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On a complete hyomandibular of the Cretaceous Moroccan notopterid *Palaeonotopterus greenwoodi* (Teleostei, Osteoglossomorpha)

Louis Taverne

Abstract

A well preserved left hyomandibular of *Palaeonotopterus greenwoodi* from the Cretaceous of Morocco is described. It is a massive bone, with its dorsal part bent forward and an articular head divided in two distinct condyles. It differs considerably from the hyomandibulars of the recent Notopteridae, Mormyridae and Gymnarchidae. Several autapomorphies of the hyomandibular of *P. greenwoodi* are noted to complete its diagnosis.

Keywords: *Palaeonotopterus greenwoodi*, Teleostei, Notopteridae, Cretaceous, Morocco, hyomandibular.

Zusammenfassung

Ein gut erhaltenes linkes Hyomandibulare von *Palaeonotopterus greenwoodi* aus der Kreide von Marokko wird beschrieben. Es ist ein massiver Knochen, dessen dorsaler Teil nach vorn gekrümmt ist und dessen Gelenkkopf zweigeteilt ist. Es unterscheidet sich deutlich von den Hyomandibulria rezenter Notopteridae und Gymnarchidae. Mehrere Autapomorphien des Hyomandibulare ergänzen die Diagnose von *P. greenwoodi.*

1. Introduction

The primitive Cretaceous notopterid *Palaeonotopterus greenwoodi* Forey, 1997 from southern Morocco is only known from incomplete braincases, lower dental plates, parts of a shoulder girdle, a few vertebrae, some ribs and scales (Forey 1997, Taverne & Maisey 1999, Taverne 2000, Cavin & Forey 2001).

Until now, only a very eroded fragment of a right hyomandibular has been described (Cavin & Forey, 2001, figs. 1, 6). Recently the Staatliches Museum für Naturkunde Stuttgart (Germany) has purchased a complete and well preserved left hyomandibular of *P. greenwoodi* which brings unknown osteological information on this fish and new elements of comparison with the four modern notopterid genera and with mormyroids, the sister-lineage of notopterids.

The purpose of the present paper is thus to describe this bone, to compare it with the hyomandibular of recent Notopteridae, Mormyridae and Gymnarchidae, and to complete the diagnosis of *P. greenwoodi*.

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2. Materials and methods

SMNS 87961: a complete left hyomandibular of *Palaeonotopterus greenwoodi* from southern Morocco (Kem Kem Beds, Albian/Cenomanian boundary).

The drawings were compiled by the author.

3. Description

The left hyomandibular SMNS 87961 (Fig. 1) is a heavily built bone, almost as wide (50 mm) as high (61 mm). Such a robustness of the hyomandibular is probably linked to the strong stresses supported by the bones of the suspensorium and their associated muscles and induced by the highly specialized palato-lingual bite of *P. greenwoodi* with enormous upper and lower dental plates (TAVERNE 2000, figs. 2, 3, 6, 7; CAVIN & FOREY 2001, figs. 2 B, 4).

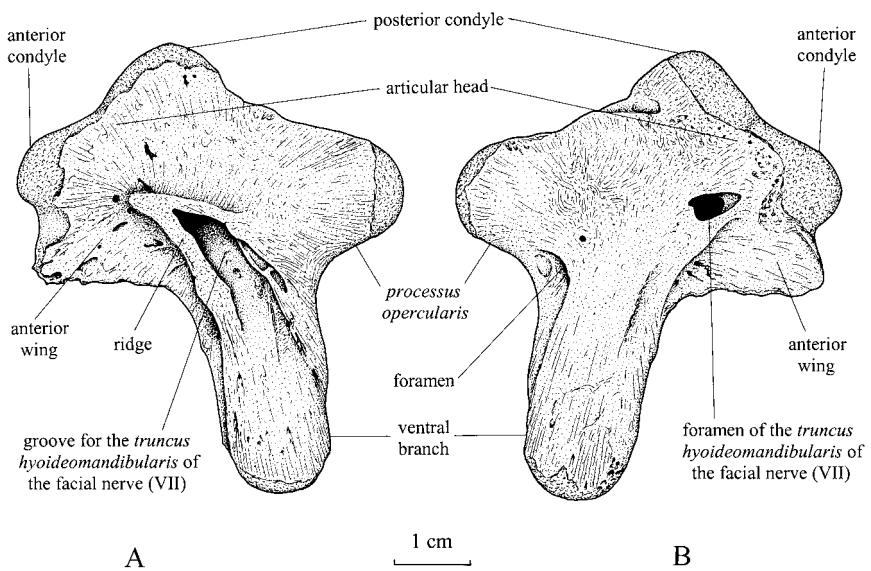

Fig. 1. *Palaeonotopterus greenwoodi* FOREY, 1997. The left hyomandibular SMNS 87961. **A:** External face; **B:** Inner face.

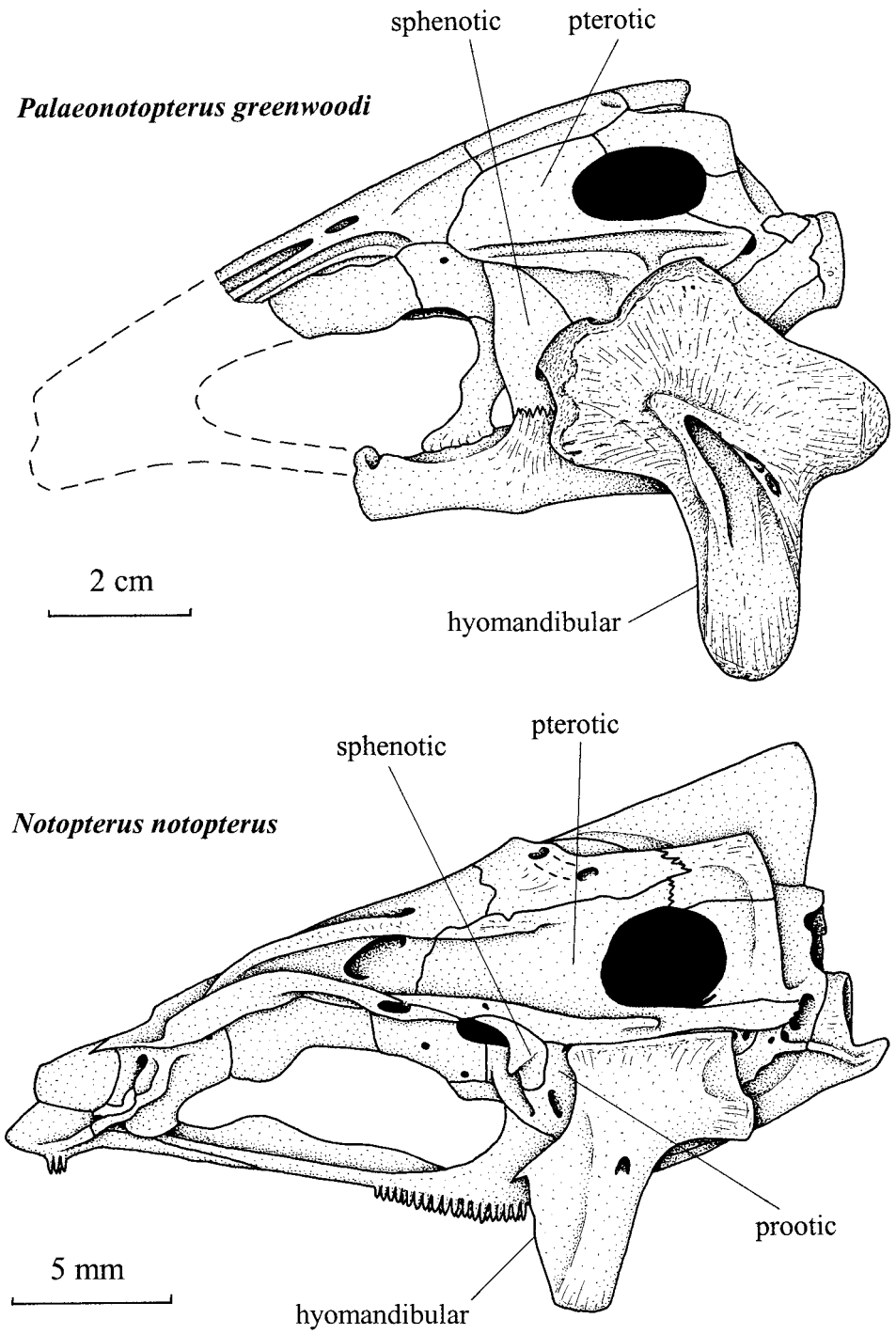

Fig. 2. The hyomandibular articulated with the neurocranium: a comparison between *Palaeonotopterus greenwoodi* FOREY, 1997 (above) and the modern Notopteridae examplified by *Notopterus notopterus* (PALLAS, 1769) (below). [*N. notopterus* modified from TAVERNE 1978, figs. 61, 62, 69]

The broad dorsal part of the hyomandibular is bent forward and so the articular head for the neurocranium is directed mainly antero-dorsally. This articular facet is elongated and divided in two distinct large hemispherical condyles of about the same size. The anterior condyle fits into a large deep fossa on the autosphenotic, the pterotic and the prootic, and the posterior one articulates in another large fossa entirely located on the ventro-posterior surface of the pterotic (Fig. 2; TAVERNE 2000, fig. 1). Anteriorly, below the first condyle, the head of the hyomandibular produces a small and thin wing of bone. Posteriorly, the margin of the hyomandibular projects as a short, bulky prominent processus opercularis which is horizontally oriented and has a rounded condyle. The ventral branch of the bone is a short but stout element, as broad as the processus opercularis but longer, and has a more or less vertical orientation.

The truncus hyoideomandibularis of the facial nerve (VII) enters the hyomandibular in a foramen on the inner side of the bone near the anterior condyle. From this foramen two canals run through the bone in a posterior direction. The dorsal and longest one opens on the inner side of the hyomandibular by a foramen located in a hollow just at the meeting point of the processus opercularis and the ventral branch. The ventral canal is very short and emerges on the external face of the bone in a long, broad and ventro-posteriorly oriented groove ending on the ventral branch. The groove is surrounded on each side by a prominent ridge, the antero-ventral one being thicker and longer than the dorso-posterior one. The antero-ventral ridge probably served as a bony basis for the connection of some layers of the muscle adductor mandibulae and the dorso-posterior one for a portion of the muscle levator arcus palatini. The short ventral canal and the broad external groove following it certainly carry the main branches of the truncus hyoideomandibularis. The use of the long and thin dorsal canal is more problematic. That could be the way of emergence for a small nervous branch, such as the ramus hyoideus or the ramus opercularis, or for a blood vessel.

4. Discussion

4.1. The hyomandibular in Notopteridae, Mormyridae and Gymnarchidae

From their observations on an incomplete right hyomandibular of *P. greenwoodi*, CAVIN & FOREY (2001: 36) conclude that "the morphology [of this bone] is strikingly like that of notopterids and short-snouted (i. e. primitive) mormyroids." Such an assertion is false. Quite the contrary, the hyomandibular of *P. greenwoodi* greatly differs in shape and morphology from those of modern Notopteridae, Mormyridae and Gymnarchidae as the comparison hereafter will show. Apparently, CAVIN & FOREY (2001) were led in error by the bad preservation and incompleteness of the hyomandibular in their material.

When fitted in the two corresponding articular fossae of the neurocranium, it becomes obvious that the hyomandibular is proportionally much larger and stronger in *P. greenwoodi* (Fig. 2, above) than in the recent notopterids (Fig. 2, below). Moreover the four modern notopterid genera, *Notopterus* LACÉPÈDE, 1800, *Chitala* FOWLER, 1934, *Xenomystus* GÜNTHER, 1868 and *Papyrocranus* GREENWOOD, 1963, exhibit the dorsal part of the hyomandibular located in the axis of the ventral branch

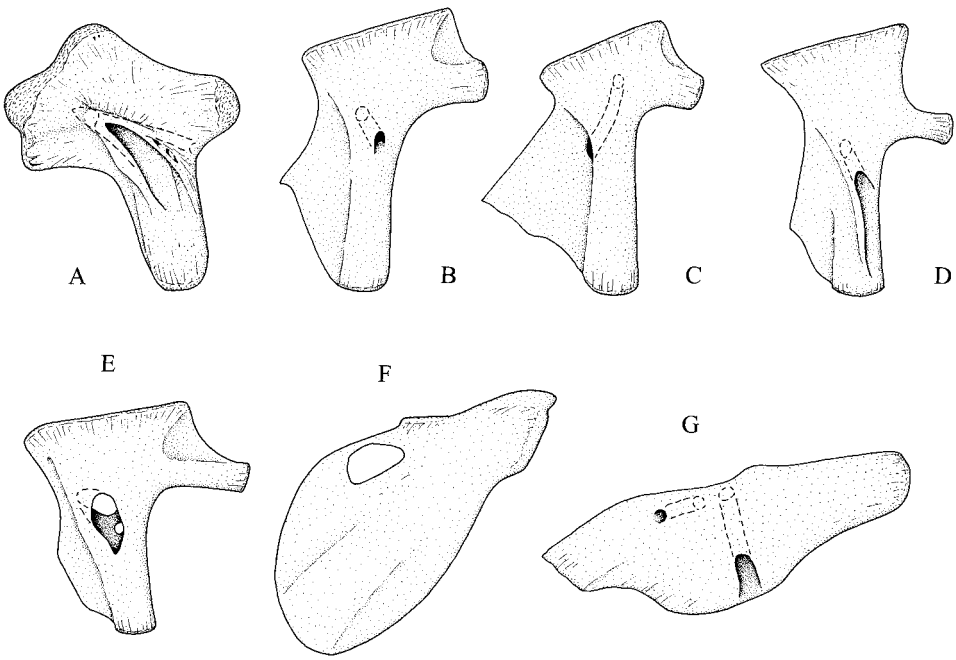

Fig. 3. A comparison between the hyomandibulars of **(A)** *Palaeonotopterus greenwoodi* FOREY, 1997, the four recent notopterid species **(B)** *Notopterus notopterus* (PALLAS, 1769), **(C)** *Chitala chitala* (HAMILTON, 1822), **(D)** *Xenomystus nigri* GÜNTHER, 1868, and **(E)** *Papyrocranus afer* (GÜNTHER, 1868), the mormyrid **(F)** *Mormyrus rume* CUVIER & VALENCIENNES, 1846, and the gymnarchid **(G)** *Gymnarchus niloticus* CUVIER, 1829 (not to scale). [B, C, D and E modified from TAVERNE 1978, figs. 61, 69, 83, 86, 90, 104, 113, 124; F and G modified from TAVERNE 1972, figs. 7, 104].

and thus not bent forward (Fig. 3 B, C, D, E). The elongate articular facet is always single (Fig. 3 B, C, D, E). The anterior wing-like part of the bone is located more ventrally than in *P. greenwoodi*; this wing-like zone is well developed in *Notopterus* and *Chitala* (Fig. 3 B, C) but more reduced in *Xenomystus* and *Papyrocranus* (Fig. 3 D, E). In recent notopterids the processus opercularis is not as bulky as in *P. greenwoodi*. *Notopterus* and *Chitala* possess a processus opercularis of approximately the same length as in *P. greenwoodi* (Fig. 3 A, B, C) but *Xenomystus* and *Papyrocranus* have a longer one (Fig. 3 D, E). In *Notopterus*, *Xenomystus* and *Papyrocranus* the canal for the truncus hyoideomandibularis of the facial nerve (VII) is short and ventro-posteriorly oriented as in *P. greenwoodi* (Fig. 3 A, B, D, E). *Chitala* offers a long canal ventro-anteriorly directed (Fig. 3 C). *Xenomystus* is the only modern notopterid in which the truncus emerges in a long groove on the external face of the hyomandibular as in *P. greenwoodi* (Fig. 3 A, D). But this groove is less broad than in the fossil species and there is a bony ridge only along its anterior border (Fig. 3 D). Such a groove is a derived feature but independently acquired by both genera and not indicating a closer relationship between them. A second canal penetrating the hyomandibular as in *P. greenwoodi* never exists in modern notopterids (Fig. 3 B, C, D, E, TAVERNE 1978).

The hyomandibular in Mormyridae and Gymnarchidae presents a quite different shape (Fig. 3 F, G) than the one of *P. greenwoodi* and recent Notopteridae. The bone is very broad, rather thin, with a large anterior wing-like portion, and is devoid of an individualized narrow ventral branch. The elongate articular facet is single or very slightly divided in two condyles, the posterior one then notably longer than the anterior. The processus opercularis is extremely short, reduced to a big bony knob. Gymnarchidae still retain two long canals penetrating the hyomandibular but not connected together (Fig. 3 G). The anterior one carries a blood vessel (TAVERNE 1972: 146) and the posterior one only the ramus hyoideus, the ramus mandibularis emerging from the neurocranium with many other nervous branches by a large foramen opened between the pleurosphenoid, the autosphenotic and the prootic (TAVERNE 1971, fig. 3). In Mormyridae there is no longer a canal and the truncus passes through a large hole pierced in the antero-dorsal border of the bone (Fig. 3 F).

4.2. New autapomorphies for the diagnosis of *Palaeonotopterus greenwoodi*

FOREY (1997: 565) provided the first diagnosis of *P. greenwoodi*. This diagnosis was considerably improved by TAVERNE (2000: 13–14), who enumerated fourteen autapomorphies characterizing this teleost and separating it from the four modern notopterid genera. CAVIN & FOREY (2001) also mentioned some new derived characters of *P. greenwoodi*. The present study allows to add seven new autapomorphies to this list:

(1) The hyomandibular is proportionaly much larger and stronger than in modern notopterids.

(2) The dorsal part of the hyomandibular is bent forward.

(3) The articular facet of the hyomandibular is divided in two big hemispherical condyles.

(4) The processus opercularis is short but much thicker than in modern notopterids.

(5) The anterior wing-like part of the hyomandibular is reduced and located more dorsally than in modern notopterids.

(6) Two connected canals run in a posterior direction through the hyomandibular from the inner foramen of the truncus hyoideomandibularis of the facial nerve (VII), the long dorsal one opening in another foramen on the inner side of the bone and the short ventral one in a groove on the external side.

(7) There is a long and broad groove on the external face of the hyomandibular. This groove, surrounded on both sides by a strong bony ridge, carries the main branches of the truncus hyoideomandibularis.

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