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A new tooth-plated lungfish from the Middle Devonian of Yunnan, China, and its phylogenetic relationships

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Abstract

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A new genus and species of tooth-plated lungfish, *Sinodipterus beibei* gen. et sp. nov., is described from the Qujing Formation (Middle Devonian, late Eifelian) of Zhaotong, Yunnan, China. The new form resembles *Dipterus* in the skull table, but differs in its tooth-plate: cosmine-like tissue absent near the midline, tooth rows fewer in number (7 to 8) and less divergent radiating, and no reparative dentine layers. Phylogenetic analysis of Devonian lungfish based on a dataset of 150 characters and 33 taxa indicates that the new taxon is more crownward than *Dipterus* and the clade comprising *Adololopas*, *Sorbitorhynchus* and *Pillararhynchus*. Our results agree broadly with previous cladistic solutions. *Diabolepis* is placed as a sister group to all other Devonian lungfish. The species referred to *Chirodipterus* fail to form a monophyletic group. The result shows a large number of convergences corresponding to early radiation of lungfish compressed in time.

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Introduction

Some lungfish specimens were collected in the 2004–2006 field seasons from Qingmen in the suburb of Zhaotong, northeastern Yunnan, China. The fish-bearing horizon was named the Qujing Formation by comparison to the type locality of this formation in Qujing district, Yunnan (Xian and Zhou 1978; Yun 1978; Zhao 1978). The age of this fauna is referred to Middle Devonian, late Eifelian, as the horizon is below the *Stringocephalus* layer, whose earliest occurrence is late Eifelian (Cai 2000; Liao and Ruan 2003). Other fish materials include some placoderms, onychodonts and tetrapodomorphs. In the same section, a Lower Devonian formation yields a diverse assemblage of agnathans, placoderms, onychodonts, tetrapodomorphs and dipnomorphs (Lu and Zhu 2008).

The new form represents the seventh Devonian lungfish genus from China since the first report of three isolated dipnoan scales (Liu and P'an 1958). The other six genera are *Dongshanodus* (Wang 1981), *Diabolepis* (Chang and Yu 1984), *Erikia* (Chang and Wang 1995), '*Chirodipterus*' (Song and Chang 1991), *Sorbitorhynchus* (Wang *et al.* 1990, 1993) and *Tarachomylax* (Qiao and Zhu 2008).

Lungfish are considered as a highly derived group of sarcopterygian fish (Miles 1975; Cloutier and Ahlberg 1996; Janvier 1996) and are the living sister group of tetrapods (e.g. Cloutier and Ahlberg 1996; Forey 1998; Zhu *et al.* 2001; Zhu and Yu 2002; Brinkmann *et al.* 2004). However, the fossil lungfish interrelationships are still widely debated (Miles 1977; Campbell and Barwick 1990; Schultze and Marshall 1993; Schultze 2001; Ahlberg *et al.* 2006; Friedman 2007). Three different phylogenetic approaches have been involved in the analysis. One is the functional-adaptive method proposed by Campbell and Barwick (1990). They defined three separate lineages mainly based on dentition: tooth-plated, dentine plated and denticulated plates. They claimed that the functional complexes, especially those concerning food reduction and respiration are the best criteria to establish the evolutionary relationships of Dipnoi. This method, nevertheless, has been rejected by the advocates of cladistics (Miles 1977; Maisey 1986; Marshall 1987; Schultze and Marshall 1993; Schultze 2001; Ahlberg *et al.* 2006). Despite the divergences of opinions among these authors using the parsimony approach, all their resolved results showed that the three lineages of Campbell and Barwick (1990) are paraphyletic or polyphyletic. Recently, Friedman (2007) tried a third method – Bayesian inference – and derived a similar result to that from the parsimony approach.

To test the robustness of the previous results and to find the phylogenetic position of the new taxon, we present a parsimony analysis based on a new dataset combining previous studies, which focused on one subset of characters, such as skull roof bones (Schultze 2001), tooth-plates and skull roof bones (Ahlberg *et al.* 2006) and neurocranial complex (Friedman 2007). The new dataset is compiled to avoid the possible weighting of characters due to the exclusion of other available subsets of characters. The phylogenetic results are compared with previous hypotheses and areas of congruence and disagreement are discussed.

Materials and Methods

Systematic methods

Included taxa and outgroup selection. The in-group consists of 31 taxa, of which 16 are found from Upper Devonian, five from Middle Devonian and 10 from Lower Devonian. *Youngolepis* and *Psarolepis* were used as outgroup taxa in parsimony analysis. *Youngolepis* is currently considered as a basal member of Dipnomorpha (Ahlberg 1991; Zhu *et al.* 2001, 2006), while *Psarolepis* is a stem-group sarcopterygian (Zhu *et al.* 2006).

For the monospecific genera or the genera whose monophyly is well supported, we only adopt the genus name for the simplicity.

Character formulation. To explore the phylogenetic position of *Sinodipterus*, we constructed a dataset of 150 characters and 33 taxa (Tables 1 and 2), mainly based on the datasets of Schultze (2001), Ahlberg *et al.* (2006) and Friedman (2007). We deleted the uninformative characters, emended some miscoded states and added four characters (characters 5, 21, 22 and 86) to reflect the character changes between *Sinodipterus* and other lungfish. Character states were coded from direct observation of specimens or through an examination of source literatures. All characters were unordered, with the exception of six multistate characters which had been ordered as they were first defined (characters 3, 40, 61, 72, 107 and 138).

Maximum parsimony analysis. The phylogenetic analyses were performed using PAUP 4.1 (Swofford 2003) on a data matrix composed in MacClade 4.0 (Maddison and Maddison 2000). Characters were assigned equal weights and state optimization was set to DELTRAN. We used heuristic tree search routines, addition sequence of taxa simple. MacClade 4.0 was used to trace character transformation in the preferred cladogram. Bremer decay indices were obtained using command files composed by TreeRot (Sorenson 1999) in conjunction with the heuristic search algorithm in PAUP.

Systematic palaeontology

Osteichthyes Huxley, 1880
Sarcopterygii Romer, 1955
Dipnomorpha Ahlberg, 1991
Dipnoi Müller, 1845
Sinodipterus gen. nov.
(Figs 1–6)

Diagnosis

Pineal foramen absent; dermal bone covered with cosmine; elongated E bones with length more than twice width; a long prepineal length; I bones separated by B bone; a small D bone; fused X and K bones; supraorbital and infraorbital canals in connection; tooth-plates; cosmine-like tissue absent in median part of tooth-plate; seven or eight tooth rows; tubercles present in clefts of inter-rows; no reparative dentine layers along posteromesial edge of tooth-plate.

Etymology

Generic name from Latin *sino-* (pertaining to China) and another genus name *-dipterus* which is a name used for many Devonian lungfishes.

Sinodipterus beibei sp. nov

Diagnosis

As for genus, only species.

Etymology

Named after one of five official mascots of the Beijing 2008 Olympic Games, which embodies a fish.

Holotype

An incomplete individual with a majority of skull roof and cheek bones, left pterygoid tooth-plate, dislocated gular bones, pectoral girdles and part of squamation. IVPP V14562.

Materials

The specimens include two complete pterygoid tooth-plates (IVPP V15038.1–2), five incomplete pterygoid tooth-plates (IVPP V15038.3–7), two prearticular tooth-plates (IVPP V15038.8–9), 14 detached skull bones (IVPP V15039.1–14) and an incomplete isolated scale (IVPP V15039.15).

Locality and horizon

Zhaotong, northeastern Yunnan, China; Qujing Formation, Middle Devonian, late Eifelian.

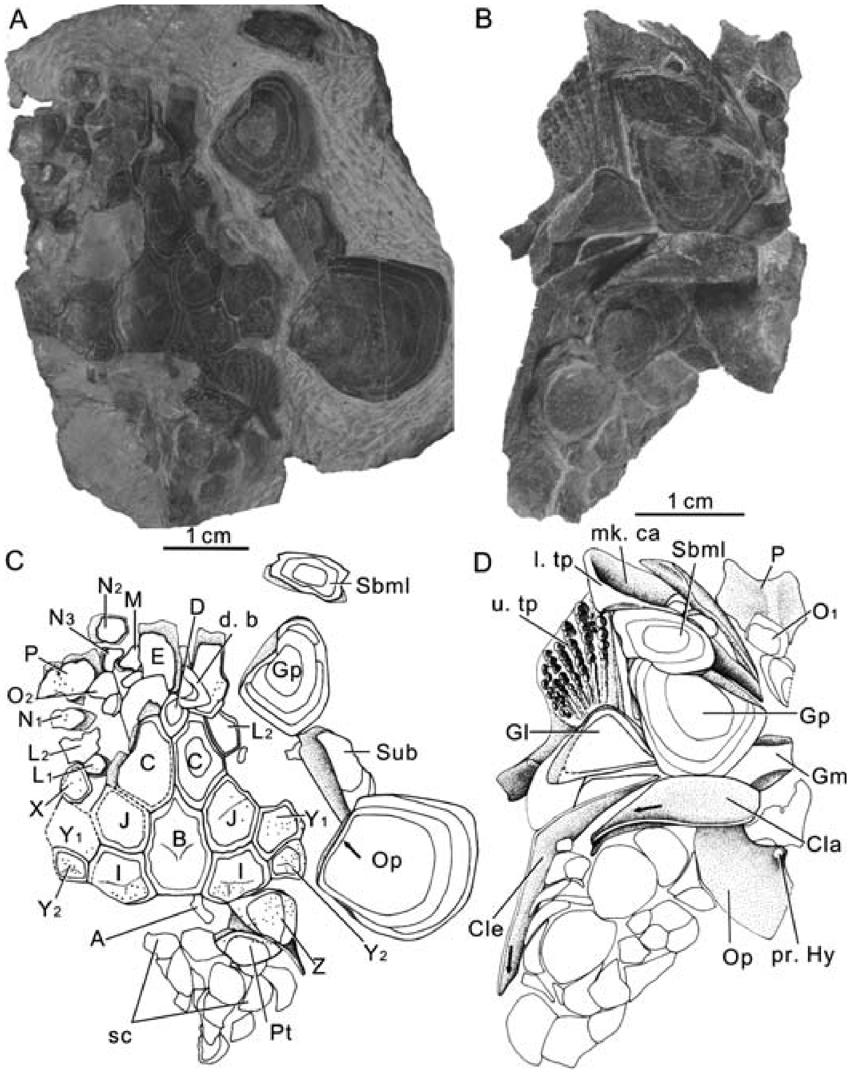

Fig. 1—*Sinodipterus beibei* gen. et sp. nov. —**A**, **C**. IVPP V14562. Dorsal view of holotype. —**B**, **D**. Ventral view of holotype. Cla, Clavicle; Cle, Cleithrum; d.b, displaced bone; Gl, lateral gular; Gm, median gular; Gp, principal gular; l.tp, prearticular tooth-plate; mk.ca, cavity for the Meckelian bone; Op, opercular; pr.Hy, process of opercular articulating with hyomandibular; Pt, post-temporal; sc, scales; Sbml, lateral submandibular; Sub, subopercular; u.tp, pterygoid tooth-plate. Arrows on the clavicle, cleithrum and opercular indicate anterior direction.

Description

Dermal skull roof. The dermal bones of the holotype clung to the grey sandstone tightly, and formed an integrated skull roof except for the rostral region. Considering the anterior part of the skull to be missing, we suggest that the length from the middle of the D bone to the posterior edge of the B bone (DBL) be used as an alternative. A restoration of the head, based on the holotype, is shown in Fig. 3(A).

The skull roof (Figs 1–3) is about 30 mm in total length and 21 mm in the DBL. Its maximum width (28 mm) is larger than the DBL and occurs at the level of the lateral corner of the Y_1 bone, being different from some early lungfish such as *Dipnorhynchus* (Campbell 1965; Thomson and Campbell 1971; Campbell and Barwick 1982; Campbell *et al.* 2000), *Speonesydrion* (Campbell and Barwick 1984) and *Erikia* (Chang and Wang 1995), in which the maximum width is always situated posteriorly at the level of the Y_2 bone. All of the dermal bones are covered with cosmine, and marked by two or three Westoll lines. Roofing bones are tightly sutured in the holotype (Fig. 1), while in V15039.1 (Fig. 2A,B) and V15039.2 (Fig. 2C) bones are partly detached from each other by weathering and distortion, making the overlapped areas along sutures visible.

The B bone is heptagonal, occupying more than 50% of the DBL. Its length is about 1.5 times as long as its width. The anterior pit-line (apl) extends to the anterolateral edge of the B bone and connects to the anterior pit-line on the J bone (Figs 1 and 2A–C). The supraoccipital commissure is not traced on the B bone, suggesting that this canal runs through the A bone. One Z bone and a small part of the A bone are preserved in the extrascapular series. The I bones are separated by the B bone and flank the posterolateral margins of the B bone, with the openings for supraoccipital commissure on their surface. The longest axis of the I bone is transverse, as opposed to *Dipterus*, where the long axis is anteroposteriorly

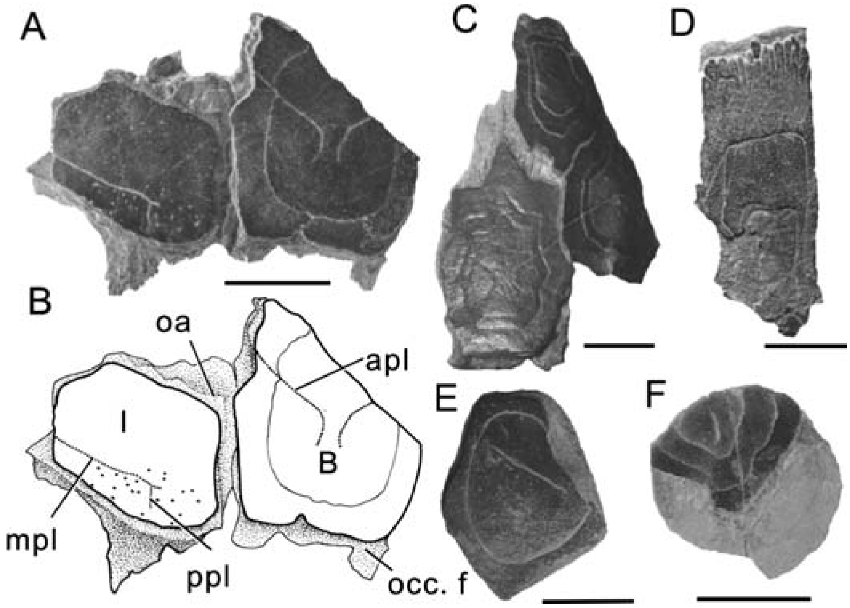

Fig. 2—*Sinodipterus beibei* gen. et sp. nov. —**A**, **B**. IVPP V15039.1. B-bone and associated left I bone. —**C**. IVPP V15039.2. B bone, and associated incomplete right C bone and J bone. —**D**. IVPP V15039.4. Left E bone in dorsal view. —**E**. IVPP V15039.5. Left J bone. —**F**. IVPP V15039.15. Isolated scale. apl, anterior pit-line; mpl, middle occ.f, occipital flange; pit-line; oa, overlapped area; ppl, posterior pit-line. Scale bars 5 mm.

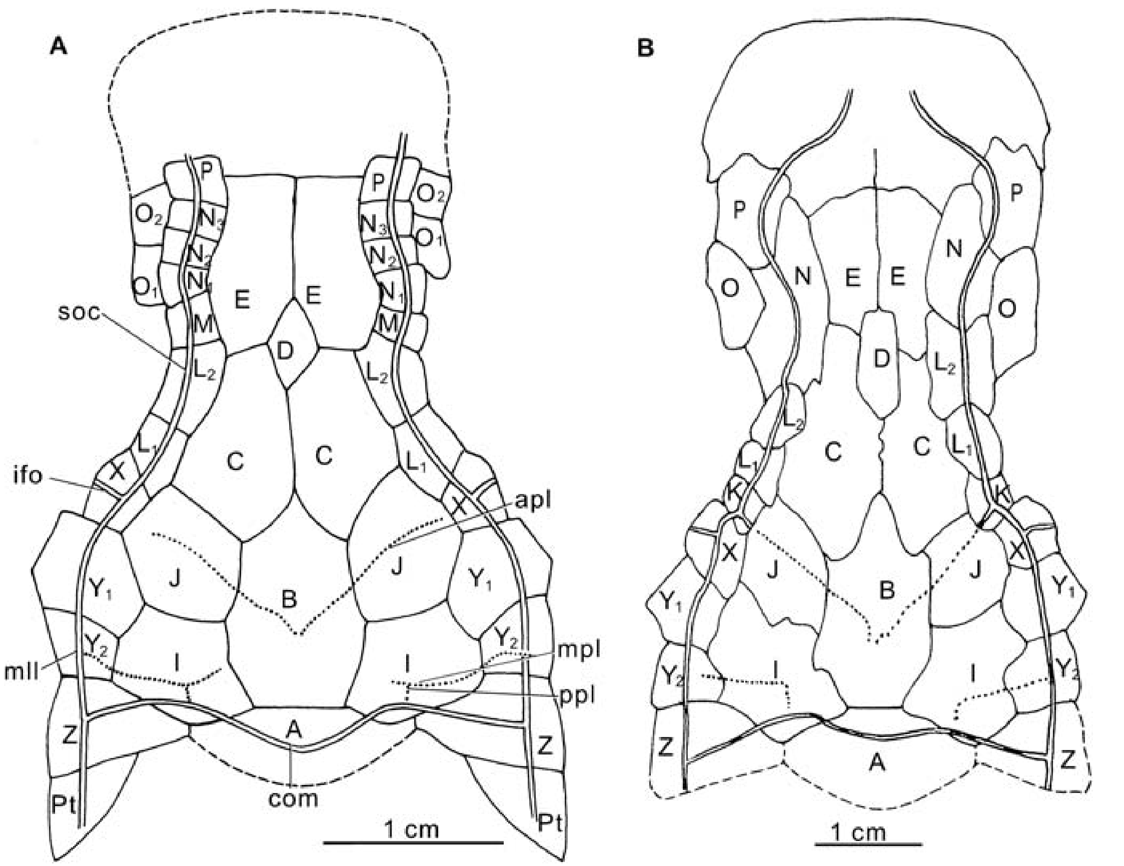

Fig. 3—**A**. *Sinodipterus beibei* gen. et sp. nov., Restoration of the head in dorsal view. —**B**. Restoration of *Dipterus* (modified from White 1965). apl, anterior pit-line; com, supraoccipital commissure; ifo, infraorbital sensory line; mll, main lateral line; mpl, middle pit-line; Orb, orbital margin; ppl, posterior pit-line; Pt, post-temporal; soc, supraorbital sensory line.

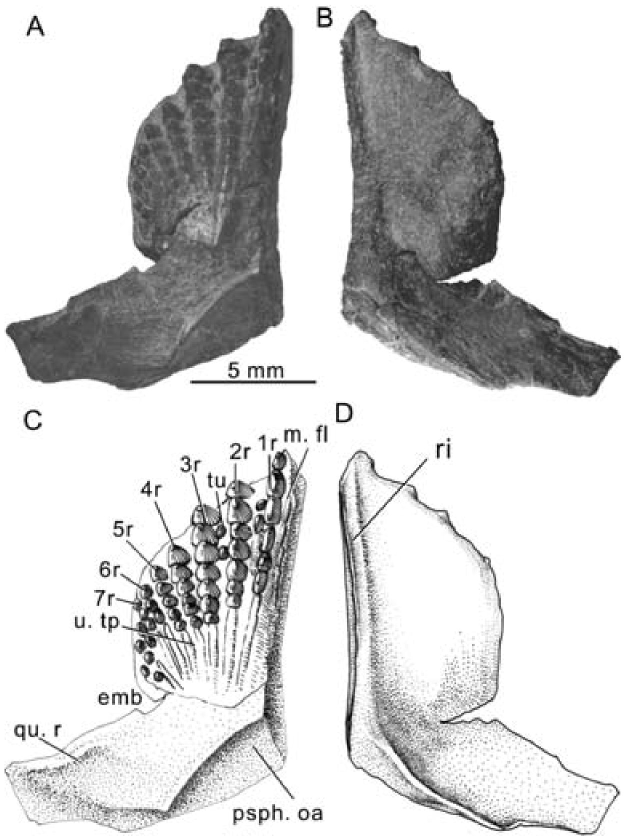

Fig. 4—*Sinodipterus beibei* gen. et sp. nov. Right pterygoid with tooth-plate. —**A**, **C**. IVPP V15038.1. Ventral view. —**B**, **D**. Dorsal view. 1r–7r, first to seventh tooth row; emb, embayment; m.fl, mesial flange; psph.oa, overlapped area for parasphenoid; qu.r, quadrate ramus; ri, ridge; tu, tubercles; u.tp, pterygoid tooth-plate.

orientated (Fig. 3). The middle and posterior pit-lines (mpl, ppl) are present on the I bones. The B bone bears long projections anteriorly serving as the overlapped areas for the C bones. Posteriorly, the B and I bones jointly send out the occipital flange (Fig. 2A,B, occ.f), which is always overlapped by the extrascapular series. This flange is supposed to cover the posterior process of the neurocranium (Miles 1977) and is well developed in some Middle and Late Devonian lungfish such as *Dipterus* (White 1965), *Gogodipterus* (Miles 1977), *Griphognathus* (Miles 1977) and *Fleurantia* (Cloutier 1996).

The anterolateral margin of the J bone (Figs 1 and 2C,E) has a small corner, suggesting the suture between K/X and L_1 bones. Its posterolateral margin is in contact with the Y_1 bone. Some pores for the sensory lateral line are present on the J bone as in some specimens of *Dipterus* (White 1965). The C bone occupies about 50% of the DBL. Its anterior end extends to the middle level of the D bone and contacts the posterior margin of the E bone. A small lozenge-shaped D bone is enclosed by the C bones posteriorly and E bones anteriorly. The D bone is covered by a small, displaced bone (Fig. 1, d.b) and no pineal opening is visible.

The elongate E bone of the holotype bears an anterior overlap area. Its length is almost twice its width. Its surface is marked with pores for branches of the supraorbital canal. Because of post-mortem distortion, the two E bones do not meet each other closely. An isolated E bone 18 mm long and 7 mm wide (V15039.4, Fig. 2D) exhibits a fimbrate anterior margin of the cosmine cover as in some specimens of *Dipterus* (White 1965, fig. 23).

The supratemporal series (X,Y_1,Y_2) can be outlined based on the preserved impression on the right part and some small bones on the left part. Two Y bones are well preserved on the right side, and a Y_2 bone on the left side. The Y_2 bone is smaller than the Y_1 bone, and carries the middle pit-line extending from the I bone. The mesial edge of the Y_2 bone and the posteromesial edge of the Y_1 bone jointly contribute to the lateral margin of the I bone. A small bone on the left side of the holotype is recognized as a composite K/X bone (Fig. 1A,C), because it carries some pores of the infraorbital sensory line (ifo) branching off the main lateral canal (Fig. 3, mll) and the anterior pitline is headed directly off the J bone and to this bone.

Seven elements with the supraorbital sensory line have been recorded: L_1, L_2, M, N_1, N_2, N_3 and P bones. The restoration of this series is largely based on the left part of the holotype, while only one bone of this series (L_2 bone) is preserved on the right part. Two L bones are present in the holotype: the L_1 bone is relatively small in comparison with the L_2 bone; the L_2 bone is weathered so strongly on the left side that no cosmine is left on the surface but is completely preserved and in contact with the C bone on the right side. The M bone is a small bone near the E bone. The O_1 bone is preserved on the ventral side of the holotype (Fig. 1B). Other small bones are referred to as N_1, N_2, N_3 and O_2 bones.

Operculo-gular and submandibular series. Detached opercular and subopercular are present in the holotype (Fig. 1). The right opercular (Op) is a little rotated and approximately 17 mm both in length and height. It bears a dorsal overlapped area for the supratemporal series and an anterior overlapped area for cheekbones. The ventral margin of the opercular is straight which matches the dorsal edge of the subopercular (Sub). On the ventral side of the holotype, an incomplete left opercular is preserved in internal view, showing the process articulating with hyomandibular (Fig. 1B,D, pr.Hy) exposed. The subopercular is an elongated bone with its length almost three times its height, bearing a well-developed dorsal overlapped area for the opercular. On the dorsal side of the holotype, detached principal gular (Gp) and lateral submandibular (Sbml) plates are preserved anterior to the subopercular. Their counterparts more or less articulate with each other in life on the ventral side of the holotype. The principal gular bears an overlapped area for

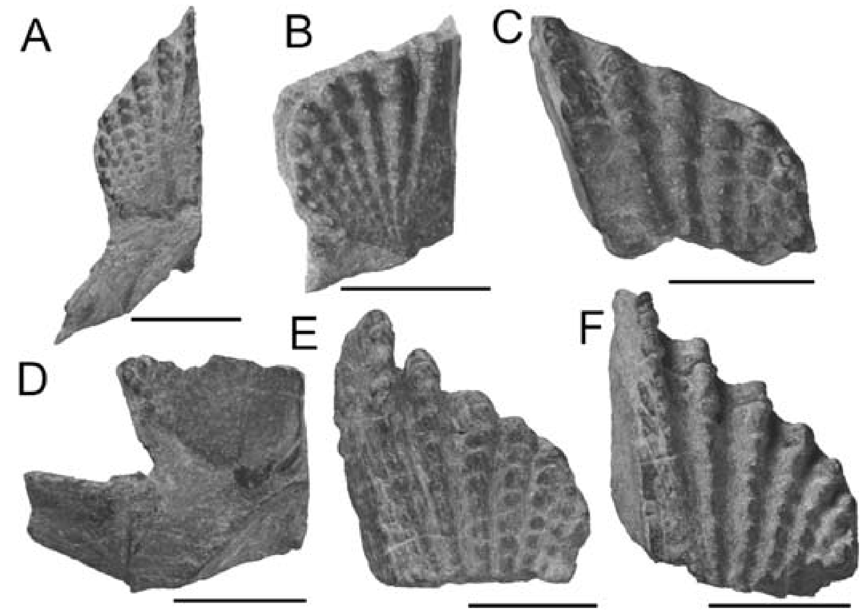

Fig. 5—*Sinodipterus beibei* gen. et sp. nov. Pterygoids with tooth-plates in ventral view. —**A**. IVPP V15038.2. Complete right pterygoid. —**B**. IVPP V15038.7. Incomplete right pterygoid. —**C**. IVPP V15038.4. Incomplete left pterygoid. —**D**. IVPP V15038.6. Incomplete right pterygoid. —**E**. IVPP V15038.5. Incomplete left pterygoid. —**F**. IVPP V15038.3. Incomplete left pterygoid. Scale bars 5 mm.

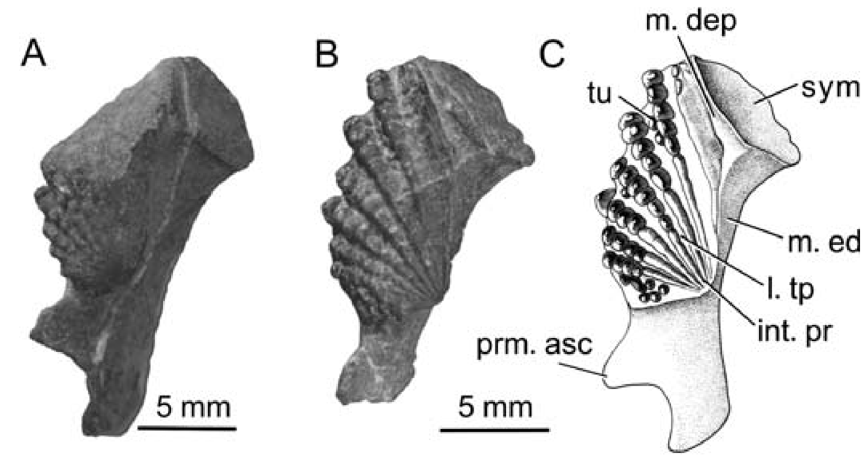

Fig. 6—*Sinodipterus beibei* gen. et sp. nov. Left prearticulars with tooth-plates. —**A**. IVPP V15038.8. —**B**. IVPP V15038.9. —**C**. Restoration of the left prearticular based on IVPP V15038.8 and IVPP V15038.9. l.tp, prearticular tooth-plate; int.pr, internal angle of prearticular; m.ed, mesial edge for prearticular; m.dep, median space for hypobranchial apparatus; prm.asc, mesial ascending process; sym, symphysial face; tu, tubercles.

the lateral gular on its dorsal edge. On the ventral side of the holotype, a symmetrical bone at the right edge represents the median gular (Gm). A triangular bone to the left of the principal gular is recognized as the lateral gular (Gl). Other displaced bones cannot be identified because they are either incomplete or incompletely exposed.

Tooth-plates. Except for the pterygoid tooth-plate (u.tp) and prearticular tooth-plate (l.tp) of the holotype (Fig. 1B,D), several detached tooth-plates of varying sizes (Figs 4–6) are assigned to *Sinodipterus*, including seven pterygoid tooth-plates (V15038.1–7) and two prearticular tooth-plates (V15038.8–9).

The following description of the pterygoid tooth-plate is largely based on V15038.1 (Fig. 4). The tooth-bearing part of the pterygoid tooth-plate has about seven ridges with discrete teeth and its origin lies slightly behind the posteromedial part of the plate. The tooth rows are separated by furrows, shallower between the more posterolateral tooth rows. The first tooth row (1r) has six elongated cone-shaped teeth, and is much narrower and higher than others. Other rows (e.g. 2r–7r) have rounded discrete teeth anteriorly and worn-out teeth posteriorly. Two or three tubercles (tu) often occur in the first and second furrows, as is the case in *Dipterus* (White 1965). This might indicate some supplementary rows of teeth inserting between the anterior sets of the rows (Blaauwen *et al.* 2005). The angle between the mesial row and the lateral row is about 70°, much smaller than that of *Dipterus.* The supporting pterygoid bone is preserved in some specimens (Figs 4 and 5A,D). The mesial flange (Fig. 4, m.fl) of the pterygoid is narrower than that of *Dipterus* and is not covered with cosmine-like tissue. The straight mesial edge indicates that the pterygoid tooth-plates meet each other closely in life position. Sharp additive mesial and posterior edges (Ahlberg *et al*. 2006) are absent on the tooth-plates. These edges are always represented by the deposition of several concentric dentine bands around the mesial and posterior margins of the tooth-plates (Ahlberg *et al*. 2006) in *Dipterus* (Blaauwen *et al*. 2005) and *Pillararhynchus* (Barwick and Campbell 1996). Along the posterolateral margin of the tooth-plate, a lateral embayment (Fig. 4A,C, emb) is poorly developed in comparison with *Dipterus*. Posteromesially, the ventral surface of the pterygoid bears a triangular overlapped area for the parasphenoid (Fig. 4A,C, psph.oa). The wide, well-developed quadrate ramus (qu.r) of the pterygoid runs posterolaterally and becomes slender distally.

In visceral view, the mesial margin of the tooth-plate-bearing area is raised into a low ridge that abuts against its antimere. The ridge (Fig. 4B,D, ri) extends posterolaterally to the quadrate ramus (qu.r) where it forms a dorsal ridge standing at the base of the quadrate, as in *Dipterus* and '*Chirodipterus*' *australis* (Miles 1977). The lateral termination of the endoskeletal subocular shelf (Friedman 2007) corresponding to the lateral thickening (Miles 1977) is not so developed as in *Holodipterus* and '*Chirodipterus*' *australis*.

A prearticular tooth-plate is preserved in ventral view in the holotype (l.tp, Fig. 1B,D), which shows the cavity for the Meckelian bone (mk.ca). In addition, two detached left prearticular tooth-plates including the supporting bone (Fig. 6) are referred to the new form. The upper edge of the prearticular is expanded horizontally to carry the tooth-plate with six tooth rows. Similar to the pterygoid tooth-plate, some tubercles (Fig. 6C, tu) are present in the first and third furrows. The tooth rows end posteromesially at a distinct angle (int.pr), as in '*Chirodipterus*' *australis* and *Dipnorhynchus sussmilchi* (Thomson and Campbell 1971; Miles 1977), but it is less prominent than that in *Dipterus valenciennesi* (Jarvik 1967; Miles 1977). The more or less lozenge-shaped symphysial face (sym) bears a smooth surface contacting with the opposing prearticular. A groove with corrugated surface is situated between the tooth-plate and the symphysial face. This groove, named as lingual furrow by Long (1992), serves the median space for hypobranchial apparatus (m.dep) and was possibly occupied by the anterior part of the basihyal in life. Posteriorly, the prearticular bears a process (prm.asc) that flanks the mesial face of the preglenoid process. The prearticular bears a broad mesial edge (m.ed) curving downwards to form a vaulted surface above the Meckelian bone. The posterior margin of the prearticular bone is almost straight and no horizontal flange has been found, in contrast to most other Devonian lungfish (e.g. *Chirodipterus australis*) (Miles 1977).

Postcranial skeleton. A triangular post-temporal (Fig. 1A,C, Pt) is a little displaced behind the Z bone in the holotype. It sends out the main lateral canal to the Z bone where the canal joins the supraoccipital commissure.

A right cleithrum (Fig. 1B,D, Cle) and a right clavicle (Cla) are preserved on the ventral side of the holotype. The cleithrum is preserved in posterointernal view. It consists of a narrow, elongate, dorsally-directed blade, and a short, anteroventrally-directed ventral part. The scapulocoracoid, if preserved, is not visible because a majority of the internal side of the cleithrum is covered by scales. The clavicle is displaced with most of its internal surface exposed. A narrow strip of cosmine-covered external surface and an overlapped area for the subopercular (or a gular) can be seen in posterior view of the specimen. The longest dimension of the exposed surface of the cleithrum is estimated to be 1.7 times that of the clavicle.

Scales. Some round body scales covered with cosmine are present at the right posterior corner of the holotype (Fig. 1). In addition, an isolated scale (V15039.15, Fig. 2F) is preserved with the overlapped area broken. The scale is thin and rounded, about 1 cm in length. The exposed area is covered by cosmine and marked by three Westoll-lines. A pit-line is visible, suggesting that this scale belongs to the lateral-line series.

Discussion

Phylogenetic analysis

All referred specimens were collected from the same bed and the same site as the holotype. They are compatible in size, and have the same cosmine, Westoll-line and dentition, so we refer them to the same species. *Sinodipterus* is a Middle Devonian tooth-plated lungfish bearing some similarities to *Dipterus* in the arrangement of the skull roof: the elongated E bones, two Y and two L bones, the I bones separated by the B bone, the Z bone posterior to the I bone; supraorbital and infraorbital canals in connection. However, it is distinguished from *Dipterus* in many aspects: the X and K bones fused; cosmine-like tissue absent near the midline; seven or eight tooth rows which are much less than in *Dipterus*; tooth rows less radiative than in *Dipterus*; no sharp additive mesial and posterior edges; medial flange of the pterygoid strongly reduced when compared with that of *Dipterus* (White 1965; Ahlberg and Trewin 1995).

The maximum parsimony analysis recovered eight equally parsimonious trees of length 436, with a consistency index (CI) of 0.4233, a retention index (RI) of 0.6374 and a rescaled consistency index (RCI) of 0.2698. These trees are summarized as a strict consensus tree (Fig. 7). The result shows a large number of convergences and reversals in the evolution of Devonian lungfish. Even one character change may result in the collapse of the cladogram, possibly relating to a radiation compressed in time (Rokas *et al*. 2005). One of the most parsimonious trees (Fig. 8A) is selected for analysis.

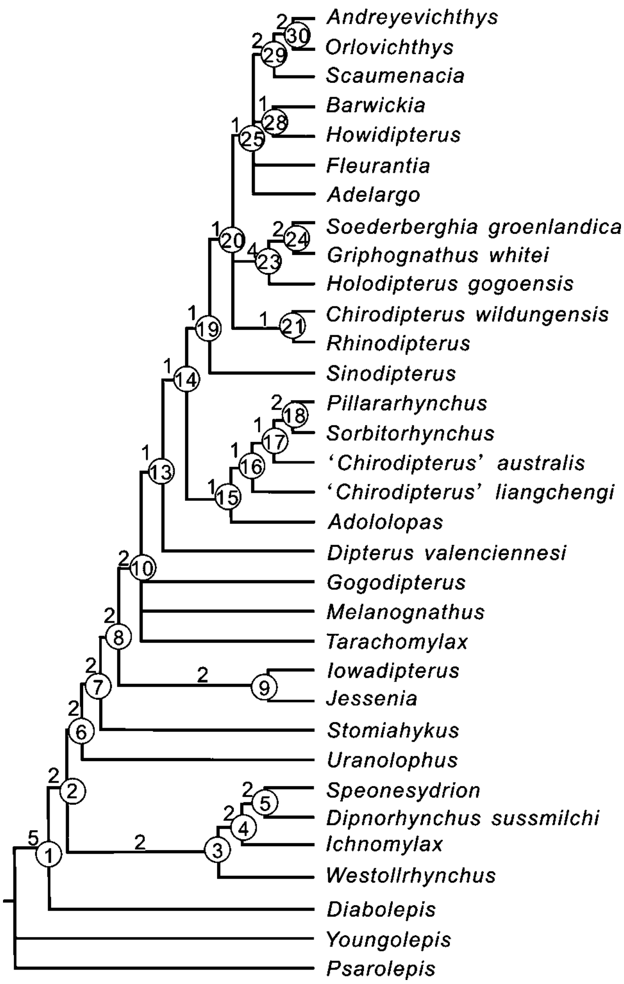

Fig. 7—Strict consensus tree from eight most parsimonious trees (L = 436, CI = 0.4233, RI = 0.6374) based on the dataset in Table 1. Numbers above nodes represent Bremer decay indices. See Table 3 for the characters supporting the numbered nodes.

Diabolepis is placed at the most basal position of Dipnoi, in agreement with many previous studies of sarcopterygian interrelationships (Smith and Chang 1990; Ahlberg 1991; Chang 1995; Cloutier and Ahlberg 1995; Zhu *et al.* 2001; Zhu and Yu 2002) but in contradiction of Campbell and Barwick (1987, 2001) who rejected the close relationship of *Diabolepis* and lungfish. This clade (Node 1, Fig. 8) is the most robust in the cladogram and supported by a Bremer decay index of 5 and by nine synapomorphies: parietals (= J bones) not meeting in midline; ratio of symphysis length to jaw length greater than 1 : 3; no coronoids; addition of large dentine elements at regular intervals to lateral margin of pterygoid and prearticular; addition of inter-row dentine along edge of pterygoid and prearticular; teeth on dentary statodont tooth rows; series anterolateral to pterygoids covered with denticles or dentine sheet; posterior nostril marginal; internasal pits strongly reduced or absent.

The clade above *Diabolepis* (Node 2) contains all in-group taxa unanimously referred to lungfish. It is supported by 18 synapomorphies, 12 of which are unambiguous: C bone; anterior nostril oral margin; posterior nostril at the palatal margin; premaxilla absent; no dentary; lip fold; braincase supporting skull roof with cristae; autostyly; palatoquadrate fused into palate; intracranial joint absent; notochord not extending to or beyond level of Nerve V; the ventral floor of the nasal capsule completely unossified. The first clade (Node 3) in this group consists of four Early Devonian genera: *Westollrhynchus* from Late-Pragian to early Emsian of Germany (Lehmann and Westoll 1952); *Ichnomylax* from Emsian of Australia and Russia (Long *et al.* 1994; Reisz *et al.* 2004), *Dipnorhynchus sussmilchi* (Campbell 1965; Thomson and Campbell 1971; Campbell and Barwick 1982; Campbell *et al.* 2000) and *Speonysydrion* (Campbell and Barwick 1984) from Emsian of Australia. *Westollrhynchus* is one of the earliest lungfishes and is the sister taxon of all remaining members of this clade. This clade is supported by a Bremer decay index of 3 and by three synapomorphies: pineal opening; 'dermopalatine 1' *sensu* Miles (1977) not paired; mostly dentine sheet on the palate.

Most of the Devonian lungfish fall into another clade (Node 6). *Uranolophus* from the Pragian of USA (Dension 1968a,b) appears at the most basal position in this lineage, consistent with its early stratigraphic appearance. Above *Uranolophus* appear *Stomiahykus* and then [*Iowadipterus* + *Jessenia*]. These members are also basally placed in previous cladograms (Schultze 2001; Ahlberg *et al.* 2006; Friedman 2007).

The clade above Node 10 is poorly resolved in the strict consensus tree, including *Gogodipterus*, *Tarachomylax*, *Melanognathus* and the clade above Node 13.

The clade above Node 13, comprising *Dipterus*, and two groups above Node 15 and Node 20 (the post-*Dipterus* grade), is supported by 12 synapomorphies as shown in Table 3.

The members in the clade above Node 15 are all from Australia and China. The sister-group relationship of *Pillararhynchus* and *Sorbitorhynchus* is also supported by Schultze (2001). Synapomorphies supporting this clade include: snout separated from skull roof with diffuse margin; angle between midline and anterolateral margin of pterygoid more than 55°; upper lip with shedding teeth. *Sorbitorhynchus* from the Emsian of China (Wang *et al.* 1990, 1993), represents the earliest member in the post-*Dipterus* grade, indicating that *Dipterus* may have diversified before the Middle Devonian.

Another species of *Chirodipterus* – '*C*'. *liangchengi* is closely related with *Adololopas* in the strict consensus tree. '*Chirodipterus*' *liangchengi* is reported from the Late Devonian of Hunan, China (Song and Chang 1991). this species is resolved here as a polyphyletic relationship with the type species of *Chirodipterus*, in agreement with Friedman (2007).

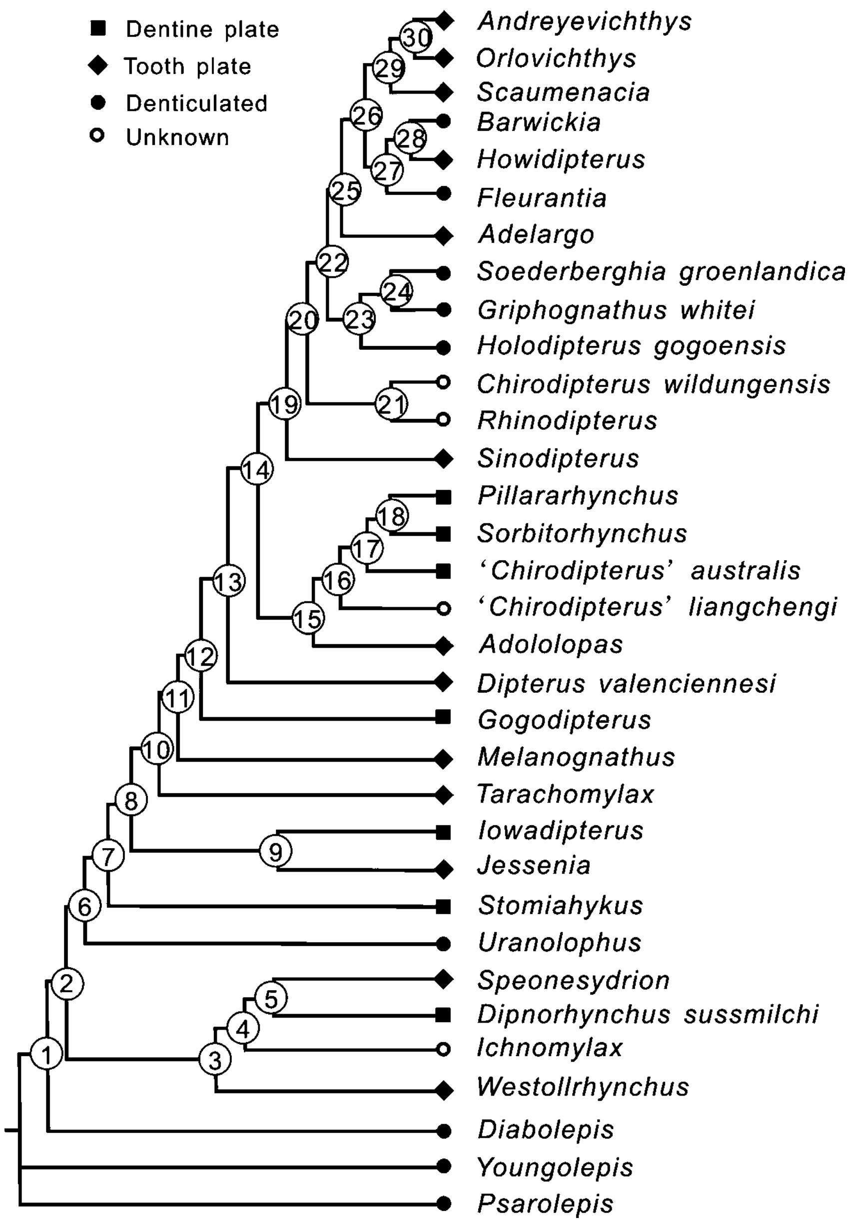

Fig. 8—One of eight most parsimonious trees. See Table 3 for the characters supporting the numbered nodes.

The clade above Node 19 is supported by a Bremer decay index of 1 and only by one synapomorphy: the K and X bones fused (Fig. 7, Table 3). However, this character has changed four times along the tree: Node 19; Node 30; *Howidipterus* and *Iowadipterus*. *Sinodipterus* is resolved as the most basal member in this clade. *Chirodipterus wildungensis* + *Rhinodipterus* and the members in the clade above Node 23 are placed in a polytomy with the lungfish in the clade above Node 25. The monophyly of *Holodipterus*, *Griphognathus* and *Soederberghia* is supported by a Bremer decay index of 4 and 12 synapomorphies (Table 3).

The clade above Node 25 is poorly resolved in the strict consensus tree. *Fleurantia*, *Adelargo*, [*Howidipterus* + *Barwickia*] are placed in a polytomy with the group containing *Scaumenacia* and [*Orlovichthys* + *Andreyevichthys*]. Geologically younger lungfishes, including the crown group, probably originated from the radiation above Node 26 (Ahlberg *et al.* 2006).

Comparison with previous studies

Early lungfish classification and phylogeny have been subjects of a series of studies. Campbell and Barwick (1990) proposed a classification based on the dentition and functional complexes including food reduction and respiration. They classified the lungfish into three suborders corresponding

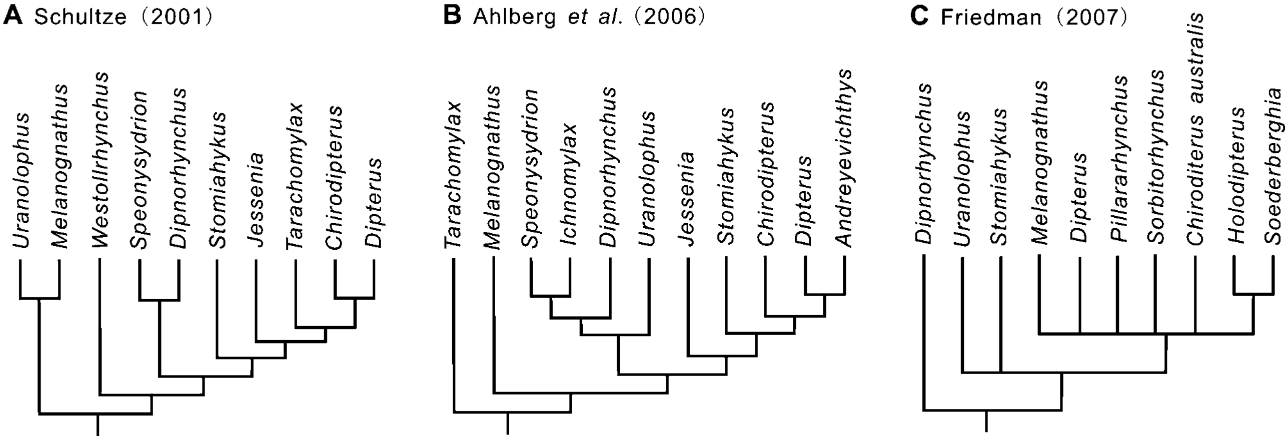

Fig. 9—Previous hypothesis of early lungfish interrelationships based on parsimony. —**A**. Schultze (2001); —**B**. Ahlberg *et al.* (2006; strict consensus topology of the analysis of their total dataset); —**C**. Friedman (2007). Cladograms have been pruned to make the comparison of the relationships of basal members.

to three types of dentition: tooth-plated, denticulated and dentine-plated. Tooth-plates carry large dental elements capped with enamel that each form from a single papilla and are added to the dentition in an organized manner; dentine plates carry radically arranged biting ridges, and are sometimes divided into discrete cusps, but they are not teeth in the accepted sense of conical enamel-coated structures but 'pseudoteeth'; dentine plates carry small 'pseudoteeth', but they are irregular arranged (Ahlberg *et al.* 2006). However, this classification is not accepted by the advocates of parsimony (Schultze and Marshall 1993; Schultze 2001; Ahlberg *et al.* 2006; Friedman 2007), who demonstrated that the division of lungfish into three groups based on 'food reduction' is untenable if other characters are given equal weight in the analysis.

Our results show that the hypothesis of separate tooth-plated, dentine-plated and denticulated lineages is not feasible. In our cladogram, the most basal members (*Psarolepis*, *Youngolepis*, *Diabolepis*) are denticulated, consistent with Ahlberg *et al.* (2006) and Schultze (2001). A denticulated group (Node 23) comprising *Soederberghia*, *Griphognathus* and *Holodipterus* appears in the strict consensus tree, in agreement with Friedman (2007). But other taxa with tooth-plates, dentine plates and denticulate plates do not separate out.

The broad phylogenetic pattern in this study agrees well with that in other parsimony analysis. The members below Node 13 (Fig. 8) are always resolved at the pre-*Dipterus* grade in previous studies (Fig. 9). The group above Node 25 is always situated at the most apical position.

The genus *Chirodipterus*, with three species considered here, is shown to be a heterogeneous assemblage as in Friedman (2007). The type species of *Chirodipterus*, *C. wildungensis*, is placed in a monophyletic group with *Rhinodipterus*; this clade is placed in a polytomy group with the clade comprising *Holodipterus*, *Griphognathus* and *Soederberghia* and the clade above Node 25. This pattern indicates the close link between *C. wildungensis* and the 'rhynchodipterids' *sensu* Friedman (2007) (*Griphognathus* and *Soederberghia*) and agrees with Friedman (2007).

However, there are also some remarkable areas of disagreement between our phylogenetic hypothesis and previous studies. The most remarkable disagreement is in the basal section of the cladogram. In our cladogram, *Diabolepis* is directly followed by two groups: one comprising [*Westollrhynchus* + *Ichnomylax* + *Dipnorhynchus* + *Speonesydrion*]; the other comprising the rest of the lungfish. Our solution reconstructs a large radiation immediately crownward of *Diabolepis*. This differs from previous solutions, which show a pectinate arrangement of smaller clades (single genus, or sister-genus pairs) in this area (Schultze 2001; Ahlberg *et al.* 2006; Friedman 2007). Another disagreement is the instable position of *Tarachomylax*. This genus is a tooth-plated genus from Emsian of Severnaya Zemlya (Siberian Arctic) (Barwick *et al.* 1997) and South China (Qiao and Zhu 2008). It appears at the most basal place above *Diabolepis* in Ahlberg *et al.* 2006) strict consensus tree based on the total dataset. However, *Tarachomylax* is sometimes placed at a relatively higher place (Schultze 2001). This lack of resolution in the basal section of lungfish evolution may a the result of the incomplete record of the Early Devonian lungfishes.

Conclusions

1. The tooth-plated lungfish *Sinodipterus* gen. nov., bears great similarity to *Dipterus* in the skull roof pattern and some differences in the tooth-plates.
2. Phylogenetic analysis of Devonian lungfish based on a dataset of 150 characters and 33 taxa indicates that the new taxon is more crownward than *Dipterus* and the clade

comprising *Adololopas*, *Sorbitorhynchus* and *Pillararhynchus*, and the genus *Chirodipterus* is a heterogeneous assemblage.

3. The phylogenetic results do not support the classification based on the tooth-plates and functional complexes proposed by Campbell and Barwick (1990).
4. The result shows a large number of convergences and reversals in the evolution of Devonian lungfish. Even a one-character change may result in the collapse of the cladogram, probably relating to the fact that the early history of lungfish was a radiation compressed in time (Rokas *et al*. 2005).

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Table 1 Character list

1. Pineal opening: 0. open; 1. closed. (A55, S1)
2. Pineal region marked by short eminence: 0. no; 1. yes. (F40)
3. Cosmine present on skull: 0. yes, full cover; 1. yes, but strongly reduced; 2. no. (A72, S40) (ordered)
4. Length of B bone: 0. short (less than twice its width); 1. long (equal or more than twice its width); 2. broad (wider than long). (S7)
5. Pit-lines on B bone: 0. absent; 1. anterior and middle pit-line present; 2. only anterior pit-line. (N)
6. C bone: 0. absent; 1. present. (A54)
7. D bone: 0. many; 1. single; 2. absent. (A56, S2)
8. Contact between E and C bones: 0. absent; 1. present. (A58, S12)
9. Paired E bones: 0. absent; 1. present; 2. mosaic. (A57, S13 modified)
10. Length of E bone: 0. less than twice their width; 1. more than twice their width. (S14)
11. Postparietals (I bones) meeting in midline: 0. yes; 1. no, separated by B bone. (A53, S20)
12. Posterior process of I bone: 0. absent; 1. present. (S21)
13. Parietals (J bones) meeting in midline: 0. yes; 1. no. (A51)
14. L bone: 0. two present; 1. one present. (S25)
15. Length of L bone: 0. similar to others in supraorbital canal series; 1. about twice as long as others in supraorbital canal series. (A65)
16. Bone K and X: 0. isolated; 1. single bone combining characteristics of K and X. (S24)
17. K bone: 0. medial to X bone; 1. anterior to X bone; 2. in sequence. (S23)
18. M bone: 0. present; 1. absent. (S26)
19. N bone: 0. present; 1. absent. (S27)
20. Q bone: 0. absent; 1. present. (S28)
21. Z bone: 0. posterior to I bone; 1. lateral to I bone. (N)
22. Maximum width of skull roof situated posterior to the level of the bone Y_1: 0. yes; 1. no (N)
23. Sutures between median series of skull roofing bones: 0. straight; 1. interdigitate. (S3)
24. Elongated snout: 0. absent; 1. present. (A70, S39)
25. Ossified upper lip in adult: 0. mosaic; 1. fused; 2. absent. (A50 modified)
26. Snout/skull roof: 0. with diffuse posterior margin; 1. with sharp posterior margin. (A71, S17 modified)
27. Supraorbital and infraorbital canals: 0. separated; 1. connected. (S33)
28. Lateral line/bone 3: 0. absent; 1. present. (A62, S35)
29. Cheek bones: 0. cheek bones 1–11 present; 1. no 11; 2. no 10, 11. (S36)
30. Length of postorbital cheek: 0. substantially longer than diameter of orbit; 1. equal to or shorter than diameter of orbit. (A66)
31. Ratio snout/cheek: 0. < 1; 1. ≥ 1. (S85 modified)
32. Bone 6: 0. reaching ventral margin of cheek; 1. excluded from ventral margin of cheek by bone 10. (A67)
33. Bone 7: 0. approximately equilateral; 1. much longer than deep. (A69)
34. Size of bone 10 (quadratojugal): 0. large, as 5 or greater; 1. much smaller than 5, or absent. (A68)
35. Subopercular: 0. two; 1. one. (S90)
36. Buccohypophysial opening: 0. present; 1. absent. (F67, S54)
37. Palatal construction: 0. parasphenoid separates pterygoids; 1. pterygoids articulate with each other with suture; 2. pterygoids fused. (A23, S55 modified)
38. Parasphenoid sutures: 0. fused; 1. visible sutures. (A29, S43)
39. Transverse curvature of palate: 0. flat; 1. arched. (A25)
40. 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. (A26) (ordered)
41. Ratio of posterior length to anterior length of parasphenoid: 0. less than 1 or about 1; 1. greater than 1. (S47)
42. Furrow on ventral surface of parasphenoid stalk: 0. absent; 1. present. (A27, S51)
43. Furrow on dorsal surface of parasphenoid stalk: 0. absent; 1. present. (S50)
44. Parasphenoid bearing denticle-lined ascending process: 0. no; 1. yes. (F62)
45. Dental material on parasphenoid: 0. present; 1. absent. (A21, F66, S53)
46. Parasphenoid reaching posterior margin of occiput: 0. no; 1. yes. (F64)
47. Shape of parasphenoid: 0. anterior elongated; 1. plough-shaped; 2. with lozenge. (S49)
48. Position of parasphenoid: 0. below ethmosphenoid; 1. below otico-occipital; 2. below both. (S44)
49. Position of anterior end of parasphenoid: 0. in front of jaw articulation; 1. not in front. (S46)
50. Ratio maximal width of parasphenoid to distance articulation points of jaws: 0. less than 1 : 3; 1. between 1 : 3 and 2 : 3; 2. greater than 2 : 3. (S45)
51. Lateral angle of parasphenoid: 0. no angle; 1. angular. (S48)
52. End of parasphenoid stalk: 0. single point; 1. bifid; 2. trifid with lateral projections. (A28, F65)
53. Margins of posterior stalk of parasphenoid: 0. converge to posterior angle; 1. subparallel. (F68)
54. ‘Vomer’ *sensu* Miles (1977): 0. present; 1. absent. (S59)
55. ‘Dermopalatine 1’ *sensu* Miles (1977): 0. median; 1. paired. (S57)
56. ‘Dermopalatine 1’ *sensu* Miles (1977) / pterygoid: 0. fused to pterygoid; 1. present, not contact; 2. isolated. (S58)
57. Series anterolateral to pterygoids: 0. present, with tusks; 1. present with denticles or dentine sheet; 2. present with tooth row. (A64)
58. Parasphenoid separating pterygoids along more than half of their length: 0. yes; 1. no. (F70)
59. Angle between midline and anterolateral margin of pterygoid: 0. less than 50°; 1. more than 55°. (A24)
60. Anterior nostril: 0. located dorsal to oral margin; 1. marginal. (F49)

Table 1 *Continued.*

61. Posterior nostril: 0. located dorsal to oral margin; 1. marginal 2. palatal. (F50) (ordered)
62. Internasal pits: 0. well developed; 1. reduced or absent. (F51)
63. Cosmine-like tissue within oral cavity: 0. no; 1. yes. (F56)
64. Premaxilla: 0. present; 1. absent. (A30)
65. Lateral lines in mandible: 0. parallel; 1. converging in one bone. (A63, S65)
66. Length of symphysis (ratio length of symphysis to length of jaw): 0. greater than 1 : 3; 1. between 1: 5 and 1: 3; 2. less than 1: 5. (S62, modified)
67. Adsymphysial plate: 0. present; 1. absent. (S66)
68. 'Dentary': 0. unpaired ; 1. paired. (S63)
69. Dentary-prearticular relationship: 0. dentition-generating gap; 1. small midline hole; 2. only no gap. (A37)
70. Slot between dentary and prearticular: 0. broad; 1. narrow; 2. no slot. (A38)
71. Adductor fossa: 0. not overhung by prearticular; 1. overhung by prearticular. (A39)
72. Length of adductor fossa: 0. more than 20% of jaw length; 1. 5%–20% of jaw length; 2. 0–5% of jaw length (A40) (ordered).
73. Morphology of adductor fossa: 0. open; 1. reduced to vestigial slit. (A41, S69)
74. Coronoids: 0. present; 1. absent. (A35)
75. Lip fold: 0. absent; 1. present. (A36)
76. Meckelian bone: 0. wholly ossified; 1. only articular ossified, or not ossified at all. (A49)
77. Retroarticular process: 0. small and poorly developed; 1. robust, squarish. (A43)
78. Skin contact surface on infradentary bones: 0. reaching up to lip of adductor fossa; 1. widely separated from lip of adductor fossa. (A45)
79. Curvature of ventral mandibular margin: 0. strongly convex; 1. essentially flat. (A42)
80. Orientation of glenoid: 0. mostly dorsally; 1. posterodorsally. (A44, modified)
81. Shape of glenoid fossa: 0. double structure; 1. single groove. (S71)
82. Angular and surangular: 0. separate; 1. fused into a single long bone. (A46)
83. Splenial and postsplenial: 0. separate; 1. fused. (A47)
84. Teeth on upper lip: 0. shedding teeth; 1. statodont tooth row; 2. teeth absent. (A20, S60)
85. Teeth on dentary: 0. shedding teeth present; 1. statodont tooth rows present; 2. teeth absent. (A19)
86. Number of tooth ridges: 0. < 10; 1. > 10. (N)
87. Teeth: 0. present; 1. absent. (A1)
88. Morphology of teeth on pterygoid and prearticular: 0. round/conical; 1. sectorial, forming distinct proximodistal cutting ridge. (A5)
89. Addition of large dentine elements at regular intervals to lateral margin of pterygoid/prearticular: 0. yes; 1. no. (A2)
90. Nature of large dentine elements: 0. teeth; 1. petrodentine cores; 2. thick irregular dentine; 3. ridges narrow regular dentine ridges. (A3)
91. Addition of marginal blisters to pterygoid/prearticular: 0. no; 1. yes. (A6)
92. Shape of marginal blisters: 0. bead-shaped; 1. elongated strips. (A7)
93. Addition of inter-row dentine along edge of pterygoid/prearticular: 0. no; 1. yes. (A8)
94. Nature of inter-row dentine: 0. always fuses or wears down into sheet; 1. separate denticles persist between some tooth rows. (A9)
95. Pulp cavity: 0. tooth-plates without pulp cavity; 1. with pulp cavity. (S77)
96. Diffuse dentine deposition on surface of palate/lower jaw: 0. yes, diffusely across whole palate; 1. no; 2. redeposition of denticles only within 'footprint' (outer circumference) of resorbed tooth-plate. (A10)
97. Relative areas of denticle 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 tooth-plate, dentine sheet on resorption areas within tooth-plate. (A11)
98. Relative areas of denticle field and dentine sheet on lower jaw: 0. all or nearly all denticles; 1. both denticles and dentine sheet; 2. mostly dentine sheet. (A12)
99. 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 tooth-plate only, not crossing edges. (A13)
100. Distinct vertically growing 'heel' on prearticular: 0. no; 1. yes. (A14)
101. Petrodentine: 0. absent; 1. present. (A17, S78)
102. Sharp 'additive' mesial and posterior edges on tooth-plates: 0. absent; 1. present. (A15)
103. Behaviour of 'additive edges' (if present): 0. quiescent; 1. active. (A16)
104. Braincase/skull table relationship: 0. broad contact; 1. supported by cristae. (A59, S9)
105. Angle between quadrate and plane of parasphenoid: 0. 90–95°; 1. 80–65°; 2. 55–35°. (A32, S42)
106. Autostyly: 0. absent; 1. present. (A30)
107. Lateral commissure: 0. separate from palatoquadrate; 1. partly fused but distinguishable; 2. wholly fused to palatoquadrate. (A34) (ordered)
108. Palatoquadrate: 0. fused into palate; 1. free. (S41)
109. Dorsolateral process on palatoquadrate: 0. absent; 1. present. (A31, F54)
110. Metotic fissure: 0. present; 1. absent. (A61, F13)
111. Intracranial joint/ventral cranial fissure: 0. mobile joint; 1. ventral cranial fissure; 2. neither fissure nor joint. (A60)
112. Occiput inset from posterior margin of neurocranium: 0. no; 1. yes. (F4)
113. Notochordal canal occluded by ossified cranial centrum: 0. no; 1. yes. (F5)
114. Neural cavity and notochordal canal separated by an ossified shelf in the occipital region, posterior to the foramen for N. X: 0. yes; 1. no. (F6, A78)
115. Ossification complete along ventral midline of notochordal canal posteriorly: 0. yes; 1. no. (F7, A79)
116. Occipital region bears transverse processes flanking foramen magnum: 0. no; 1. yes. (F8)
117. Dorsal aorta: 0. divides at or anterior to occiput; 1. divides posterior to occiput. (F9)
118. Lateral dorsal aortae: 0. run along ventral surface of neurocranium; 1. run in grooves on parasphenoid. (F10)

Table 1 *Continued.*

119. Occipital artery extramural: 0. no; 1. yes. (F11)
120. Neurocranium extends far posterior to hind margin of postparietals: 0. no; 1. yes. (F12)
121. Dorsolateral crista fenestrated: 0. no; 1. yes. (F16)
122. Median crista discontinuous: 0. no; 1. yes. (F17)
123. Little or no overlap between intersections of median and dorsolateral cristae with the dermal skull roof (median crista abbreviated): 0. no; 1. yes. (F18)
124. Lateral cristae fenestrated: 0. no; 1. yes. (F19)
125. Development of a pronounced ridge anterior to and continuous with the dorsolateral cristae: 0. no; 1. yes. (F20)
126. Articulation of first epibranchial posterior to the level of the foramen for N. IX: 0. no; 1. yes. (F22)
127. Notochord extending to or beyond level of N. V: 0. yes; 1. no. (F25)
128. Development of a deep 'spiracular recess' *sensu* Thomson and Campbell (1971): 0. yes; 1. no. (F27)
129. Separate foramina for the internal carotid artery and efferent pseudobranchial artery: 0. no; 1. yes. (F28)
130. Jugular vein: 0. little or no groove; 1. travels through deep groove along length of otic region. (F30)
131. Foramina for the jugular vein and the ramus hyomandibularis N. VII on the posterior surface of the transverse wall of the otic region: 0. confluent; 1. separate. (F31)
132. Foramina for the jugular vein and the orbital artery on the posterior surface of the transverse wall of the otic region: 0. confluent; 1. separate. (F32)
133. Foramina for the ramus hyomandibularis N. VII and the orbital artery on the posterior surface of the transverse wall of the otic region: 0. no; 1. separate. (F33)
134. Hyomandibular facet traverses fissure in transverse otic wall (hyomandibular facet extends on to palatoquadrate): 0. no; 1. yes. (F35)
135. Separate ossified canals for pineal and parapineal organs: 0. yes; 1. no. (F38)
136. Foramen for N. II above the level of foramen sphenoticum minus: 0. no; 1. yes. (F41)
137. Foramen for N. III above level of foramen sphenoticum minus: 0. no; 1. yes. (F42)
138. Ventral face of nasal capsule: 0. complete; 1. perforated by fenestration that opens posteroventrolaterally (fenestra ventralis); 2. solum nasi completely unossified. (F46) (ordered)
139. Nasal capsule set well posterior to snout margin or preoral eminence: 0. no; 1. yes. (F48)
140. Enlarged, knob-shaped protrusion on the posteroventral surface of the quadrate (hyosuspensory eminence of Miles, 1977): 0. absent; 1. present . (F55)
141. Overlap relationship between entopterygoids and parasphenoid: 0. parasphenoid overlaps entopterygoids dorsally; 1. entopterygoids overlap parasphenoid dorsally. (F61)
142. Cleithrum and clavicle: 0. with cosmine; 1. without cosmine. (S81)
143. Median fin morphologies: 0. all separate and short-based; 1. posterior dorsal fin long-based; 2. both dorsal fins long-based uninterrupted fin fringe. (A74, S83)
144. Posterior dorsal fin support: 0. all radials carried by basal plate; 1. anterior radials on basal plate, posterior radials free; 2. no basal plate. (A75)
145. Anal fin support: 0. trapezoidal with no distinct shaft; 1. cylindrical proximal shaft and triangular distal plate. (A76)
146. Median fin radials: 0. cylindrical; 1. hourglass-shaped. (A77)
147. Vertebral column: 0. unconstricted notochord; 1. disc centra. (A78)
148. Neural arches and spines: 0. separate; 1. fused. (A79)
149. Scales: 0. rhombic; 1. round. (A73)
150. Cosmine on scales: 0. present; 2. absent. (A73)

Characters used in previous analyses: S = taken from Schultze 2001; A = taken from Ahlberg *et al.* 2006; F = taken from Friedman 2007, which are all characters listed above except for new characters (N) (5, 21, 22 and 86).

Table 2 Dataset of 150 characters for the 33 taxa investigated

	00000	00001	11111	11112	22222	22223	33333	33334	44444	44445	55555	55556	66666	66667	77777
Characters	12345	67890	12345	67890	12345	67890	12345	67890	12345	67890	12345	67890	12345	67890	12345
Psarolepis romeri	0-0--	02-0?	??0--	-----	-0001	000?0	0--??	00-?0	??-?0	-?000	0?-11	200?0	00?0?	20101	00000
Youngolepis praecursor	110--	02-0?	000--	?----	-0001	000?0	0--0?	00-?0	??-?0	-0000	0?-11	200?0	00p00	20101	00000
Diabolepis speratus	110?0	02-0?	00100	??110	?1001	000?0	0????	00-00	??-?0	-0000	0?-11	21000	1100?	0?101	00010
Chirodipterus australis	10002	11-0?	11110	p1000	11001	11110	11001	11101	101?1	01110	10001	21111	21011	10001	10011
Chirodipterus liangchengi	??0??	?????	??1??	?????	??001	1????	?????	11101	10??1	01110	100??	??111	2101?	?????	????1
Chirodipterus wildungensis	??0??	1????	1????	?????	??001	?????	?????	11102	10?01	11111	1010?	??111	212??	?????	?????
Dipnorhynchus sussmilchi	0-000	1002?	00100	00000	00000	00100	00?0?	02000	??-?0	0????	??000	01?01	21010	00000	00011
Dipterus valenciennesi	10002	1p110	11100	01000	01001	01111	10000	01101	00??0	01101	10010	1?101	21111	10000	10011
Gogodipterus paddyensis	??0??	?????	?????	?????	???01	?????	????0	11101	10?00	01101	1000?	1?10?	??0?0	10001	10011
Griphognathus minutidens	10212	11011	11110	1-010	01111	01110	11100	12011	00110	12112	11110	11101	2101?	20022	12111
Holodipterus gogoensis	10112	1111?	11100	1-???	??101	?11?0	1????	12011	?0110	1?1??	?1101	21?01	21011	10012	11011
Melanognathus canadensis	100??	1102?	????-	??00?	??000	0????	?????	111?1	10?00	11201	1001?	??101	21010	10022	10011
Orlovichthys limnatis	??21?	1?-01	10111	01???	11011	1????	?????	?1102	1??01	?0200	??10?	??001	2111?	20012	10111
Pillararhynchus longi	10010	12-0?	10100	p1010	01001	110?0	0???0	11101	10?00	01110	100??	22111	2101?	01000	10111
Soederberghia groenlandica	10212	1q111	11111	1-001	11110	01010	1011?	11112	11100	?1102	111??	??101	2?01?	?????	?????
Sorbitorhynchus deleaskitus	??02?	1????	101??	01???	??00?	?1???	?????	11101	10?01	?1111	100??	??11?	??0??	210??	10111
Stomiahykus thlaodus	??0??	10?2?	???00	0001?	000??	??1??	?????	12000	???00	0????	??0??	?1?0?	??0??	?????	?????
Uranolophus wyomingensis	10000	11110	00100	00000	00000	000?0	0???0	12010	??-00	????0	???01	01001	21010	01000	00011
Speonesydrion iani	0-000	1012?	00100	0000?	?0001	0????	????0	02000	??-00	?????	???00	01?01	21010	00000	00011
Westollrhynchus lehmanni	0-100	1012?	00110	00001	?0001	000?0	0????	10000	?--00	?000?	0??10	0100?	2101?	?????	?????
Jessenia concentrica	??010	1102?	00110	0101?	10001	0????	?????	?1100	??-00	0020?	0??0?	??00?	??01?	?????	?????
Fleurantia denticulate	10201	11011	11111	1-001	11112	11121	10110	111?2	11101	12100	11111	1110?	??0??	2????	???11
Scaumenacia curta	10201	12110	11100	1-000	11002	11121	10110	p1102	1??01	?210?	1??01	2210?	??011	??0??	???11
Howidipterus donnae	10201	11110	11110	01001	11002	11121	10011	111?2	11?01	?2101	11101	2110?	??010	?????	???11
Barwickia downunda	10201	11111	11110	1-010	11102	11121	10111	011?2	11101	?2101	111??	??10?	??010	?????	???11
Andreyevichthys epitomes	1010?	12-01	11101	011??	01002	111?1	??0?0	?1102	11101	?1100	11?01	22?0?	??01?	?????	???11
Rhinodipterus ulr	10012	11111	11110	1-000	11011	01???	1???1	01102	11101	?1111	10???	??10?	??01?	00022	11111
Adelargo schultzei	??201	1????	111??	1-???	0?0??	?????	?????	11102	11001	?21??	111??	??10?	??01?	?????	?????
Ichnomylax kurnai	?????	?????	?????	?????	???0?	?????	?????	?????	?????	?????	?????	???0?	??0??	0??0?	00011
Adololopas moyasmithae	??002	1????	111??	01???	?100?	111?0	0???0	11101	10101	?1101	10001	2111?	??011	???0?	???1?
Tarachomylax oepiki	??00?	1002?	10100	0p001	00001	011?1	?0??0	?110?	??00?	?????	?????	??10?	??01?	?????	?????
Iowadipterus halli	10011	1012?	10111	1-000	10001	01110	0010?	?????	?????	?????	?????	?????	???10	1?0??	?????
Sinodipterus beibei	10002	11110	1110?	1-00?	010??	?1???	?????	?1?0?	?????	?????	?????	??10?	??0??	?????	?????

Table 2 *Continued.*

	00000	00000	00000	00000	00001	11111	11111	11111	11111	11111	11111	11111	11111	11111	11111
	77778	88888	88889	99999	99990	00000	00001	11111	11112	22222	22223	33333	33334	44444	44445
Characters	67890	12345	67890	12345	67890	12345	67890	12345	67890	12345	67890	12345	67890	12345	67890
Psarolepis romeri	00000	00000	?0?1?	0?0??	000??	0??0?	001?0	0????	??0??	- - - 0 -	?0-00	0000?	- - 00?	-0???	?????
Youngolepis praecursor	00000	00000	?0?1?	0?0?**1**	000?0	0??0?	001**?**0	10000	00010	- - - 0 -	10-01	000??	- - 100	-0???	???00
Diabolepis speratus	00010	?0011	?0000	0?11**0**	03020	00?0?	0?110	1????	??0??	- - - 0 -	?0-0**1**	000??	- - 10?	-????	?????
Chirodipterus australis	01111	**0**0022	01?03	1110**1**	1??00	11011	12000	20001	10000	11000	011p0	11011	00201	0?0?**0**	**0**0010
Chirodipterus liangchengi	?????	???1?	0?00?	0?10?	1??0?	?1011	12001	20**0**00	00000	**0**?10?	0?111	?1?1?	0?201	?????	?????
Chirodipterus wildungensis	?????	???2?	0?00?	0?10?	1??0?	???11	12001	21000	01000	00101	?1111	111?1	01201	1????	?????
Dipnorhynchus sussmilchi	00000	10022	?1?02	10100	02201	00?10	11010	**2**00?1	??01?	00000	01000	00000	00200	?**?**???	???0?
Dipterus valenciennesi	01111	00022	10000	0?10**1**	1??00	11111	12001	2000?	00001	0000?	0?111	111??	01201	11000	0001?
Gogodipterus paddyensis	0?111	100??	01?01	1010?	01100	**11**011	12000	20000	10000	0?000	0?100	1101?	0???1	0????	?????
Griphognathus minutidens	01111	01111	?1?1?	1010**0**	00010	00?12	12000	211?1	111**0**0	10111	1?101	p1111	11211	11000	01011
Holodipterus gogoensis	01111	10111	?0000	10100	01111	10?11	12000	21010	01010	00101	0?111	11111	11201	?????	???11
Melanognathus canadensis	00??**1**	00121	?0000	0?0??	00010	?0?1?	1?0??	?00?0	0100?	00000	??1??	?????	??20?	?????	?????
Orlovichthys limnatis	01**1**11	**1**1111	00100	0?0??	1??00	?11**1**?	1?0**01**	2001?	??000	00101	?????	?????	0020?	1????	?????
Pillararhynchus longi	01111	01111	01?01	1110?	1??00	11111	12001	20000	00001	11000	1?101	1111?	00201	01???	???10
Soederberghia groenlandica	1????	?????	?1?1?	?????	00**?**00	?0??**?**	????0	?01??	10110	0?11?	????0	?????	??21?	1?**0**?**1**	**11**???
Sorbitorhynchus deleaskitus	01111	001??	?1?1?	1110**?**	1??00	11011	1?00?	2????	??0?0	01000	??1??	011??	0???1	?????	???10
Stomiahykus thlaodus	?????	???0?	01?01	1110?	01?0?	10?11	11010	?000?	00010	0000?	0?011	00000	11??1	?????	?????
Uranolophus wyomingensis	00000	10022	?1?1?	0?100	00010	00?10	1?01?	?00?1	??010	?00??	?????	?????	??201	000??	?0100
Speonesydrion iani	00001	000?1	01000	10100	02101	00?**1**?	1?01?	?0??0	????0	?????	??1??	?????	??20?	0????	???10
Westollrhynchus lehmanni	?????	?????	00000	0?10?	02?0?	0????	1?0??	?????	?????	?????	??1??	?????	??20?	0????	?????
Jessenia concentrica	?????	???**2**?	0**1**?01	0?0??	00?0?	**1**0???	1??**1**?	?????	?????	?????	?????	?????	?????	?????	?????
Fleurantia denticulate	11111	?112?	00100	0?0??	20?1?	?????	1??**0**?	?????	?????	?????	?????	?????	?????	01121	10111
Scaumenacia curta	??**1**1?	?112?	00100	0?0?1	1??00	110?**1**	1????	?????	?????	?????	?????	?????	?????	01221	10**1**11
Howidipterus donnae	1??1?	11022	10000	0?0??	22?10	?**?**???	1????	?????	?????	?????	?????	?????	?????	?11**11**	**1**0?11
Barwickia downunda	?1?11	01?2?	?0000	0?11?	20010	?????	1??0?	?????	?????	?????	?????	?????	?????	?11**11**	**1**0**1**11
Andreyevichthys epitomes	?1?1?	?1111	00100	0?11?	1??00	111??	1??0?	?????	?????	?????	?????	?????	?????	?????	?????
Rhinodipterus ulr	0???1	1???2	00000	??0??	1???0	?10??	1?0??	2????	?????	?????	?????	?????	?????	?00**?0**	??**?**10
Adelargo schultzei	?????	?????	10000	0?11?	1??0?	0??1?	?????	?????	?????	?????	?????	?????	?????	0???1	?????
Ichnomylax kurnai	0?00**0**	**000**?1	00000	1010?	0?101	1????	?????	?????	?????	?????	?????	?????	?????	?????	?????
Adololopas moyasmithae	?????	?0?1?	00000	0?10**1**	1??00	111??	1?00?	?????	?????	?????	?????	?????	?????	11???	???10
Tarachomylax oepiki	?????	???1?	00000	0?**1**11	00?00	00???	1????	?????	?????	?????	?????	?????	?????	0????	???10
Iowadipterus halli	?????	???2?	?????	?????	?????	?????	?????	?????	?????	?????	?????	?????	?????	?????	???10
Sinodipterus beibei	?????	?????	00000	0?11?	1??0?	110??	?????	?????	?????	?????	?????	?????	?????	1????	???10

'–' = inapplicable; '?' = unknown; 'p' = 0/1; 'q' = 1/2. Underlined characters have been emended.

Table 3 Characters and character states defining major clades shown in Fig. 8. Asterisks indicate ambiguous character states resolved using DELTRAN. Character state is (1), unless marked otherwise

Node1 : 13;57;61;62;66(0);74;85;89(0);93;
Node2 : 6;7(0);9(2);56(0);60;61(2);64;68(0);70(0);75;84*; 104;106;107*;108(0);111(2);127;138(2);
Node3 : 1(0);55(0);97(2);
Node4 : 91;98*;100*;
Node5 : 37*;54*;87;
Node6 : 2*;36*;37*;54*;87;140;
Node7 : 28;101;105;137*;
Node8 : 17;27*;29*;37;38;48*;66*;149*;
Node9 : 4;14;21;
Node10 : 11*;58;87(0);95*;
Node11 : 7;40*;47*;50*;51*;71*;80*;119*;
Node12 : 48;56*;78*;79*;102;107*;109*;131*;132*;134*;
Node13 : 5*;9*;12*;22*;65;77*;96;110;129*;133;141;142*;
Node14 : 43*;45;56(2);135*;
Node15 : 26;59;84;
Node16 : 49;50(0);
Node17 : 9*;87*;91;92*;122*;137*;141*;
Node18 : 12(0);67;73*;83*;
Node19 : 16;
Node20 : 10;31*;46*;53*;70*;73*;81*;117*;123*;125*;
Node21 : 40*;49;
Node22 : 3;33*;52;69*;83*;114;150;
Node23 : 4*;23;39;45(0);72*;84;91;95(0);96(0);102(0);110(0);136;
Node24 : 3*;14*;24;50*;87;89;113;116;118;124;139;147*;
Node25 : 3*;5;40*;42;47*;94;141(0);145*;
Node26 : 21*;25*;26*;29*;30*;34*;66*;82*;93(0);144*;146*;148*;
Node27 : 14*;76;96(2);99;143*;
Node28 : 35;65*;144;
Node29 : 7(2);57(2);88*;
Node30 : 9(0);15;16(0);50*;84;103;