A Notopterid Skull (Teleostei, Osteoglossomorpha) from the Continental Early Cretaceous of Southern Morocco

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ABSTRACT

Palaeonotopterus is an extinct osteoglossomorph and represents the oldest known fossil notopterid, coming from the continental late Albian or early Cenomanian of southern Morocco. The taxon is founded upon a single isolated braincase, and the discovery of a second braincase of *Palaeonotopterus greenwoodi* (described here) permits the original description to be expanded. *Palaeonotopterus* is more closely related to modern notopterids than to mormyrids and gymnarchids, but it is more primitive than all four modern notopterid genera, which share at least six cranial synapomorphies not observed in either of the fossil braincases.

INTRODUCTION

A large teleost braincase is described from the continental late Albian or early Cenomanian Kem-Kem Beds (Tegana Formation) of southern Morocco, near the Algerian frontier. The skull is preserved three-dimensionally and displays characters diagnostic of notopterids (Teleostei, Osteoglossomorpha). The braincase is 91 mm long but the mes- ethmoid, vomer, lateral ethmoids, parasphenoid, and the most anterior part of the frontals are missing. Assuming the body proportions were similar to those of modern notopterids, the total length of the individual would have been approximately 1 m.

Notopteridae is a family of fresh and brackish-water fishes, with an elongate and

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strongly compressed body, a paired series of scutes between the shoulder girdle and pelvic fins, an anteriorly located vent, and a reduced tail with the caudal fin continuous with a very long anal fin. Four modern genera are now recognized within the family: *Notopterus* de Lacepede, 1800, from India, Thailand, Malaysia, Sumatra, and Java; *Chitala* Fowler, 1934, from India, Malaysia, Thailand, Cambodia, Laos, Borneo, and Sumatra; *Xenomystus* Günther, 1868, from tropical Africa; and *Papyrocranus* Greenwood, 1963, from West Africa and Congo (Roberts, 1992). *Notopterus* is also known from the late Eocene of Sumatra (Günther, 1876; Sanders, 1934). Notopterid sagittae from the Upper Cretaceous–Paleocene boundary in India have been described and named "*Notopteridarum*" *nolfi* (Singh Rana, 1988). The fossil notopterid from Morocco is thus and by far the most ancient representative of the family.

MATERIALS AND METHODS

Specimen AMNH 19559 is an incomplete braincase preserved in three dimensions, with a preserved length of approximately 91 mm. It is supposedly from the Kem Kem Beds of Morocco, and is probably from the same area as the holotype. The new specimen was studied using a Wild M5 stereomicroscope and was drawn by one of us (LT) using a camera lucida. Subsequently the specimen suffered some damage and is now slightly less complete than is shown in the drawings.

We had intended to name our new fish in honor of the late P. Humphrey Greenwood and his notable work on Notopteridae. During the time we were writing the present paper, Peter Forey of the Natural History Museum (London, England) informed us that he had also studied a Lower Cretaceous notopterid skull from Morocco, and that his paper was submitted for publication (Forey, 1997). By an amazing chance, he had named his fossil *Palaeonotopterus greenwoodi*, with only one letter of difference from our own planned name. A comparison of the AMNH braincase with Forey's (1997) illustrations clearly showed that the two skulls are similar enough to belong to the same species. The existence of an Albian notopterid is impor-

tant enough to justify this separate description of the AMNH specimen, especially since it shows some osteological details not clearly visible on the BMNH skull.

ABBREVIATIONS

Institutional

AMNH American Museum of Natural History, New York
BMNH Natural History Museum, London

Anatomical

BO	basioccipital
BSP	basisphenoid
C1	first vertebral centrum (sutured to basioccipital)
EPI	epioccipital
EXO	exoccipital
FR	frontal
ORS	orbitosphenoid
PA	parietal
PRO	prootic
PTO	pterotic
PTS	pterosphenoid
SOC	supraoccipital
SPH	sphenotic
af	auditory fenestra
ag	aortic groove
c circ	anterior supraocular branch of the otic sensory canal
c pop	uppermost part of the preopercular sensory canal on the pterotic
c porb	otic sensory canal (= postorbital sensory canal)
c sorb	supraorbital sensory canal
df	dilatator fossa
fm	foramen magnum
foa	foramen for the orbital artery
hf	hypophysial fenestra
hyf	hyomandibular fossa
jug a	anterior opening of pars jugularis for the jugular vein, palatine ramus, and pretrematic branch of the facial nerve
jug p	posterior opening of pars jugularis for

	the jugular vein and hyomandibular branch of the facial nerve
my	roof of myodome
pj	pars jugularis
pn	pits for neural arch on centrum fused to basioccipital
sef	subepiotic fossa
slc	sacculo-lagenar chamber
stf	subtemporal fossa
tf	temporal fossa
I	foramen for olfactory nerve
II+III	foramen for optic and common oculomotor nerves
II g	groove on orbitosphenoid for the optic nerve
IV	foramen for trochlear nerve
V+VII	foramen for trigeminal and profundus ramus (V) and facial nerve (VII)
V+VII (so)	foramen for superficial ophthalmic ramus
VI	foramen for external oculomotor (abducens) nerve
VII(o)	foramen for otic ramus of facial nerve
IX(st)	foramen for supratemporal ramus of glossopharyngeal nerve
X	foramen for vagus nerve

DESCRIPTION

DIVISION TELEOSTEI

SUPERORDER OSTEOGLOSSOMORPHA

ORDER MORMYRIFORMES

SUBORDER NOTOPTEROIDEI

FAMILY NOTOPTERIDAE

Genus *Palaeonotopterus* Forey

Species *Palaeonotopterus greenwoodi* Forey

HOLOTYPE: BMNH P.64799, incomplete braincase in three dimensions, preserved length approximately 133 mm, late Albian or early Cenomanian, Kem Kem Beds, Taouz, SE Morocco (Sereno et al., 1996).

REFERRED MATERIAL: AMNH 19559, incomplete braincase preserved in three dimensions, preserved length approximately 91 mm, Kem Kem Beds, probably from the same area as the holotype.

CRANIAL MORPHOLOGY

The preserved length of the AMNH specimen is slightly less than that of the holotype (Forey, 1997). The cranial roof in both examples is a little broader posteriorly and more flattened than in modern notopterids. Additionally, the basioccipital region protrudes farther posteriorly than in modern species.

The **frontals** are slightly wider posteriorly than anteriorly and do not extend posteriorly beyond the level of the orbit. They meet at the midline in a sinuous suture but do not form a small median crest between them as in *Notopterus* (Ridewood, 1904: pl. 24, fig. 13; Taverne, 1978: fig. 63). The supraorbital sensory canal traverses the frontal. Anteriorly this canal is carried in a broad groove, part of which is roofed over (unlike the canal in modern notopterids where the groove is completely open); our fossil agrees with the holotype of *Palaeonotopterus greenwoodi* in this respect (Forey, 1997). Posteriorly the canal is contained within the bone (shown by a dashed line in fig. 2), and opens by a small pore near the pterotic border. Lateral to the supraorbital canal, there is another narrower open groove for the anterior supraocular branch of the otic sensory canal (Kapoor, 1964, 1966; Sharma, 1964; Taverne, 1975, 1978), which is autapomorphic for notopterids (Forey, 1997). In modern notopterids, however, an opening in the frontal allows communication between the supraorbital and supraocular canals (Kapoor, 1964: fig. 3; Taverne, 1978: figs. 62, 84, 91, 114). Such an opening does not exist in *Palaeonotopterus* and the two canals remain completely separate. Three foramina for branches of the superficial ophthalmic nerve are below the supraorbital canal, on the ventral side of the frontal.

The large **parietals** are smooth, more elongate than in modern notopterids, and meet at the midline along an extensive suture (Forey, 1997). A longitudinal ridge runs from the posterior part of the frontal to the lateral border of the parietal. In the holotype of *Palaeonotopterus* there is apparently no trace of a bony transverse crest for the supratemporal commissure (in modern notopterids the canal is contained by bone on the parietal; Taverne, 1978: figs. 62, 63, 91, 92, 114, 115). In the AMNH example the right parietal has a short ridge at its posterolateral corner, which may have served as an anterior support for the canal, but otherwise the canal was not enclosed by bone. The surface of the
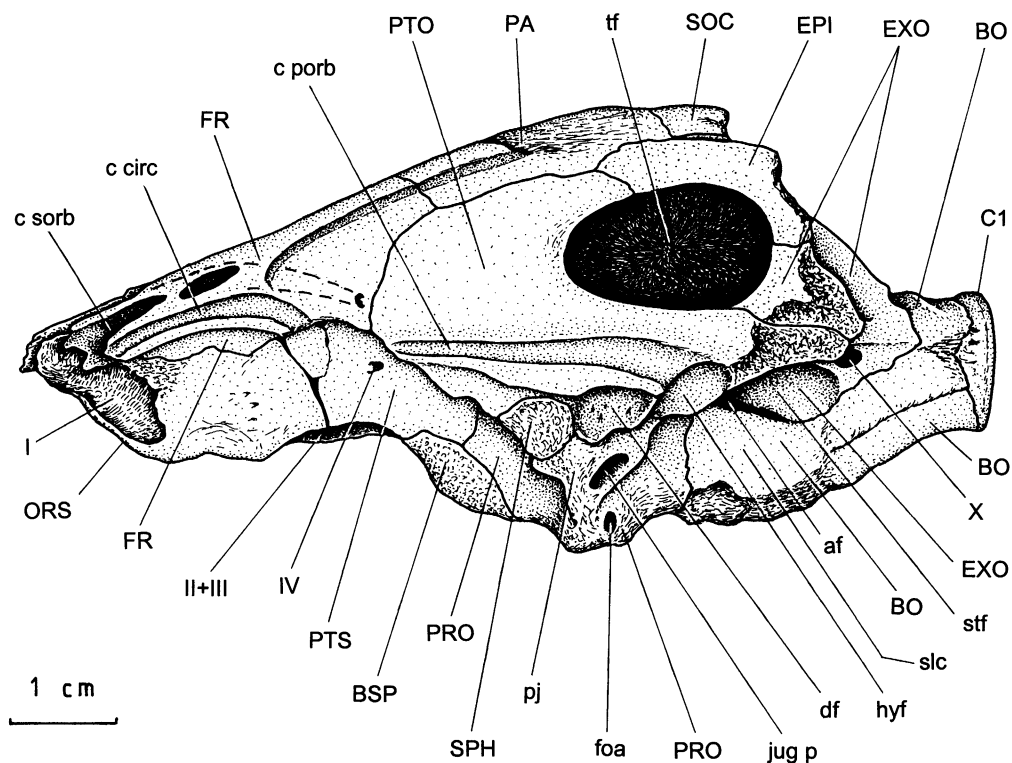
Fig. 1. *Palaeonotopterus greenwoodi,* AMNH 19559. Neurocranium as originally preserved in left lateral view. Dashed lines mark the position of the supraorbital canal within the frontals.

left parietal is broken in this region. No such small ridge is present on the parietal of the holotype but that is perhaps due to preservation.

The **supraoccipital** is a small bone. In AMNH 19559 the median crest is broken but was probably large. It is uncertain whether the supraoccipital reaches the foramen magnum; in the holotype the supraoccipital just fails to reach it.

The **epioccipitals** meet above the foramen magnum in the holotype. In AMNH 19559 the supraoccipital may have originally extended down over the contact between the epioccipitals. On either side of the supraoccipital, the epioccipitals form a buttress which marks the posterodorsal shoulder of the neurocranium. The posterior part of the left epioccipital is broken, showing the posterior semicircular canal. There is a small irregular bony knob at the top of the right epioccipital, near its posterior border, that

probably served as an attachment for epaxial ossified tendons as in *Notopterus* (Taverne, 1978: fig. 61). The corresponding region of the left epioccipital is not preserved.

The **pterotics** are large bones extending forward well before the sphenotic, with a high and broad dorsal part enclosing part of the temporal fossa and a long ventral portion carrying the otic sensory "canal" as an open groove. There is a small vertical open groove for the upper part of the preopercular sensory canal on the BMNH specimen (Forey, 1997: fig. 1), but this is not preserved here (its presumed position is indicated in fig. 2 by a dotted line). The left pterotic of our specimen shows a well-developed dilatator fossa ventrally, just behind the sphenotic (figs. 2, 3). The anterior part of the hyomandibular facet is situated a little farther posteriorly. The posterior part of this facet is missing on both sides of the skull.
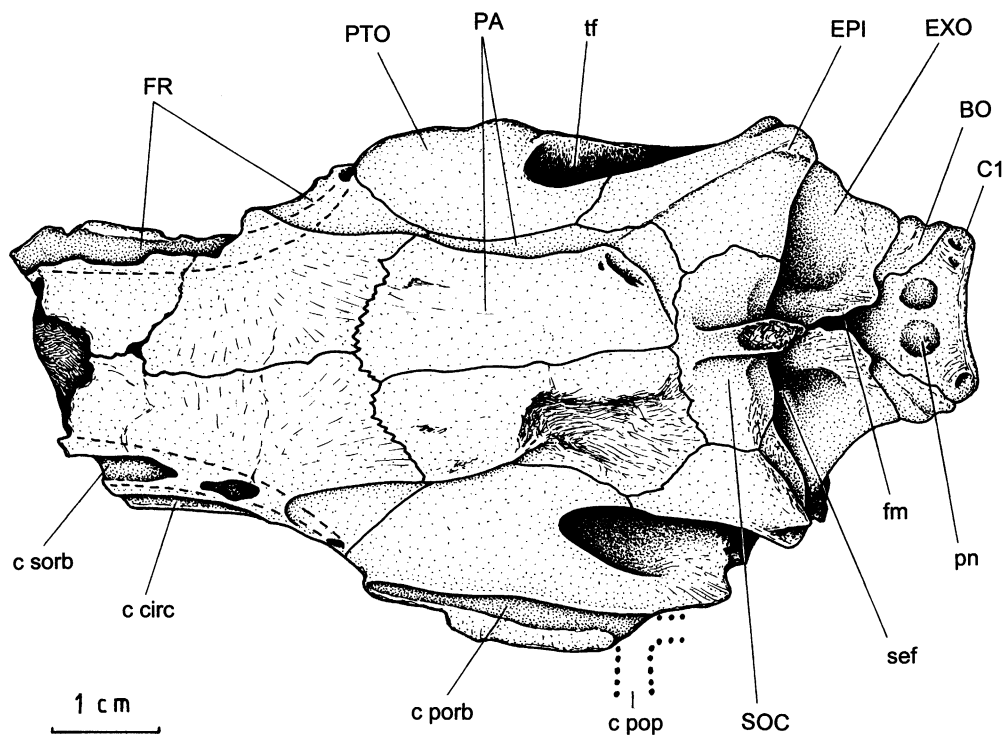
There is a very large temporal fossa on the

Fig. 2. *Palaeonotopterus greenwoodi*, AMNH 19559. Neurocranium in dorsal view, anterior end to the left. Dashed lines mark the position of the supraorbital canal within the frontals. The inferred position of the preopercular sensory canal is indicated by dotted lines.

lateral wall of the neurocranium. Each fossa opens directly into the cranial cavity and is bounded anteriorly and ventrally by the pterotic, dorsoposteriorly by the epioccipital, and ventroposteriorly by the exoccipital. It is not known if an extrascapular (supratemporal) covered the fossa as in modern notopterids.

The large **orbitosphenoid** lies anterior to the **pterosphenoids**. The two olfactory nerves emerge via a large opening between the ventral face of the frontals and the anterior margin of the orbitosphenoid. The trochlear nerve passes through a small foramen in the pterosphenoid. Another large and elongated foramen opens dorsally along the suture between the pterosphenoid and the prootic, for the trigeminal nerve, profundus branch of the ophthalmic nerve, and superficial ophthalmic branch of the facial nerve. This foramen is largely separated from the pars jugularis and from other foramina for branches of the facial nerve located farther

posteriorly on the prootic, as in most modern notopterids. The **basisphenoid** contacts the pterosphenoids and the prootics but unfortunately its entire surface is broken and it is uncertain whether a basisphenoid process was present. The very large foramen for the optic and common oculomotor nerves opens ventrally between the orbitosphenoid, pterosphenoids, and basisphenoid. Farther anteriorly the optic nerve lies in a short but wide groove on the posteroventral part of the orbitosphenoid. More posteriorly, between the basisphenoid and the prootics, there is another large medioventral opening, the hypophysial fenestra. In the BMNH skull, the basisphenoid is missing (Forey, 1997); therefore, the optic foramen and the hypophysial fenestra seem to be confluent.

The very small **sphenotics** are only partially preserved on both sides of the skull, lying far backward from the anterior level of the pterotic. The canal for the otic ramus of
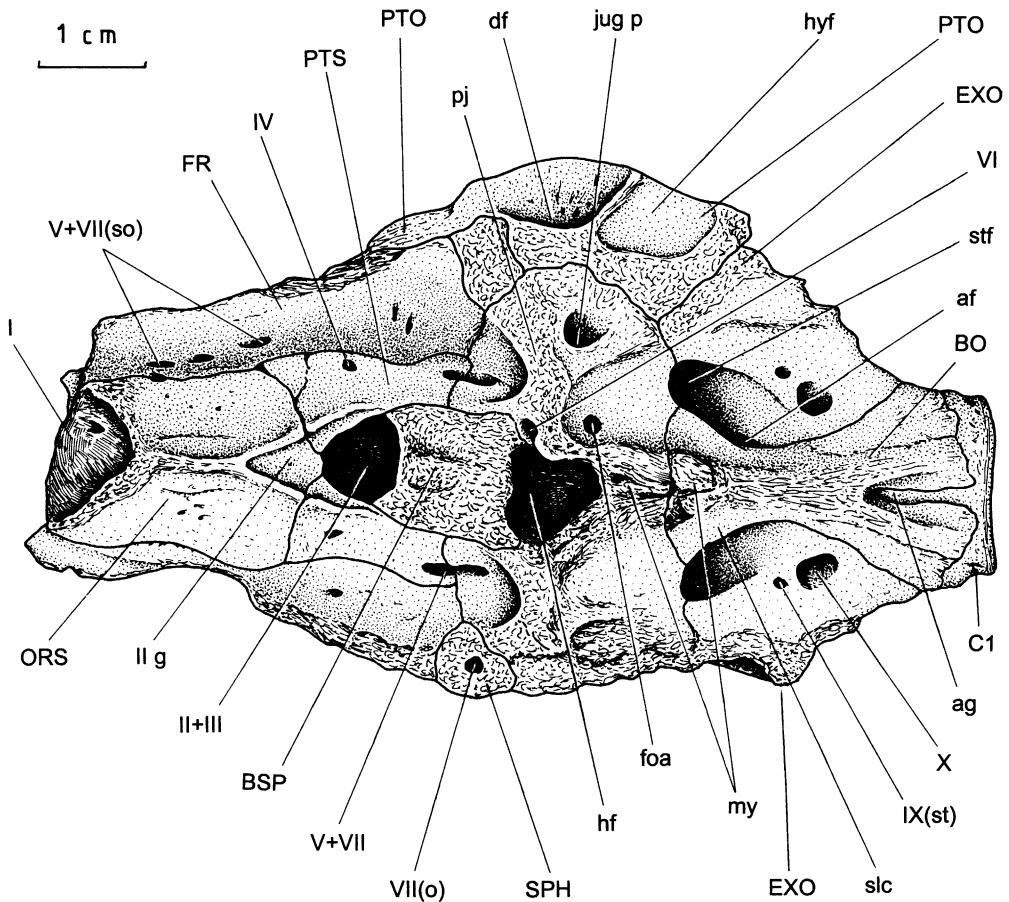
Fig. 3. *Palaeonotopterus greenwoodi,* AMNH 19559. Neurocranium in ventral view, anterior end to the left. Note that many features of the ventral surface are weathered and incomplete.

the facial nerve is visible within the crushed right sphenotic.

The **prootics** are large bones, reaching the basisphenoid and the pterosphenoids anteriorly, and the basioccipital and the exoccipitals posteriorly. Ventrally the prootics meet at the midline in a horizontal plane to form the prootic bridge above the myodome. The foramen for the external oculomotor (abducens) nerve is visible on the left prootic, just lateral to that bridge. The dorsovertical plane of the prootic carries a narrow vertical bony bridge, the pars jugularis, which is completely preserved on the left side of the AMNH skull. The anterior opening of the pars jugularis allows passage of the palatinus and pretrematic branches of the facial nerve. The

posterior myodome roof is formed essentially by the prootic bridge but also in its more posterior part by the basioccipital. We know nothing of the myodome floor because the parasphenoid is not preserved.

The **exoccipitals** exhibit a ventrohorizontal and a posterovertical face. On the rear of the skull, they surround the foramen magnum. The high and narrow preserved shape of this opening may be an artefact of preservation, and the upper slitlike part may represent a cartilage-filled gap between the exoccipital of either side. Lateral to the foramen magnum, each exoccipital is depressed in a large and shallow subepiotic fossa. Ventrally, the exoccipital forms a conspicuous subtemporal fossa, which is perforated by a
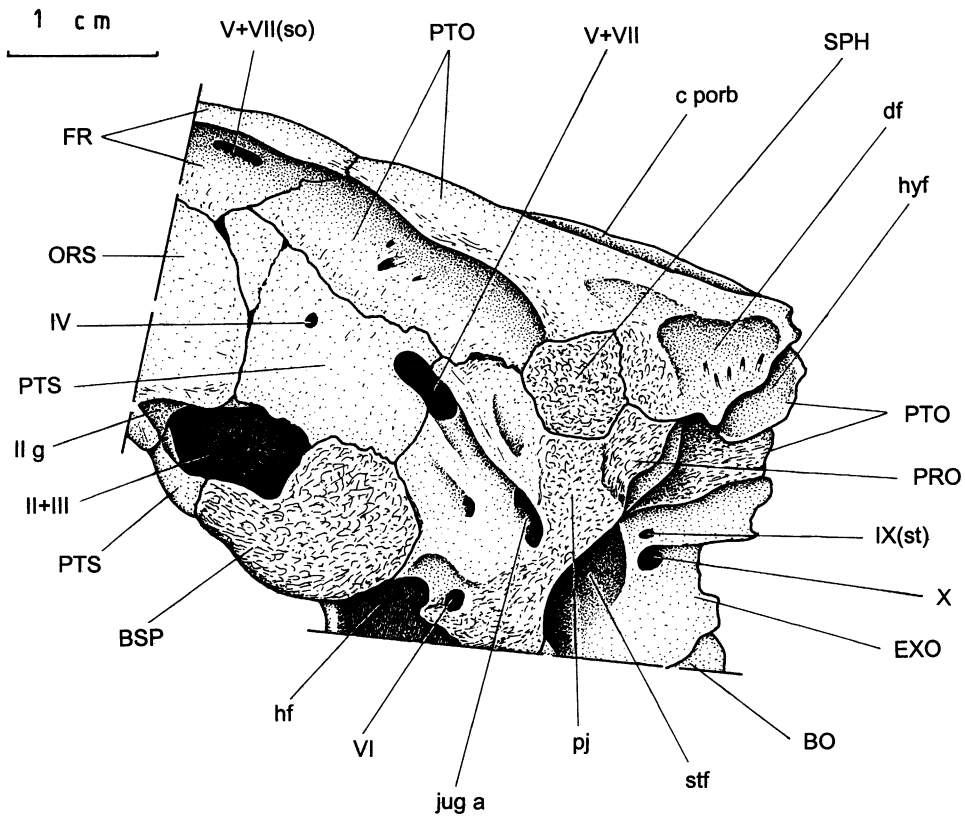
Fig. 4. *Palaeonotopterus greenwoodi,* AMNH 19559. Oblique view of neurocranium (left side, viewed from anterior and below), showing features of postorbital wall including the anterior opening of the jugular canal. Scale is approximate in oblique view.

long auditory fenestra at the borders of the prootic and the basioccipital. The fossa probably received a cranial diverticulum from the swimbladder in the living fish like the one in *Notopterus* (Bridge, 1990: pl. 36, fig. 3; De-hadrai, 1957: fig. 5). The subtemporal fossa is less pronounced in the BMNH specimen (Forey, 1997: fig. 2). The foramen for the glossopharyngeal nerve is located in the fossa. Just behind the fossa, there are two other foramina, a small one for the supratemporal branch of the glossopharyngeal nerve, and a bigger one for the vagus nerve.

The **intercalar** is missing on both sides of the neurocranium. The left intercalar is partially preserved in the BMNH skull (Forey, 1997: figs. 1, 3).

The **basioccipital** is a very large bone, firmly united with the narrow first vertebral centrum that forms the occipital condyle. Un-

like the bones in the BMNH skull (Forey, 1997), the contact between the basioccipital and centrum is clearly visible from all sides in our example, and we are therefore able to confirm that a vertebral centrum is incorporated into the braincase (cf. Forey, 1997: 568). Dorsally, the centrum bears a pair of small pits, presumably for a neural arch (although the arch itself is not preserved). An occipital neural arch also exists in *Heterotis* Cuvier et Valencienes, 1846, and *Arapaima* Muller, 1843 (Taverne, 1977: figs. 97, 105, 125, 126). The basioccipital meets the prootics anteriorly just below the auditory fenestra and defines with them the two sacculolagenar chambers. Those chambers are less developed than in *Notopterus* (Taverne, 1978: figs. 62, 64, 65). Ventrally the posterior portion of the basioccipital bears a deep medial aortic groove bordered by two bony
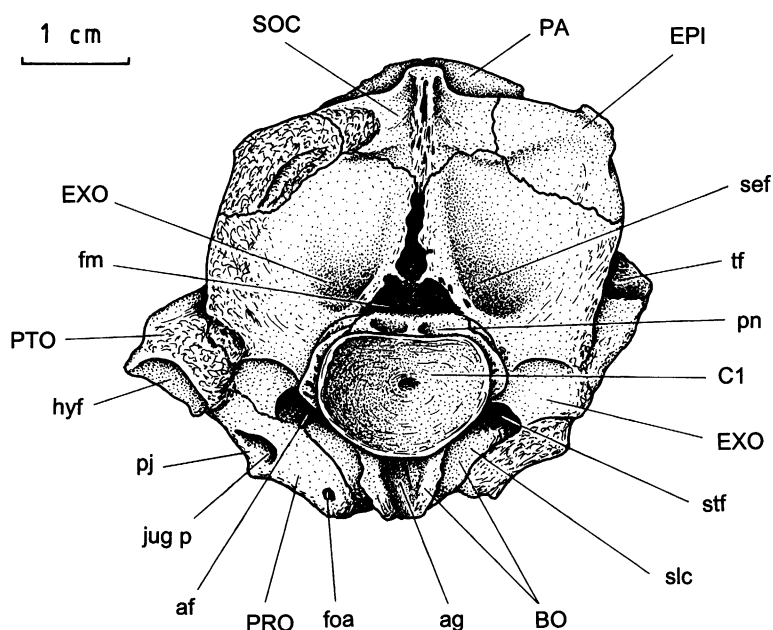
Fig. 5. *Palaeonotopterus greenwoodi,* AMNH 19559. Neurocranium in posterior view showing vertebral centrum fused to basioccipital and pits for neural arch.

crests. The two ventroanterolateral processes of the basioccipital that Forey (1997: figs. 2, 3) identified as an autapomorphy of the genus *Palaeonotopterus* are not preserved here.

DISCUSSION

The AMNH and the BMNH skulls are very similar but some slight differences are noted. The optic foramen is smaller, more posteriorly located, and apparently confluent with the hypophysial fenestra in the BMNH neurocranium, perhaps because the basisphenoid is missing (Forey, 1997: figs. 2, 3). Additionally, the subtemporal fossa is less pronounced in that specimen and the basioccipital comes close to but does not reach the foramen magnum. These differences may reflect individual variation or could be related to differences in preservation; neither case justifies the erection of a new specific taxon for the AMNH specimen.

Two specialized characters place *Palaeonotopterus* within the order Mormyriformes (see fig. 6):

(1) The large temporal fossa is located completely on the lateral wall of the neuro-cranium, opening directly into the cranial cavity and surrounded by the pterotic, the epioccipital, and the exoccipital, with a very broad dorsal wing of the pterotic as antero-dorsal border. Among teleosts such an arrangement of the fossa also occurs in *Hiodon,* mormyrids, and notopterids (Bridge, 1900; Ridewood, 1904; Greenwood, 1963; Taverne, 1968a, b, 1969, 1971, 1972, 1978), although among notopterids only *Notopterus* has this feature; in *Chitala, Papyrocranus,* and *Xenomystus* the epioccipital is excluded from the temporal fossa border (Greenwood, 1963: fig. 3A; Taverne, 1978: figs. 84, 91, 114).

(2) A completely open otic sensory canal is located on the pterotic. This apomorphic character is shared by mormyrids and most notopterids (Bridge, 1900; Ridewood, 1904; Greenwood, 1963; Taverne, 1968a, b, 1969, 1971, 1972, 1978). *Xenomystus* is again an exception, because the anterior part of the otic canal is roofed (Taverne, 1978: fig. 91). While this is the presumed primitive condition, according to the phylogenies presented here (fig. 6) and by Forey (1997: fig. 4) it would represent a reversal in *Xenomystus.*
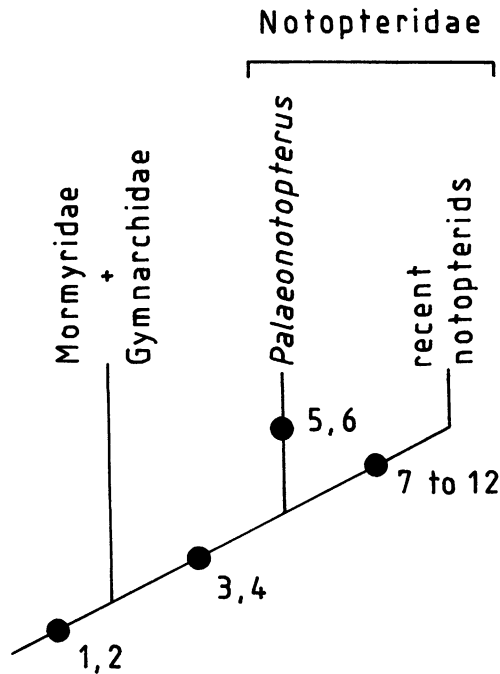
Fig. 6. Phylogenetic relationships of *Palaeonotopterus greenwoodi* within the order Mormyriformes. The numbers refer to characters discussed in the text.

Two apomorphic characters of *Palaeonotopterus* support its inclusion in the family Notopteridae.

(3) Supraocular groove for an anterior branch of the otic sensory canal lies on the frontal, parallel and external to the supraorbital canal (Kapoor, 1964, 1966; Sharma, 1964; Taverne, 1975, 1978, 1979).

(4) Foramen for the combined trigeminal nerve, profundus branch of the ophthalmic nerve, and superficial ophthalmic branch of the facial nerve is separated from the narrow pars jugularis and from the foramen for the main branches of the facial nerve. A similar arrangement occurs in *Notopterus, Chitala,* and *Papyrocranus* (Taverne, 1978: figs. 62, 66, 84, 114, 116). Again *Xenomystus* is exceptional, as the trigeminal foramen is smaller, remote on the prootic, and closer to the pars jugularis (ibid.: figs. 91, 93), which is considered to be a more primitive condition.

Two other characters strengthen the notopterid relationship of *Palaeonotopterus* though they are not unique features of the group. First, among osteoglossomorphs a completely or partially open supraorbital sensory canal on the frontal is characteristic of notopterids, certain mormyrids, and pantodontids (Bridge, 1900; Ridewood, 1904; Greenwood, 1963; Kapoor, 1964; Taverne, 1969, 1971, 1972, 1978; Kershaw, 1970). Secondly, notopterids and hiodontids are the only osteoglossomorphs with an auditory fenestra between the prootic, exoccipital, and basioccipital (Greenwood, 1973: figs. 3A, 4, pl. 1; Taverne, 1977: figs. 3, 10, 11, 1978: figs. 62, 64, 66, 67, 114, 116).

Among notopterids, *Palaeonotopterus* is distinguished by:

(5) The presence of a pair of ventrolateral processes on the basioccipital (Forey, 1997). They are unfortunately broken away on the AMNH skull.

(6) Protrusion of the basioccipital posteriorly beyond the exoccipitals. In primitive teleosts generally, and especially in modern notopterids, such a protrusion does not exist (Bridge, 1900; Ridewood, 1904; Greenwood, 1963; Taverne, 1978).

Forey (1997) was uncertain whether the

first vertebral centrum is fused to the basioccipital in *Palaeonotopterus.* In general among nonhiodontid osteoglossomorphs the occipital condyle is formed only by the basioccipital. In the heterotid *Arapaima,* the suture between the basioccipital and the fused centrum is still partially visible (Taverne, 1977: figs. 125–127). Conversely in hiodontids the occipital condyle is tripartite, formed by the exoccipitals and the basioccipital, and does not include the first vertebral centrum (Ridewood, 1904: pl. 25, fig. 21; Taverne, 1977: fig. 6).

Recent notopterids are collectively more derived than *Palaeonotopterus,* with at least six synapomorphies not shared by that taxon:

(7) The orbitosphenoid does not border the large medioventral foramen for the optic and common oculomotor nerves between the pterosphenoids and the basisphenoid (Taverne, 1978: figs. 66, 84, 93, 98) except for *Papyrocranus* where the basisphenoid is lost (ibid.: fig. 114). Additionally, in the modern taxa there is no optic groove on the orbitosphenoid. In *Palaeonotopterus* the orbitosphenoid contributes to the border of the large optic foramen and there is an optic groove (figs. 3, 4), as in pholidophorids and other basal teleosts (Rayner, 1937: fig. 10; Taverne, 1974: fig. 11; Patterson, 1975: figs. 63, 89).

(8) The medial part of the extrascapular sensory canal is enclosed by parietal bone (Taverne, 1978: figs. 62, 63, 84, 91, 92, 114, 115); the canal was apparently not enclosed in *Palaeonotopterus.*

(9) The supraorbital sensory canal has lost its posterior bony roofed portion, and does not reach the otic canal on the pterotic (Kapoor, 1964: fig. 3; Taverne, 1978: figs. 62, 63, 84, 91, 92, 114, 115).

(10) The grooves for the anterior part of the supraorbital canal communicate via an opening with those for the supraocular branch of the otic canal on the frontal (Kapoor, 1964: fig. 3; Taverne, 1978: figs. 62, 63, 84, 91, 92, 114, 115).

(11) The otic sensory canal groove on the pterotic is greatly enlarged (Taverne, 1978: figs. 62, 84, 114). *Xenomystus* is the only exception, with its otic canal anteriorly roofed (ibid.: fig. 91).

(12) There is no neural arch associated with the basioccipital (Taverne, 1978: fig. 63).

Several hypotheses have been proposed regarding the interrelationships of modern Notopteridae: ((*Xenomystus* (*Notopterus, Papyrocranus*)) in Greenwood (1963), Taverne (1979), and Li and Wilson (1996); ((*Notopterus* (*Papyrocranus, Xenomystus*)) in Nelson (1969) and Forey (1997); and ((((*Chitala* ((*Papyrocranus* (*Notopterus, Xenomystus*))) in Taverne (in press). Being more primitive than the four modern genera, *Palaeonotopterus* unfortunately does not shed any new light on that issue. Recent notopterid phylogeny is not the concern of this paper and the interested reader should refer to the five publications cited above for a detailed discussion.

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