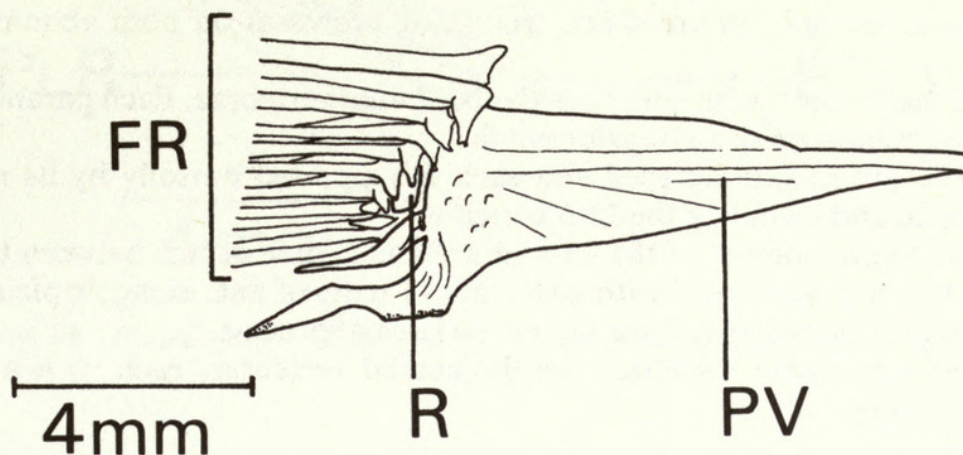


Fig. 16 *Hydrocynus forskahlii* left pelvic girdle, dorsal view.

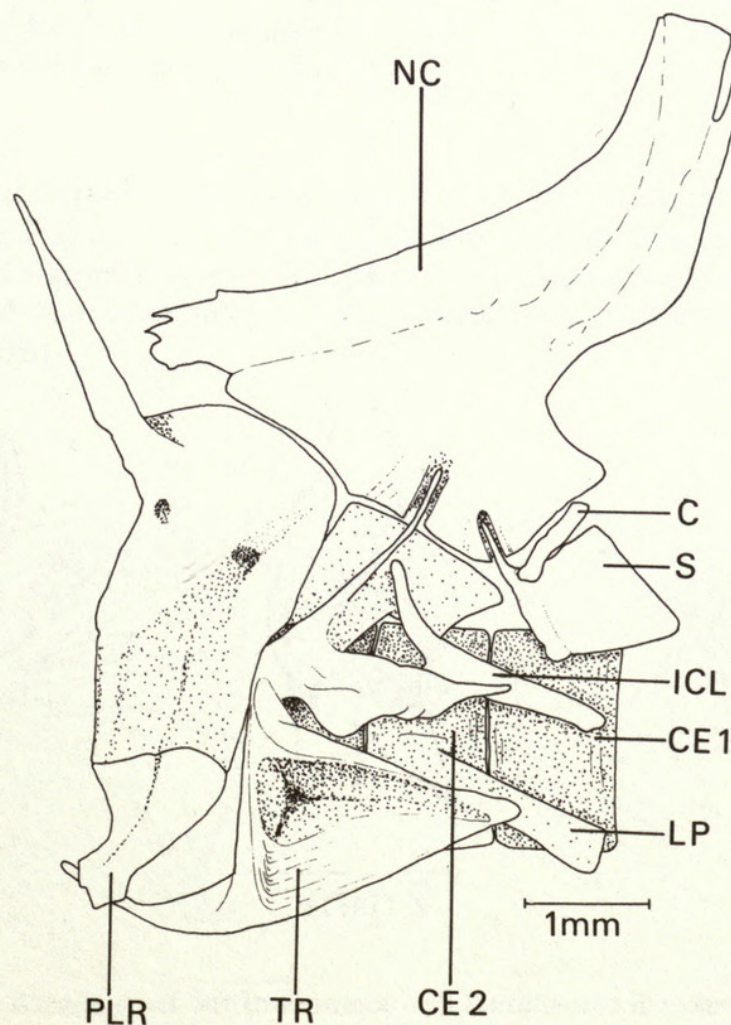


Fig. 17 *Hydrocynus forskahlii* Weberian apparatus, right side, lateral view.

Vertebrae

There are 28–32 abdominal vertebrae, most of which support pleural ribs. The first four contribute to the Weberian apparatus and support the Weberian ossicles. *Hydrocynus* Weberian apparatus is like that described by Weitzman (1962) in *Brycon meeki* but the tripus is fan-shaped in lateral view, (not triangular) and the neural complex is crescentic (Fig. 17).

The other abdominal vertebrae have a large neural spine. The *neural prezygapophysis* of the 5th vertebra is a thick, nub-like process, whereas those of the 6th to 11th vertebrae are elongate processes. The neural prezygapophysis of the 12th and all successive vertebrae, including the caudal elements, is a short, thumb-like process.

The *neural postzygapophyses* are short, triangular processes on both abdominal and caudal vertebrae.

Parapophyses are present on the 6th to 20th abdominal vertebrae. Each parapophysis supports a scimitar-shaped *pleural rib* in a posterior notch.

The *pleural ribs* are scimitar-shaped and each is supported dorsally by its respective lateral parapophyses up to and including the 20th vertebra.

The transitional development of the haemal arch and spine occurs between the 21st and 31st vertebrae (Fig. 18A–C), associated with which are 11 pairs of fine, elongate pleural ribs (Fig. 19) articulating with the posteroventral surface of the haemal process.

The 32nd and subsequent vertebrae are the caudal vertebrae, each with a fully developed haemal arch and spine.

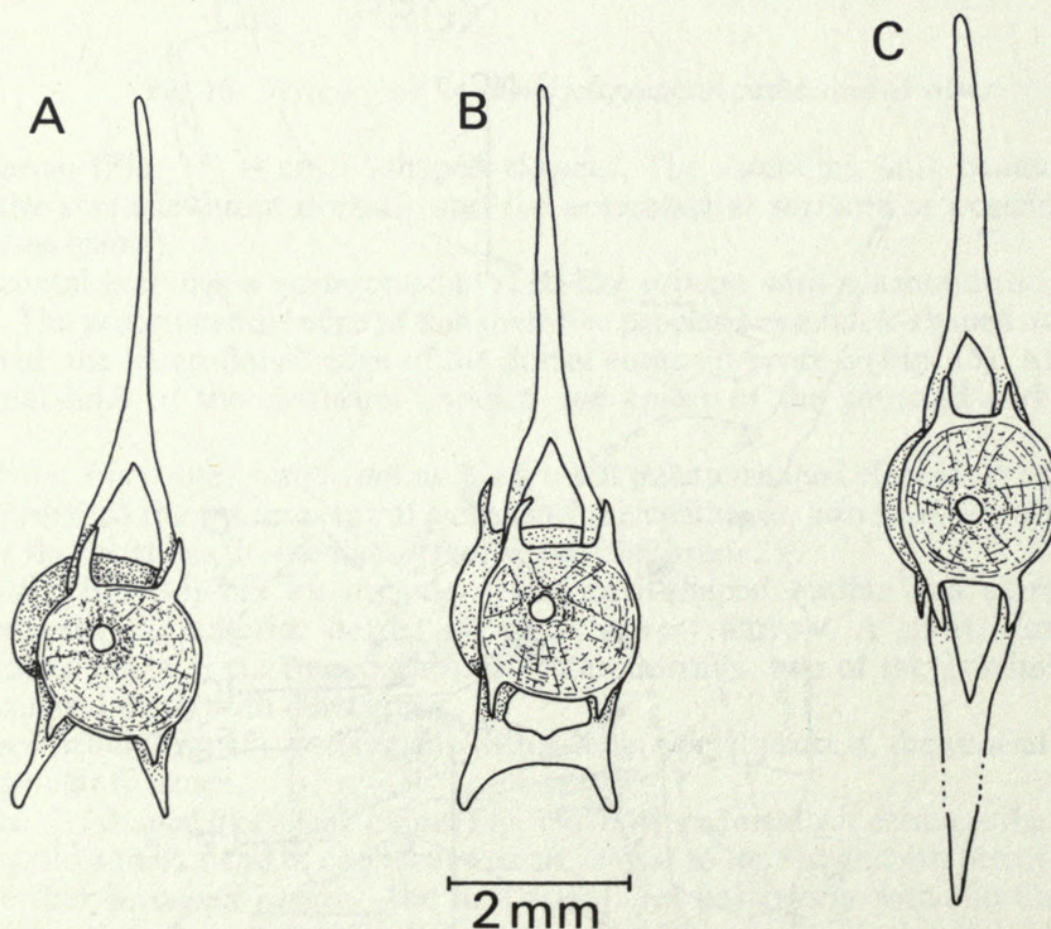


Fig. 18 *Hydrocynus forskahlii* transitional development of the haemal arch and spine. Vertebrae in anterior view. A, 21st vertebra showing haemal processes; B, 25th vertebra, the haemal processes form the canal but are bifurcate ventrally. C, 35th vertebra showing fully developed haemal spine.

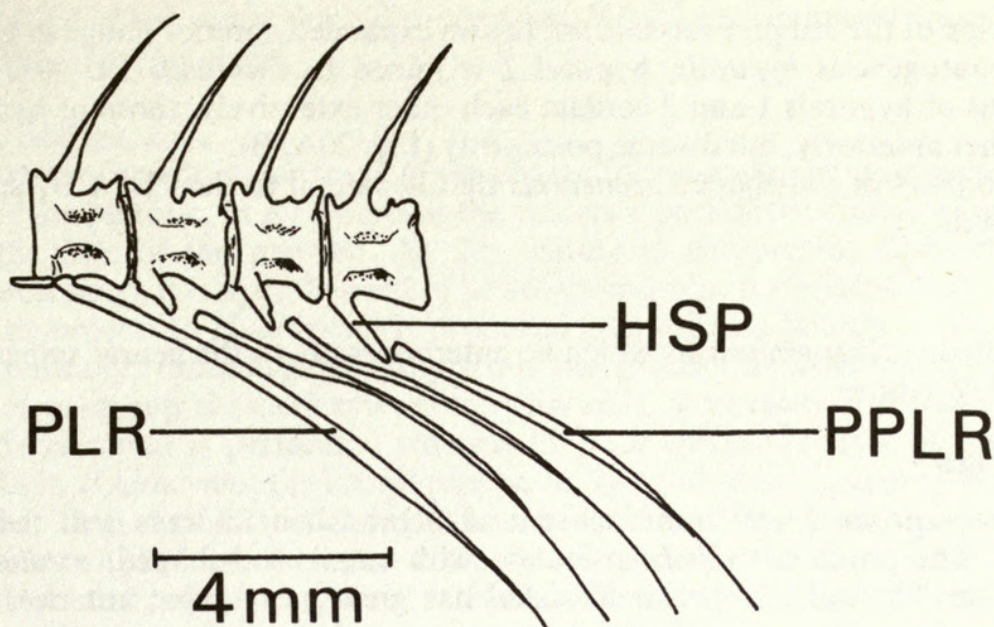


Fig. 19 *Hydrocynus forskahlii* 20th–23rd vertebrae, left side, lateral view.

Epineural and epipleural ribs

There are 44 pairs of *epineural ribs*, all of which are posterodorsally directed and forked proximally.

There are 27 pairs of *epipleural ribs*, all of which project posteroventrally; apart from the first and last pair, all are forked. The epipleurals lie lateral to the last 15 pleural ribs and the series continues posteriorly to the base of the caudal fin.

Caudal fin

Sexual dimorphism is exhibited in the *caudal fin skeleton* of all species of *Hydrocynus*. In females, the neural spines on the 2nd and 3rd preural centra are of approximately the same length, with expanded anterior and posterior flanges (Fig. 20A). The neural spines of preural centra 3 and 4 of males are more elongate than in females and curve backwards over the neural spine on the 2nd preural centrum (Fig. 20B).

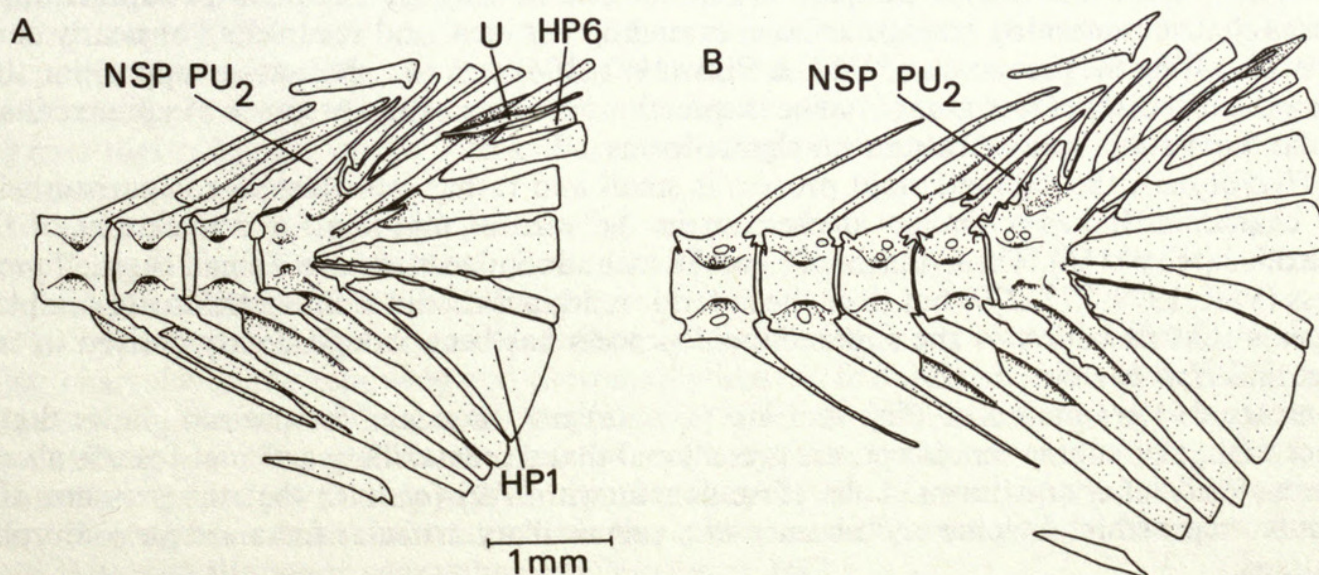


Fig. 20 *Hydrocynus forskahlii* caudal fin skeleton, left side, lateral view: A, female (uroneural is displaced); B, male.

The neural spine of the 3rd preural centrum has an expanded anterior flange in both sexes.

There are 5 autogenous *hypurals*, hypural 2 is joined to the fused $PU_1 + U_1$ centra. The adjacent margins of hypurals 1 and 2 contact each other extensively, those of hypurals 2 and 3 contact each other anteriorly, but diverge posteriorly (Fig. 20A, B).

There are two pairs of rod-shaped *uroneurals* that lie lateral to the $PU_1 + U_1$ spine and three rod-shaped *epurals*.

Supraneurals

There are 11 rod-shaped *supraneurals* which lie anterodorsally to the neural spines of the 4th to 14th abdominal vertebrae.

Dorsal and anal fins

The *dorsal fin* comprises 2 soft unbranched and 8 branched fin rays and their supporting pterygiophores. The *proximal radials* articulate with small, rod-shaped, *medial radials* at a cartilage interface. The anterior proximal radial has greatly expanded anterior and posterior flanges.

The medial radials articulate with the small, triangular *distal radials* at a cartilage interface.

The *anal fin* comprises 3 soft, unbranched and 12 branched fin rays and supporting pterygiophores which are similar in morphology to those described for the dorsal fin (see above).

Character analysis

On the basis of jaw and tooth structure, tooth replacement, three openings to the posttemporal fossa and the presence of a tubular orbitosphenoid process, Roberts (1966: 215; 1967: 242; 1969: 443) considered *Hydrocynus* to be related to the genus *Alestes*, stating the former 'very probably had *Alestes*-like ancestors'. Therefore, the question to be answered is whether *Hydrocynus* and *Alestes* are sister-groups, or, whether *Hydrocynus* is either most closely related to one group of *Alestes* species or some other genus currently included in the Characidae. In order to resolve this problem, the derived features of *Hydrocynus* must be established.

Those features not included in the following discussion are either dealt with later (see p. 193–201) or are symplesiomorphies for characids.

Neurocranium

The ethmoid

According to Vari (1979: 277) the plesiomorphic condition of the characiform supraethmoid process is '... an anteriorly triangular bone extending between, and completely or nearly completely separating the premaxillae.' Fink & Fink (1981: 306) make an alternative supposition that the absence of a distinct mesethmoid spine (supraethmoid process) and presence of a premaxillary articular fossa are primitive features for characiforms.

In *Hydrocynus*, the supraethmoid process is small and rather indistinct in comparison with other characins. It has a shallow depression in the vertical mid-line for articulation of the premaxillae (see p. 166). The Citharinidae and Distichodontidae also have a small supraethmoid process (Vari, 1979: 277–279) but since the anterior margin is modified into a trifurcate complex, it appears that reduction of the supraethmoid process has been independently derived in this lineage and *Hydrocynus*.

Contrary to the opinion of Fink & Fink (*op. cit.*) my outgroup comparison shows that a distinct triangular supraethmoid spine is present and that a premaxillary articular fossa is absent in the majority of characiforms. I therefore concur with Vari (*op. cit.*) that the presence of a triangular supraethmoid spine and absence of a premaxillary articular fossa are plesiomorphic conditions.

The lateral supraethmoid wings are primitively triangular processes, whereas in *Hydrocynus* these are blunt, thick straight processes.

The morphology of the supraethmoid process and lateral supraethmoid wings of *Hydrocynus* are autapomorphic for this genus.

Dilatator fossa and sphenotic

The posterior part of the dilatator fossa of the characiforms examined, just encroaches onto the anterior face of the pterotic. In *Hydrocynus*, the posterior part of the dilatator fossa is formed as a groove in the face of the pterotic. As this feature is not present amongst the outgroup characiforms examined, it is hypothesized to be autapomorphic for *Hydrocynus*.

The sphenotic process in *Hydrocynus* is produced laterally as a bluntly triangular shelf which slopes anteroventrally; extending medially from the process as a sharp-edged ventral strut. Examination of outgroup characiforms reveals that only *Serrasalmus* possesses a similar strut. The strut in *Serrasalmus* is perforated whereas in *Hydrocynus* the strut of bone is thick and imperforate. As in *Hydrocynus*, the lateral process in *Serrasalmus* is anteroventrally directed, but is spinous rather than shelf-like. Although the sphenotic in *Hydrocynus* and *Serrasalmus* has a generally similar morphology, there are marked differences in the shape of the spine, furthermore, in the absence of any other shared, derived features between these genera, the similarity is reasoned to be independently derived and autapomorphic for each genus.

Parasphenoid

Roberts (1969: 406) considers a straight parasphenoid to be primitive for characiforms, and the 'strongly ventrally depressed' parasphenoid characteristic of many members of the Characidae to be a specialized feature. According to Vari (1979: 288) the characiform parasphenoid is plesiomorphically a flat, straight or ventrally convex element extending posteriorly to below the basioccipital. My outgroup comparisons suggest that the parasphenoid which is markedly convex ventrally, anterior to the ascending processes (which is typical of the Characidae) appears to be the derived condition. I therefore, agree with Vari that the flat, straight parasphenoid is plesiomorphic for characiforms.

In comparison with the parasphenoid in other members of the Characidae, that of *Hydrocynus* is straight, its morphology resembling that of the plesiomorphic type.

Jaw bones

The plesiomorphic condition for the upper jaw of characiforms is immovably attached to the supraethmoid via large, triangular-shaped premaxillary ascending processes, which are almost entirely separated in the mid-line by the supraethmoid process (Weitzman, 1962: 32; Vari, 1979: 271 & pers. obs.) *Lepidarchus adonis* is exceptional within the Characidae in the extreme reduction of the premaxillary ascending processes and triangular supraethmoid spine. The supraethmoid region of the cranium of *L. adonis* closely resembles that of a 10 mm SL specimen of *Alestes* sp. (BMNH 1981.2.17: 1699–1734) in which the cranium is largely cartilaginous and the premaxillary ascending processes and supraethmoid spine are not yet fully developed. However, *Lepidarchus* displays reduction in many other morphological characters which suggests that reduction of the premaxillary ascending process and supraethmoid spine may be paedomorphic features.

In some *Alestes* species the premaxillae are united by a weak symphysial 'hinge' joint, comprising at the most, two interdigitating processes. The distal part of the characid premaxilla (excluding *Hydrocynus*) is tapered (Fig. 21).

The upper jaws of *Hydrocynus* (described on pp. 171–172) are seen to differ from those of other characids in the following and presumably derived features: presence of medial interdigitations along the vertical length of the premaxillae, forming a loose symphysial hinge; a short premaxillary ascending process; the distal part of the premaxilla dorso-ventrally expanded.

Another derived jaw feature in *Hydrocynus* is the presence of a double premaxillary (ethmoid) facet. The anterior facet articulates with the supraethmoid process whilst the posterior facet articulates with the lateral supraethmoid wing (see. p. 166).

Vari (1979: 271) reported the presence of a medial premaxillary articular fossa in the Distichodontidae and Citharinidae, which he hypothesized to be synapomorphic for these families.

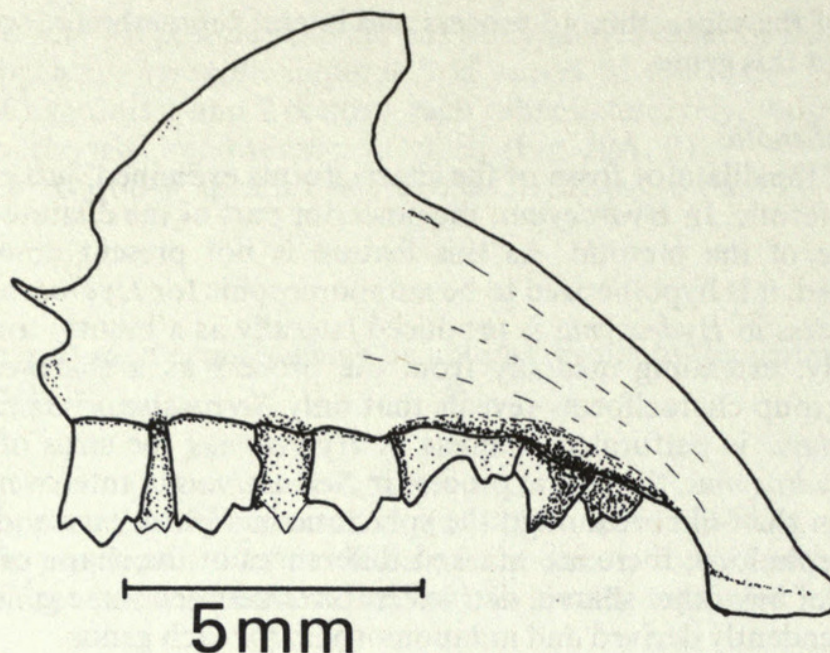


Fig. 21 *Alestes baremose* premaxilla, left side, lateral view.

However, the morphology of this socket differs from that in *Hydrocynus* in being a deep horizontal depression, open to its partner across the symphysis in *Xenocharax* (Distichodontidae). Other derived modifications of the premaxillary articular fossa amongst the citharinid-distichodontid lineage are: a conical pit; transversely directed pit, or, the fossa roof is reduced to a small shelf at the lateral margin of the depression (Vari, 1979: 271–272). The citharinids and distichodontids have a single articulation with the ethmoid rather than the double articulation of *Hydrocynus*. In view of these several differences and the absence of any other synapomorphies uniting these taxa, it is most likely that the anterior premaxillary facet of *Hydrocynus* is homoplastic with that in the Distichodontidae and Citharinidae.

The maxilla of the African characids is an edentulous comma-shaped bone, considerably thickened posteriorly. Posteromedially, the maxilla is grooved for the reception of the maxillary-mandibular ligament. In contradistinction, the maxilla of *Hydrocynus*, although edentulous, is a lamellar bone ankylosed to the premaxilla (Roberts, 1969: 415 and personal observation). In members of the neotropical characiform family Erythrinidae, the maxilla is also lamellar bone, but unlike that of *Hydrocynus*, it bears a large number of teeth and has an elongate, medially curved anterior ascending process. No other synapomorphies were found to unite these taxa, thus the apomorphous lamellar nature of the maxillae in *Hydrocynus* and the Erythrinidae is most parsimoniously explained as being independently derived.

The attachment of the maxillary-mandibular ligament to the anterolateral face of the maxilla (see p. 172) is unique to *Hydrocynus*.

The mobile articulation of the upper jaw in *Hydrocynus* is absent amongst other African characids, although found in other characiforms. Like *Hydrocynus*, the Citharinidae and some genera of Distichodontidae have a premaxillary articular fossa (see above), and lack a prominent premaxillary ascending process. The mechanism by which mobility of the upper jaw is achieved in Citharinidae and Distichodontidae is quite different from that in *Hydrocynus* (Vari, 1979: 272) and must be considered as being independently derived. A mobile premaxillary-supraethmoid articulation occurs in the neotropical characiform families Anostomidae, Chilodontidae, Prochilodontidae, Parodontidae and Hemiodontidae (Roberts, 1974: 412 & 425; Vari, 1979: 272). The morphology of the premaxillae and ethmoid region in these families is dissimilar to that of *Hydrocynus*. In the absence of any other shared, derived characters, the premaxillary mobility in these South American families appears to be non-homologous with that in *Hydrocynus*.

Dentition

Roberts (1967: 238–239) found the multicuspid teeth of characiforms to be compound elements, each cusp representing a separately formed conical element. The individual conical elements equate to a single tooth, a group of which are held together by a hard base of variable development. Roberts also thought that conical teeth are primitive for characiforms but the conical teeth of *Hydrocynus* are derived. My observations agree with those of Roberts regarding the formation of multicuspid teeth in *Alestes* and *Hydrocynus*. The tricuspid condition of *Hydrocynus* is evidently derived in each case by fusion of three 'juvenile' conical teeth and the 'adult' conical teeth are secondarily derived from the tricuspid teeth in which the median cusps are dominant (see p. 172). The juvenile conical dentition found in *Hydrocynus* and *Alestes* suggests the presence of conical teeth is the primitive condition for characiforms; the multicuspid dentition of non-juvenile *Alestes* and *Hydrocynus* of more than 23 mm SL but less than 50 mm SL is the derived condition. The conical teeth of *Hydrocynus* are considered to be secondarily derived from the tricuspid condition. This is in agreement with Roberts's hypothesis that the 'adult' conical teeth of *Hydrocynus* are derived.

The teeth of the Characidae are usually tightly bunched and contact one another in the anterior part of the relatively short jaws. In *Hydrocynus* the teeth are few in number, and are widely and evenly distributed along elongate jaws (see p. 171). Elongate jaws are characteristic of a number of supposedly primitive characiform genera, such as *Hepsetus*, *Ctenolucius*, *Salminus*, *Hoplias* and *Acestrorhynchus*, but with the exception of *Hydrocynus* and *Acestrorhynchus*, the teeth of these taxa are numerous, usually contiguous and are uniserial. The teeth of *Acestrorhynchus* are more numerous than in *Hydrocynus* and have large, irregularly situated diastemata.

Roberts (1969: 439) considered wide spacing of jaw teeth to have resulted from secondary elongation of the jaws. Apart from the wide spacing of the jaw teeth of *Hydrocynus*, there is no other morphological evidence to suggest that the jaws in this taxon are secondarily elongate, or indeed that this is the derived condition.

The conical 'juvenile' dentition as found in *Hydrocynus* is hypothesized to be plesiomorphic for characiforms (see above). Apparently such conical 'juvenile' teeth are the first to develop from the embryonic dental lamina, which is continuous, so that the emergent teeth all contact one another. In specimens of *Hydrocynus* larger than 16 mm SL, the dental lamina appears to be in regular, discrete units that each produce 3 tooth buds; these fuse as the tooth develops and form a tricuspid tooth.

Contra Roberts (1969: 439), I consider the wide, even spacing of the teeth of *Hydrocynus* to be the primary derived condition and not a result of secondary elongation of the jaws. Such wide, even spacing of the teeth was not found in any other characiform examined and is considered to be autapomorphic for *Hydrocynus*.

Roberts (1966, 1967) dealt with characiform tooth replacement in some detail. He described the replacement trenches of *Hydrocynus* as '... roofed over but ... pierced by large foramina for each of the replacement teeth ...' For the reason given on p. 171 I have referred to these trenches as 'replacement cavities'. The replacement cavities are most probably derived from a single trench because the posterior cavity contains two or more replacement teeth. Roberts (1967: 233) described the replacement trenches of five genera of African characids as greatly excavated in the lower jaw, with the replacement teeth lying considerably below the bases of the corresponding functional teeth. The replacement teeth of *Hydrocynus* lie horizontally, with their tips projecting posteriorly through the cavities. The replacement teeth are also horizontally aligned in the replacement trenches of the supposedly primitive characiforms *Hepsetus* and members of the Cynodontini, however, the knowledge of distribution of this character within the characiforms is such that no polarity can be assigned to this character.

Teeth are replaced on alternate sides of the jaw in *Alestes* species, but in several specimens of *Hydrocynus* that are in the process of replacing teeth, the entire functional dentition is lost simultaneously. In the jaws of a specimen of 25 mm SL (BMNH 1981.2.17: 2600–2609) in the process of replacing teeth, the bone of the dentary surrounding the functional teeth and replacement cavities has been resorbed. The complete loss of the functional dentition is reported by

Begg (1973) who noted high proportions of toothless *Hydrocynus* being caught by anglers. The stomach contents of some of these specimens included shed teeth, so it is assumed the teeth are often swallowed. Begg kept eight tigerfish in captivity for a month and found dozens of teeth on the floor of the tank at the end of this period; he presumed that all the fish had shed their teeth and successfully replaced them. Tweddle (1982) also reported the complete loss of functional dentition in a species he called *Hydrocynus vittatus*. Roberts (1967: 238) reported only *Schizodon fasciatus* (Characiformes: Anostomidae) as losing and replacing its entire dentition in one stage. Too few data are available on the occurrence of complete vs incomplete tooth loss amongst characiforms for any polarity assignment to be given to these characters.

Circumorbital bones

Roberts (1969: 419) considers the characiform series to be primitively comprised of eight bones: a supraorbital, antorbital and six infraorbitals. All characids examined for outgroup comparison in this study have a circumorbital series comprising these eight bones as follows and as exemplified by *Alestes dentex*:

The antorbital is spear-shaped (Fig. 22) and tightly bound by connective tissue to the anterolateral margin of the frontal; it lies anterior to the supraorbital and the posterodorsal margin of the first infraorbital; the first infraorbital, or lachrymal is narrow and rectangular, and lies lateral to the ascending process of the maxilla; the second infraorbital is of similar shape, but lies posterior to the maxilla; the third, fourth and fifth infraorbital bones are large, cover the cheek, and are similar to those described for *Hydrocynus* (see p. 173); the dermosphenotic is a rectangular bone with an anterodorsal process, and is bound by connective tissue to the lateral edge of the frontal and to the posterior part of the supraorbital; the supraorbital is an elongate, thick, rod-like bone lying anterior to the dermosphenotic; it contacts the lateral edge of the frontal and the antorbital anteriorly.

The laterosensory canal runs along the orbital margin of the circumorbital series and bifurcates in the dermosphenotic, as described for *Hydrocynus* (see p. 173).

The first infraorbital of *Hydrocynus* is a broad bone relative to that in other characiforms, and lies lateral to the premaxilla as well as the ascending limb of the maxilla. The second infraorbital is also greatly enlarged, concealing most of the maxilla. Such enlargement of the first and second infraorbital bones is unique to *Hydrocynus*.

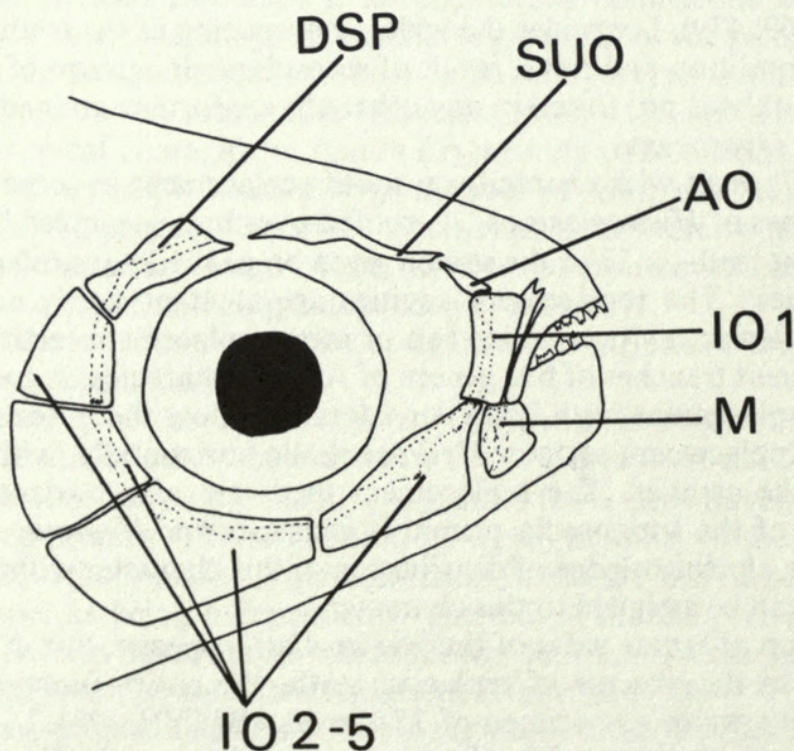


Fig. 22 *Alestes dentex* circumorbital series, right side.

Suspensorium

The hyomandibula of *Hydrocynus* is similar to that of other characiforms except for the presence of a dorsolateral spine (see p. 174). As this spine is not found in any other outgroup characiform examined, it is recognized as autapomorphic for *Hydrocynus*. Amongst other teleosts, there is a process on the posterolateral surface of the hyomandibula in the Clupeidae. This process projects as an anteriorly directed flange along the length of the hyomandibular shaft, and is unlike that found in *Hydrocynus*. In the absence of any synapomorphies suggesting a relationship between these taxa, the hyomandibular spine of *Hydrocynus* and hyomandibular process in the Clupeidae are proposed to be independently derived.

The modal (and presumably plesiomorphic) condition for the ectopterygoid in characiforms is an elongate, ovate, toothed bone which contacts the quadrate ventrally and extends along the anterior margin of the endopterygoid. The shortened, disc-like ectopterygoid of *Hydrocynus* was not found in any other characiform examined and is hypothesized to be autapomorphic for *Hydrocynus*. Roberts (1969: 418) states that the presence of ectopterygoid teeth in characiforms has a mosaic distribution. However, none of the African characids that I examined possess ectopterygoid teeth (see also p. 203).

Interrelationships of *Hydrocynus*

From the above analysis, the following apomorphic characters have been identified for *Hydrocynus*, and will form the basis of a discussion concerning the interrelationships of the genus.

1. Supraethmoid process small but specialized with a shallow depression for articulation of the premaxillae. The supraethmoid of other characiforms is usually large and triangular, separating the premaxillae.
2. Supraethmoid wings blunt, thick, straight processes. The supraethmoid wings of outgroup characiforms are plesiomorphically small triangular processes.
3. Pterotic grooved posteriorly, such a groove is absent in all other characiforms examined.
4. Sphenotic with a ventromedial strut, which with the exception of *Serrasalmus* (see p. 185) is absent in all other characiforms.
5. Upper jaw articulates with the supraethmoid. With the exception of the Citharinidae and Distichodontidae (see p. 186), the upper jaw of characiforms is immovably attached to the supraethmoid.
6. Premaxillae with synarthritic connection, such a connection is absent in other characiforms.
7. Premaxillary ascending processes short, which in other characiforms are present as large triangular processes.
8. Premaxilla deepened distally. The distal part of the premaxilla in other characiforms is tapered.
9. Premaxillary facet present. This facet is absent in other characiforms with the exception of the Distichodontidae and the Citharinidae (see p. 186).
10. Premaxillary dorsomedial facet present, this facet was not found in any other characiform examined.
11. Maxilla lamellar, edentate and ankylosed to premaxilla, whereas the maxilla of other characiforms is comma-shaped and thickened posteriorly, with the exception of the Erythrinidae (see p. 186).
12. Maxillary-mandibular ligament attached to anterolateral face of maxilla. In other characiforms this ligament is attached to the posteromedial surface of the maxilla.
13. Tooth replacement cavities present, as opposed to the open trenches found in other characiforms.
14. Conical teeth, secondarily derived from a tricuspid condition. The teeth of other characids are multicuspid.
15. Teeth widely and evenly spaced. In other characiforms, the teeth are usually contiguous, or have irregularly situated diastemata.

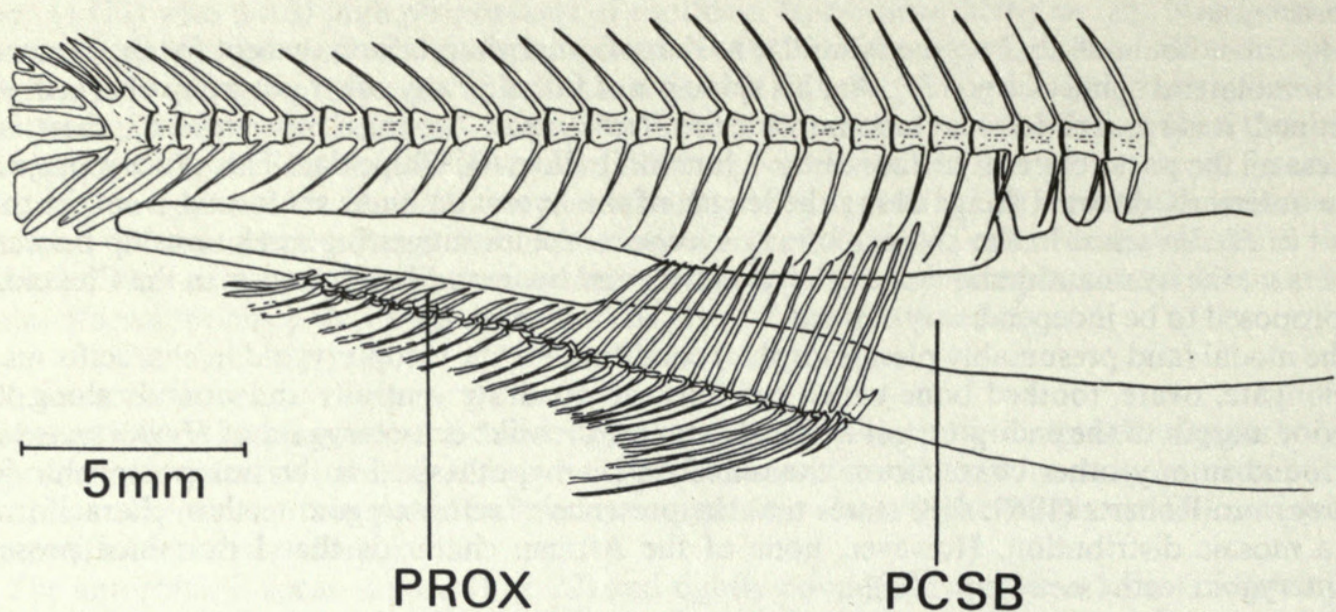


Fig. 23 *Alestes dentex* anal fin, posterior portion of vertebral column and swimbladder, right side, lateral view.

16. 1st and 2nd infraorbital bones enlarged, in other characiforms these are both narrow and rectangular, with the latter lying posterior to the maxilla.
17. Hyomandibular spine present. No such spine occurs in any other characiform.
18. Ectopterygoid reduced in length. The ectopterygoid of other characiforms is an elongate, ovate bone.

Roberts (1966, 1967 & 1969) suggested that *Hydrocynus* was derived from an *Alestes*-like ancestor, interpreting *Alestes* in the sense used by Boulenger (1907). Myers (1929), Poll (1976) and Géry (1968: 1977) recognizing that Boulenger's '*Alestes*' is polyphyletic have, however, reinstated the genera *Brycinus* Cuvier & Valenciennes 1849 and *Myletes* Peters 1852, taxa which Boulenger incorporated in his concept of *Alestes*. My continuing studies on the osteology of '*Alestes*' (*sensu* Boulenger) tend to confirm the opinions of Myers, Poll and Géry, that it incorporates at least three taxa each of which has closer relatives with species in other genera and furthermore, that one of these is more closely related to *Hydrocynus* than are the others. This latter group of species, which, pending a revision of the genus, is referred to as *Alestes sensu stricto*, includes the species: *dentex* (type species of the genus), *baremore*, *ansorgii*, *macrophthalmus*, *stuhlmanni* and *liebrechtsii*. It is characterized by the two following apomorphies:

19. Posterior chamber of the swimbladder extends to the haemal spine of the third preural centrum (Fig. 23). In all other species of '*Alestes*' and other outgroup characiforms examined, the swimbladder extends to the origin of the anal fin.
20. The posterior proximal radials of the anal fin are short and curved anteriorly (Fig. 23). These radials in the anal fin of all other '*Alestes*' species, and other characiforms examined, are straight, aligned anterodorsally and not conspicuously shortened.

Those characters which are thought to be synapomorphic features uniting *Alestes s.s.* with *Hydrocynus* are considered below, and will be compared with those in remaining species in *Alestes sensu lato*, and other characiform taxa.

Dilatator fossa and sphenotic process

According to Vari (1979: 317, 319 & 326) and Howes (1981: 15) the plesiomorphic characiform dilatator fossa is small, is formed by almost equal contributions from the frontal, sphenotic and pterotic and is roofed or partially roofed by the frontal. This form of the dilatator fossa is Type 1

sensu Howes (1978: 56). In *Hydrocynus*, *Alestes s.s.* and *Oligosarcus*, the fossa is long and deep, with an extensive frontal contribution. It approximates to Type 2 *sensu* Howes (1978: 56).

The anterior margin of the dilatator fossa is formed by the sphenotic process, which in *Hydrocynus* and *Alestes s.s.* is thick and ventrally directed (see below) so that the fossa is broad in lateral view. In *Oligosarcus*, the sphenotic process is thin, sickle-shaped and directed backwards, thus the fossa is narrow in lateral aspect. Although the dilatator fossae of *Hydrocynus*, *Alestes s.s.* and *Oligosarcus* are long and deep, there are differences in the way the sphenotic, frontal and pterotic contribute to them, indicative of their independent derivation. Thus, the long, deep dilatator fossa shared by *Hydrocynus* and *Alestes s.s.* is thought to be synapomorphic for these genera.

The sphenotic process of characiforms is thin and directed ventrally forming part of the posterior wall of the orbit. In *Hydrocynus* and *Alestes s.s.* the process is well-developed and thickened ventrally. A similar form of the sphenotic process was not found in any other characiform examined, and thus is considered a derived feature shared by *Hydrocynus* and *Alestes s.s.*

Parasphenoid

In the absence of any synapomorphies indicating that *Hydrocynus* is more closely related to any characiform taxon outside the Characidae, the straight parasphenoid characteristic of this genus is most parsimoniously explained as homoplastic with that of other characiform taxa sharing this feature.

Pleural ribs

All species of *Hydrocynus* have 10 or 11 pairs of fine, elongate pleural ribs that articulate with the posteroventral surface of the haemal process and are associated with the transitional development of the haemal arch and spine between the 21st, or 22nd and 31st vertebrae, (see p. 182). In *Alestes s.s.* the counts are: *ansorgii*, *baremore*, *macrophthalmus* 8; *stuhlmanni* 9; *dentex* 10–11; *liebrechtsii* 10–11. The counts for *Alestes s.l.* are: *minutus*, *stolatus* 2; *lateralis*, *longipinnis* 3; *carolinae*, *tholloni*, *dageti*, *leuciscus* 4; *nurse*, *jacksoni*, *opisthotaenia*, *senegalensis* 5; *nigricauda*, *sadleri*, *poptae*, *lemairii*, *grandisquamis*, *macrolepidotus* 6.

In other characiforms, there are also pleural ribs articulating with the posteroventral surface of the haemal process. Counts on those taxa examined are: *Charax* 2; *Rhabdalestes*, *Bryconaethiops* 2–3; *Brycon*, *Triportheus*, *Scissor*, *Lebiasina* 3; *Acestrorhynchus* 4; *Hydrolicus* 5; and *Hepsetus* 6. Exceptionally, *Lepidarchus* does not have any pleural ribs articulating with the posteroventral surface of the haemal process.

On the basis of those outgroup comparisons within the Characiformes the higher number of 8 or more paired 'posterior pleural' ribs occurring in *Hydrocynus* and *Alestes s.s.* seem to represent the derived condition and is considered to be synapomorphic for these taxa.

Orbitosphenoid tube

Starks (1926: 167) described a bony orbitosphenoid process surrounding the olfactory tract and bulb in *Alestes liebrechtsii* and *A. grandisquamis*. Roberts (1969: 441) also observed this process in *Alestes baremore*, *A. imberi*, *A. macrolepidotus*, *Bryconaethiops* and *Hydrocynus* (see p. 170). Vari (1979: 341) added *Alestes dentex* and *A. macrophthalmus* to those taxa listed above, and suggested that a tubular orbitosphenoid process is an apomorphy shared by these taxa. Although Weitzman (1962: 20) and Howes (pers. comm.) noticed that *Brycon* also has a bony tubular process that encases the olfactory nerve, this is a process developed from the lateral ethmoid and not a homologue of the tube under discussion.

In addition to those taxa mentioned, the following also share this feature: *Alestes sensu stricto*; *A. nurse*; *A. grandisquamis*; *A. macrolepidotus* and *A. jacksoni*. It seems the tubular orbitosphenoid process is either apomorphic for this lineage, or, that this feature has a mosaic distribution in the African Characidae. However, pending a revision of the genus '*Alestes*' no polarity can be assigned to this character.

Caudal neural spines

Sexual dimorphism in the neural spine morphology of preural vertebrae 1 and 2 as seen in *Hydrocynus* (see p. 183), occurs in all members of the African Characidae examined, except for *Lepidarchus*. Vari (1982, p. 4), describes dimorphism in the neural spines of preural vertebrae 2 and 3 in the neotropical genus *Curimatopsis* (Curimatidae). Here, the neural spines in males have greatly expanded anterior and posterior flanges, a condition unlike that in the males of African characid species which have a reduced neural spine on preural 2 and elongate, curved neural spines on preurals 3 and 4. This difference, together with the absence of any other shared, derived features, and furthermore since Vari (1983: 46) lists a series of characters indicating curimatids are related to the Neotropical family, Prochilodontidae, suggests this form of sexual dimorphism has been independently derived in the two groups.

On the basis of the above analysis, the following characters are proposed as synapomorphies for *Hydrocynus* and *Alestes s.s.*, which taxa are thus considered to be sister-groups (see Fig. 24):

21. long, deep dilatator fossa;
22. well-developed, ventrally thickened sphenotic process;
23. 8–11 pairs of fine, elongate pleural ribs articulating with the posteroventral surface of the haemal process.

Géry (1968) studied the classification of '*Alestes*', (including *Bryconaethiops microstoma*), utilizing numerical taxonomy to analyse data obtained from a number of morphometric, meristic and colour features. His results, produced as a phenogram, show the group of characids referred to here as *Alestes s.s.* to be more closely related to *Bryconaethiops* than either genus is to any other species or group of species included in *Alestes sensu lato*. Géry's hypothesis that *Alestes s.s.* and *Bryconaethiops* are sister-groups is in contradiction to the relationship between *Alestes s.s.* and *Hydrocynus* proposed here. I have been unable to detect any osteological characters to

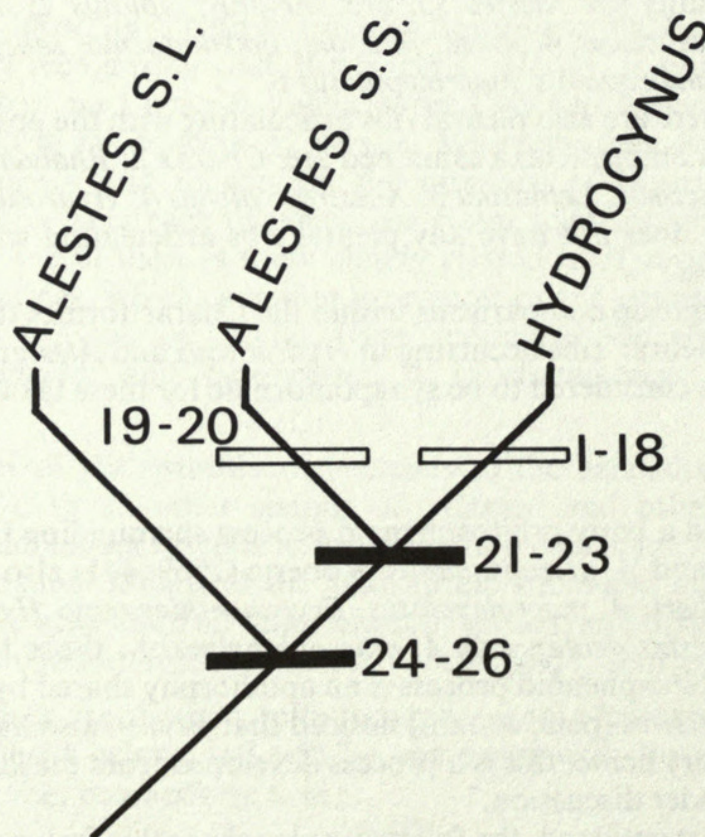


Fig. 24 Synapomorphy diagram of relationship between *Hydrocynus*, *Alestes s.s.* and *Alestes s.l.* Open bars indicate autapomorphies, black bars indicate synapomorphies, numbers 24–26 are as follows: (24) unique upper jaw morphology; (25) absence of ectopterygoid teeth; (26) sexual dimorphism exhibited in the posterior neural spines (see p. 183).

support Géry's findings and consider *Bryconaethiops* to be more closely related to some other 'Alestes' lineage than to either *Alestes s.s.* or *Hydrocynus*.

The proposed relationship of *Hydrocynus* and *Alestes s.s.* is discussed further on pp. 202.

Revision of *Hydrocynus* species

As stated earlier (see p. 164), there is some confusion regarding the validity of certain nominal species of *Hydrocynus*. Previous authors (Günther, 1864; Boulenger, 1901; 1907) relied on meristic characters to differentiate between species. Four species of *Hydrocynus* are recognized here, based on morphometric, meristic and osteological characters.

Hydrocynus forskahlii Cuvier (Fig. 25B)

Hydrocynus forskahlii Cuvier 1819 *Memoires du Muséum d'Histoire Naturelle* 5: 354–357

Characinus dentex (non Lacepède) Geoffroy Saint Hilaire 1809 *Description de l'Egypte* 24: 236–244, pl. 4

?*Hydrocynus vittatus* Castelnau 1861 *Memoire sur les Poissons de l'Afrique Australe*: 65–66

Hydrocyon lineatus (attributed to Schlegel) Bleeker, 1863 *Natuurkundige Verhandelungen van de Bataafsche Hollandsche Maatschappye der Wetenschappen te Haarlem Z. Verz.* 18: 125

NOTE ON THE SYNONYMY. The type specimen of *Hydrocynus vittatus* Castelnau 1861 is no longer extant (Boulenger, 1907: 106). Castelnau's description is undoubtedly that of a tigerfish; he gives the collection locality as Lake Ngami (Okovango drainage, Botswana) and *H. forskahlii* is the only species known to occur in that area. It therefore seems most likely that *H. vittatus* is a synonym of *H. forskahlii*.

I have examined the type of *H. lineatus*, which is in poor condition comprising little more than the skull, caudal skeleton and skin. On the basis of morphometric and meristic data, together with radiographs of the skull, I am satisfied that *H. lineatus* is a synonym of *H. forskahlii*.

NOTE ON THE HOLOTYPE. The holotype of *H. forskahlii* is in the collections of the Muséum National d'Histoire Naturelle, Paris (MNHN 1691). In addition to this specimen, the following MNHN specimens A9705, A9708, A9707, A9709, A9710, A8548, A8607, A9711 and 1692 are listed by Bertin (1939) as part of a syntypic (*sic*) series of *H. forskahlii* and are labelled as such. I disagree that these specimens should be included in the type series for the following reasons: Specimens A9705 and A9710 were collected from the Nile by Joannis in 1834, subsequent to Cuvier's 1819 description. The following specimens were collected from Sénégal A9707 by Heudelot; A9708, A9711 by Jubelin (the latter in 1828) finally, A9709 and 1692 by Leprieur, whereas Cuvier's description gives the type locality as the Nile. Specimens A8548 and A8607 were collected from the White Nile by Darnaud in 1843.

I note that Daget *et al.* (1984: 170) state only MNHN 1691, A9705, A9707, A9708 and A9709 are syntypes.

The holotype is in poor condition, with few scales remaining on the body; the infraorbitals of the right hand side are loose and the right upper jaw is disarticulated.

DIAGNOSIS. The body of *H. forskahlii* (Fig. 25B) tends to be less deep (mean = 22.6 expressed as a percentage of the standard length) than that of its congeners, and the lateral stripes are prominent. It differs from *H. brevis* with which it is sympatric, in having slender gill rakers, which are approximately equal to the gill filaments in length.

DESCRIPTION. Based on the holotype and 175 other specimens, ranging in size from 51.2–442 mm standard length. Depth of body 17.2–27.8 (mean = 22.6) per cent of standard length, length of head 15.3–25.3 (mean = 19.8) per cent. The dorsal profile of the head is straight. Interorbital width 6.1–10.8 (mean = 7.9) per cent, width of 4th infraorbital 5.1–7.5 (mean = 6.1); snout length 6.1–10.2 (mean = 8.3) per cent; depth of premaxilla 1.7–3.9 (mean = 2.7) per cent of standard length.

Gill rakers: Long and slender, approximately as long as the gill filaments; 8–10 (mode 9) rakers on the first ceratobranchial.

Scales: Lateral line with 46 (f. 10), 47 (f. 31), 48 (f. 30), 49 (f. 26), 50 (f. 31), 51 (f. 19), 52 (f. 12) or 53 (f. 7).

Fins: Dorsal with 2 soft, unbranched rays and 8 branched rays in all specimens. Anal with 3 soft, unbranched rays and 11 (f. 6), 12 (f. 132), 13 (f. 9) or 14 (f. 1) branched rays.

Teeth: In the upper jaw caniniform, large and widely spaced anteriorly, and smaller and tricuspid posteriorly, numbering 9 (f. 2), 10 (f. 10), 11 (f. 4), 12 (f. 126), 13 (f. 4) or 14 (f. 19). Lower jaw with 8 (f. 4), 9 (f. 4), 10 (f. 56), 11 (f. 15) or 12 (f. 66) teeth, identical in morphology to those of the upper jaw. Of those specimens with 14 upper jaw teeth, 16 are from coastal flowing rivers in Liberia and Ivory Coast and 3 are from L. Rudolf. This difference in tooth number appears to be a populational variation as there is no osteological or other evidence to suggest these specimens are not *H. forskahlii*.

Vertebrae: 45–51, counted as abdominal + caudal elements: 28 + 16 (f. 1); 28 + 17 (f. 2); 28 + 18 (f. 4); 29 + 16 (f. 1); 29 + 17 (f. 12); 29 + 18 (f. 1); 30 + 17 (f. 6); 30 + 18 (f. 1); 32 + 18 (f. 6) or 32 + 19 (f. 1).

Osteology: *Hydrocynus forskahlii* differs from its congeners in the following osteological features:

The lateral ethmoid wing is dorsally thickened and sickle-shaped in lateral view (Fig. 1B). In the other *Hydrocynus* species, it is narrow and crescentic in shape.

In the region of the dilatator fossa, the frontal is produced as a lip that partially roofs the fossa. In *H. brevis* the dilatator fossa is extensively roofed by the frontal (see p. 196) and in *H. goliath* and *H. tanzaniae*, the dilator fossa is unroofed.

DISTRIBUTION. Nilotic drainage; Senegal, Guinea, Sierra Leone; Liberia, Ivory Coast, Ghana, Nigeria, Cameroun, Zaire drainage, Zambesi drainage including L. Malawi, Limpopo, the Pongolo River system, Okovango basin, L. Ngami and as far south as L. Sibaya N. Natal.

MATERIAL EXAMINED. Holotype: MNHN 1691, River Nile; BMNH: 1937.4.20: 1–6, L. Gandjule, Ethiopia; 1907.12.2: 481–486, Nile, Beni Suef, Egypt; 1907.12.2: 511–519, Nile, Luxor and Aswan; 1949.10.20: 22–23, R. Volta; 1905.7.25: 79–80, L. Gandjule, Ethiopia; 1953.4.28: 129–130, Ogun R. Nigeria; 1953.4.28: 129–130, Ogun R. Nigeria; 1907.12.2: 487, Sanhur R. Nile; 1907.12.2: 526, Upper Nile, Korosko; 1907.12.2: 537, Mouth of L. No, White Nile; 1907.12.2: 527–528, Ibrim, Upper Nile; 1907.12.2: 474, L. Edkon; 1907.12.2: 524, Abu Hoor, Upper Nile; 1899.8.23: 58–59, Niger; 1934.8.31: 36, Volta, Ashanti Forest; 1904.1.19: 5, Tsutyaba, Albert Nile; 1932.6.13: 25–34, L. Rudolf; 1976.11.12: 52–58, Little Scarcies R., Sierra Leone; 1932.12.16: 39, Luangwa Valley; 1929.1.24: 60, Victoria Nile; 1907.12.2: 541–544, Mouth of L. No, Nile; 1907.12.2: 545–547, Gondokoro, (Sudan) Nile; 1943.7.27: 169–171, R. Chambezi and Bangwelu Swamps; 1899.9.26: 74, Leopoldville, Congo (Kinshasa, Zaire); 1908.11.6: 6–12 Upper Zambezi, above Victoria Falls; 1977.6.27: 275–298; L. Sibaya, N. Natal; 1975.6.20: 62, Luhra, Zaire; 1975.6.29: 59–60, L. Tomphwe, Zaire; 1975.6.20: 65, Ituri Bridge, Zaire; 1969.3.25: 38, Sokoto R. Nigeria; 1978.12.5: 2–3 Manantali Dam Site, Senegal; 1975.6.20: 66 Luhra, Zaire; 1975.6.20: 67, Lukuga R. Zaire; 1981.2.17: 1258–1259, L. Rudolf (Turkana); 1932.6.13: 25–34, L. Rudolf (Turkana); 1903.4.24: 181, R. Offin; 1981.2.17: 590–591, L. Rudolf (Turkana); 1907.12.2: 3738 Nile; 1864.5.3: 1, R. Shire; MRAC 79.1.P. 362, L. Upemba, Belgian Congo (Zaire); 78.6.P. 463–464, R. Cuango, Angola; 183706–183707, Kariba Lake, Rhodesia (Zimbabwe); 79.1.P. 1361, Lufira, Belgian Congo (Zaire); 82.13.P. 1223–1226, R. Oubangui, Central African Republic; 183708–710, Sanyati R., Rhodesia (Zimbabwe); 166415–416, Ubangi R., Belgian Congo (Zaire); 158580, Dundo, Angola; 158581, R. Karai, Angola; 78.14.P. 127, Gorom R., Senegal; 189342, Wilia, Zaire; 76.14.P. 607–610, Koum, Cameroun; 154071–073 Fort Archambault, Tchad; 73.26.P. 40, Karaska, Tchad; 179926, Dungu R., Belgian Congo (Zaire); 76.14.P. 889–890 Mieri R., Doume, Cameroun; 73.10.P. 981–982, Toyebli, R. Cerr, Ivory Coast; 73.12.P. 81–83, Mopti, S. Mali; 73.12.P. 85, Mopti, S. Mali; 73.14.P. 53–54, Ogbone, Mono R., Togo; 82.28.P. 150–152, L. Abaya, Ethiopia; 73.12.P. 84, Mopti, S. Mali; 73.7.P. 28 Kete Krachi, Ghana; 73.5.P. 481, R. Ouime, Whedda, Dahomey; 73.10.P. 993–994, Mano R., Liberia; 73.10.P. 908 Toyebli, R. Cerr, Ivory Coast; 73.7.P. 29 Yetji, Ghana; 73.18.P. 776–782, Lagdo, R. Benoue, Cameroun; 73.15.P. 323–326, Garoua, R. Benoue, Cameroun; 73.10.P. 996–997, St Paul R., Mt Coffee, Liberia; 74.14.P. 291, L. Kossou, Ivory Coast; 74.14.P. 289–290, L. Kossou, Ivory Coast; 74.14.P. 2712, L. Kossou, Ivory Coast; 73.10.P. 998–1003, St Paul R., Mt Coffee, Liberia; 74.14.P. 2895–2802, L. Kossou, Ivory Coast; 80.19.P. 44, Sassandra R., Ivory Coast; 80.36.P. 816, Liberia; RMNH: 3279 (holotype of *Hydrocyon lineatus*) Ashantee, Guinea; MRHN: 8892, Rhodesia (Zimbabwe); 7539, Stanleyville (Kisangani, Zaire).

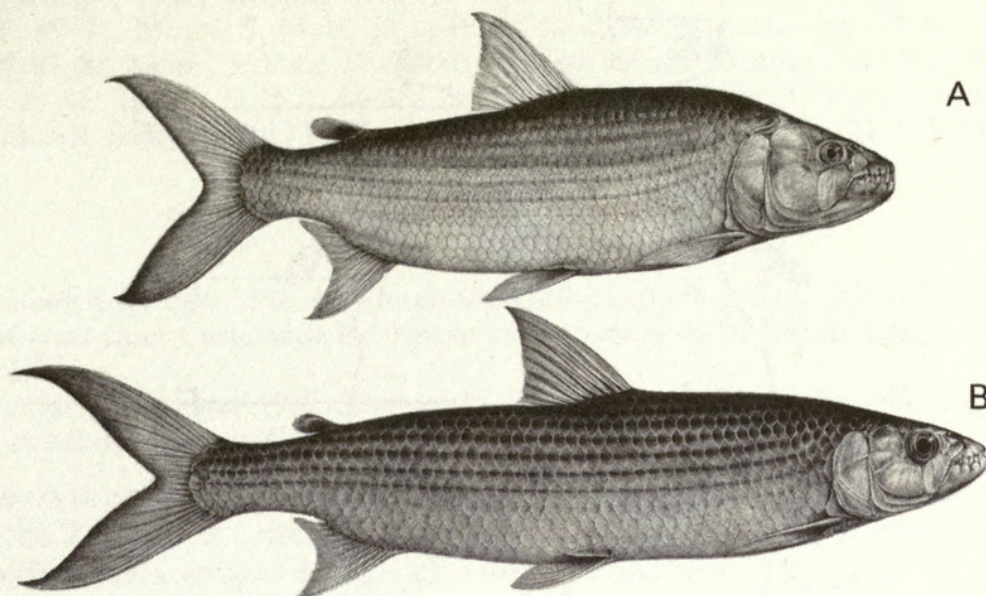


Fig. 25 A, *Hydrocynus brevis*; B, *Hydrocynus forskahlii* (taken from Boulenger 1907 *The fishes of the Nile*. Plate xv).

Hydrocynus brevis Günther
(Fig 25A)

Hydrocynus brevis Günther 1864 *Catalogue of Fishes* 5: 351

?*Hydrocynus somonorum* Daget 1954 *Memoires de l'I. F. A. N.* no. 36: 116–117.

LECTOTYPE. Günther's description is based on three females in the collections of the BMNH. A specimen of 247 mm standard length, from Khartoum (BMNH 1862.6.17: 94) is designated here as the lectotype. The remaining two specimens, of 232 mm and 275 mm standard length (BMNH 1862.6.17: 95–96) thus become paralectotypes.

NOTE ON THE SYNONYMY. The types of *H. somonorum* are no longer extant (M. L. Bauchot, pers. comm.). I have examined the single non-type specimen labelled as *H. somonorum* and am satisfied this is a specimen of *H. brevis*. Daget's description of *H. somonorum* agrees with that of *H. brevis*, and he comments on the close resemblance of the two nominal forms but considers them distinct species on the basis of the short head; very small eye; position of the dorsal fin; number of scales above and below the lateral line and the fewer vertebrae in *H. somonorum*. I find Daget's morphometric and meristic data for the types of *H. somonorum* lie within the ranges of those of *H. brevis*.

DIAGNOSIS. *Hydrocynus brevis* has a deeper body (mean = 24.4 per cent of the standard length) than the other species. The lateral stripes are less conspicuous than those of either *H. forskahlii* or *H. tanzaniae*. The infraorbital width is greater in this species (mean = 7.7 per cent of the standard length) and the gill rakers are short, approximating to one third the length of the gill filaments.

DESCRIPTION. Based on the lectotype 247 mm SL., paralectotypes 232; 275 mm SL and 83 other specimens, ranging from 41.3–442 mm SL. Depth of body 19.1–29.6 (mean = 24.4) per cent of standard length, length of head 18.5–24.5 (mean = 21.3) per cent. The dorsal profile of the head is straight to the posterior margin of the parietals, the supraoccipital is slightly crested. Interorbital width 8.0–10.3 (mean = 9.2) per cent; 4th infraorbital width 6.9–8.9 (mean = 7.7) per cent; snout length 8.1–13.8 (mean = 10.0) per cent; depth of premaxilla 3.0–5.3 (mean = 3.8) per cent of standard length.

Gill rakers: Short, approximately one third the length of the gill filaments, 7–10 (mode 8) rakers on the first ceratobranchial.

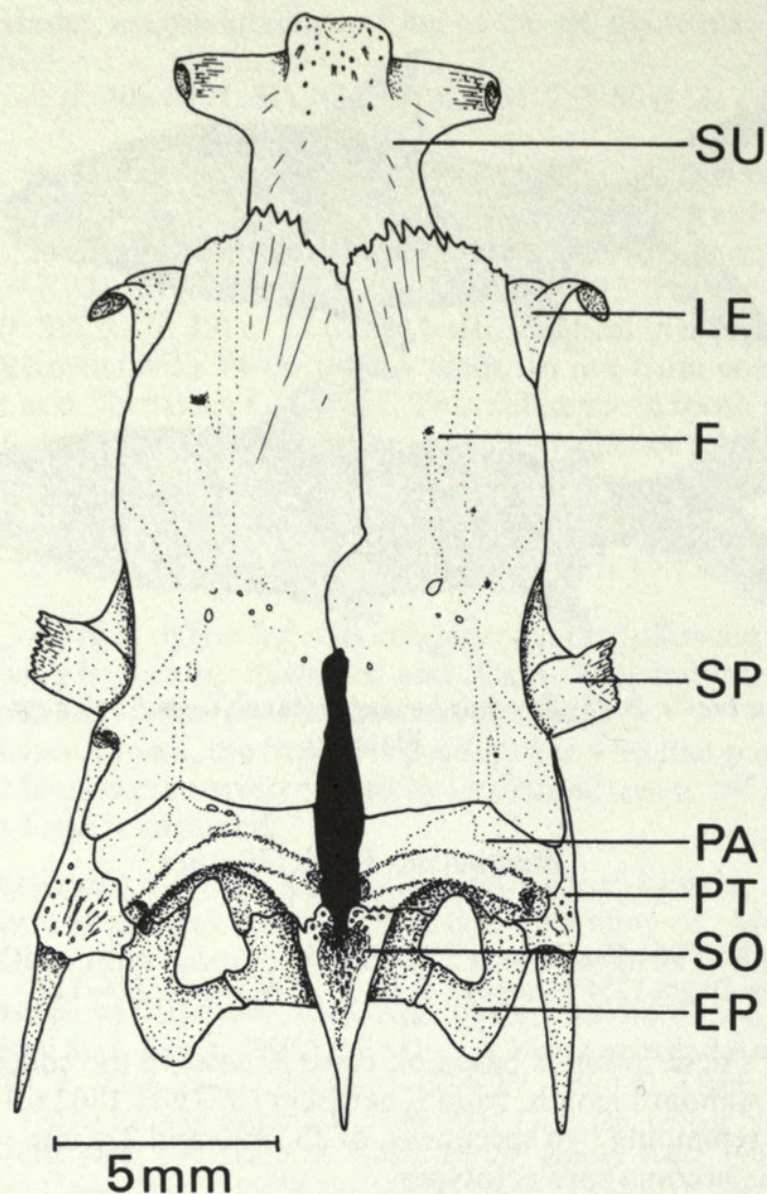


Fig. 26 *Hydrocynus brevis* neurocranium, dorsal view.

Scales: Lateral line with 47 (f. 2), 48 (f. 2), 49 (f. 11), 50 (f. 22), 51 (f. 21), 52 (f. 13), 53 (f. 11), 54 (f. 2) or 55 (f. 1) scales.

Fins: Dorsal with 2 soft unbranched and 8 branched rays in all specimens. Anal with 3 soft unbranched rays and 11 (f. 4), 12 (f. 61) or 13 (f. 16) branched rays.

Teeth: Are like those described for *H. forskahlii*, with 10 (f. 27), 11 (f. 2) or 12 (f. 55) in the upper jaw and 8 (f. 7), 10 (f. 51), 11 (f. 3), 12 (f. 22) or 13 (f. 1) in the lower jaw.

Vertebrae: 49–51; counted as abdominal + caudal elements: 31 + 18 (f. 6), 31 + 19 (f. 3), 32 + 16 (f. 1); 32 + 18 (f. 3).

Osteology: The osteology of *H. brevis* differs from that of *H. forskahlii* in the following features: The region of the frontals which roofs the dilatator fossa is produced as a thin, flat ledge of bone (Fig. 26), this region of the frontals in *H. forskahlii* partially overlaps the medial border of the fossa, whilst in *H. goliath* and *H. tanzaniae* the fossa is not overlapped by the frontals (Fig. 28 & 31).

The sphenotic process is very short and peg-like in contrast to the other species of *Hydrocynus* which have a well-developed, ventrally thickened process.

DISTRIBUTION. Nilo-Sudan, Upper Guinea, Cameroun, Togo, Ghana and Ivory Coast.

MATERIAL EXAMINED. BMNH: lectotype 1862.6.17: 94, Khartoum; paralectotypes 1862.6.17: 95–96, Khartoum; 1907.12.2: 3768–3776, nr. Luxor; 1982.4.13: 744, Sokoto R., Nigeria; 1949.10.20: 24, Dasikope, Gold Coast (Ghana); 1905.3.15: 6, Shari R.; 1907.12.2: 559–573, nr. Luxor; 1900.6.28: 77, Matam, Senegal; 1907.12.2: 549–558, nr. Luxor; 1862.9.19: 10 Nile; MNHN: A8548, White Nile; A8607, White Nile; A9710,

Nile; A9711, Senegal; 1692, Senegal. MRAC: 78.14.P. 34–36, Mbane, Senegal; 73.13.P. 57–58, R. Ori, Togo; 73.12.P. 89–91, Mopti, S. Mali; 73.15.P. 307–311, Waga, Cameroun; 75.5.P. 491, Doropo, Ivory Coast; 73.12.P. 87–88, Mopti, S. Mali; 73.7.P. 30–31, Kete Krachi, Ghana; 73.15.P. 312–313, Waga, Cameroun; 73.26.P. 41–43, Tchad; 73.26.P. 44–45, Tchad; 82.28.P. 37, Nile; 75.66.P. 1, Siquiri, Guinea; 70.2.P. 178–181, Gambia R. Senegal; 73.13.P. 55–56, San Sargon R., Togo; 79.2.P. 171–177, Mbane, Senegal.

Hydrocynus goliath Boulenger
(Fig. 27)

Hydrocynus goliath Boulenger 1898 *Annales du Musée du Congo Belge. Zoology* 1: 23, plate xi.

Hydrocynus vittatus (non Castelnau) Boulenger 1898 *Annales du Musée du Congo Belge. Zoology* 1: 24, plate x, fig. 2.

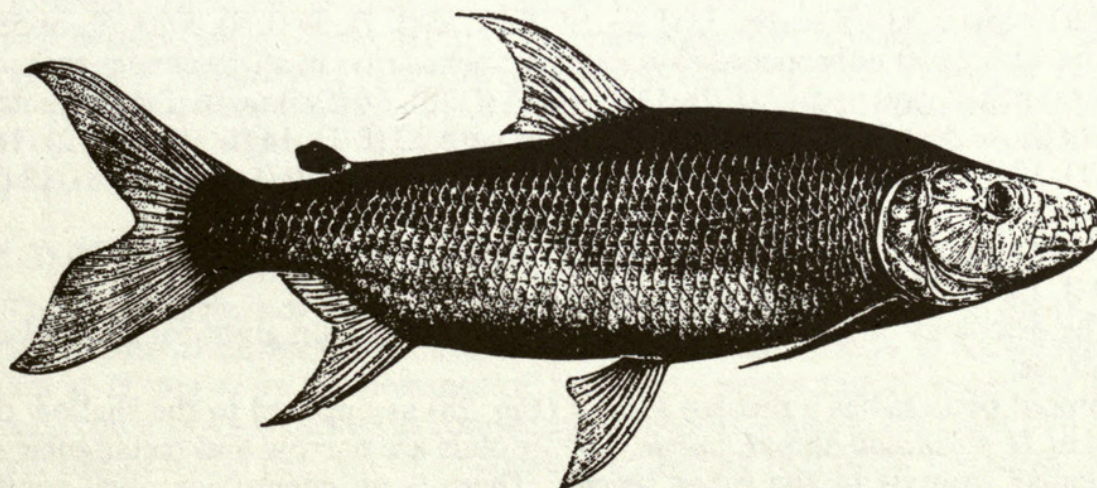
Hydrocynus vittiger Boulenger 1907 *Zoology of Egypt: The Fishes of the Nile*. Egyptian Government Publishers; as a footnote on p. 106.

NOTE ON THE SYNONYMY. Boulenger described both *H. goliath* and *H. vittiger* from specimens collected in the Zaire river system. He distinguished them on morphometric and meristic characters, in which there is some overlap. In his description, Boulenger stated *H. vittiger* had only 10 upper jaw teeth, but the types have at least two additional teeth on each premaxilla at the rictus of the jaws, which Boulenger failed to notice. Since the osteology and external morphology of the two species are identical, I consider *H. vittiger* a junior synonym of *H. goliath*. The latter name has precedence because *H. vittatus* Boulenger 1898 was invalid as it was preoccupied by *H. vittatus* Castelnau 1861; also according to Daget *et al.* (1984: 171–172) it has been more widely used.

LECTOTYPE. Of the six original specimens described, two were deposited in the collections of the BMNH and four in the MRAC, Tervuren. One of the specimens in the BMNH, collected by Captain Wilverth from New Antwerp, cannot be traced. The other, a female of 672 mm standard length (BMNH 1898.11.17: 4) is designated here as lectotype. The following MRAC, Tervuren specimens become paralectotypes: 77(117) Manyanga, coll. Wilverth; 166(267) Umangi, coll. Wilverth; 116 Leopoldville, coll. Wilverth and 117 Leopoldville coll. Wilverth.

DIAGNOSIS. The lateral stripes of *Hydrocynus goliath* are the least distinctive within the species of this genus. There are between 2–8 small teeth at the posterior margin of the upper jaw which just protrude through the skin. The anal fin has 3 soft unbranched rays and usually 14 branched rays; in all other *Hydrocynus* species there are usually 12 branched rays.

This species has a higher vertebral count of between 52–54 vertebrae compared with a range of 45–51 vertebrae in other species. Similarly, there are a larger number of scales in the lateral line series, ranging from 53–58 scales, whilst the range for the remaining species is 43–55 scales.



Hydrocyon goliath.

Fig. 27 *Hydrocynus goliath* (taken from Boulenger, 1909 *Catalogue of the freshwater fishes of Africa in the British Museum* p. 185).

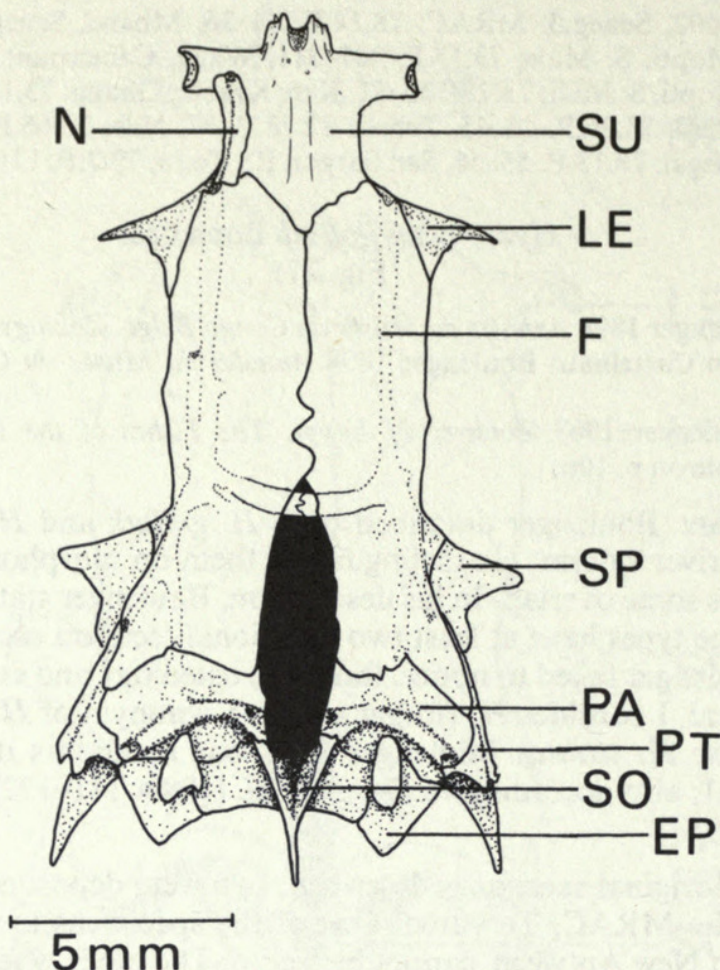


Fig. 28 *Hydrocynus goliath* neurocranium, dorsal view.

DESCRIPTION. Based on the lectotype, paralectotypes and 26 other specimens, ranging in size from 36.1–672 mm standard length. Depth of body 19.4–32.7 (mean = 23) per cent of standard length; length of head 19.2–23.1 (mean = 21.2) per cent. The dorsal profile of the head is straight. Interorbital width 6.2–8.5 (mean = 7.9) per cent; 4th infraorbital width 5.5–8.0 (mean = 6.5); snout length 8.6–10.9 (mean = 9.6) per cent; depth of premaxilla 3.8–4.4 (mean = 4.3) per cent.

Gill rakers: Very short, less than one-third the length of the gill filaments; 8–9 rakers on the first ceratobranchial.

Scales: Lateral line with 53–58 scales, 53 (f. 2), 54 (f. 2), 55 (f. 7), 56 (f. 9), 57 (f. 5), or 58 (f. 4).

Fins: Dorsal fin with 2 soft unbranched rays and 8 branched rays in all specimens examined. Anal with 3 soft unbranched rays and 12 (f. 2), 13 (f. 2), 14 (f. 20), 15 (f. 5) or 16 (f. 1) branched rays.

Teeth: Are like those described for *H. forskahlii* but with 12 (f. 1), 14 (f. 1), 15 (f. 2), 16 (f. 9), 17 (f. 2), 18 (f. 11), 19 (f. 1) or 20 (f. 2) in the upper jaw, and 8 (f. 2), 10 (f. 5), 12 (f. 8), 13 (f. 1) or 14 (f. 13) in the lower jaw.

Vertebrae: 52–54; counted as abdominal + caudal elements: 32 + 20 (f. 1); 33 + 20 (f. 5); 33 + 21 (f. 1); 34 + 19 (f. 1); 34 + 20 (f. 3); 35 + 19 (f. 2) or 36 + 20 (f. 1).

Osteology: The osteology of *H. goliath* differs from the description given for *H. forskahlii* in the following features:

The supraethmoid process has a median groove (Fig. 28) as opposed to the shallow depression characteristic of *H. forskahlii* and *H. brevis*. The frontals are narrow and rectangular unlike the broad rectangular frontals of the other species. There is an edentulous, oval toothplate on basibranchial 4 (Fig. 29) a character which is unique to this species within the characiforms.

DISTRIBUTION Restricted to the Oubangui R. (Waters, pers. comm.), the central and upper Zaire basin.

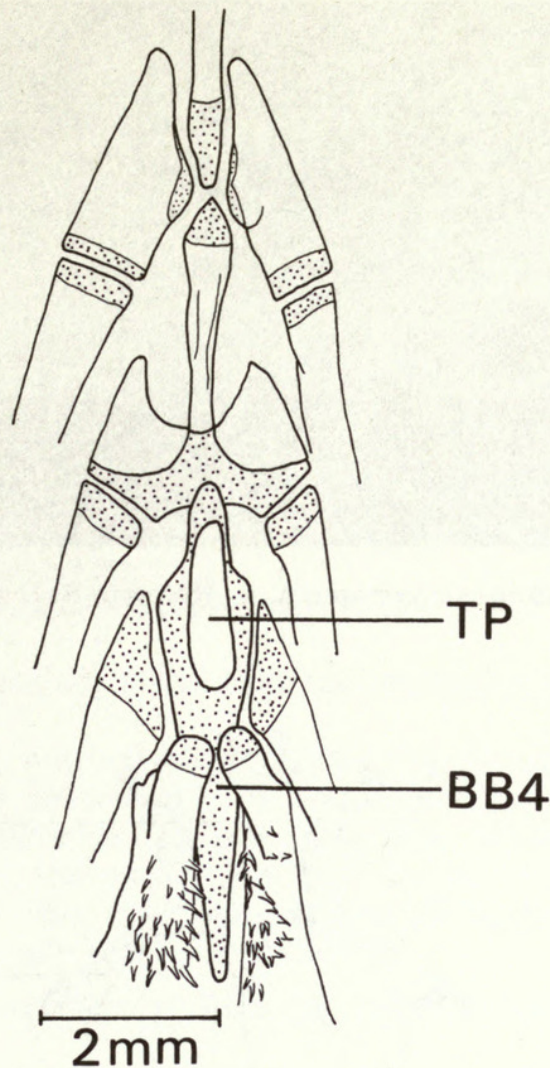


Fig. 29 *Hydrocynus goliath* basibranchial 4, dorsal view.

MATERIAL EXAMINED. BMNH: 1898.11.17: 4 (lectotype) Manyanga Belgian Congo (Zaire); 1919.9.10: 96, Leopoldville (Kinshasa, Zaire); 1907.5.2: 18, Bolobo Belgian Congo (Zaire); 1919.9.10: 97 Busabangi Belgian Congo (Zaire); 1899.8.22: 10, Monsembe Belgian Congo (Zaire); 1901.12.12: 21, Monsembe Belgian Congo (Zaire); 1898.11.17: 5 (syntype of *H. vittiger*), Manyanga Belgian Congo (Zaire); 1919.9.10: 95, Leopoldville (Kinshasa, Zaire); 1975.6.20: 69, Monganga-Ilewa, Zaire, MRAC: 77 (paralectotype) Manyanga Belgian Congo (Zaire); 166 (paralectotype) Umangi Belgian Congo (Zaire); 74.59.P. 1, Zaire; 189340–341, Kisangani, Zaire; 149 (syntype of *H. vittiger*) Upoto Belgian Congo (Zaire); 165 (syntype of *H. vittiger*) Umangi Belgian Congo (Zaire); 120625 Yangambi Belgian Congo (Zaire); 48032 Matadi Belgian Congo (Zaire); 120624 Yangambi Belgian Congo (Zaire); 120622–120623 Yangambi Belgian Congo (Zaire); 48074–48077 R. Kalamu Belgian Congo (Zaire); 2319 Leopoldville (Kinshasa, Zaire). MRHN 10749 Yangambi Belgian Congo (Zaire); 10748, Yangambi Belgian Congo (Zaire); 15238, Leopoldville (Kinshasa, Zaire).

Hydrocynus tanzaniae sp. n. fig. 30

DIAGNOSIS. The lateral stripes of *H. tanzaniae* are distinct and it differs from all other *Hydrocynus* species in the presence of elongated 3rd and 4th dorsal and anal fin rays. It is distinguished from *H. forskahlii* and *H. brevis* by the presence of at least 14 upper and 12 lower jaw teeth and a lateral line scale count of 43–47 scales as compared with 46–55 scales in the other two species. The body is deeper (mean = 23.8 per cent of standard length) than that of *H. forskahlii* (mean = 22.6 per cent of standard length) but does not quite approach the body depth of *H. brevis* (mean = 24.4 per cent of standard length).

Hydrocynus tanzaniae has 3 soft, 12–13 (mode 12) branched anal fin rays compared with 3 soft, 12–16 (mode 14) in *H. goliath*.

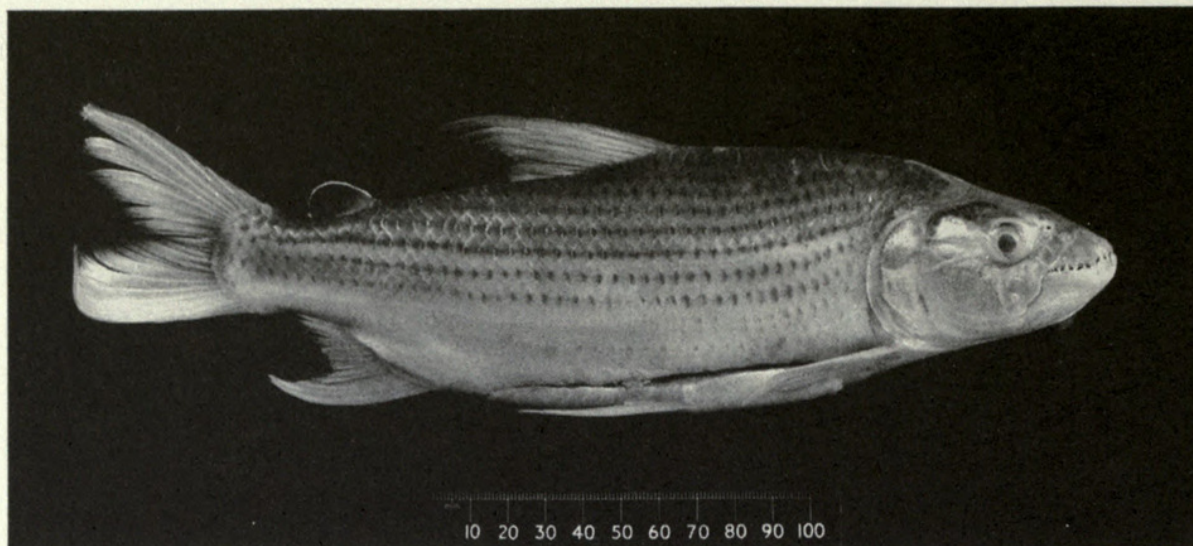


Fig. 30 *Hydrocynus tanzaniae* n. sp. Holotype BMNH 1976.10.21: 130

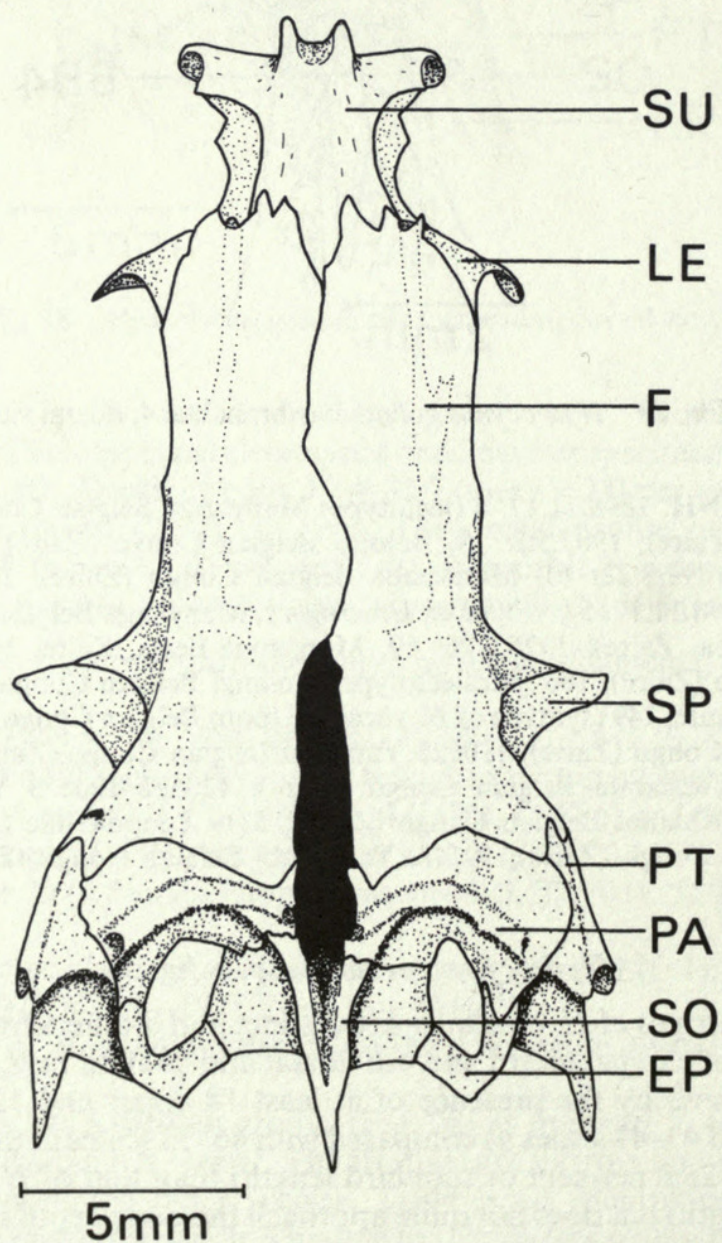


Fig. 31 *Hydrocynus tanzaniae* neurocranium, dorsal view.

DESCRIPTION. Based on the holotype, a female of 247 mm standard length, from Lower Ruvu River, Tanzania, collected by R. G. Bailey, BMNH 1976.10.21: 130, two paratypes of 141.5 mm and 191 mm standard length from the Rufiji River, Tanzania, collected by A. I. Payne, BMNH 1981.7.7: 41–42, and 17 other specimens.

Depth of body 20.0–26.6 (mean = 23.8) per cent of standard length; length of head 18.3–22.2 (mean = 20.4) per cent. The dorsal profile of the head is straight. Interorbital width 6.5–8.1 (mean = 7.3) per cent; 4th infraorbital width 6.0–7.6 (mean = 6.3) per cent; snout length 7.1–9.0 (mean = 8.0) per cent; depth of premaxilla 2.2–3.4 (mean = 2.7) per cent of standard length.

Gill rakers: Short, approximately one-third the length of the gill filaments; 8–9 (mode 9) rakers on the first ceratobranchial.

Scales: Lateral line with 43–47 scales, 43 (f. 2), 44 (f. 1), 45 (f. 7), 46 (f. 5) or 47 (f. 5).

Fins: Dorsal with 2 soft, unbranched rays and 8 branched rays in all specimens examined. Anal fin with 3 soft, unbranched rays and 12 (f. 16), or 13 (f. 4) branched rays.

Teeth: Similar to those in *H. forskahlii*, with 13 (f. 1), 14 (f. 7), 15 (f. 1) or 16 (f. 11) in the upper jaw and 10 (f. 1) or 12 (f. 19) in the lower jaw.

Vertebrae: 46–47; counted as abdominal + caudal elements: 28 + 18 (f. 1), 28 + 19 (f. 1) or 29 + 17 (f. 2).

Osteology: The osteology of *H. tanzaniae* differs from the description given for *H. forskahlii* in the following features:

The supraethmoid process is deeply notched in the mid-line (Fig. 31) unlike that of *H. forskahlii* and *H. brevis* which has a shallow depression or *H. goliath* which has a median groove. The lateral supraethmoid wings are anterolaterally orientated (Fig. 31) and the supraethmoid is narrow posteriorly so that in dorsal view part of the dorsal surface of the vomer is visible. The lateral supraethmoid wings of the other *Hydrocynus* species are horizontal, the supraethmoid obscures the vomer in dorsal view and is not markedly narrow.

DISTRIBUTION. The eastward flowing rivers of Tanzania, in the Wami Ruaha and Rufiji river systems.

MATERIAL EXAMINED. BMNH: 1976.10.21: 130 (holotype), Lower Ruvu river; 1981.7.7: 41–42 (paratypes), Rufiji River; 1976.10.21: 128–129, Lower Ruvu R.; 1972.11.28: 3–4, Ruaha R.; 1981.1.14: 44 Kilombero R.; 1981.1.14: 45–46, Kilombero R.; 1981.1.14: 33–43 Makulinzo. MRAC 188963–968, Gt Ruaha R.; 191468, Ruaha R.

Nomen dubium

Salmo dentex (non Linnaeus) Forsskål, 1775 *Descriptiones Animalium* p. 67, number 97.

The type of *Salmo dentex* is no longer extant (Klausewitz & Nielsen, 1965); however, Forsskål's description of this Nilotic fish clearly refers to a specimen of *Hydrocynus*. *Salmo dentex* is usually included in the synonymy of *H. forskahlii* but I consider it a *nomen dubium* since both *H. forskahlii* and *H. brevis* are sympatric in the Nile and there are insufficient data in Forsskål's description to assign his material to one or other of the two species.

Key to species

The description of the four species of *Hydrocynus* recognized here are summarized as follows:

- | | | |
|---|--|---|
| 1 | Usually with 14 or more teeth in the upper jaw | 2 |
| – | Usually with 12 teeth in the upper jaw | 3 |
| 2 | Gill rakers very short, less than one-third the length of the gill filaments; lateral line with 53–58 pored scales; anal fin with 3 soft, unbranched and usually 14 branched rays; vertebrae 52–54; lateral stripes not distinctive; found in the Oubangui R., central and upper Zaire | |

H. goliath

- Gill rakers approximately one-third the length of the gill filaments; lateral line with 43–47 pored scales; anal fin with 3 soft, unbranched and usually 12 branched rays; vertebrae 46–47; lateral stripes distinct; confined to the eastward flowing rivers of Tanzania *H. tanzaniae*
- 3 Gill rakers long, approximately equal in length to the gill filaments; 4th infraorbital width approximately 6.1 per cent (range 5.1–7.5 per cent) of the standard length; body not deep, usually 22.6 per cent of the standard length (range 17.2–27.8 per cent of SL); lateral line with 46–53 pored scales; vertebrae 45–51; lateral stripes prominent; widespread throughout Africa *H. forskahlii*
- Gill rakers approximately one-third the length of the gill filaments; 4th infraorbital broad, approximately 7.7 per cent of standard length (range 6.9–8.9 per cent of SL); body deep, approximately 24.4 per cent of standard length (range 19.1–29.6 per cent of SL); lateral line with 47–55 pored scales; vertebrae 49–51; lateral stripes conspicuous; found from the Nilo-Sudan region to the west coast of northern Africa *H. brevis*

Concluding remarks

An osteological study of four *Hydrocynus* species has revealed eighteen features which appear to be autapomorphic for the genus.

In view of Roberts's (1966, 1967 & 1969) idea of relationship between *Alestes* and *Hydrocynus*, species of the former taxon were examined in detail. During the course of this study it became apparent that Roberts's *Alestes* (*sensu* Boulenger, 1907) is a non-monophyletic assemblage, containing species having their affinities with species in at least three other genera. Of those genera, *Alestes sensu stricto* (see p. 190) is, on the basis of three synapomorphies, apparently the sister-group of *Hydrocynus* (see p. 192). However, the relationship of *Hydrocynus* and *Alestes s.s.* to the *Alestes sensu lato* group of species cannot be resolved until a detailed anatomical revision and phylogenetic analysis of all their constituent species has been undertaken.

Roberts (1969: 441) commented on the upper jaw morphology of African Characidae, and pointed out that the morphology of the premaxilla and maxilla differs from that of the Neotropical Characidae. Amongst outgroup Neotropical characids examined, I find the maxilla is typically dentate, large, ovate and lamellar, with a medially directed ascending process. The maxilla of the African Characidae (excluding *Hydrocynus*, see p. 172) is edentulous, pediculate posteriorly, and has a well-developed, anteriorly curved ascending process; possibly this represents the derived condition within the Characiformes.

The majority of Characiformes have two posttemporal fossae, although in concurrence with Vari (1979: 341) I find that with the exception of *Lepidarchus*, all African Characidae have a third posttemporal fossa contained entirely within the epioccipital. A third posttemporal fossa contained entirely within the epioccipital occurs in the Neotropical characiform families Hemiodontidae, Paradontidae and Curimatidae (Roberts, 1974: 416 & 425; Vari, 1983: 37).

The African characiform families Distichodontidae and Citharinidae and the neotropical characid tribe Cynodontini, also have a third posttemporal fossa, but it is bordered by both the epioccipital and exoccipital bones (Vari, 1979: 289; 1983: 37).

Vari (1983) gives a series of characters uniting the Curimatidae to the Prochilodontidae; the Hemiodontidae have a rhinosphenoid bone present, in common with various other Neotropical characids. In the absence of any synapomorphies indicating a close relationship between the Hemiodontidae, Paradontidae, Curimatidae and the African Characidae, the presence of a third posttemporal fossa contained entirely within the epioccipital is most parsimoniously explained as a homoplasy.

Sexual dimorphism in the posterior neural spines (see p. 183), occurs in all African Characidae examined (with the notable exception of *Lepidarchus*) and in one genus (*Curimatopsis*) of the Neotropical characiform family Curimatidae (Vari, 1982, 4). The morphology of these modified neural spines in *Curimatopsis*, however, differs from that in the African Characidae (see p. 192). Thus, it is unlikely this feature represents a synapomorphy uniting the African Characidae with the Curimatidae. The particular morphology of the modified neural spines, shared only amongst African characids, indicates that this character is synapomorphic for those taxa

possessing it, namely *Hydrocynus*, *Alestes sensu stricto*, *Alestes sensu lato*, *Bryconaethiops*, *Micralestes* and *Rhabdalestes*.

The African characid genus *Lepidarchus* apparently lacks all those features hypothesized above as synapomorphies for African Characidae. It is, therefore possible either that *Lepidarchus* should not be included in the family Characidae, or since it shows reduction in many morphological features, this genus is paedomorphic and represents a miniaturized characid.

The unique upper jaw morphology, absence of ectopterygoid teeth (see p. 189) and secondary sexual dimorphism exhibited in the posterior neural spines are hypothesized to be synapomorphies that indicate the African characids form a monophyletic subunit within the Characiformes, an idea already suggested by Vari (1979: 342). However, since a number of African characid genera were unavailable for outgroup comparison, formal designation of such a category cannot be made at this stage.

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Appendix 1

MATERIAL EXAMINED

EtOH = ethanol preserved; A = Alcian blue/Alizarin red stained; S = skeleton

Characidae			
<i>Alestes affinis</i>		A	
<i>Alestes ansorgii</i>		A	
<i>Alestes baremose</i>	EtOH	A	S
<i>Alestes chaperi</i>		A	
<i>Alestes dentex</i>	EtOH	A	S
<i>Alestes ferox</i>		A	
<i>Alestes humilis</i>		A	
<i>Alestes imberi</i>		A	
<i>Alestes jacksoni</i>		A	
<i>Alestes lateralis</i>		A	
<i>Alestes leuciscus</i>		A	
<i>Alestes liebrechtsii</i>	EtOH	A	
<i>Alestes macrolepidotus</i>		A	S
<i>Alestes macrophthalmus</i>	EtOH	A	S
<i>Alestes minutus</i>	EtOH	A	
<i>Alestes stuhlmanni</i>	EtOH	A	
<i>Bryconæthiops microstoma</i>	EtOH	A	S
<i>Micralestes acutidens</i>		A	S
<i>Rhabdalestes rhodesianus</i>	EtOH	A	
<i>Hemigrammopetersius barnardi</i>	EtOH	A	
<i>Phenacogrammus interruptus</i>		A	
<i>Virilia pabrensis</i>	EtOH	A	
<i>Alestopetersius leopoldianus</i>			S
<i>Lepidarchus adonis</i>	EtOH	A	
<i>Serrasalmus humeralis</i>	EtOH		S
<i>Rhaphiodon vulpinus</i>			S
<i>Hydrolycus scomberoides</i>			S
<i>Hydrolycus pectoralis</i>			S
<i>Charax gibbosus</i>			S
<i>Acestrorhynchus falcatus</i>			S

continued overleaf

Appendix 1—continued

EtOH = ethanol preserved; A = Alcian blue/Alizarin red stained; S = skeleton

<i>Oligosarcus bolivianus</i>		A	S
<i>Oligosarcus hepsetus</i>			S
<i>Roeboides</i> sp			S
<i>Salminus maxillosus</i>			S
<i>Brycon falcatus</i>		A	S
<i>Brycon dentex</i>			S
<i>Triportheus angulatus</i>			S
<i>Poptella orbicularis</i>			S
<i>Astyanax bimaculatus</i>		A	S
<i>Moenkhausia lepidura</i>			S
<i>Bryconops caudomaculatus</i>			S
<i>Scissor macrocephalus</i>			S
Hepsetidae			
<i>Hepsetus odoe</i>	EtOH	A	S
Distichodontidae			
<i>Distichodus lusosso</i>			S
<i>Xenocharax spilurus</i>			S
<i>Ichthyborus besse</i>			S
<i>Ichthyborus quadrilineatus</i>			S
Citharinidae			
<i>Citharinus citharus</i>			S
Erythrinidae			
<i>Erythrinus erythrinus</i>		A	
<i>Hoplias malabaricus</i>		A	S
<i>Hoplerythrinus unitaeniatus</i>		A	S
Ctenoluciidae			
<i>Ctenolucius</i> sp			S
<i>Boulengerella lucium</i>			S
Lebiasinidae			
<i>Lebiasina multimaculata</i>			S
<i>Lebiasina erythrinoides</i>			S
Curimatidae			
<i>Curimatorbis spilurus</i>			S



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