

**A NEW SPECIES OF *CLADOCYCLUS*
(TELEOSTEI: ICHTHYODECTIFORMES)
FROM THE CENOMANIAN OF MOROCCO**

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ABSTRACT

A species of ichthyodectiform fish, *Cladocyclus pankowskii* sp.nov. is described based on a single well-preserved braincase specimen from the Cenomanian Kem Kem beds of southern Morocco. It differs from the type species, *C. gardneri*, in the proportions of the skull roof. The presence of a species of *Cladocyclus* in Morocco adds yet another vicariant taxon shared between Brazil and Africa in the mid-Cretaceous, when Africa was separating from South America during the formation of the South Atlantic.

Key Words: new species; anatomy; actinopterygian; palaeobiogeography

INTRODUCTION

The braincase described here belongs to an ichthyodectiform teleost. It shows a well-developed ethmopalatine (a synapomorphy of all but the most primitive of ichthyodectiforms), as well as the following combination of features: median parietals meeting in front of a large supraoccipital, large intercalar that forms a significant part of the hyomandibular facet as well as the skull roof, a jugular canal opening into the floor of a deep subtemporal fossa and continuing to run posteriorly beneath the intercalar. Some of these features are only found in

more derived ichthyodectiforms (see below). Ichthyodectiforms are an extinct group of about 30 species of primitive teleosts ranging in time from the Bathonian to Maastrichtian. Most were marine fishes and many had structural adaptations suggesting they were fast open water swimmers. Some must have been the top predators of their day. The phylogeny of ichthyodectiforms has been addressed on several occasions (Bardack 1965; Patterson and Rosen 1977; Maisey 1991; Stewart 1999; Taverne and Chanet 2000). There is broad agreement among these authors; at least for the better known taxa. The phylogeny and derivative

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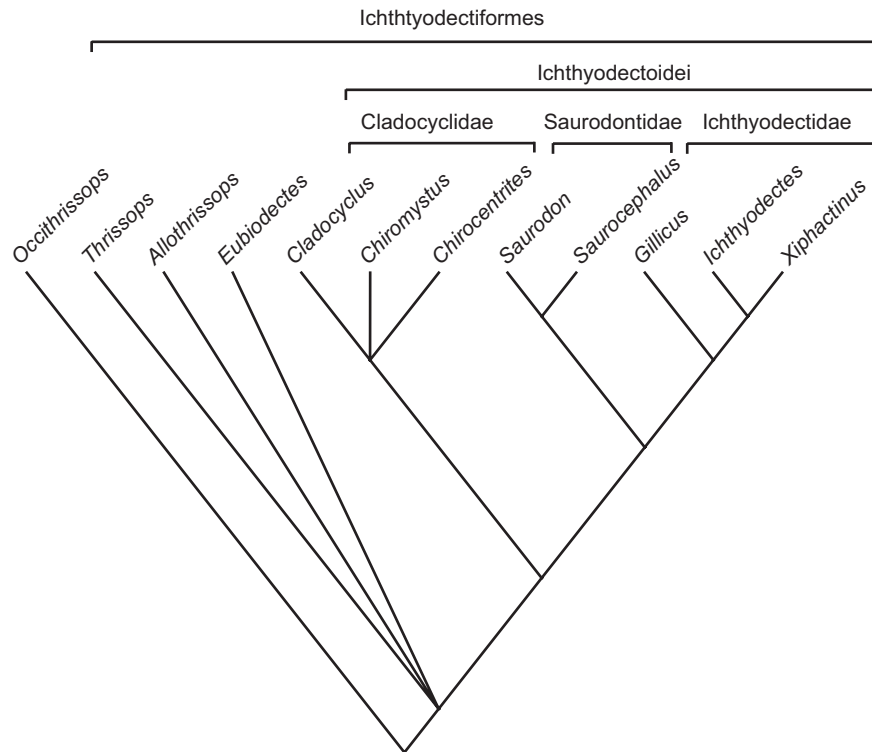


FIGURE 1. Reference phylogeny and classification of ichthyodectiform fishes. From Maisey (1991).

classification given in Figure 1 is that of Maisey (1991) and may be used as reference for the following description.

Detailed information on braincase structure is not known for all ichthyodectiforms, and therefore comparisons of this braincase with others are more detailed for some taxa than for others. The braincase of the most primitive ichthyodectiforms such as *Occithrissops* and *Allothrissops* remain largely unknown, except for the skull roof and ethmoid regions. At the other extreme, species of *Ichthyodectes*, *Gillicus* and *Xiphactinus* are virtually completely known. Therefore, comparisons are inevitably biased towards those taxa.

SYSTEMATIC DESCRIPTION

Subdivision TELEOSTEI Müller, 1846
 Plesion (Order) ICHTHYODECTIFORMES Bardack and Sprinkle, 1969
 Suborder ICHTHYODECTOIDEI Romer, 1966
 Family ICHTHYODECTIDAE Crook, 1892
 Genus *Cladocyclus* Agassiz, 1841
Cladocyclus pankowskii sp. nov.

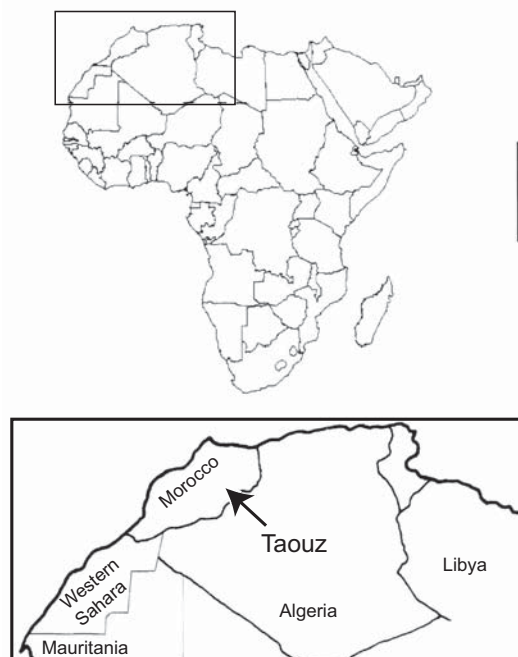
Diagnosis. *Cladocyclus* differing from the type species in the proportions of the skull roof; being 2.1 times as long as wide (excluding the supraoc-

cipital crest) versus 3.1 times as long as wide in the type species: no fenestra present between the parietal, supraoccipital and epioccipital (present in type species): rostrodermethmoid with blunt anterior margin versus anteriorly-projecting margin in type species: angle of parasphenoid is 155° versus 130° in type species.

Holotype. United States National Museum of Natural History USNM PAL 521360. Nearly complete braincase missing only part of the left basiptyergoid process and edge of supraoccipital spine. Currently the only specimen known.

Horizon and locality. Tafilalt Region, Kem Kem Basin, south of Taouz (Figure 2). As is usual with specimens from this region the precise locality and horizon is unknown. Many specimens are found lying loose on the surface and detailed stratigraphic work has not been done. Specimens from the Kem Kem Beds of Taouz area, southeastern Morocco are well-known. The vertebrate-bearing horizons in this region occur at the base of an escarpment formed by Cenomanian-Turonian carbonates. These beds have been informally divided into an upper marly unit and lower sandstone unit, collectively referred to as Kem Kem beds. The specimen described here clearly comes from the

2.1



2.2

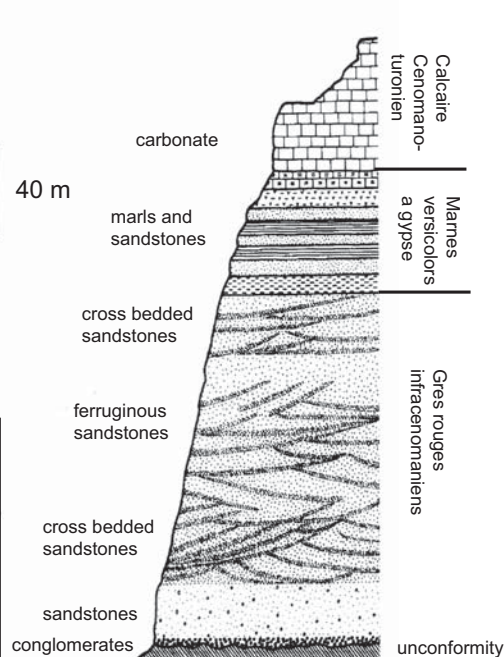


FIGURE 2. 2.1. Type locality of *Cladocyclus pankowskii* sp. nov. The holotype was not found in situ, and the locality may only be identified as the Taouz area. **2.2.** Section through Kem Kem beds. The holotype and jaw specimen described here undoubtedly come from the ferruginous sandstone horizon. After Forey and Grande (1998).

lower Sandstone unit and almost certainly from within the ferruginous sandstones (Figure 2). This unit has been dated to the Cenomanian, based on the contained shark fauna and is thought to represent a deltaic deposit (Serenio et al. 1996).

Etymology. Species named after Mr. Mark Pankowski of Rockville, Maryland, who kindly donated the specimen to the United States National Museum of Natural History, Washington.

Description. The braincase measures 102 mm from the tip of the vomer to the occipital condyle. In dorsal view (Figure 3) the roof narrows above the orbit and widens considerably at the levels of the ethmoid, autosphenotic spines and intercalars: the width at these three levels being 41 mm, 47 mm and 43 mm, respectively. These proportions are very similar to those of *Cladocyclus gardneri*, but unlike those of *Xiphactinus*, *Ichthyodectes*, *Gillicus* or *Saurocephalus*, in which the ethmoid region is considerably narrower than the width of the skull at the level of the autosphenotic or intercalar. Also, in *Cladocyclus gardneri*, as in the braincase described here, the lateral margins of the frontals above the orbit are parallel, whereas the frontal margin of *Xiphactinus*, *Ichthyodectes* and *Gillicus*

is inflated above the orbit. That of *Saurocephalus* is parallel sided but relatively much wider.

The ethmoid region is completely ossified. All of the ethmoid bones are securely sutured to one another. This is usual for most ichthyodectiforms except for the more primitive forms (*Allothrissops*, *Eubiodectes*, *Thrissops* and *Occithrissops* where many spaces persist between the bones). The rostrodermethmoid is relatively small (cf. *Saurocephalus*) and carries anterolaterally and ventrally projected processes that suture with the ethmoplatine of either side. On the dorsal surface the rostrodermethmoid extends posteriorly as paired splints of bone that suture with the frontals. The diverging splints of the median rostrodermethmoid are matched by opposing diverging ends of the paired frontals, such that there is a median fenestra left between these three bones. A small portion of the supraethmoid is seen to partially occlude the fenestra. A similar fenestra and dorsal expression of the supraethmoid is seen in *Cladocyclus gardneri*. It is absent from other ichthyodectiforms in which this region of the skull is sufficiently well-known.

The supraethmoid forms the dorsal wall of the nasal capsules. As usual the lateral ethmoid is

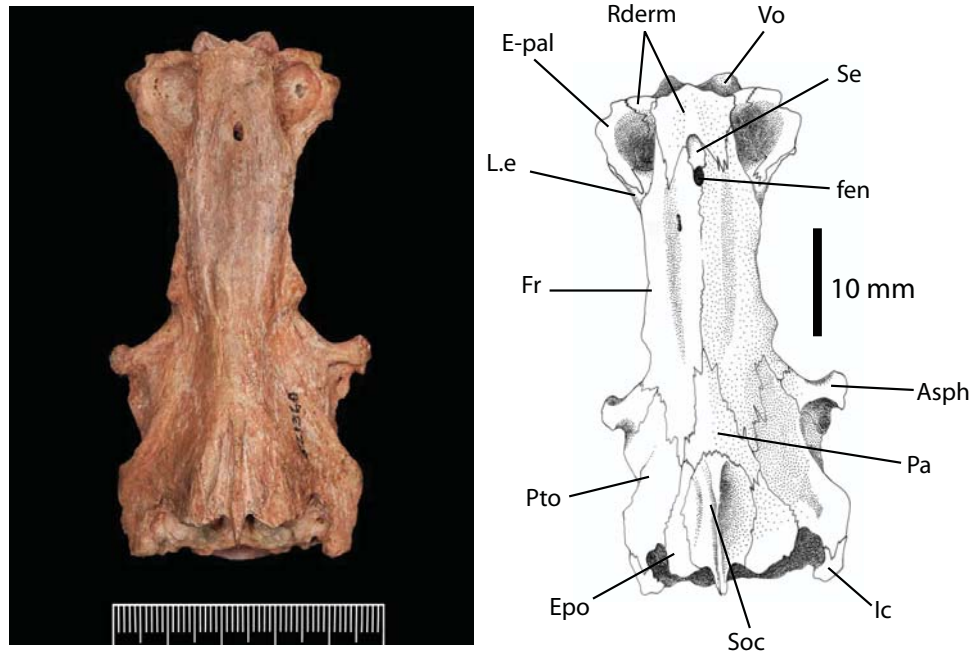


FIGURE 3. *Cladocyclus pankowskii* sp. nov. USNM PAL 521360 braincase in dorsal view together with interpretive camera lucida drawing. Scale bar in millimeters. Abbreviations: Asp, autosphenotic; E-pal, ethmopalatine; Epo, epioccipital; fen, fenestra; Fr, frontal; Ic, intercalar; L.e, lateral ethmoid; Pa, Parietal; Pto, pterotic; Rderm, rostrodermethmoid; Se, supraethmoid; Soc, supraoccipital; Vo, vomer.

robust and tightly sutured to the supraethmoid, rostrodermethmoid and ethmopalatine. With the last mentioned bone it forms the articular facet for palatine. This facet is transversely elongate as it is in *Cladocyclus gardneri* but unlike the rounded facet seen in *Xiphactinus*, *Ichthyodectes* and *Gilliscus*. The extreme ventral edge of the lateral ethmoid is open-ended and must have passed into cartilage in life. The lateral ethmoid is pierced by a large olfactory foramen.

The ethmopalatine ('rhinal' of Taverne 1977, 'parethmoid' of Bardack 1965) is very well-developed and forms much of the floor, as well as the inner and posterior walls of the nasal capsule. Anteriorly the ethmopalatine contacts the rostrodermethmoid through a complex suture. The anterior margin of the ethmopalatine is sutured to the vomer, and these two bones form a cup-shaped articular facet for the head of the maxilla. Posteriorly it overlies the lateral ethmoid in a splint-like suture. The size and mutual relationships of the ethmopalatine to surrounding bones is very similar to that of *Cladocyclus gardneri* and saurodontids and ichthyodectids such as *Xiphactinus*, *Ichthyodectes* and *Gilliscus*. In primitive ichthyodectiforms such as *Allothrissops* the ethmopalatine is very small and lies wholly beneath the lateral ethmoid and rostrodermethemoid, which contact each other

(Patterson and Rosen 1977, figure 7A); *Occithrissops* appears to lack an ethmopalatine (Schaeffer and Patterson 1984).

The frontal is a long narrow bone resembling most closely that of *Cladocyclus gardneri*. Differences from other ichthyodectiforms in the lateral margins have already been mentioned. One or two pores are seen on the frontals but there is no clear indication of the path of the supraorbital sensory canal. Posteriorly, there are sinusoidal sutures with the median parietal and the pterotic. On the left side of USNM PAL 521360 there is a very short contact with the epioccipital, which is due to the extreme forward projection of this latter bone in this species, not seen in *Cladocyclus gardneri* or, indeed, other ichthyodectiforms.

The median parietal is placed well-forward at the level of the autosphenotic and lies wholly anterior to the supraoccipital. This is the condition in ichthyodectoids and like those taxa the parietal is pointed anteriorly and expanded posteriorly. Among primitive ichthyodectiforms such as *Occithrissops* (Schaeffer and Patterson 1984, figure 25), *Allothrissops* (Patterson and Rosen 1977, figure 5) and *Thrissops* (Taverne 1977, figure 5) the parietals are small, paired and confined to the hind margin of the skull and meet in the midline above the supraoccipital (the usual condition in primitive

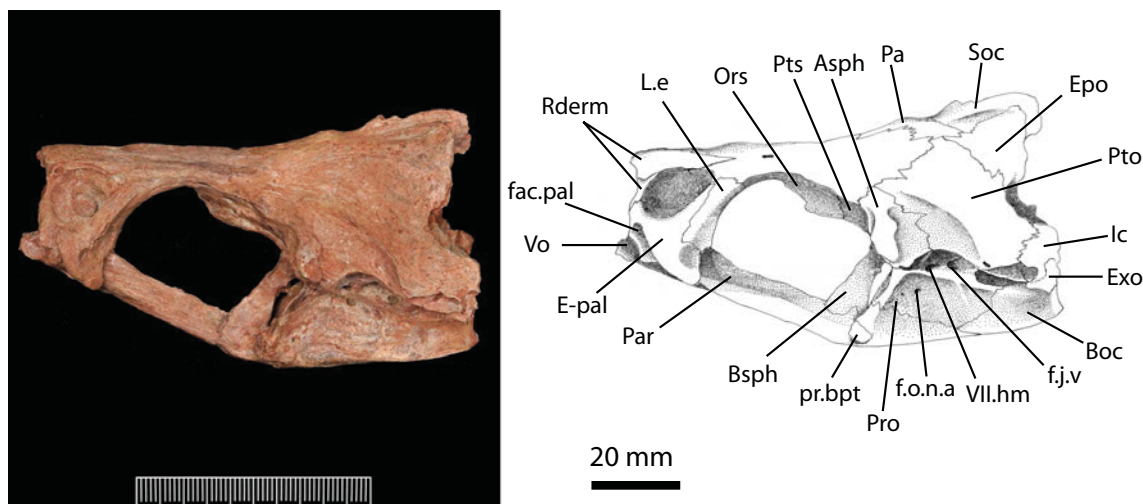


FIGURE 4. *Cladocyclus pankowskii* sp. nov. USNM PAL 521360 braincase in left lateral view together with interpretive camera lucida drawing. Scale bar in millimeters. Abbreviations: Asph, autosphenotic; Boc, basioccipital; Bsph, basisphenoid; E-pal, ethmopalatine; Epo, epioccipital; Exo, exoccipital; fac.pal, facet for palatine; f.j.v, foramen for jugular vein; f.o.n.a, foramen for orbitonasal artery; Ic, intercalar; L.e, lateral ethmoid; Ors, orbitosphenoid; Pa, Parietal; Par, parasphenoid; pr.bpt, basipterygoid process; Pro, prootic; Pto, pterotic; Pts, pterosphenoid; Rderm, rostrodermethmoid; Soc, supraoccipital; Vo, vomer; VII.hm, foramen for hyomandibular trunk of the facial nerve.

teleosts). The parietal is smooth. There is no trace of a pit line as is present in *Cladocyclus gardneri*. However, this absence may be preservational since such pit line grooves are easily abraded post-mortem.

The supraoccipital is large and well-expressed on the dorsal surface. Again, this is similar to the supraoccipital in ichthyodectoids, including *Cladocyclus gardneri*. The remains of the base of a supraoccipital crest are preserved but clearly most of the crest has been broken off, and it is impossible to be certain of its extent. It must have extended down the posterior face of the supraoccipital as well as the dorsal surface, a similarity with *Cladocyclus gardneri*. In most ichthyodectoids the crest is very large. In dorsal view the margins of the supraoccipital describe an ellipse. This is very similar to the supraoccipital in *Cladocyclus gardneri* but is unlike the narrow parallel-sided profile seen in *Xiphactinus*, *Ichthyodectes* and *Gillicus*. In *Saurocephalus* the supraoccipital outline is also approximately ellipsoidal but the posterior margins are excavated by the neighbouring epioccipitals (Stewart 1999, figure 7).

The epioccipital contacts the supraoccipital, parietal, pterotic and frontal through complex interdigitating sutures. It is perfectly smooth: that is, there is no parietal-epioccipital crest as prominently developed in *Xiphactinus*, *Ichthyodectes*, *Gillicus* and *Saurocephalus*. The contact between

the epioccipital and the supraoccipital extends for only about half the length of the supraoccipital. This is similar to *Cladocyclus gardneri* and also *Saurocephalus lanciformis* (Stewart 1999, figure 7) but unlike conditions in *Xiphactinus*, *Ichthyodectes* and *Gillicus* where the epioccipital lies along the greater part of the supraoccipital. According to Maisey (1991:195) *Chiromystus* and *Chirocentrites* are similar to *Cladocyclus* in this respect.

The pterotic is a large bone as in most ichthyodectiforms. It reaches well-forward above the autosphenotic and carries the otic branch of the sensory canal. It also forms most of the dilatator fossa as well as the posterior half of the anterior facet for the hyomandibula and the anterior half of the posterior facet for the hyomandibula. In posterior view it can be seen to form the roof of the small posttemporal fossa. The autosphenotic is developed as a prominent process that projects directly laterally, not forward as in *Xiphactinus*, *Ichthyodectes* and *Gillicus*. The process is of complex shape and must have provided firm anchorage for dilatator operculi muscles. The autosphenotic forms a small portion of the anterior facet for the hyomandibula.

The prootic is developed as in most other ichthyodectiforms. It is best exposed in lateral view (Figure 4). There is a prominent lateral ridge that forms the posterior margin of the orbit and is sutured with the short ascending process of the

parasphenoid. The lateral wall of the lower half of the prootic is deeply concave: so much so that, with its contralateral partner, the posterior myodome is severely restricted. The dorsal half of the lateral wall of the prootic contributes to the anterior facet for the hyomandibula and to the anterior wall of the deep subtemporal fossa. The lateral face is perforated by three principal foramina. The foramen for the hyomandibular trunk of the facial nerve is the largest and is located just beneath the anterior facet for the hyomandibula. This foramen is directed laterally and slightly dorsally. Beneath and slightly anterior to the above foramen there is a smaller opening for the orbitonasal artery. This opening is angled dorsally and emerges on the inner wall of the posterior myodome. The third principal foramen opens along the lower margin of the subtemporal fossa, very close to the mutual suture of prootic, exoccipital and basioccipital. This is the posterior opening of the jugular canal and allowed the jugular vein to pass out and run posteriorly within a notch in the intercalar. In saurodontids and ichthyodectids the jugular canal was completely enclosed within the intercalar until it emerged onto the posterior face of the braincase. The anterior face of the prootic is pierced by the large anterior opening of the jugular canal. The inner wall of the jugular canal is perforated by two foramina allowing the trigeminal to pass from the brain cavity through one and the facial through the other into the jugular canal. On the left side only of the braincase there is a small, dorsally directed foramen that opens immediately behind the foramen for the hyomandibular trunk. This foramen may have allowed the otic branch of the facial to course dorsally to innervate the otic sensory canal. It probably followed a completely intraosseous course on the right side.

The exoccipital forms the posterior wall of the subtemporal fossa and part of the posterior wall of the braincase. It has complex interdigitating sutures with the basioccipital and intercalar but a simple suture with the prootic and pterotic. The exoccipitals of either side meet in the midline to form the floor of the cranial cavity. On the lateral aspect a small, posteriorly directed foramen can be seen exiting the cranial cavity immediately behind the posterior exit of the jugular vein. The size of this foramen suggests that it carried the supratemporal branch of the glossopharyngeal nerve. On the posterior face of the exoccipital there is a very large foramen that leads to a canal penetrating the floor of the cranial cavity. This is the combined foramen for the glossopharyngeal and vagus

nerves. Such a large combined foramen is a common feature in ichthyodectoids. However, in saurodontids and ichthyodectids this foramen also carried the jugular vein.

The intercalar is developed in typical ichthyodectiform fashion, having complex sutures with all surrounding bones. It is exposed on the dorsal surface of the skull where it is developed as a boss above the foramen for the glossopharyngeal+vagus. It is probable that the ventral limb of the posttemporal anchored to the braincase at this point. The intercalar forms the posterior end of the posterior facet for the hyomandibula.

The basioccipital forms the entire occipital condyle and becomes constricted as it extends anteriorly to contact the prootic.

There is a median orbitosphenoid, perforated anteriorly to allow the passage of the olfactory tracts through the roof of the orbit.

The vomer (Figure 5) is very broad anteriorly where it is sutured with the ethmopalatine. Its contribution to the facet for the maxilla has been mentioned above. The vomer continues posteriorly as a splint-like shaft, interdigitating with the anterior end of the parasphenoid. There is a low median crest on the ventral surface. No vomerine teeth were seen.

The pterosphenoid forms part of the margin of the optic foramen. The surface is marked by a prominent longitudinal groove that presumably carried the anterior dorsal lateral line nerve.

The basisphenoid is robust. Dorsally there are laterally diverging wings that subtend the ventral border of the optic foramen. These wings suture with the pterosphenoid and prootic of either side. The basisphenoid pedicel is broad, laterally compressed with a tight suture with the parasphenoid.

The parasphenoid extends nearly the entire length of the braincase, being sutured to the vomer anteriorly and ending as posteriorly diverging wings that embrace the basioccipital. Below the orbit the parasphenoid is triangular in section. Beneath the otic region it is flat. In lateral profile there is a marked angle at the level of the basiptyergoid processes and separating the orbital from the otic limbs. The angle between these two limbs is 155°. The basiptyergoid process of either side is stout and extends laterally and slightly dorsally (in most ichthyodectoids it reaches anteroventrally). The base of the basiptyergoid process is penetrated by two foramina. The anterior foramen carried the efferent pseudobranchial artery into the base of the orbit. The posterior foramen carried the internal carotid artery.

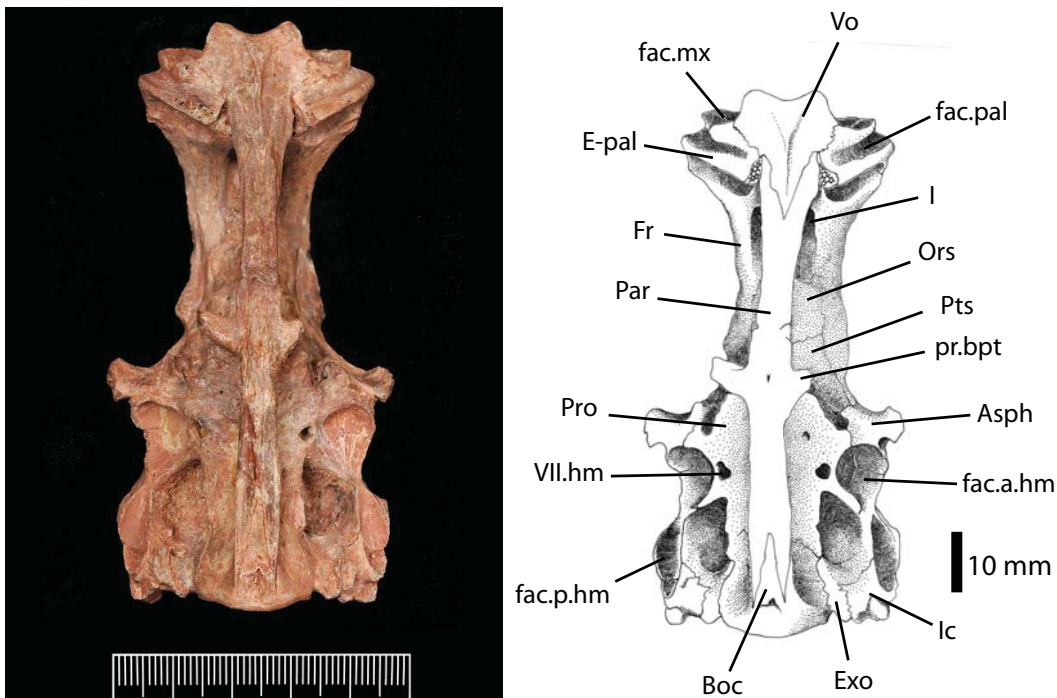


FIGURE 5. *Cladocyclus pankowskii* sp. nov. USNM PAL 521360 braincase in ventral view together with interpretive camera lucida drawing. Scale bar in millimeters. Abbreviations: Asph, autosphenotic; Boc, basioccipital; E-pal, ethmo-palatine; Exo, exoccipital; fac.a.hm, anterior facet for hyomandibula; fac.mx, facet for maxilla; fac.pal, facet for palatine; fac.p.hm, posterior facet for hyomandibula; Fr, frontal; Ic, intercalar; Ors, orbitosphenoid; Par, parasphenoid; pr.bpt, basipterygoid process; Pro, prootic; Pts, pterosphenoid; Vo, vomer; I, foramen for the olfactory tract; VII.hm, foramen for hyomandibula trunk of the facial nerve.

The hyomandibular facet is clearly divided to an anterior and a posterior facet separated by a narrow bridge of perichondral-covered bone. This appears different from *Cladocyclus gardneri* where the facet, although clearly bilobed, is continuous. In saurodontids and ichthyodectids it is also continuous. The subtemporal fossa is extremely deep as in all ichthyodectoids. It reaches well dorsally, so much so that there is a fenestra between it and the posttemporal fossa.

Ichthyodectiform jaw. From the same geographic region and sedimentary beds there is also a fragment of a large jaw with teeth (Figure 6). This represents the greater part of a left dentary. It measures 110 mm in length. It is clearly from an ichthyodectiform fish. It cannot be taxonomically associated with the braincase and hence is left in open nomenclature. The symphysis is very deep (45 mm), an ichthyodectiform character. On the median surface of the symphysis the bone surface is roughened, and this presumably provided a firm anchorage point for ligaments connecting left and right mandibles. Along the ventral surface there are three openings for the mandibular sensory canal (presumably more were present but the jaw is bro-

ken along the ventral margin). The dentition is very similar to that of *Cladocyclus gardneri*, both in tooth shape and size distribution. It is also similar to the dentition of *Xiphactinus* except that in that taxon there is usually a small diastema between the symphyseal teeth and those more posteriorly (not seen in this specimen), and there are usually more teeth in the jaw (about 20).

The dorsal, oral margin of the dentary is sinusoidal in outline, rising to a low coronoid process posteriorly. The most characteristic feature is the nature of the dentition. There are 15 teeth or sockets arranged in a single row. The size of the teeth varies. The two anterior teeth are very large. Although the tips of these teeth are not preserved, the diameters of the bases (6.4mm) are larger than those of the complete teeth (5.6 mm) seen more posteriorly. These complete teeth measure 22 and 23 mm in length, suggesting that the symphyseal teeth were longer. Behind the symphyseal teeth there is the base of a broken tooth of about the same diameter. This is followed by sockets and bases of much smaller teeth. At the level of the dorsal convexity in the oral margin there are three large teeth, two complete with the base of a partic-

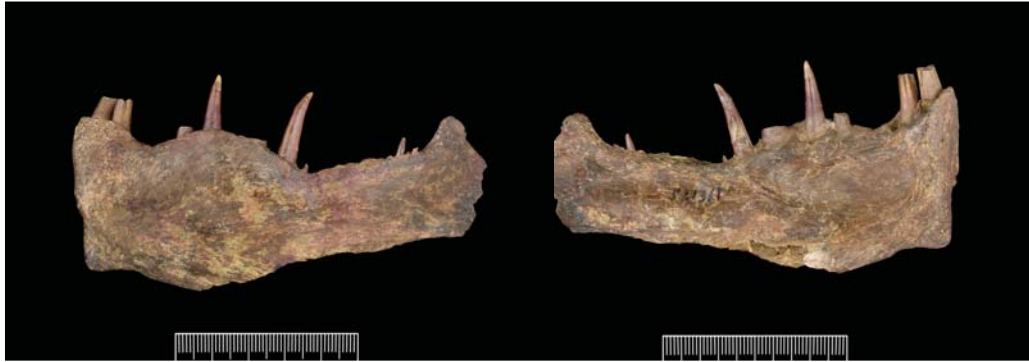


FIGURE 6. Ichthyodectid jaw. USNM PAL 521361. Left dentary with partial dentition. Left, lateral view. Right, medial view. Scale bar in millimeters.

ularly large tooth between them. The base of this large tooth measures 7.7 mm and appears to be the largest in the jaw. These teeth are followed by seven smaller teeth. There is no simple gradation of tooth size: rather, adjacent teeth may be of very different sizes. It is possible that this is due to replacement teeth lying alongside mature teeth. Each tooth is rounded or slightly ovoid in cross section. The bases are hollow, the surface is smooth and the complete teeth are slightly curved posteriorly. They also show acrodin caps at their tips.

COMPARISONS AND SIGNIFICANCE

The following features suggest that this braincase should be referred to the genus *Cladocyclus*. The ethmoid region is deep and especially wide, nearly as wide as the skull at the level of the autosphenotics. The frontals are parallel-sided above the orbit. There is a deep transverse groove (as opposed to a rounded facet seen in many ichthyodectiforms) on the ventral surface of the ethmopalatine for articulation with the palate. There is a fenestra between the frontals and rostrodermethmoid partially occluded by the supraethmoid. There are no parietal-epioccipital crests (a feature shared with more plesiomorphic ichthyodectiforms). The dorsal profile of the supraoccipital shows rounded lateral margins, and the pterotic extends only part way along the length of the supraoccipital (*Saurocephalus* shows a somewhat similar relationship). Some of these features are evident in the comparison of dorsal outlines shown in Figure 7. The basipterygoid processes project anteriorly and slightly dorsally. It is true that some of these features need to be checked on ichthyodectiforms in which the braincases are currently unknown or

unstudied but on current evidence this braincase can be referred to the genus *Cladocyclus*.

There are two nominal species of *Cladocyclus*; the type species *C. gardneri* Agassiz 1841 and *C. ferus* Silva Santos 1950 from the Apto-Albian Romaldo Member of the Santana Formation of Brazil. Patterson and Rosen (1977) noted that there were considerable differences between some of their specimens that they regarded as *C. gardneri* and cf. *C. ferus*, chiefly in the nature of the margins of the opercular bones. Castro Leal and Brito (2004) found specimens showing combinations of both these features and concluded that the genus was monospecific. We have no knowledge of the opercular bones in the specimen from the Kem Kem Beds described here but note that there is a marked difference in the skull roof proportions between *C. pankowskii*: length/breadth ratio = 2.1 versus 3.1 in *C. gardneri*, the rostrodermethmoid is blunt in *C. pankowskii* and pointed in *C. gardneri*, and the angle of the flexure of the parasphenoid at the level of the basipterygoid process is 155° in *C. pankowskii* and 130° in *C. gardneri*. The hyomandibular facet of *C. pankowskii* is divided by a narrow bridge of perichondral bone not present in *C. gardneri*.

Other ichthyodectiforms with which *C. pankowskii* might be compared are *Chiromystus mawsoni* Cope 1886 from the Late Hauterivian – early Barremian of Recôncavo Basin and Aptian-early Albian of Sergipe basin, Brazil (Maisey 2000), *Ichthyodectes bardacki* Cavin 1997 from the Turonian of Goulmima, Morocco, and *Unamichthys espinosai* Alvarado-Ortega 2004 from the middle or late Albian of the Tlayúa Formation, Mexico. *Chiromystus* shows well-developed parieto-epioccipital crests and thus differs in this respect. However, the

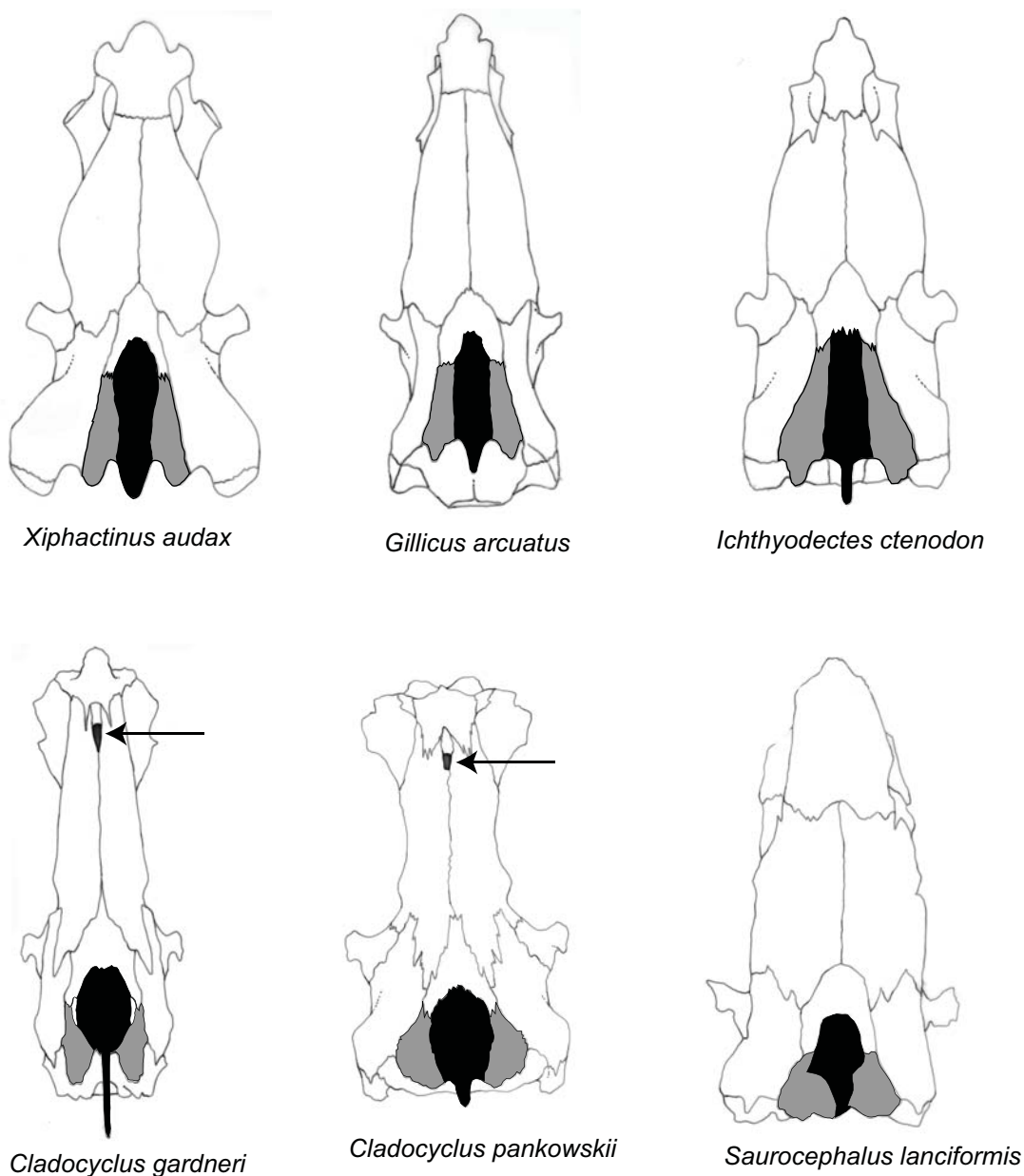


FIGURE 7. Outlines of skull roofs of some ichthyodectiforms to show similarities between the two species of *Cladocyclus* as well as differences from other members of the group. Note shape and extent of supraoccipital and epioccipital bones (black and grey respectively), overall proportions of the ethmoid, sphenotic and occipital widths, presence of fenestra in the dorsal aspect of the snout in *Cladocyclus*. *Xiphactinus*, *Gillicus* and *Ichthyodectes* from Bardack (1965); *Cladocyclus gardneri* from Patterson and Rosen (1977); *Saurocephalus* from Stewart (1999).

palatine articulatory surface upon the ethmopalatine is developed as a groove as in *Cladocyclus*. *Ichthyodectes bardacki* differs in that the parieto-epioccipital crests are well-developed, the ethmopalatine has a complex double faceted articulatory condyle and the jugular vein appears to have been completely bone enclosed through its traverse through the otic portion of the braincase. In all of these features *I. bardacki* appears more derived

and similar to *Xiphactinus*, *Ichthyodectes* and *Gillicus*. *Unamichthys espinosai* differs in that it shows paired parietals (Alvarado-Ortega 2004).

The presence of species of *Cladocyclus* in the mid-Cretaceous of Morocco and North Eastern Brazil is concordant with other similar distributions of sister-group taxa of fishes and increases an already large body of evidence suggesting the contiguity of these two parts of the world at this time.

Maisey (2000, figure 3) plots many of these comparisons that involve at least six separate fish clades. To this we can now add sister species of *Calamopleurus* (Forey and Grande 1998) and now a sister species of *Cladocyclus*.

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