

New osteichthyans (bony fishes) from the Devonian of Central Australia

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Abstract

Osteichthyan remains described from two localities in Central Australia (Mount Winter, Amadeus Basin, and southern Toomba Range, Georgina Basin) include the dipnoan *Amadeodipterus kencampbelli* n. gen., n. sp., the osteolepidid *Muranjilepis winterensis* n. gen., n. sp., and the onychodontid *Luckeus abudda* n. gen., n. sp., as well as indeterminate holoptychiid scales, osteolepidid scales of a new type from the Georgina Basin locality, and indeterminate onychodontid remains from both localities. *Amadeodipterus* n. gen. is a short-headed dipterid dipnoan with bones A and H enclosed into the skull roof; *Muranjilepis* n. gen. is a small form with short postparietal and parietoethmoidal shields, large orbits, and large pores of the sensory line system. It is closest to *Thursius*, and some Chinese osteolepidid material. *Luckeus* n. gen. is based on an onychodontid lower jaw with Meckel's cartilage separately ossified perichondrally from the dentary and infradentary, and carrying the parasymphysial tooth whorl. Different osteichthyan taxa at the two localities indicate a difference in age and/or palaeoenvironment within the Early-Middle Devonian.

Schlüsselwörter: Knochenfische, Dipnoi, osteolepidide und onychodontide Sarcopterygier, Devon, Zentralaustralien.

Zusammenfassung

Knochenfischreste aus zwei Fundorten Zentralaustraliens (Mount Winter, Amadeus Becken und südlicher Toomba Rücken, Georgina Becken) umfassen den Lungenfisch *Amadeodipterus kencampbelli* n. gen., n. sp., den osteolepididen Sarcopterygier *Muranjilepis winterensis* n. gen., n. sp., und den onychodontiden Sarcopterygier *Luckeus abudda* n. gen., n. sp., sowie unbestimmte holoptychiide und osteolepidide Schuppen eines neuen Typs aus dem Fundort im Georgina Becken und unbestimmte onychodontide Reste von beiden Fundorten. *Amadeodipterus* n. gen. ist ein kurz-schädeliger Lungenfisch, bei dem die Knochen A und H in das Schädeldach miteingeschlossen sind. Bei *Muranjilepis* n. gen. handelt es sich um einen kleinen Osteolepididen mit kurzem Postparietal- und Parietoethmoidal-Schild, großen Augenhöhlen und großen Poren des Sinneskanalsystems; er ist am nächsten mit *Thursius* und einigen chinesischen Osteolepididen verwandt. Ein unbestimmter onychodontider Unterkiefer zeigt ein wahrscheinlich primitives Merkmal in der perichondralen Verknöcherung des Meckelschen Knorpels getrennt von Dentale und Infradentale, der die Unterlage der parasymphysialen Zahnspirale bildet. Verschiedene Knochenfischtaxa treten an den beiden Lokalitäten auf; das deutet auf unterschiedliches Alter und/oder Palaeoenvironment an der Unter-Mitteldevongrenze zwischen beiden Lokalitäten hin.

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Introduction

The osteichthyans (true bony fishes) from the Devonian of Australia are still poorly known,

with some exceptions. The Dipnoi (lungfishes) are the best documented group, first reported from the Lower Devonian of Burrinjuck in southeastern Australia (Etheridge 1906; Camp-

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bell et al. 2000). Hills (1929) identified lungfish toothplates in the Middle-Upper Devonian sequence of Victoria, Long (1987a, 1992) documented much more complete remains from this sequence, and Ahlberg et al. (2001) compared the Late Devonian lungfish *Soederberghia* from New South Wales with the same genus in North America and Greenland. Miles (1977) first monographed the exceptionally preserved lungfish material from the Upper Devonian (Frasnian) Gogo deposit in Western Australia (Campbell & Barwick 1999 summarised extensive subsequent work on Gogo dipnoans). Other major osteichthyan groups are documented from the same regions: Actinopterygii (ray-finned fishes) from the Lower Devonian of Burrinjuck (Schultze 1968; Basden et al. 2000a; Basden & Young 2001), the Middle-Upper Devonian of Victoria (Long 1988), and the Gogo fauna (Gardiner 1984), and various sarcopterygians from southeastern Australia (Thomson 1973; Young & Gorter 1981; Long 1985, 1987b; Johanson &

Ahlberg 1997, 1998; Ahlberg & Johanson 1997). The first Australian Devonian coelacanth comes from Victoria (Long 1999), and the exceptionally preserved osteolepidid *Gogonassus* and onychodontid *Onychodus* from the Gogo fauna provide a wealth of new morphological data (Long et al. 1997; Andrews et al., in press). Fragmentary Early Devonian onychodont remains are known from Burrinjuck (Ørvig 1969; Lindley 2002), and otherwise the widespread occurrence of osteichthyans is indicated by a significant component in various microvertebrate assemblages (e.g. Basden et al. 2000b; Burrow 1994, 1995a, b, 1997; Turner et al. 2000).

All of the localities mentioned so far lie either in the sedimentary basins of the western continental margin (locality 21 [Gogo], Fig. 1A), or in the Lachlan Fold Belt in the eastern part of the continent (localities 1 [Mount Howitt], 2 [Buchan], 5 [Taemas, Wee Jasper], 7 [Canowindra], Fig. 1A). These areas were subject to repeated marine incursions during the Palaeozoic. From

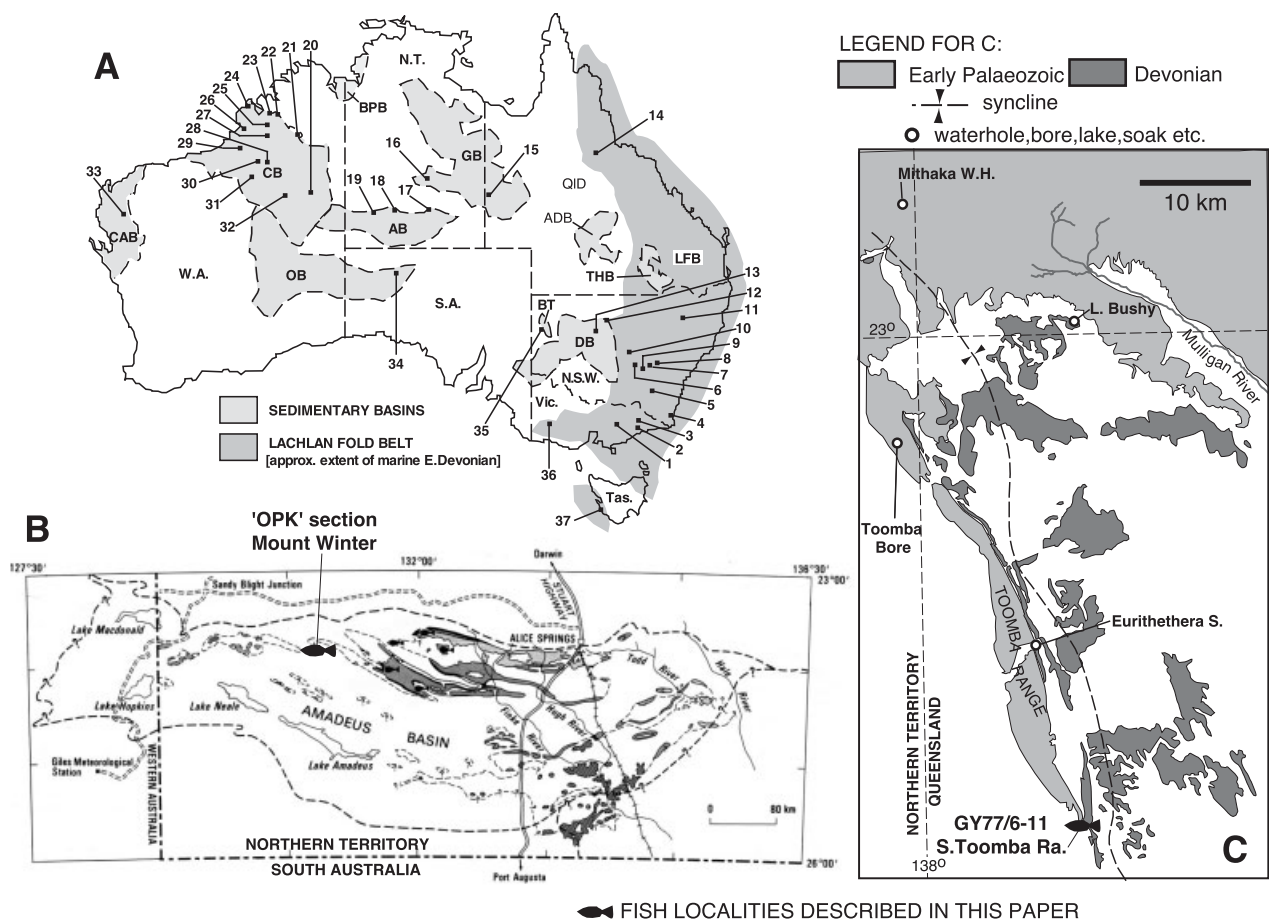


Fig. 1. **A** – Locality map for Devonian vertebrate occurrences in Australia (modified from Young & Turner 2000). Material described in this paper comes from the Amadeus Basin (AB, locality 19) and the Georgina Basin (GB, locality 15). For full explanation of locality numbers and abbreviations see Young & Turner (2000). **B** – Devonian rocks in the Amadeus Basin, showing the location of the OPK ('Orange Peel Knob') measured section at Mt. Winter (locality 19, Fig. 1A). **C** – Devonian rocks of the Cravens Peak Beds (dark grey) in the Toko Range – Toomba Range area, Georgina Basin (locality 15, Fig. 1A).

the central part of the Australian craton, Devonian fish remains (placoderms) were first described by Hills (1959) from the Georgina Basin (locality 16 [Dulcie Range], Fig. 1A), and Gilbert-Tomlinson (1968) reviewed all known occurrences, which were mainly placoderm remains (a 'possible dipnoan fragment' from the Georgina Basin was an erroneous determination; Young & Goujet 2003: 66). The first indication of a diverse osteichthyan fauna was an associated lungfish skull and rhipidistian remains documented by Young (1985) from the central Macdonnell Ranges of the Amadeus Basin (locality 18 [Stokes Pass], Fig. 1A). From the Georgina Basin (localities 15 [Toomba Range], 16 [Dulcie Range], Fig. 1A), Young & Goujet (2003) have recently documented incomplete remains provisionally assigned to three osteichthyan groups (onychodontids, porolepiforms, rhizodontids).

In this paper we describe some osteichthyan remains from two central Australian localities presumed to be about the same age (Emsian-Eifelian): Mt. Winter in the western Amadeus Basin, and the southern Toomba Range in the Georgina Basin (localities 19, 15, Fig. 1A). These are the first named osteichthyans from the Devonian of central Australia, and the first described forms from the Mt. Winter locality.

Field occurrences

A. Mount Winter, western Amadeus Basin (locality 19, Fig. 1A)

Field work near Mount Winter in the western part of the Macdonnell Ranges in 1991 (G. C. Young and S. Turner) led to discovery of a diverse assemblage of micro- and macrovertebrate remains in a calcareous sandstone-siltstone sequence 20–30 m above a fossil fish plate occurrence at the top of the Mereenie Sandstone. The measured section at this locality, briefly described by Young & Turner (2000: 464), is presented with lithological and palaeontological marker beds and sample numbers in Figure 2A. The base of the Mount Winter section is a fragmentary placoderm horizon from the transition beds between the Mereenie Sandstone and the overlying Pertnjara Group, provisionally assigned to the *Wuttagoonaspis* assemblage (Young & Turner 2000: 464). The main evidence is a spinal plate assigned to *Wuttagoonaspis* from a nearby locality illustrated by Young (1988: fig. 13). The main fossil fish interval is overlain by a lime-

stone unit some 30 m thick, and at the 60 m level sandstone-siltstone interbeds mark the return to a clastic sequence interpreted as the base of Harajica Sandstone equivalents (Young & Turner 2000: fig. 4, column C). However, in the type section for the Parke Siltstone in the central Macdonnell Ranges (locality 18, Fig. 1A), summarised in Figure 2B, the basal Deering Siltstone Member beneath the Harajica Sandstone Member is considerably thicker (200 m), so these lithological correlations are only approximate (for details of Pertnjara Group geology see Wells et al. 1970; Jones 1972, 1991).

B. Southern Toomba Range, Georgina Basin (locality 15, Fig. 1A)

Young & Turner (2000: fig. 4, columns C, E) compared the Mount Winter section just discussed with that for the Cravens Peak limestone unit in the Georgina Basin. This limestone was originally assumed to have a conformable and basal position beneath the *Wuttagoonaspis* assemblage (hence termed the 'basal calcareous unit'). A diverse fish fauna including *Wuttagoonaspis* is well represented in associated sandstone lithologies of the Cravens Peak Beds (Fig. 1C), as recently described by Young & Goujet (2003). The only known Devonian limestone outcrop was initially assumed to be of Ordovician age, but sampling for microfossils revealed an assemblage of Devonian fish scales (thelodonts and acanthodians), first described by Turner et al. (1981). Further collecting of macrovertebrate remains (Young 1977) revealed a fauna including antiarch placoderms (Young 1984) and teeth of the chondrichthyan *Mcmurdodus* (Turner & Young 1987). Turner (1995) revised the thelodonts, and noted associated shark scales, onychodont teeth, sarcopterygian scales, lepidotrichia, and acanthodian remains. The acanthodians are described by Burrow & Young (2005), and include a new genus and two new species, based on disarticulated fin spines, scales, and a perichondrally ossified palatoquadrate and scapulocoracoids.

Turner (1991) and Young (1993) noted that the microvertebrate assemblages described by Turner et al. (1981) contained conflicting evidence of age, and Young (1995: 20) discussed the possibility that the assemblage may have mixed material from older (shot-point samples) and younger (outcrop) horizons. Young (1996: 103) considered the fauna attributed to the 'basal cal-

careous unit' of the Cravens Peak Beds to include a component which was younger (?Eifelian) than the Early Devonian age assigned by Turner et al. (1981). Of the eight taxa first documented from this 'basal calcareous unit', five were listed by Turner et al. (1981: fig. 4) as common to the limestone and shot-point samples. Subsequently the two thelodonts from the former were reassigned to a new species by Turner (1995). The best preserved illustrated ostracods (*Healdianella* and *Bashkirina*?) only come from the shot-point samples, and the eridostracan *Cryptophyllus* is best represented only from the limestone sample (Turner et al. 1981: fig. 15). Gi-

ven the possibility that different levels may have been sampled, the poorly preserved unfigured remains of these crustacean taxa are in need of restudy (P. J. Jones, pers. comm.). Because of this uncertainty, Young & Turner (2000: fig. 4, column E) gave alternative late Pragian-Emsian, or late Emsian-Eifelian, ages for this assemblage, which was provisionally assigned to microvertebrate assemblage zone MV6 in the macrovertebrate (MAV) and microvertebrate (MV) biostratigraphic scheme for East Gondwana proposed by Young (1995, 1996; updated summary in Young & Turner 2000: fig. 2). The two alternative stratigraphic positions for the 'basal calcar-

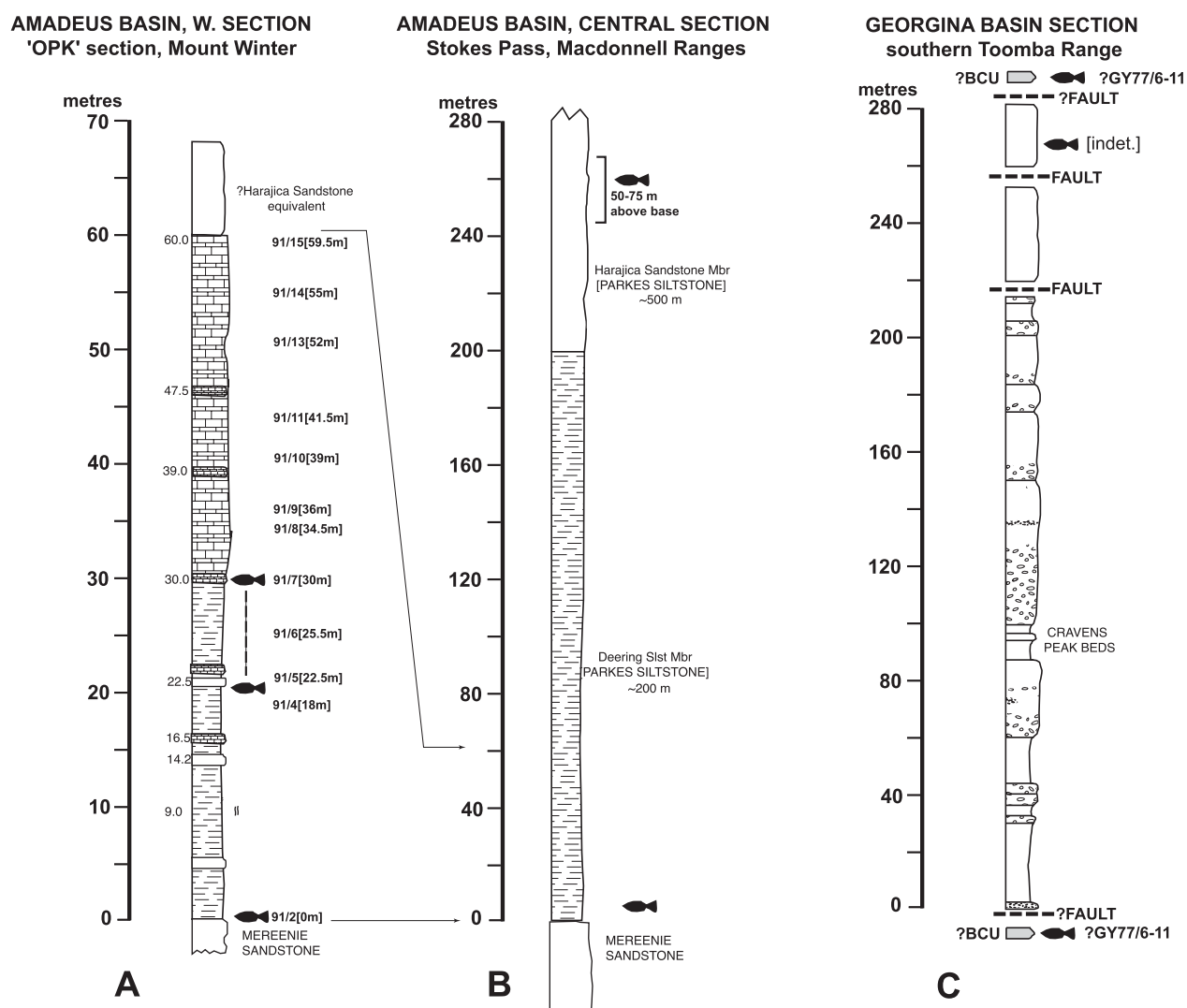


Fig. 2. Summary stratigraphic sections at three localities across central Australia. **A** – 'OPK' section, Mt. Winter (locality 19, Fig. 1A, B). All Amadeus Basin material described here comes from the horizon 30 m above the base in this section. **B** – Type section for the Devonian Pertnjara Group at locality 18 in the Amadeus Basin (Fig. 1A). The upper fish fauna (?Givetian; 50–75 m above the base of the Harajica Member) is documented by Young (1985, 1988, 2005). **C** – Southern Toomba Range (locality 15, Fig. 1A), showing the measured section of Draper (1976) through the Cravens Peak Beds, with two possible stratigraphic positions for the 'basal calcareous unit' (BCU), depending on interpretation of geological faults. All Georgina Basin material described here comes from the only known limestone outcrop attributed to this unit (field localities GY77/6–11, Fig. 1C). The fish fauna in sandstones of the Cravens Peak Beds is documented by Young (1991) and Young & Goujet (2003).

eous unit' (BCU) are indicated on the stratigraphic section in Figure 2C. Turner (1995, 1997) compared the thelodonts with younger (Middle Devonian) turiniid scales from the Broken River sequence of Queensland and the Aztec sequence of Victoria Land, Antarctica. The acanthodian assemblage also indicates a mixing of older and younger elements in the fauna (Burrow 2002; Burrow & Young, 2005).

The few osteichthyan remains described below were collected from the only surface outcrop of limestone, and are assumed to belong to the younger component in the assemblage. A 280 m thick measured section of Cravens Peak Beds only 100 m from the limestone outcrop begins with a basal pebbly unit first assumed to overlie it (Turner et al. 1981: fig. 3), but a faulted contact noted in the original field assessment (Draper 1976: fig. 4, section 1) places some uncertainty on the stratigraphic relationship. Many localities in the adjacent sandstone lithology have yielded a diverse fish assemblage (Young 1991; Young & Goujet 2003). Young & Goujet (2003) discussed the geological evidence in more detail, and concluded that the *Wuttagoonaspis* fauna from the Cravens Peak Beds and lower Dulcie Sandstone in the Georgina Basin was probably no older than Pragian, and no younger than early Eifelian, but a more precise age assessment was not possible. Full systematic documentation of the faunas involved will clarify the age relationships, and the description of osteichthyans presented in this paper is a contribution to that result.

Material and methods

All specimens are housed in the Department of Earth & Marine Sciences, Australian National University, Canberra (ANU V). Material from the Mount Winter locality was prepared mechanically, and that from the Georgina Basin was etched in acetic acid. ANU V2969, a small onychodont lower jaw acid-prepared in 2001 in the palaeontological laboratory of the Museum für Naturkunde, Berlin, has produced a range of other taxa in the residues which are described below (acanthodian remains described by Burrow & Young 2005). Measurements for osteolepidid skull remains follow Jarvik (1948), as updated by Jarvik (1985: fig. 2).

Systematic palaeontology

Class **Osteichthyes** Huxley, 1880
 Subclass **Sarcopterygii** Romer, 1955
 Infraclass **Dipnoiformes** Cloutier in Schultze, 1992a
 Order **Dipnoi** Müller, 1845
 Family *incertae sedis*

Amadeodipterus n. gen.

Diagnosis: A short-headed dipnoan (interorbital distance nearly as wide as the skull is long) with a B-bone broader than long. Bones A and H enclosed in the skull roof; short C-bones; large, possibly unpaired E-bone; bone I larger than bone J.

Type species: *Amadeodipterus kencampbelli* n. sp.

Age: Early/Middle Devonian.

Derivatio nominis: After the Amadeus Basin, a major Palaeozoic sedimentary basin of central Australia, from Lake Amadeus, first named in 1872 by the explorer Ernest Giles in honour of his benefactor Baron Ferdinand von Müller, who later apparently insisted that King Amadeus of Spain be honoured instead of himself; combined with dipterus, name used for many Devonian lungfish.

Amadeodipterus kencampbelli n. sp.

Figs 3A, 4, 5A

1993 'dipnoans (?dipterid)' – Young: 223.

2000 'dipnoan remains' – Young & Turner: 464.

Diagnosis: See diagnosis of genus.

Holotype: ANU V2709, an incomplete skull roof.

Additional material: ANU V2708 (left pterygoid tooth plate with bones J, K, L, X and 3); ANU V2960 (right pterygoid tooth plate with bones K, L and 3); ANU V3037 (indefinite bone portion); ANU V2968 (incomplete branchiostegal or subopercular); ANU V3036, V3038 (scales with Westoll lines).

Locality and Age: 30 m above the base of the 'OPK' section (see Fig. 2A), about 3.7 km northwest of the summit of Mount Winter, Amadeus Basin, central Australia (Fig. 1A, B; southwestern corner of the Mount Liebig 1:250 000 sheet, see Scrimgeour et al. 2005); Emsian – Eifelian.

Derivatio nominis: To acknowledge the major contribution to the study of Palaeozoic lungfishes by Professor Ken Campbell, Australian National University, Canberra.

Description: The holotype (Fig. 3A) is an incomplete portion of a skull roof about 33 mm long. It is notable for the very asymmetrical shape and arrangement of bones of the left and right sides (Fig. 4A, B). The two additional skull specimens add to the total variability of the skull roofing bones. All bones in the holotype are covered with cosmine, which is weathered in some posterior central parts to expose canals of the pore canal system (Fig. 3A). Normally one Westoll line follows the outer contour line of each bone. A unique feature of this skull is that bone A is incorporated within the skull roof (Fig. 4A, B), a condition seen in no other lungfish. Not only is it sutured with bones B and I, but bone A is bounded by bone H through a posteromedial running suture, clearly seen on the left side of the posterior preserved margin (Fig. 3A). Another unusual feature is the proportion of the B-bone, which is wider than long (114%), rather than longer than wide

as in other Devonian lungfish. This bone has straight borders posteriorly and laterally, forming sutures with bone A and the paired I-bones. The lateral and anterolateral borders of bone B are more irregular. A group of four smaller bones, two median and two lateral ones, lie in the midline in front of bone B. The lateral bones are interpreted as C-bones; the median bones may be called C'- or D'-bones, with only the anterior median bone (D', Fig. 4A) approaching the normal position of bone D (between C- and E-bones as seen in other lungfish skulls). There are no complete bone sutures in front of the C- and D-bones. The large central bone with sutures to C-, D'- and J-bones posteriorly and to LM- and KLM-bones laterally may represent a large unpaired E-bone.

On the left side of the posterior preserved margin a square H-bone lies lateral to bone A (its posterior and lateral margins are abraded, but apparently complete). It has some pores of the lateral line system, also seen on the lateral part of the left I-bone in front. This bone is wider than long, whereas the I-bone of the right side appears longer than wide, but is incomplete. There are no pores on its preserved part. The left I-bone is expanded laterally, and shorter medially, whereas the right I-bone has a longer medial suture with bone B. A square bone J and a large bone X occupy the space in front of the left I bone. The square J-bone may only represent part of bone J, with its anterior part perhaps fused with bone K. Alternatively, bone K may have taken over the anterior space of bone J (labelled KJ in Fig. 4B). Bones X and K on the left side show no external pores of the lateral line system. The left bone LM is longer than wide. The large median bone has its continuation anteromedial to the snout, with an evagination with an overlap area for the missing bones of the anterior left side.

The right side of the holotype shows a different bone pattern. The anterior extension of bone I separates bone J from bone X. Bone J has otherwise the normal relationship to surrounding bones I, B, C and K. It reaches anteriorly to the anterior level of bone C, and thus completely separates bone C from bones K and L. In contrast to the left side, there is a long bone lateral to the right J-bone, which carries the supraorbital canal as indicated by the many sensory pores. This long bone represents the space of bones K + L + M. Bones X, 3 and O lie lateral to it, with many sensory pores on the X-bone (incompletely preserved). The left bone X borders

bones I, J and KJ. The anterior bone in front of bone 3 is not preserved. The bone Y₁ must have attached laterally because the posterior border of bone X sutures with bone I. The right X-bone shows many pores of the sensory line whereas these are missing on the left side. The preserved anterior part of the right X-bone borders bones I, KLM and 3. It is separated from J by a posterior process of bone KLM and an anterior process of bone I. Bone 3 is positioned between bones X and O. Its anterolateral corner is broken, so the margin of the orbit is only preserved for a short distance.

No traces of pit lines were observed on any part of the skull.

Two other pieces of skull, each with parts of the pterygoid tooth plates attached, show even more variability in the arrangement of skull roofing bones. Bones K and L form separate bones in both specimens (Fig. 4C, D). Bone K has many pores of the supraorbital canal, which are lacking on the left side of the more complete skull roof of the holotype. In ANU V2708 (Fig. 4C) bone K is surrounded by bones J, X, 3, and L, but all are only partly preserved. Bone 3 is the most complete preserved bone in ANU V2960 (Fig. 4D).

The skull roof is broad, broader than in other lungfish (even broader than the skull of *Chirodipterus*). The reconstruction of the skull roof (Fig. 4E) requires two small Y-bones lateral to bone I and without contact to bone J. Still bone Y₁ may have contact to bone J in ANU V2708 (Fig. 4C). Bone Z lies lateral to bone H as in other Early Devonian lungfish and has no contact to bone A. The supraorbital canal ends in bone X, where the temporal canal splits into infra- and supraorbital canals.

The pterygoid tooth plates of ANU V2708 and V2960 have at least 15 tooth ridges. They are strongly weathered, so it is difficult to give a good description. The ridges radiate anteriorly, lateral and posterolateral from a point close to the midline, in contrast to *Tarachomylax* and *Stomiahkyus*, for example, where the ridges radiate anteriorly from a posterior point at the posterior margin of the toothplate. The tooth plates meet in midline. The teeth are smaller and closer together on the posterior ridges. These are typical tooth plates of dipterid type, which are otherwise first recorded from the Lower Devonian (Barwick et al. 1997).

ANU V2968 is an incomplete lungfish subopercular showing an anterodorsally pointing cosmine cover with one surrounding Westoll line

and wide bony overlapped dorsal and anterior margin.

Another bone fragment (ANU V3037) shows the posterior part of a 15 mm broad bone with straight lateral margins sutured with narrow bone pieces. A Westoll line follows the margins, a second one is placed away from the margin, and a third close to the centre. This bone may be a B-bone of the skull.

Isolated dipnoan scales from the same locality (ANU V3036, V3038) are up to 14 mm across,

and thus from a much larger fish than the skull remains, but assumed also to belong to *Amadeodipterus kencampbelli* n. sp. These are round scales with cosmine cover and Westoll lines. They show tubercles with shallow depressions on their top face (Fig. 5A). Such scales are described from *Iowadipterus* (Schultze 1992b: fig. 9A) and from *Tarachomyx* (Barwick et al. 1997: fig. 6) within dipnoans, and from holoptychiid rhipidistians. The free field is covered with small pores as in *Tarachomyx*. These scales

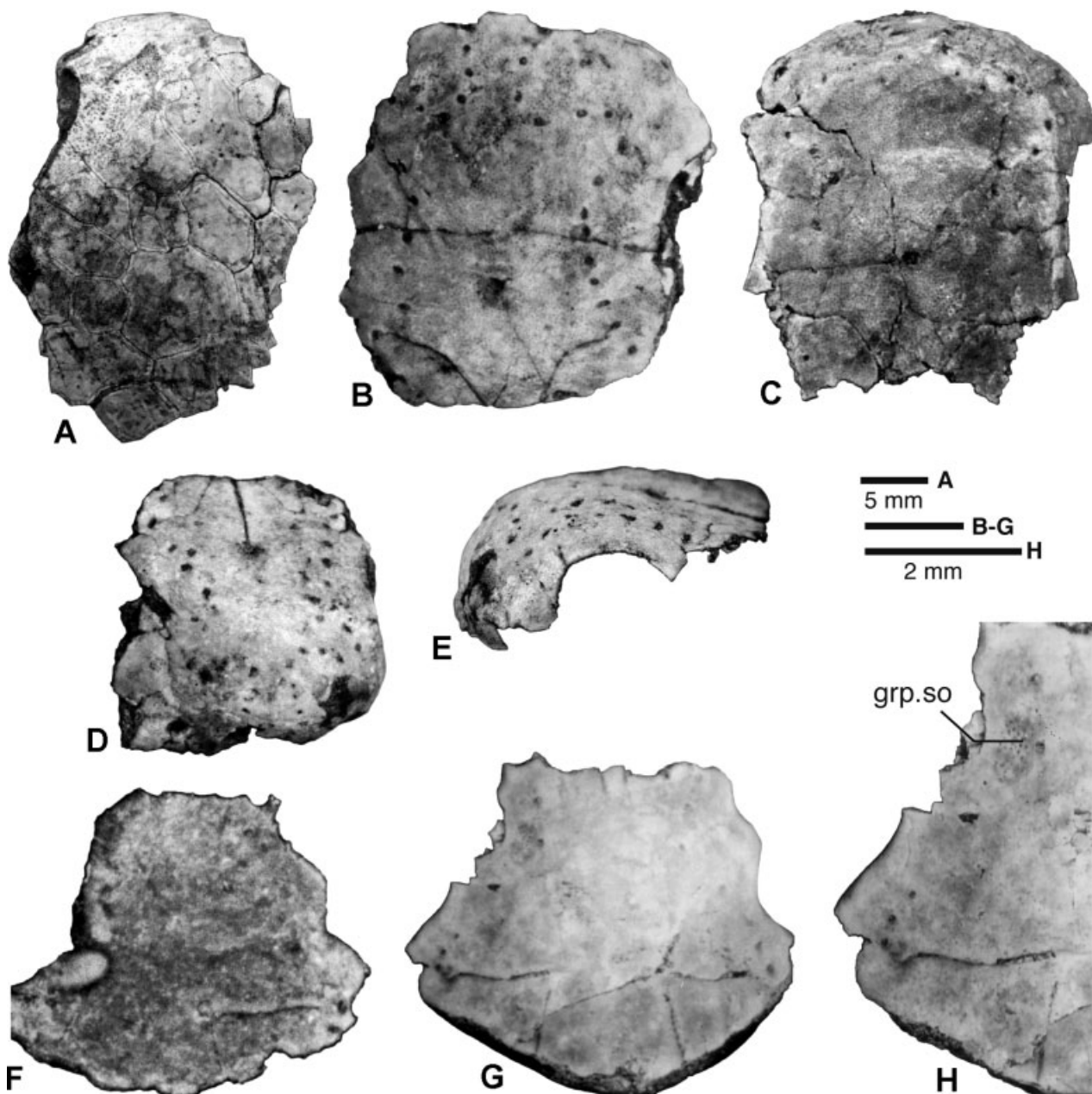


Fig. 3. **A** – Skull roof of *Amadeodipterus kencampbelli* n. gen., n. sp., dorsal view (holotype, ANU V2709); **B–H** – *Muranjilepis winterensis* n. gen., n. sp.; **B, C** – Parietoethmoidal shields in dorsal view (ANU V2961, 2963); **D, E** – Parietoethmoidal shield in anterodorsal and left lateral views (ANU V2962). **F, G** – Postparietal shields in dorsal view (ANU V2964, 3035); **H** – Detail of ANU 3035, showing sensory pores. All specimens from near Mt. Winter, Amadeus Basin, central Australia (locality 19, Fig. 1A); **grp.so** – pore groups indicating cutaneous sensory organs.

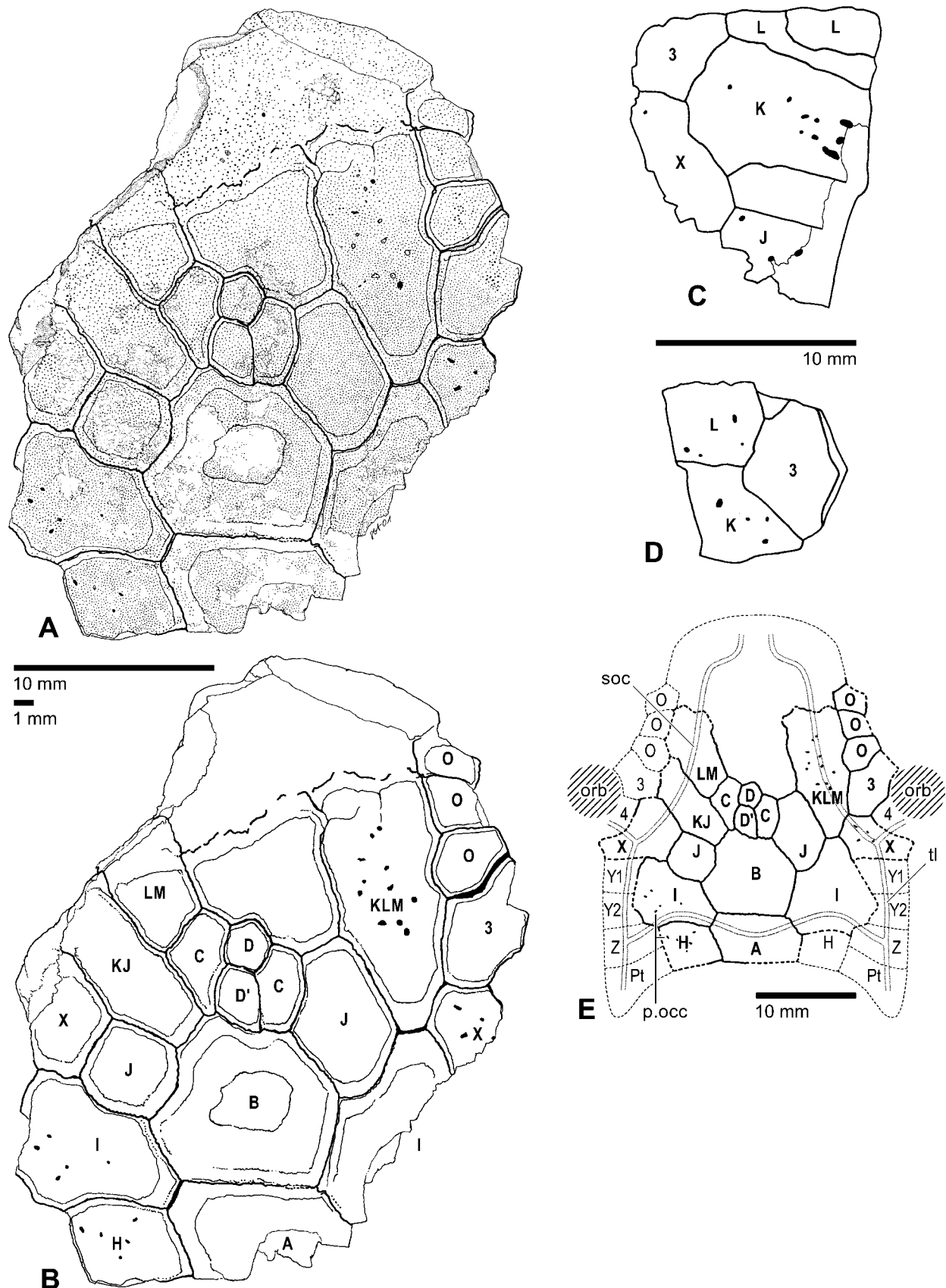


Fig. 4. **A, B** – Preserved skull roof pattern of *Amadeodipterus kencampbelli* n. gen., n. sp., dorsal view (holotype, ANU V2709); **B** – Interpretation of the skull roof pattern; **C** – Drawing of ANU V2708, left lateral portion of skull roof; **D** – Drawing of ANU V2960, right lateral portion of skull roof; **E** – Attempted skull roof restoration, based on holotype. Mt. Winter, Amadeus Basin, central Australia (locality 19, Fig. 1A). **A, B, C, D, D', H, I, J, K, KJ, KLM, L, O, X, Y_{1,2}, Z, 3, 4** – dipnoan skull roofing bones; **orb** – orbit; **p.occ** – pores of the occipital commissure; **p.tl** – pores of the temporal canal; **soc** – supraorbital canal.

may be contrasted with isolated scales from the Toomba Range locality described below, which lack the broad field of tubercles, and have the free field covered by fine ridges (Fig. 5B–F).

Comparisons: Taken together, these incomplete dipnoan specimens show considerable disparity in the arrangement and shapes of skull bones. However, given the variability of the skull pattern in other dipnoans there is no reason on available evidence not to place them in the same taxon. The size difference between left and right bones I and J is rare in lungfish. Westoll (1949) and Parrington (1950) figured such differences in *Dipterus valenciennesi* (Westoll 1949: fig. 2B; right side with two I-bones, figs 3E, 4D; lack of bone J on one or both sides). Schultze & Bolt (1996: fig. 2C) showed two J-bones and a wide I-bone on the left side in *Tranodis*. The bone ser-

ies along the supraorbital canal is also very variable in dipnoans (Cloutier 1997; Schultze & Bolt 1996; Kemp 1999), and this new form is no exception. A bone D' is also known from *Dipterus* (White 1965: figs. 19, 25), *Tranodis* (Schultze & Bolt 1996: fig. 2D) and other dipnoans (Kemp 1999: table 6).

The enclosure of bones A and H into the skull table is unique for the new genus, whereas the separation of bone A from bone Z by bone H is a primitive feature, reconstructed in *Uranolophus*, *Dipnorhynchus*, *Westollrhynchus*, and present in *Chirodipterus*, *Griphognathus*, and *Rhino-dipterus*. Bone H lies behind bones Z and A in *Dipterus*. Unusual for lungfish is the broad B-bone; bone B broader than long is otherwise only recorded in one specimen of *Scaumenacia* (Cloutier 1997: fig. 7B).

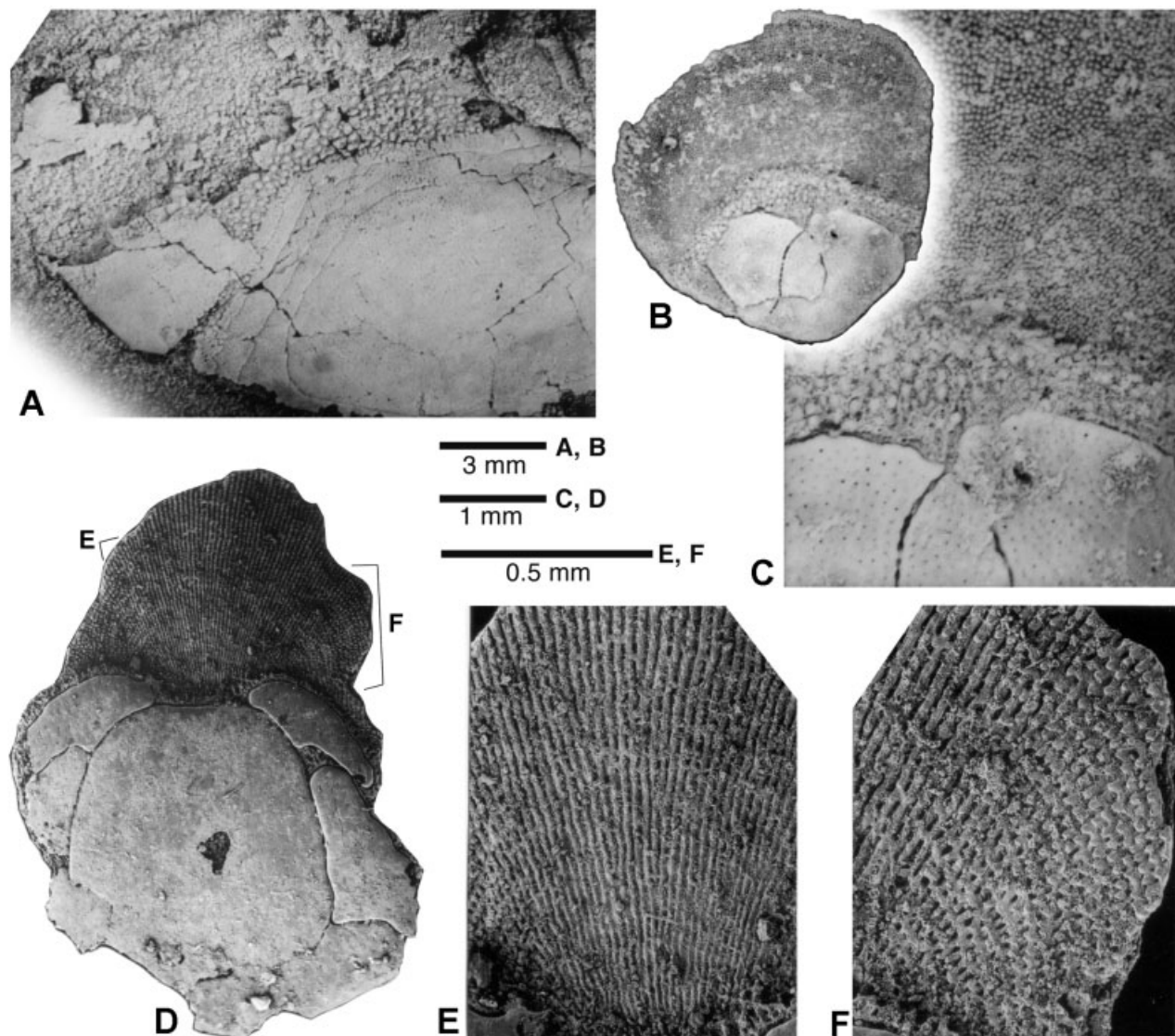


Fig. 5. Various isolated dipnoan scales in external view. **A** – ANU V3038 from Mt. Winter, Amadeus Basin, central Australia (locality 19, Fig. 1A); **B–F** – Scales from Toomba Range, Georgina Basin, central Australia (locality 15, Fig. 1A); **B, C** – ANU V3087; **D–F** – ANU V3086.

The possession of true lungfish tooth plates and the branching of supra- and infraorbital canal from the temporal canal in bone X places the new genus above node 6 in the cladogram of Schultze (2001), and the scale structure, as in *Lo-wadipterus* and *Tarachomylax*, is consistent with this (both genera also above node 6).

Dipnoi gen. et sp. indet.

Fig. 5B–F

1984 'dipnoan remains' – Young: 66.

2000 'possible dipnoan' – Turner et al.: 502.

2003 'dipnoan remains' – Young & Goujet: 66.

Material: Isolated scales (ANU V3086–3097).

Locality and Age: Southern part of the Toomba Range, western Queensland, approximate latitude 23°23'47" S, longitude 138°08'10" E (Abudda Lakes 1:100 000 sheet); horizon uncertain (?BCU, Fig. 2C); Emsian – Eifelian.

Description: Eleven round dipnoan scales were extracted from the residue of ANU V2969, and one similar scale (Fig. 5D) was scanned on the electron microscope by Dr. C. Burrow from a sample provided for etching to Dr. S. Turner. These scales show cosmine cover on the free field, with some Westoll lines; four of the scales carry a pit line. The free field descends abruptly to the covered field. There are few tubercles visible on a narrow field anterior to the cosmine cover (Fig. 5C). The covered field is characterised by radial, finely serrated ridges (Fig. 5E), with a texture that is much more linear than in the 'honeycomb' structure of the covered field illustrated for Gogo dipnoans (e.g. Pridmore & Barwick 1993: fig. 13).

These scales can be distinguished from the smaller isolated scales of *Amadeodipterus ken-campbelli* n. sp. described above by the ridges of the anterior covered field, and the step between the free and covered field.

Infraclass **Rhipidistia** Cope, 1887

Order **Osteolepidida** Boulenger, 1901

Family **Osteolepididae** Cope, 1889

Muranjilepis n. gen.

Diagnosis: A small osteolepidid with a very short and wide postparietal shield, large orbits compared to parietoethmoidal length, very short preorbital length, large pores of the sensory line system, supraorbital lines forming an excessive lateral extension in front of orbits, downwards arched snout, and marginal position of anterior external naris. Lacrimal notch is separated from notch for anterior tip of maxilla.

Type species: *Muranjilepis winterensis* n. sp.

Derivatio nominis: After Muranji Rockhole, an important water source for the original Aboriginal inhabitants of the desert (located in the base of the Mereenie Sandstone, 5 km NNW of the summit of Mount Winter, and about 2 km N of the type locality).

Muranjilepis winterensis n. sp.

Figs 3B–H, 6, 7

1993 'osteolepids' – Young: 223.

2000 'osteolepid remains' – Young & Turner: 464.

Diagnosis: See diagnosis of genus.

Holotype: ANU V2961 (parietoethmoidal shield).

Additional material: Three parietoethmoidal shields (ANU V2962, 2963, 2967); five postparietal shields (ANU V2964, 2965, 2966, 3035, 3098).

Locality and Age: 30 m above the base of the 'OPK' section (see Fig. 2A), about 3.7 km northwest of the summit of Mount Winter, Amadeus Basin, central Australia (Fig. 1A, B; southwestern corner of the Mount Liebig 1:250 000 sheet, see Scrimgeour et al. 2005); Emsian – Eifelian.

Derivatio nominis: After Mount Winter, the locality where the material was found.

Description: These nine examples of osteolepidid shields are all of similar small size (7–8 mm length), and covered completely by cosmine, obscuring most bone sutures. Measurements and proportions are summarised in Table 1.

On the parietoethmoidal shields (Fig. 3B–E), the median suture between the parietals posterior to the pineal opening is clearly visible only in ANU V2962 (Fig. 3D), which also shows a suture between the parietal and intertemporal, and possibly for the left premaxilla (Fig. 7A). The contact to the postparietal encompasses 66% of the length of the parietoethmoidal shield. The parietal pitline (pa.pl, Fig. 6B) in the posterior part of the parietoethmoidal shield forms a shallow arch from near the midline to the pores of the supraorbital sensory line behind the orbits (po.soc). The large pineal opening (pi) lies a third of the length of the parietoethmoidal shield in front of the contact with the postparietal shield and between the posterior parts of the rim of the orbit (orb). The posterior contact to the postparietal shield is nearly straight; a nearly straight line runs from the posterolateral corner to the post-orbital corner. The dorsal orbital rim is well preserved in ANU V2961 and V2962 (Figs 3E, 6B, C). The orbit was relatively large, occupying about 40% of the length of the parietoethmoidal shield. The rounded preorbital corner (proc, Fig. 6B, C) separates the orbital notch from the lacrimal notch in front, which also shows a shallow overlap area for the anterior tip of the max-

Table 1

Measurements and proportions of nine osteolepidid shields from Mt. Winter, Amadeus Basin, central Australia (locality 19, Fig. 1A) after Jarvik (1948). [e] = estimate based on one side to midline measurement.

Spec. No.	a	b	c	d	e	f	g	h	r	s	t
ANU V2961		7.5	2.5	8[e]	6[e]	~5			2.5	3.5	1.5
ANU V2962		6	2.4	7[e]	5.5	~4					
ANU V2963		8.5	~3	7.5	6.5	~4					
ANU V2967		7	2.9	~7		4.5					
ANU V2964	5.5						6.5	7.5			
ANU V2965	5						~4.4	6[e]			
ANU V2966	~7										
ANU V3035	7					4.5	6	~9			
ANU V3098	~6.5					4.5	~6.5	9			

a – median length of postparietal shield; **b** – median length of parietoethmoidal shield; **c** – distance from center of pineal foramen to posterior margin of parietal; **d** – breadth of cranial roof at preorbital corner; **e** – breadth of cranial roof at the deepest point of the orbital notch; **f** – breadth of cranial roof at the deepest point of the postorbital notch; **g** – breadth of cranial roof at the spiracular notch; **h** – breadth of cranial roof at posterolateral corner of the postparietal shield; **r** – median length of preorbital division of parietoethmoidal shield; **s** – median length of orbital division of parietoethmoidal shield; **t** – median length of postorbital division of parietoethmoidal shield.

illa. The lacrimal notch (la.n) is 45% the length of the orbit.

The pores of the supraorbital sensory canal (soc) are noteworthy for their relatively large size. They start close to the posterolateral corner of the parietoethmoidal shield, curve medially and then laterally inside the dorsal rim the orbit, and return in a sharp loop towards the midline in front of the orbit (Figs 6B, C, 7A). Close to the midline they turn anteriorad and a little away from the row of the other side. The pores are not expressed so clearly on ANU V2967. A few depressions with pores larger than the normal cosmine pores probably correspond to the 'groups of pores probably transmitting nerves to groups of cutaneous organs' noted in the Scottish Middle Devonian osteolepidids by Jarvik (1948: 137–139).

Of the five postparietal shields, ANU V2964 and V3035 are best preserved. ANU V3035 shows an undulated anterior margin, with shallow invaginations for the parietals on each side of a short median process (Fig. 3G). Lateral to these, and separated by short processes, are two short invaginations marking the contact with the intertemporal. The right margin with two invaginations is complete, whereas the posterior and the left margin are broken. The anterior lateral invagination receives the postorbital, and the second marks the position of the spiracular slit. The anterior-posterior running posterior pit-line and the medio-laterad running middle pit-line are preserved. The pores of the temporal sensory line appear close to the lateral margins, together with groups of pores probably for cutaneous sensory organs (Fig. 3H).

ANU V2964 (Fig. 3F) is broader than long (4:3), and shows no sutures. As in the previous example, two pit-lines are developed, a short posterior and a long middle one (p.pl, m.pl, Fig. 7B). The left and right margins show the two invaginations for the postorbital and spiracular slit. The sensory line pores are as large as on the parietoethmoidal shield. ANU V2965 is distorted with an angled fracture along the midline, reducing original breadth between the two postparietals. ANU V2966 is broken through the midline so only the left side is incompletely preserved.

Taking into consideration the relatively large orbits and large pores of the sensory line system in these specimens, it is possible that the small size indicates remains of a juvenile, even though the disappearance of bone sutures contradicts such an interpretation.

Comparisons: The parietoethmoidal shield of this new taxon is more elongate, and the postparietal shield shorter and broader, than in *Gyroptichius? australis* described by Young & Gorter (1981). The orbital position of the pineal opening is similar to that of *Thursius* and *Osteolepis*, and closest to *Thursius pholidotus* (Jarvik 1948), and *Th. wudingensis* Fan, 1992. The preorbital length is shorter and the postparietal shield broader and shorter than in all other described osteolepidids. A lateral loop of the supraorbital sensory canal is typical for osteolepidids (e.g. Jarvik 1948: figs 14, 32), but the extreme loop of this sensory line described above is seen also in *Thursius wudingensis* (Fan 1992: fig. 2B), and *Kenichthys campbelli* (Chang & Zhu 1993: figs 2A, 3D).

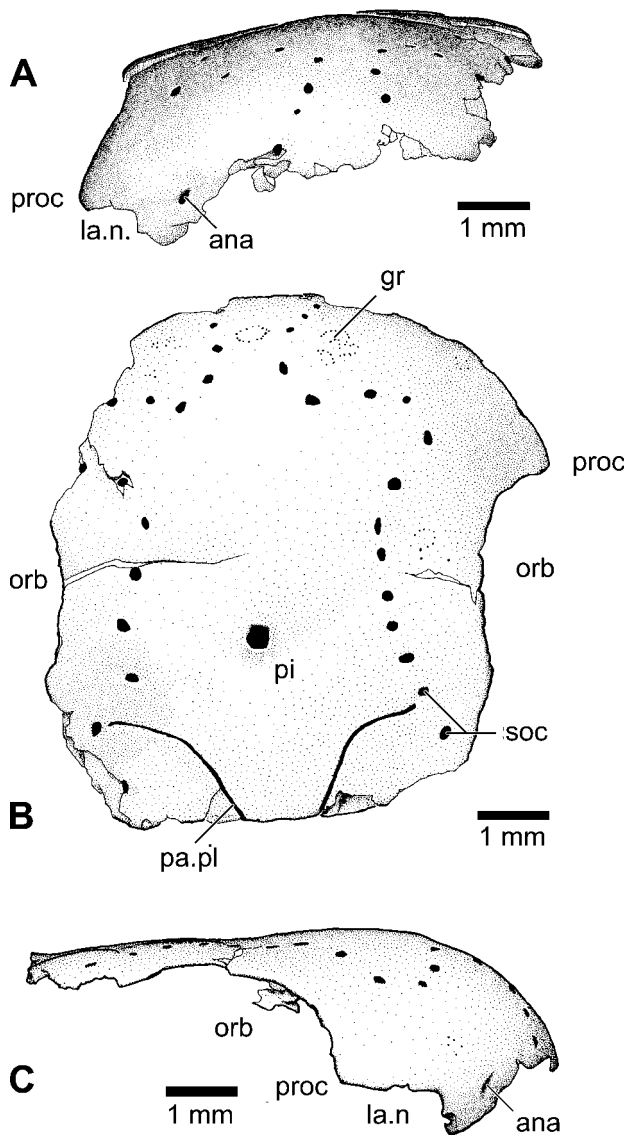


Fig. 6. *Muranjilepis winterensis* n. gen., n. sp., parietoethmoidal shield in anterior (A), dorsal (B) and right lateral (C) views (holotype, ANU V2961). Mt. Winter, Amadeus Basin, central Australia (locality 19, Fig. 1A). **ana** – anterior external nasal opening; **gr** – vascular groove; **la.n** – lacrimal notch; **orb** – orbit; **Pa** – parietal; **pa.pl** – parietal pit line; **pi** – pineal foramen; **proc** – preorbital corner; **soc** – pores of the supraorbital sensory canal.

Chang & Zhu (1993: 195) noted that the Chinese osteolepidid *Kenichthys* shares the greatest number of similarities with the Scottish form *Gyroptychius*, but differs in its very short and broad snout (the shortest amongst known osteolepidids), and its long postorbital division (the longest amongst known osteolepidids). In its very short, broad snout, grooved nasal opening, and deep embayment behind the postorbital corner, *Kenichthys* resembles *G. ? australis* Young & Gorter, 1981, the only previously described pre-Late Devonian osteolepidid from Australia. These are features not present in *Muranjilepis winterensis* n. gen., n. sp.

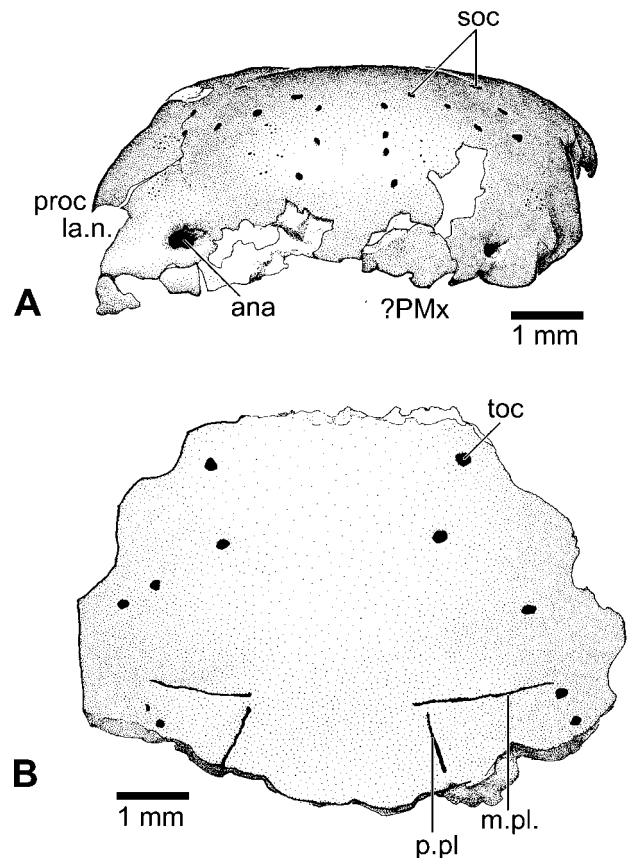


Fig. 7. *Muranjilepis winterensis* n. gen., n. sp. A – Parietoethmoidal shield in anterior view (ANU V2962); B – Postparietal shield in dorsal view (ANU V2964). Mt. Winter, Amadeus Basin, central Australia (locality 19, Fig. 1A). **ana** – anterior external nasal opening; **la.n** – lacrimal notch; **m.pl** – middle pit line; **?PMx** – premaxilla; **p.pl** – posterior pit line; **proc** – preorbital corner; **soc** – pores of the supraorbital sensory canal; **toc** – pores of the temporal sensory canal.

osteolepidid n. gen., n. sp.

Figs 8, 9A–D

1987 'crossopterygian remains' (pars) – Turner & Young: 233.

?1995 'scales of a sarcopterygian' (pars) – Turner: 683.

Material: Isolated scales (ANU V3099-3106).

Locality and Age: Southern part of the Toomba Range, western Queensland, approximate latitude 23°23'47" S, longitude 138°08'10" E (Abudda Lakes 1: 100 000 sheet); horizon uncertain (?BCU, Fig. 2C); Emsian – Eifelian.

Description: A small sample of eight similar scales of a new form of osteolepidid were extracted from the residue of ANU V2969. These scales were initially thought to belong to a palaeoniscid, because of the posterior serrations. However, under alcohol they revealed the cosmine and pore system. One example of a thick scale (Fig. 8A) shows the smooth cosmine surface with a finely serrated posterior border. The anterior border of the cosmine cover has leaf-like extensions. The dorsal overlapped border

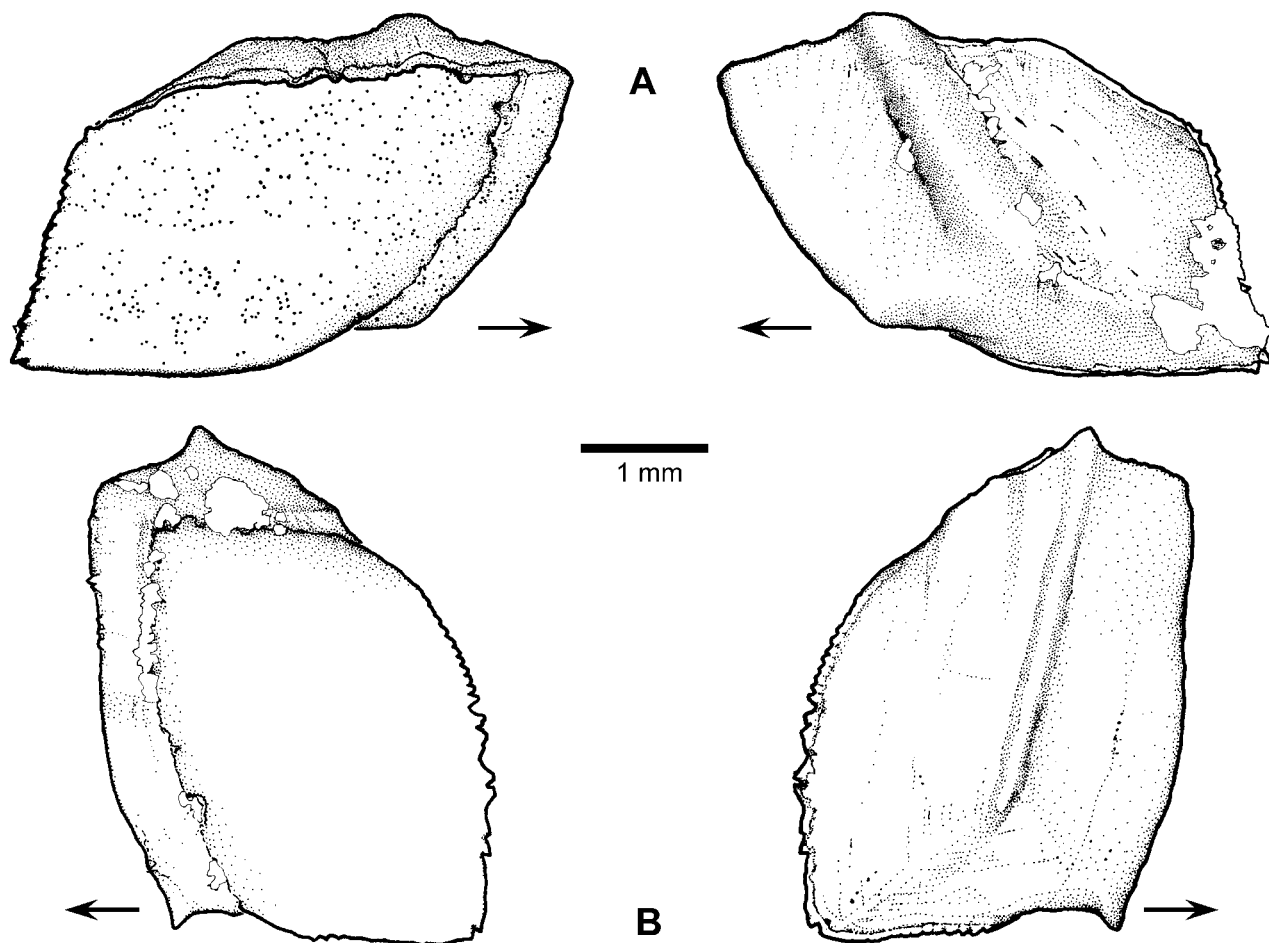


Fig. 8. Osteolepidid n. gen., n. sp. Two scales from the southern Toomba Range (locality 15, Fig. 1A), Queensland. **A** – ANU V3099; **B** – ANU V3100. External view on left; internal view on right; arrows point antieriad.

carries a small short-based peg. A ridge corresponding to the peg divides the inner surface into a short and a wide inner surface. This scale, and a second very similar example (Fig. 9A, B) may have come from the middle or posterior part of the flank. A second illustrated scale type (Fig. 8B) has a higher rhombic shape, and is evidently a typical flank scale. Two other more elongate scales (ANU V3103, 3104) show a similar distinct groove surrounding the cosmine field. The inner ridge is more narrow, and in ANU V3104 has the appearance of an attached separate structure, rather than an integral part of the scale.

Comparisons: We do not know of any similar osteolepidid scales from the Devonian; such scales with a serrated posterior margin have not previously been recorded. These scales evidently belong to a new osteolepidid taxon, but until more material is available we leave them in open nomenclature.

Order **Holoptychiida** Andrews, 1967
Family **Holoptychiidae** Owen, 1860

? holoptychiid indet.

Fig. 9E

?1995 'scales of a sarcopterygian' (pars) – Turner: 683.

2000 'porolepiform crossopterygian' – Turner et al.: 502.

Material: One scale (ANU V3107).

Locality and Age: Southern part of the Toomba Range, western Queensland, approximate latitude 23°23'47" S, longitude 138°08'10" E (Abudda Lakes 1:100 000 sheet); horizon uncertain (?BCU, Fig. 2C); Emsian – Eifelian.

Description: Extracted from the residue of ANU V2969 was a single round scale (4 × 4 mm) with ridged ornament of 'holoptychiid' type. It has a depressed anterior rim, and a raised free field with about nine subparallel slightly nodose ridges covering its anterior half (Fig. 9E). The ridges decrease in width posteriorly, reducing to a series of short ridges and posteriorly directed tubercles becoming smaller towards the posterior edge. The inner scale surface, which lacks any internal ridge or boss, is thickened and gently convex anteriorly, with a few pores, and forms a thinner porous posterior flange which would have overlapped the scale behind.

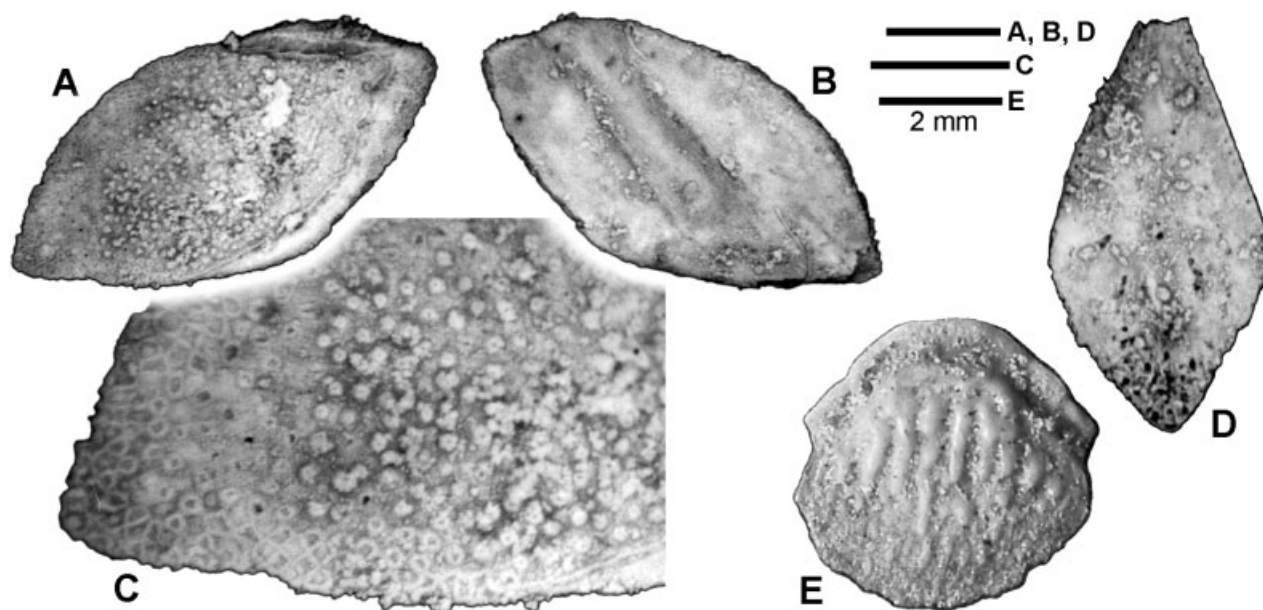


Fig. 9. **A–D** – *Osteolepidid* n. gen., n. sp. **A–C** – ANU V3101 in external (**A**) and internal (**B**) views, with detail of the posteroventral external surface (**C**); **D** – ANU V3102, external view; **E** – holoptychiid gen. et sp. indet., scale in external view (ANU V3107). Southern Toomba Range (locality 15, Fig. 1A), Queensland.

Infraclass **Onychodontida** Andrews, 1973

Family **Onychodontidae** Woodward, 1891

***Luckeus* n. gen.**

Diagnosis: An onychodontid in which the lower jaw dentition comprises a main row of larger lingually curved antero-posteriorly compressed teeth alternating with sockets of sub-rectangular shape, a lateral row of smaller teeth alternating with tooth sockets in a less regular pattern, and an outer marginal laterally projecting ridge of crowded denticles, some enlarged as curved small teeth; inner dentary ridge reduced in thickness anterior to tooth row; anterior part of Meckel's cartilage perichondrally ossified, and with a deep fossa for the parasymphysial tooth whorl with minimal dermal attachment. Jaw symphysis with combined cartilaginous and dermal connection. Parasymphysial teeth with a barbed tip and striated at a density of 30–50/mm.

Type species: *Luckeus abudda* n. sp.

Derivatio nominis: From the nick-name 'Lucke' of the late Dr. Hans Ludolph Jessen (Köln), to acknowledge his major contribution to the study of Palaeozoic osteichthyans, in particular onychodontids (Jessen 1966) and rhipidistians (Jessen 1968, 1980).

Remarks: The new taxon differs from previously named onychodontid genera in the number of tooth rows, cross section of teeth, shape of teeth in the outer row, and the form of the parasymphysial tooth whorl attachment to Meckel's cartilage.

***Luckeus abudda* n. sp.**

Fig. 10A–E

1984 'onychodontid remains' – Young: 66.

1987 'crossopterygian ... remains' – Turner & Young: 233.

1995 'onychodontid teeth' – Turner: 683.

2000 'onychodontids' – Turner et al.: 502.

2003 'smaller onychodontid' – Young & Goujet: 75.

Diagnosis: See diagnosis of genus.

Holotype: ANU V2969 (left lower jaw).

Additional material: Various isolated teeth (ANU V3108–3112).

Locality and Age: Southern part of the Toomba Range, western Queensland, approximate latitude 23°23'47" S, longitude 138°08'10" E (Abudda Lakes 1:100 000 sheet); horizon uncertain (?BCU, Fig. 2C); Emsian – Eifelian.

Derivatio nominis: From Abudda Lakes, located in the Simpson Desert about 15 km ESE of the fossil locality.

Description: ANU V2969 is a small onychodontid left lower jaw preserved in two pieces (Fig. 10B), which was prepared using acetic acid digestion in Berlin in 2001. The Cravens Peak limestone material is exceptionally fragile during preparation, and the specimen is not yet completely extracted. We provide this preliminary description to document the interesting morphology of this specimen. The residue from the acid digestion yielded a variety of osteichthyan scales as described above, as well as antiarch bones like those described by Young (1984), various acanthodian remains (Burrow & Young 2005), and a perfectly preserved typical tooth of the chondrichthyan *Mcmurdodus whitei* Turner & Young, 1987. This is still partly embedded in the limestone matrix (tth, Fig. 10B).

The lower jaw has a preserved length of about 60 mm, but the posterior margin is not fully prepared. The outer dermal surface carries external ornament of indistinct elongate partly anasto-

mosing ridges, and includes a well preserved dentary inflected upwards at the front, and a prominent ventral expansion formed by the inwardly inflected anterior infradentary (De, Id₁, Fig. 10A). There is no anterodorsal notch in the

dentary, of the type described in *Psarolepis* by Zhu & Schultze (1997) and Yu (1998), but the ventral expansion of the dermal cover corresponds to the extended anterior infradentary of *Strunius* as illustrated by Jessen (1966: fig. 10),

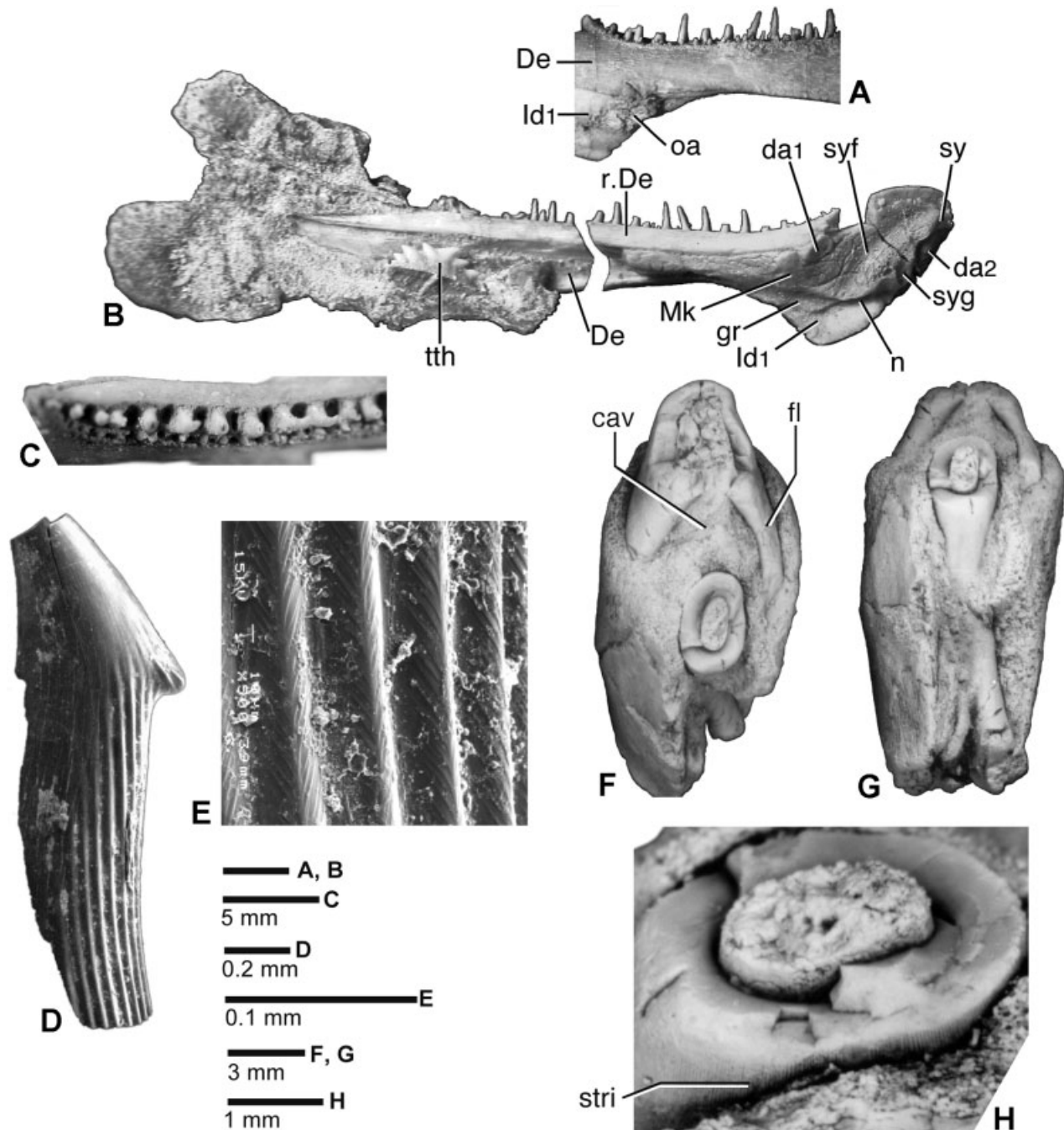


Fig. 10. Onychodontid remains from central Australia. **A–E** – *Luckeus abudda* n. gen., n. sp. from Southern Toomba Range, Georgina Basin, Queensland (locality 15, Fig. 1A); **F–H** – Specimen from Mt. Winter, Amadeus Basin, central Australia (locality 19, Fig. 1A); **A–C** – Left lower jaw (holotype, ANU V2969); part of external surface (**A**), the preserved internal surface (**B**), and an occlusal view of the anterior part of the dentition (**C**, anterior to left); **D** – Isolated fragment of parasymphysial tooth (ANU V3112), with detail of striated enamel (**E**); **F–H** – Incomplete parasymphysial tooth whorl (ANU V3039) in dorsal (**F**) and posterior (**G**) views, with detail of striated enamel (**H**). **cav** – posterior cavity at base of onychodont tooth; **da₁** – small boss of presumed dermal bone for tooth whorl attachment; **da₂** – presumed dermal attachment as part of jaw symphysis; **De** – dentary; **fl** – posterior process on tooth base; **gr** – vascular groove; **Id₁** – first infradentary; **Mk** – Meckel's cartilage (perichondrally ossified); **n** – notch; **oa** – contact for adjacent infradentary; **r.De** – inner ridge of dentary; **stri** – fine striation; **sy** – inner lamina of Meckel's cartilage enclosing parasymphysial tooth whorl; **syf** – attachment fossa for parasymphysial tooth whorl; **syg** – area for lower jaw symphysis on Meckel's cartilage; **tth** – chondrichthyan tooth (*McMurdochodus whitei*).

the 'anterior infradentary flange' illustrated by Chang & Yu (1997: fig. 3), and the 'ventro-mesial flange of the splenial' in *Psarolepis* (Zhu & Yu 2004: fig. 1B). The suture between the dentary and anterior infradentary is visible externally, running forward along an angle in the dermal surface such that the external surface of the dentary faces laterally, and that of the anterior infradentary faces ventrolaterally. In lateral view the first infradentary is more triangular than restored for *Strunius* (Jessen 1966: fig. 10D), with a deeper less rounded ventral angle, and the sharp anterior angle slightly behind the anterior end of the dentary. The rounded anterior expansion of the dorsal edge of the dentary is more elongate than in *Strunius*, but less elongate than in an isolated onychodontid dentary from China (Zhu & Janvier 1994), which has a more pointed anterior margin. The posterior margin of the anterior infradentary shows a roughened surface (oa, Fig. 10A) for interlocking with an adjacent bone (second infradentary), not identified in *Strunius*, nor in *Grossius* or *Onychodus sigmoides*, although a series of infradentaries is present in the Gogo *Onychodus* (Long 2001: fig. 1). Several deep pits entering the bone in this overlap presumably include a foramen for the passage of the mandibular sensory canal.

The inner surface of the dentary shows a thickened upper ridge (r.De, Fig. 10B), which carries the dentition. This comprises a main row of larger socketed teeth up to 2 mm long, most of which alternate with sockets where teeth have been lost. There are seven larger teeth on the posterior and 13 on the anterior preserved section. These decrease in size towards the front, with a small tooth cluster at the anterior end of the row. The teeth are antero-posteriorly compressed, with a marked lingual curvature at their tips. The tooth surface appears smooth, so if striations are present in the enamel they are very fine. Such striations on the lingual surface were said to be characteristic of the teeth of *Strunius* and *Onychodus* by Jessen (1966: 363). The sockets show the tooth bases to be about 1 mm in the lingual-labial dimension, and about 0.5 mm antero-posteriorly. Similar sockets, with a 'sub-rectangular' shape in a dentary ascribed to '*Onychodus* sp.' by Turner et al. (2000: fig. 5.5), can be contrasted with the rounded tooth sockets of *Onychodus sigmoides* and *Onychodus jaekeli* (Jessen 1966: fig. 12C, pl. 20, fig. 1).

In occlusal view (Fig. 10C) the main tooth row is flanked by a lateral row of about 26 smaller teeth (approaching 1 mm in length) which again

tend to alternate with tooth sockets, but in a less regular pattern. The outer margin of the dentition comprises a ridge of crowded denticles, some clearly enlarged as curved immature teeth (maximum length about 0.5 mm). Jessen (1966: 375) distinguished *Strunius* from *Onychodus* lower jaws by the thickened elevated oral rim in the latter, which was contrasted with the flat rim in *Strunius* (Jessen 1966: figs 10, 12C, D). In ANU V2969 this outer rim also projects laterally from the main dermal bone surface (Fig. 10A). The lateral row of smaller socketed teeth was evidently not developed in *Onychodus sigmoides* (Jessen 1966: fig. 12C), nor in the Gogo *Onychodus* (K. S. W. Campbell, pers. comm.). However the latter has at least four coronoids fused inside the marginal dentition (Long 2001), whereas in primitive osteichthyans the coronoids were evidently loosely attached and readily lost (Zhu & Yu 2004). There is no evidence of coronoids in *Strunius*, nor in *Luckeus abudda* n. sp., but outgroup comparison would suggest that they were either non-preserved, or secondarily lost.

ANU V2969 includes the anterior end of a perichondrally ossified Meckel's cartilage attached to the inner surface beneath the thickened dentary ridge (Mk, Fig. 10B). The ossified cartilage is hollow posteriorly, with an inner perichondral layer completely separate from the dermal bone to which it is attached, presumably the primitive condition for osteichthyans. Another early osteichthyan with a similar structure preserved is the 'mentomeckelian bone' on the lower jaw illustrated by Zhu & Schultze (1997: fig. 4) belonging to *Psarolepis* Yu, 1998 from the Lower Devonian (Lochkovian) of China (see also Zhu & Yu 2004: fig. 4). In *Luckeus abudda* n. sp. the anterior end of the cartilage is expanded both dorsally and ventrally, with an extensive concave area on its mesial surface covered with vascular grooves (syf) that must have been the attachment area for a parasymphysial tooth whorl. The large ventral expansion is completely different to the anterior end of Meckel's cartilage in *Psarolepis* or *Achoania* as described by Zhu & Yu (2004: figs 3, 4), which carries a large oval anterior fenestra in this position. Assuming this area is completely preserved (i.e. that the 'anterior fenestra' is not an opening into the 'interperichondral space'; see Miles & Young 1977: 145), then the ventral expansion of Meckel's cartilage to support the parasymphysial tooth plate in *Luckeus abudda* n. sp. would be a specialised feature. Posterodorsally, this 'para-

symphyseal lamina' of Meckel's cartilage partly surrounds a rounded projection (da₁) apparently continuous with the dentary ridge, which represents a small dermal attachment area for the parasymphyseal tooth whorl. Anterodorsally the lamina has a clear edge about 1 mm inside the thin dorsal margin of the dentary, where it curves up in front of the dentary ridge. The smaller vascular grooves covering the perichondral attachment surface arise from a large groove running along the ventral ossified surface of the cartilage (gr), from which the contained vessel passed to the anterior in a deep notch (n) between the expanded anterior end of Meckel's cartilage and the inner dermal bone surface. Small branches from the main groove can be seen passing around the mesial surface of the cartilage near its posterior preserved end (Fig. 10B). In a similar position is the 'infradentary foramen' associated with the posterior end of the 'anterior Meckelian fenestra' in *Psarolepis*, and the ventral indentation 'for nerves and blood vessels' in the lower jaw of *Achoania* (Zhu & Yu 2004: figs 3, 4).

The anterior edge of the tooth whorl attachment area forms a deep notch, with a mesial lamina (broken posteriorly) that would have enclosed the tooth whorl in a deep groove as reconstructed for *Strunius rolandi* (Gross) by Jessen (1966: fig. 10A, B). Several examples show the detail of this structure (Jessen 1966: pl. 16, figs 6–9, pl. 17, fig. 1), which may be a specialisation of early onychodontids, lost in later forms or modified by reduction of the ossified cartilage and more extensive dermal support (see below). At the anteroventral edge of Meckel's cartilage in ANU V2969 there is a separate deep depression for the jaw symphysis (syg, Fig. 10B), also in a similar position to that of *Strunius*. The depression is incomplete dorsally because of the broken mesial lamina, and may have been an elongate vertical groove as illustrated for *Strunius rolandi* by Jessen (1966: pl. 17, fig. 1). The symphysis has an anterior dermal component in the form of a rounded boss delineated by shallow grooves (da₂), with a flat attachment surface. This may correspond to the smaller anterior symphyseal connection illustrated by Jessen (1966: pl. 16, fig. 8). This attachment has the same more opaque bone texture as the attachment developed posterodorsally (da₁), and both are interpreted as dermal components of the symphyseal and tooth whorl attachments (alternatively they could be part of the edge of the cartilage separated off by vascular grooves).

As just described, the anterior end of the lower jaw of *Luckeus abudda* n. sp. is rather different from that of other onychodontids. The large 'symphyseal area' delimited by a low ridge illustrated for *Onychodus sigmoides* (sya, Jessen 1966: fig. 12D) probably indicates the extent of attachment to the dentary of the expanded anterior end of Meckel's cartilage (unossified, or not preserved). Above this, the parasymphyseal tooth whorl was placed on a thickened dentary ridge, and a similar arrangement, with Meckel's cartilage only in the symphysis, is seen also in porolepiforms, for example *Glyptolepis* and *Holoptychius* (Gross 1942: figs 2A–C, 6). In *Onychodus* from Gogo (Long 2001: fig. 3C, D) the tooth whorl apparently sits inside and against the thickened anterior end of the dentary ridge, as in holoptychiids (but its alignment with the braincase suggests a gap filled with cartilage; J. A. Long, pers. comm.). The essential difference from the holotype of *Luckeus abudda* n. sp. is that the inner dermal ridge of the dentary, which sits above the groove for Meckel's cartilage (unossified in *Onychodus*), expands anteriorly to provide a support for the tooth whorl, whereas in ANU V2969 the dentary ridge reduces to a narrow strip, with only a small dermal attachment process (da₁), and Meckel's cartilage is expanded to carry the major part of the tooth whorl attachment. In contrast, both the jaw symphysis and the attachment for the parasymphyseal dental plate for *Psarolepis* were described as being on the inner surface of the dentary (Yu 1998: figs 5, 6). Zhu & Yu (2004: fig. 7) illustrate a sequence of lower jaw character transitions on a cladogram of major sarcopterygian groups, with a 'mesial horizontal ledge of the dentary' as a new character of onychodontids (their character 5). The lower jaw of *Luckeus abudda* n. sp. shows that the posterior part of this structure developed first, as may also be indicated by an indeterminate dentary from Yunnan, China, considered by Zhu & Yu (2004: fig. 6A–F) to be a possible onychodontid. Still unclear is the primitive osteichthyan arrangement for dermal versus endochondral connections at the jaw symphysis and parasymphyseal dental plate attachment, but the *Psarolepis* specimen illustrated earlier by Zhu & Schultze (1997: fig. 4B, C) suggests that both attachments were carried on a perichondrally ossified 'mentomeckelian bone'.

The posterior preserved end of Meckel's cartilage is a broken edge, with a thick perichondral layer (slightly perforated ventrally in the main

vascular groove), so it is uncertain whether Meckel's cartilage was unossified posteriorly, or whether it was lost during preparation of the posterior part of the jaw. The corresponding 'mentomeckelian bone' of *Psarolepis* apparently has a similar posterior termination (Zhu & Schultze 1997: fig. 4).

Additional to this lower jaw are various isolated onychodont teeth from the southern Toomba Range locality. These are not uncommon in the limestone samples, and we assume they belong to the same taxon. The examples documented here, in unetched limestone samples (ANU V3108–3111), range in size up to 13 mm long. In the Gogo *Onychodus* the parasymphysial teeth may be 2–3 times the length of dentary teeth (Long 2001: fig. 1A), so these isolated teeth probably came from parasymphysial tooth whorls associated with somewhat larger lower jaws. ANU V3109 is missing the tip, but would have been about 13 mm long, with the proximal preserved part (about one third tooth length from the base) being 2 mm in diameter, oval in cross section, and showing 45–50 striations right around the exposed half of the enamel surface (density about 25/mm). ANU V3111 is a broken tooth with 6 mm length preserved, and 1.5 mm across at the basal preserved part. Again the tooth is laterally compressed, with a striated enamel surface at a density of about 25/mm. ANU V3108 was at least 12 mm long (mainly an eroded impression in limestone), but with 3 mm of the tip of the tooth preserved, showing that it had a barbed end, a feature first described by Gross (1965) in *Onychodus jaekeli* from Wildungen, and 'Hamodus' from the Middle Devonian of the Russian platform. Similar barbed teeth occur in an undescribed species from Lode, Latvia (Frasnian) assigned to *Onychodus* by Upeniece (1995). ANU V3110 is another tooth 13 mm long, probably also with a barbed end (covered by matrix). The barbed structure is well shown in the SEM of the tip of another parasymphysial tooth (V3112; Fig. 10D), a 1.6 mm long fragment presumably from a tooth at least 5–6 mm long. Higher magnification (Fig. 10E) shows the distinctive 'herringbone' or chevron pattern of ribs along the longitudinal ridges, just as illustrated by Smith (1989: fig. 4C) in *Onychodus* from Gogo, and said to be a specialised feature of onychodonts (*Onychodus* and *Strunius*). The striations are reduced with wear, but the large parasymphysial teeth of *Onychodus* from Gogo are mainly smooth (K. S. W. Campbell, pers. comm.). The 6–7 striations across the prox-

imal preserved end of V3112 (Fig. 10D) suggests a density of ~30/mm.

onychodontid gen. et sp. indet.

Fig. 10F–H

Material: ANU V3039 (incomplete tooth whorl).

Locality and Age: 30 m above the base of the 'OPK' section (see Fig. 2A), about 3.7 km northwest of the summit of Mount Winter, Amadeus Basin, central Australia (Fig. 1A, B; southwestern corner of the Mount Liebig 1:250 000 sheet, see Scrimgeour et al. 2005); Emsian – Eifelian.

Description: ANU V3039 is a weathered incomplete onychodont tooth whorl showing the basal portion of two teeth enclosed in the bony lamina of the parasymphysial dental plate (Fig. 10F). Comparison with similar elements in the Gogo collection indicates that the preserved portion represents the anterior end of the whorl. The basal part of the larger anterior tooth shows paired posterior processes (fl) enclosing a large posterior cavity at the tooth base (cav), just as figured for *Onychodus* by Gross (1965: fig. 1e, d). The second tooth shows the basal 10 mm enclosed in the parasymphysial plate (Fig. 10G), with its crenellated base again typical of onychodonts (Gross 1965; Schultze 1969). The broken tooth sections in dorsal view are laterally compressed (anterior tooth 5 × 4 mm; posterior 4 × 2.8 mm). Higher magnification (Fig. 10H) shows the fine striations in the tooth enamel. These have a density of ~30/mm, similar to the parasymphysial teeth from the previous locality.

Comparisons: Previously named onychodontid genera are *Onychodus* Newberry, 1857, *Strunius* Jessen, 1966 and *Grossius* Schultze, 1973. *Quebecius* Schultze, 1973, first described as an onychodontid, was later re-assessed as a porolepiform (Schultze & Arsénault 1987; Cloutier & Schultze 1996). Onychodontids are mainly represented in the fossil record by many occurrences of isolated teeth in Devonian and Carboniferous strata (Schultze 1973). Records of more complete remains include jaw remains from the Pragian of China and Emsian of Australia (Zhu & Janvier 1994; Ørvig 1969; Lindley 2002), and associated skull remains from the Eifelian of Morocco (Aquesbi 1988), said to resemble *Grossius* from the Eifelian of Spain. Exceptionally preserved acid-prepared material from the famous Upper Devonian (Frasnian) Gogo deposit, Western Australia, is by far the most complete onychodont material, and represents a new species

of *Onychodus* (Long 2001; Andrews et al. in press).

Assuming all material from the Cravens Peak limestone locality belonged to the same taxon, it cannot be referred to the much smaller genus *Strunius* (total length of fish 100 mm; Jessen 1966: 334), whilst the type and only known species of *Grossius* was much larger (Schultze 1973). The only named taxon with parasymphysial teeth with a barbed tip is *Onychodus jaekeli* from Wildungen (Frasnian), but in that form the parasymphysial whorl is mainly attached to the dentary, not Meckel's cartilage, and the tooth sockets on the dentary are round (Jessen 1966: pl. 20), both significant differences from the holotype of *Luckeus abudda* n. sp. described above. Both features are also seen in *Onychodus sigmoides* and the Gogo *Onychodus* (Jessen 1966: fig. 12C; Long 2001: fig. 3C, D), whereas *Luckeus abudda* n. sp. differs from other onychodontids in that the dentary ridge is reduced anteriorly in front of the tooth row, and the parasymphysial tooth whorl is carried mainly or entirely on Meckel's cartilage. The 'subrectangular' tooth sockets resemble those on a dentary from the Eifelian of Queensland ascribed to '*Onychodus* sp.' by Turner et al. (2000: fig. 5.5), but this lacks the lateral row of smaller socketed teeth, as do the lower jaws of other *Onychodus* and *Strunius*.

Regarding the characteristic striations of onychodont teeth, Lindley (2002: 122) described a contrasting anastomosing pattern in teeth named *Onychodus yassensis* from the Emsian of Burrinjuck, but other teeth from this locality also show the chevron pattern (Young, unpublished data). The striations of Lindley's material are much finer (160–2000/mm) than in the teeth described here (and would appear smooth under low magnifications). He suggested a trend of decreasing density of the striations through the Middle-Late Devonian of Australia, by comparison with Middle Devonian material from Queensland (Turner et al. 2000: pl. 2). However, striations on Emsian teeth from Broken River have a density of about 25/mm (De Pomeroy 1996: fig. 5B), and some Eifelian teeth are at least twice the density (Turner et al. 2000: pl. 2, fig. 2), so such a trend is not clearcut. Isolated teeth from China illustrated by Wang (1992: pl. 4, figs 1–5) show the typical resorbed base, and striated enamel on the distal end of one tooth (fig. 1). The age of these remains is Pragian-Emsian (Zhu et al. 2000). The small dentary described by Zhu & Janvier (1994) as the oldest onychodontid is of Pragian age, and they suggested that lack of striations on its teeth was a

generalised osteichthyan condition by which the jaw could be distinguished from all other onychodontids. Similar isolated teeth that are apparently 'smooth' (or with very fine striations) also occur commonly in Pragian deposits of central NSW (Burrow 1997, 2002). An indeterminate isolated dentary from China illustrated by Zhu & Yu (2004: fig. 6A–F) and interpreted to have possible onychodontid affinity is slightly older (late Lochkovian Xitun Formation; Zhu et al. 2000).

The single onychodontid specimen from Mount Winter (gen. et sp. indet.) evidently came from a somewhat larger form than that from the Cravens Peak locality. The striations on the parasymphysial teeth had a similar density (30–50/mm) to *Luckeus abudda* n. sp., but this applies also to other onychodontids, for example *Grossius* (40–50/mm; Schultze 1973: 203), and *Onychodus jaekeli* (30–40/mm; Gross 1965).

Discussion

Biostratigraphy and correlation

Revised faunal lists of the Devonian fish assemblages from the two studied localities are summarised in Table 2. The osteichthyan component comprises three major osteichthyan groups represented in both assemblages: dipnoans, osteolepidids, onychodonts. A fourth group (Porolepiformes) is represented at the Toomba Range locality by a single scale. The fact that within these groups different taxa are represented at the two localities indicates that they are either not the same age, or did not sample the same palaeoenvironments. Turner (1995, 1997) compared the thelodonts from the southern Toomba Range in the Georgina Basin with younger (Middle Devonian) turiniid scales from the Broken River sequence of Queensland, and the acanthodian assemblage also resembles Broken River forms (Burrow 2002; Burrow & Young, 2005). Some resemblance was noted above between the holotype of *Luckeus abudda* n. sp. and onychodont jaw remains documented from the 'Fish Hill' locality at Broken River (Turner et al. 2000). This has been dated as middle Eifelian (*costatus-australis* conodont zones; for a review of Broken River Devonian fish ages see Young 2004). Thus there may be consistent evidence from thelodonts, acanthodians and now onychodontids for a similar Eifelian age for the Cravens Peak limestone in the southern Toomba Range. The apparently primitive position of the

Table 2

Faunal lists of the Lower/Middle Devonian at Mt. Winter (locality 19, Fig. 1A) and at Southern Toomba Range (locality 15, Fig. 1A), central Australia.

MOUNT WINTER	SOUTHERN TOOMBA RANGE
AGNATHA	AGNATHA
Thelodontida	Thelodontida
thelodont scales (Turner 1997: 309)	<i>Turinia gavinyoungi</i> Turner, 1997 <i>Turinia</i> sp. Turner, 1997
GNATHOSTOMATA	GNATHOSTOMATA
Placodermi	Placodermi
?groenlandaspid arthrodire indet.	asterolepid antiarch indet. Young, 1984
	Chondrichthyes
	<i>Mcmurdodus whitei</i> Turner & Young, 1987
Acanthodii	Acanthodii
?climatiid acanthodian (spine)	<i>Nostolepis</i> sp. cf. <i>N. striata</i>
acanthodian indet.	<i>Radioporacanthodes</i> sp.
	<i>Teneracanthus toombaensis</i> Burrow & Young, 2005
	<i>Machaeracanthus pectinatus</i> Burrow & Young, 2005
Osteichthyes	Osteichthyes
Osteolepidida	Osteolepidida
<i>Muranjilepis winterensis</i> n. gen., n. sp.	osteolepid n. gen., n. sp.
	Holoptychiida
	holoptychiid indet.
Onychodontida	Onychodontida
onychodontid indet.	<i>Luckeus abudda</i> n. gen., n. sp.
Dipnoi	Dipnoi
<i>Amadeodipterus kencampbelli</i> n. gen., n. sp.	dipnoan gen. et sp. indet.

tooth whorl in *Luckeus abudda* n. sp. might not be expected in such a young taxon (already lost in the Eifelian *Onychodus sigmoides*), but there are close similarities in this respect to *Strunius rolandi* from Kokenhusen (Latvia, Frasnian), so the onychodontid evidence of age remains equivocal.

Biogeography

Other groups from central Australia have provisionally indicated some faunal connections with South China in the Early-Middle Devonian, for example the arthrodire *Toombalepis* from the Cravens Peak Beds was grouped with *Yujiangolepis* from South China within the family Antartaspidae by Young & Goujet (2003). For osteichthyans, Long (2001) has suggested a close relationship between onychodontids and the Chinese *Psarolepis*, based on endocranial similarities indicated by the Gogo *Onychodus*. The apparently primitive position of the tooth whorl in the lower jaw of the new onychodontid *Luckeus* n. gen. may support this idea, consistent with the co-occurrence of onychodontid remains in pre-Emsian strata in China and Australia (see above). The new osteolepidid taxon *Muranjilepis* shows some characters also recorded in Chinese forms *Thursius wudinensis* and *Kenichthys*

campbelli. Relationships of *Amadeodipterus* n. gen. are uncertain, but it was evidently an endemic dipnoan, in contrast to the more typical 'dippterid' lungfish from younger strata (Harajica fauna; Fig. 2B) in central Australia (e.g. the undescribed skull of Young 1985: fig. 8J).

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