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A new genus of lungfish from the Givetian (Middle Devonian) of central Australia

ALICE M. CLEMENT

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A new *Dipterus*-like lungfish, *Harajicadipterus youngi*, is described from the Givetian (Middle Devonian) Harajica Sandstone Member of central Australia. The material is comprised of five specimens representing the skull roof, orbital bones, tooth plates, operculo-gular bones, a partial pectoral girdle, centra and scales. *Harajicadipterus* can be distinguished from other dipnoans by its long postorbital cheek, broad B bone, lack of contact between E and C bones, and radiating tooth rows with some denticles evident between the rows. Results of a cladistic analysis of 81 characters for 33 dipnoan taxa resolved *Harajicadipterus* below the holodontid clade but as more derived than *Dipterus* and the chirodipterid clade.

Key words: Dipnoi, phylogeny, Devonian, Givetian, Harajica Formation, Australia.

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Introduction

Dipnoans, or lungfish, first appeared in marine deposits in the Early Devonian over 400 million years ago (Lehmann and Westoll 1952; Denison 1968; Chang and Yu 1984), before reaching their peak of diversity later in the Devonian (Marshall 1986). Over time, dipnoans diversified into a variety of body forms and appear to have occupied a wide range of ecological niches (Campbell and Barwick 1990).

Devonian vertebrate fossil sites in Australia stretch across the continent (Young and Turner 2000). Those in the west are typically marine, in eastern Australia they are either marine or non-marine and in central sites such as the Amadeus and Georgina Basins they are predominantly non-marine (Young 1993). Remains of Devonian fish were first discovered in the Amadeus Basin of central Australia in 1963 (Gilbert-Tomlinson 1968) during regional geological mapping across the area, published by Wells et al. (1970). The Harajica Sandstone Member belongs to the Parke Siltstone of the non-marine Pertnjara Group of central Australia (Jones 1972). The siltstones, sandstones and conglomerates indicate a fluviatile environment (Wells et al. 1970).

The first dipnoan remains discovered in the Harajica Sandstone Member were described by Young (1985) who estimated a Givetian–Frasnian age for the strata. Other Devonian vertebrates known from the Amadeus Basin include thelodontids (Turner 1997), placoderms such as *Bothriolepis* spp. and *Phyllolepis* (Young 1985, 2005), the dipnoan *Amadeodipterus kencampbelli*, and the osteolepid *Muranjilepis winterensis* (Young and Schultze 2005). Young (1985) also described some fragments of acanthodian and rhipidistian crossopterygian material. Late Devonian lungfish from Australia are more common (Miles 1977; Campbell and Bell 1982; Campbell and Barwick 1991, 1998; Ahlberg et al. 2001) than the comparatively rare Middle Devonian forms (Long 1992).

The dipnoan skull roof previously described by Young (1985) was not attributed to any specific taxon. However, Young (1985) discussed various features that are sufficient to distinguish it from any of the long-snouted forms, and also from *Scaumenacia*, *Phaneropleuron*, and *Pentlandia*. He concluded from the skull-roofing pattern that the lungfish from Harajica is most like *Dipterus* or *Chirodipterus*, but recognised that further material was required to conclusively identify the species or erect a new taxon. Further material has since been discovered and the purpose of this paper is to describe and analyse the new specimens.

Institutional abbreviations.—CPC, Commonwealth Palaeontological Collection (Geosciences Australia), Canberra; NMV, National Museum of Victoria, Melbourne.

Material and methods

A collection of five specimens was studied, collected by Gavin Young in 1973 and 1991. All specimens came from locality 6 (as defined by Young 1985), which is southwest of Stokes Pass in the Harajica Sandstone Member. The material was prepared by removing any existing bone or tissue from the matrix through immersion in 7–10% hydrochloric acid

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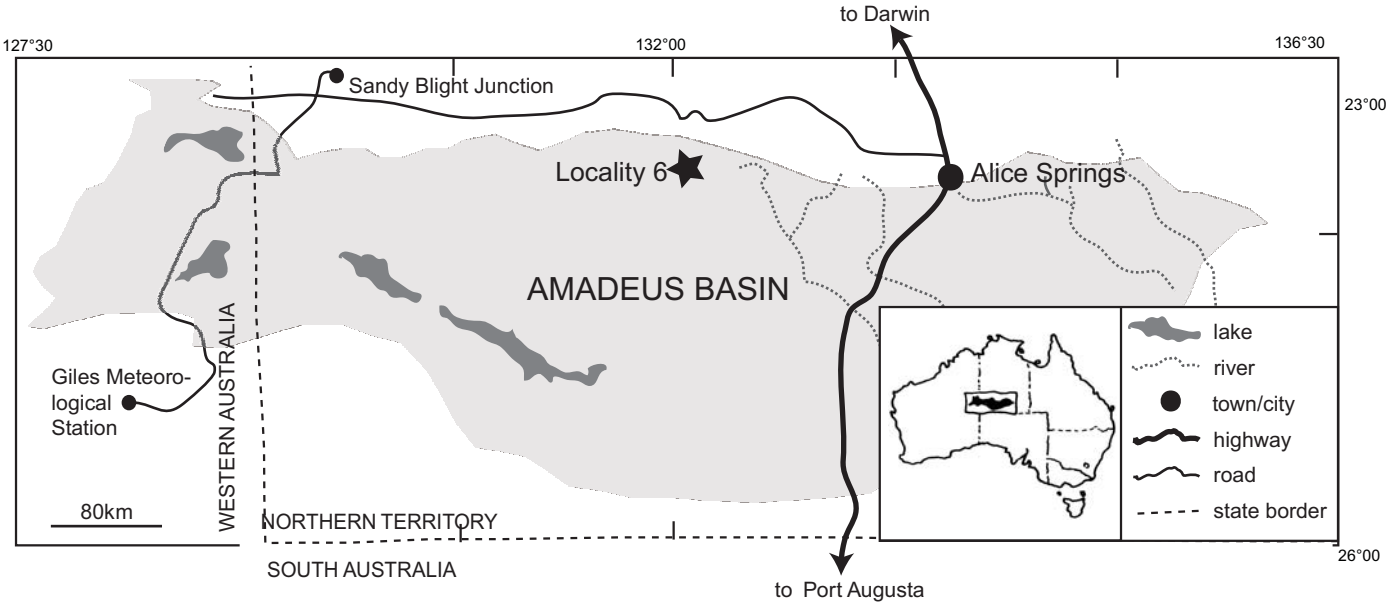

Fig. 1. The Amadeus Basin in central Australia (for location see small map), showing Devonian vertebrate localities (re-drawn from Young 2005). *Harajicadipterus youngi* gen. et sp. nov. is known from locality 6.

for one day. Following acid preparation, the specimens were rinsed and allowed to dry.

The examination of the specimens involved using black latex casts of the impressions preserved in the sandstone rock, and dusting them with a sublimate of ammonium chloride to enhance contrast prior to photography. The nomenclature used is that of Forster-Cooper (1937) with additions from Miles (1977).

The data matrix used for cladistic analysis was that of Ahlberg et al. (2006) with 79 morphological characters and 33 taxa with amendments from the erratum (Ahlberg et al. 2007) (Appendix 1). Two additional characters were identified through the course of this research. Of the total 81 characters, 22 are binary and the remainder are multistate. The data matrix was assembled in MacClade 4.05 (Maddison and Maddison 2001) and *Diabolepis* was specified as the outgroup. The analysis was performed using the phylogenetic package PAUP* 4.0b10 (Swofford 2001). A heuristic search was used, with 1000 replicates of random stepwise addition under the tree bisection-reconnection algorithm. All characters were equally weighted and all but five were unordered. Bremer support values were calculated using TreeRot v.3 (Sorenson and Franzosa 2007) in accordance with the heuristic search algorithm of PAUP.

Systematic paleontology

Osteichthyes Huxley, 1888

Sarcopterygii Romer, 1955

Dipnomorpha Ahlberg, 1991

Dipnoi Müller, 1844

Genus *Harajicadipterus* nov.

Etymology: In reference to the Harajica Sandstone, the formation in which the specimens were preserved.

Type and only known species: *Harajicadipterus youngi* gen. et sp. nov.

Diagnosis.—As for the type species by monotypy.

Harajicadipterus youngi sp. nov.

1985 "dipnoan"; Young 1985: 246, 249, fig. 8J.
1993 "dipnoan indet."; Young 1993: 248.

Figs. 2, 3, 5J–K.

Etymology: In honour of Dr. Gavin Young who has contributed much time and effort in the study of the Amadeus Basin geology and fauna.

Type material: Holotype: NMV P228725, skull roof and cheek bones, with also tooth plates, operculum and partial pectoral girdle (Fig. 2A–D); paratype: CPC 24697, a cranium showing the pattern of most skull roofing bones (Fig. 2E, F).

Type locality: All specimens were collected from "locality 6" of the Amadeus Basin, Northern Territory, Australia. Locality 6 is 2km southwest of the southern end of Stokes Pass.

Type horizon: The Harajica Sandstone Member of the Parke Siltstone has been dated as Givetian–Frasnian (Young 1985). Locality 6 has three horizons that contain fish material, most of which is referable to the antiarch *Bothriolepis*, but that also contains some osteichthyans (Young 1985).

Material.—NMV P229314, an isolated left pterygoid tooth plate (Fig. 3A, B); CPC 24698, 7 vertebral centra (Fig. 3C, D); and CPC 24699 contains some possible partial operculogulars and an isolated dermal scale (Fig. 3E, F).

Diagnosis.—*Dipterus*-like pterygoid tooth plates with seven tooth rows; teeth that coalesce towards the postero-mesial margin of the tooth plate; scattered denticles between tooth rows. Broad B bone with median projection; K present; single D bone separates C from F; paired C and E bones; C bones elongate. Postorbital cheek longer than orbit diame-

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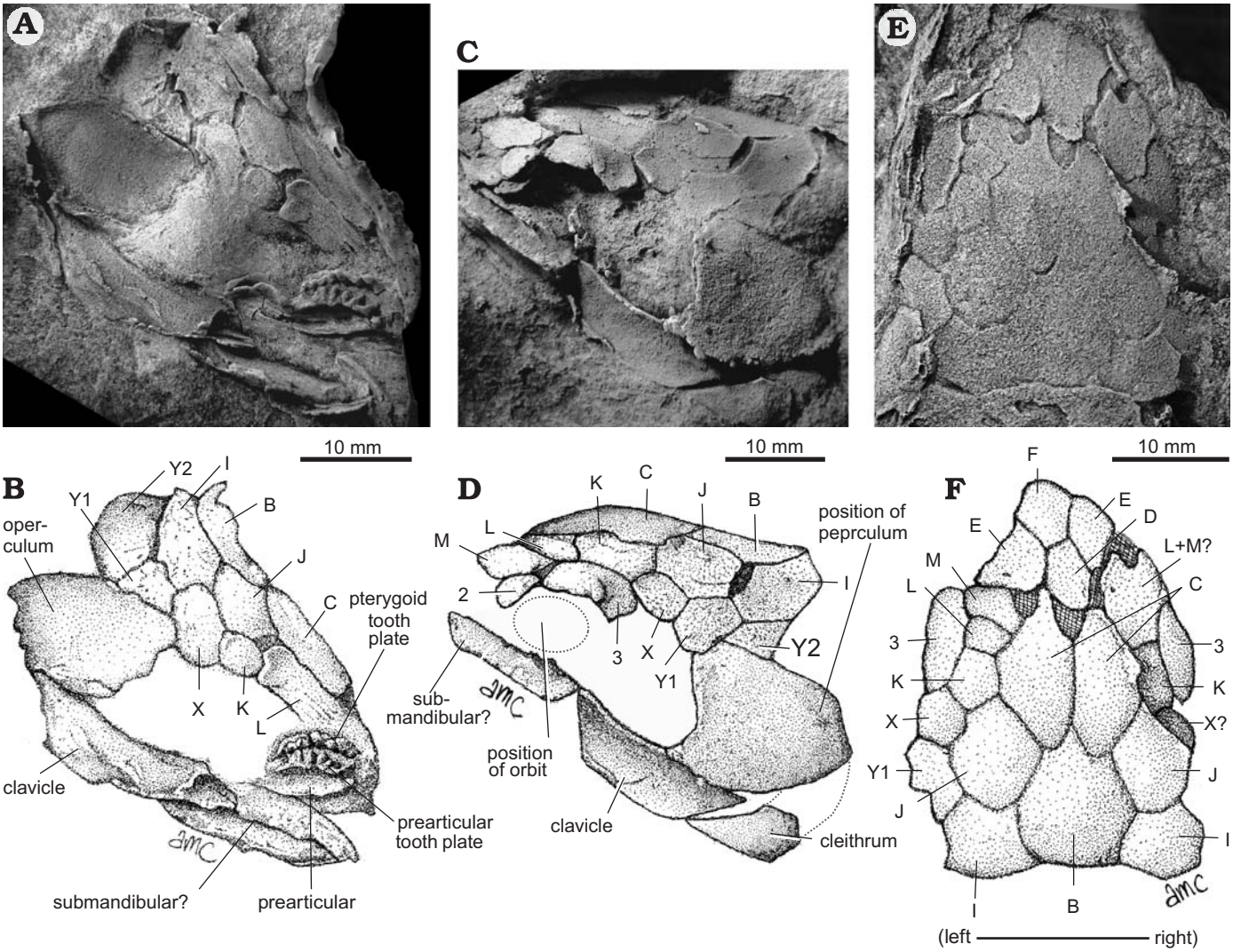

Fig. 2. Dipnoan fish *Harajicadipterus youngi* gen. et sp. nov. from the Harajica Sandstone Member (Givetian), central Australia. Holotype, NMV P228725, skull-roofing bones, operculum, tooth plates and pectoral girdle in opposing views (**A**, **C**); interpretive drawing of same (**B**, **D**). **E**. CPC 24697, skull roof in dorsal view. **F**. Interpretive drawing of same. All specimens are latex casts of impressions in rock and whitened with ammonium chloride. Dashed lines represent approximate extent of cleithrum in D and approximate position of orbit.

ter. Ossified, differentiated disc centra; rounded scales partially covered with ridged dermal ornament.

Description

General features.—A small to mid-sized dipnoan with a *Dipterus*-like skull roof pattern (White 1965) and a long postorbital cheek. Specimen NMV P228725 consists of two parts of the same individual, labelled herein as A and B. NMV P228725-A shows detail of the skull roof, operculum, shoulder girdle and the tooth plates. NMV P228725-B shows skull-roofing bones, the shoulder girdle and the position of the orbit relative to the operculum. CPC 24697 is an impression of a second dipnoan skull of the same taxon that was first figured by Young (1985: text-fig. 8J) but will be re-described here. NMV P229314 is an isolated left pterygoid tooth plate. CPC 24698 shows 7 vertebral centra, and CPC 24699 contains some possible partial operculo-gulars and scales.

Skull roof.—*Harajicadipterus youngi* has a short and broad median B bone with a distinctive median projection and elongate, paired C bones (Figs. 2E, F, 5G, H). There is a single D bone, and paired E bones lying anteriorly. The I and J bones are both large relative to Y1 and Y2 which seem to be variable in size between specimens. Unlike *Dipterus* where the X bone can sometimes fail to develop (White 1965), both X and K bones are present in these specimens of *Harajicadipterus* (Fig. 2). Bones L and M have fused on the right side of CPC 24697 to form a compound bone (Fig. 2E, F). There has been some disarticulation of the anterior portion of the skull roof, with the D, E and F bones displaced slightly.

Bone 3 has a long orbital margin and is strongly curved (Fig. 2C, D). Pores and a thickening of the bone indicate the path of the lateral line branch passes into bone 3. Bone 2 (Fig. 2C, D) is very small with a short orbital margin. Although very few of the cheek bones have been preserved, the dis-

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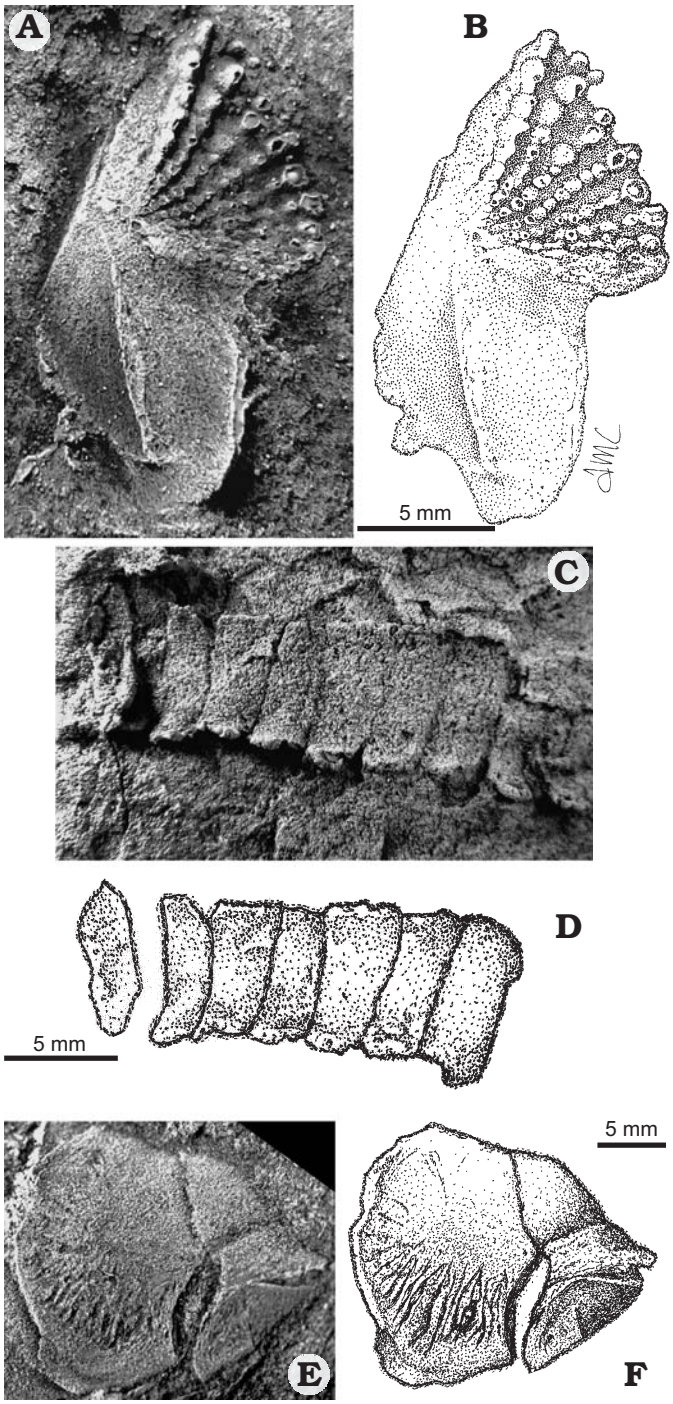

Fig. 3. Dipnoan fish *Harajicadipterus youngi* gen. et sp. nov. from the Harajica Sandstone Member (Givetian), central Australia. **A**. Photograph of upper left pterygoid tooth plate, NMV P229314, latex cast impression whitened with ammonium chloride. **B**. Interpretive drawing of same. **C**. Articulated vertebral centra, CPC 24698. **D**. Drawing of same. **E**. Isolated scale in external view showing ornament CPC 24699. **F**. Drawing of same.

tance between the orbit and the median skull roof bones (B and C) is comparable to that of other "long-cheeked" dipnoans such as *Iowadipterus* (Schultze 1992), *Adololopas* (Campbell and Barwick 1998) and primitive dipnoans such as *Dipnorhynchus* (Campbell and Barwick 1982) and *Uranolophus* (Denison 1968). There is no ornamentation on the skull roof bones, indicating that they were possibly covered by cosmine unlike the distinct dermal ornamentation seen on the Mount Howitt lungfishes *Howidipterus* and *Barwickia*, which were also studied from latex casts (Long 1992, 1993). Unfortunately the state of preservation is too poor to more accurately determine the presence or absence of this tissue. The canal entering bone 3 is the only evidence of sensory canals or pit-lines.

Operculum and pectoral girdle.—The size and shape of the operculum can be determined from NMV P228725 A and B (Fig. 2A–D). The operculum measures approximately 19 mm in diameter and has a horizontal dorsal edge. The specimens have not preserved evidence of muscle attachment scars or any ornamentation.

Specimen NMV P228725 shows the clavicle on parts A and B, and the cleithrum on part B only. The clavicle (Fig. 2A–D) is a long, thin bone, which is slightly trapezoidal in shape. The cleithrum is loosely articulated with the clavicle on part B, and the ventral portion is pentagonal in shape with an elongated point. The dorsal shaft is not seen (Fig. 2C, D). The clavicle and cleithrum in Fig. 2C, D comprise the right shoulder girdle which shows no evidence of dermal ornamentation on its external surface, however, this is possibly an artefact of poor preservation. There is a large bone at the anterior end of the specimen lying below the tooth plates that appears narrow and elongate, and this is likely to be part of the submandibular or subopercular series disarticulated and partially exposed (Fig. 2A–D).

Mandible.—Some of the prearticular (the main internal dermal bone) can be seen still attached to the lower tooth plate on the holotype (Fig. 2A, B). The visible portion shows that it is a thick, smooth bone that supports the radial tooth plates.

Tooth plate.—NMV P229314 is an isolated upper left tooth plate with the oral surface exposed. It resembles that of the holotype (Fig. 2A, B) and has been assigned to *Harajicadipterus*. The discovery of further material will be vital to either support or disprove this association. The tooth plate is deeply concave and triangular in shape, not ovoid like *Eoctenodus* (Long 1987). Seven well-defined tooth rows are visible, and there is a possibility of an eighth (Fig. 3A, B). The tooth plate contains 8 or 9 teeth in the medial rows, and as few as 6 in the lateral rows. The angle between the medial row and the lateral-most row is 67°. Like those in lungfish such as *Tarachomylax* (Barwick et al. 1997) and *Stomiahykus* (Bernacsek 1977), all tooth rows originate from the posterior of the pterygoid and radiate anteriorly and antero-laterally. There are no postero-laterally radiating ridges. The teeth are rounded and they decrease in size and coalesce towards the centre of radiation. They appear neither sharp nor pointed, possibly due to wear. The tooth rows are not as clearly defined or widely separated as in *Adololopas* (Campbell and Barwick 1998), and there are relatively shallow clefts between the rows without any obvious wear facets. Unlike the condition seen in *Dipterus* (White 1965; Jarvik 1980), *Harajicadipterus* has some small denticles between

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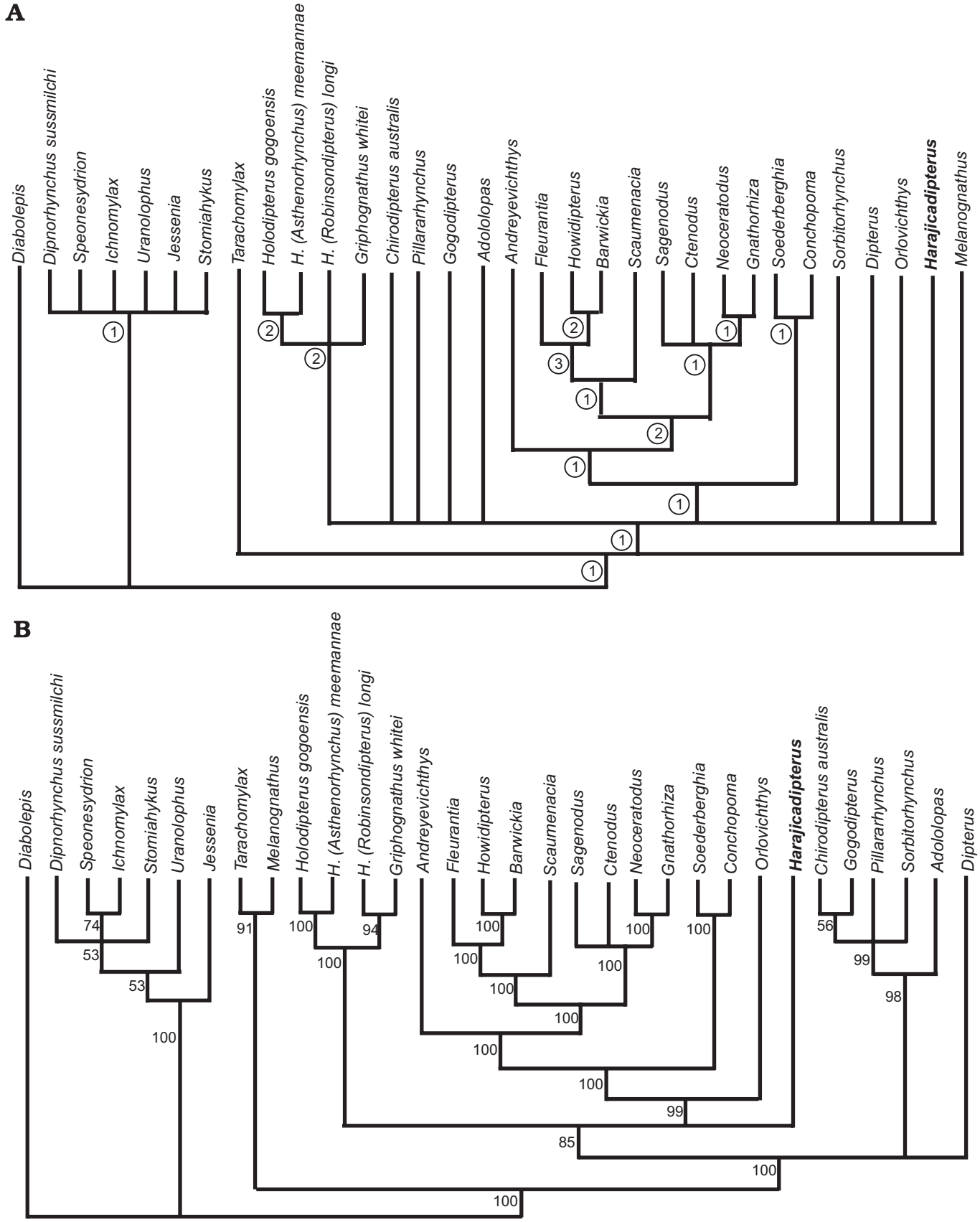

Fig. 4. **A**. Strict consensus tree of the 525 most parsimonious trees generated for the position of *Harajicadipterus youngi* gen. et sp. nov. within the Dipnoi. Consistency index (CI) = 0.4369, retention index (RI) = 0.6906, homoplasy index (HI) = 0.5631. Encircled numbers indicate Bremer support values. **B**. 50% Majority-rule consensus tree. Node support bootstrap values indicated.

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the tooth rows. The outline of the shape and size of the corpus (the anterior portion of the parasphenoid) can be inferred from the shape of the tooth plates. The corpus appears short and broad, with long pterygoid to pterygoid contact. The pterygoid reaches backwards towards the mandibular articulation and there is a prominent ridge extending posterolaterally (Fig. 3A, B), similar to that seen in *Dipterus* (White 1965). The pterygoid distinctly differs in shape from those of *Tarachomylax* (Barwick et al. 1997) and *Adololopas* (Campbell and Barwick 1998) which have a distinct edge into which a ploughshare-shaped parasphenoid can fit, the posterior edge of the pterygoid is not so prominent in *Harajicadipterus* (Fig. 3A, B). The tooth plates of *Howidipterus*, another Australian Middle Devonian tooth-plated genus, differ from *Harajicadipterus* in having twice as many tooth rows, with only three to five cusps in each tooth row (Long 1992).

Vertebrae.—Like the Recent genera, most Devonian dipnoans do not possess ossified vertebral centra (Ahlberg and Trewin 1995; Arratia et al. 2001), however, some impressions of centra are evident in CPC 24698. There appears to be a row of seven centra, six of which are articulated and none of the associated vertebral elements such as neural or haemal arches or spines are preserved (Fig. 3C, D). Unlike *Howidipterus* or *Barwickia* that exhibit a mineralised column rather than individual centra (Long and Clement in press), those of *Harajicadipterus* are clearly differentiated. The average height of the centra is 6.5 mm. *Harajicadipterus* does not have prominent neural arches or supraneural spines, which is unlike the condition seen in *Dipterus* (Ahlberg and Trewin 1995) and *Uranolophus* (Denison 1968). The centra are compact and independent and resemble those of *Rhynchodipterus* (Schultze 1969; Arratia et al. 2001). They may be comparable to the disc centra of genera such as *Griphognathus* (Campbell and Barwick 2002) and *Soederberghia* (Ahlberg and Trewin 1995), but further comparisons cannot be made due to the state of preservation in *Harajicadipterus* (Fig. 3C, D).

Scales.—Some isolated scales present in CPC 24699 are poorly preserved, but dermal ornament is present and cosmine was most likely absent. The scales are cycloid and approximately 20 mm in diameter. Individual scales may overlap, and the thin, wavy ridged ornament covers a roughly triangular area one-third the length of the scale (Fig. 3E, F). The ornament is less dense than that of *Scaumenacia* (Cloutier 1996) and more pronounced than that of *Eoctenodus* (Long 1987). It resembles most closely that of *Howidipterus* (Long 1992).

Phylogenetic analysis

The results of the cladistic analysis are shown in Fig. 4. As in Ahlberg et al. (2006), in both the strict and 50% majority rule consensus trees, Early Devonian taxa such as *Dipnorhynchus*, *Uranolophus*, and *Melanognathus* dominate the bottom of the tree and Late or post Devonian genera appear near the top of the tree. The Mount Howitt *(Howidipterus* and *Barwickia)* and Escuminac (*Scaumenacia* and *Fleurantia*) taxa form a distinctive clade, as do *Sagenodus*, *Ctenodus*, *Gnathoriza*, and *Neoceratodus*.

Two new characters were added to the Ahlberg et al. (2006) matrix: character (80), whether Bone 10 has contact with bones 5–7 in the cheek; and character (81), which concerns the shape of the anterior corpus of the parasphenoid. This resulted in the removal of the tooth-plated *Adololopas* from alongside *Dipterus*, and the appearance of a "chirodipterid" clade (Campbell and Barwick 1990), containing *Adololpas*, *Pillararhynchus*, *Sorbitorhynchus*, *Chirodipterus*, and *Gogodipterus*. This differs from the tree of Ahlberg et al. (2006) through clarifying the monophyly of the Chirodipteridae, a result not seen in the cladistic parsimony analyses of other authors (Schultze 2001; Ahlberg et al. 2006; Friedman 2007). There is also slight re-adjustment of the Early Devonian taxa that branch from the bottom of the tree.

The strict consensus tree results in a polytomy for most of the Early Devonian genera, and another for many of the Late Devonian genera, including the chirodipterids, *Dipterus*, and *Harajicadipterus*. The clade containing the Mount Howitt fauna, *Fleurantia*, *Scaumenacia* and Recent genera is well supported, as is the Gogo Holodontid clade (Fig. 4A).

Harajicadipterus youngi was placed toward the middle of the tree just above *Dipterus* and the chirodipterid clade in the 50% majority-rule consensus tree (Fig. 4B). The 50% majority-rule consensus tree shows the inferred monophyletic groups that occurred in a majority of the bootstrap samples. *Harajicadipterus* sits below the Gogo holodontid clade (*Holodipterus* spp. and *Griphognathus*) and all other Late Devonian and post-Devonian taxa, however it results in a polytomy in the strict consensus tree (Fig. 4). *Harajicadipterus* shares paired E bones and a narrow angle between the midline and anterolateral margin of pterygoid with the more derived dipnoans. The presence of rounded scales without cosmine is a synapomorphy of this group. Node support was evaluated for the strict consensus tree using Bremer support indices (Bremer 1988, 1994). The indices are a means of assessing support in a maximum parsimony analysis and can be used as an alternative to bootstrap analysis (Fig. 4).

Discussion

Tooth plates with distinct cusps organised into many discrete rows are found in numerous other Devonian dipnoans. They have been documented in many species, including *Dipterus* (White 1965), *Stomiahykus* (Bernacsek 1977; Smith and Campbell 1987), *Scaumenacia* (Cloutier 1996), *Tarachomylax* (Barwick et al. 1997), *Speonesydrion* (Campbell and Barwick 1984), *Rhinodipterus* (Campbell and Barwick 1999), and *Andreyevichthys* (Ahlberg et al. 2006). Whilst tooth plates are relatively common in the fossil record and useful

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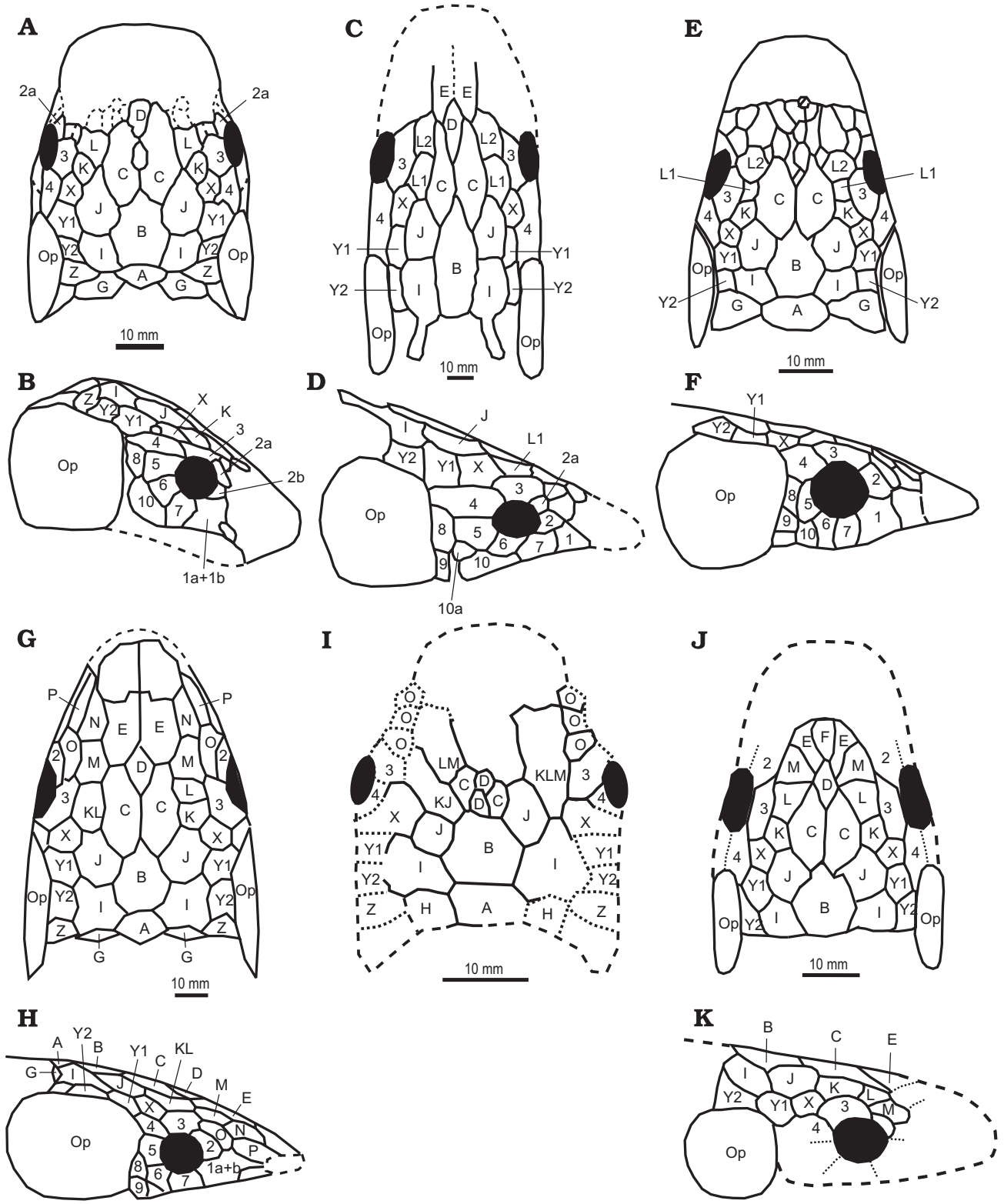

Fig. 5. Comparison between dorsal and right lateral views of skull roof pattern of Devonian dipnoans. **A**, **B**. *Chirodipterus australis* from the Gogo Formation (Frasnian), Australia, redrawn from Miles (1977:232-233); comparison between dorsal and right lateral views. **C**, **D**. *Holodipterus* (*Asthenorhynchus*) *meemannae* from the Gogo Formation (Frasnian), Australia, redrawn from Pridmore et al. (1994: 152). **E**. *Dipterus valenciennesi* from the Old Red Sandstone (Middle Devonian) of Scotland, redrawn from Campbell and Barwick (1990: 154). **F**. *Dipterus valenciennesi* from the Old Red Sandstone (Middle Devonian) of Scotland, redrawn from Jarvik (1980: 413). **G**, **H**. *Howidipterus donnae* from Mount Howitt (Givetian), Victoria, Australia, redrawn from Long (1992: 306). **I**. *Amadeodipterus kencampbelli* from the Amadeus Basin (Emsian–Eifelian), central Australia, redrawn from Young and Schultze (2005:20). **J**, **K**. *Harajicadipterus youngi* gen. et sp. nov. from the Harajica Sandstone Member (Givetian), central Australia, drawn from specimens NMV P228725 and CPC 24697. Abbreviation: Op, operculum.

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when identifying or classifying taxa, identification of a taxon cannot rely on tooth plates alone. Wear and resorption can alter tooth plate form, making identification of isolated tooth plates difficult (Reed 1985). Similarly, Kemp (1997) showed that the form of tooth plates might vary dramatically during ontogeny in *Neoceratodus*. Juvenile *Neoceratodus* tooth plates are triangular, whereas adult ones are elongate or oval. Thus, tooth plates are most useful in the identification of taxa when used in conjunction with a suite of other characteristics. However, the mode of growth of the dentition can be phylogenetically informative. The radial tooth plates of *Harajicadipterus* were formed by the addition of isolated teeth at the end of each row, rather than by deposition of successive dentine layers as seen in genera such as *Dipnorhynchus* (Campbell and Barwick 1990). There is no evidence of any growth from between the dentine and the underlying bone. Additionally, *Harajicadipterus* also differs from *Dipterus* significantly (Campbell and Barwick 1995) in having some small denticles scattered between the tooth rows.

Harajicadipterus youngi, known from the central section of the Amadeus Basin was noted by Young (1985) to have a "*Dipterus*-like" skull-roofing pattern, both genera retain a short, broad B bone. While *Harajicadipterus* is similar in pattern to both *Dipterus* (White 1965; Jarvik 1980) and *Chirodipterus* (Miles 1977), it differs in some significant features (Fig. 5A–K). *Harajicadipterus* has the primitive feature of a much longer postorbital cheek relative to the size of the orbit. Young (1985) noted that *Harajicadipterus* possesses a D bone, unlike *Scaumenacia*, *Phaneropleuron* or *Pentlandia* (Fig. 2E, F); the D bone is smaller in *Harajicadipterus* compared to that of *Chirodipterus* (Miles 1977). *Harajicadipterus* also differs from *Dipterus* in having fewer tooth rows, a separate K bone, no contact between the E and C bones, and a single D bone when *Dipterus* frequently has many. Therefore, whilst maintaining the primitive long cheek, *Harajicadipterus* appears more derived than *Dipterus* in other features of the skull roof.

Like *Dipterus*, the massive dental plates of *Harajicadipterus* are strongly denticulated indicating that they are capable of masticating tough food (White 1965). The long cheek seen in *Harajicadipterus* like that in *Holodipterus* (*Asthenorhynchus*) *meemannae* and *Iowadipterus*, would have housed large adductor muscles (Schultze 1992). These two features of *Harajicadipterus* suggest that it had a very powerful bite.

Other long-cheeked dipnoans include *Iowadipterus*, *Holodipterus*, *Adololopas* (Campbell and Barwick 1998), *Uranolophus* (Denison 1968), *Dipnorhynchus* (Campbell and Barwick 1982), and *Soederberghia* (Lehman 1959). *Harajicadipterus*, however, has differentiation of D and E bones unlike that of the Middle Devonian *Iowadipterus* (Schultze 1992), and radically different dentition to that of *Holodipterus* (Pridmore et al. 1994). While *Adolopas* has a long-cheeked, tooth-plated form like *Harajicadipterus*, it has a greater elongate B bone and a more anterior X bone relative to the orbit. The most striking difference is that of the tooth plates. There are fewer rows and fewer cusps per row in *Adololopas*, and the tooth rows radiate from across the posterior of the plate (Campbell and Barwick 1998) instead of radiating from the postero-medial corner as in *Harajicadipterus.* Of course, the way in which the radial tooth plates develop differs among many of these genera (Campbell and Barwick 2008) but this cannot always be readily and accurately determined from incomplete specimens.

Amadeodipterus is a short-headed "dipterid" dipnoan known from the Emsian–Eifelian western section of the Amadeus Basin (Young and Schultze 2005). *Amadeodipterus* differs quite remarkably from *Harajicadipterus*. *Amadeodipterus* has a very short and broad head, very small C bones, no obvious paired E bones, and an extremely short and wide B bone (Fig. 5I). There are also up to 6 more tooth rows per pterygoid tooth plate. However, the number of tooth rows and cusps in each row can increase during growth, as documented in *Eoctenodus* (Long 1987). Despite this, *Amadeodipterus* differs strongly from *Harajicadipterus* and is known only from the Mt. Winter site of the Amadeus Basin so far (Young and Schultze 2005). The nearby Georgina Basin has an endemic faunal assemblage containing placoderms, acanthodians, osteichthyans and agnathan groups (Young and Goujet 2003). The only dipnoan material from this site is some isolated scales (Young and Schultze 2005).

There have been numerous attempts to clarify the interrelationships of Devonian dipnoans (Miles 1977; Marshall 1986; Schultze 2001; Ahlberg et al. 2006; Friedman 2007). Campbell and Barwick (1990) developed a phylogeny based on adaptive functional complexes rather than cladistic parsimony analysis, which resulted in a phylogeny of three lineages centred around broad dentition types. If *Harajicadipterus* were to be placed in Campbell and Barwick's (1990) phylogeny, it would sit alongside *Pentlandia*, *Scaumenacia*, and *Rhinodipterus* in the "tooth-plated" lineage. However, this phylogeny is contradicted by a series of morphological characters such as the known distribution of cranial ribs (Long 1993) and many features of the skull roof. *Howidipterus* (Fig. 5G, H), another Late Devonian dipnoan from East Gondwana differs in the overall proportions and in aspects of the skull-roof pattern (Long 1992).

In the cladistic analysis, *Harajicadipterus* sits above the chirodipterid clade and *Dipterus* in the middle of the tree. Despite the similarity in tooth plate morphology and skull roof pattern, *Harajicadipterus* is more derived than *Dipterus* and is more closely related to the Late Devonian taxa. Further specimens will be required to determine whether a separate K and a single D bone are always present. The Bremer decay indices, which show support for individual branches were highest for the clades containing *Holodipterus gogoensis, H.* (*Asthenorhynchus*), *Fleurantia* with the Mount Howitt fauna respectively. Overall support for the tree as indicated by Bremer support values, was low with most clades only one step longer than that of the shortest tree.

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Conclusions

- The new tooth-plated lungfish *Harajicadipterus* gen. nov., displays similarities to the well-known Middle Devonian genus, *Dipterus*, in both skull roof pattern and the tooth plates.
- The position of *Harajicadipterus youngi* above *Dipterus* in the cladistic analysis suggests it is a more derived taxon.
- *Harajicadipterus* also sits above the "chirodipterid" clade, and is more closely related to the Late and post-Devonian taxa.
- *Harajicadipterus* is especially significant as a Middle Devonian lungfish from Australia, of which there are only five described, and contributes important information regarding early dipnoan radiation in Australia.

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Appendix 1

Description of characters used in phylogenetic analysis.

1. Teeth: (0) present; (1) absent.
2. Addition of large dentine elements at regular intervals to lateral margin of pterygoid/prearticular: (0) yes; (1) no.
3. Nature of large dentine elements: (0) teeth; (1) petrodentine cores; (2) thick irregular dentine ridges; (3) narrow regular dentine ridges.
4. Pattern of tooth addition on pterygoid/prearticular: (0) teeth/petrodentine added in linear proximo-distal sequence; (1) teeth added in oblique series away from biting surface.
5. Morphology of teeth: (0) round/conical; (1) sectorial, forming distinct proximodistal cutting ridge.
6. Addition of marginal blisters to pterygoid/prearticular: (0) no; (1) yes.
7. Shape of marginal blisters: (0) bead-shape; (1) elongated strips.
8. Addition of inter-row dentine along edge of pterygoid/prearticular: (0) no; (1) yes.
9. Nature of inter-row dentine: (0) always fuses or wears down into a sheet; (1) separate denticles persist between some tooth rows.
10. Diffuse dentine deposition on palate/lower jaw: (0) yes; diffusely across the whole palate; (1) no, (2) redoposition of denticles only within "footprint" or resorbed tooth plate.
11. Relative areas of dentine field/thin dentine sheet on palate: (0) all or nearly all denticles; (1) both dentine sheet and denticles; (2) mostly dentine sheet; (3) denticles outside toothplate; dentine sheet on resoorption areas within toothplate.
12. Relative areas of dentine field/thin dentine sheet on lower jaw: (0) all or nearly all denticles; (1) both dentine sheet and denticles; (2) mostly dentine sheet.
13. Resorption of dentition on pterygoid/prearticular plate origin: (0) little or no resorption, origin left unmodified; (1) extensive resorption, removing mesial parts of plate; (2) resorption and deposition of dentine sheet within toothplate only, not crossing edges.
14. Distinct vertically growing "heel" on prearticular: (0) no; (1) yes.
15. Sharp "additive" mesial and posterior edges on tooth plates: (0) absent; (1) present.
16. Behaviour of "additive edges" (if present): (0) quiescent; (1) active.
17. Petrodentine: (0) absent; (1) present.
18. Median callus on palate: (0) absent; (1) present.
19. Teeth on dentary: (0) shedding teeth present; (1) statodont tooth rows present.
20. Teeth on upper lip: (0) shedding teeth; (1) statodont tooth row; (2) teeth absent.
21. Dental material on parasphenoid: (0) present; (1) absent.
22. Palatal construction: (0) parasphenoid separates pterygoids; (1) short pter-pter contact, long parasphenoid; (2) long pter-pter contact, short parasphenoid.
23. Parasphenoid stalk: (0) no stalk; (1) simple stalk without sharp division into tapering proximal portion and parallel-sided distal portion; (2) stalk with sharp division into tapering proximal portion and parallel-sided distal portion.
24. Ventral furrow on parasphenoid stalk: (0) absent; (1) present.
25. End of parasphenoid stalk: (0) single point; (1) bifid, (2) trifid with lateral projections.
26. Parasphenoid sutures: (0) fused; (1) visible sutures.
27. Premaxilla: (0) present; (1) absent.
28. Dorsolateral process on palatoquadrate: (0) absent; (1) present.
29. Angle between quadrate and plane of parasphenoid: (0) more than 90°; (1) 80–65°; (2) 55–35°.
30. Autostyly: (0) absent; (1) present.
31. Lateral commissure (joint): (0) separate from palatoquadrate; (1) partly fused but distinguishable; (2) wholly fused to palatoquadrate.
32. Coronoids: (0) present; (1) absent.
33. Gape of mouth: (0) long, no lip fold; (1) short, with lip fold.
34. Dentary-prearticular relationship: (0) dentary separated from prearticular by dentition-generating gap that housed a dental lamina; (1) small midline hole only; (2) no gap.
35. Slot between dentary and prearticular: (0) broad; (1) narrow.
36. Adductor fossa: (0) not overhung by prearticular; (1) overhung by prearticular.
37. Adductor fossa length: (0) more than 20% jaw length; (1) 5–20% jaw length; (2) 0–5% of jaw length.
38. Adductor fossa morphology: (0) open; (1) reduced to a vestigial slit.
39. Curvature of ventral mandibular margin: (0) strongly convex; (1) essentially flat.
40. Retroarticular process: (0) small and poorly developed; (1) robust, squarish.
41. Glenoid shape and orientation: (0) cupped, faces dorsally; (1) horizontally cylindrical, faces posterodorsally.
42. Skin contact surface of infradentary bones: (0) reaches up to lip of adductor fossa; (1) widely separated from lip of adductor fossa.
43. Angular and surangular: (0) separate; (1) fused into a single bone.
44. Splenial and postspenial: (0) separate; (1) fused.
45. Ossified dentary in adult: (0) present; (1) absent.
46. Meckelian bone: (0) wholly ossified; (1) only articular ossified, or not ossified at all.
47. Ossified upper lip in adult: (0) present; (1) absent.
48. Parietals meet in midline: (0) yes; (1) no.
49. B bone: (0) absent; (1) present.
50. Postparietals meet in midline: (0) yes; (1) no, separated by B bone.
51. C bones: (0) absent; (1) present.
52. Pineal foramen: (0) present; (1) absent.
53. D bones: (0) many, (1) single; (2) absent.
54. Paired E bones: (0) absent (mosaic); (1) present.
55. Contact between E and C bones: (0) absent; (1) present.
56. Braincase/skull table relationship: (0) broad contact; (1) supported by crisate.
57. Intracranial joint/ventral cranial fissure: (0) mobile joint; (1) ventral cranial fissure; (2) neither fissure nor joint.
58. Metotic fissure: (0) present; (1) absent.
59. Lateral line branch in bone 3: (0) absent; (1) present.
60. Lateral lines in mandible: (0) parallel; (1) converging in one bone.
61. Series anterolateral to pterygoids: (0) present, with tusks; (1) present with denticles/dentine sheet; (2) present with tooth row.
62. Length of L bone: (0) similar to others in supraorbital canal series; (1) about twice as long as other in series.
63. Length of postorbital cheek: (0) substantially longer than diameter of orbit; (1) equal to or shorter than diameter of orbit.

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64) Bone 6: (0) reaches ventral margin of cheek; (1) excluded from ventral margin by bone 10.
65. Size of bone 10: (0) large, as 5 or greater; (1) much smaller than 5, or absent.
66. Bone 7: (0) approximately equilateral; (1) much longer than deep.
67. Elongated snout: (0) absent; (1) present.
68. Fused cosmine-covered snout: (0) absent; (1) present with diffuse posterior margin; (2) present with sharp posterior margin.
69. Cosmine present on skull: (0) yes, full cover; (1) yes, but strongly reduced; (2) no.
70. Scale morphology: (0) rhomboid, cosmine-covered; (1) semi-rounded, cosmine covered; (2) rounded, no cosmine.
71. Median fin morphologies: (0) all separate and short-based; (1) posterior dorsal fin long-based; (2) both dorsal fins long-based; (3) uninterrupted fin fringe.
72. Posterior dorsal fin support: (0) all radial carried by basal plate; (1) anterior radials on basal plate, posterior radials free; (2) no basal plate.
73. Anal fin support: (0) trapezoidal with no distinct shaft; (1) cylindrical proximal shaft and triangular distal plate.
74. Median fin radials: (0) cylindrical; (1) hourglass-shaped.
75. Vertebral column: (0) unconstricted notochord; (1) disc centra.
76. Neural arches and spines: (0) separate; (1) fused.
77. Angle between midline and anterolateral margin of pterygoid: (0) less than 50°; (1) more than 55°.
78. Transverse curvature of palate: (0) flat; (1) arched.
79. Position of pterygoid toothplate centre relative to first and last tooth rows: (0) not recessed, tooth rows essentially straight and diverging by 100° or less; (1) slightly recessed into curving posteromesial margin of tooth plate.
80. Bone 10 in contact with bones 5–7 in cheek: (0) no; (1) yes.
81. Shape of anterior corpus of parasphenoid: (0) Thin, not conspicuously thickened anteriorly; (1) ploughshare-shaped.

Appendix 2

Character-taxon matrix used for phylogenetic analysis.

Character:	0000000001	1111111112	2222222223	3333333334	4444444445	5555555556	6666666667	7777777778	8
	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1
Diabolepis	000000?110	30200?0011	000???01?0	?110100010	0000000110	010??01?0?	100???010?	??????000?	0
Dipnorhynchus	102??10100	22010?0022	0?0??01101	1110000000	0000000110	1000?11010	100???0100	???????00?0	0
Speonesydrion	0000010100	21010?001?	0????011?1	?110000000	0000000110	1000?????0	10????0101	???????00??	0
Ichnomylax	0000010100	?101??1?1?	??????????	?110?0000?	?0??00????	??????????	??????0???	??????0???	0
Uranolophus	11???0?100	00100?0?22	020??01101	?110000000	0000000110	111101??00	100???0000	0???0101??	0
Tarachomylax	000000?0?0	0?000?00?1	?2???11??1	??????????	??????0111	11000???1?	?010??0101	??????000?	?
Jessenia	1010?0?0?0	0?0?0??0??	010??111?1	??????????	??????0110	1?10??????	?0????020?	??????000?	0
Stomiahykus	1010?11100	1?0?0?10??	020??0?111	1?????????	??????????	1?00?1?01?	10????0?0?	??????000?	?
H. gogoensis	0000010100	11110?1111	0210101011	2111?11011	1101000111	1111112011	100??00012	??????01?1	0
Robinsondipterus	0000010100	00100?101?	021??010?1	?111?12011	1101000???	??????????	??????0?12	??????01?1	0
Asthenorhynchus	0000010110	11110??11?	02101??0?1	?111??????	??0101?111	11111???11	1001000?2	??????01?1	0
Griphognathus	11???10100	00100?0011	0210101021	2112?12111	1111000111	111101201?	1001001022	00001001?1	0
Chirodipterus	1030?11101	??00101022	1210011011	2110110011	1100000111	1110112011	1001000201	0?00001001	1
Pillararhynchus	1010?11101	??00111011	0210011011	2110010111	1111000111	1???11210?	200???0201	??????1001	1
Gogodipterus	1010?10100	11000?10??	021?01?011	211011001?	110000????	?????120??	??????0?0?	??????1001	1
Adololopas	000000?101	??001110?1	12100110?1	?1?0??????	??0?0?0111	1????????11	1?0???0201	??????100?	1
Andreyevichthys	000010?111	??00111011	12211110?1	?11?????11	??111?0111	11211???1?	211??0102?	??????000?	1
Sorbitorhynchus	11???11101	??001010??	121001?011	?11??10111	1101?0?111	1????12???	??????0?01	???????00??	0
Fleurantia	000010?0?2	0?1????0?2	12211110?1	?11?????11	1111?11111	11110???11	1110111022	1211010???	1
Dipterus	000000?101	2?00111022	1210011??1	21100100?1	1100000111	1101?12111	?010000101	0000000000	0
Howidipterus	000000?0?2	2?101??022	1221111??1	?11?????1?	??10011111	11111???1?	1010100022	11110?0?10	0
Barwickia	000000?112	0010???0?2	12211110?1	?11?????11	1?1???1111	11111???1?	?010110022	1111010??0	0
Scaumenacia	000010?0?1	??001010?2	122??11??1	?11?????1?	?1111?1111	11211???11	2010110022	2211010000	0
Sagenodus	000110?101	??001010?2	1221011??1	?11?????1?	?111111111	1121????11	2010?00022	32?00?0010	0
Ctenodus	000100?101	??001010??	122???1??1	?1????????	????111111	1??1??????	?00???0022	32????0010	0
Neoceratodus	000110?101	??10101012	1120211011	211????111	1?11111111	?12??1210?	2?10110022	32?000001?	0
Melanognathus	000000?0?0	00100??012	0210011??1	?112?110?0	??01000???	111001???0	??????010?	???????0??0	0
Soederberghia	11????????0	00000??0??	0221111?21	??????????	?????10111	11?11???0?	?1?0111022	0?111?01??	0
Conchopoma	11???0???0	00??0??011	0020?11??1	?1????????	??110?1111	11211???0?	2?101?0022	32?0000??0	0
Gnathoriza	000?10?101	??001010??	1120211??1	?11?????1?	1?11111111	11211???0?	2?10100022	??????001?	0
Orlovichthys	000010?0?1	??0011?011	012??110?1	?111?10111	1111000111	1??11121??	??????120?	??????000?	0
Harajicadipterus	000000?111	2?0?11?01?	?2???1????	??????????	????0??111	11110?211?	?10?1?0002	?????1000?	?

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