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A new Palaeocene albulid (Teleostei: Elopomorpha) from the Ouled Abdoun phosphatic basin, Morocco

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Abstract – A new albulid fish, *Phosphonatator oxyrhynchus*, based on a single large neurocranium, is described from the deposits of the Ouled Abdoun phosphatic basin, Morocco. The matrix of the fossil contains an elasmobranch assemblage indicating a Danian age (with some redeposited Maastrichtian elements). *P. oxyrhynchus* is characterized notably by its elongated snout and by a reduced patch of teeth on the parasphenoid. Up to now, fossil fishes from the Ouled Abdoun phosphatic basin were mainly known by isolated remains, and the recovery of this specimen should be ranked equal to the recent discovery of important, very well-preserved new material of vertebrates in the Sidi Daoui area.

1. Introduction and geological setting

The phosphatic deposits of Morocco have been exploited since the 1920s and are one of the principal economic resources of the country. Since the extensive palaeontological work of Arambourg (1952), the phosphates of Morocco have also been known worldwide for their richness in fossil vertebrates.

During French–Moroccan palaeontological fieldwork in April 1998 in collaboration with the OCP (Cherifian Office of Phosphates) and the Moroccan geological survey (Ministère de l'Energie et des Mines), we obtained a large bony fish neurocranium through a fossil dealer of the Ouled Bouali Douar, between Oued Zem and Khouribga, in the Eastern part of the Ouled Abdoun Basin (Fig. 1).

Although the exact location is unknown, it is certain that it comes from 'Grand Daoui', an actively mined area for phosphate. The sediment containing the albulid skull has yielded a small elasmobranch assemblage. This assemblage contains *Dasyatis hexagonalis*, *D. tetraedra*, *Palaeogaleus brivesi*, *Plicatoscyllium youssoufiaense*, *Coupatezia fallax*, *Ixobatis mucronata* and incomplete odontaspidid teeth. The stratigraphic range of the elasmobranch assemblages of phosphate deposits are now well known after a series of faunal studies (Arambourg, 1952; Cappetta, 1981; Noubhani & Cappetta, 1997). The fauna associated with the albulid skull shows a mixture of uppermost Maastrichtian (*Plicatoscyllium youssoufiaense*, *Coupatezia fallax*, *Ixobatis mucronata*) and Danian species (*Dasyatis hexagonalis*, *D. tetraedra*, *Palaeogaleus brivesi*). This situation is classical in all of the 'Grand Daoui' area; indeed, in this area, the Danian deposits overlie directly the 'Sillon X', which represents the last Maastrichtian deposits, due to a condensing of the series. In this situation, bioturbation in very soft sediments produced a mixture of Cretaceous and Palaeocene elements of small size. In the Ganntour Basin, where the phosphate series is much thicker, the 'Sillon X' is well separated from the first Danian level and no faunal mixture can be noted between Cretaceous and Palaeocene deposits (Cappetta, 1981, 1987). On this basis, it can be asserted that the albulid skull is Danian in age.

The type and only known specimen was first mechanically prepared with a compressed air engraver. Final preparation was carried out with a needle and diluted acetic acid.

Albulids, the bonefishes, are an extant family of Elopomorph comprising today the single genus *Albula*. Albulids are grouped with the extant family pterothrissids in the suborder Albuloidei. Albuloids have a fossil record extending back to the Late Cretaceous where species from both families are known. The Cretaceous osmeroidids (see Forey, 1973*a*), the Early Cretaceous *Brannerion* (see Blum, 1991) and possibly *Paraelops* (see Maisey & Blum, 1991) from the Santana Formation, Brazil, and the Late Cretaceous *Deltaichthys albuloides* (Fielitz & Bardack, 1992) from Kansas, USA, are close relatives of albuloids and grouped together in the order Albuliformes (Forey *et al.* 1996).

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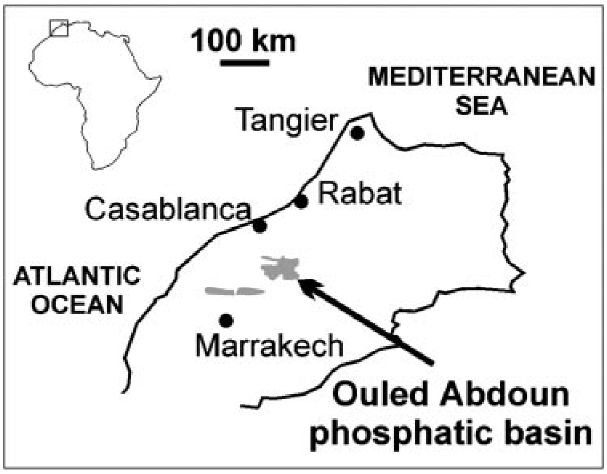

Figure 1. Location map of Morocco showing the position of the Ouled Abdoun phosphatic basin.

2. Systematic palaeontology

Subdivision TELEOSTEI *sensu* Patterson & Rosen, 1977
Cohort ELOPOMORPHA Greenwood *et al.* 1966
Order ALBULIFORMES *sensu* Forey *et al.* 1996
Suborder ALBULOIDEI *sensu* Forey *et al.* 1996
Family ALBULIDAE Bleeker, 1859

Phosphonatator gen. nov.

Diagnosis. Albulid in which the preorbital distance is longer than half of the total neurocranial length; parasphenoid teeth present only beneath the anterior half of the orbit; vomer with a patch of minute teeth situated anteriorly; presence of a fused vertebral centrum to the neurocranium. *Phosphonatator* differs from other albulids by the following set of characters: no ossified interorbital septum; dermethmoid with a prominent median ridge pierced by a large transverse fenestra and pierced laterally by paired antero-posteriorly oriented canals probably for the supraorbital sensory canals.

Derivation of name. From phosphate and from *natator* (Latin) meaning swimmer.

Phosphonatator oxyrhynchus sp. nov.

Diagnosis. As for genus, only species.

Holotype. SGM-P1. Palaeontological Collections of the Geological Survey of Morocco (CPSGM). Nearly complete crushed neurocranium. Preservation of the specimen is good but the crushing makes difficult to describe its lateral faces.

Horizon and locality. Danian of 'Grand Daoui', Eastern part of the Ouled Abdoun phosphatic basin, Morocco.

Derivation of name. From *oxys* (Greek) meaning pointed and *rhynchos* (Greek) meaning beak.

2.a. Description (Figs 2–5)

The size of the specimen is large (Table 1). Compared to the general size of *Albula vulpes*, the total length of the fish should have been about two metres. The extant elopomorph *Megalops atlanticus* may reach such a large size.

The comparisons with *Pterothrissus gissu*, *Albula vulpes* and *A. oweni* are based on the descriptions of these three species by Forey (1973*a*), and with *Deltaichthys albuloides* on the description of Fielitz & Bardack (1992).

*Neurocranium***.** The neurocranium is elongate: its length is 2.7 times longer than its width at the level of the autosphenotic. This proportion is greater than that of *P. gissu* (2.4), of *A. oweni* (2.3), of *A. vulpes* (2.6) and of *Deltaichthys albuloides* (2.0).

The frontal (Fr) is well developed and bears a deep and large depression posteriorly as in *A. oweni*. Forey (1973*a*) suggested that the presence of this depression in *A. oweni* may be a consequence of absolute size, this being greater in *A. oweni* than in *A. vulpes*. This suggestion is reinforced and expanded to another albulid species by the observation of such a depression in the large specimen of *P. oxyrhynchus* described herein. Another character probably linked to the large absolute size of the specimen described herein and the large specimen of *A. oweni* illustrated by Forey (1973*a*, fig. 85) is the absence of visible suture between both frontals. *P. oxyrhynchus* and *A. oweni* share an ornamentation on the frontal above the orbit. The anterior pore of the supraorbital sensory canal (aossc) opens apparently at the level of the lateral ethmoid as in *Albula* and not above the posterior part of the orbit as in *P. gissu*. The frontal forms a shallow trough lateral to the median dermethmoid that should have contained the unknown nasal. The supraorbital sensory

Table 1. Measurements of the neurocranium of *Phosphonatator oxyrhynchus* gen. et sp. nov.

Morphometric characteristics (SGM-P1)	Size (mm)	Percentage of snout–occipital condyle length
Snout–occipital condyle length	363	–
Preorbital length	200	55
Width at the level of the autosphenotic spines (estimated)	136	37
Width at the level of epiotic process	93	26
Maximal width of the dermethmoid	35	10

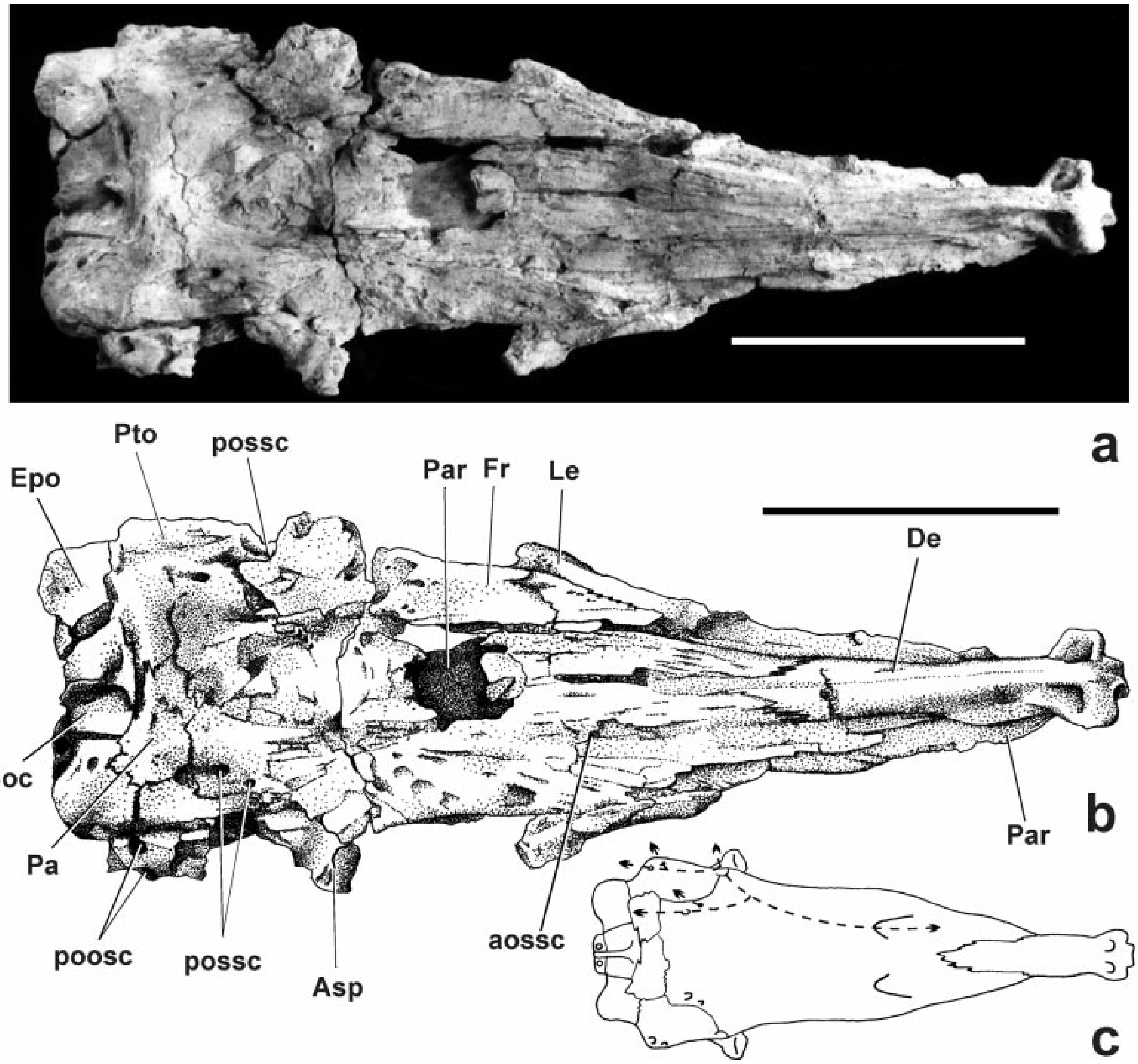

Figure 2. *Phosphonatator oxyrhynchus* gen. et sp. nov. Holotype (SGM-P1), neurocranium in dorsal view. Scale bar: 100 millimetres. (a) photograph, (b) drawing, (c) reconstruction. Course of sensory canals shown by dotted line on the left side. Abbreviations: aossc, anterior opening of the supraorbital sensory canal; Asp, autosphenotic; De, dermethmoid; Epo, epiotic; Fr, frontal; Le, lateral ethmoid; Pa, parietal; Par, parasphenoid; poosc, posterior opening of the otic sensory canal; possc, posterior opening of the supraorbital sensory canal; Pto, pterotic; Soc, supraoccipital.

canal opens posteriorly by three pores (possc), two directed posteriorly near the suture with the parietal, the other directed laterally above the autosphenotic spine and joining with the otic sensory canal.

The parietal (Pa) meets its fellow medially. It is wider than it is long as in *A. vulpes* and unlike *P. gissu*.

The pterotics (Pto) are not completely preserved: the lateral part of that of the right side is incomplete and displaced dorsally. It shows posteriorly two pores for the exit of the otic sensory canal (poosc), one directed laterally and one directed postero-laterally. The former received the preopercular canal and the latter received the supratemporal commissure and the lateral line. As in *Albula* and in contrast to *Pterothrissus*, the pterotic does not bear a groove for the supratemporal commissure. The lateral wall of the pterotic forms the posterior part of the deep dilatator fossa (df) and the posterior part of the hyomandibular facet (fahm). The ventro-lateral walls of the otic region are not preserved. On the right side of the skull, the ventral margin of the pterotic shows in the thickness of the bone an arc-shaped groove in ventral view which probably contained the horizontal semicircular canal (hsc). In *P. gissu*, the horizontal semicircular canal is marked by a swelling on the lateral face of the pterotic. The pterotic forms the anterior part of the roof, the lateral wall and part of the floor of the posttemporal fossa. The state of preservation of the specimen does not allow us to observe in posterior view a possible 'isolated' portion of the pterotic representing

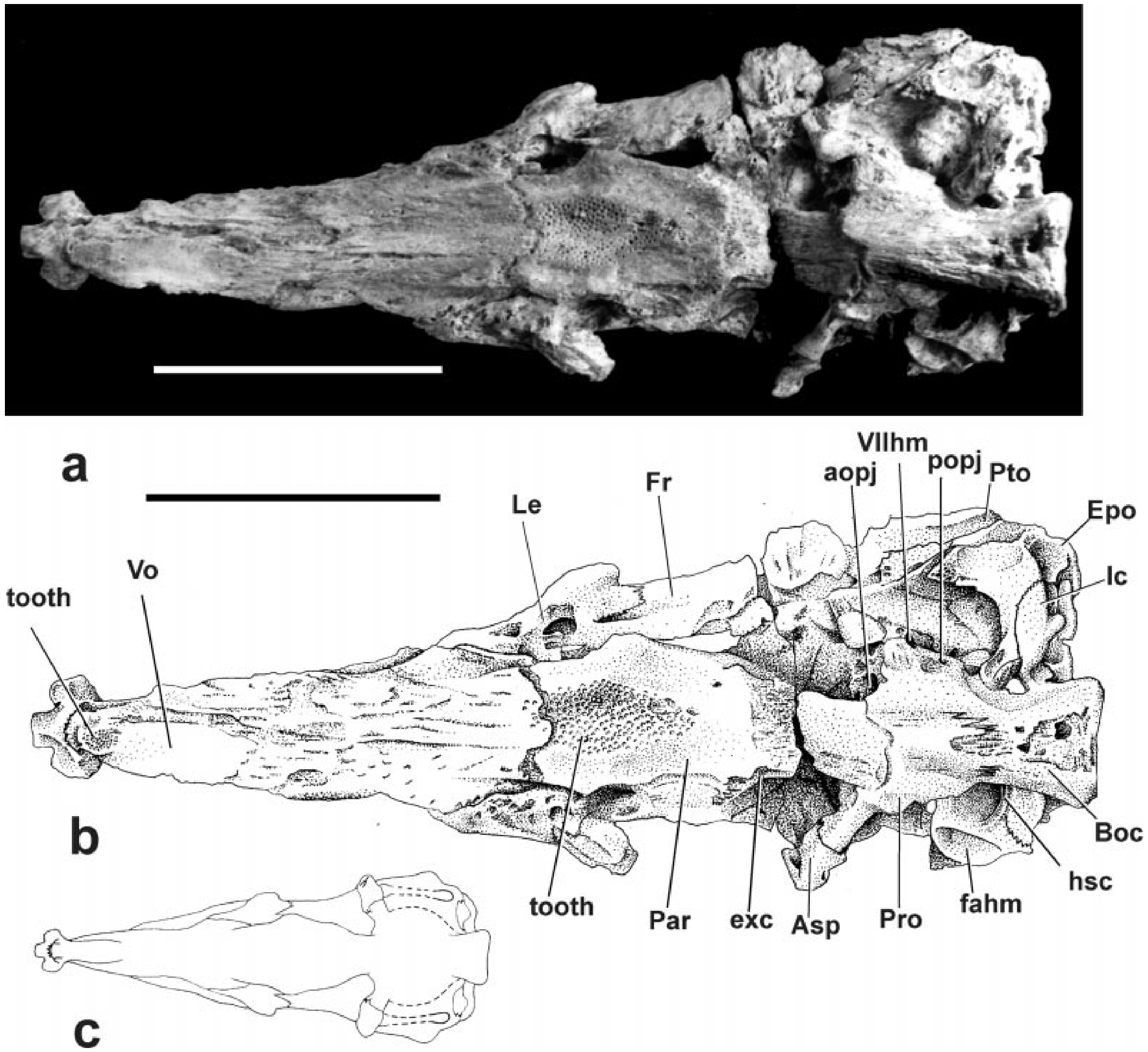

Figure 3. *Phosphonatator oxyrhynchus* gen. et sp. nov. Holotype (SGM-P1), neurocranium in ventral view. Scale bar: 100 millimetres. (a) photograph, (b) drawing, (c) reconstruction. Abbreviations: aopj, anterior opening of the pars jugularis; Asp, autosphenotic; Boc, basioccipital; Epo, epiotic; exc, excavation; fahm, facet for articulation with hyomandibular; Fr, frontal; hsc, horizontal semicircular canal; Ic, intercalar; Le, lateral ethmoid; Par, parasphenoid; popj, posterior opening of the pars jugularis; Pro, prootic; Pto, pterotic; Vo, vomer; VIIhm, hyomandibular trunk of the facial nerve.

the wall of the caecal end of the subtemporal fossa as those described in *A. vulpes* (Forey, 1973*a*). Although the arrangement of the posterior part of the neurocranium could have been distorted by the crushing, the pterotics probably did not reach the postero-lateral edge of the braincase as in other albuloids and consequently, the epiotics (Epo) form most of the roof of the post-temporal fossa (ptf) in posterior view.

The supraoccipital (Soc) and epiotics are more developed in dorsal view than in other albulids and in pterothrissids. The external surface of the supraoccipital is regularly curved from its horizontal dorsal face to its vertical posterior face. The supraoccipital crest is incompletely preserved: it is thin and apparently like that of *A. vulpes*. The epiotic forms a posteriorly oriented process. In posterior view, the epiotic forms the medial wall of the post-temporal fossa, the roof of the deep triangular sub-epiotic fossa (sef) and the posterior part of the roof of the post-temporal fossa. The post-temporal fossa is small and directed antero-medially.

The exoccipital (Exo) is poorly known. It meets its fellow above and below the foramen magnum (fm). The suture between both exoccipitals below the foramen magnum is not visible in posterior view because of the well-developed occipital condyle (Fig. 5). The exoccipital forms the floor of the sub-epiotic fossa where two pores open, probably for the occipital nerve

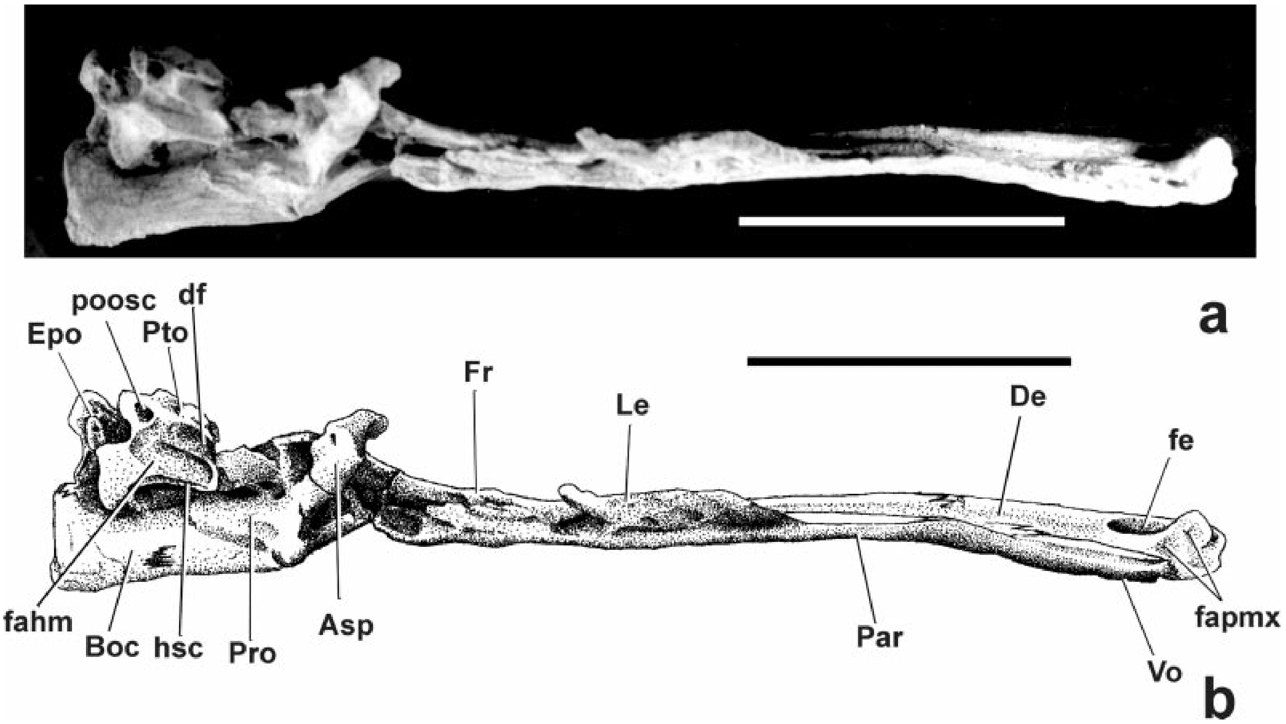

Figure 4. *Phosphonatator oxyrhynchus* gen. et sp. nov. Holotype (SGM-P1), neurocranium in right lateral view. Scale bar: 100 millimetres. (a) photograph, (b) drawing. Abbreviations: Asp, autosphenotic; Boc, basioccipital; De, dermethmoid; df, dilatator fossa; Epo, epiotic; fahm, facet for articulation with hyomandibular; fapmx, facet for articulation with premaxilla; fe, fenestra; Fr, frontal; hsc, horizontal semicircular canal; Le, lateral ethmoid; Par, parasphenoid; poosc, posterior opening of the otic sensory canal; Pro, prootic; Pto, pterotic; Vo, vomer.

(fon). Most of the medial wall of the sub-epiotic fossa was probably formed by a stout vertical ridge as in *A. oweni* and osmeroidids. As in *A. oweni*, an interspace between supraoccipital and exoccipitals seems to be present.

The intercalar (Ic) forms a rounded process at the ventro-medial edge of the post-temporal fossa. Its exact shape is unknown but there is probably no prootic–intercalar bridge. The intercalar contacts the epiotic dorsally.

The basioccipital (Boc) forms a very large occipital condyle. The dorsal face of the condyle bears a pair of deep pits (pna), presumably for the reception of a neural arch, suggesting that a centrum element has been incorporated into the basioccipital as in the Cretaceous *Rhacolepis buccalis* and *Pachyrhizodus megalops* (Forey, 1977), among others. In these species and *P. oxyrhynchus* the suture between the centrum and the basioccipital is not visible, unlike in the extant elopids and megalopids and the fossil osmeroidids (Forey, 1973*a*). The dorso-lateral suture of the basioccipital is not visible. It meets the parasphenoid (Par) anteriorly in an antero-dorsal directed interdigitate suture.

In albuloids, a large bulla containing the sacculith is formed mainly by the exoccipital, basioccipital and prootic (Pro). This character is not preserved in the holotype of *P. oxyrhynchus* and was probably less developed in this taxon than in the extant albulids and pterothrissids. The crushed left prootic is laterally well developed and swollen, and shows the anterior part of the subtemporal fossa. A small pore for the posterior opening of the pars jugularis (popj) is present near the posterior margin of this bone. Anterior to the subtemporal fossa there is a large foramen for the hyomandibular trunk of the facial nerve (VIIhm). The foramen for the orbital artery, generally situated immediately above the ascending wing of the parasphenoid in albuloids, was not observed. The orbital face of the prootics is poorly preserved; there is apparently a large lateral foramen for the anterior opening of the pars jugularis (aopj), a medial foramen for the oculomotor and a large ventral opening for the posterior myodome. However, the interpretation of this part of the neurocranium is still uncertain.

The autosphenotic (Asp) forms the anterior extremity of the deep dilatator fossa. It meets the prootic at a rectilinear suture laterally and with a zigzag suture on the orbital face. The autosphenotic is produced laterally as a tetrahedral process. A deep and large depression is present on the anterior face of this process. A small foramen pierced the bottom of this depression and opens on the postero-lateral face of the process.

The parasphenoid is very wide. Almost 200 alveoli are present beneath the anterior half of the orbit. Some small (almost 1 mm in diameter) hemispherical

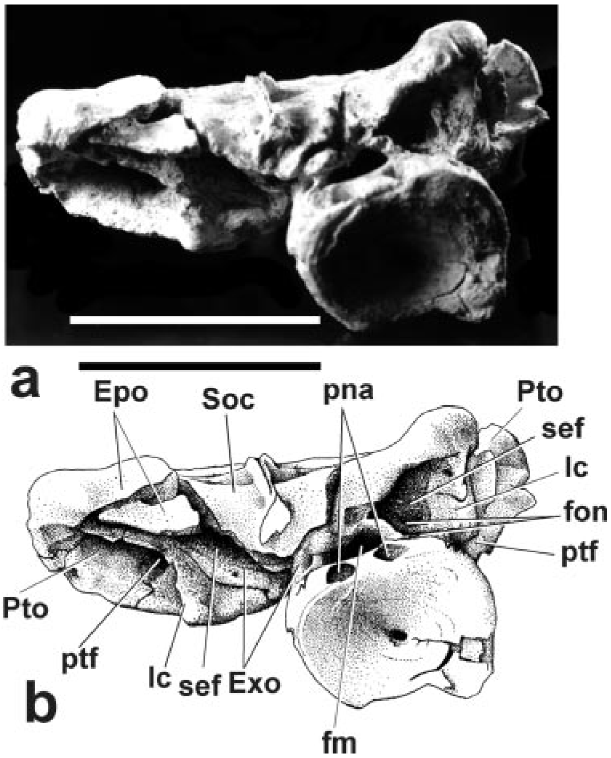

Figure 5. *Phosphonatator oxyrhynchus* gen. et sp. nov. Holotype (SGM-P1), neurocranium in posterior view. Scale bar: 50 millimetres. (a) photograph, (b) drawing, (c) reconstruction. Abbreviations: Epo, epiotic; Exo, exoccipital; fm, foramen magnum; fon, foramen for the occipital nerve; Ic, intercalar; pna, pit for the reception of the neural arch; ptf, post-temporal fossa; Pto, pterotic; sef, subepiotic fossa; Soc, supraoccipital.

smooth teeth are still present. These teeth look like those of *A. oweni* and *A. vulpes*, but in these two species the teeth are present between the level of the autosphenotic spines and the level of the lateral ethmoid, and are not restricted to a patch in the anterior half of the orbit. The parasphenoid bears a lateral wing at the level of the teeth. There is a well-developed excavation on each side of the parasphenoid posterior to the patch of teeth, situated approximately beneath the posterior third of the orbit (exc). These excavations may correspond to the point of articulation for the first infrapharyngobranchials. In the pachyrhizondontid *Rhacolepis buccalis*, the articular facets for the first infrapharyngobranchials are marked by a low prominence situated immediately posterior to the ascending wings of the parasphenoid (Forey, 1977). If the excavations observed on *P. oxyrhynchus* are correctly interpreted, they are situated more anteriorly than on *R. buccalis*; this position could be linked with the elongated snout of *P. oxyrhynchus*. Forey (1973*a*, p. 202) described in albuloids ‘a deep depression at the base of the parasphenoid ascending wing, the significance of which is not known’. Because the holotype of *P. oxyrhynchus* is crushed, we cannot reconstruct the neurocranium in three dimensions and it remains unclear if the excavations observed on our specimen are homologous with those reported by Forey. A piece of the skull roof is missing on the holotype of *P. oxyrhynchus* and one can see through the gap a part of the dorsal face of the orbital region of the parasphenoid (Fig. 2, Par), which does not show any trace of an ossified interorbital septum.

In ventral view, the vomer (Vo) of *P. oxyrhynchus* has the same shape as those of *A. vulpes*. However, the suture between the vomer and the parasphenoid is not visible. A patch of almost 50 alveoli is present at the anterior extremity of the vomer. The alveoli are smaller than those of the parasphenoid. Teeth are no longer preserved. The vomerine teeth of *P. oxyrhynchus* differ from those of *A. vulpes* because they must have been more numerous and more anteriorly situated.

The lateral ethmoid (Le) is large and stout as in other albulids. Both lateral ethmoids extend laterally beyond the frontal profile in dorsal view, but this condition is probably due to the crushing of the specimen. Antero-ventrally, the lateral ethmoid is sutured with a lateral wing of the parasphenoid.

The dermethmoid (De) is proportionally more elongate than in other species of *Albula*. It forms a prominent median ridge pierced by a large fenestra (fe). There is no well-marked central groove as in *A. vulpes*. The dermethmoid bears anteriorly two lateral well-developed rounded wings beneath each of which there is an antero- and a postero-ventrally oriented facet for articulation with the premaxilla (fapmx). Each wing is pierced by an antero-posterior canal which opens posteriorly at the level of the transverse fenestra. The anterior tip of the dermethmoid bears two small processes. The structure of the dermethmoid is discussed below.

Other bones of the neurocranium are unknown.

2.b. Relationships and comparison

The analysis of characters of *P. oxyrhynchus* is conducted according to the work of Forey (1973*a*) on elopiform fishes. The diagnoses presented in the work of Forey are based on a combination of primitive and advanced characters. A comprehensive phylogenetic study of fossil and living elopomorphs is outside the scope of our work; we only indicate herein the derived characters with an asterisk (*), and mention references for further discussion.

The Elopomorph (regarded as Elopiformes by Forey in 1973*a*) characters observed in *P. oxyrhynchus* are: (1) dermethmoid large; (2) parietals meeting in the mid-line (Taverne, 1989; Forey, 1973*b*); (3) roofed post-temporal fossa (Forey, 1973*b*; Forey, 1977); (4) pars jugularis long (Forey, 1973*b*; Forey, 1977); (5) jugular vein and hyomandibular branch of the facial with separate openings on the lateral face of the prootic (unknown for opening of the orbital artery); (6) parasphenoid extending to, or near the posterior limit of, the neurocranium, with teeth beneath the orbit (Arratia, 1999); (7) basipterygoid process absent (*) (Forey, 1977).

The Albuliformes (regarded as Albuloidei by Forey in 1973*a*) characters observed on *P. oxyrhynchus* are: (8) shallow cranium, broad at the occiput (*); (9) sensory canals developed as a cavernous system, incompletely covered by bone (*); (10) post-temporal fossa small, directed antero-medially (*) (Forey, 1973*b*); (11) sub-epiotic fossa well developed (*) (Forey, 1973*b*; Forey *et al.* 1996); (12) dilatator fossa narrow, with a roof (*) (Forey, 1977); (13) autosphenotic spine and epiotic process weakly developed; (14) intercalar small and prootic-intercalar bridge absent (*) (Taverne, 1989); (15) lateral ethmoid in contact with the parasphenoid (*).

The Albuloidei (*sensu* Forey *et al.* 1996. This taxon, containing the Albulidae and Pterothrissidae only, was not named by Forey in 1973*a*) characters observed on *P. oxyrhynchus* are: (16) snout elongated (*); (17) ethmoid commissure incomplete (uncertain) (*) and (18) supraorbital sensory canal not extending onto parietal (*) (Taverne, 1989). A possible additional albuloid character proposed by Maisey & Blum (1991) in their description of *Paraelops* and observed on *P. oxyrhynchus*, is (19) a sutural contact between the intercalar and epiotic. Although these authors pointed out this character in several non-related groups of actinopterygians, its presence among elopomorphs seems to be restricted to the Albuloidei and to *Osmeroides lewesiensis*

Following Forey (1973*a*), the albulid characters observed on *P. oxyrhynchus* are: (20) lateral ethmoid sutured with a broad parasphenoid (*); (21) vomer with small teeth; (22) parasphenoid with crushing dentition. In *P. oxyrhynchus*, however, the set of parasphenoid teeth is less prominent and less extensive than in other albulids. *P. oxyrhynchus* shares with *Albula vulpes* the (23) first vertebral centrum incorporated in the neurocranium (Rosen, 1985, fig. 9C). The lateral ethmoids sutured with the parasphenoid is a synapomorphy of Albulidae unique among teleosts. Other characters uniting *Phosphonatator* and *Albula* and separating them from *Pterothrissus* are the position of the (24) anterior opening of the supraorbital canal at the level of the lateral ethmoid *contra* above the posterior part of the orbit, and (25) the absence of grooves on the pterotics and parietals for the supratemporal commissure.

P. oxyrhynchus differs from other albulids by (26) the absence of ossified interorbital septum. The ethmoid ossification looks like those of *A. vulpes* with (27) the double premaxillary facet (*). However, in *Albula* the dermethmoid bears dorsally a ridge with a well-marked central groove whereas in *P. oxyrhynchus* (28) the dermethmoid is simpler: the median prominent ridge shows no groove and looks like those of pterothrissids (*Pterothrissus* and *Istieus*) and probably those of *Lebonichthys gracilis* (Forey, 1973*a*). In pterothrissids and *Phosphonatator oxyrhynchus* (29) the ridge of the dermethmoid is pierced by a large fenestra in which the supraorbital sensory canals of either side unite (*). In *Phosphonatator*, however, there are two supplemental canals antero-posteriorly crossing the lateral wings of the dermethmoid. These canals are here regarded as the path for the supraorbital sensory canal and could foreshadow the formation of the anterior nasal ossicles observed in *Pterothrissus gissu* and in some specimens of *Albula vulpes* (Forey,1973*a*). Nybelin (1956, 1967) has suggested that the lateral rostral ossicle in *Elops* arose by fragmentation of the dermethmoid (his rostral): the structure observed herein could confirm that the different ossicles bearing sensory canals in the snout of elopomorphs may arise by fragmentation of the dermethmoid.

Compared with fossil albulids, *P. oxyrhynchus* shares with the Late Cretaceous *Lebonichthys* from Lebanon described by Forey (1973*a*) a dermethmoid with a median prominent ridge (28), but differs in having a longer snout, the organization of the posterior part of the skull roof (arrangement and relative size of the parietals, pterotics, epiotics and supraoccipital), the disposition of the otic sensory canal, and in the shape and dentition of the parasphenoid.

The Late Cretaceous *Deltaichthys albuloides* from Texas (Fielitz & Bardack, 1992) shares with *P. oxyrhynchus* a primitive albuloid character: (23) a centrum element incorporated into the basioccipital, and a primitive albulid character: (26) absence of ossified interorbital septum. *Deltaichthys albuloides* differs from *P. oxyrhynchus* by its non-elongated snout, by the dorsally visible posterior part of its autosphenotic, and by the shape and dentition of the parasphenoid.

P. oxyrhynchus shares similarities with *A. oweni*, known in the Early Eocene of southeastern England, France, Belgium and the Middle Eocene of Belgium: (30) the ornamentation of the frontals and (31) an interspace between supraoccipital and exoccipitals. *P. oxyrhynchus* differs from *A. oweni* in the proportions of the skull roof, the structure of the dermethmoid and the arrangement of teeth on the parasphenoid and vomer. *A. oweni* differs from *A. vulpes* in the position of the posterior opening of the pars jugularis situated far forward, and in the presence of a lateral bridge of bone spanning the jugular groove behind the posterior opening, whereas in *A. vulpes*, and probably in *P. oxyrhynchus*, the opening is close to the posterior margin of the prootic. However, this bridge is probably subject to individual variation in *A. oweni* (Forey, 1973*a*) and of little use in indicating phylogenetic relationships. Arambourg (1952) referred isolated micoremains from the Thanetian of the Ouled Abdoun basin to *A. oweni* on the basis of similarities with parasphenoid teeth of *Albula* and for stratigraphical reasons. It is now more parsimonious to refer these teeth to *P. oxyrhynchus*.

P. oxyrhynchus differs significantly from the albulid *Coriops amnicolus* known by isolated parasphenoids and basibranchials, described by Estes (1969) in the Maastrichtian Lance and Hell Creek Formations, USA. *P. oxyrhynchus* can not be compared with *Albula dunklei* known by remains other than braincase, described by Applegate (1970) in the Campanian of the Moorville Chalk, USA.

P. oxyrhynchus is not related to one of the primitive albuliform plesions (*Paraelops*, *Brannerion*, osmeroidids) and is placed within the albuloidei (characters (1) to (19)). The neurocranium of *P. oxyrhynchus* shares six diagnostic characters with albulids, four being plesiomorphic for Albuloidei ((21), (22), (24), (25)) and two being synapomorphies of the family ((20) and (27)). It shares with pterothrissids two diagnostic characters, one being plesiomorphic for Albuloidei ((26)) and one being a synapomorphy of the family ((29)). Character (28) is apparently present in forms of both families: *Pterothrissus*, *Istieus* and *Lebonichthys*.

Consequently, we regard (a) *P. oxyrhynchus* as a primitive albulid; (b) the simplest structure of the dermethmoid and the lack of an ossified interorbital septum in *P. oxyrhynchus, Deltaichthys albuloides* and pterothrissids as primitive characters of albuloids preserved in the three taxons; and (c) the ridge of the dermethmoid pierced by a large fenestra in which the supraorbital sensory canals of either side unite in *P. oxyrhynchus* and pterothrissids as either a plesiomorphic character for Albuloidei preserved in both taxons or an apomorphic character acquired independently in both taxons.

3. Conclusion

True albulids and pterothrissids are recorded as early as Late Cretaceous times, so it is surprising that the Palaeocene *P. oxyrhynchus* cannot be placed in either family without any reservation. A cladistic study could establish either that another albuloid lineage, containing *P. oxyrhynchus*, has evolved parallel to albulids and pterothrissids at least up to the Palaeocene, or that phylogenetic relationships among albuloids are now not clearly understood. However, it is not time to draw up a cladogram because the polarity of some concerned characters is unclear and because phylogenetic relationships based exclusively on neurocranial characters are highly likely to be only partially resolved; the recovery of other cranial and post-cranial elements of *P. oxyrhynchus* is necessary.

The recovery of this specimen should be ranked equal to the recent discovery of important, very well-preserved new material of vertebrates in the Sidi Daoui area of Ouled Abdoun Basin. This material, which is the object of collaborative Franco-Moroccan research (with the help of the Office Cherifien des Phosphates and the Moroccan Geological Survey), will considerably enhance our knowledge of several groups from phosphatic deposits of Morocco such as bony fishes, but also Cretaceous mosasaurs, chelonians, crocodilians, snakes, birds and mammals (Gheerbrant, Sudre & Cappetta, 1996; Gheerbrant *et al.* 1998), aside from selachians which were until now known mainly by fragmentary remains.

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