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Gondwanodus irwinensis gen. et sp. nov., a new elasmobranch from the Early Permian (Late Sakmarian) Fossil Cliff Member of the Holmwood Shale, Perth Basin, Western Australia

Stephen M. Daymond

68 Osprey Drive, Yangebup, Western Australia 6164, Australia

Abstract – A new elasmobranch is described from the Early Permian (Sakmarian, Sterlitamakian) of Western Australia. *Gondwanodus irwinensis* gen. et sp. nov. is represented by a single tooth which has a lingually prominent rectangular coronal base, a long, wide, robust tooth root and a low, medially acuminate crown. The tooth shares the lingually prominent coronal base with the petalodonts and *Heteropetalus* Lund, 1977. The morphology of the tooth suggests a specialized durophagous diet that may have included small decapod crustaceans or phyllocarids. The specimen was recovered from residue obtained through acid etching of small limestone blocks collected from Fossil Cliff in the northern part of the Perth Basin. The sediments are glacio-marine in origin and were formed when the Perth Basin was located at a latitude of approximately 70°S. To date a vertebrate fauna comprising symmoriid and stethacanthid shark teeth, a variety of placoid scales, and teeth and scales of palaeoniscoid fish, has been recovered.

INTRODUCTION

Australian Permian vertebrate microremains are generally rare (Turner, 1991) and the Permian fish fauna of Australia is poorly known. This is particularly true for Western Australia where the only described fauna has been *Crassidonta subcrenulata* Teichert, 1943, *Helodus* sp. Teichert, 1943, *Helicoprion davisii* H. Woodward, 1886 (rec: Woodward, 1886; Teichert, 1940, 1943), all from the Wandgee Series of the Carnarvon Basin, and a cryphiolepidid, gen. et sp. indet. Archbold, 1981 from the Byro Group, also in the Carnarvon Basin (Long and Turner, 1984). Fossil vertebrate remains from the Fossil Cliff Member of the Holmwood Shale at Fossil Cliff have previously been reported by the author (Daymond, 1993). Numerous palaeoniscoid teeth and scales, and rarer shark teeth were recovered from the limestone by Ferdinando (1992). Further work by the author on small limestone blocks collected from the type section at Fossil Cliff has revealed a new elasmobranch tooth along with several teeth of symmorriid and stethacanthid sharks, some placoid scales, and teeth and scales of palaeoniscoid fish. The fauna shows similarities with that of the Upper Pennsylvanian Shawnee Group, Kansas, as illustrated in Tway and Zidek (1982: figures 27A–E, 38A–E, 60A–E, 1983 figures 1A,B, 2A,B, 5A,B, 7A,B, 18A,B). Until the discovery of the large stethacanthid specimens described by Daymond (1993), in the sandy shale facies of the Fossil Cliff Member, all Permian fish records from Western Australia were from marine limestones (Turner, 1993). It is proposed that future collection and study of microvertebrate specimens from this locality will increase our knowledge of the Permian marine vertebrate fauna from this part of the world.

LOCALITY INFORMATION

Fossil site

Fossil Cliff (lat. 28°56'35"S, long. 115°32'30"E) is situated on the north branch of the Irwin River (Mingenew District) in the northern part of the Perth Basin (Irwin Sub-basin), 400 kilometres NNE of Perth, Western Australia (Figure 1).

Approximately 2600 metres of Permian sediments are contained within the Irwin Sub-basin (Playford, *et al.* 1976). The Holmwood Shale consists of 450 metres of micaceous and jarositic shale, siltstone, and discontinuous coquinitic limestone. It conformably overlies the glacial Nangetty Formation, which is the lower-most Permian formation in the sub-basin, and is conformably overlain by the near-shore marine sediments of the High Cliff Sandstone. The Fossil Cliff member is the uppermost unit of the Holmwood Shale. The type section of the Fossil Cliff Member outcrops on the west bank of the river, which is normally dry and flows only after heavy rain, consists of sandy siltstones, shales and mudstones with lenticles of indurated grey to yellow limestone. It contains a rich invertebrate fauna of brachiopods, pelecypods,

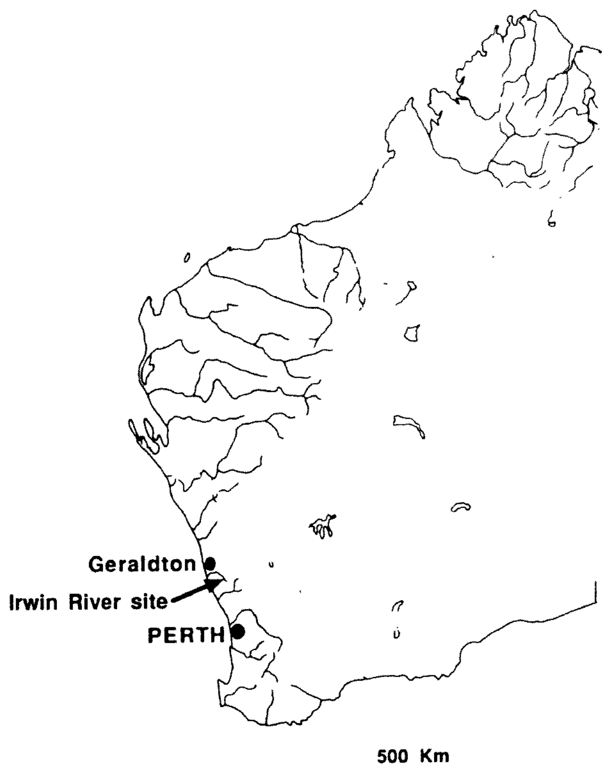

Figure 1 Map showing location of the Irwin River site, Fossil Cliff, Western Australia.

crinoids, bryozoans and rare cephalopods (Clarke, *et al.* 1951; Playford, *et al.* 1976). The type section of the Fossil Cliff Member is 12 metres thick and has recently been mapped in detail by D. Ferdinando (pers. comm. 1998). The associated ammonoid (*Metalegoceras kayi*) and pelecypod fauna indicates a Sakmarian (Sterlitamakian) age for the unit (Playford, *et al.* 1976; Archbold, *et al.* 1993; Glenister, *et al.* 1993).

Stratigraphic occurrence

The type, and only specimen, comes from a grey indurated silty limestone facies, massive to weakly bedded, occurring between 8.5 to 9.5 metres above the base of the Fossil Cliff Member of the Holmwood Shale (Figure 2). It was recovered from a 5 cm band that is particularly rich in small fragments of brachiopods, bryozoans and crinoids. This bed occurs as small, irregular lenses within the limestone suggesting that the deposit was the result of a gentle winnowing current on the sea-bed (Ferdinando, pers. comm.).

MATERIALS AND METHODS

Acetic acid etching of the limestone blocks was carried out following methods described by Rixon (1976). Whitelaw and Kool (1993) reported that during acid preparation, matrices with a high clay content posed difficulties as the clay quickly forms a skin over the rock surface and acts as a buffer, limiting the effect of the acid and necessitating frequent rinsing. Because of the high clay content of the Fossil Cliff matrix, a relatively high concentration of 15% glacial acetic acid at an initial temperature of 40°C was found to allow maximum dissagregation before the formation of a skin with no detrimental effects on the microvertebrate specimens. The residue was washed in a 180 µm aperture mesh seive, dried, then sorted under a binocular dissecting microscope. Vertebrate remains in the limestone are rare with a specimen being recovered every 4 or 5 inspections. The quality of preservation is excellent with even the most delicate structures intact. Previous specimen recovery by Ferdinando was done by initial mechanical disaggregation and then boiling of the matrix (Ferdinando pers. comm. 1998) which showed a collecting bias toward the survival of the generally more robust palaeoniscoid specimens. The quantities of chondrichthyan and palaeoniscoid specimens so far recovered by the author are nearly equal. This reflects the gentler method of acid preparation which ensures the survival of the more delicate shark remains.

The SEM photographs were made using a Phillips 505 Scanning Electron Microscope. The specimen is lodged in the collections of the Western Australian Museum (WAM).

ENVIRONMENT OF DEPOSITION

Recent palaeomagnetic studies have shown that during the early Permian, the Perth basin was situated in eastern Gondwana at a latitude of approximately 70°S (Li, Z.-X., *et al.* 1993). Work in the area by D. Ferdinando (pers. comm. 1995) has supported the hypothesis that the Irwin Sub-basin sediments were deposited in a barred basin (Clarke, *et al.* 1951). A model proposed by Le Blanc Smith and Mory (1995) suggests that the Holmwood Shale is glaciomarine in origin, with the sediments being deposited by glacial meltwaters into a large standing waterbody created by the retreat of the continental ice sheet as the climate warmed. The presence of recognised cold-water pelecypods such as *Deltopecten* and *Lyonia* is evidence of a cold water temperature (Dickens, 1993). The impoverished invertebrate fauna in the lowermost strata of the Holmwood Formation suggests that the water was probably initially brackish and then marine. The envisioned embayment had an ocean connection to the north (Le Blanc Smith and Mory, 1995).

During deposition of the Holmwood Shale sediments the water was relatively shallow; the sea-bed having only a very slight gradient so that water depth was rather uniform over the entire basin (Ferdinando, pers. comm. 1995). The presence of appreciable amounts of gypsum, jarosite and

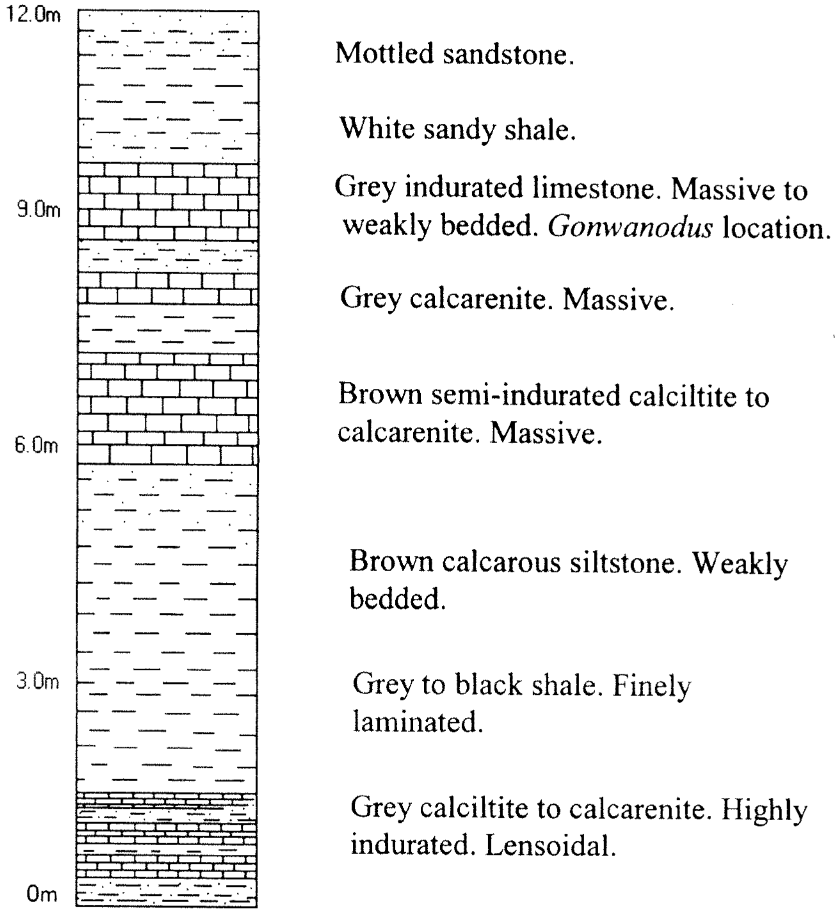

Figure 2 Stratigraphic section of the type locality, Fossil Cliff member, Holmwood Shale Formation (after Ferdinando).

marcasite in some layers indicates periodic inundation of the barred basin with fresh sea water that led to the deposition of alternating aerobic and disaerobic sediments. The abundant invertebrate fauna in the Fossil Cliff sediments indicates that conditions were ameliorating and marine life was prolific. The high clay content of the limestone suggests that the limestone lenses were formed in depressions on the sea-bed. The preservation of delicate spines on some brachiopods, and fine cusps on the tiny stethacanthid shark teeth, indicates that there was little transportation of the organic remains and therefore suggests that it was a low energy environment.

SYSTEMATIC PALAEONTOLOGY

Class Chondrichthyes Huxley, 1880

Subclass Elasmobranchii Bonaparte, 1838

Order incertae sedis

Family incertae sedis

Gondwanodus gen. nov.

Type Species

Gondwanodus irwinensis, sp. nov.

Diagnosis

An elasmobranch tooth that is microscopic (2 mm wide measured across the base), robust and low-crowned. Crown base is rectangular and labiolingually elongate with thick, smooth, rounded margins. The coronal basal margin is lingually prominent. Crown down-curved labiolingually and has a single, short acuminate cusp lacking surface ornamentation. The tooth root is deep, wide, flared, hexagonal and robust with lower half lingually prominent. The tooth root is twice as long as the crown is high. Shallow nutritive foramina occur on both the lingual and labial surfaces of the tooth root.

Etymology

Named after the Gondwana landmass to which Australia belonged during the Permian period.

Gondwanodus irwinensis **sp. nov.**
Figures 3A–E, 4A–D

Holotype and Only Specimen

WAM 98.7.1. single complete tooth from Fossil Cliff, Western Australia, Australia.

Diagnosis

As for genus.

Description

The crown is down-curved labiolingually with the prominent, rounded lingual margin of the coronal base overhanging the tooth root by one third of the coronal labiolingual length (Figures 3C, E, 4C). The rounded labial margin of the coronal base protrudes only slightly over the line of the tooth root (Figures 3B, 4C). The low cusp extends vertically from the centre of the coronal base (Figures 4A, C). The lateral surfaces of the cusp are initially perpendicular to the crown then rapidly converge to form an apex (Figures 3F, 4A, B). The labial and lingual surfaces are gently curved to the apex of the cusp (Figure 4C). No surface ornamentation is visible on the crown or cusp (Figure 3D). Dorsally the crown is rectangular; being labiolingually elongate with the long margins showing a slight medial constriction (Figures 3B, 4D). The crown is narrow, being just half the width of the rostrocaudal dimension of the tooth root. The lingual margin is slightly wider than the labial margin (Figure 4D). All margins of the crown are thick, smooth and rounded. Dorsally, the lingual coronal surface is flat with two shallow depressions, separated by a narrow ridge, located lingual to the cusp (Figures 3E, 4B, D). The labial coronal surface is concave; the concavity narrowing and deepening from the cusp to the labial margin (Figures 3A, C, 4A).

The tooth root is wide with the lateral margins flaring from underneath the crown to approximately two-thirds of the tooth root length and then converging to a truncated bottom margin forming a hexagonal shape (Figures 3A, F, 4A, B). The length of the tooth root is twice the height of the crown. The lingual basal surface exhibits small nutritive foramina on each side extending from under the crown to the points where the lateral margins converge toward the bottom margin of the tooth base (Figure 4B). Large nutritive foramina occur in a line on the lingual basal surface (Figures 3F, 4B). Labially the tooth root is smooth with only 3 or 4 nutritive foramina (Figure 4A).

The tooth root is thickest (labiolingually) at its junction with the crown and thins to a feather-edge along the lower margin (Figures 3E, 4C). Both labial and lingual root surfaces are approximately parallel for half the basal length and then the labial surface converges sharply toward the lingual surface to meet the latter slightly forward of the medial line of the tooth; resulting in the lower half of the tooth root being lingually prominent (Figures 3E, 4C). Lingually the tooth root is slightly concave from the anterior margin to the posterior margin (Figure 3B) which may be an accommodation for a replacement tooth.

Discussion

Taxonomic placement of the tooth is difficult as it shows few affinities to any known taxa, with perhaps the exception of the petalodonts and *Heteropetalus* Lund, 1977. The strong feature of the *Gondwanodus* tooth is the lingually prominent coronal basal margin, a feature shared only with petalodonts and *Heteropetalus.* Hansen (1985) has listed four basic aspects of external tooth morphology in petalodonts. Only two features of *Gondwanodus,* the lingually prominent coronal basal margin and a medially acuminate crown, are shared with the petalodonts. The lingually prominent coronal basal margin is imbricated in the petalodonts and petalodont crowns are labiolingually compressed. However these characters are absent in *Gondwanodus.* Additionally, there are no visible osteons on the surface of the crown and therefore no indication of tubular dentine which is a diagnostic character of the microscopic anatomy of petalodont teeth (Zangerl, *et al.* 1993). The coronal basal margin of *Heteropetalus* is lingually prominent and like *Gondwanodus* is not imbricated (Lund, 1977). However, although the teeth of *Heteropetalus* show some variation depending on their position in the dentition, none of the illustrated tooth families (Zangerl 1981, figure 67A–D; Hansen, 1985, figure 12A–D; Lund, 1977, figure 10A–D) closely resemble *Gondwanodus.* The tooth is therefore sufficiently unique to be a new genus with a possible relationship to the petalodonts and *Heteropetalus.* There is a fifty million year interval between the occurrence of *Heteropetalus* in the Lower Carboniferous (Chesterian) and *Gondwanodus* in the Lower Permian (Sakmarian). It is possible that *Heteropetalus* is related to *Gondwanodus* and the lingually prominent coronal basal margin may be a derived character linking them, being extremely pronounced in the latter. Histological examination is presently not possible as the described specimen is the holotype and the only one known.

The lack of an open pulp cavity in this specimen precludes the possibility that it is perhaps a dermal denticle or cephalic spine which can be very tooth-like in appearance and structure (e.g. Maisey 1989, figure 32A–C). Additionally, it has a long root with nutritive foramina on the root surface.

Etymology

Named after the Irwin River where Fossil Cliff sediments are exposed.

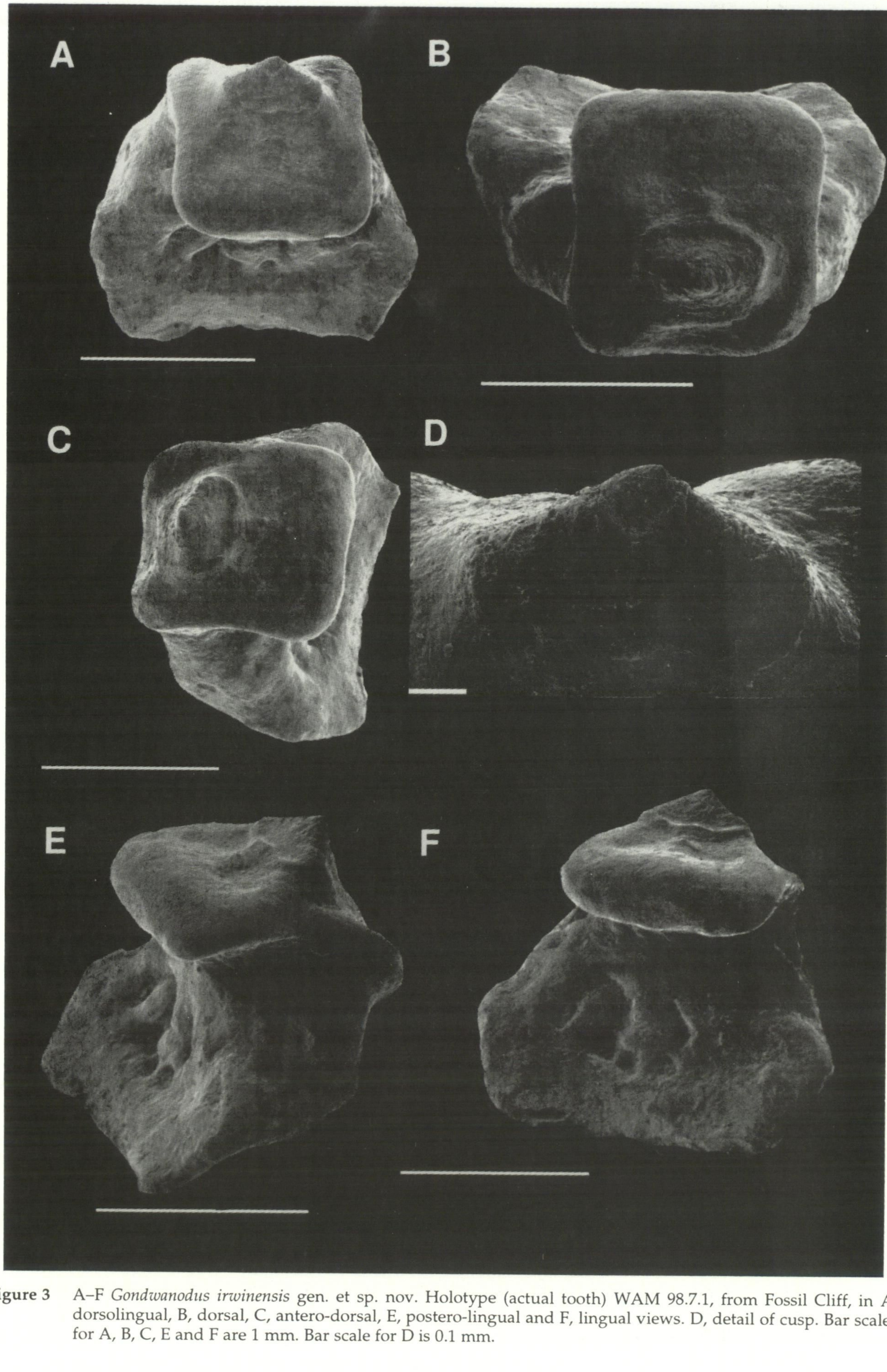

Figure 3 A–F *Gondwanodus irwinensis* gen. et sp. nov. Holotype (actual tooth) WAM 98.7.1, from Fossil Cliff, in A, dorsolingual, B, dorsal, C, antero-dorsal, E, postero-lingual and F, lingual views. D, detail of cusp. Bar scales for A, B, C, E and F are 1 mm. Bar scale for D is 0.1 mm.

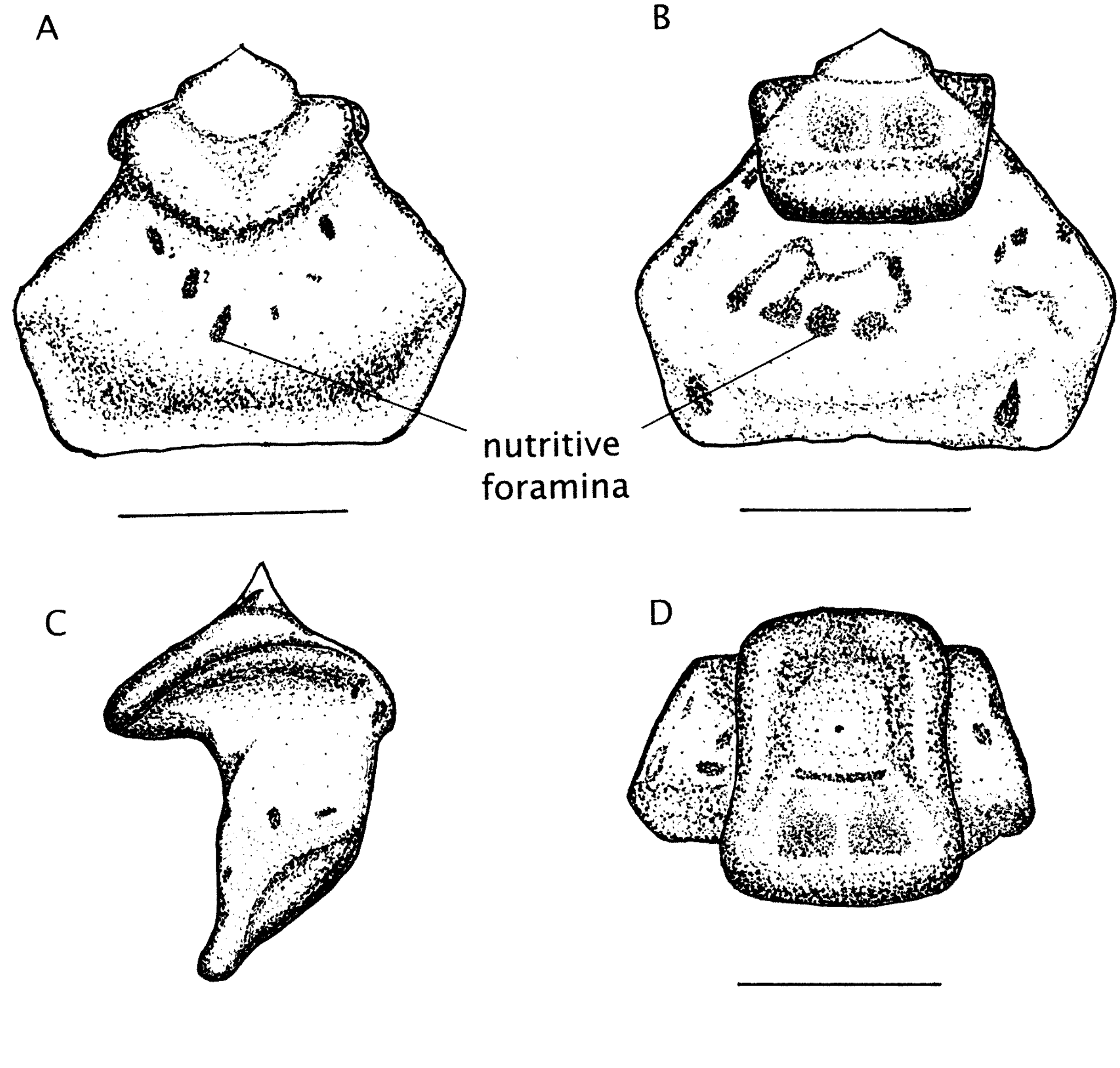

Figure 4 A–D *Gondwanodus irwinensis* gen. et sp. nov. Holotype WAM 98.7.1, in A, labial, B. lingual, C, lateral and D, dorsal views. Bar scales are all 1mm.

PALAEOECOLOGY

The robust morphology of the tooth suggests that it could withstand considerable forces and indicates a durophagous diet. The deep, wide, flaring root would have provided a solid attachment in the jaw tissue and suggests infrequent replacement (Hansen, pers. comm.). The acuminate cusp, albeit short, suggests a specialised puncturing function which possibly assisted in the splitting of hard exoskeletons rather than the crushing of brachiopod and pelecypod shells which would have required a pavement-like dentition. Therefore, it is envisioned that creatures such as small decapod crustaceans or phyllocarids may have been a food source for *Gondwanodus*. Fragments of crustacean shell have been found in the limestone of the Fossil Cliff Member.

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