BioOne COMPLETE

The First Record of the Ichthyodectiform Fish Cladocyclus from Eastern Gondwana: A New Species from the Lower Cretaceous of Queensland, Australia

Authors: Berrell, Rodney W., Alvarado-Ortega, Jesús, Yabumoto, Yoshitaka, and Salisbury, Steven W.

Source: Acta Palaeontologica Polonica, 59(4) : 903-920

Published By: Institute of Paleobiology, Polish Academy of Sciences

URL: https://doi.org/10.4202/app.2012.0019

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

The first record of the ichthyodectiform fish *Cladocyclus* from eastern Gondwana: A new species from the Lower Cretaceous of Queensland, Australia

RODNEY W. BERRELL, JESÚS ALVARADO-ORTEGA, YOSHITAKA YABUMOTO, and STEVEN W. SALISBURY



Berrell, R.W., Alvarado-Ortega, J., Yabumoto, Y., and Salisbury, S.W. 2014. The first record of the ichthyodectiform fish *Cladocyclus* from eastern Gondwana: A new species from the Lower Cretaceous of Queensland, Australia. *Acta Palaeontologica Polonica* 59 (4): 903–920.

Cladocyclus is a genus of ichthyodectiform fish that is best known from fossils found in shallow marine Cretaceous deposits in Brazil and Morocco. Herein, a new species of *Cladocyclus* is described on the basis of a fossil that comprises an articulated skull and anterior part of the body, preserved as part and counter-part in what was originally a single eroded nodule of fluvially-deposited volcanolithic sandstone from the Lower Cretaceous (upper Albian) portion of the Winton Formation near Isisford, central-western Queensland, Australia. This specimen represents the first record of *Cladocyclus* in eastern Gondwana, and indicates that species of this fish may also have inhabited freshwater environments. The new species is assigned to the genus *Cladocyclus* based on the morphology of the cleithrum (the arms are oriented at approximately 90° to each other) and a mandibular articular facet that incorporates portions of the angular, the articular and the retroarticular. *Cladocyclus geddesi* sp. nov. can be distinguished from other congeners based on the possession of a more elongate horizontal arm of the cleithrum and a supraoccipital crest that is gently convex posteriorly. This discovery greatly expands the geographic range of *Cladocyclus*, and supports the idea of a distinct southern fish fauna in the seas surrounding the fragmenting Gondwanan landmasses during the mid-Cretaceous.

Key words: Teleostei, *Cladocyclus*, Cretaceous, Winton Formation, Australia.

Rodney W. Berrell [rodneyberrell@yahoo.com] and Steven W. Salisbury [s.salisbury@uq.edu.au] (corresponding author), School of Biological Sciences, The University of Queensland, Brisbane, Qld 4072, Australia;
Jesús Alvarado-Ortega [alvarado@geol-sun.igeolcu.unam.mx], Departamento de Paleontología, Instituto de Geología, Universidad Nacional Autónoma de México, Circuito de la Investigación S/N, Ciudad Universitaria, Coyoacán, Distrito Federal, 04510 México;
Yoshitaka Yabumoto [yabumoto@kmnh.jp], Kitakyushu Museum of Natural History and Human History, 2-4-1, Higashida, Yahatahigashiku, Kitakyushu, Fukuoka, 805-0071, Japan.

Received 8 February 2012, accepted 6 June 2013, available online 17 June 2013.

Copyright © 2014 R.W. Berrell et al. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Introduction

Ichthyodectiforms were a common element of shallow marine fish faunas during the latter part of the Mesozoic (Bardack 1965; Bardack and Sprinkle 1969; Patterson and Rosen 1977; Alvarado-Ortega 2004; Cavin et al. 2013). At least 20 genera and double that number of species of these predatory teleosts have been erected based on fossils from North and South America, Europe, Asia, Africa, Antarctica, and Australia. The majority of ichthyodectiforms were between 1 and 5 m in length, but some, such as *Xiphactinus audax* Leidy, 1870 from the Western Interior Seaway of North America, reached lengths in excess of 6 m (Everhart 2005). Although most ichthyodectiform fossils derive from shallow marine and estuarine environments, rare specimens are known from brackish and freshwater deposits (Patterson and Rosen 1977; Nesov 1981, 1985, 1997; Maisey 2000; Mkhitaryan and Averianov 2011).

One of the best-known ichthyodectiform taxa is *Cladocyclus* Agassiz, 1841. The type species, *Cladocyclus gardneri*, is based on well preserved skeletons from the Lower Cretaceous (Aptian–Albian) of north-eastern Brazil, specifically in the Araripe, Parnaiba and Sergipe-Alagoas basins (Leal and Brito 2004; Brito and Yabumoto 2011). Other Brazilian species of *Cladocyclus* have been proposed, but these have

 http://dx.doi.org/10.4202/app.2012.0019

Downloaded From: https://bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

been either synonymized with *C. gardneri* (e.g., *C. ferus*; Leal and Brito 2004) or are based on isolated or poorly preserved material, such that their precise taxonomic identity is doubtful (e.g., *C. lewensis, C. occidentalis, C. strehlensis*).

Cladocyclus has also been recorded in the Upper Cretaceous of south-eastern Morocco. Forey and Cavin (2007) erected *Cladocyclus pankowskii* based on a partial skull from the Cenomanian Kem Kem Beds near Taouz (Sereno et al. 1996; Wellnhofer and Buffetaut 1999; Cavin et al. 2010). While the validity of this species has not been questioned, Mkhitaryan and Averianov (2011) proposed that it should be removed from *Cladocyclus* and placed in *Aidachar* Nesov, 1981. Despite this issue, Martill et al. (2011) reported the occurrence of complete skeletons of a possible new species of *Cladocyclus* in the overlying upper Cenomanian–lower Turonian marine sediments at Gara Sbaa, also in the Kem Kem area (Martill et al. 2011), reaffirming the occurrence of *Cladocyclus* spp. in south-eastern Morocco.

Here we describe the first confirmed record of *Cladocyclus* from eastern Gondwana. The new specimen comes from the upper Albian portion of the Winton Formation near Isisford, central-western Queensland, and represents the most complete teleost fossil from a likely freshwater deposit in the Cretaceous strata of the Eromanga Basin.

Institutional abbreviations.—AMNH, American Museum of Natural History, New York, USA; DNPM, Departamento Nacional de Producao Mineral, Rio de Janeiro, Brazil; IGM, Instituto de Geología, Universidad Nacional Autónoma de México, Distrito Federal, Mexico; MV, Museum Victoria, Melbourne, Australia; QM, Queensland Museum, Brisbane, Australia; UERJ-PMB, Universidade do Estado do Rio de Janeiro (Paulo Brito´s collection), Brazil; UQ, The University of Queensland, Australia; USNM, United States National Museum of Natural History, Washington DC, USA.

Material and methods

Preparation of the fossil.—The specimen was discovered within a sandstone nodule when it was split along a sagittal plane, producing a part and counter-part specimen. Following its discovery in the field, the exposed bones were stabilized with acrylic plastic (Paraloid B 72, also known as Butvar, an ethyl methacrylate copolymer) dissolved in acetone (30 g of Paraloid beads to 1 l of acetone). Exposed cracks were filled with cyanoacrylate (Superglue). Laboratory preparation followed the chemical techniques described by Toombs and Rixon (1959), and closely matched that outlined in Maisey (1991b) for similarly preserved Santana Formation fishes. The exposed surface of each part of the fossil was initially set in a 2–3 cm deep tablet of acrylic resin. The embedded parts were then immersed in a 10 per cent dilution of acetic acid for four to seven days. Following immersion in the acid bath, each part was washed in water for 2–3 days and then allowed to dry. Newly exposed bones were then hardened with Mowital B30 (polyvinyl butyral powder) dissolved in pure ethanol (one teaspoon to 200 ml ethanol). This process was repeated for approximately 25 weeks until the desired amount of matrix had been removed. In total, 50 l of acid were used to remove approximately 4 kg of sediment (each acid bath removed approximately 120 g of sediment). The residual sediment from each acid bath was dried and sorted under a binocular microscope for associated microfossils such as scales and teeth.

Comparative material examined.—During the course of this study, the following specimens were examined firsthand. Other comparisons were made using photographs, along with published descriptions and illustrations: *Occithrissops willsoni* Schaeffer and Patterson, 1984, AMNH 10873, the impression of a complete specimen from Sundance Formation, Wyoming, USA; *Chiromystus alagoensis* Jordan, 1910, AMNH 10015 and AMNH 10016, complete specimens collected near Riacho Doce, Alagoas, Brazil; *Cladocyclus gardneri* Agassiz, 1841, AMNH 11877, AMNH 11992, AMNH 19129, and AMNH 19528, specimens from the Santana Formation, Ceará, Brazil; *Proportheus kameruni* Jaekel, 1909, AMNH 8394, a complete skeleton, and AMNH 6302, a specimen lacking the caudal region, both from San Benito River, Equatorial Guinea; *Xiphactinus audax* Leidy, 1870, AMNH 1673 and AMNH 19528, skulls from Niobrara Formation, Kansas, USA; *Unamichthys espinosai* Alvarado-Ortega, 2004, IGM 8373 and IGM 8374, complete specimens from the Tlayúa Formation, Mexico; *Saurodon leanus* Hays, 1830, IGM 6762, lower jaw and fragments of the pectoral girdle from La Mula quarry, Coahuila, Mexico; *Cooyoo australis* Lees and Bartholomai, 1987, QM F12711, QM F12327, QM F6346, complete skulls and associated vertebrae, Allaru Mudstone, Hughenden area, north central Queensland, Australia; *Ogunichthys triangularis* Alvarado-Ortega and Brito, 2010, UERJ-PMB 100 (holotype skeleton), UERJ-PMB, 93, 94, 95, 97, 98, 99 (paratypes), DNPM 533-P, 534-P, and 544-P.

Geological setting

The specimen was discovered by Kerry Geddes in April 2005, during a University of Queensland expedition to Isisford, central-western Queensland, Australia (Fig. 1). It comes from the same locality that produced the paratype skull of the basal eusuchian crocodyliform *Isisfordia duncani* (QM F44320; Salisbury et al. 2006a). Local grazier Ian Duncan discovered the first vertebrate-bearing fossil locality near Isisford in 1995–1996. Subsequent exploration by The University of Queensland between 2003 and 2013 has revealed a number of other localities in the surrounding area.

All the vertebrate fossils collected from Isisford thus far derive from the Winton Formation. The Winton Formation extends over a large area of western Queensland, north-eastern South Australia and north-western New South Wales (Gray et al. 2002). It is the uppermost unit of the Manuka Subgroup

Downloaded From: https://bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

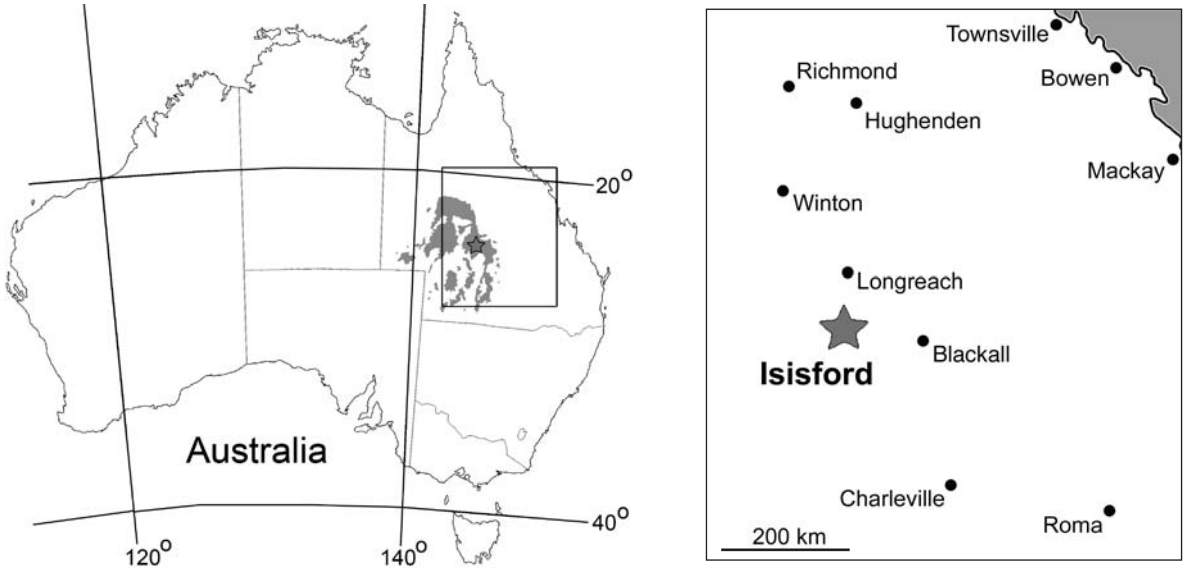


Fig. 1. Map showing the discovery site of *Cladocyclus geddesi* sp. nov. (QM F44329) near the town of Isisford, central-western Queensland, Australia. Gray area indicates the extent of the upper Albian–lower Turonian Winton Formation.

within the Rolling Downs Group, and constitutes the uppermost Cretaceous strata of the Eromanga Basin (Gray et al. 2002). U-Pb isotope dating of detrital zircons by laser ablation from a number of vertebrate-bearing localities indicates that deposition of the Winton Formation commenced no earlier than latest Albian (~103.0–100.5 Ma), continuing to roughly at or just after the Cenomanian–Turonian boundary (93.9 Ma) (Tucker et al. 2013). This age range corresponds to the upper *Phimopollenites pannosus* and *Appendicisporites distocarinatus* spore-pollen zones of Helby et al. (1987) and Partridge (2006). Fossil localities near Isisford, including the one that yielded the new fish fossil described herein, occur approximately 200 m above the inferred contact with the underlying shallow marine and paralic sediments of the Mackunda Formation, and have a maximum depositional age of 100.5–102.2 Ma (i.e., upper Albian; Tucker et al. 2013) (Fig. 2).

The Winton Formation comprises repeated facies that represent major channels, flood basins and mires, all signifying a freshwater fluvial-lacustrine environment deposited on a broad coastal plain as the epicontinental Eromanga Sea withdrew (Exon and Senior 1976; McLoughlin et al. 1995; Tucker et al. 2011, 2013). Vertebrate fossils in the uppermost Winton Formation are often found in low-energy fluvial settings, such as point bar deposits, crevasse splays from flood events and ox-bow lakes (Salisbury et al. 2006b; Tucker et al. 2011, 2013). Vertebrate fossils at Isisford, however, occur in medium-high energy fluvial deposits, and are typically preserved in medium-course grain Fe-oxide and calcite-cemented volcaniclastic-volcanolithic sandstone nodules (Salisbury et al. 2006a; Tucker et al. 2011, 2013).

Other fossils found within the Winton Formation include titanosauriform sauropods (Coombs and Molnar 1981; Molnar 2001; Molnar and Salisbury 2005; Salisbury et al. 2006b; Hocknull et al. 2009), megaraptoran theropods (Hocknull et al. 2009; Benson et al. 2010c; Agnolin et al. 2010; White et al. 2012, 2013), dolicosaurian squamates (Scanlon and Hocknull 2008), and vertebrate microfossil remains that belong to theropod, thyreophoran, and ornithopod dinosaurs, turtles, fish, crocodyliforms, possible cynodonts and basal mammaliaforms, and possible plesiosaurs (Salisbury 2005; Molnar and Salisbury 2005; Salisbury et al. 2006a; Hocknull and Cook 2008; Musser et al. 2009). Upward of 50 species of plant macrofossils are also known, dominated by conifers and angiosperms (Dettmann et al. 1992 and references therein; Dettmann et al. 2009; McLoughlin et al. 1995, 2010; Pole 1999, 2000a, b; Pole and Douglas 1999; Dettmann and Clifford 2000; Clifford and Dettmann 2005). Occasional in-

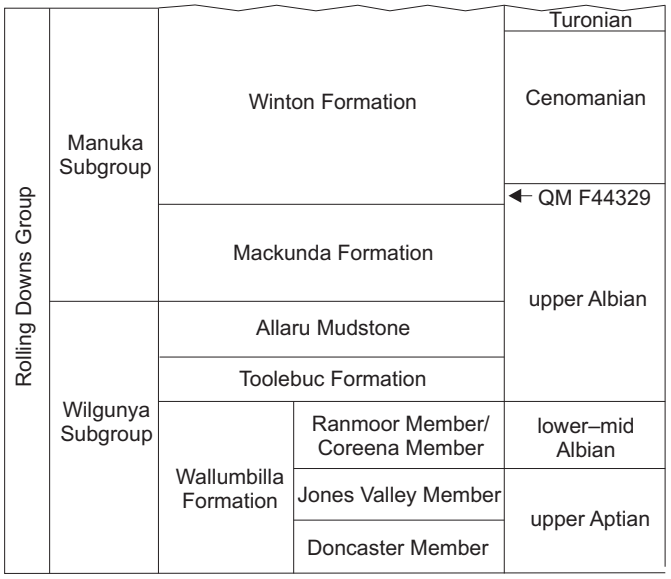


Fig. 2. Stratigraphy of the Eromanga Basin, western Queensland, after Gray et al. (2002) and Tucker et al. (2013). *Cladocyclus geddesi* sp. nov. (QM F44329) comes from the lower part of the Winton Formation, and is upper Albian in age.

Downloaded From: https://bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

vertebrate fossils have also been recorded (Hocknull 1997, 2000; Jell 2004; Cook 2005). Trace fossils from the Winton Formation include dinosaur tracks at Lark Quarry Conservation Park, indicative of two types of ornithopods (Thulborn and Wade 1984; Romilio and Salisbury 2011; Thulborn 2013; Romilio et al. 2013). An internal mould of a chelonian carapace has also been identified (Molnar 1991).

At present, the only freshwater fishes to be described from the Winton Formation are three species of ceratodont lungfish, all based on isolated tooth plates: *Ceratodus* sp., *Metaceratodus wollastoni*, and *Metaceratodus ellioti* (Kemp 1991, 1997; Dettmann et al. 1992). Faggotter et al. (2007) reported a possible halecomorph from the Winton Formation at Isisford, but further work on this specimen is required to confirm this identification.

Systematic palaeontology

Teleostei Müller, 1845

Ichthyodectiformes Bardack and Sprinkle, 1969

Ichthyodectoidei Romer, 1966

Cladocyclidae Maisey, 1991a

Genus *Cladocyclus* Agassiz, 1841

Type species: *Cladocyclus gardneri* Agassiz, 1841; near Jardim village, Ceará, Brazil, Aptian–Albian strata of the Santana Formation.

Emended diagnosis.—Medium-sized icthyodectiform fishes (adults >80 cm total standard length) that can be diagnosed from other ichthyodectoids based on the following unique combination of features (autapomorphies marked with "a"; amended from the diagnosis presented in Leal and Brito 2004): approximately 64 vertebrae (not known for *C. geddesi* sp. nov.); premaxillary, maxillary, and dentary with teeth (shared with all ichthyodeciforms except the toothless *Heckelichthys vexillifer*); dentary possesses a single large fang-like tooth ("a"); juveniles bearing short intercalar, adults with a large intercalar process extending posteriorly ("a"); long axes of the vertical and horizontal arms of the cleithrum oriented approximately perpendicular to each (shared with *Vallecillichthys multivertebratum*); mandibular articular facet in which the articular surface comprises portions of the angular, the articular and the retroarticular; caudal fin endoskeleton with two ural centra, eight hypurals, one epural and six uroneurals ("a"; not known for *Cladocyclus geddesi*).

Stratigraphic and geographic range.—Mid-Cretaceous of western and eastern Gondwana: Aptian–Albian of north-eastern Brazil; upper Albian of Australia; upper Cenomannian–lower Turonian of Morocco.

Cladocyclus geddesi sp. nov.

Etymology: After Kerry Geddes, in recognition of his discovery of the holotype specimen and outstanding preparation work on the Isisford fossil material.

Holotype: QM F44329, part and counter-part of an articulated cranial and mandibular skeleton, the anterior part of the body, along with associated neural spines and isolated scales (Fig. 3).

Type locality: The specimen comes from a University of Queensland field locality (UQL-Isis-IX) on private land near the town of Isisford, central-western Queensland, Australia (24°15.460'S, 144°26.207'E).

Type horizon: Winton Formation, Manuka Subgroup, Rolling Downs Group; Lower Cretaceous (upper Albian, 100.5–102.2 Ma; Fig. 2).

Diagnosis.—*Cladocyclus geddesi* sp. nov. can be diagnosed from other congeners based on the following features: supraoccipital crest that is gently convex posteriorly; horizontal arm of the cleithrum approximately twice as long as the vertical arm.

Description

General features.— Preserved elements of QM F44329 include an almost complete skull, shoulder girdle, pectoral fin, and the first 19 vertebrae. Ribs and some scales are preserved, but the opercular is obscured as a result of the specimen now being embedded in resin. The head is slightly rotated clockwise and the shoulder girdle is disarticulated. The length from the anteriormost end of the head to the posteriormost edge of the 18th vertebrae is 270 mm. The head length (from the tip of the upper jaw to the middle of the corner of lower and upper arms of the cleithrum that represent the posterior border of the opercular is about 121 mm. The depth of the head (from the dorsal end of the supraoccipital crest to the ventral margin of the interopercular is 101 mm. The body depth is almost the same as the depth of the head.

The anterodorsal part of the skull has been flattened mediolaterally slightly, such that the palatine is partly disarticulated from the palatine condyle of the maxilla. For most bones only the lateral surface is visible. Surface colouration on the bones consists of a marbled pattern of yellow, rust orange, chocolate brown and black.

In all the complete ichthyodectiform specimens so far described, the head length (including the opercle) represents 15–25% of the total length (see Bardack 1965; Taverne and Bronzi 1999; Alvarado-Ortega 2004, 2005). The head length of QM F44329 (measured from the tip of the ethmoid area to the anterior border of vertical limb of the cleithrum that represent the posterior border of the opercle, which is missing in the specimen) is about 150 mm. This means that the total length of QM F44329 could be around 600–1050 mm.

The large, oblique, dorsally opening mouth is formed by a well-developed upper and lower jaw bones (assuming that paired bones such as the dentaries are identical) with a single series of conical, slender, pointed teeth. In lateral view, the braincase is triangular in outline, being approximately 1.4 times longer than it is deep. Based on the length of the preserved ribs that enclose the abdominal region, and the height of the preserved neural spines, the anterior part of the trunk of QM F44329 was not deeper than the posterior part of the skull.

Skull and braincase.—The ethmoid region is proportionately very deep dorsoventrally, being almost the same depth as the

Downloaded From: https://bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

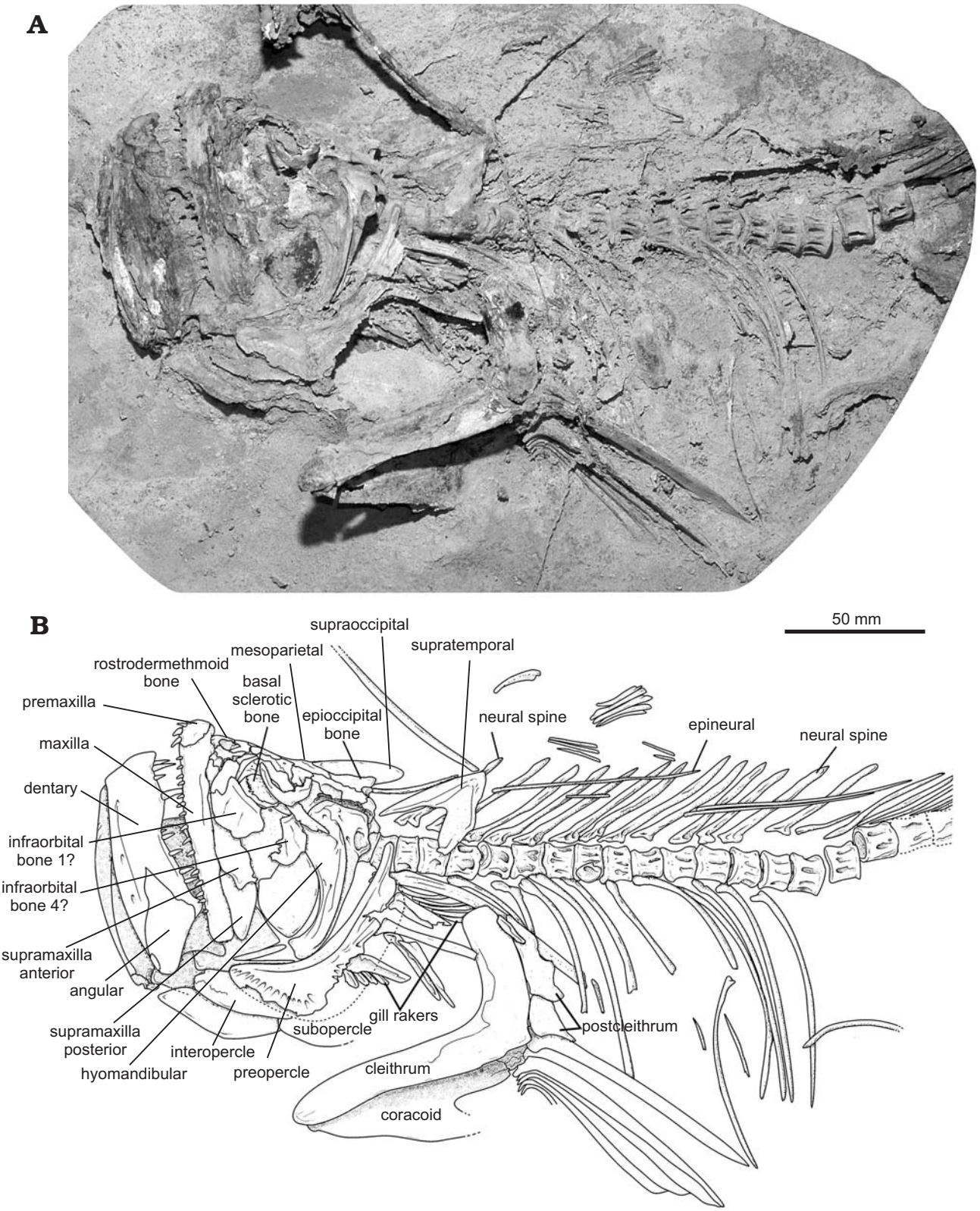


Fig. 3. Ichthyodectiform fish *Cladocyclus geddesi* sp. nov. (QM F44329) from near Isisford, central-western Queensland, Australia; Lower Cretaceous (upper Albian) strata of the Winton Formation, in lateral view. Photograph (**A**) and interpretive drawing (**B**).

postorbital portion of the braincase. The orbit is also large, with a diameter that is slightly shorter than the length of the posterior part of the cranium. The rostrodermethoid is a complex bone that forms the roof and anterior border of the nasal capsule. It has a posterior projection that is sutured to the frontals. It also shows a rounded anterior tip and a ventral

Downloaded From: https://bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

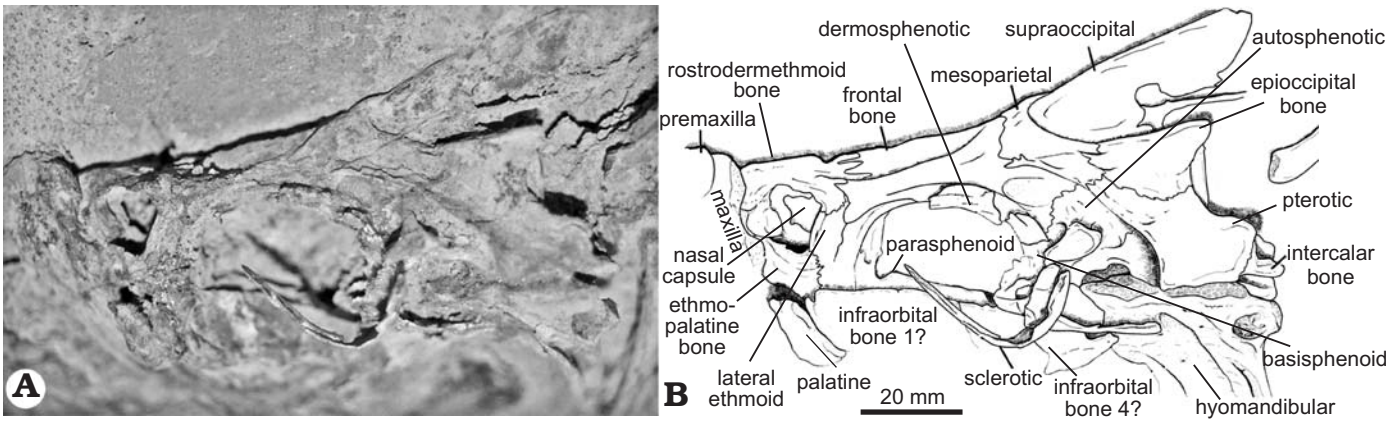


Fig. 4. Ichthyodectiform fish *Cladocyclus geddesi* sp. nov. (QM F44329) from near Isisford, central-western Queensland, Australia; Lower Cretaceous (upper Albian) strata of the Winton Formation, braincase in dorsolateral view. Photograph (**A**) and interpretive drawing (**B**).

section that is expanded laterally to form two semi-circular, wing-like lateral projections.

The ethmopalatine is a well ossified bone (only the left element is visible) that forms the floor of the nasal capsule. Bony outgrowths attach this bone to the rostrodermethoid anteriorly and to the lateral ethmoid posteriorly. Although the lateral ethmoid is not well preserved, it forms a solid bar that firmly attached to the frontal and the ethmopalatine bone. It additionally separates the nasal capsule from the orbit.

Similar to the condition in most ichthyodectiforms, the frontal is a long smooth bone located above the orbit, being about two thirds of the maximum cranium length. The frontal is attached to the rostrodermethoid anteriorly by a serrated suture, and the mesoparietal, pterotics, and sphenotics posteriorly. Medially, the suture between the two frontals forms a shallow median sulcus, best developed between the orbits.

The parietals are fused elements, forming the mesoparietal, which in dorsal view has a C-shaped outline, with a posterior section that is concave and a central section joining the supraoccipital, just above the posterior margin of the orbit. The posterior projections of the mesoparietal extend laterally to the base of the supraoccipital, and also contact the epioccipitals. The mesoparietal does not form part of the supraoccipital crest. The supraoccipital bone is proportionately very large and the anterior margin reaches to above the posterior edge of the orbit. The supraoccipital crest is well developed, being gently convex anteriorly with a rounded posterior margin. The epioccipital, which is located along the lateral side of the supraoccipital, is a proportionately large bone with a massive, rounded posterior crest that extends over the middle of the supraoccipital crest. The epioccipital bone is sutured to the mesoparietal anteriorly and sits medial to the middle of the supraoccipital.

The pterotic is the largest bone in the posterior part of the cranium. Posteroventrally, the pterotic contacts the intercalar, while dorsally it contacts the epioccipital and mesoparietal. Ventrally the pterotic forms the middle part of the hyomandibular fossa, while anteriorly it contacts the frontal and the autosphenotic. The pterotic has a long groove that forms a dilator fossa, obscuring its suture with the autosphenotic.

The autosphenotic forms the anterior part of the hyomandibular fossa and has a stout lateral process. The intercalar is a complex bone that forms the posterior part of the hyomandibular fossa. The parasphenoid forms a large, straight, toothless rod along the orbit; although its postocular section is not exposed, the ventral border of the postocular skull section is observable in X-rays. The angle between the orbital and postorbital sections of the parasphenoid is about 130°.

In QM F44329 the hyomandibular fossa is occupied by the articular head of the hyomandibular bone, as when the specimen was alive, such that the longitudinal axes of the hyomandibular head and the hyomandibular fossa have the same inclination. The anterior projection of the hyomandibular fossa crosses the paraesphenoid bone behind the ethmoid area.

Circumorbital and sclerotic bones.—The circumorbital series is not well preserved. Preserved elements include the partial remains of infraorbitals II and IV, which are located along the ventral border of the orbit. These bones are thin and fragile. The preserved sclerotic bones are flimsy, with semicircular laminar structures that surround the circular basal sclerotic bone with surrounding serrated borders. While the dermosphenotic in most ichthyodectiforms is rarely preserved (Patterson and Rosen 1977), it is visible on QM F44329 as a small, subrectangular bone that is located dorsal to the preserved sclerotic ring (Fig. 4).

Hyopalatine bones.—The hyomandibula, metapterygoid, quadrate and palatine are partially exposed in lateral view. The exposed dorsal part of the hyomandibula is stout and appears to be elongated and continuous. Just at the base of this opercular condyle, the hyomandibula shows a large deep cavity, regarded by Bardack (1965) as a depression for the adductor hyomandibular muscle in other ichthyodectiforms. The foramen for the hyomandibular branch of cranial nerve VII is visible anterior to the latter depression. The ventral section of the hyomandibula becomes progressively narrower as it curves slightly anteriorly to meet the symplectic. The anterior border of the preopercle matches with a groove that opens dorsoventrally along the ventral section of the hyomandibula.

Downloaded From: https://bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

The quadrate is triangular in outline, with a straight dorsal border. Its articular condyle is directed anteriorly and located below the posterior edge of the orbit. Even though the dorsal tip of the symplectic seems to be broken, this nail-shaped bone is as high as the quadrate, where it is attached in a deep posterior notch. The metapterygoid is a smooth bone located between the anterior border of the hyomandibula and the dorsal border of the quadrate. Only the head of the palatine is visible as a malleolus-like element that fits between the palatine condyle of the maxilla and the ethmopalatine bone (Fig. 4). The arrangement and number of branchiostegal rays are uncertain.

Gill arch skeleton.—Elongated gill rakers are preserved between the posterior edge of the preopercle and the anterior end of the anterodorsal border of the cleithrum. The gill rakers comprise hollow tubes and L-shaped projections. No denticles are visible on the lateral surface of each individual gill-raker.

Lower jaw.—In lateral view, the lower jaw is rectangular in outline. The dentary symphysis is almost as deep as the posterior section of the lower jaw along the sinuous alveolar border. The ventral border of the lower jaw is slightly convex, and the coronoid process is reduced to a rounded structure that partially overhangs the dentary teeth. The teeth of the lower jaw are robust, conical, elongate and slightly recurved. The teeth within the dentary are longer than those in the maxilla and premaxilla. The size (crown height) of individual, complete dentary teeth is highly variable along the tooth row, ranging from 2.9–6.4 mm. As in the maxilla and the premaxilla, the dentary teeth form a single line rising from the alveolar border. The left dentary possesses 13–14 alveoli in total, with 4–5 teeth lacking.

In lateral view, the angular bone occupies the posterior third of the lower jaw. It possesses a short, rounded postarticular process. The retroarticular bone is a proportionately small bone, located at the posterior end of the angular, between the posterior border of the dentary and the postarticular process of the angular. The articular, retroarticular and angular bones participate in the articular facet for the quadrate (Fig. 5).

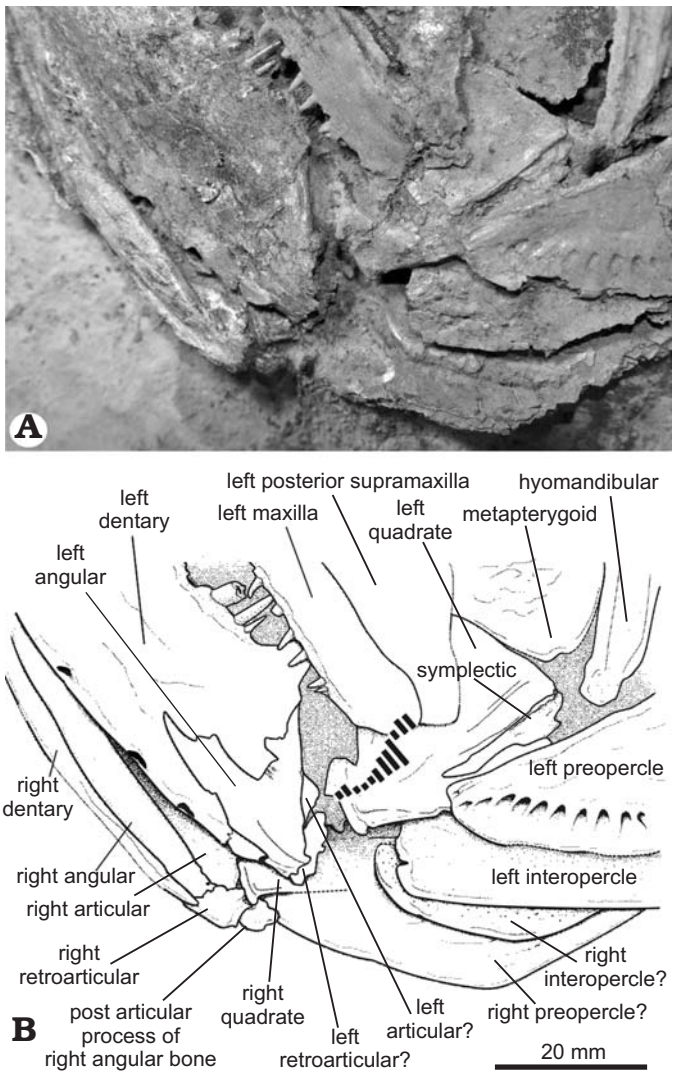


Fig. 5. Ichthyodectiform fish *Cladocyclus geddesi* sp. nov. (QM F44329) from near Isisford, central-western Queensland, Australia; Lower Cretaceous (upper Albian) strata of the Winton Formation, area of articulation for the lower jaw. Photograph (**A**) and interpretive drawing (**B**). Hatched area indicates broken bone.

Upper jaw.—The maxilla is a long rectangular-shaped bone, about seven times longer than it is deep. The maxillary teeth are similar in shape to those of the lower jaw, but are smaller and more regular in size, ranging from 2.7–3.9 mm. As in the lower jaw, these teeth are singularly implanted within the jaw, such that they are almost equally spaced.

The premaxilla is ovoid in lateral view, and carries the first four teeth of the upper jaw. These teeth increase in size posteriorly from 3.6–1.3 mm. The premaxilla and maxilla attach to each other along their entire height. The left premaxilla bears four alveoli, all with teeth, while the left maxilla has 22 alveoli in total, with five teeth lacking. Patterson and Rosen (1977) state that all ichthyodectiforms possess two supramaxilla bones except for the saurodontids. In QM F44329 both supramaxillary bones are preserved. The anterior supramaxilla is an irregularly shaped, elongated bone with a posterior keel. The posterior supramaxilla has a triangular outline with a notch in its anterior part where it intersects with the bony outgrowth of the anterior supramaxilla (Fig. 3).

Opercular series.—The opercle is not visible on the exposed section of the specimen. Although the posterior edge of the preopercle is not well preserved, it is a flat boomerang-shaped bone with wide limbs, the vertical limb being twice as long as the horizontal one. The dorsal posterior edge of the preopercle shows fine grooves giving the appearance of a wide-toothed comb. The preopercle has five openings with short grooves of the preopercular sensory canal along its vertical limb, and about 14 on its horizontal limb. The interopercle is a thin, laminar, and gently curved bone placed below the ventral limb of preopercles. Behind the interopercle, the anterior part of the subopercle is preserved showing the same laminar aspect.

Pectoral girdle and fin.—In lateral view, the cleithrum is boomerang-shaped, with the long axes of the two arms oriented at

Downloaded From: https://bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

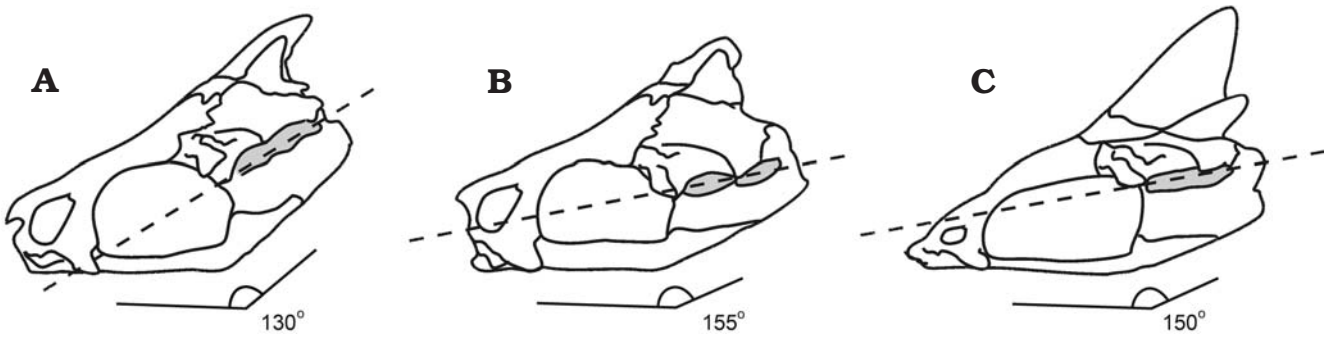


Fig. 6. Projection of the hyomandibular facet and angle of the parasphenoid in three ichthyodectiform fishes. **A**. *Cladocyclus gardneri* Agassiz, 1841 (based on AMNH 19129). **B**. *Aidachar pankowskii* (Forey and Cavin, 2007) (after Forey and Cavin 2007: fig. 4). **C**. *Ichthyodectes ctenodon* Cope, 1871 (after Badack 1965: 14). Also, note differences in proportions of the skull in these ichthyodectiforms. QM F44329 (*Cladocyclus geddesi* sp. nov.) has the same angle of the parasphenoid as *Cladocyclus gardneri*.

approximately 90° to each other. The length of the horizontal arm of the cleithrum is about twice the length of the vertical arm. The coracoid is as long as the horizontal arm of the cleithrum, and has a rounded ventral border. Only a small surface of the scapula is visible, just in the posterior angle formed by both arms of the cleithrum, at the point where these bones meet the upper posterior part of the coracoid. Two poorly preserved postcleithra sit behind the vertical arm of the cleithrum. These elements are only partially exposed, but X-rays reveal their presence and full extent. The dorsalmost part of the postcleithrum has a rectangular shape with an undulating posterior margin. The ventralmost part of the postcleithrum has a hammer-like outline anteriorly, and a tear-drop-like outline posteriorly. The supracleithrum is not preserved. The supratemporal is a large triangular plate. At least seven rays of the pectoral fin are present in this specimen. The two anterior rays of each fin are saber-shaped, being wider and longer, while the posterior ones tend to be shorter and narrower.

Vertebral column.—Only the anterior 19 abdominal centra are preserved. These are proportionately massive, well ossified, and slightly longer in an anteroposterior direction than they are wide. All centra have long, longitudinally ovoid fossae on their ventral and lateral surfaces, except for the two anterior-most ones, which have essentially smooth surfaces. All the neural arches are autogenous and fused to neural spines. There is no evidence of supraneurals, but the remains of several large, fine epineurals are preserved. The ribs enclose the abdominal area.

Scales.—Although very fragmentary, the preserved scales are all oval-shaped, with a dorsoventrally-aligned long axis. The external surface of each scale displays numerous concentric circuli.

Comparisons

Referral of QM F44329 to *Cladocyclus*.—Among basal teleosts, QM F44329 compares best with taxa typically referred to Ichthyodectiformes, and specifically Ichthyodectoidei. Comprehensive phylogenetic analyses investigating the relationships of ichthyodectiform fishes have been published by Stewart (1999), Mhitaryan and Averianov (2011) and Cavin et al. (2013). Other useful comments on the evolution of these fishes come from studies in which formal phylogenetic analysis was not carried out (e.g., Patterson and Rosen 1977; Teverne 1986; Maisey 1991a; Taverne and Chanet 2000; Alvarado-Ortega 2004, 2005). The recognition of QM F44329 as an ichthyodectiform is supported by its possession of a nasal capsule that is occupied by the ethmopalatine bones. This character was first defined by Patterson and Rosen (1977) and has since been identified as an unequivocal synapomorphy of Ichthyodectiformes in subsequent cladistics analyses (Stewart 1999; Mhitaryan and Averianov 2011; Cavin et al. 2013). The assignment of QM F44329 to Ichthyodectoidei is further supported by its possession of the following four characters: (i) a long and high triangular-shaped supraoccipital crest, with well-developed epioccipital crests extending posteriorly either side of the supraoccipital crest (compare Figs. 4 and 6); (ii) parietals that are set far from the posterior border of the cranium (in QM F44329 and the majority of the ichthyodectoid fishes, these bones are fused to form a mesoparietal); (iii) an intercalar bone that forms the posterior part of the hyomandibular fossa; and (iv) a massive palatine head that forms a disc-shaped, malleolus-like bone.

Within Ichthyodectoidei, QM F44329 can be considered more derived than *Thrissops* on account of the following characters listed in Mhitaryan and Averianov (2011): a parietal devoid of sensitive pit openings (character 7); a proportionately deep premaxillomaxillary contact (character 22), and dentary symphysis (character 28); an angular that contributes to part of the mandibular facet (character 30); and a first pectoral fin ray that is stout and blade-like (character 42).

Among described ichthyodectoids, the preserved osteology of QM F44329 most closely resembles that of specimens referred to *Cladocyclus*. It lacks key synapomorphies of Saurodontidae (Stewart 1999), Ichthyodectidae (Romer 1966), and Unamichthyidae (Alvarado-Ortega 2004), as listed in the analyses of Patterson and Rosen (1977), Maisey (1991a) and Mhitaryan and Averianov (2011). However, it should be noted that the monophyly, taxonomic content and phylogenetic relationships of the latter three taxa within Ichthyodectoidei requires a detailed review, re-description of

Downloaded From: https://bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

both a large number of poorly-known ichthyodectiform taxa (e.g., *Cooyoo australis*, *Chiromystus* spp., *Proportheus,* and *Prymnetes longiventer*), and the inclusion of these taxa in more inclusive phylogenetic analyses.

Cladocyclus gardneri is unusual among ichthyodectiforms with respect to the morphology of its cleithrum. The cleithrum in *C. gardneri* has a horizontal arm that is aligned at approximately 90° to the vertical arm (Maisey 1991a: 198, 205). In all other ichthyodectiforms, the angle between the horizontal and vertical arms of the cleithrum is more obtuse. In common with *C. gardneri*, QM F44329 also has a cleithrum with arms that are perpendicular to each other (Fig. 7D, E). The morphology of the cleithrum in closely related taxa such as *Aidachar* is not known. *Vallecillichthys* may also have a cleithrum with perpendicular arms (Fig. 7F). The cleithrum of QM F44329 can be distinguished from that of *C. gardneri* and *Vallecillichthys* on account of the horizontal arm being approximately twice the length of the vertical arm. In both these taxa and *Allothrissops mesogaster*, the two arms are approximately the same length, and in most other ichthyodectiforms the vertical arm is longer than the horizontal arm (Fig. 7).

Although the nature of the articulation with the lower jaw for the quadrate remains unknown in *Occithrissops*, *Thrissops*, *Eubiodectes*, *Chiromystus*, *Chirocentrites*, *Cooyoo*, *Prymnetes*, *Faugichthys*, *Saurocephalus*, and *Proportheus*, Alvarado-Ortega (2004, 2005) regarded the participation of the articular, retroarticular and angular bones in the mandibular articular facet in *Cladocyclus* (Patterson and Rosen 1977: fig. 7B) as a likely apomorphic condition. Significantly QM F44329 also shows this condition. The inclusion of the articular and retroarticular in the mandibular articular facet is widely distributed among ichthyodectiforms (e.g., *Aidachar*, *Unamichthys*, *Prosaurodon*, *Saurodon*, *Vallecillichthys*, *Gillicus*, *Xiphactinus*, and *Ichthyodectes*) that are either more derived or more plesiomorphic than *Cladocyclus* (see Alvarado-Ortega 2004). The same condition also occurs in *Allothrissops*, "leptolepids" and other basal teleosteans, in which it is considered symplesiomorphic (Nelson 1973; Patterson and Rosen 1977). Also consistent with *Cladocyclus gardneri*, the visible portion of the hyomandibular facet of QM F44329 appears to be elongated and continuous, unlike *Aidachar* (*Cladocyclus*) *pankowskii* and *A. paludalis*, where it is clearly divided into a deep anterior and a shallow posterior facet (Forey and Cavin 2007; Mhitaryan and Averianov 2011).

Forey and Cavin (2007) diagnosed *Aidachar* (*Cladocyclus*) *pankowskii* using two characters relating to the morphology of the orbital and postorbital sections of the parasphenoid. Angles ranging from 149–160° occur in the ichthyodectids *Xiphactinus*, *Ichthyodectes*, and *Vallecillichthys*, as well as *Cooyoo* and *Faugichthys* (see Bardack 1965; Taverne 1986; Lees and Bartholomai 1987; Taverne and Chanet 2000; Blanco-Piñón and Alvarado-Ortega 2007; Forey and Cavin 2007). In contrast, this angle is about 130° in *Cladocyclus gardneri* (Maisey 1991a), QM F44329 and other Jurassic and Lower Cretaceous ichthyodectiforms, whilst in *A. pankowskii* the angle is 155°.

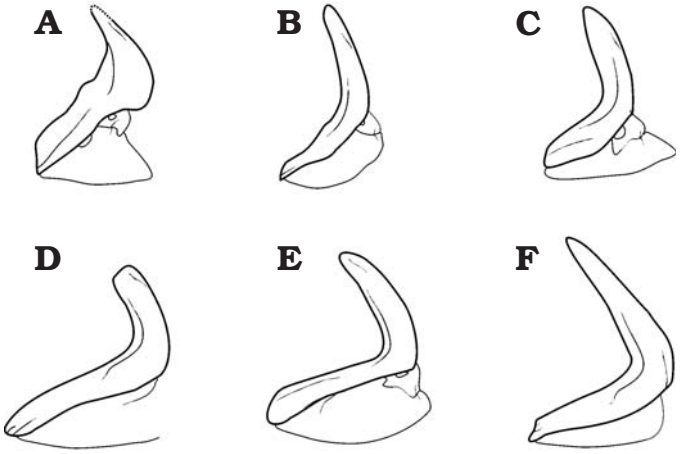


Fig. 7. Outlines of various ichthyodectiform pectoral girdle (cleithrum, coracoid, and scapular) arrangements in lateral external view. **A**. *Allothrissops mesogaster* (Agassiz, 1843) (redrawn from Patterson and Rosen 1977: fig. 10). **B**. *Thrissops formosus* Agassiz, 1833 (redrawn from Taverne 1977: fig. 5). **C**. *Unamichthys espinosai* Alvarado-Ortega, 2004 (IGM 8373). **D**. *Cladocyclus geddesi* sp. nov. (QM F44329). **E**. *Cladocyclus gardneri* Agassiz, 1841 (AMNH 11877). **F**. *Vallecillichthys multivertebratum* Blanco and Cavin, 2003 (redrawn from Blanco-Piñón 2003: fig. 9.2).

The second character used by Forey and Cavin (2007) in their diagnosis of *Aidachar* (*Cladocyclus*) *pankowskii* relates to the projections of the longitudinal axes of the hyomandibular facet and the orbital section of the parasphenoid intersecting each other beyond the anterior border of the skull (i.e., in the ethmoid area). This condition also occurs in *Xiphactinus*, *Ichthyodectes*, and *Vallecillichthys*. In *Cladocyclus gardneri* and QM F44329, these projections cross each other in the ethmoid area of the skull (see Figs. 3 and 6).

Based on the peculiar morphology of the cleithrum (the long axes of the horizontal and vertical arms being perpendicular to each other), and mandibular articular facet (articular surface comprises three bones: the angular, the articular, and the retroarticular), we refer QM F44329 to the ichthyodectiform genus *Cladocyclus*. QM F44329 can be distinguished from other species of *Cladocyclus* based on a more elongate horizontal arm of the cleithrum and a supraoccipital crest that is gently convex posteriorly (in specimens referred to *C. gardneri*, the posterior margin of the supraoccipital crest is always concave (see Patterson and Rosen 1977: figs. 1, 3). The number of dentary and maxillary teeth is also different. In light of these differences, its Australian provenance and upper Albian age, we therefore propose that the specimen can be assigned to a new species, *Cladocyclus geddesi* sp. nov. With the collection of more material, in particular specimens that include a caudal skeleton, we hope that the diagnosis of *C. geddesi* will be further strengthened.

Comments on other Australian Cretaceous ichthyodectiforms.—*Cooyoo australis* is the only other ichthyodectiform known from Australia. The taxon is represented by thirteen specimens, all from the shallow marine limestone of the Lower Cretaceous (upper Albian) Allaru Mudstone and Toolebuc Formation of western Queensland.

Downloaded From: https://bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

Cooyoo australis was initially described by Woodward (1894) based on a single fragmented teleostean skull (Lees and Bartholomai 1987) under the name *Portheus australis*. Hay (1898) subsequently determined that *Portheus* was a junior synonym of *Xiphactinus*, such that the classification became *Xiphactinus australis* (Hay 1898). This name was maintained for 90 years until Lees and Bartholomai (1987) recognized it as a distinct genus, *Cooyoo*.

There are a number of differences between *Cooyoo australis* and *Cladocyclus* (including QM F44329). For instance, the lower jaw on *Cladocyclus* has an anteroventral keel, whilst in *Cooyoo australis* the lower jaw is simple with no keel-like projection. The basic outline of the lower jaw also differs in that *Cooyoo australis* has a shallow lower jaw profile resulting in a sharp rectangular outline. On the other hand, *Cladocyclus* has a deeper profile to the lower jaw resulting in a more rounded outline than the condition in *Cooyoo australis*.

The supraoccipital crest also differs between the two taxa. *Cooyoo australis* has a high and sharp crest forming an equilateral triangle that rises dorsally from the dorsal surface of the cranium at an angle of approximately 15°. In *Cladocyclus*, the supraoccipital forms an obtuse triangle, overhanging the occiput and rising from the dorsal surface of the cranium at 30°.

The construction, shape and morphology of the preopercle and preopercular canal are also different between *Cooyoo australis* and *Cladocyclus*. *Cooyoo australis* has a solidly constructed preopercle with an I-shaped outline (Lees and Bartholomai 1987: fig. 7), similar to *Xiphactinus,* with simple anterior pits in the base of the preopercule for the preopercular cannal. On the other hand, the preopercular of *Cladocyclus* (inclusive of QM F44329) has a boomerang- or L-shaped outline, with a complex preopercular canal morphology, comprising a single canal running down the arm of the preopercular that branches anteriorly.

Both QM F44329 and available material of *Cooyoo australis* lack caudal regions. This seems to be a taphonomic feature of all of Australia's Lower–mid-Cretaceous fish fossils that are preserved in nodules.

Comments on "*Cladocyclus sweeti*" Woodward, 1894.—Woodward (1894) described some fish remains from the "Rolling Downs Formation" of Afton Downs Station, southwest of Hughenden, Queensland. These specimens were accessioned to Museum Victoria, and Woodward (1894) assigned them to *Cladocyclus sweeti.* Woodward (1894) included five isolated scales and a string of five caudal vertebrae (MV P15571, MV P15572, MV P15573, MV P15574, MV P15575, MV P24127), with five of these having originally been collected by George Sweet, a geologist. It is not known, if these specimens were all found within the same area of outcrop or if they were found from various localities on Afton Downs Station.

The "Rolling Downs Formation" is now referred to as the Rolling Downs Group, and includes a number of distinct formations that crop out across western Queensland (Fig. 2), all of which contain fish remains. Based on the location of Afton Downs Station and the sediment in which the specimens are preserved, it seems likely that these fossils derive from the upper Albian Toolebuc Formation.

The vertebrae could quite possibly belong to a cladocyclid fish, although it is most likely that they pertain to *Cooyoo australis* (see above). The vertebrae of *Cooyoo australis* are very similar to those of other ichthyodectids (including *Cladocyclus*) and basal teleost genera, so a precise referral is hard to establish. Similarly, the vertebrae of *Cooyoo australis* and *Cladocyclus* are constructed much the same as in other basal teleosts in that they are robust with a series of longitudinal groves laterally.

The morphology of the scales assigned to "*Cladocyclus sweeti*" by Woodward (1894) is typical of most basal teleosts (Schultze 1996). The scales of *Cooyoo australis* are not described, making comparisons to *Cladocyclus* or any other ichthyodectiform problematic.

As with most fossils from the Toolebuc Formation, the remains assigned to "*Cladocyclus sweeti*" occur as isolated bones and scales in bonebed-like layers, such that some bones may have accumulated together during storm and tidal events. The only way to know if certain bones and scales belong to individual fish is to find complete articulated specimens with the same morphology.

Until more Lower Cretaceous fish fossils with associated scales are described, the material referred to "*Cladocyclus sweeti*" by Woodward (1894) should be regarded as Teleostei incertae sedis.

Phylogenetic relationships

To test the validity of our assignment of QM F44329 to *Cladocyclus*, we included the specimen in a phylogenetic analysis using the taxon-character-matrix of Cavin et al. (2013). Character definitions and scores that we used were the same as for Cavin et al. (2013), except that in order to remove ambiguity around *C. gardneri* we only used scores for adult specimens, such that characters 22 (scored as 0 in our analysis), 24 (scored as 0) and 45 (scored as 1) were not considered polymorphic (in Cavin et al. 2013) these characters included scores for both juvenile and adult specimens). We also added a new character (70) relating to the morphology of the cleithrum (see Appendix 1 for character description and taxon character matrix). The data were analysed using a heuristic search (1000 replicates in "Traditional search" with TBR branch swapping) in T.N.T. 1.1 (Goloboff et al. 2003), with *Amia calva*, *Hiodon alosoiodes*, *Leptolepis coryphaenoides*, and *Elops hawiensis* as outgroups, following Cavin et al. (2013). All characters were treated as unordered, characters that were not visible on available specimens were scored with a question mark, and characters that were not applicable to specific taxa were scored as gaps (–).

Analysis of all 26 ingroup taxa and 70 characters revealed three equally most-parsimonious trees of 223 steps, with a consistency index (CI) of 0.45 and a retention index (RI)

Downloaded From: https://bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

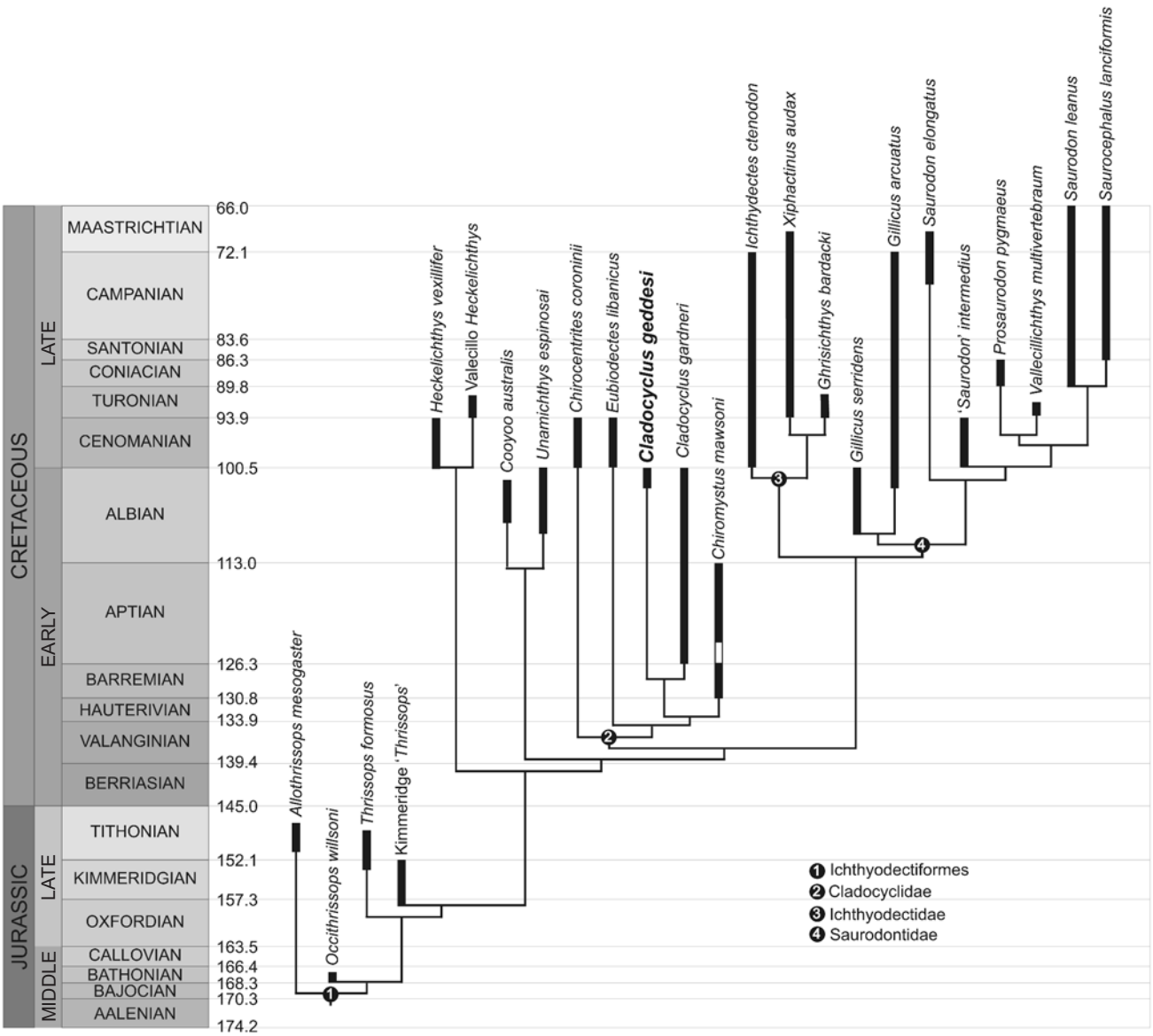


Fig. 8. Phylogenetic relationships of *Cladocyclus geddesi* sp. nov. (QM F44329). Stratigraphically calibrated strict consensus of 3 most-parsimonious trees (length 223, CI 0.45, RI, 0.67) analysed using T.N.T. 1.1 (Goloboff et al. 2003), with a heuristic search (1000 replicates in "Traditional search" with TBR branch swapping). See Appendix 1 for new character descriptions, taxon-character matrix, and a list of character state transformation for each taxon. Age ranges correspond to those provided in Cavin et al. (2013).

of 0.67. A strict consensus for the ichthyodectiform part of these trees is shown in Fig. 8. The overall topology of this consensus tree is consistent with that of the preferred consensus tree from Cavin et al. (2013: figs 40, 42), with the only uncertainty relating to the position of *Pachythrissops* at the base of the tree in a polytomy with *Hioden alosoides*, one of the outgroup taxa, indicating that it is probably not an ichthyodectiform as was proposed by Cavin et al. (2013). Significantly, in this consensus tree QM F44329 was recovered as the sister taxon to *C. gardneri* within Cladocyclidae, supporting its assignment to *Cladocyclus* based on comparative morphology. Within the framework of our data, *C. gardneri* and *C. geddesi* are united by the presence of uniformly sized maxillary teeth, a condition they share with all other ichthyodectiforms except *Chirocentrites coroninii* and *Xiphactinus audax*. The possession of this character state in *C. gardneri* and *C. geddesi* is most parsimoniously regarded as a reversal from the derived condition where the size of the maxillary teeth varies. Cladocyclids are united by the presence of 8 hypurals, but the condition in *C. geddesi* is unknown. The inclusion of character 70 (which relates to the morphology of the cleithrum) did not seem to affect the topology of the trees or the sister-group relationship between *C. gardneri* and *C. geddesi*; the same result was recovered when character 70 was excluded for the analysis. This could be because this character is scored for just over 50% of taxa in the matrix. With the addition of new taxa and improved sampling, we suspect that this character may help to strengthen the relationships among some taxa, particularly cladocyclids such as *C. gardneri* and *C. geddesi*.

Downloaded From: https://bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

Discussion

The occurrence of *Cladocyclus geddesi* in the Winton Formation of central-western Queensland has interesting palaeobiological and palaeobiogeographic implications. Previously, confirmed occurrences of *Cladocyclus* have been restricted to the presence of the type species, *C. gardneri,* in the Aptian–Albian of north-eastern Brazil (Leal and Brito 2004; Brito and Yabumoto 2011) and the upper Cenomanian–lower Turonian *Cladocyclus* sp. of Morocco (Martill et al. 2011). Although the upper Albian age of the new Australian specimen falls within the current temporal range of the genus, geographically it is very much an outlier, and its occurrence in a likely freshwater depositional setting is unusual.

Cladocyclus gardneri had a preference for epicontinental or shallow marine habitats, as is best exemplified by the relative abundance in the Santana Formation. Rarer specimens of *C. gardneri* from the laminated limestone of the Crato Formation are now thought to represent juvenile individuals, with the thermally and salinally stratified lacustrine habitat of the Crato lagoon and surrounding fluvial systems likely serving as a nursery area, as occurs with many extant teleosts (Leal and Brito 2004). Migration to and from the Crato lagoon to the epicontinental seaway that extended from the Carribbean Tethys to the south (Alvarado-Ortega and Brito 2010) most likely occurred via the fault-bounded grabens of the Recôncavo-Tucano-Jatobá Basin complex to the south, the Portigua Basin to the north, or the Parnaíba Basin to the west (Berthou 1990; Martill 1993; Leal and Brito 2004).

The occurrence of a possible new species of *Cladocyclus* in a coastal setting in the upper Cenomanian–lower Turonian marine sediments of Gara Sbaa, in the Kem Kem area of Morocco, is not unexpected given close proximity of that region to north-eastern Brazil (Martill et al. 2011), and involves only a short dispersal route along the north Atlantic coastline of western African. However, explaining the intercontinental dispersal of *Cladocyclus* from equatorial western Gondwana (north-eastern Brazil) to mid-low latitudinal eastern Gondwana (central-western Queensland) is more complex. We propose two scenarios.

The first scenario requires *Cladocyclus* to have been widespread in freshwater environments throughout Gondwana during the Early Cretaceous. This scenario is similar to the hypothesis of Maisey (2000), who suggested that Gondwanan freshwater cladocyclids existed in small, interconnected rift lakes in western Gondwana (South America and Africa) prior to the development of an equatorial seaway and the rifting of South America from Africa. However, this hypothesis is weakened because fossils that Maisey (2000) considered closely related or synonymous with *Cladocyclus* (placed within his family Cladocyclidae) have been either assigned to new taxa outside Cladocyclidae (e.g., *Ogunichthys*), better characterized as individual genera in their own right (e.g., *Proportheus*), or shown to not be closely related to *Cladocyclus* at all (e.g., *Chirocentrites*, *Chiromystus*) (see Taverne 2009, 2010; Alvarado-Ortega and Brito 2010).

Additionally, the occurrence of *Cladocyclus* in fluvial habitats in the late Albian of central-western Queensland would require that the most recent common ancestor of the Australian and Brazilian/African *Cladocyclus* existed prior to the Aptian, and would predict the occurrence of this genus in the intervening freshwater environments of southern South America, Antarctica, and possibly India-Madagascar during the mid-Cretaceous. Although by no means implausible, we do not consider this explanation very likely. Given the apparent ability of *Cladocyclus* to tolerate both marine and freshwater conditions, the need to invoke vicariant events that preclude a marine dispersal phase is not essential to explain the presence of *Cladocyclus* in eastern Gondwana during the late Albian.

The second, and probably more parsimonious, scenario involves the marine dispersal of *Cladocyclus* along the fragmenting Gondwanan coastlines, and its subsequent invasion of freshwater systems. Such a scenario would be similar to the Miocene–Pliocene intercontinental dispersal and radiation of *Crocodylus* through the sub-tropical Indo-Pacific, Europe, and New World (Brochu 2000; Delfino et al. 2007; Meganathan et al. 2010). During the late Albian and early Cenomanian, the marine entrance to the Eromanga Sea was from the north through the Carpentaria Basin (Dettmann et al. 1992: fig. 9; Bryan et al. 1997: fig. 12). *Cladocyclus* could have dispersed to this part of Australia from north-eastern Brazil via the coastlines surrounding Africa, Antarctica, and possibly India-Madagascar, along two possible routes: a southerly route along the margin of the incipient South Atlantic–Indian Ocean or a northerly route along the margin of the equatorial Tethys Sea. Both routes seem equally plausible. As with the aspidorynchid *Richmondichthys* (Brito 1997; Maisey 2000; Bartholomai 2004), *Cladocyclus* may therefore represent part of a distinct southern fish fauna that existed in the seas and adjacent coastal areas surrounding Gondwana during the mid-Cretaceous. These two scenarios may be tested through future discoveries of *Cladocyclus* in either marine or freshwater deposits in India, Madagascar, or Antarctica.

Palaeogeographical reconstructions place Isisford at approximately 55°S during the late Albian. Dettmann et al. (1992) postulated that the climate in the Eromanga Basin at this time was similar to that experienced today in warm-temperate regions. Thus, in addition to a broad temporal and geographic distribution, the occurrence of *Cladocyclus* in the Winton Formation demonstrates that species of this fish existed across a wide latitudinal gradient, and that it could potentially tolerate a broad range of water temperatures.

Similar to other species of *Cladocyclus*, *C. geddesi* was very likely a fast-swimming, predatory fish, best suited to open water conditions. Given the occurrence of other species of *Cladocyclus* in shallow marine depositional settings elsewhere, the discovery of *C. geddesi* in a fluvial setting in the Winton Formation at Isisford is unusual but not unex-

Downloaded From: https://bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

pected. During the early late Albian, the fluvial sediments of the Winton Formation at and near Isisford were deposited by distal channel settings associated with extensive river systems that opened into the broad lagoonal, estuarine and marginally developed backwater swamp environments around the edge of the Eromanga Sea, currently represented by the mudstone, siltstone, and carbonaceous rich mud of the lowermost Winton Formation and uppermost Mackunda Formation. The shallow waters of the seaway and the more marginal paralic areas would have been an ideal habitat for fast-swimming, open water fishes. Some of these fishes, such as *C. geddesi* presumably swam upstream into more proximal fluvial settings, as is common for analogous fishes in similar environments today. At some point, we would therefore expect to see the remains of *C. geddesi* or a closely related ichthyodectiform in the Mackunda Formation, or even the shallow marine sediments of the Toolebuc Formation and Allaru Mudstone.

To date, the remains of large, fast swimming teleosts like *Cladocyclus* have yet to be discovered in younger (Cenomanian–lower Turonian; Tucker et al. 2013) parts of the Winton Formation. The only fish remains known from the Upper Cretaceous part of the Winton Formation are isolated tooth plates of three species of ceratodont lungfish: *Ceratodus* sp., *Metaceratodus wollastoni*, and *Metaceratodus ellioti* (Kemp 1991, 1997; Dettmann et al. 1992), all of which derive from fine-grained sandstone and silt suggestive of deposition in point bar deposits, crevasse splays from flood events and ox-bow lakes (Salisbury et al. 2006b; Tucker et al. 2011). Despite over ten years of searching, no dipnoan remains have been recovered from Isisford. Although the dataset is limited, these differences seem to reflect a change in the Winton Formation's fish fauna that corresponds with a temporal shift from predominately lower energy, potentially tidally influenced distal channel sets (the lowermost Winton Formation) to higher flow flood plain and meandering channel regimes (the uppermost Winton Formation) as the Eromanga Sea retreated northward and gradually infilled with terrestrial sediments. The lungfish seem to be restricted to backwater habitats associated with the latter depositional environments, while the fast-swimming teleosts like *C. geddesi* the open water habitats of the former.

The discovery of *Cladocyclus geddesi* in the upper Albian of Queensland also provides evidence for faunal interchange between eastern and western Gondwana during the Early to mid-Cretaceous, as predicted from palaeogeographic reconstructions (Smith et al. 1994; Hay et al. 1999; Scotese 2001; Sereno et al. 2004). Other elements of Australia's continental vertebrate fauna that support this palaeobiogeographic scenario include the likely occurrence of the otherwise South American megaraptoran theropod *Megaraptor* in the upper Aptian–lower Albian of southern Victoria (Salisbury et al. 2007; Smith et al. 2008), and, also in the Winton Formation, the closely related *Australovenator wintonensis* (Benson et al. 2010c; Agnolin et al. 2010; White et al. 2012, 2013) and somphospondyl titanosauriform sauropods (Salgado 1993; Molnar 2001; Molnar and Salisbury 2005; Salisbury et al. 2006b; Hocknull et al. 2009). Reports of Australian dinosaurs with potential palaeobiogeographic connections to Asia, such as ornithomimosaurs, oviraptorosaurs, neoceratopsians, and tyrannosaurids (Rich and Vickers-Rich 1994, 2003; Currie et al. 1996; Benson et al. 2010a, b, 2012) have also recently been questioned, with alternative interpretations supporting links to terrestrial vertebrate faunas from adjoining Gondwanan landmasses (Salisbury et al. 2007; Agnolin et al. 2010; Herne et al. 2010). Other elements of Australia's continental vertebrate fauna were most likely either endemic (e.g., the styracosternan iguanodontian *Muttaburrasaurus*; Bartholomai and Molnar 1981; Agnolin et al. 2010), or possible relicts of ancient lineages (e.g., temnospondyl amphibians, Warren et al. 1997; ausktribosphenid and monotrematan mammals, Pridmore et al. 2005, australosphenidans sensu Kielan-Jaworowska et al. 2004; dicynodont? synapsids, Thulborn and Turner 2003).

Despite its position at the eastern extremity of the eastern Gondwanan peninsula, it now seems likely that Australia's continental fauna was not overly isolated from the rest of Gondwana during the Early to mid-Cretaceous, as has often been proposed (e.g., Vickers-Rich et al. 1988; Molnar 1992; Thulborn and Turner 2003). Any geographic or climatic barriers that did exist during this time probably only acted as filter, and some taxa, such *Cladocyclus*, appear to have made it through.

Acknowledgements

The authors thank Ian Duncan and members of the Isisford community for their hospitality and assistance during fieldwork. We are grateful to Kerry Geddes (UQ) for assistance with preparation of the specimen, Peter Colls (UQ) for rock-cutting and assistance with resin embedding, Anthony O'Toole (UQ) for photography, Carole Burrow (UQ) and John Long (Museum Victoria, Melbourne, Australia) for advice on acid preparation, and Jay Nair (UQ) for help with the use of TNT. Kerry Geddes, Matt Herne, Tim Holt, Lucy Leahey (all UQ), Nick Milne (University of Western Australia, Perth, Australia), Selwin Smith (Barcaldine, Queensland, Australia) and Murray Williams (Mount Perry, Queensland, Australia) are all thanked for their contributions during the 2005 UQ Isisford Expedition. John Stewart and John Maisey (AMNH) are also thanked for their comments on ichthyodectiform phylogeny and identification. Insightful comments from Lionel Cavin (Villa de Genève, Switzerland) and Gloria Arratia (University of Kansas, Lawrence, USA) on ichthyodectiforms, and from Ryan Tucker (James Cook University, Townsville, Queensland, Australia) on the sedimentology of the Winton Formation greatly improved earlier versions of this paper. We also thank Ana María Rocha (Coyoacán, Mexico City, Mexico) for technical assistance with illustrations and translations. RWB would also like to acknowledge the support of the Lorna Milgate Scholarship Trust. This research was funded in part by the Australian Research Council (LP0347332 and LP0776851) and The University of Queensland (to SWS), in association with Isisford Shire Council, Longreach Regional Council, Winton Shire Council, Land Rover Australia, the Queensland Museum and Carnegie Museum of Natural History. J.A.O. was supported by UNAM through project PAPIIT-106011.

Downloaded From: https://bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

References

Agassiz, L. 1833–1844. *Recherches sur les poissons fossiles*. 5 volumes, with atlas. 1420 pp. Neuchâtel, Petitpierre.

Agnolin, F.L., Ezcurra, M.D., Pais, D.F., and Salisbury, S.W. 2010. An overview of the Cretaceous non-avian dinosaur faunas from Australia and New Zealand: evidence for their Gondwanan affinities. *Systematic Palaeontology* 8: 257–300.

Alvarado-Ortega, J. 2004. Description and relationships of a new ichthyodectiform fish from the Tlayúa Formation (Early Cretaceous: Albian), Puebla, Mexico. *Journal of Vertebrate Paleontology* 24: 802–813.

Alvarado-Ortega, J. 2005. *Systematica de Los Peces Ichthyodectiformes de las Cantera Tlayua, Puebla Mexico*. 302 pp. Unpublished Doctoral Thesis, Instituto de Geologica, Instituto de Geología, Universidad Nacional Autónoma de México, Mexico City.

Alvarado-Ortega, J. and Brito, P.M. 2010. A new ichthyodectiform fish (Teleostei) from the Early Cretaceous Marizal Formation, Northeast Brazil. *Palaeontology* 53: 297–306.

Bardack, D. 1965. Anatomy and evolution of chirocentrid fishes. *The University of Kansas paleontological contributions: Vertebrata* 10: 1–88.

Bardack, D. and Sprinkle, G. 1969. Morphology and relationships of saurocephalid fishes. *Fieldiana Geology* 16: 297–340.

Bartholomai, A. 2004. The large aspinorhynchid fish, *Richmondichthys sweeti* (Etheridge Jnr and Smith Woodward, 1891) from Albian marine deposits of Queensland, Australia. *Memoirs of the Queensland Museum* 49: 521–536.

Bartholomai, A. and Molnar, R.E. 1981. *Muttaburrasaurus*, a new iguanodontid (Ornithischia: Ornithopoda) dinosaur from the Lower Cretaceous of Queensland. *Memoirs of the Queensland Museum* 20: 319–349.

Benson, R.B., Barrett, P.M., Rich, T.H., and Vickers-Rich, P. 2010a. A southern tyrant reptile. *Science* 327: 327 1613.

Benson, R.B., Barrett, P.M., Rich, T.H., Vickers-Rich, P., Pickering, D., and Holland, T. 2010b. Response to Comment on "A southern tyrant reptile". *Science* 329: 1013-d.

Benson, R.B., Carrano, M.T., and Brussatte, S.L. 2010c. A new clade of archaic large bodied predatory dinosaurs (Theropoda: Allosauroidea) that survived to the latest Mesozoic. *Naturwissenschaften* 97: 71–78.

Benson, R.B.J., Rich, T.H., Vickers-Rich, P., and Hall, M. 2012. Theropod fauna from southern Australia indicates high polar diversity and climate-driven dinosaur provinciality. *PLoS One* 7(5): e37122.

Berthou, P.Y., 1990. Le bassin d'Araripe et les petits bassins intracontinentaux voisins (NE du Brésil): formation et évolution dans le cadre de l'ouverture de l'Atlantique équatorial. Comparaison avec les bassins ouest-africains situés dans le même contexte. *In*: D. de A. Campos, M.S.S. Viana, P.M. Brito, and G. Beurlen (eds.), *Atas do I Simpósio sobre a Bacia do Araripe e Bacias Interiores do Nordeste*, *Crato*, 113–134. Departmento Nacional da Produção Mineral (DNPM), Crato (CE), Brazil.

Blanco, A. and Cavin, L. 2003. New Teleostei from the agua Nueva Formation (Turonian), Vallecillo (NE Mexico). *Comptes Rendus Palevol* 2: 299–306.

Blanco-Piñón, A. 2003. *Peces fósiles de la Formación Agua Nueva (Turoniano) en el municipio de Vallecillo, Nuevo León, NE de México*. 330 pp. Unpublished Doctoral Thesis, Facultad de Ciencias de la Tierra, Universidad Autónoma de Nuevo León, Linares, México.

Blanco-Piñón, A. and Alvarado-Ortega, J. 2007. Review of *Vallecillichthys multivertebratum* (Teleostei: Ichthyodectiformes), a Late Cretaceous (early Turonian) "Bulldog fish" from northeastern Mexico. *Revista Mexicana de Ciencias Geológicas* 24: 450–466.

Brito, P.M. 1997. Révision des Aspidorhynchidae (Pisces, Actinopterygii) du Mésozoïque: ostéologie, relations phylogénétiques, donnéss environmentales et biogéografiques. *Geodiversitas* 19: 681–772.

Brito, P.M. and Yabumoto, Y. 2011. An updated review of the fish fauna from the Crato and Santana Formations in Brazil, a close relationship to the Tethys faunas. *Bulletin Kitakyushu Museum of Natural History, Serie A* 9: 107–136.

Brochu, C.A. 2000. Phylogenetic relationships and divergence timing of *Crocodylus* based on morphology and the fossil record. *Copeia* 2000: 657–673.

Bryan, S.E., Constantine, A.E., Stephens, C.J., Ewart, A., Schön, R.W., and Parianos, J. 1997. Early Cretaceous volcano-sedimentary successions along the eastern Australian continental margin: implications for the break-up of eastern Gondwana. *Earth and Planetary Science Letters* 153: 85–102.

Cavin, L., Tong, H., Boudad, L., Meiser, C., Piuz, A., Tabouelle, J., Aarab, M., Amiot, R., Buffetaut, E., Dyke, G., Hua, S., and Le Loeuff, J. 2010. Vertebrate assemblages from the early Late Cretaceous of southeastern Morocco: an overview. *Journal of African Earth Sciences* 57: 391–412.

Cavin, L., Forey, P.L., and Giersch, S. 2013. Osteology of *Eubiodectes libanicus* (Pictet & Humbert, 1866) and some other ichthyodectiformes (Teleostei): phylogenetic implications. *Journal of Systematic Palaeontology* 11: 115–177.

Clifford, H.T. and Dettmann, M.E. 2005. First record from Australia of the Cretaceous fern genus *Tempskya* and the description of a new species, *T. judithae*. *Review of Palaeobontany and Palynology* 134: 71–84.

Cook, A.G. 2005. First record of fossil freshwater gastropods within the Winton Formation. *Memoirs of the Queensland Museum* 51: 406.

Coombs, W.P. and Molnar, R.E. 1981. Sauropoda (Reptilia, Saurischia) from the Cretaceous of Queensland. *Memoirs of the Queensland Museum* 20: 351–373.

Cope, E.D. 1871. Note of some Cretaceous vertebrata in the State Agricultural College of Kansas, U.S.A. *Proceedings of the American Philosophical Society* 12: 168–170.

Currie, P.J., Vickers-Rich, P., and Rich, T.H., 1996. Possible oviraptorosaur (Theropoda, Dinosauria) specimens from the Early Cretaceous Otway Group of Dinosaur Cove, Australia. *Alcheringa* 20: 73–79.

Delfino, M., Böhme, M., and Rook, L. 2007. First European evidence for transcontinental dispersal of *Crocodylus* (late Neogene of southern Italy). *Zoological Journal of the Linnean Society* 149: 293–307.

Dettmann, M.E. and Clifford, H.T. 2000. Gemmae of the Marchantiales from the Winton Formation ("mid"-Cretaceous), Eromanga Basin, Queensland. *Memoirs of the Queensland Museum* 45: 285–292.

Dettmann, M.E., Clifford, H.T., and Peters, M. 2009. *Lovellea wintonensis* gen. et sp. nov.—Early Cretaceous (late Albian), anatomically preserved, angiospermous flowers and fruits from the Winton Formation, western Queensland, Australia. *Cretaceous Research* 30: 339–355.

Dettmann, M.E., Molnar, R.E., Douglas, J.G., Burger, D., Fielding, C., Clifford, H.T., Francis, J., Jell, P., Rich, T.H., Wade, M., Vickers-Rich, P., Pledge, N., Kemp, A., and Rozefelds, A. 1992. Australian Cretaceous terrestrial faunas and floras: biostratigraphic and biogeographic implications. *Cretaceous Research* 13: 207–262.

Everhart, M.J. 2005. *Oceans of Kansas—A natural history of the Western Interior Sea*. 320 pp. Indiana University Press, Bloomington.

Exon, N.F. and Senior, B.R. 1976. The Cretaceous geology of the Eromanga and Surat Basins. *Bureau of Mineral Resources, Geology and Geophysics, Bulletin* 1: 33–50.

Faggotter, S.J., Salisbury, S.W., and Yabumoto, Y. 2007. A new possible halecomorph fish from the mid-Cretaceous (Albian–Cenomanian) Winton Formation of Isisford, central-western Queensland, Australia. *In*: A. Warren (ed.), *11th Conference of Australian Vertebrate Palaeontology, Evolution and Systematics, Abstracts*, 26–27. Geological Society of Australia, Melbourne.

Forey, P.L. and Cavin, L. 2007. A new species of *Cladocyclus* (Teleostei: Ichthyodectiformes) from the Cenomanian of Morocco. *Palaeontologia Electronica* 10 (3): 1–10. http://palaeo-electronica.org/2007_3/133/

Goloboff, P.A., Farris, J.S., and Nixon, K.C. 2003. *T.N.T.: Tree analysis using new technology*. Version Willi Hennig Society Edition 1.1. Willi Hennig Society. http://www.zmuc.dk/public/phylogeny/TNT/.

Gray, A.R.G., McKillop, M., and McKellar, J.L. 2002. Eromanga Basin stratigraphy. *In*: J.J. Draper (ed.), *Geology of the Cooper and Eromanga Basins, Queensland*, 30–56 + references and figures. Department of Natural Resources and Mines, Brisbane.

Downloaded From: https://bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

Hay, O.P. 1898. Observations on the genus of fossil fishes called by Professor Cope, *Portheus*, by Dr. Leidy, *Xiphactinus*. *Zoological Bulletin* 2: 25–54.

Hay, W.W., Deconto, R.M., Wold, C.N., Wilson, K.M., Voigt, S., Schulz, M., Wold, A.R., Dullo, W.-C., Ronov, A.B., Balukhovsky, A.N., and Söding, E. 1999. Alternative global Cretaceous paleogeography. *Special Papers of the Geological Society of America*, 332: 1–47.

Hays, I. 1830. Description of a fragment of the head of a new fossil animal discovered in a marl pit, near Mooretown, New Jersey. *Transactions of the American Philosophical Society, Series 2*, 3: 471–477.

Helby, R., Morgan, R., and Partridge, A.D. 1987. A palynological zonation of the Australian Mesozoic. *Association of Australian Palaeontologists Memoir* 4: 1–94.

Herne, M.C., Nair, J.P., and Salisbury, S.W. 2010. Comment on "A southern tyrant reptile". *Science* 329: 1013-c.

Hocknull, S.A. 1997. Cretaceous freshwater bivalves from Queensland. *Memoirs of the Queensland Museum* 42: 223–226.

Hocknull, S.A. 2000. Mesozoic freshwater and estuarine bivalves from Australia. *Memoirs of the Queensland Museu*m 45: 405–426.

Hocknull, S.A. and Cook, A.G. 2008. Hypsilophodontid (Dinosauria: Ornithischia) from the latest Albian, Winton Formation, central Queensland. *Memoirs of the Queensland Museum* 52: 212.

Hocknull, S.A., White, M.A., Tischler, T.R., Cook, A.G., Calleja, N.D., Sloan, T., and Elliott, D.A. 2009. New mid-Cretaceous (latest Albian) dinosaurs from Winton, Queensland, Australia. *PloS ONE* 4 (7): 1–51, e6190.

Jaekel, O. 1909. Beiträge zur Geologie von Kamerun: X. Fischreste aus der Mamfe-Schiefern. *Königlische Preussische Geologische Landesantstalt, Abhandlung, Neue Serie*, 6: 392–398.

Jell, P.A. 2004. The fossil insects of Australia. *Memoirs of the Queensland Museum* 50: 1–124.

Jordan, D.S. 1910. Description of a collection of fossil fishes from the bituminous shale at Riacho Doce, State of Alagoas, Brazil. *Annals of Carnegie Museum* 7: 23–34.

Kemp, A. 1991. Australian Mesozoic and Cainozoic lungfish. *In*: P. Vickers-Rich, J.M. Monaghan, R.F Baird, and T.H. Rich (eds.), *Vertebrate Palaeontology of Australasia*, 465–496. Pioneer Design Studio, Lilydale.

Kemp, A. 1997. Four species of *Metaceratodus* (Osteichthyes: Dipnoi, Family Ceratodontidae) from Australian Mesozoic and Cenozoic deposits. *Journal of Vertebrate Paleontology* 17: 26–33.

Kielan-Jaworowska, Z., Cifelli, R.L., and Luo, Z.-X. 2004. *Mammals from the Age of Dinosaurs: Origins, Evolution, and Structure*. 630 pp. + i–x. Columbia University Press, New York.

Leal, M.E.C. and Brito, P.M. 2004. The ichthyodectiform *Cladocyclus gardneri* (Actinopterygii: Teleostei) from the Crato and Santana Formations, Lower Cretaceous of Araripe Basin, North-Eastern Brazil. *Annales de Paléontologie* 90: 103–113.

Lees, T. and Bartholomai, A. 1987. Study of a Lower Cretaceous actinopterygian (Class Pisces) *Cooyoo australis* from Queensland, Australia. *Memoirs of the Queensland Museum* 25: 177–192.

Leidy, J. 1870. Remarks on *Ichthyodorulites* and on certain fossil mammalians. *American Philosophical Society, Proceedings* 22: 12–13.

Maisey, J.G. 1991a. *Cladocyclus* Agassiz, 1841. *In*: J.G. Maisey (ed.), *Santana Fossils: an Illustrated Atlas*, 190–207. Tropical Fish Hobbyist Publications, Neptune City.

Maisey, J.G. 1991b. *Santana Fossils: an Illustrated Atlas*, 459 pp. Tropical Fish Hobbyist Publications, Neptune City.

Maisey, J.G. 2000. Continental break up and the distribution of fishes of western Gondwana during the Early Cretaceous. *Cretaceous Research* 21: 281–314.

Martill, D.M. 1993. *Fossils of the Santana and Crato Formations, Brazil*. 159 pp. The Palaeontological Association, London.

Martill, D.M., Ibrahim, N., Brito, P.M., Baider, L., Zhouri, S., Loveridge, R., Naish, D., and Hing, R. 2011. A new Plattenkalk Konservat Lagerstätte in the Upper Cretaceous of Gara Sbaa, south-eastern Morocco. *Cretaceous Research* 32: 433–446.

McLoughlin, S., Driannan, A.N., and Rozefelds, A.C. 1995. A Cenomanian flora from the Winton Formation, Eromanga Basin, Queensland, Australia. *Memoirs of the Queensland Museum* 38: 273–331.

McLoughlin, S., Pott, C., and Elliott, D. 2010. The Winton Formation flora (Albian, Cenomanian, Eromanga Basin): implications for vascular plant diversification and decline in the Australian Cretaceous. *Alcheringa* 34: 303–323.

Meganathan, P.R., Dubey, B., Batzer, M.A., Ray, D.A., and Haque, I. 2010. Molecular phylogenetic analysis of genus *Crocodylus* (Eusuchia, Crocodylia, Crocodylidae) and the taxonomic position of *Crocodylus porosus*. *Molecular Phylogenetics and Evolution* 57: 393–402.

Mkhitaryan, T.G. and Averianov, A.O. 2011. New material and phylogenetic position of *Aidachar paludalis* Nesov, 1981 (Actinopterygii, Ichthyodectiformes) from the Late Cretaceous of Uzbekistan. *Proceedings of Zoological Institute RAS* 315: 181–192.

Molnar, R.E. 1991. Fossil reptiles in Australia. *In*: P. Vickers-Rich, J.M. Monaghan, R.F. Baird, and T.H. Rich (eds.), *Vertebrate Palaeontology of Australasia*, 606–702. Pioneer Design Studio, Lilydale.

Molnar, R.E. 1992. Paleozoogeographic relationships of Australian Mesozoic tetrapods. *In*: S. Chatterjee and N.I. Hotton (eds.), *New Concepts in Global Tectonics*, 259–266. Texas Tech University Press, Lubbock.

Molnar, R.E. 2001. A reassessment of the phylogenetic position of Cretaceous sauropod dinosaurs from Queensland, Australia. *In*: H.A. Leanza (ed.), VII International Symposium on Mesozoic Terrestrial Ecosystems. *Asociación Paleontologica Argentia, Buenos Aires*, *Publicación Especial* 7: 139–144.

Molnar, R.E. and Salisbury, S.W. 2005. Observations on Cretaceous sauropods from Australia. *In*: K. Carpenter and V. Tidell (eds.), *Thunder-lizards: The Sauropodomorph Dinosaurs*, 454–465. Indiana University Press, Bloomington.

Müller, J. 1845. Über den Bau und die Grenzen der Ganoiden and über das naturliche System der Fische. *Archiv für Naturgeschichte* 11 (for 1846): 91–141.

Musser, A., Luo, Z., Martinelli, A.G., Lamanna, M.C., Weisbecker, V., Wroe, S., and Salisbury, S.W. 2009. First Australian non-mammalian cynodont: new evidence for the unusual nature of Australia's Cretaceous vertebrates. *In*: K.J. Travouillon, T. Worthy, S.J. Hand, and P. Creaser (eds.), *2009 Conference on Australasian Vertebrate Evolution, Palaeontology and Systematics, 2009 Sydney, Abstracts 93*, 47. Geological Society of Australia, Sydney.

Nelson, G.J. 1973. Relationship of clupeomorphs, with remarks on the structure of the lower jaw in fishes. *In*: P. Greenwood, R.S. Miles, and C. Patterson (eds.), *Interrelationships of Fishes*, 333–349. Academic Press, London.

Nesov, L.A. 1981. Flying reptiles of Late Cretaceous of Kyzylkum [in Russian]. *Paleontogičeskij žurnal* 1981 (4): 98–104.

Nesov, L.A. 1985. Rare bony fishes, terrestrial lizards and mammals from the zone of estuaries and coastal plains of the Cretaceous of Kyzylkum [in Russian]. *Ežegodnik Vsesoûznogo Paleontologičeskogo Obšestva* 28: 199–219.

Nesov, L.A. 1997. *Nemorskie pozvonočnye melovogo perioda severnoj Evrazji*. 218 pp. Sankt-Peterburgskij Gosudarstvennyj Universitet, Naučno-Issledovatelskij Institut Zemnoj Kory, Sankt Petersburg.

Partridge, A.D. 2006. Jurassic–Early Cretaceous spore-pollen and dinocyst zonations for Australia. *In*: E. Monteil (ed.), *Australian Mesozoic and Cenozoic Palynology Zonationas—Updated from the 2004 Geologic Time Scale*, 1–4. Geoscience, Canberra.

Patterson, C. and Rosen, D.E. 1977. Review of ichthyodectiform and other Mesozoic teleost fishes and the theory and practice of classifying fossils. *American Museum of Natural History, Bulletin* 158: 81–172.

Pole, M. 1999. Latest Albian–earliest Cenomanian monocotyledonous leaves from Australia. *Botanical Journal of the Linnean Society* 129: 177–186.

Pole, M. 2000a. Dicotyledonous leaf macrofossils from the latest Albian–earliest Cenomanian of the Eromanga Basin, Queensland, Australia. *Paleontological Research* 4: 39–52.

Pole, M.S. 2000b. Mid-Cretaceous conifers from the Eromanga Basin, Australia. *Australian Systematic Botany* 13: 153–197.

Pole, M.S. and J.G. Douglas. 1999. Bennettitales, Cycadales, and Gink-

Downloaded From: https://bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

goales from the mid Cretaceous of the Eromanga Basin, Queensland, Australia. *Cretaceous Research* 20: 523–538.
Pridmore, P.A., Rich, T.H., Vickers-Rich, P., and Gambaryan, P.P. 2005. A tachyglossid-like humerus from the Early Cretaceous of south-eastern Australia. *Journal of Mammalian Evolution* 12: 359–378.
Rich, T.H. and Vickers-Rich, P. 1994. Neoceratopsians and ornithomimosaurs: dinosaurs of Gondwana origin. *Research and Exploration* 10: 129–131.
Rich, T.H. and Vickers-Rich, P. 2003. Protoceratopsian? ulnae from Australia. *Records of the Queen Victoria Museum* 113: 1–12.
Romer, A.S. 1966. *Vertebrate Paleontology*. 687 + ix pp. University of Chicago Press, Chicago.
Romilio, A. and Salisbury, S.W. 2011. A reassessment of large theropod tracks from the mid-Cretaceous (late Albian–Cenomanian) Winton Formation of Lark Quarry, central-western Queensland, Australia: a case for mistaken identity. *Cretaceous Research* 32: 135–142.
Romilio, A., Tucker, R.T., and Salisbury, S.W. 2013. Re-evaluation of the Lark Quarry dinosaur tracksite (late Albian–Cenomanian Winton Formation, central-western Queensland, Australia): no longer a stampede? *Journal of Vertebrate Paleontology* 33: 102–120.
Salgado, L. 1993. Comments on *Chubutisaurus insignis* Del Corro (Saurischia, Sauropoda). *Ameghiniana* 30: 265–270.
Salisbury, S.W. 2005. A new vertebrate assemblage from the mid-Cretaceous (Albian–Cenomanian) Winton Formation, central-western Queensland. *In*: L. Reed, D. Bourne, D. Megirian, G. Prideaux, G. Young, and A. Wright (eds.), Proceedings of CAVEPS 2005. *Alcheringa, Special Issue* 1: 465
Salisbury, S.W., Molnar, R.E., Frey, E., and Willis, P.M.A. 2006a. The origin of modern crocodyliforms: new evidence from the Cretaceous of Australia. *Proceedings of the Royal Society of London, Series B* 273: 2439–2448.
Salisbury, S.W., Molnar, R.E., and Lamanna, M.C. 2006b. A new titanosauriform sauropod from the mid-Cretaceous (Albian–Cenomanian) Winton Formation of central-western Queensland, Australia. *Journal of Vertebrate Paleontology* 26 (Supplement to 3): 118A.
Salisbury, S.W., Agnolin, F., Ezcurra, M., and Pais, D. 2007. A critical reassessment of the Cretaceous non-avian dinosaur faunas of Australia and New Zealand. *Journal of Vertebrate Paleontology* 27 (Supplement to 3): 138A.
Scanlon, J.D. and Hocknull, S.A. 2008. A dolichosaurid lizard from the latest Albian (mid-Cretaceous) Winton Formation, Queensland, Australia. *In*: M.J. Everhart (ed.), Proceedings of the Second Mosasaur Meeting), 2007, Fort Hays State University, Hays, Kansas, USA. *Fort Hays Studies, Special Issue* 3: 131–136.
Schaeffer, B. and Patterson, C. 1984. Jurassic fishes from the Western United States, with comments on Jurassic fish distribution. *American Museum Novitates* 2796: 1–86.
Schultze, H.-P. 1996. The scales of Mesozoic actinopterygians. *In*: G. Arratia and G. Viohl (eds.), *Mesozoic Fishes 1: Systematics and Paleoecology*, 83–94. Verlag Dr. Friedrich Pfiel, Munchen.
Scotese, C.R. 2001. *Atlas of Earth History*. 52 pp. Paleomap Project, Arlington.
Sereno, P.C., Dutheil, D.B., Iarochene, M., Larsson, H.C.E., Lyon, G.H., Magwene, P.M., Sidor, C.A., Varricchio, D.J., and Wilson, J.A. 1996. Predatory dinosaurs from the Sahara and the Late Cretaceous faunal differentiation. *Science* 272: 986–991.
Sereno, P.C., Wilson, J.A., and Conrad, J.L. 2004. New dinosaurs link southern landmasses in the mid-Cretaceous. *Proceedings of the Royal Society of London, Series B* 271: 1325–1330.
Smith, N.D., Makovicky, P.J., Agnolin, F.L., Ezcurra, M.D., Pais, D.F., and Salisbury, S.W. 2008. A *Megaraptor*-like theropod (Dinosauria: Tetanurae) in Australia: support for faunal exchange across eastern and western Gondwana in the mid-Cretaceous. *Proceedings of the Royal Society, Series B* 275: 2085–2093.
Smith, A.G., Smith, D.G., and Funnell, B.M. 1994. *Atlas of Mesozoic and Cenozoic Coastlines*. 99 pp. Cambridge University Press, London.
Stewart, J.D. 1999. A new genus of Saurodontidae (Teleostei: Ichthyodectiformes) from the Upper Cretaceous rocks of the Western Interior of North America. *In*: G. Arratia and H.-P. Schultze (eds.), *Mesozoic Fishes 2. Systematics and fossil record*, *Proceedings of the International Meeting, Buckow, 1997*, 335–360. Verlag Dr. Friedrich Pfeil, München.
Taverne, L. 1986. Ostéologie et affinités systématiques de *Chirocentrites vexillifer* du Crétacé supérieur de la Mésogée Eurafricaine. Considérations sur la phylogénie des Ichthyodectiformes, poissons téléostéens du Jurassique et du Crétacé. *Annales de la Société Royale Zoologique de Belgique* 116: 33–54.
Taverne, L. 2009. Les poissons du Santonien (Crétacé supérieur) d'Apricena (Italie du Sud). 2°. *Garganoichthys decosmoi* gen. et sp. nov. (Teleostei, Ichthyodectiformes, Ichthyodectidae). *Bollettino del Museo Civico di Storia Naturale di Verona, Geologia Paleontologia Preistoria* 33: 27–39.
Taverne, L. 2010. Les Ichthyodectidae (Teleostei, Ichthyodectiformes) des schistes bitumineux de l'Aptien (Crétacé inférieur) de Guinée Équatoriale et du Gabon. *Bulletin de l'Institut Royal des Sciences Naturalles de Belgique, Sciences de la Terre* 80: 115–143.
Taverne, L. and Bronzi, P. 1999. Les poissons Crétacés de Nardò. 9°. Note complementaire sur le saurodontinae (Teleostei, Ichthyodectiformes): *Saurodon elongatus*, sp. nov. *Verona, Museo Civico di Storia Naturale, Studi e Ricerche sui Giacimenti Terziari di Bolca* 8: 105–116.
Taverne, L. and Chanet, B. 2000. *Faugichthys loryi* n. gen., n. sp. (Teleostei, Ichthyodectiformes) de l'Albien terminal (Crétacé Inférieur marin) du vallon de la Fauge (Isére, France) et considérations sur la phylogénie des Ichthyodectidae. *Geodiversitas* 22: 23–34.
Thulborn, R.A. 2013. Lark Quarry revisted: a critique of methods used to identify a large dinosaurian track-maker in the Winton Formation (Albian–Cenomanian), western Queensland, Australia. *Alcheringa* 37: 312–330.
Thulborn, R.A. and Turner, J.S. 2003. The last dicynodont: an Australian Cretaceous relict. *Proceedings of the Royal Society of London, Series B* 270: 985–993.
Thulborn, R.A. and Wade, M. 1984. Dinosaur trackways in the Winton Formation (mid-Cretaceous) of Queensland. *Memoirs of the Queensland Museum* 21: 413–517.
Toombs, H.A. and Rixon, A.E. 1959. The use of acids in the preparation of vertebrate fossils. *Curator* 2: 304–312.
Tucker, R.T., Roberts, E.M., and Salisbury, S.W. 2011. New information on the stratigraphy, depositional environment and taphonomy of the mid-Cretaceous Winton Formation, central-western Queensland, Australia. *13th Conference on Australasian Vertebrate Evolution, Palaeontology and Systematics, Program and Abstracts*, 84. Geological Survey of Western Australia, Perth.
Tucker, R.T., Roberts, E.M., Hu, Y., Kemp, A.I.S., and Salisbury, S.W. 2013. Detrital zircon age constraints for the Winton Formation, Queensland: contextualizing Australia's Late Cretaceous dinosaur faunas. *Gondwana Research* 24: 767–779.
Vickers-Rich, P., Rich, T.H., Wagstaff, B.E., McEwen Manson, J., Douthitt, C.B., Gregory, R.T., and Felton, E.A. 1988. Evidence for low temperatures and biologic diversity in Cretaceous high latitudes of Australia. *Science* 242: 1403–1406.
Warren, A., Rich, T.H., and Vickers-Rich, P. 1997. The last labyrinthodont? *Palaeontographica, Abteilung A* 247: 327–332.
Wellnhofer, P. and Buffetaut, E. 1999. Pterosaur remains from the Cretaceous of Morocco. *Paläontologische Zeitschrift* 73: 133–142.
White, M.A., Cook, A.G., Hocknull, S.A., Sloan, T., Sinapius, G.H., and Elliott, D.A. 2012. New forearm elements discovered of holotype specimen *Australovenator wintonensis* from Winton, Queensland, Australia. *PLoS One* 7 (6): e39364.
White, M.A., Falkingham, P.L., Cook, A.G., Hocknull, S.A., and Elliott, D.A. 2013. Morphological comparisons of metacarpal I for *Australovenator wintonensis* and *Rapator ornitholestoides*: Implications for their taxonomic relationships. *Alcheringa* 37: 1–7.
Woodward, A.S. 1894. On some fish remains of the genera *Portheus* and *Cladocyclus* from the Rolling Downs Formation of Queensland. *Annals and Magazine of Natural History, Series 6* 14: 444–447.

Downloaded From: https://bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

Appendix 1

Character scores for icthyodectiforms considered in this analysis. Character numbers, descriptions and scores (but see below for *Cladocyclus gardneri*) follow those listed in Cavin et al. (2013). Characters that were not visible on available specimens were scored with a question mark, and characters that were not applicable to specific taxa were scored as gaps (–). Polymorphic characters states are shown in curly brackets {01}. Scores for *Cladocyclus gardneri* for characters 22, 24, and 45 have been modified from those given in Cavin et al. (2013) to reflect the condition in adult individuals only. We have also added a new character relating to the morphology of the cleithrum.

70. *Cleithrum*. [Long axes of vertical and horizontal arms aligned at an obtuse angle = 0; long axes of vertical and horizontal arms aligned approximately perpendicular to each other = 1]. The derived state is seen in *Cladocyclus geddesi*, *Cladocyclus gardineri*, and *Vallecillichthys multivertebratum.*

Amia calva
0-0000000000001000101000010000000000001001000000000100000100000000020000
Hiodon alosoides
02011100011100104210000000000002201001000007011011101001023102213200000
Leptolepis coryphaenoides
00000001000001001100100000000002200000007001?000000000107100000120000?
Elops hawaiensis
00000000000001101101000000000002200001000000000000000000011000213100 0?
Allothrissops mesogaster
00001001001011101100100000000?010000?01000110107100111002 1?0012201000
Ascalabotrissops voelkli
???????010?001?0?10110000000000???0000?0?0??????00010?01000010 1?13?000?
Chirocentrites coroninii
11???1???1??????2321110101001007?01???????1?11101100111111207???23?1?0?
Heckelichthys "Vallecillo"
121?1??111??21?123022--?0--010???2101?1??00101?01100310 1?22?11?24???0?
Heckelichthys vexillifer
12101??11???21?123022--?0--010???210100???0?01?0????3111?12????????00?
Chiromystus mawsoni
1?1?111?11??2????1211001?10010???0120?0???1?1?10???101?11120????2??110?
Cladocyclus gardneri
12101112117?03101211110001100100010120001111011100101110 1?1201212321101
Cladocyclus geddesi
121011??????31?121?11000?10010001?120???????1?????????????????????????1
Cooyoo australis
11101112100?320122111007?{01}0?10???010??0?????0??0??0????????2??????????0?
Eubiodectes libanicus
12101??2111?2??1232110011100107??11?0?0?00??1110?10011011220117?23?1000
Ghrisichthys bardacki
111111?1101?3?0123111007?000100??112010??0101?11??00???1??207???21???00
Gillicus arcuatus
1111111211?132?1232110000000101111111111117?11?10?1001111?1201?222?110?
Gillicus serridens
111?11???1??32??2321100101??10??111?????11??1110??0?????1?2???????????
Ichthyodectes ctenodon
11111111101?31?12311100000001 0?1101?11?1??????10?????????????01?222?1100
Occithrissops willsoni
0000?1??11??2??01100???0000?00???0100?0110??1?10010111 1??2201011210?00
Pachythrissops
?00?????0?1???1?1?0010000?0?00???00????1??????10????10000111107?13?0?00
Prosaurodon pygmaeus
12111111?1?1?2?13?021021?11012?1111111?1??????1?????????????1?????????
Saurocephalus lanciformis
1111111??????2???3121010000111 1?????????0?????????????????????????????

Downloaded From: https://bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

Saurodon intermedius
11101?????????2??2312101110101????11???0?00??0??????????????????????????
Saurodon leanus
1111111111113 2?033121010001111111111?1?01????0?1???????????201?221??110
Thrissops formosus
120011?110?12?1112101000000000??0100?0010??1110010111111111011111000
Thrissops "Kimmeridge"
120111??001?210?1100100010000000?010000???0?0?1????0111???1???????100?
Unamichthys espinosai
110011?111??32012201100001 0?10?1101???????1?0110??0011?1?220?0?222?100
Xiphactinus audax
1111111110003101231111010100100110121111?01?01111100 21?11120 1?222?1100
Vallecillichthys multivertebratum
121111?111?132?133021021010012 11?112111????00101100110101201?222?1111
Saurodon elongatus
?????1???1???????3221 0???01?1{01}?1??1??10???????1??1101101012 01?222?111?

List of character state transformations for taxa included in the phylogenetic analysis, based on the strict consensus of 3 most parsimonious trees. For the relationships of icthyodectiform taxa, see Fig. 8.

Amia calva
Char. 14: 1 → 0
Char. 18: 1 → 0
Char. 19: 0 → 1
Char. 26: 0 → 1
Char. 41: 0 → 1
Char. 57: 0 → 1
Char. 64: 1 → 0
Char. 65: 3 → 0

Hiodon alosoides
Char. 2: 0 → 2
Char. 4: 0 → 1
Char. 10: 0 → 1
Char. 12: 0 → 1
Char. 14: 1 → 0
Char. 17: 1 → 4
Char. 18: 1 → 2
Char. 19: 0 → 1
Char. 21: 1 → 0
Char. 35: 0 → 1
Char. 49: 0 → 1
Char. 51: 0 → 1
Char. 56: 0 → 1
Char. 59: 1 → 3
Char. 62: 0 → 2

Leptolepis coryphaenoides
Char. 8: 0 → 1
Char. 15: 1 → 0
Char. 38: 1 → 0
Char. 43: 0 → 1
Char. 65: 3 → 2

Elops hawaiensis
No autapomorphies

Allothrissops mesogaster
Char. 64: 1 → 2

Ascalabotrissops voelkli :
Char. 9: 0 → 1
Char. 20: 0 → 1
Char. 60: 0 → 1
Char. 62: 0 → 1

Chirocentrites coroninii
Char. 22: 0 → 1

Heckelichthys "Vallecillo"
Char. 39: 0 → 1
Char. 55: 1 → 0

Heckelichthys vexillifer
No autapomorphies

Chiromystus mawsoni
Char. 53: 1 → 0

Cladocyclus gardneri
No autapomorphies

Cladocyclus geddesi (QM F44329)
No autapomorphies

Cooyoo australis
Char. 8: 1 → 2
Char. 10: 1 → 0
Char. 19: 0 → 1

Eubiodectes libanicus
Char. 34: 0 → 1
Char. 41: 1 → 0
Char. 58: 1 → 2
Char. 68: 1 → 0

Ghrisichthys bardacki
Char. 34: 0 → 1
Char. 37: 1 → 0
Char. 65: 2 → 1

Gillicus arcuatus
Char. 24: 1 → 0

Gillicus serridens
Char. 26: 0 → 1

Ichthyodectes ctenodon
Char. 24: 1 → 0

Occithrissops willsoni
Char. 10: 0 → 1
Char. 59: 1 → 2

Pachythrissops
Char. 61: 0 → 1

Prosaurodon pygmaeus
No autapomorphies

Saurocephalus lanciformis
Char. 27: 1 → 0

Saurodon intermedius
Char. 4: 1 → 0
Char. 25: 0 → 1

Saurodon leanus
No autapomorphies

Thrissops formosus
Char. 12: 0 → 1
Char. 18: 1 → 2
Char. 19: 0 → 1
Char. 40: 1 → 0
Char. 65: 2 → 1

Thrissops "Kimmeridge"
Char. 4: 0 → 1
Char. 9: 1 → 0
Char. 25: 0 → 1

Unamichthys espinosai
Char. 3: 1 → 0

Xiphactinus audax
Char. 11: 1 → 0
Char. 22: 0 → 1
Char. 26: 0 → 1
Char. 39: 0 → 1

Vallecillichthys multivertebra
Char. 27: 1 → 0

Saurodon elongatus
Char. 51: 0 → 1

Downloaded From: https://bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use