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Pycnodont fishes (Actinopterygii, Pycnodontiformes) from the Upper Cretaceous (lower Turonian) Akrabou Formation of Asfla, Morocco

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The Upper Cretaceous (upper Cenomanian–middle Turonian) Akrabou Formation of Asfla, southeast Morocco is renowned for exceptionally preserved, often three-dimensional bony and cartilaginous fish fossils. Teleosts, rare holosteans and chondrichthyans are well known from the so-called “Goulmima ichthyological assemblage”, however pycnodonts (Actinopterygii, Pycnodontiformes) have received scant attention and remain undescribed until now. Five nominal species are recognised in the assemblage, including two new forms: Neomesturus asflaensis gen. et sp. nov. and Paranursallia cavini sp. nov. The Italian genus Polazzodus is reported in Morocco for the first time. Specimen taphonomy is examined in the context of substrate consistency and oxygenation of an outer shelf carbonate platform setting. Diversity and ecological disparity of the Goulmima assemblage is revised in regard to trophic partitioning with durophagy seemingly more diverse than previously recognised. Comparisons with other pycnodont-bearing horizons of similar age demonstrate strong faunal affinities between the Asfla pycnodonts and those in the western Tethys and South Atlantic.

1. Introduction

The order Pycnodontiformes represents a successful, monophyletic clade of extinct neopterygian fishes in part characterised by a highly specialised feeding apparatus of robust, domed teeth. They have a temporal range of Late Triassic (Norian) to late Eocene (Ypresian) and were highly speciose throughout the Mesozoic but their diversity declined in the Paleogene. They are typically rec...
vertebrate assemblage also contains rare selachian, platyrhiniid batoids (Claeson, Underwood and Ward, 2013), sawsharks (Villalobos-Segura et al., 2019) as well as marine reptiles including polycotylid pliosauras (Bardet et al., 2003a), pliosaurs, tethysaurus (Tethysaurus nopscai, Bardet et al., 2003b) and turtles (Cavin et al., 2010). Dubar (1949) first recorded well preserved “fish remains [preserved] in nodules … associated with Turonian ammonites” from the Akrobou Formation in the Midelt area. These remains went unstudied until Cavin (1995) described the pachyrhizodontid (Teleostei: Crossognathiformes) *Goulminichthys arambourgi* from the Akrobou Formation at Goulmima. *Goulminichthys arambourgi* is the most abundant vertebrate in the assemblage and is also present at Asfla (Veysey et al., 2020; pers. obs. SC). Cavin (1997, 1999) also recorded several other teleosts from the Akrobou Formation, including *Osmeroides* sp., *Ichthyodectes* sp. (an ichtyodectid), the tetraitaliform *Araripichthys* sp. and *Enchodus* sp. based on a juvenile endocranium preserved in a coprolite. More recently, Veysey et al. (2020) described from Asfla a new crossognathiform, *Kradimus asfuenis* with unusually hypertrophied fins which shows an apparent convergence with extant Flyingfishes (Teleostei: Exocoetidae). Recently a large marine lepisosteiform (Gar) was discovered at Asfla (undescribed) and is under study (SC).

Pycnodont fishes are poorly documented from the Akrobou Formation. Prior to this analysis, only a single, poorly preserved vomer discovered in the stomach contents of an ichthyodectid has been documented (Cavin, 1996). Cavin identifies the conspicuous vomer as “cf. *Palaeobalistum* sp.” but does not describe the specimen. More likely it is an example of *Paranursallia* sp. due to characteristic dentition similar to new material figured here (see *Systematic palaeontology*).

Pycnodonts were later mentioned in the Akrobou Formation by Cavin et al. (2010), simply stating “there is also a pycnodont”, insinuating a single taxon, when discussing the diversity of the ‘Goulmina Assemblage’. These authors regard their pycnodont remains as “indeterminate” and consisting only of “isolated teeth” preserved “within coprolites”, although do not figure any examples. These studies, while rather uninformative, do confirm the occurrence of pycnodontiforms in the Akrobou Formation, but they suggest pycnodonts are poorly preserved, taxonomically undiagnostic and in low diversity. New data presented here strongly conflicts this interpretation. Below we describe a diverse assemblage of pycnodont fishes from the Akrobou Formation at Asfla consisting of complete dental elements (vomer and prearticulars) as well as evidence of exceptionally preserved, complete pycnodont skeletons.

2. Geological context

The Akrobou Formation is an outer shelf carbonate succession with a stratigraphic range from the upper Cenomanian to lower Turonian (Ettachfini and Andreau, 2004). In Morocco, the formation crops out along the southern flank of the Atlas Mountains (Preafrican Trough) between Tinghir and Errachidia (west to east) and Tazzouguert to Ain et Ati (north to east) encompassing an area of ~175 km x ~65 km respectively (Lézin et al., 2012). The fossil-bearing unit of the Akrobou Formation at Asfla (Asfla Member Fig. 1B) is assigned to the lower Turonian as indicated by an abundance of *Mammites* sp., indicating the *Mammites nodosoides* ammonite biozone (Kennedy et al., 2008). At Asfla the formation comprises a sequence of alternating facies succession of fossiliferous packstones, chalk dominated marls, cherts and a vertebrate-yielding Konservat-Lagerstätten nodular horizons (Asfla Member), the latter of which is mined commercially for its beautiful fossils. The Akrobou Formation stratigraphically succeeds non-sequentially the ?Albian–Cenomanian Ifezouane and Aoufous formations of the fluvial, and fluvio-lagoon Kem Kem Group (see Ibrahim et al., 2020).

Cavin et al. (2010) defined two distinct vertebrate assemblages within the Akrobou Formation; a lower, so-called Agoult (Gara Sbaa) assemblage, and an upper Goulmina assemblage. The Agoult assemblage occurs within outcrops exposed at Gara Sbaa (named the Gara Sbaa Member by Martill et al., 2011), situated approximately 10 km south west of Agoult. The Agoult fauna consists of exceptionally preserved fishes (including pycnodonts, see discussion), crustaceans, rare reptiles and plants, within finely laminated, marginal marine limestones (Martill et al., 2011; Roberts et al., 2020). The palaeoichthyological component of the Agoult assemblage is composed of at least two pycnodontiforms (undescribed), clupeomorphs, macrosemiids, aspidorhynchids and dercets (Martill et al., 2011; Veysey et al., 2020) and demonstrates strong faunal affinities with the central Tethys (Cavin et al., 2010). Fossils at Gara Sbaa are preserved flat (crushed) on bedding planes and always fully articulated, suggesting preservation by microbial mats (Cavin et al., 2010). The upper, so-called Goulmina assemblage was coined by Cavin (1997; 1999) and Cavin et al. (2010). It occurs in outcrops along the southern flank of the High-Atlas Mountains, in the region of Goulmima, Tadirhout, Asfla and Timizguir in Errachidia Province (Fig. 1). The Tadirhout fossil occurrence extent remains to be established. In contrast to the Agoult assemblage, fossil fishes of the Goulmina assemblage at Asfla are usually preserved as three-dimensional, exceptionally preserved individuals enclosed within calcareous nodules (Asfla Member). Preservation of fishes in this horizon is likely attributed to soupgrounds with comparable preservation recognised in the Early Cretaceous Santana Formation of Brazil (e.g. Brito and Yabumoto, 2011). Rare instances of soft-tissue preservation in the Asfla Member fishes was first reported by Cavin (1999) who records preservation of the alimentary tract, muscles, gill filaments and cartilage in fishes enclosed within the nodules. Early diagenesis of these nodules has preserved fishes in three-dimensions with minimal flattening or distortion (Cavin, 1999, 2001). Nodules typically form around only part of the fish, usually the head and abdominal region (Veysey et al., 2020), with few nodules preserving extremities such as the caudal fins or distal parts of the pectoral fins. It is rare for the entire fish to be enclosed within a nodule (pers. obs. SC and DMM). These remarkable instances of exceptional preservation have been attributed to dysoxic conditions in all but the highest portions of the water column (Lebedel et al., 2015).

3. Materials and methods

All specimens in this study were obtained directly from local fossil collectors directly at the dig site or from their homes in the Asfla oasis (Fig. 1). Almost all specimens are preserved within a cream coloured chalky marl matrix confirming their origin from the Asfla Member fossil conservation Lagerstätte nodule horizon. One specimen (AK-PYC 24) is preserved on a piece of bioclastic limestone and was collected near the top of the Akrobou Formation at Asfla. All of the material described here was obtained between December 2017 and January 2020. One additional specimen consisting of a near complete pycnodont skeleton (NHMUK P. 73411, Fig. 2) was identified in the collection of the NHMUK by one of the authors (SC). The specimen is figured here but because of logistical challenges brought about by the Covid-19 pandemic, will be described at a later date. All material studied in this work has been accessioned into the palaeontology collection of the London Natural History Museum, (NHMUK), Cromwell Road, South Kensington, London, United Kingdom.
4. Systematic palaeontology

OSTEICHTHYES Huxley, 1880.
ACTINOPTERYGII Cope, 1888.
NEOPTERYGII Regan, 1923 (sensu Rosen et al., 1981)
HALECOSTOMI Regan, 1923 (sensu Patterson, 1973)
PYCNODONTIFORMES, Nursall, 1996b.

Family PYCNODONTIDAE, Agassiz, 1833 (sensu Nursall, 1996b)

Genus Anomoeodus Forir, 1887.
Type species: Anomoeodus subclavatus (Agassiz, 1833)

Material. Twenty specimens: AK-PYC 6—11, 13, 14, 16—24 from the Akrobou Formation are confidently assigned to Anomoeodus (see below).

Remarks. All twenty specimens show affinities with the type species A. subclavatus (Agassiz, 1833; Forir, 1887). Two distinct vomer and two prearticular morphotypes of Anomoeodus are identified and are informally identified here as Anomoeodus sp. A and Anomoeodus sp. B. Vomer and prearticular morphotypes are tentatively matched based on similar morphologies of the medial teeth seen in both elements. Usually vomer and prearticular elements are described separately in the absence of associated material (e.g. Longbottom, 1984). However, as only two morphologies of each element are present from a sample consisting of multiple individuals of each form, with distinct ontogenetic sizes present, it is parsimonious to assume that only two species of Anomoeodus are present in the Akrobou Formation.

Fig. 1. Locality maps of Morocco and stratigraphic log of the Akrobou Formation at Asfla. (A), locality maps of Morocco: (Top left), simplified map of Morocco with the Errachidia Province indicated by a rectangle. (Top centre), map of the Errachidia province showing the position of Asfla in relation other major towns. (Bottom), Localised map of the Asfla area with the position of the main fossil mines indicated along the Asser N’ Tadirhouch escarpment. (B) Simplified stratigraphic log of the Akrobou Formation outcropped at the Asfla oasis, with the Asfla Member indicated.
Anomoeodus sp. A

Material. AK-PYC 6, large complete vomer (Fig. 3). AK-PYC 8 and 12 (Fig. 4), left prearticulars. AK-PYC 7, 9, 10, 11, right prearticulars.

Locality. Asfla fossil mines on the escarpment called Assemer N’Tadirhoust, 4 km south-east of the oasis village Asfla, Errachidia province, south-east Morocco, 31°52’01”N 4°52’30”W.

Horizon. Mammites ammonite biozone, Chalky-Marl facies, Asfla Member, Akrabou Formation. Upper Cretaceous (Turonian).

Description. Anomoeodus sp. A is described from a single well-preserved vomer and a composite of six prearticular elements. Both elements show medial teeth which are thin and laterally elongate (as opposed to short and wide in Anomoeodus sp. B, below) and hence are tentatively described as single species here.

Vomer. Specimen AK-PYC 6 consists of a near complete vomer lacking only the ascending process on matrix exposed in occlusal view. The vomer is narrow and elongate (as opposed to short and wide in Anomoeodus sp. B, below) and hence are tentatively described as single species here.

Teeth on the medial row are short and laterally expanded with a width more than twice as great as the anteroposterior crown length (Fig. 5A). The teeth are convex and unornamented with lateral tooth faces curved slightly anteriorly; a condition typical of Anomoeodus (Forir, 1887; Kriwet, 2002). Teeth on the medial row are separated longitudinally by a wide diastema while teeth of the lateral rows are tightly interspaced both laterally and longitudinally. Tooth size on the medial row decreases slightly towards the anterior, with tooth dimensions ranging between 15 mm × 5 mm posteriorly and 13 mm × 4 mm anteriorly in width and anteroposterior length. At the most anterior end of the medial row, a small sub-rectangular tooth is situated in succession to the anterior most medial tooth (Fig. 5A). This strange tooth is distinguished from the medial teeth by the presence of an oval contour and a central occlusal facet; similar to that of the lateral teeth. This tooth is unlike a typical second generational replacement tooth observed in other taxa, which are always spherical and unornamented (Longbottom, 1984; Cooper and Martill, 2020, fig. 5A). Its function is unclear; however, it is possibly a consequence of a morphological change associated with ontogeny.

The paired primary lateral tooth rows are composed of at least fifteen pisiform to sub-lachrymiform convex teeth, ranging in size...
from 7 mm × 6 mm posteriorly and 4 mm × 4 mm anteriorly in width and anteroposterior length. Each lateral tooth is steeply convex with a single, unornamented occlusal wear facet, present on the dorsolateral face of the dental crown.

The secondary (outer) lateral row is composed of no less than fourteen sub-pisiform to reniform convex teeth, ranging in size from 5 mm × 5 mm posteriorly to 4 mm × 5 mm in width and anteroposterior length. Similar to the primary lateral row, these teeth are strongly convex with a small occlusal facet present on the dorsolateral face of the tooth crown. However, unlike the primary lateral row, the secondary lateral teeth are slightly smaller and show a greater anteroposterior elongation in occlusal view (Fig. 3).

Prearticular. Six prearticular specimens: AK-PYC 6 are assigned to Anomoeodus sp. A based on characteristic dentitions (Fig. 4). All specimens are partial or somewhat damaged except for AK-PYC 7 which consists of a complete pallet with coronoid process intact. AK-PYC 7 measures 62 mm, 37 mm and 17 mm in anteroposterior length, width and prearticular thickness respectively (anteroposterior length of the dental pavement in 2.2 x greater than the width of the occlusal pavement posteriorly). Three continuous tooth rows are present on the prearticular, consisting of one medial (main) and two laterals. The presence of any labial dentition along the medioventral lamina is unknown because this element is poorly preserved in all 6 specimens. The prearticular is concavely elliptical in cross section and relatively thicker compared to the dentition (approximately 5.2 x greater in AK-PYC 10).

The medial (main) row is positioned medio-labially on the dental pavement and composed of at least ten lozenge-shaped medial teeth. Medial teeth are laterally elongate, convex, unornamented and slightly sigmoidal with the labial face of each tooth curved antero-labially. Some specimens do not show curved faces (AK-PYC 8, 12) and thus this feature is regarded as natural variation of no taxonomic significance. Tooth dimensions on the medial row decrease slightly towards the anterior, ranging from 5 mm × 16 mm (posterior) to 4 mm × 9 mm (anterior) in AK-PYC 7. Each medial tooth is separated longitudinally by a prominent diastema, whilst the lateral rows lack this diastema – a condition also encountered in the vomer. Specimen AK-PYC 7 displays two
Fig. 4. Pycnodont prearticulars from Asfla. (A–B), AK-PYC 7, left element of *Anomoedus* sp. A. in occlusal (A) and latero-ventral view (B). Notice the complete coronoid process and unerupted medial teeth exposed at the posterior end of the dental pavement (arrow). (C), AK-PYC 23, gigantic right prearticular of *Anomoedus* sp. B. The posterolateral region of the
partially unerupted teeth at the posterior extremity of the pre-articular, just preceding the first erupted medial tooth (Fig. 4A). These unerupted teeth are positioned deeper into the bone than the active teeth on the occlusal pavement and show poorly developed enamel crowns with a distinctive variation in enamel colour as a result. The presence of new, partially developed teeth preserved in the act of eruption is rarely seen in pycnodonts and suggests a sub-mature individual.

The primary lateral row is composed of up to thirteen (AK-PYC 9), laterally elongated oval to reniform teeth which measure between 4 mm × 11 mm (posterior) and 3 mm × 5 mm (anterior) in AK-PYC 7. Crown topography is slightly concave, as opposed to convex in the adjacent medial teeth. Each tooth on the row is ornamented with a shallow, slit-like occlusal fossa encompassed by marginal micro-crenulations, positioned medially along the crown apex (Fig. 7). The primary lateral teeth are less wide than the medial teeth and never show curvature of lateral or labial tooth faces.

The secondary (outer) lateral row is composed of at least twelve rhombic to sub-pisiform teeth, measuring between 5 mm × 7 mm posteriorly to 4 mm × 3 mm in anteroposterior length and width in AK-PYC 7 (Figs. 4 and 5). Dental topography of this row is gently convex with a short and narrow occlusal fossa on the crown apex with ornamentation similar to that on the primary lateral teeth. Lateral faces of these teeth are relatively flat, creating a straight lateral profile of the dental pavement in occlusal view, as opposed to antero-labially curving in Anomoeodus sp. B (see below).

The coronoid process protrudes 90° adjacent to the dental pavement and is only complete on AK-PYC 7 and poorly preserved in AK-PYC 9 and 10. The shaft of the coronoid is short and thick with a rectangular cross section. The head of the coronoid has an ax head-like, narrow and anteroventrally elongate outline in occlusal view, with the posterior lobe of the process more elongate than the anterior lobe.

Remarks. Specimens are assigned to Anomoeodus Forir (1887) due to similar characters shared with the type species A. subclavatus (Agassiz, 1833) from the Late Cretaceous of Maastrict, Belgium. These are: medial teeth on the prearticular are more than twice as wide as the laterals; lateral faces of the medial teeth are curved anteriorly; primary and secondary lateral tooth rows on the vomer are of near equal size and are closely interspaced whilst the medial teeth are not. Anomoeodus sp. A differs from A. subclavatus by: primary lateral teeth on the prearticular more elongate than the secondary lateral, opposed to equally proportioned in the type species; only the labial faces of the medial teeth are curved anteriorly. A. subclavatus possesses a discontinuous labial tooth row situated along the anterior region of the medioventral lamina (Friedman, 2012). This feature is absent in Anomoeodus sp. A, possibly due to damage of the symphysis region in all specimens. A similar medial tooth morphology with only the labial face curved anteriorly is also present in Anomoeodus cretaceous (Agassiz, 1833), A. barberi Hussakof, 1947 and A. pauciseriale Kriwet, 2002. Anomoeodus cretaceous from the Cretaceous of Bohemia possesses laterally elongate medial teeth with anteriorly curved labial tooth faces and two lateral tooth rows similar to the Asfla form. Unlike Anomoeodus sp. A, the lateral tooth rows of A. cretaceous are of equal size respectively. Fritsch (1878, table 2, figs. 3 and 4) first figured the prearticular of A. cretaceous and labels five tooth rows, consisting of the medial row, two lateral rows and an irregular cluster of smaller teeth anteriorly. Capasso (2019, fig. 1a) illustrates a specimen of Anomoeodus sp. from the Turonian of Gabon with a similar dental configuration to that figured by Fritsch (1878, table 2, figs. 3 and 4), which also shows unorganised replacement teeth situated within cavities of broken first-generation teeth. This taxon is reappraised here as only possessing four tooth rows (one labial, one medial and two lateral) and we consider that the “fifth tooth row” are second generational teeth which should not be regarded as taxonomic in diagnosing pycnodont tooth rows. Anomoeodus barberi Hussakof, 1947 from the Upper Cretaceous Marlbrook Marl of Arkansas (USA), varies drastically from the Asfla forms by the presence of two labial rows, one medial, two organised laterals and several other lateral rows which are poorly organised, representing at least four additional lateral tooth rows. Cooper and Martill (2020) regard Anomoeodus as a taxonomic waste bin genus and erected a new genus, Agassizilla to accommodate specimens of Anomoeodus with more than four true tooth rows. We disagree with the assignment of A. barberi to Anomoeodus due to the striking difference in tooth row number and reassign it as Agassizilla barberi (Hussakof, 1947). Shimada and Everhart (2009) figured an incomplete paratype specimen of A. barberi which is broken between the secondary and third lateral tooth row. The authors suggest that the absence of these additional tooth rows is due to “considerable amount in variation … in A. barberi”. This opinion is tentative and disregarded here. The paratype the authors figure is incomplete and the additional tooth rows present in the holotype have likely just broken off.

The medial teeth of Anomoeodus pauciseriale Kriwet (2002) from the English Chalk Group is partially diagnosed by medial teeth with a “rhomboid outline” and an “outer extremity [that] is truncated with a straight lateral margin and a rounded posterolateral edge”. Furthermore, Kriwet (2002) diagnoses only seven teeth on the medial row, as opposed to eight to nine in Anomoeodus sp. A.

**Anomoeodus** sp. B

**Material.** Complete vomer — AK-PYC 14 and incomplete vomer AK-PYC 13 (Fig. 3B–C). Prearticular — AK-PYC 16-24 (Fig. 4C, F–I).

**Locality.** Asfla fossil mines on the escarpment called Assemer N’Tadirhoust, 4 km south-east of the oasis village Asfla, Errachidia province, south-eastern Morocco, 31°52′01”N 5°52′30”W.

**Horizon.** Mammites ammonite biozone, chalky-marl facies, Asfla Member, Akrabou Formation. Upper Cretaceous (Turonian).

**Description.** Anomoeodus sp. B is described from a composite of two vomer and ten prearticular specimens which all show a unanimous medial tooth dentition which is distinct from that in Anomoeodus sp. A. Anomoeodus sp. B is characterised and distinguished from A. sp. A by oval medial teeth which possess an ornamented fossa on the crown apex — as opposed to thin, laterally elongated unornamented teeth in Anomoeodus sp. A.

**Vomer.** The vomer of Anomoeodus sp. B is known from a medium-sized complete specimen (AK-PYC 14) and one incomplete larger vomer (AK-PYC 13) which is broken anteriorly. Both specimens are preserved within pieces of chalky limestone and have been prepared in occlusal view. The ascending process of the vomer is not...
visible in either specimen. Specimen AK-PYC 14 measures 46 mm × 20 mm × 9 mm in anteroposterior length, width (posterior) and palatal thickness. The anteroposterior length of AK-PYC 13 is unknown due to anterior damage, however the posterior width is 27 mm (compared to only 20 mm in AK-PYC 14) insisting a larger, more mature individual of Anomoedus sp. B. Cross sectional topography of both specimens is steeply convex, with medial teeth elevated slightly higher than the adjacent laterals (Fig. 5A). This differs from Anomoedus sp. A which has a relatively flat vomer with no medial dental elevation.

The median row of Anomoedus sp. B is composed of at least nine oval to sub-reniform teeth, each possessing an antero-dorsally set, lip to slit-like occlusal fossa with a mildly crenulated anterior margin ornamented with micro-granules. Medial teeth decrease in size towards the anterior, measuring between 5 mm × 6 mm (posterior) and 3 mm × 4 mm (anterior) in anteroposterior length and width for AK-PYC 14. The medial teeth of AK-PYC 13 (a larger individual) are slightly more elongate, and less quadrato-rectangular than in AK-PYC 14; but as elongate as in Anomoedus sp. A (above). Both AK-PYC 13 and 14 possess an ornamented dental fossa on each tooth which is absent in Anomoedus sp. A.

The paired primary lateral row is composed of at least ten (AK-PYC 14) reniform to sub-pisiform convex teeth, each possessing an anteroposteriorly orientated, elliptical to circular dental fossa with ornamentation similar to the medial teeth. Teeth which are reniform, especially in the more mature specimen (AK-PYC 13) are mildly elongated towards the anteroposterior plane of the palle (Fig. 4D). Teeth in AK-PYC 14 are more pisiform than reniform, suggesting the tooth morphology in this row changes gradually with ontogeny. Tooth size remains similar along the primary lateral row, only varying by 1 mm in both length and width between the first (posterior) and last (anterior-most) tooth in both AK-PYC 13 and 14.

At least nine reniform to triangularly lachrymiform teeth are present on the paired secondary (outer) lateral row. Secondary lateral teeth are convex and tightly interspaced both longitudinally along the row but also laterally with the adjacent primary lateral tooth row. Teeth on this row each possess a single, anteroposteriorly orientated fossa which is narrowly oval, shallow and mildly ornamented with micro-granules. As with adjacent primary lateral teeth, tooth size on the secondary lateral row remains near enough uniform anteriorly, with dimensions varying less than 1 mm between the anterior most and posterior most tooth in both specimens. Both lateral tooth rows are tightly interspaced with tooth crowns orientated approximately 45° postero-laterally to the dorsal occlusal surface of the medial teeth in cross section - this is a consequence of the steep convex curvature of the vomer which has elevated the medial teeth dorsal of the lateral teeth on the occlusal pavement (Fig. 5B).

Prearticular. The prearticular of Anomoedus sp. B is known from seven specimens (AK-PYC 16, 18, 20–24) of varying condition and different ontogenetic sizes including juvenile (AK-PYC 20, 21), subadult (AK-PYC 16, 18, 24) and mature individuals (AK-PYC 22–23). Specimens are assigned to Anomoedus sp. B and differentiated from Anomoedus sp. A by medial teeth which are shorter laterally, relatively thicker anteroposteriorly and are inclined towards the antero-labial margin when seen in occlusal view (as opposed to 90° parallel to the mandibular symphysis in Anomoedus sp. A). Anomoedus sp. B is further characterised by a gradually curving lateral profile of the occlusal pavement as opposed to straight in Anomoedos sp. A (Fig. 5C and D).

Juvenile specimen AK-PYC 21 measures 18 mm × 16 mm and 4 mm in anteroposterior length, width posteriorly and prearticular thickness. Sub-adult specimen AK-PYC 24 measures 37 mm × 31 mm and 6 mm in the same dimensions; whilst mature specimen AK-PYC 23 measures 60 mm, 77 mm and 22 mm in these dimensions.

The medial tooth row is composed of no more than seven (average six) convex, rhombic to reniform teeth with well-rounded tooth faces. In more mature specimens, teeth narrow towards the labial, with the labial tooth face slightly curved antero-labially, as per the condition seen in the type species A. subclavatus. Some juvenile and sub-adult specimens (AK-PYC 18, 20, 21, 24) show a poorly developed, weakly ornamented and short furrow-like fossa positioned along the dorsal anterior margin of the dental crown. Most specimens only preserve this feature on the posterior most (first) tooth of the medial row. Successive anterior teeth are older and therefore

![Fig. 5. Comparative line drawings of Anomoedus spp. (A), vomer of Anomoedus sp. A. in occlusal view. Notice the irregular morphology of the anterior-most tooth on the medial row (arrow). (B) vomer of Anomoedus sp. B in occlusal view. Notice that the medial teeth are narrower and more reniform than those in Anomoedus sp. A which are short and very wide. (A–1–A–2), stylised cross sections of each Anomoedus vomer morphotype showing variation between the relative height of width of teeth and vomerine bone. (C–D), comparative line drawings of Anomoedus spp. prearticulare (C), sp. A and (D), sp. B. The medial teeth of sp. A are more elongated and often sigmoidal, unlike sp. B which are narrower and sub-reniform. The lateral teeth of sp. A are weakly ornamented but always unornamented in sp. B. The lateral profile of sp. A is always straight whilst in sp. B it often curves antero-labially. All scale bars are equal to 10 mm.](image-url)
are more worn due to durophy; thus, any ornamentation was destroyed and replaced by largely undiagnostic wear facets. Adult individuals do not show any dental ornamentation on the medial rows, even on the youngest teeth (posterior-most) which are un-affected by wear faceting. Medial teeth show a gradual tooth size reduction anteriorly. Teeth in juvenile specimens (AK-PYC 21) range from 3 mm × 6 mm (posterior) to 2 mm × 4 mm (anterior), whereas adult median teeth (AK-PYC 23) range from 6 mm × 17 mm (posterior) to 5 mm × 16 mm in anteroposterior length and width respectively. Successive medial teeth are closely interspaced down row in juvenile specimens and some sub-mature specimens, while more mature specimens (AK-PYC 22 and 23) show a prominent diastema separating these teeth longitudinally. Between seven and ten (average nine) reniform to oval teeth are present on the primary lateral tooth row. These teeth are slightly laterally elongate with shallowly concave crowns, each possessing a weakly ornamented fossa along the occlusal apex. Teeth on this row are approximately one third smaller than the medial teeth in all dimensions. Anteroposterior length and width of these teeth range from 1 mm × 4 mm posteriorly to 0.5 mm × 1.5 mm anteriorly in juvenile specimen AK-PYC 21; 3 mm × 7 mm posteriorly to 2 mm × 3.5 mm anteriorly in sub-mature specimen AK-PYC24 and 6 mm × 12 mm posteriorly to 5 mm × 12 mm anteriorly in AK-PYC 23. The secondary (outer) lateral tooth row is composed of nine to eleven teeth which are sub-lachrymiform to reniform or triangular depending on ontogeny. Teeth are slightly wider than they are long and are closely spaced longitudinally, with some teeth preserving a minorly ornamented, oval fossa on the dental apex - similar to those on the other tooth rows. Anteroposterior length and width of these teeth ranges from 1.5 mm × 2 mm (post.) to 0.5 mm × 0.5 mm (ant.) in AK-PYC 21 (juvenile), 3 mm × 4 mm (post.) to 2 mm × 2 mm (ant.) in AK-PYC 24 (sub-adult) and 6 mm × 7.5 mm (post.) to 5.5 mm × 5 mm (ant.) in AK-PYC 23 (mature adult). In juvenile and sub-adult individuals, tooth morphology is sub-lachrymiform to oval or reniform posteriorly, gradually becoming sub-rectangular to pisi-form anteriorly. Mature adult specimens (AK-PYC 22 and 23) show a more triangular tooth morphology posteriorly, becoming more sub-lachrymiform to oval anteriorly. The overlap of dental morphologies between different sized individual is evident that the sample represents a complete prearticular ontogenetic series of Anomoeodus sp. B (Fig. 4). Due to a combination of a reducing tooth size and morphology change of teeth along this row, the lateral profile of the occlusal pavement forms a distinctive curvature towards the anterior labial margin anteriorly (Fig. 5D). This lateral curvature is not present in species A, which instead has a straight lateral profile of the dental pavement, likely due to less variation in tooth morphology along the row.

A single sub-adult individual, AK-PYC 18, shows an unusual cluster of three small, perfectly spherical teeth at the anterior most margin of the occlusal pavement (Fig. 4G). These teeth are distinct and do not show organised alignment with either the lateral tooth rows, inferring they are second generational teeth which have grown to replace those lost to damage or shedding (Longbottom, 1984; Sally Collins, pers. comm. 2020). A similar dental anomaly was recently reported for the vomer of Neoprosocinetes africus from the Moroccan Kem Kem Group at Tarda (Cooper and Martill, 2020). The presence of these teeth on a sub-mature specimen and their absence in the mature specimens, suggests that this phenomenon is not dictated by ontogeny as suggested by Longbottom (1984), but rather is a consequence of individual variation.

The coronoid process is well preserved in AK-PYC 23 and AK-PYC 24, and is remarkably similar to Anomoeodus sp. A, by possessing a short shaft, but with a large anteroposterior elongate condyle with is recurved posteriorly with an oval dorsal profile. The mandibular symphysis is flat and straight, originating laterally adjacent of the diastema separating the first and second medial tooth and extends longitudinally, anterior of the last medial tooth. The mandibular symphysis and the labial faces of the medial teeth are separated by a wide medioventral lamina which is edentulous, concave and constitutes roughly one third the total lateral width of the prearticular in occlusal view.

Remarks. Specimens AK-PYC 6, 8, 7, 9, 10, 11 and 12 are assigned to Anomoeodus for the same justification as specimens of Anomoeodus sp. A discussed above. Although not yet found associated, vomer and prearticular elements are tentatively matched on the basis of medial (main) tooth morphologies which are near identical across all specimens and sufficiently characteristic to differentiate them from Anomoeodus sp. A. The medial teeth in Type B are significantly less laterally elongate and relatively thicker anteroposteriorly than Anomoeodus sp. A. Pre-articular medial teeth of Anomoeodus sp. A are unornamented and sigmoidal, compared to sub-reniform with mild ornamentation in Anomoeodus sp. B. Both Anomoeodus sp. A and sp. B have near identical lateral tooth configurations on both the vomer and prearticulats (Fig. 5).

Both Asila Anomoeodus spp. vomer are longitudinally elongated and narrow. The medial teeth of Anomoeodus sp. A are laterally elongate, unornamented and thin, with lateral tooth faces subtly curved anteriorly on some teeth. These teeth in Anomoeodus sp. B are instead narrower and thicker with a weakly ornamented dental fossa (Fig. 5D). Nine medial teeth are present on the vomer of Anomoeodus sp. B, as opposed to at least sixteen in Anomoeodus sp. A. In cross-section, the vomer of Anomoeodus sp. A is flat with no dental elevation, whereas Type B is steeply convex with medial teeth elevated above the laterals.

The possibility of Anomoeodus types A and B being synonymous is rejected with good justification: juvenile and mature prearticular specimens of both Anomoeodus types are present in the assemblage, demonstrating that the unique dental morphologies which differentiate them remain constant throughout their ontogeny. This excludes the possibility of one type representing a junior synonym of the other. The vomer of Anomoeodus sp. A (AK-PYC 6) and a mature vomer of Anomoeodus sp. B (AK-PYC 13) represent similar sized individuals, but display distinct morphologies (listed above), confirming the presence of two distinct species of Anomoeodus in the assemblage.

Anomoeodus is also known from the coeval Turonian “Series of Azilé” of Gabon, which like the Moroccan Akrabou Formation, is composed of outer shelf limestones, marls and dolomites (Capasso, 2019). Similar to Asila, pycnodont remains are rare in the Turonian of Gabon according to Capasso (2019) who records a single form of Anomoeodus sp. based on a composite of isolated vomer, prearticular and prehensile remains. The Gabon Anomoeodus sp. appears to share strong affinities with Anomoeudos sp. B from Asila. Both posses sub-reniform medial teeth which lack diastemas on the prearticular but are prevalent on the vomer; the secondary lateral row on the prearticular both show anterior-labial curved lateral profiles. However, Asila Anomoeodus sp. B and the Gabon Anomoeodus sp. specimens cannot be confidently synonymised due to the following: vomer teeth in Gabon Anomoeodus sp. are strongly triangular, whereas in Anomoeodus B they are oval to sub-reniform. Furthermore, the secondary lateral teeth on the prearticular of the Gabon Anomoeodus sp. shows strong anterior curvature of both the lateral and labial tooth faces. By contrast, these teeth in the Asila Anomoeodus sp. B lack any anterior curvature. Therefore, it is concluded that the pycnodont material from Gabon represents a species distinct from Anomoeodus sp. A and sp. B from the Turonian of Asila.
Family PYCNODONTIDAE, Agassiz, 1833 (sensu Norsall, 1996b)
Subfamily NURSALLINAE, Poyato-Ariza and Wenz, 2002.

Genus Paranursallia, Taverne et al., 2015.
Type species: Paranursallia spinosa Taverne et al., 2015.

Paranursallia cavini sp. nov.

Holotype. AK-PYC 4, isolated left partial with complete dental pavement (Fig. 4J and K).

Referred specimen. AK-PYC 1, complete vomer with ascending process preserved (Fig. 3E).

Type locality. Asfla fossil mines, escarpment of Assemer N'Tadirhoust, 4 km south-east of the oasis village Asfla, Errachidia province, south-eastern Morocco. 31°52′01″N 4°52′30″W

Horizon. Mammites ammonite biozone, Asfla Member, Akrabou Formation. Upper Cretaceous (Turonian).

Etymology. Named in honour of Lionel Cavin for his pioneering work on the Goulmima ichthyological assemblage and who first recorded pycnodonts in the Akrabou Formation.

Diagnosis. Paranursallia cavini is distinguished from the type species P. spinosa Taverne et al., 2015 and P. gutturosa (Arambourg, 1954) by the following autapomorphies: A nuralline-like prearticular dental pavement composed of six distinctive tooth rows, as opposed to four in P. gutturosa and two in the closely related genus Nursallia Blot (1987).

Paranursallia cavini is further diagnosed on a unique combination of the following synapomorphies: Five vomerine tooth rows with the primary lateral teeth significantly smaller and intercalated between the medial and outer lateral rows; lateral teeth on the vomer are ‘D’ shaped with flattened lateral profiles forming an acute cutting edge on the occlusal surface; outer lateral teeth on the prearticular are monocuspid with cingulum due to presence of a modified central papilla forming a serrasalmid-like cutting edge; medial teeth on the prearticular lachrymiform with longitudinal orientation almost antero-posteriorly; mandibular symphysis short, anteriorly set and lacking labial elongation of a medoventral lamina (Figs. 3E, 4 and K, 6A and C).

Description. Paranursallia cavini sp. nov. is described from an isolated vomer and left prearticular. Although not yet found associated, we combine these elements in a single taxon due to close similarities with the dentition of an articulated individual of the closely related form Paranursallia gutturosa (Arambourg, 1954) figured by Amalitano et al. (2020) from the Cenomanian Bonarelli Level of north-eastern Italy. Furthermore, only a single morphotype of each element is known from extensive collecting, suggesting that only a single nuralline pycnodont species was present in the Akrabou Formation.

Vomer. AK-PYC 1 consists of a single vomer, measuring 35 mm long anteroposteriorly and 11 mm wide wide. The vomer is longitudinally elongate and narrow with curved lateral tooth faces creating an elliptical profile in occlusal view (Fig. 6A). Five tooth rows are present although teeth in the paired primary lateral rows are discontinuous, small and randomly intercalated between the medial and secondary lateral rows. The medial row is composed of six, sub-spherical to sub-rectangular molars that lack ornamentation or pitting. Posterior medial teeth are sub-rounded posteriorly but become more laterally compressed towards the anterior until becoming sub-triangular to elliptical when seen in occlusal view. Teeth in the paired primary lateral rows are small (2–3 mm), spherical or oviform and tightly intercalated between the medial and secondary lateral teeth.

Teeth on the secondary lateral rows are sub-rectangular to ‘D’ shaped with straight and flattened lateral tooth faces. Longitudinal alignment of the lateral tooth faces creates a pair of curved profiles on each side of the vomer when combined, appears strongly elliptical in occlusal view (Fig. 6C). Eight pairs of teeth were present on the secondary lateral rows of P. cavini, their morphology changing progressively along the row. The first five posterior teeth are almost identically sub-rectangular to ‘D’ shaped with the occlusal faces steeply inclined towards the labial margin. This morphology is reminiscent of that seen in the serrasalmid pycnodonts (see Vullo et al., 2017). The three anterior teeth of the secondary lateral row are slightly more sub-spherical with similar angles of inclination of the lateral and labial tooth faces creating a medially placed tooth ridge longitudinally in occlusal view. The ascending process is obtusely convex with a medially set apex and extends from the posterior-most to the anterior-most tooth margins of the pallet in lateral view. The process measures 36 mm, 24 mm and 0.4 mm in anteroposterior length, height and lateral width, respectively. The height of the process is approximately five times greater than the height of the secondary lateral teeth.

Prearticular. AK-PYC 4 (holotype) is a well-preserved left prearticular which is complete with some minor damage to the head of the coronoid process. It is 44 mm long anteroposteriorly and 20 mm wide. Six distinct tooth rows are present on the prearticular comprised of one medial row, two lateral rows and three labial rows. The medial row is positioned just lateral of the medial margin of the element when seen in occlusal view. Eight obtusely elliptical teeth are present on the medial row (6 mm × 4 mm av.), with lateral faces of each tooth longitudinally orientated almost fully anteroventrally. The primary lateral row consists of eleven spherical teeth which are less than half the diameter of the associated medial and secondary lateral teeth (3 mm × 2 mm av.). This condition is similar to that observed in the vomer (AK-PYC 1) where the primary lateral teeth are intercalated between the medial and secondary laterals. However, the primary lateral teeth on the prearticular form a regular, better defined tooth row compared to those on the vomer.

Ten teeth of approximately equal proportion to those on the medial row are present on the secondary lateral row (5 mm × 4 mm av.). Secondary lateral teeth are distinctively monocuspid with a shallow cingulum and longitudinal occlusal ridge forming a ‘cutting’ edge, vaguely comparable to the Serrasalmidae (see Vullo et al., 2017). The apparent ‘cutting edge’ is smooth and blunt, inferring a very different feeding strategy for P. cavini than the supposed “flesh eating” serrasalmid pycnodonts described by Vullo et al. (2017).

Three labial tooth rows are present between the medial row and the mandibular symphysis. Labial rows are set more anteriorly than the laterals, with the first tooth of the primary labial row positioned approximately halfway towards the anterior of the occlusal pavement, with the second and third labial rows beginning approximately two-thirds towards the anterior in occlusal view (Fig. 6C). Most prominent is the primary labial row situated just labially of the medial margin. Teeth here are sub-rounded posteriorly, becoming more oval anteriorly, and are only slightly smaller than the adjacent medial teeth (4 mm × 3 mm av.). Eight sub-spherical teeth are present on the secondary labial row and all of near equal size measuring 3 mm × 3 mm (av.). The third labial row is discontinuously situated tightly between the secondary labial teeth and the narrow articulatory surface of the mandibular symphysis. Teeth on this row are of equal size and proportionate to those in the primary lateral row, which both have average longitudinal and lateral tooth dimensions of 3 mm × 2 mm. The reduction of these tooth rows may be the result of dental overcrowding on the prearticular due to extrapolation of larger teeth in the medial and secondary lateral rows which likely played a more prominent role during occlusion.

All teeth on both the prearticular and vomer of P. cavini are smooth and lack any ornamentation on the occlusal faces. A few teeth on
the prearticular display a pitted surface on occlusal faces. However, examination of these surfaces under light microscopy reveals they are actually associated with dental wear and are absent on unworn surfaces.

The prearticular is laterally compressed and anteroventrally elongated in dorsal view (Figs. 3] and K. 6C). This morphology is likely associated with a specialised feeding strategy, as the secondary lateral ‘cutting’ teeth have become dorsally elevated, well above other rows on the occlusal surface. The mandibular symphysis is placed anteriorly, is broad and flat due to a reduction of the medioventral lamina. This is unlike other pycnodontiforms which have a thinner, longitudinally elongated symphysis supported by a wide, often tooth-bearing medioventral lamina (e.g. Anomoedodus [Forir, 1887; this paper], Macromesodon [Woodward, 1890; Blake, 1905] and Pycnodus [Longbottom, 1984; Poyato-Ariza, 2013]). A similar modification of the mandibular symphysis also occurs in the prearticular of Phacodus (Dixon, 1850; Arambourg, 1952) and other species of Paranursallia (Arambourg, 1954; Taverne et al., 2015).

Remarks. Paranursallia cavini sp. nov., is a new narsalline pycnodont recognised presently only from the Turonian Akrabou Formation at Asfla, SE Morocco. The holotype (AK-PYC 4) and referred specimen (AK-PYC 1), are confidently assigned to the subfamily Nusrallinae (Poyato-Ariza and Wenz, 2002) due to close dental affinities shared with both Nusrallia Blot, 1987 and Paranursallia Taverne et al., 2015, most notably: lateral-most teeth on the prearticular are specialised into a blunt cutting edge with a cingulum formed by a slightly convex central papilla; medial prearticular teeth elongated anteroventrally; medial teeth on the vomer convex while the lateral teeth are slightly concave with a single ‘cutting’ occlusal ridge. Nusrallia has a stratigraphic range of Upper Cretaceous (Cenomanian) to upper Eocene (Monte Bolca, Italy) and is diagnosed with only two tooth rows on the prearticular of N. tethysensis (Cenomanian, Capasso et al., 2009) and N. veronae (Eocene, Blot, 1987). The sister genus, Paranursallia is restricted to the Upper Cretaceous (Cenomanian–Turonian). Paranursallia gutturosa (formerly ‘Paleobalistum’ gutturosa, Arambourg, 1954) from the Cenomanian Jebel Tsfast of Morocco and the upper Cenomanian Bonarelli Level of Northeast Italy (Amalfitano et al., 2020) possesses three or four tooth rows on the prearticular (n.b. Amalfitano et al., 2020 describe only three tooth rows, however a fourth tooth row is clearly present in figs. 7–9). The prearticular of the type species P. spinosa Taverne et al., 2015 from the Cenomanian ‘Tunisian Trough’ in Tunisia, differs greatly from that of both P. gutturosa and P. cavini sp. nov. The prearticular of the type species is “triangular” and “as deep as it is long” (Taverne et al., 2015), with only five teeth of unequal size along the outer lateral row, compared to P. gutturosa and P. cavini sp. nov. which both have ten teeth on the lateral-most row and a prearticular which is almost twice as long as it is deep. The exact number of tooth rows is unknown in P. spinosa because the specimens consist of articulated individuals with the majority of the dental surfaces of the oral cavity obscured by the lateral profile of the prearticular.

The vomer of Paranursallia spinosa is poorly preserved, consisting of “three teeth” from “the lateral row” (Taverne et al., 2015), and thus is regarded here as taxonomically undiagnostic. However, the vomer of P. gutturosa from Morocco and north-eastern Italy is known from several well-preserved individuals, often partially disarticulated with the vomer visible in occlusal view (Amalfitano et al., 2020, figs. 7 and 8). The vomerine and prearticular dental pavements of P. gutturosa and the Asfla narsalline are remarkably similar and therefore we assign the new form, with confidence, to the genus Paranursallia. Paranursallia cavini sp. nov. represents the third recorded species of Paranursallia and extends the genera’s stratigraphic range from the Cenomanian into the Turonian (P. spinosa = Cenomanian; P. gutturosa = Cenomanian; P. cavini sp. nov. = middle Turonian).

Both P. cavini sp. nov. and the closest comparable species, P. gutturosa share the following characters: circular to subcircular medial teeth that decrease in size anteriorly on the vomer; Prearticular has a “high and straight dorsal boarder” and is longer than it is deep; Prearticular medial teeth show an “oval contour” and are “weakly ornamented” with nine teeth present on the medial row of both species; lateral-most teeth on the vomer and prearticulars are slightly concave due to the presence of a specialised cingulum forming a weak ‘cutting edge’–like occlusal ridge. However, the new form is distinguished from P. gutturosa due to the following: three to four prearticular tooth rows in P. gutturosa as opposed to six in P. cavini; the vomer of P. cavini is elliptical in occlusal view, as opposed to triangular in P. gutturosa. Both Arambourg (1954) and Amalfitano et al. (2020) record “coarsely serrated cutting edges” on both the prearticular and vomerine lateral teeth of P. gutturosa. These teeth in P. cavini are blunt and lack serrations, even along the so called ‘cutting edges’. Furthermore, Amalfitano et al. (2020) note that vomerine teeth possess “coarse granulations on the occlusal ridge” which are not present in the new species. A similar vomerine configuration of three tooth rows is also present in Phacodus Dixon, 1850, Cocodus Pictet, 1850 and Neoprosocinutes Silva Santos, 1970. Phacodus has similar unornamented teeth to those of Paranursallia, with the inclusion of numerous fine punctations which cover the occlusal tooth surfaces. These punctations are autapomorphic for Phacodus and thus it is easily distinguished from Paranursallia. The three dental rows of Cocodus are often well ornamented with triangular medial teeth; both characters are absent in the new form. Neoprosocinutes possess three vomerine tooth rows, however the morphology varies considerably from Paranursallia, most notably by a reoccurring series of “one large tooth followed by two smaller paired teeth” along the medial row (Figureiredo and Silva Santos, 1987; Wenz, 1991; Cooper and Martill, 2020). Furthermore, the presence of small additional teeth intercalated between the medial and lateral rows of P. cavini is unseen in these other genera.

The small pycnodont vomer tentatively reported as ‘cf. Palaeobalistum sp.’ by Cavin (1996) from “Goulmima”, shows greater affinity to Paranursallia cavini. Both specimen AK-PY 1 and Cavin’s specimen comprise three tooth rows, longitudinally elongated anterior medial teeth, and slightly concave lateral teeth which possess a cutting edge and cingulum. Due to the fragmentary nature of Cavin’s specimen, it is unclear whether it belongs in Nusrallia or Paranursallia, as both have the same number of tooth rows. The Goulmima specimen does differ from P. cavini by the presence of bicuspoid occlusal surfaces on lateral teeth. Lateral teeth of P. cavini are monocuspid with a single occlusal ridge and therefore the Goulmima specimen cannot be synonymised with the new species. The distinctive morphology of the lateral teeth in the Goulmima specimen is absent in Palaeobalistum and is reassigned as ‘cf. Paranursallia sp.’ It is possible that the Goulmima pycnodont may represent a different species of Paranursallia or even a junior synonym of P. cavini; but more material is needed to investigate this.

Family ?PYCNODEONTIDAE, Agassiz, 1833 (sensu Nursall, 1996b) Subfamily ?NUSRALLINAE, Poyato-Ariza and Wenz, 2002.

Neomesturus gen. nov.

Etymology. Named for the apparent convergent dental configuration with the Late Jurassic pycnodont Mesturus (Wagner, 1862), with Neo (G) for new.

Diagnosis. As for the type and only species. See below.

Neomesturus aslaensis gen. et sp. nov.
Diagnosis. Neomesturus is diagnosed on a single dental autopod-
somey: paired primary lateral rows composed of small, rounded
and ascending process. Referred specimen AK-PYC 2 represents a
slightly larger individual but shows damage to the posterior end of
the right secondary lateral tooth row. Comparable to the Late
Jurassic form Mesturus, the dental pavement of Neomesturus con-
sists of approximately three regular rows and two discontinuous
rows (Poyato-Ariza and Wenz, 2002).

The vomer is triangular in occlusal view and is relatively thin (3.8
mm maximum) in cross section and lacks any convex elevation of
the medial teeth above those on the adjacent lateral rows.

The medial teeth are convex, unornamented and slightly wider
than they are long. Eight to nine teeth are present on the medial
row, collectively showing a slight decrease in tooth size anteriorly
(0.3 mm × 0.4 mm posterior; 1.0 mm × 1.5 mm anterior). These
teeth are oval posteriorly to pisiform anteriorly and all possess
well-rounded lateral and occlusal faces. Teeth are tightly inter-
spaced longitudinally due to lack of diastemas between success-
se teeth on the row.

Teeth on the paired, primary lateral row are significantly smaller
and poorly organised compared to teeth on the medial and sec-
ondary lateral rows. Teeth along this row show wide variation of
size, dental shape and occlusal morphology. On the holotype
(AK-PYC 3), primary lateral tooth diameter ranges from 0.3 mm to
2 mm apparently randomly. Both specimens show a random tooth
size distribution along the rows, with larger teeth apparently interca-
lated between smaller ones, and vice versa (Fig. 7). Teeth are all
convex, but their morphology varies between circular and oval to
almost sub-elliptical at random intervals longitudinally. Dental
topography also varies with smooth, unornamented domes on
larger teeth, whilst some smaller teeth possess a small, nipple-like

Holotype. AK-PYC 3 (Fig. 3H), isolated vomer with complete dental
series and ascending process.

Referred specimen, AK-PYC 2, isolated vomer with an incomplete
dental series (Fig. 3G).

Type locality. Asflia fossil mines, Asseme N’Tadirhout, 4 km southeast
of Asflia, Errachidia province, south-east Morocco. 31°52’01”N 4°52’30”W.

Horizon. (?) Mammites ammonite biozone, Chalky-Marl facies, Asflia
Member, Akrabou Formation. Upper Cretaceous (Turonian).

Etymology. Named after the small oasis village of Asflia (Errachidia
Province) where the holotype was obtained.

Fig. 6. Comparative line drawings of Paranursallia cavini sp. nov. and other closely related taxa. (A), AK-PYC 1, Paranursallia cavini vomer in occlusal view. Notice the strongly elliptical shape of dental pallet, presence of small intercalated teeth and longitudinal ‘cutting’ ridges on the lateral teeth. (B) Paranursallia gutturosa (Arambourg, 1954) vomer from the Cenomanian of Italy (Amalfitano et al., 2020, figs. 7 and 8). By contrast to P. cavini, the dental pavement of P. gutturosa is triangular and lateral teeth lack longitudinal cutting ridges. (C), AK-PYC 4 Holotype of P. cavini sp. nov., left prearticular showing six clearly defined tooth rows with the medial row (see key) positioned on the lateral side of the dental pavement. (D), prearticular of P. gutturosa figured in Amalfitano et al., (2020; fig. 9), showing four tooth rows with the medial row positioned medially on the dental pavement. (E), left prearticular of Nursallia tethysensis Capasso et al., 2009 from the Cenomanian of Italy (Amalfitano et al., 2020, fig. 12D). Although closely allied with Paranursallia, N. tethysensis possesses only two tooth rows composed of laterally concave teeth with serrated cutting margins. All scale bars are equal to 10 mm.
Another tooth row on adjacent teeth - e.g. Paranursallia cavini, see above). Unlike Neomesturus, the vomerine and prearticular teeth of Mesturus are strongly ornamented (Martill and Hudson, 1991). By contrast the vomerine teeth of Neomesturus asaensis are completely devoid of crown ornamentation and therefore differs from Mesturus. According to Nursall (1996b), Mesturus belongs to the family Mesturidae based on the following synapomorphies: a well ossified, partially ankylosed endocranium (possibly cartilaginous in other pycnodont families); an elongate maxilla; dermal patterns distinct from other pycnodonts; and low, well rounded dorsal and anal fins which are highest at their midpoint. These skeletal elements are unknown for Neomesturus. Therefore, presently it is unjustifiable to assign Neomesturus to Mesturidae. Furthermore, Mesturus is restricted to the Middle and Upper Jurassic (Callovian – Tithonian) with the type species: M. verrucosus Wagner, 1862, restricted to the Tithonian Solnhofen-Archipelago (Solnhofen Limestone) of southern Germany (Poyato-Ariza and Wenz, 2002) and the only other species, M. leedsi Woodward (1895) from the Callovian Peterborough Member of the Oxford Clay Formation in eastern England (Martill and Hudson, 1991). Neomesturus gen. nov. is presently known only from the Turonian Akrabou Formation – the age of which postdates the stratigraphic range of Mesturus by at least 51 million years. It is concluded on stratigraphic considerations that Neomesturus is likely not a mesturid, rather a member of distinct pycnodont lineage (Pycnodontidae?) which has convergently evolved a dental configuration similar to that of Mesturus. The dental pavement of Neomesturus asaensis shares some similarities with Paranursallia cavini sp. nov. (see above). Notably the shared trait of ‘D-shaped’ outer lateral teeth with a shallow cingulum and longitudinal ridge (cutting edge) on the dorso-lateral margin of dental crowns (Fig. 7A–B). This character appears to be restricted to the Nursallinae, notably in the genera Paranursallia and Nursallia. Both Paranursallia cavini and Neomesturus asaensis lack serrated carinae on these so-called ‘cutting edges’ distinguishing them from both Nursallia and the two other species of
Paranursallia (see above). *Neomesturus* is easily distinguished from *Paranursallia* due to the presence of five true vomerine tooth rows as opposed to only three in the latter. Furthermore, the vomer of *P. cavini* is elliptical, whilst in *Neomesturus* it is strongly triangular with straight lateral margins. *Neomesturus* is tentatively interpreted as a possible nursalline (7*Nursallinae*) which has evolved from a vomerine dental apparatus convergent on *Mesturus* and is unique from all other pycnodontiforms. The lower Alban pycnodont *Paranursallia stuehmeri* Taverne, 1981 from Helgoland, Germany, possesses complex skull ornamentation also convergent on *Mesturus* but the dentition is unlike that of *Neomesturus*.

Family Pycnodontidiae, Agassiz, 1835 (sensu Nürsall, 1996a). ?Subfamily Pycnodontinae, Poyato-Ariza and Wenz, 2002.

Genus *Polazzodus* Poyato-Ariza, 2010.

Type species: *Polazzodus coronatus* Poyato-Ariza, 2010.

**Polazzodus** sp.

**Material.** AK-PYC 5 (Fig. 3D), complete vomer in occlusal view. **Locality.** Asfla fossil mines, escarpment of Asser N’Tadirhoust, 4 km south-east of Asfla, Errachidia province, south-eastern Morocco. 31°52’01” N 4°52’30” W. **Horizon.** (7)Mammelites ammonite biozone, Chalky-Marl facies, Asfla Member, Akrabou Formation, Upper Cretaceous (*Turonian*).

**Description.** *Polazzodus* sp. is identified in the Akrabou Formation from a single, isolated vomer measuring 21 mm by 11 mm (max.) in anteroposterior length and maximum width posteriorly. The vomer is strongly triangular in occlusal view, with perfectly straight lateral profiles of the outermost teeth (Figs. 3D and 8A). Teeth on the vomer are organised into five distinct tooth rows. The element is relatively thin (4 mm), with minor elevation of the medial and primary lateral rows slightly above the secondary lateral rows in cross section.

The medial teeth are strongly triangular with rounded corners - similar to *Coccodus* Pictet, 1850 and *Icthyoceros* Gayet, 1984. Seven medial teeth are present in AK-PYC 5, although slight damage to the anterior margin suggest possibly eight or more teeth were originally present. The occlusal surface of each tooth in the row is moderately ornamented with numerous fine crenulations radiating outwards from a shallow central fossa. Medial teeth decrease in size anteriorly, ranging from 3 mm × 3.5 mm posteriorly to 2 mm × 2.3 mm anteriorly. Each medial tooth is separated longitudinally by a narrow diastema measuring on average half the length of the associated tooth.

The primary lateral and secondary lateral teeth are of near equal size relative to their position along the element. Seven lachrymiform to sub-pisiform teeth are present on the primary lateral rows. A short longitudinal ridge is present medially on each dental crown. These ridges are poorly developed and unornamented with occlusal wear facets only situated on the lateral slope of each ridge. Teeth on this row measure 4 mm × 3 mm posteriorly and 2 mm × 1 mm anteriorly in length and width respectively. Seven teeth are also present on the secondary lateral row, measuring between 4 mm × 3 mm posteriorly and 2 mm × 1 mm anteriorly in length and width respectively. Secondary lateral teeth are longitudinally elongate and reniform to sub-lachrymiform. The lateral faces of these teeth are flat, forming a perfectly straight lateral topography of the vomer (Fig. 8A). Due to the specimen being prepared in occlusal view, the ascending process of the vomer (if present) is concealed by matrix.

**Remarks.** Specimen AK-PYC 5 is assigned to the genus *Polazzodus* due to the dentition being near identical to vomer specimens of the type (and only) species, *P. coronatus* figured by Poyato-Ariza (2010, fig. 5D) from the type locality. Both *P. coronatus* from the Upper Cretaceous of Polazza (northeastern Italy) and the new Asfla specimen share a very similar dental pavement in regards to tooth shape, tooth count and number of tooth rows: both possess five tooth rows with no more than seven teeth on the medial row; medial teeth are strongly triangular with curved faces; lateral teeth are sub-triangular to lachrymiform; secondary lateral teeth are oval to reniform; all lateral teeth are elongated longitudinally. However, the triangular medial teeth of AK-PYC 5 are more equilateral than in the Italian specimens. Furthermore, Poyato-Ariza (2010) diagnoses *Polazzodus coronatus* with “eight to nine teeth on the lateral rows”, whereas the Asfla specimen show no more than seven on the lateral rows (Fig. 8). Despite the minute variations observed between *P. coronatus* and AK-PYC 5, we do not deem it appropriate to erect a new species of *Polazzodus* for the Asfla specimen at this time. The slight variation in medial tooth shape and number of teeth on the lateral row may be a consequence of interspecies variation or ontogeny. More Asfla specimens are needed to investigate how these variations change with ontogeny, in order to determine if AK-PYC 5 is a distinct species of *Polazzodus* or a synonym of *P. coronatus*.

Regardless of species level assignment, AK-PYC 5 represents the first occurrence of *Polazzodus* outside of Italy, suggesting a wider geographic distribution than previously considered. The vicarious distribution of *Polazzodus* between northeast Italy and south-eastern Morocco is direct evidence of faunal dispersal within the western Neotethys. The type species *Polazzodus coronatus* is known from complete articulated specimens from the Upper Cretaceous (lower Santonian) of Polazza (Italy) and therefore assignment to Pycnodontidiae is justified and agreed upon here. The presence of *Polazzodus* in the Akrabou Formation represents the oldest occurrence of the genus and extends its stratigraphic range from the middle Turonian to lower Santonian. *Polazzodus* is a small (97 mm maximum standard length [Poyato-Ariza, 2010,]), low-bodied pycnodont, rather than round-bodied like the closely related *Oropycnodus* Poyato-Ariza and Wenz, 2002. The snout is elongate and gently downturned with a shallow caudal region creating an overall truncated lateral topography (Fig. 8C). A similar bauplan is seen in some extant coral reef fishes (e.g. Butterflyfishes and Leaffishes) which use their elongated rostrum to aid extraction of small prey items from narrow crevasses and burrows in hard ground substrates. It is likely that *Polazzodus* occupied a similar niche within the Goulmima assemblage (see discussion), feeding on smaller, perhaps more difficult to access prey items than the larger pycnodonts present in the assemblage.

**5. Discussion**

**5.1. Diversity of pycnodonts in the Akrabou Formation**

Pycnodonts were initially considered rare and “indeterminate” in the Akrabou Formation (Cavin, 1997, 1999; Cavin et al., 2010) with only a single, poorly preserved vomer of “cf. *Palaeobalistum* sp.” figured (Cavin, 1997; reassigned here to *Paranursallia* sp., see systematic palaeontology). However, from new data presented here, pycnodonts in the Akrabou Formation are proven to be both diverse and well preserved in the Asfla area, with five nominal species now recorded and formally described: *Anomoedus* sp. A. *Anomoedus* sp. B. *Paramursallia cavini* sp. nov., *Neomesturus asflaeensis* gen. et sp. nov. and *Polazzodus* sp. The apparent discrepancy for the lack of pycnodont material described before this study is unknown, although it is likely the result of a research bias due to their material being rather abundant and well preserved in the formation. This high diversity of pycnodont fishes is typically seen in many other Mesozoic marine (reef) assemblages (e.g. Nürsall, 1996a; Kriwet, 2001; Poyato-Ariza, 2013), but we note that the
Akrabou Formation generally lacks reef facies (Ettachfini and Andreau, 2004).

Two vomer and two prearticular morphotypes of *Anomoedus* are identified, and are tentatively grouped under two preliminary taxa: *Anomoedus* sp. A and *Anomoedus* sp. B (see above). Despite both *Anomoedus* species in the Akrabou possessing autapomorphic characters, they have not been erected as new species at this time. As previously discussed, *Anomoedus* in its current state is a ‘taxonomic waste bin’ (Cooper and Martill, 2020) and adding further taxa to this genus would be inappropriate as the genus requires a thorough review. Collectively, *Anomoedus* sp. A and *Anomoedus* sp. B. comprise approximately 79% of the pycnodont assemblage at Asfla (*Anomoedus* sp. A = 29%, *Anomoedus* sp. B = 50%. See Fig. 9). The reason for this high abundance is unknown. However, one plausible explanation could be interpreted from specimen size. Most vomer and prearticular specimens of *Anomoedus* are much larger than those of other taxa in the assemblage, and likely represent large individuals (>1 m). The larger size of these elements in contrast to those of smaller pycnodont taxa (e.g. *Pollazodus* sp., this paper) better-favoured preservation due to their more robust nature and advanced ossification. It is also plausible that (post-decay) these elements were heavier and more easily sank into soupy substrates than the smaller examples. Juvenile *Anomoedus* specimens are rare in the assemblage, only comprising 20% of the *Anomoedus* sample. Juveniles experience high mortality rates from predation by larger piscivorous fishes and reptiles (e.g. selachians, ichthyodectids, tethysaurus) while adults experience reduced predation rates (Stewart and Jones, 2001) which would
infer juvenile pycnodonts had a much lower preservation potential than adult forms. Small fishes in general are scarce in the Asfla Member Lagerstätte, except within the stomach contents of larger individuals (Cavin, 1997, 1999; Cavin et al., 2010).

5.2. Ecology of the Akrabou pycnodonts

The Asfla pycnodonts show robust durophagous dental pallets with blunt teeth arranged into sophisticated rows as per the typical pycnodontiform condition (e.g. Poyato-Ariza and Wenz, 2002; Kriwet, 2005). This specialised dental apparatus strongly suggests a bottom feeding ecology (benthic) as their jaws are well equipped to predate on sessile and recumbent benthos. The precise diet of the Asfla pycnodonts is unknown due to a current lack of articulated material with in-situ stomach contents. However, a rich diversity of benthos including bivalves (Astarte and Rynchostreon, Lebedel et al., 2015), foraminifera, indeterminate gastropods, scleractinian corals, irregular echinoids (Etachiffini and Andreau, 2004) and possible crustaceans (indicated by Thalassinoides burrows) may hint at the varied diet of the Asfla pycnodonts. This variety of potential prey resources may explain the high diversity of pycnodonts at Asfla and the sustainability of an apparently over-crowded benthic durophagous niche in the assemblage (Fig. 10). Firstly, examination of rare pycnodont stomach contents from other Konservat Lagerstätten by Kriwet (2001; 2005) and Capasso (2019) demonstrate them to be monospecific feeders, with each pycnodont species typically feeding exclusively on one prey item, sometimes specific to genus level (e.g. echinoderms, bivalves, crustaceans). This niche partitioning would have allowed for pycnodontiforms to diversify and reduce intraspecies competition within a single assemblage as each pycnodont species was adapted to feed on a unique prey resource. The considerable variation in dental size and morphology between pycnodonts described here strongly suggest a similar niche partitioning was present in the Asfla pycnodont assemblage. Theorising which prey resource specific pycnodonts preyed on would be completely speculative without associated stomach contents, however it is likely that larger forms like Anomoeodus spp. fed on larger invertebrates with tougher shells like oysters (Rynchostreon sp.) and echinoderms. Smaller forms on the other hand with smaller teeth (Polazzodus sp. and Neomesturus asflaensis gen et sp. nov.) were better suited to feed on smaller and softer shelled prey like small crustaceans and benthic foraminifera.

Paranursallia outside of the Akrabou Formation is known from complete individuals from the Jebel Tsafate (Morocco, Arambourg, 1954) the Agua Nueva Formation of Mexico (e.g. Stinnesbeck et al., 2019) and the Cenomanian of Italy (Amalitano et al., 2020) although no stomach contents have been recorded for this genus. The apparent ‘cutting edges’ present on the lateral tooth rows of both Paranursallia cavini sp. nov. and Neomesturus asflaensis gen. et sp. nov. are rarely observed in Pycnodontiformes and hint at a
specialised feeding niche perhaps unrelated to durophagy. The presence of a cingulum with longitudinal occlusal ridges on these teeth is comparable to that of the so-called ‘Piranha jawed’ Serrasalmimidae pycnodonts of the Upper Cretaceous to Eocene (Vullo et al., 2017) which possess a cingulum and modified papilla forming incisor-like teeth with prominent cutting edges. These ‘cutting teeth’ in the Asfla Member forms are smoother, less concave and lack a modified papilla. Despite the apparent convergency, the cutting edges in the new forms are less developed and somewhat blunt, suggesting a different feeding strategy to Serrasalmimidae.

Polazzodus sp. is only known in Morocco from a single isolated vomer, but the type species P. coronatus Poyato-Ariza (2010), from the Upper Cretaceous of Polazzo (northeastern Italy) is known from complete articulated specimens. Unfortunately, stomach contents have not yet been recorded in these specimens. The bauplan of Polazzodus is strongly convergent on extant butterflyfishes (Chaetodontidae) that possess slightly elongate rostrums used to forage on small invertebrates (e.g. polyps and small crustaceans); hidden within high ground crevasses of coral reefs (Hastings et al., 2014). Hard grounds are mostly absent in the Akrubou Formation, however rare scleractinian coral fragments present in the fossiliferous packstone beds near Asfla (pers. obs. SC) hints at isolated patches of hard ground suitable to this proposed ecological niche.

5.3. Pycnodont diversity in the cretaceous of Morocco

Pycnodont fishes are surprisingly diverse across the Cretaceous of Morocco (see Table 1). The oldest confirmed occurrence of pycnodonts in Morocco are from the ?Albian–Cenomanian Kem Kem Group in the Tafiltalt area (South-East Morocco). Cooper and Martill (2020) identified four distinct genera in the Kem Kem Group, consisting of: Neoprosocinetes africanaus, Agassizella erfoadina, cf. Coelodus sp. and cf. Macromesodon sp.. The Kem Kem Group pycnodont assemblage shows strong taxonomic affinities with both central Tethys and South American faunas, suggesting an interchange of these two faunas occurred in the vast Kem Kem river systems.

Sigogneau-Russel et al. (1998) record possibly older occurrence of pycnodonts remains from the “Lower Cretaceous” Anoual Basin of Morocco. The vertebrate-bearing-horizon in the Anoual Basin has recently been reappraised to Middle Jurassic (Bathonian) (Haddoumi et al., 2016). The pycnodonts from this locality were not described or figured and consequently are disregarded here.

Rare, complete pycnodont specimens attributed to Paramurusallia gutturosa (syn. Palaebalistum gutturosa, Arambourg, 1954) are recorded from the Cenomanian Jebel Tselfat (Arambourg, 1954; Taverne et al., 2015; Amalfitano et al., 2020). This taxon is also recorded from the upper Cenomanian of Italy (Amalfitano et al., 2020) as well as the new species, P. cavini (this paper) from the lower Turonian of Asfla. The vicarious distribution of Paramurusallia between southern Europe and Northern Africa suggest the pycnodont was well distributed across the western Tethys during the late Cenomanian and early Turonian.

At least two different pycnodont taxa are present in the upper Cenomanian so-called ‘Agoult assemblage’ (Cavin, 1997, 1999) of the Gara Sbaa Plattenkalk Konservat Lagerstätte (Gara Sbaa Member). Martill et al. (2011) figured a complete individual of cf. Pycnodus sp. from this horizon but did not formally describe it. The specimen shows closer affinities with that of Sylvienodus (Poyato-Ariza, 2013) from the Cenomanian of Portugal than it does to Pycnodus which is now considered restricted to the Eocene. Therefore, it is justified to reassign the specimen here as cf. Sylvienodus sp. A second pycnodont specimen, distinctive from that of cf. Sylvienodus sp. was figured by Murray et al., (2013; fig. 4), but again, no systematic description was provided. Determining a possible taxonomic assignment of the Murray et al. specimen is problematic based on the scarce data available. Therefore, the specimen is referred here as ‘Gara Sbaa pycnodont A’ (Table 1).

Pycnodont remains from the successive Upper Cretaceous (Maastrichtian) Ouled Abdoun phosphatic basin of Oued Zem (north central Morocco) are relatively abundant but demonstrate a low diversity. Most abundant of these remains are the vomer and prearticular elements of Phacodus punctatus Dixon, 1850 as first reported by Arambourg (1952). Arambourg (1964) also records the occurrence of Stephanodus and Hadrodus from the formation, however the taxonomic validity of the latter as a pycnodont is disputed (Poyato-Ariza and Wenz, 2002) and is therefore disregarded here in the context of pycnodont diversity. Vullo et al. (2017) erected a new pycnodont family, the Serrasalmimidae based on type material from the Moroccan phosphates.

Table 1

| Pycnodont taxa | Jurassic | Cretaceous | Paleoz. |
|----------------|----------|------------|---------|
|                | Anoual Basin (?Bathonian) | Kem Kem Group (?Albian–Cen.) | Gara Sbaa (upper Cen.) | Jebel Tselfat (upper Cen.) | Asfla (Turonian) | Oued Zem Phos. (Maastrichtian) | Oued Zem phos. (Paleogene) |
| Agassizia erfoadina | X | X | X | | | |
| Anomoeodus sp. A | | | | | | |
| Anomoeodus sp. B | | | | | | |
| cf. Coelodus sp. | | | | | | |
| Eoserrasalmimus cattoi | | | | | | |
| Gara Sbaa type A | | | | | | |
| cf. Macromesodon sp. | | | | | | |
| Neomesturus aslaoensis | | | | | | |
| Neoprosocinetes africanaus | | | | | | |
| Paramurusallia cavini | | | | | | |
| Paramurusallia gutturosa | | | | | | |
| Phacodus punctatus | | | | | | |
| Polazzodus sp. | | | | | | |
| Pycnodus peitei | | | | | | |
| Pycnodus multicuspidatus | | | | | | |
| Serrasalmimus secans | | | | | | |
| Stephanodus sp. | | | | | | |
| cf. Sylvienodus sp. | | | | | | |
| pycnodontiform indet. | X | X | X | X | X | X | |
Serrasalmimid pycnodonts are recorded across the Cretaceous-Palaeogene (K-Pg) boundary with a single representative, *Eoserrasalmimus cattoi* Vullo et al. (2017) present in the Upper Cretaceous of Morocco. Pycnodonts are also present in the Palaeogene horizons of the Moroccan phosphates (e.g. Vullo et al., 2019) but we recognised only three distinctive forms from the Cretaceous layer; *Phaco- codus punctatus*, *Stephanodus* sp. and *Eoserrasalmimus cattoi* (see Table 1).

5.4. Reappraisal of the ‘Goulmima assemblage’

Prior to this study, the trophic structure of the Goulmima assemblage was considered to have been dominated by pelagic piscivores (Cavin, 1997; Cavin et al., 2010); with a few benthic forms consisting of rare batoids and saw fish (Claeson, Underwood and Ward, 2013; Villalobos-Segura et al., 2019). A revised trophic model is proposed here to include the new Asfla pycnodontiforms and other recently discovered fishes (Asflapristis, Villalobos-Segura et al., 2019; *kradimus*, Veysey et al., 2020; Lepisosteiformes indet., pers. obs. SC, DM). Our revised trophic model for the fish assemblage at Asfla (Fig. 16) shows a dynamic increase in durophagous forms with the addition of the five newly recognised pycnodontiforms, which are now the most diverse fish group in the Akrabou Formation.

The Goulmima ichthyological assemblage shows biogeographical affinities with the northern South Atlantic and the western Tethys (Cavin et al., 2010; Veysey et al., 2020). Despite amonites which are ubiquitous, there is no evidence for North Atlantic influence in the Akrabou Formation according to Cavin et al. (2010). Close faunal affinities can be drawn between the Goulmima assemblage and the Aptian–Albian Santana Formation of Brazil (northern South Atlantic). Both formations record representatives of similar fish groups, notably batoids, pycnodonts, lepisosteiforms, pachyrhizodonts, Ichthyodectids and arapichthids. *Arapichthys* for example was originally regarded endemic to Brazil (Silva Santos, 1985), but extends from the Aptian–Albian (Brazil, Mexico and Venezuela, Maisey and Moody, 2001; Alvarado-Ortega and Brito, 2011) to the Turonian of Morocco (Cavin et al., 2010) and Mexico (Blanco and Cavin, 2003). The pycnodont fishes in the Santana Formation however share no resemblance to those in the Akrabou Formation. The Santana pycnodonts show closest affinities with those in the Aptian–Cenomanian Kem Kem Group, with *Neo- proscinotes* shown to have a vicaric distribution between the two locations (Cooper and Martill, 2020).

Closer South Atlantic faunal affinities are present with the upper Cenomanian–middle Turonian Agua Nueva Formation of Mexico. The teleost assemblage is strikingly similar to the Akrabou Formation with the shared occurrence of Goulmimichthys and Aripichthys in both formations. A single pycnodont, “Nursallia gutturosus” (now reclassified as *Paranursallia gutturosus*, see above) is present in the Vallecillo platy member of the Agua Nueva Formation (Blanco-Piñón et al., 2005; Stinesbeek et al., 2019). *Paranursallia gutturosus* is also recorded in the Cenomanian Jebel Tselfat of Morocco, with the new species, *P. cavini* (this paper) restricted to the Turonian of Asfla. A second nursalline pycnodont *Nursallia tethysensis* Capasso et al. (2009) is also present in the Cenomanian of Italy (Amalfitano et al., 2020) but has not yet been confirmed in the Moroccan Akrabou Formation.

The Cenomanian Plattenkalk konservat Lagerstatte of Mount Lebanon is famous for a variety of exceptionally preserved fishes including a diverse assemblage of pycnodonts (*Pictet*, 1850; Marama et al., 2016; Cawley and Kriwet, 2019). However, there are no generic pycnodont faunal affinities with this horizon, suggesting that there was no faunal influence in the Akrabou Formation from the north-eastern Tethys.

Overall, the greater ‘Goulmima ichthyological assemblage’ shares similarities with both South Atlantic and Tethyan faunas, whereas the pycnodont assemblage at Asfla has stronger affinities with western Tethys faunas than South American assemblages and no faunal influence from the eastern Tethys.

6. Conclusions

New material described here demonstrates pycnodonts to be significantly more diverse than previously considered in the Upper Akrabou Formation at Asfla. Five nominal species are described, each showing disparity in jaw and tooth morphology emphasising that each was specialised to predate of unique prey resources, theoretically allowing for high speciation whilst reducing intraspecies competition in the assemblage. A new
genus Neomesturus possesses a venerable dental pavement convergent on the European Jurassic form Mesturus. The stratigraphic range of Paranurshlia is extended into the middle Turonian by the presence of the new species P. cavini. The Italian form Polazodus is recorded for the first time outside of the type locality (Polazzo, northeastern Italy) demonstrating a vicariant distribution and extending its stratigraphic range from the Santonian (Italy) back to the middle Turonian. The revised ‘Goulimima ichthyological assemblage’ shows a larger durophagous eco-space occupation due to the addition of the new pycnodont genera and benthic chondrichthyanas. Comparisons between other pycnodont-bearing horizons of similar age to the Akarabou Formation suggest a strong eastern Tethys faunal influence, notably from north-eastern Italy.

CRediT authorship contribution statement

**Samuel L.A. Cooper:** data acquisition, interpretation, formal analysis, fieldwork, Writing - original draft. **David M. Martill:** data acquisition, interpretation, formal analysis, fieldwork, Writing - original draft.

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