

A new Thai Mesozoic lungfish (Sarcopterygii, Dipnoi) with an insight into post-Palaeozoic dipnoan evolution

LIONEL CAVIN^{1*}, VARAVUDH SUTEETHORN², ERIC BUFFETAUT³ and HAIYAN TONG³

¹Department of Palaeontology, The Natural History Museum, Cromwell Road, London SW7 5BD, UK

²Department of Mineral Resources, Rama VI Road, Bangkok 10400, Thailand

³CNRS (UMR 5125, Paléoenvironnements et Paléobiosphère), 16 cour du Liégat, 75013 Paris, France

Received April 2005; accepted for publication January 2006

We describe a new species of lungfish, *Ferganoceratodus martini* sp. nov., based on a single specimen discovered in the Late Jurassic – Early Cretaceous of the Phu Nam Jun locality, north-eastern Thailand. The material comprises an almost complete skull roof with associated upper and lower jaws, as well as some postcranial remains. *F. martini* shows characters unexpected and/or unknown in other Mesozoic lungfishes, such as pieces of a ‘hard snout’. The microstructure of the ‘hard snout’ provides support to the Bemis and Northcutt interpretation of the cosmine tissue of Palaeozoic lungfishes as homologous to the complex cutaneous vasculature of the living *Neoceratodus*. Because the homologies of the ossifications of the skull roof among lungfishes and among piscian sarcopterygians are unsatisfactorily understood, we use a topological nomenclature in the description of the specimen and in the discussion of post-Devonian dipnoan skull roof characters. We define a few characters for the cladistic analysis only, but these are regarded as less theory-laden. We propose a hypothesis of phylogenetic relationships for most of the post-Devonian forms known by skull remains. The main feature is the ancient dichotomy between the *Neoceratodus* lineage and most of the other Mesozoic forms, including the Lepidosirenids. The palaeobiogeographical pattern shows a series of vicariant events between Laurasia and Gondwana in the Late Triassic – Early Jurassic, followed by a vicariant event between Africa and South America. © 2007 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2007, 149, 141–177.

ADDITIONAL KEYWORDS: histology – new taxon – palaeoecology – palaeogeography – phylogeny – tooth plate.

INTRODUCTION

Dipnoi, or lungfishes, form a well-defined clade of sarcopterygian fishes first recognized from Mesozoic deposits by Agassiz in 1838 with the genus *Ceratodus*. Then, living representatives were discovered in freshwaters from South America (*Lepidosiren* Fitzinger, 1837), Africa (*Protopterus* Owen, 1839) and eventually Australia (*Neoceratodus* de Castelnau, 1876). Lungfishes rapidly played a key-role in theories of the origin of tetrapods. They were first regarded as direct ancestors of amphibians, then dismissed as intermediates throughout most of the 20th century, before

being regarded as the living sister group of tetrapods following reinterpretation of some of their characters (Rosen *et al.*, 1981).

The fossil record of lungfishes shows a remarkable pattern since their appearance in the Early Devonian. Several Devonian taxa are represented by heavily ossified, articulated specimens preserved in anatomical articulation. The first lungfishes diversified in shallow marine environments (Campbell & Barwick, 1986) and rapidly dispersed worldwide (Reisz, Krupina & Smith, 2004). Schultze (2001) recently proposed a hypothesis of phylogenetic interrelationships of the taxa forming this first radiation. His analysis is based on 90 osteological characters, thanks to the well-preserved material used as terminal taxa. Fossil lungfishes occurred in the Carboniferous and Permian in marine, as well as in brackish and freshwater deposits. The skull roof pattern of these fishes is, in a way, intermediate between the Devonian and the post-

*Corresponding author. Current address: Département de Géologie et Paléontologie, Muséum d’Histoire naturelle de la Ville de Genève, 1 Route de Malagnou, Case Postale 6434, CH-1211 Genève 6, Switzerland. E-mail: lionel.cavin@ville-ge.ch

Palaeozoic forms. As far as we know, all post-Devonian lungfishes possessed tooth plates. This feature strongly modifies the quality of the lungfish fossil record since the beginning of the Mesozoic onwards. In the Triassic most lungfish occurrences are known by isolated tooth plates, except for a handful of skull remains sometimes associated with jaw and postcranial material described from Austria (Teller, 1891), Madagascar (Lehman *et al.*, 1959; Beltan, 1968), Kyrgyzstan (Vorobyeva, 1967), Germany (Schultze, 1981), Morocco (Martin, 1979, 1981a), Australia (Woodward, 1890; Wade, 1935) and South Africa (Kemp, 1996). In post-Triassic deposits, isolated tooth plates are common but other cranial remains are very rare. There are, however, a few exceptional occurrences consisting of dental remains preserved alongside other cranial remains. One of these is *Ferganoceratodus jurassicus* from the Middle Jurassic of Kyrgyzstan, known by various isolated elements of the skull roof associated with tooth plates in the same deposit (Nessov & Kaznyshkin, 1985). Another consists of some skull material from the Cainozoic of Australia referable to the Recent *Neoceratodus* lineage (Kemp, 1991, 1998). The shift observed in the type of lungfish fossil material through time, from complete articulated skeletons in the Devonian to almost exclusively isolated tooth plates in the Mesozoic and Cainozoic, is directly related to evolutionary trends that affected the mineralization of the skeleton of these fishes. Devonian species were heavily ossified, with dermal bones sometimes covered by a unique kind of hypermineralization, cosmine. The strongly ossified skeleton became reduced in most post-Devonian lungfishes, which possessed only thin dermal skull bones deeply embedded in the skin. As a parallel trend the tooth plates became stronger and more mineralized thanks to the presence of a specialized kind of dentine, petrodentine (*sensu* Reisz *et al.*, 2004). This feature helps fossilization and explains the relative abundance of isolated tooth plates in the Mesozoic and Cainozoic sedimentary record. But the shift observed in the type of the fossil record makes any phylogenetic analyses difficult, because of the highly incomplete post-Palaeozoic record. The difficulty is increased by another trend in lungfish evolution, which is the simplification of the pattern of ossifications in the skull roof. This feature hinders the recognition of homologies among all taxa. Accordingly, each discovery of post-Palaeozoic skull material associated with tooth plates is very important for the understanding of post-Palaeozoic lungfish evolution.

Here we describe a new species, based on a single well-preserved specimen (incomplete skull roof with associated upper and lower jaws and tooth plates, parasphenoid and pieces of the first six vertebral elements) from the Late Jurassic – Early Cretaceous of

north-eastern Thailand. This material provides an opportunity to assess character recognition and to suggest homologies in the Mesozoic lungfish skeleton, and to propose a new phylogenetic analysis and to discuss palaeoecological and palaeobiogeographical implications.

GEOLOGICAL SETTING

The specimen described here was found in 2002 during systematic excavation of the locality of Phu Nam Jun, Kalasin Province, north-east Thailand. The locality of Phu Nam Jun is situated in the upper part of the Phu Kradung Formation, which was regarded by some authors as a separate formation, the Waritchaphum Formation (Philippe *et al.*, 2004). The Phu Kradung Formation, here including the Waritchaphum Formation, is the lowest Formation of the Khorat Group as currently defined (Racey *et al.*, 1996). It has yielded no strong evidence for dating so far. According to age constraints provided by palynological data from the overlying formations, the Phu Kradung Formation may be regarded as either Late Jurassic or basal Cretaceous in age (Racey *et al.*, 1994, 1996). The sediments of the Phu Kradung Formation were deposited in continental environments, varying from river channels to lacustrine settings. The presence of large silicified logs in the lower part of the formation and their near absence in the upper part and following formations may indicate a shift from a subarid to a wetter climate (Philippe *et al.*, 2004). Figure 1 shows the location of the site and a simplified overview of the vertebrate assemblages from the Mesozoic formations of the Khorat Plateau.

The locality of Phu Nam Jun has been regularly excavated since 2001. The faunal assemblage contains mostly semionotiform fishes referred to *Lepidotes budhabutrensis* Cavin *et al.*, 2003, which is represented by more than 200 complete or subcomplete articulated specimens so far. A single specimen belonging to a new derived semionotiform (Cavin & Suteethorn, 2006) and a single isolated tooth of a hybodont shark (G. Cuny, pers. comm., 2003) are the only other vertebrates alongside the lungfish described here. An array of evidence indicates that the semionotiform fishes accumulated in a drying pool and that the lungfish was probably fossilized *in situ* during aestivation and, accordingly, that the environment was subaerial (Cavin *et al.*, 2004).

Abbreviations used in figures and text: a.f, articular facet; a.m.b, anterior medial bone; a.ml.b, anterior mediolateral bone; a.p, ascending process; c, canal; c.a.a.ml.b, contact area with the anterior bone of the mediolateral series; c.a.p.m.b, contact area with the posterior bone of the medial series; c.a.p.ml.b, contact

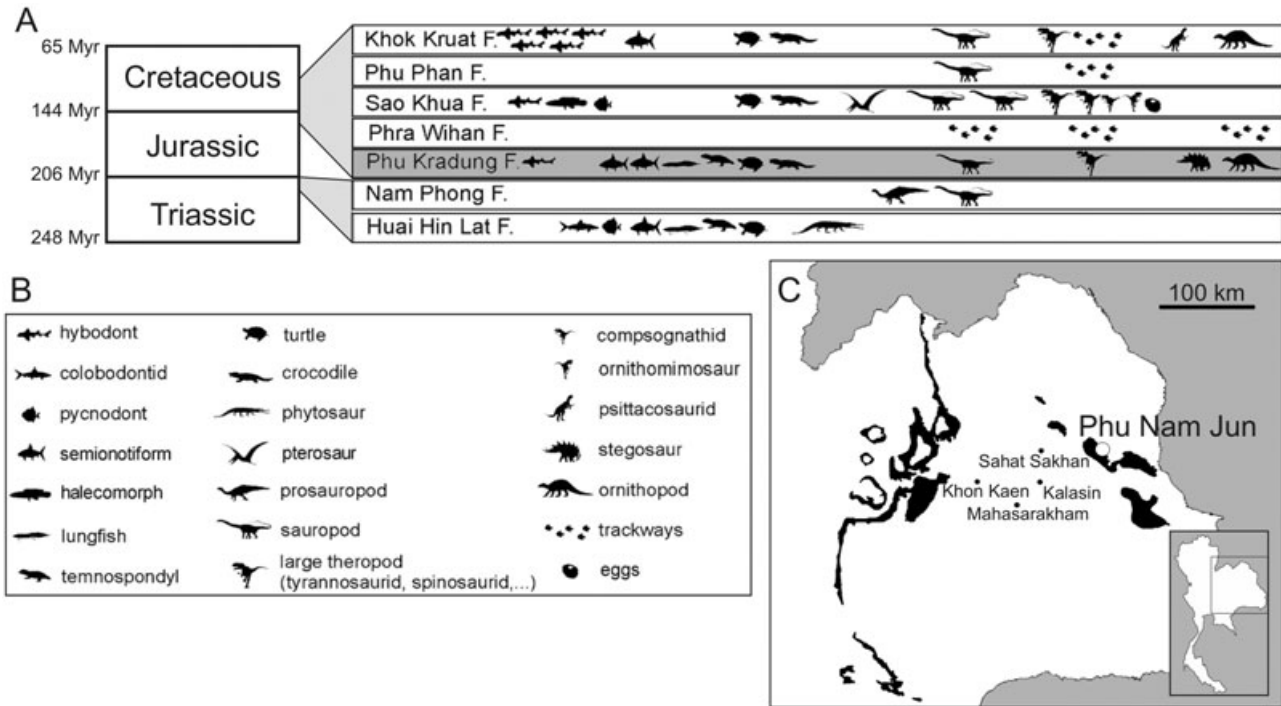


Figure 1. A, Mesozoic formations of the Khorat Plateau with vertebrate assemblages. B, caption for the silhouettes in A. C, the Khorat Plateau, north-east Thailand (frame), with the extent of the Phu Kradung Formation outcrops (in black) and the location of the Phu Nam Jun locality (white spot). Modified from Cavin *et al.* (2004).

area with the posterior bone of the mediolateral series; c.l, capillary loops; co, cosmine; c.pV, canal for the profundus branch of the trigeminal nerve; d, dentine; de, dermis; d.e.p, deeper horizontal plexus; d.p, descending process; Dsph, dermosphenotic; en, enamel; ep, epidermis; f.c, flask cavities; g, groove; i.o.s.c, infraorbital sensory canal; la.b, labial bone; l.b, lamellar bone; li.b, lingual bone; o, orbit; o.s.c, otic sensory canal; p, process; p.a, anterior process; p.c, pulp canal; pi, pit; p.m.b, posterior medial bone; p.ml.b, posterior mediolateral bone; po, pore; p.o, orbital process; Pt, pterygoid; R, pleural rib (numbered); r, ridge; s.c.t, subcutaneous tissue; s.e.p, subepidermal plexus; sp, spine; s.p, spongy bone; sy.b, symphyseal bone; s.o.s.c, supraorbital sensory canal; t.p, tooth plate; tu, tubuli.

Institutional abbreviations: BMNH, The Natural History Museum, London, UK; TF, Thai Fossils, Sahat Sakhan Dinosaurs Research Centre, Kalasin Province.

SPECIMENS EXAMINED

Dipterus valenciennesi Sedgwick & Murchison, 1835. Middle Old Red Sandstone. BMNH P.61663: Skull roof.

Chirodipterus australis Miles, 1977. Upper Devonian of Gogo, Australia. BMNH P.52562: Skull.

Protopterus sp.: half dry skull, BMNH, no number.

Ariguna formosa (Wade, 1935). Early Triassic of New South Wales, Australia. BMNH P.16828, holotype: almost complete individual.

Ferganoceratodus jurassicus Kaznyshkin & Nessov, 1985. Middle Jurassic of Kirghizstan. nos. 1-13/12217 and 26-90/12217 (Geological Institute, Saint Petersburg): isolated cranial bones and tooth plates.

SYSTEMATIC PALAEOLOGY

SARCOPTERYGII ROMER, 1955

ORDER DIPNOI MÜLLER, 1845

FERGANOCERATODUS KAZNYSHKIN & NESSOV, 1985

Diagnosis (emended): Skull roof with two unpaired bones in the median series, two paired bones on the mediolateral series and two bones on the lateral series; bones of the median series suture through a short contact; dental plates of cutting type, with five radiating ridges on the upper plates and four radiating ridges on the lower plates separated by deep notches.

Type species: *Ferganoceratodus jurassicus* Kaznyshkin & Nessov, 1985 (Fig. 2).

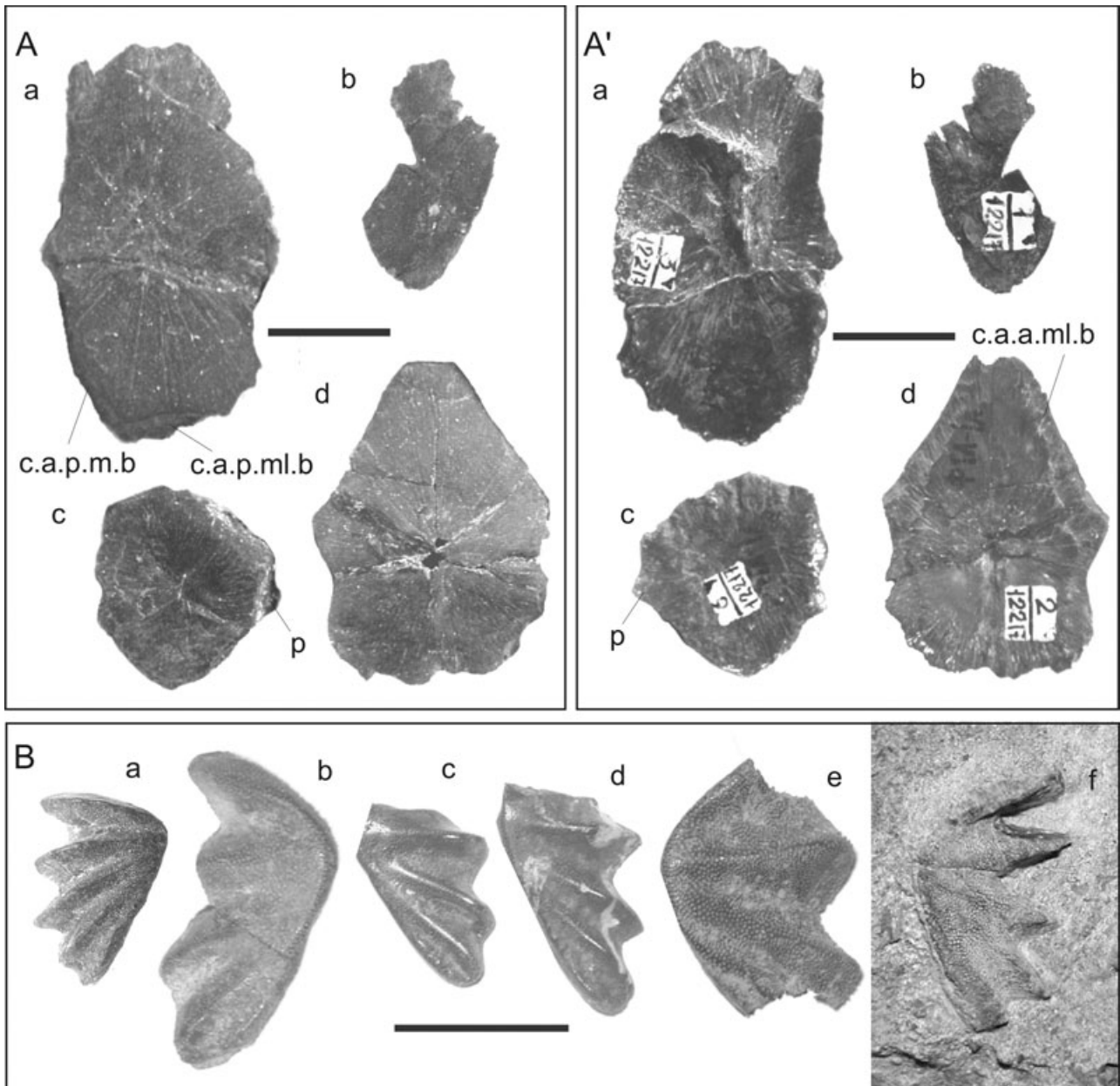


Figure 2. A, *Ferganoceratodus jurassicus* Kaznyshkin & Nesso, 1985: ossifications of the skull roof. A, dorsal views; A', internal views. a, right anterior bone of the mediolateral series (holotype, no. 3/12217); b, anterior bone of the median series; c, left posterior bone of the lateral series; d, posterior bone of the median series. B, occlusal views of upper (a, f) and lower tooth plates (b–e) (material: no. 1–13/12217 and 26–90/12217). Scale bars: 10 mm.

Diagnosis (emended): *Ferganoceratodus* with an overlapping suture between the posterior bone of the median series and the paired anterior bones of the mediolateral series (Fig. 2, c.a.a.ml.b and c.a.p.m.b); posterior bone overlapping the anterior bone of the mediolateral series along a narrow strip; posterior bone of the mediolateral series with a median process covered by the bone of the median series (Fig. 2A, A', p); lower tooth plates with a first notch significantly

deeper than the following ones, with an inner angle of about 90°.

***FERGANOCERATODUS MARTINI* SP. NOV.**

Holotype (Fig. 3): TF 7712, an incomplete skull roof with articulated palatine tooth plates, lower jaw with tooth plates, parasphenoid, isolated pieces of the 'hard snout', elements of the first six vertebral elements and

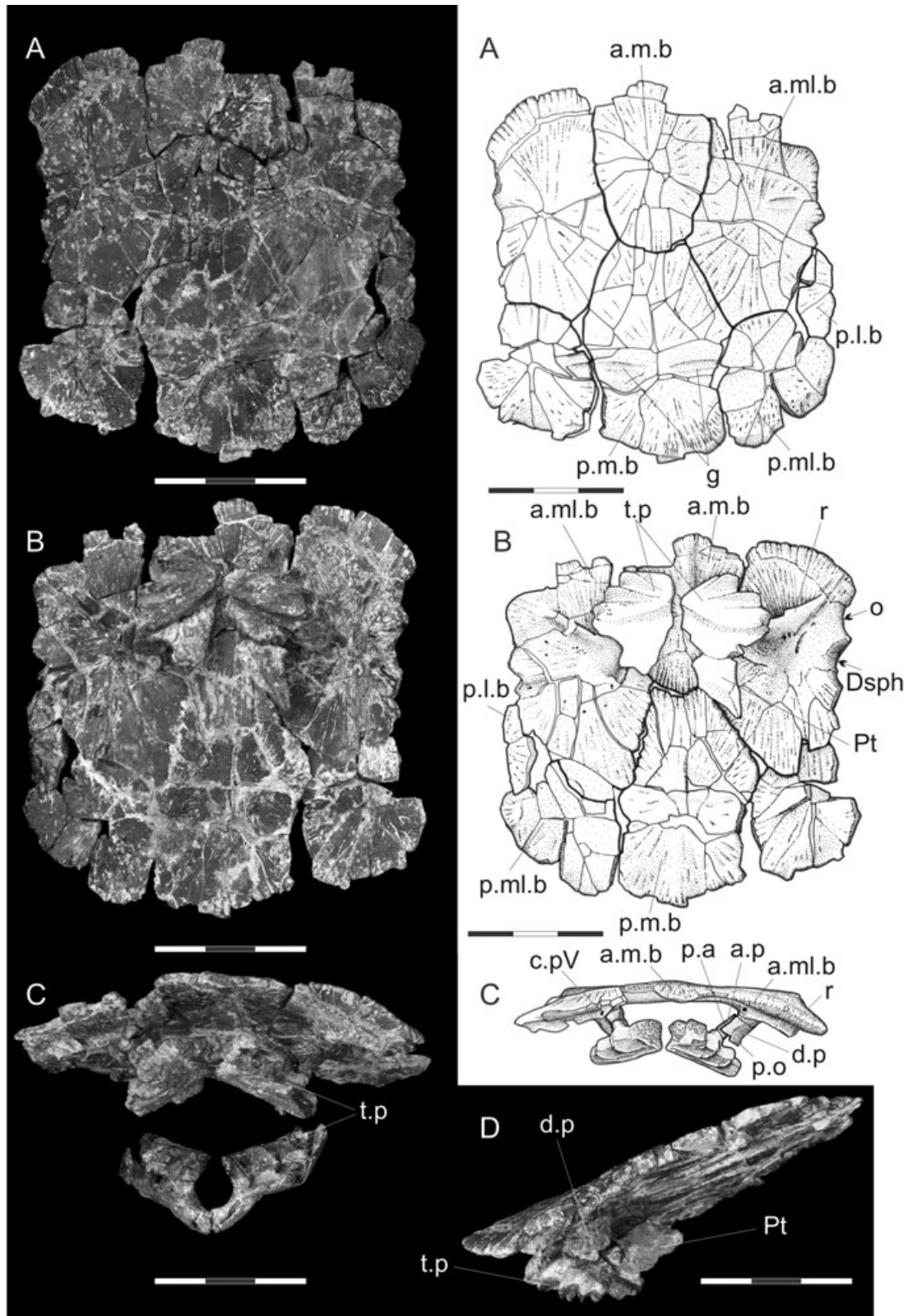


Figure 3. *Ferganoceratodus martini* sp. nov. Holotype TF 7712. Photographs and interpretative drawings of the skull roof and upper tooth plates in dorsal views (A), internal views (B), anterior view with the lower jaw (C) and photograph in left lateral view (D). Scale bars: 30 mm.

fractured scales. The fragments of 'hard snout' have not been found in connection with the rest of the skull, but were discovered during the mechanical preparation of the skull roof in its plaster jacket. They belong beyond doubt to the same individual because the pieces have been found a few centimetres apart and because of the similar structure in the bone of the skull roof and the pieces of the snout (see below).

Etymology: Species dedicated to Dr Michel Martin for his contribution to the study of lungfishes.

Type locality: Phu Nam Jun, Kalasin Province, north-east Thailand, upper part of the Phu Kradung Formation, Late Jurassic or basal Cretaceous.

Diagnosis: *Ferganoceratodus* with a vertical non-overlapping suture between the posterior bone of the median series and the paired anterior bones of the mediolateral series; posterior bone overlapping the anterior bone in the mediolateral series over a proportionally large area; posterior bone of the mediolateral series with no median process; lower toothplates with a first notch not significantly deeper than the following ones, with an inner angle of more than 90°; a straight and broad anterior margin of the skull roof, axes of the orbits orientated laterally, anteriormost bone of the mediolateral series proportionally large; tip of the snout with mineralized tissue.

COMPARATIVE DESCRIPTION

REMARK ON NOMENCLATURE

The homology between the ossifications of the skull roof and lower jaw of lungfishes with the ossifications of the skull roof and lower jaw in other osteichthyans on the one hand, and within the lungfish taxa on the other hand, is far from being accepted. Table 1 gives some of the different names applied by authors to supposedly homologous bones of the skull roof in derived lungfishes. These assumptions of homologies are primary homologies *sensu* Patterson (1982). They imply fusions between two or more ossifications, or topo-

graphic invasion of one ossification over the area of other ossifications. None of these assumptions is based on ontogenetic series observed in fossil or Recent taxa.

Bemis (1984) suggested that paedomorphosis played an important role in the evolution of several lungfish features, including a reduction in the ossification of endochondral bones of the skull. Arratia, Schultze & Casciotta (2001: 164) also suggested that the reduction in exoskeletal bones of the skull of lungfish is a feature affected by paedomorphosis. The study of ontogenetic series of fossil taxa would be the way to detect paedomorphic processes and perhaps aid in recognizing primary homologies among the various patterns of lungfish skull roofs. Such an example is now known: *Dipterus valenciennesi* Sedgwick & Murchison, 1835 is a well-known Middle Devonian lungfish. It shows a complex pattern of skull-roofing ossifications, with a median series of alternately unpaired and paired bones (from A to F bones according to White, 1965), plus paired mediolateral and lateral series composed of a variable number of bones. But small skull-roofs of adult individuals of *D. valenciennesi* often show fewer ossifications in the marginal series of the skull roof than larger individuals (White, 1965: figs 25–27), indicating that the number of ossifications increased during ontogeny. The Devonian '*Palaeospondylus gunni*' is now regarded as the larval stage of *Dipterus valenciennesi* (Forey & Gardiner, 1981; Thomson, Sutton & Thomas, 2003). It has a dermal roof bone pattern with apparently a single median dermal element in the otico-occipital position and two pairs of dermal elements in the C and D positions (Thomson *et al.*, 2003), showing that the ossification pattern in the larva is still simpler than in the young adult. This ontogenetic series of *D. valenciennesi* – larva, young adults, large adults – shows that a simpler pattern with fewer bones on the skull roof was present in the early growth stages of this species and indicates that post-Devonian lungfishes may have acquired their simpler skull-roof pattern through a paedomorphosis process. This example, however, is unique and not sufficiently documented to allow us to

Table 1. Synonyms of the ossifications present in *Ferganoceratodus martini* sp. nov.

Martin (1981a)	Schultze (1981)	Bemis (1986)	Thomson (1990)	Kemp (1998)	Present study
rostral	EC/EQ-bones	dermal ethmoid	F-bone	EC/EQ-bones	anterior medial bone
central frontoparietal	AB-bone	frontoparietal	B-bone	ABC-bone	posterior medial bone
lateral frontal	KLMN+3-bone	supraorbital	L-bone	KLMN	anterior mediolateral bone
lateral parietal	IJ-bone	squamosal	I-bone	IJ-bone	posterior mediolateral bone
preangular	angular	angular		angular	labial bone
splenic	prearticular	prearticular		prearticular	lingual bone
'os median'		postsplenic		splenicpostsplenic	symphysal bone

recognize homologies with bones of the ontogenetically older or phylogenetically more derived lungfishes. But it shows a way for further studies.

In the present paper, the new material comprises a skull roof with a very simple bone pattern. During the description, we rapidly encountered difficulties in naming the bones of the skull roof, i.e. in the recognition of homologous ossifications with other lungfishes. Choosing one nomenclature over another may have a strong impact on the way we define the characters for cladistic analysis and may deeply affect the phylogenetic results. Accordingly, we prefer to use for the main central bones of the skull roof a nomenclature referring to topographic locations only (the bones are named according to their location, respectively, to each other), in order to avoid arbitrary primary homologies. This topographic approach is also used in the way we coded the characters in the phylogenetic analysis (see 'Characters'). The choice we made implies that only a few characters can be defined and used in the construction of the cladogram. But these characters are expected to be less theory-laden of any unjustified primary homologies. The lower jaw has a small set of ossifications too and here also we choose to use a topographical nomenclature (labial, lingual and symphyseal bones).

Nessov & Kaznyshkin (1985) also found it difficult to recognize homologies when they described *Ferganoceratodus jurassicus*, and they suggested that both actual fusions between bones and decrease in the number of bones occurred during lungfish evolution, rendering difficult or even impossible the recognition of homologies. Kemp (1996: 415, 1998: 44) avoided using presumed fusion patterns of the medial series for taxonomic purposes because of the lack of agreement regarding the identity of the bones that have fused.

The method we propose here is an attempt to define a procedure for comparing simple skull-roof patterns observed in post-Palaeozoic lungfishes in order to avoid using arbitrary primary homologies. We regard it as a stopgap, pending the definitions of better supported homologies. We are aware that the method may lead us to overlook some well-established homologies recognized in the skull roofs of Palaeozoic lungfishes, some of them being used in our phylogenetic analysis, but we prefer to miss data for those taxa rather than to use unsupported data for Mesozoic taxa.

SKULL ROOF (FIG. 3)

The skull roof, as preserved, is almost square in shape (slightly longer than wide). The complete skull roof was probably slightly wider than long and comprised two median unpaired bones, two mediolateral paired bones and probably two lateral paired bones. As indi-

cated by the articulated palatine tooth plates and the associated jaws, the specimen was only weakly distorted during fossilization and the skull roof has kept its original transverse curvature: the anterior part of the skull roof is slightly arched and the posterior part is almost perfectly flat (Fig. 3C).

Both external and internal faces of the skull roof bones bear shallow grooves radiating from the ossification centres. The grooves are slightly deeper on the internal than on the external side. Such a difference in grooves between both faces of bones is also present in *Ferganoceratodus jurassicus* (Nessov & Kaznyshkin, 1985; compare Fig. 2A and 2A') and, in a more pronounced way, in *Ptychoceratodus serratus* Agassiz, 1838 (Schultze, 1981). This character is probably size-dependent.

The anterior medial bone (Fig. 3, a.m.b, see Table 1 for other names) is slightly wider anteriorly than posteriorly. The anterior margin of the bone is damaged, but it seems to have been straight with only a very small medial process extending slightly forwards beyond the level of the anterior margin of the paired mediolateral ossifications. It is, however, unlikely that the snout extended as a long bony rostrum bearing the anterior part of the supraorbital sensory canals as in *Beltanodus*, *Microceratodus* and *Neoceratodus*, or even a short anamestic rostrum as present in other Mesozoic lungfishes (also in *Ptychoceratodus serratus* Agassiz, 1838; Schultze, 1981: fig. 5 *contra* Kemp, 1998: fig. 14. For comparisons among the taxa, see Fig. 4). However, the presence of isolated pieces of a 'hard snout' (see below) indicate that the snout region was probably more elongated on the living fish than shown by the anterior silhouette of the preserved ossified skull roof. Detached snouts of Devonian lungfishes are sometimes found (Bemis & Northcutt, 1992), indicating that a weaker zone was present in these fishes between the 'hard snout' and the part of the skull roof located posteriorly to the upper tooth plate attachments. We suggest that a gap of ossification was present in *F. martini* between the skull roof proper and the 'hard snout'. The latter was probably restricted to a narrow margin covering the upper lip only. The posterior margin of the anterior medial bone is gently curved and fits in a concavity in the anterior border of the posterior medial bone. In gross morphology, the anterior medial bone is more reminiscent of *Arganodus atlantis* Martin, 1979 and *Ferganoceratodus jurassicus* than of any other taxa, as far as we can judge from the available material.

The posterior bone of the medial series (Fig. 3, p.m.b) is narrower anteriorly than posteriorly, with the maximum width situated almost at the mid-length of the bone (the bone is scarcely more than 1.5 times longer than wide). Anterior to this level the margin of the bone is straight and forms the suture with the

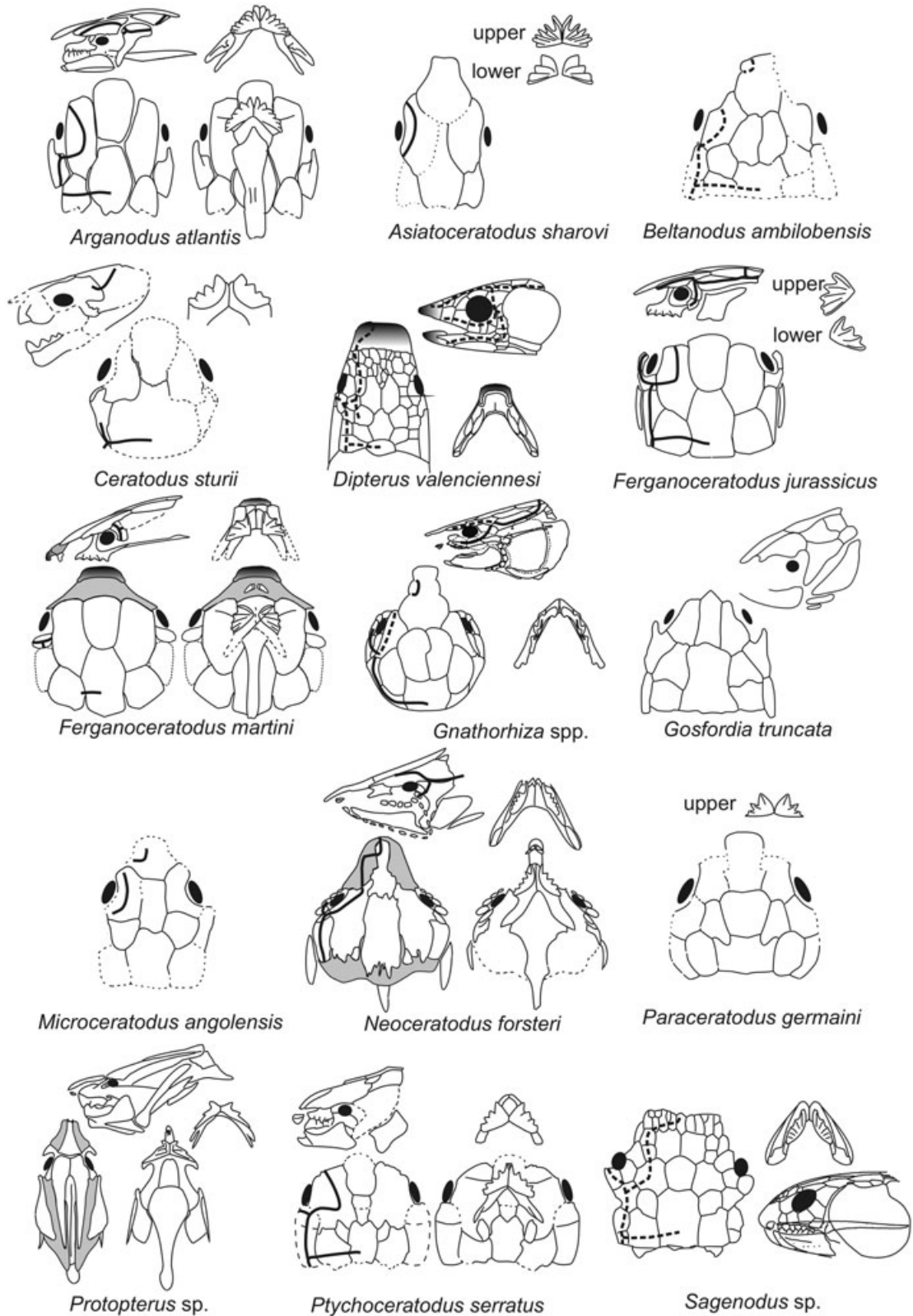


Figure 4. Semi-schematic drawings of the skulls of various taxa mentioned in the text. The sensory lines and canals are shown on the left part of the skull roofs with bold lines (canals above the bones) and dotted lines (canals bone-enclosed). Grey tone indicates cartilage (in dorsal views only) and shading tone indicates mineralization of the 'hard snout'.

anterior mediolateral bone (Fig. 3, a.ml.b). Posterior to the mid-point, the margin is concave and forms the suture with the posterior mediolateral bone. The posterior margin of the bone is slightly convex. In ventral view, the posterior medial bone does not show the deep median groove for the anchorage of the endocranium as described in most lungfishes except *Neoceratodus* in which the ossification is separated from the roof of the chondrocranium by a space for the adductor mandibulae (de Beer, 1937: 173). The posterior bone of the medial series is one of the more constant within post-Devonian lungfishes. It is generally regarded as homologous in the post-Palaeozoic species (AB-bone), except, however, in *Neoceratodus forsteri* (Kreff, 1870) (ABC-bone) and *Ceratodus sturii* Teller, 1891 (ABIJ-bone) (Schultze, 1981; Fig. 4).

The anteriormost bone of the mediolateral series (Fig. 3, a.ml.b) is large, scarcely less than 1.5 times longer than wide in dorsal view. The anterior margin of the ossification is regularly curved and its anterolateral edge, forming the anterior margin of the orbit, marks the widest level of the preserved skull roof. The dorsal margin of the orbit is visible as a shallow concavity on the lateral border of the bone (Fig. 3, o). Thus, the orbits were orientated fully laterally. Posteriorly to the orbit, the left anteriormost bone of the mediolateral series is marked by another concavity, that probably received the dermosphenotic (Fig. 3, Dsph). In dorsal view, the posterior margin is concave for the contact with posterior bone of the mediolateral series (Fig. 3, p.ml.b). In ventral view, however, the anterior mediolateral ossification extends as a lamina of bone underneath the anterior quarter of the posterior mediolateral ossification (compare Fig. 3A and 3B). The structure is similar in *Arganodus atlantis* (Martin, 1981a: fig. 3) and in *Ptychoceratodus serratus* (Schultze, 1981: fig. 4), but in the latter the superimposition occurs only on the posterolateral edge of the anterior bone. In *Ferganoceratodus jurassicus*, the posterior bone overlaps the anterior bone along a narrow margin only (Fig. 2, c.a.p.ml.b). The ventral side of the anterior bone of the mediolateral series shows the structures associated with articulation with the pterygopalatine and olfactory capsule. Both descending processes (Fig. 3C, d.p) are preserved and articulate with ascending processes of the pterygopalatine (Fig. 3C, a.p). According to the angle formed between the axes of the paired shafts of ascending processes of the tooth-plate-bearing bones and of the paired descending processes preserved on the specimen, both pterygoids (Fig. 3B, Pt) have probably shifted slightly anteriorly during fossilization. However, the displacement from the position in the living specimen was probably not important, and may be in accordance with the range of mobility of the upper jaws during life. The resulting profile in lateral view is an open

angle formed by the skull roof and the upper tooth plate (Fig. 3D), more reminiscent of some Palaeozoic forms (*Dipterus*) and the deep-bodied Mesozoic *Gosfordia* with an inclined lateral profile, than that of most post-Palaeozoic taxa with a flat profile. The descending process for the articulation with the pterygopalatine develops as a strong, flat shaft orientated anteroventromedially from the skull roof. The axis of the shaft forms an angle of about 60° with the profile of the skull roof in lateral view. The ventral extremity of the shaft bears two small processes. Laterally is the small, blunt orbital process (Fig. 3C, p.o) and anteriorly is another process (Fig. 3C, p.a) that is developed as a slightly medially orientated wing forming a groove in which rests the anterior border of the ascending process of the pterygopalatine. The descending process of the skull roof obscures the ascending process of the pterygopalatine. On the ventral surface of the skull roof a ridge (Fig. 3, r) extends anterolaterally from the base of the descending process delimitating an anterior groove, into which was inserted the cartilage of the olfactory capsule (Kemp, 1998). At the base of the descending process a canal crosses the ridge (Fig. 3C, c.pV), probably for the profundus branch of the trigeminal (Berman, 1976a). The general outline of the anterior mediolateral bone is reminiscent of that of *Arganodus atlantis*, *Ferganoceratodus jurassicus* and *Ptychoceratodus serratus*. As in the last of these, the ossification shows its widest width at the anterior level of the orbit.

Because of the presence of a ventral lamina on the posterior margin of the anterior bone from the mediolateral series, the surface of the posterior bone of the mediolateral series (Fig. 3, p.ml.b) appears smaller in ventral view than in dorsal view. The general shape of the bone is oval, with the long axis anterolaterally orientated. The bone has gently curved medial and anterior margins contacting two adjacent ossifications, and a regularly curved indistinct posterolateral margin. The latter margin shows no hint of suture indicating that the posterior bone of the lateral series (Fig. 3, p.l.b), preserved as a small fragment on the specimen, did not extend posteriorly to that level.

On the right side of the skull roof is attached a fragment of bone regarded here as a piece of a posterior ossification from the lateral series (Fig. 3, p.l.b). The bone develops along the limit between both ossifications of the mediolateral series, and extends slightly underneath the ventral rim of the posterior bone of the mediolateral series. In *Ferganoceratodus jurassicus* Nessov & Kaznyshkin (1985) described on the lateral series a large single posterior bone in addition to the dermosphenotic (Fig. 2A, A', c). We assume that the situation was similar in *F. martini*.

On the ventral side of the skull roof two small bones lay free *in situ* in the specimen at the level of the ante-

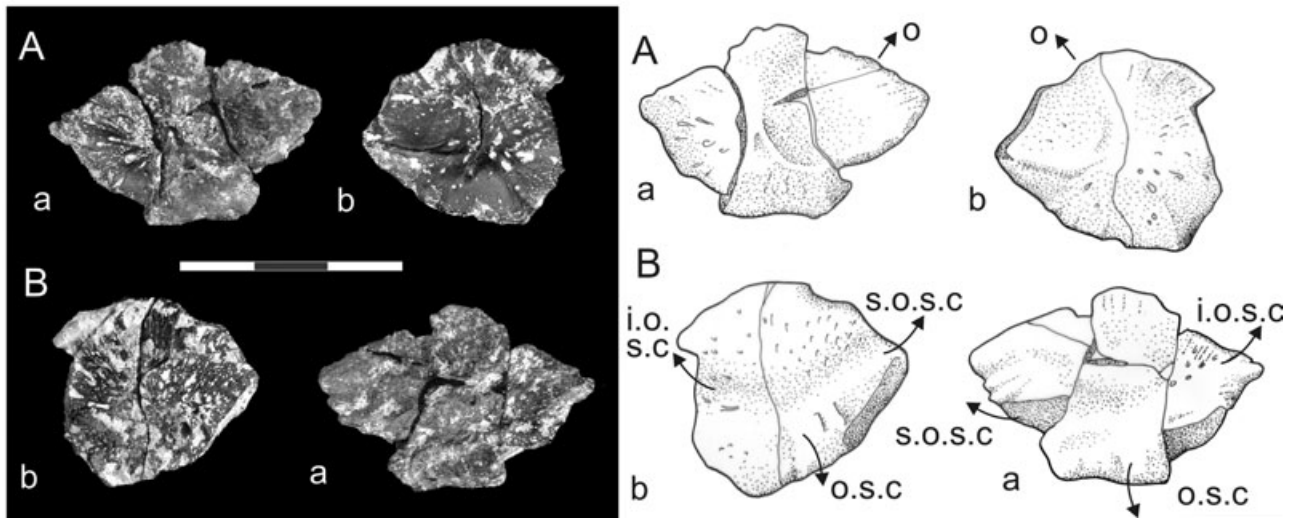


Figure 5. *Ferganoceratodus martini* sp. nov. Holotype TF 7712. Photographs and interpretative drawings of the right (a) and left (b) dermosphenotic in ventral (A) and dorsal (B) views. Scale bar: 15 mm.

rolateral edges of the ridges extending anterolaterally from the descending processes. The two bones were removed during the mechanical preparation of the specimen. They are regarded here as the paired dermosphenotics (Fig. 5), but their identification and interpretation should be considered with caution. The original outline of the ?dermosphenotic is lozenge shaped, with the longer axis of the ossification being perpendicular to the axis of the body. Along the long axis of the ?dermosphenotic is a faint curved groove that probably marked the connection between the infraorbital and supraorbital canals (Fig. 5B, i.o.s.c. and s.o.s.c). Posterior to the groove and in the middle of the width of the bone is a faint depression, which marks the connection with the otic sensory canal (Fig. 5B, o.s.c). The ventral side of the bone shows a thickening on the posterior margin and a thin anterior area, which formed the rim of the orbit (Fig. 5A, o).

'HARD SNOOT'

Among several detached fragments of the skull found loose in the matrix surrounding the specimen, two of them belong to a 'hard snout' and are worth describing here. One is a polygonal plate, about 1 cm² in surface area (Fig. 6). One side of the plate is smooth and presumably corresponds to the internal face, whilst the external side is partly covered with rounded openings. One of the lateral margins of the fragment is a natural border of the ossification. The edge of this margin is swollen and forms a rounded ridge (Fig. 6A, r) that extends as a smooth surface in the buccal cavity. This ridge is reminiscent of the contours of the ossified lip observed in some Devonian taxa (Campbell & Barwick, 1986), but we are unable to decide if it comes

from the upper or from the lower lips. The anterior margin of the skull roof, as well as the anterior extremity of the mandible, shows no surface of contact for the nasal capsule and ossified lips, and it is likely that the 'hard snout' and/or lower lip were separated from their posterior respective ossifications by cartilage. The contact area between the 'hard snout' and the skull roof was a weak zone in some Devonian species and it is quite common to find isolated detached snouts (Bemis & Northcutt, 1992: 122). The second fragment is a piece of bony plate with no natural margin. It also shows a smooth internal face and an external face with openings, which are denser than on the first fragment. Both fragments were probably pieces of a single element, but no matching contact between them has been found.

The microstructure of the two pieces is similar. In section, the internal smooth face is composed of lamellar bone (Fig. 6C, D, lb). This layer is overlain by spongy bone excavated with large cavities near the lamellar bone and smaller, but more regularly spaced cavities towards the external face. The smaller cavities are arranged on several levels, parallel to the external face, and they communicate between themselves through vertical and oblique canals (Fig. 6D, c). Some of the cavities near the surface send off canals that open on the external surface. In external view (Fig. 6A, E), the density of the openings is high in some places, low in others and pores are absent near the natural border of the ossification (Fig. 6A). The tissue forming the uppermost 70 µm near the external surface is much denser than the deeper spongy bone and is tentatively regarded here as dentine (Fig. 6D, d), although this interpretation has not been confirmed by histological examination of thin sections.

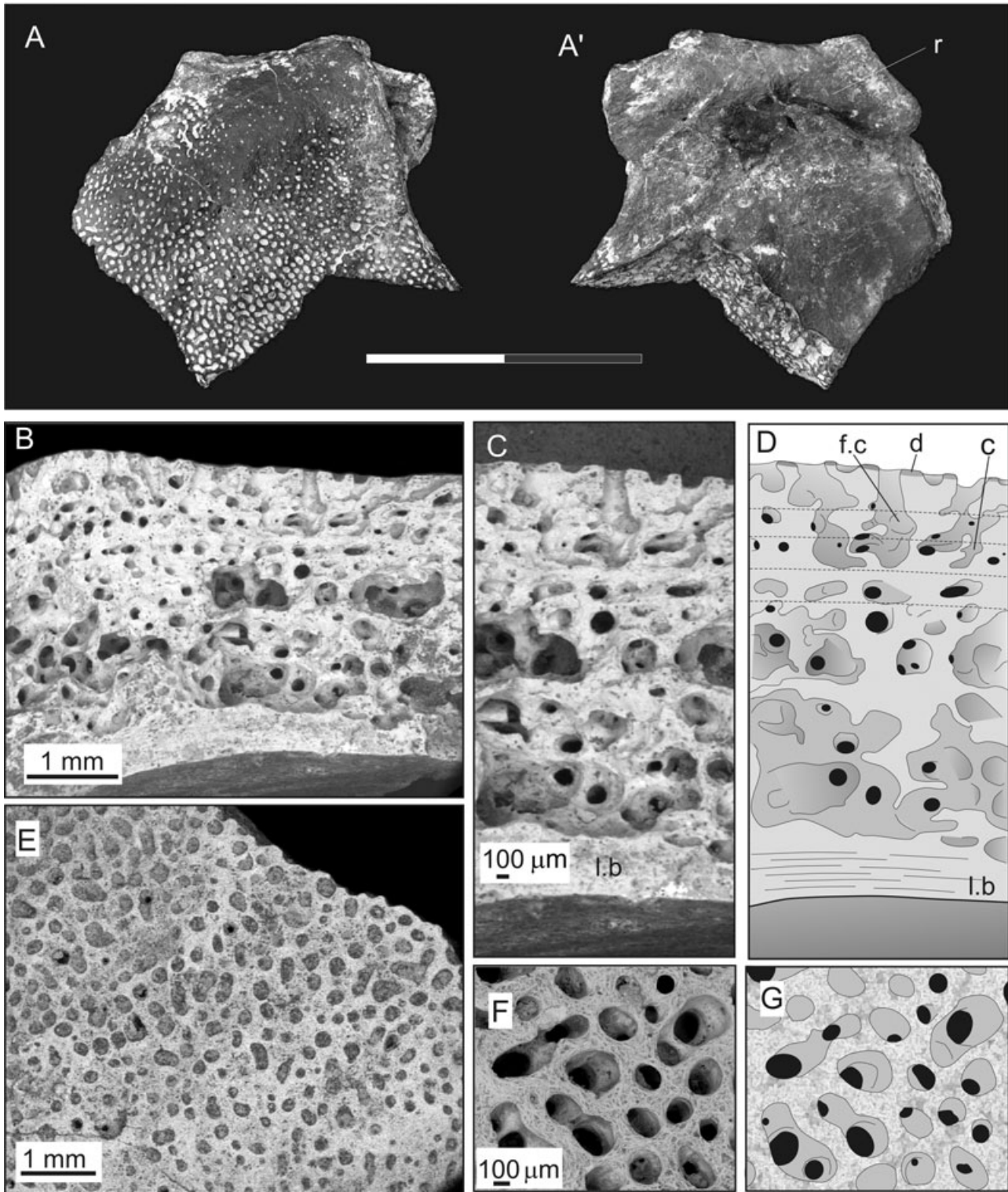


Figure 6. *Ferganoceratodus martini* sp. nov. Holotype TF 7712. General external (A) and internal (A') views (scale bar: 10 mm) and details (B–G) of a piece of 'hard snout'. B, complete section showing the basal lamellar bone and the network of cavities arranged in successive layers in the upper part; C, detail of the section and D, interpretative drawing, with the levels of cavities indicated with dotted lines. E, external surface showing the variable density of openings; F, detail of the surface and G, interpretative drawing.

There is no trace of enameloid on the external surface. Some of the cavities sending canals to the surface are basally enlarged and reminiscent of the flask cavities (Fig. 6D, fc) from the cosmine pore canal system, but they are much larger in size. The interpretation of this structure is discussed below (see 'Characters').

PALATINE REGION (FIGS 3B–D, 7, 9)

Both pterygoids are poorly preserved. They each show a piece of their posterior processes curving posterodorsally. They were probably fused together in front of the parasphenoid, but the symphyseal portion is not preserved. The upper tooth plates bear five ridges. The anteriormost three ridges are sharp and the posterior two are blunt. The surface of the plates shows a fine pattern of pits corresponding to the underlying individual pulp canals and the labial cutting edge of each ridge bears low denticles. The tooth plates are relatively deep and growth bands of enamel are visible on their lateral faces. The first ridge is shorter than the lingual length, and the first notch is as broad as the second one. The inner angle, formed by the symphyseal and lingual sides, equals nearly 90°. Although both upper tooth plates shifted a little during the taphonomic process, it is probable that there were not in contact during life.

Both vomerine teeth (Fig. 8) have been found loose during the preparation of the specimen. They are roughly triangular in shape. One of the cutting edges is steep with a slightly sinusoidal margin and the other is gently curved and bears three faint cusps. Growth bands of enamel are visible. In basal view, the

pulp cavity is pierced by the pulp canals (Fig. 8C, p.c). We suppose that these teeth would have protruded from the palate anterior to the pterygoid tooth plates, as they do in Recent lungfishes and as they probably did in all lungfishes since the end of the Palaeozoic, i.e. in *Sagenodus* (Schultze & Chorn, 1997). The vomerine teeth of *F. martini* are proportionally deeper than the vomerine teeth from the Upper Jurassic of India referred to *Ceratodus* sp. by Jain (1968) and the apex is less curved than in the teeth referred to *Ptychoceratodus serratus* by Schultze (1981). Peyer (1959) described vomerine teeth from the Upper Triassic of Switzerland with a cutting edge bearing several pointed cusps. He referred them to juvenile specimens of *Ceratodus parvus* Agassiz, 1838.

The parasphenoid (Fig. 9) is preserved in anatomical connection with the pterygoids, but the ossification was parted from the skull in order to prepare mechanically the bone, which was covered with hard concretions. The parasphenoid is made up of a poorly preserved diamond-shaped anterior extremity and a long posterior stem. A shallow groove runs on the ventral face along the posterior quarter of the stem (Fig. 9, g). At this level, the lateral rims of the bone develop faint wings extending posteriorly as two tapered processes (only the right one is preserved, Fig. 9, p). Anterior to the lateral wings, the lateral rims are slightly excavated (Fig. 9, a,f). In a dry skeleton of *Protopterus*, such excavations of the lateral margins of the parasphenoid are also present at this same level and mark the ventral border of a paired articular facet in the lateral face of the cartilaginous braincase, which accommodates a cranial rib. Because

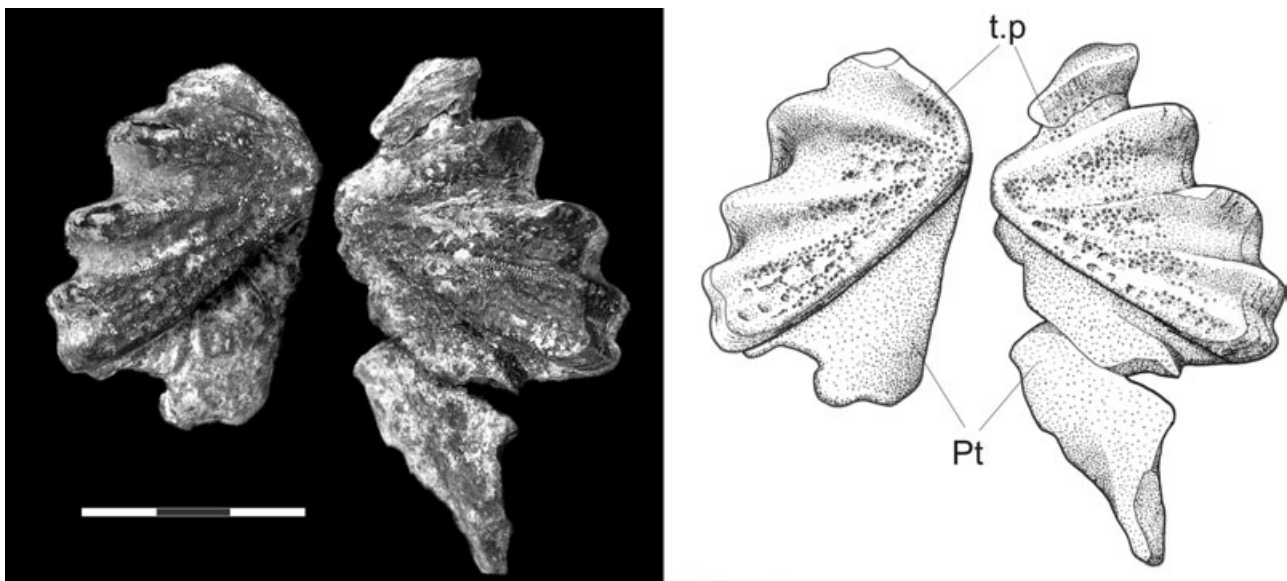


Figure 7. *Ferganoceratodus martini* sp. nov. Holotype TF 7712. Photographs and interpretative drawings of the pterygoids and upper tooth plates in occlusal view. Scale bars: 15 mm.

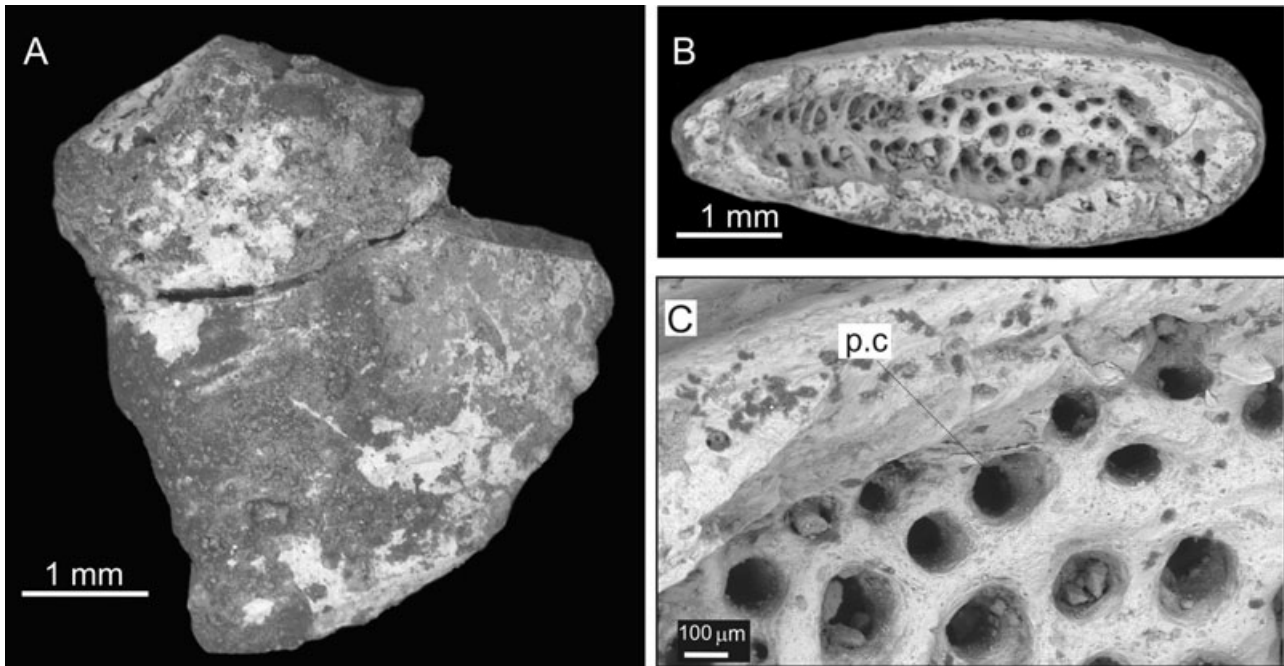


Figure 8. *Ferganoceratodus martini* sp. nov. Holotype TF 7712. Vomerine tooth. A, anterior or posterior view; B and C, basal views.

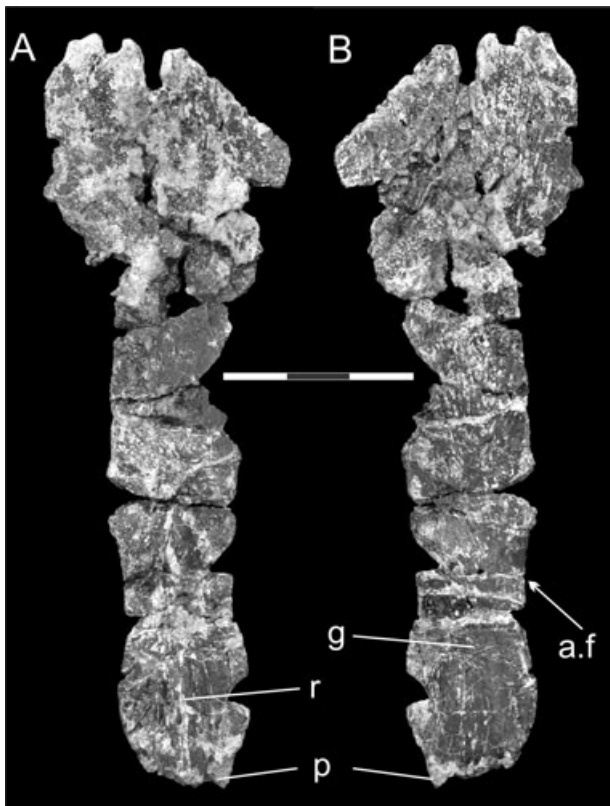


Figure 9. *Ferganoceratodus martini* sp. nov. Holotype TF 7712. Photographs of the parasphenoid in dorsal (A) and ventral (B) views. Scale bars: 15 mm.

of the similarity in parasphenoid structure, we infer that such a pair of cranial ribs was also present in *F. martini*. The dorsal surface of the parasphenoid was applied to the cartilaginous neurocranium. It has a cancellous texture and it is marked with a prominent median ridge in its posterior quarter (Fig. 9, r).

MANDIBLE (FIG. 10)

The mandible is complete, except for the anterior extremity of the symphysis and both posterior articular extremities. Both arms are slightly displaced. The structure of the mandible is conservative within post-Devonian lungfishes, as exemplified by *Ferganoceratodus martini*. There are three pairs of ossifications that surround a cavity for the Meckel's cartilage: a labial pair, a lingual pair and a ventral symphysal pair. The labial bone (Fig. 10, la.b) (see Table 1 for other names) is a plate-like dermal ossification, which twists through nearly 90° from one end to the other. The posterior part of the bone makes up the lateral wall of the mandible. The base of a coronoid process is present at the level of the posterior edges of the tooth plates. Both processes, however, are broken and therefore their dorsal extension is unknown. The hemi-mandible of lungfishes generally bears a coronoid process. It may be very shallow and formed with both the labial and the lingual ossifications in *Neoceratodus* (Bemis, 1986), or deep and formed with the lingual ossification only in *Protopterus* (Bemis, 1986). The anterior part of the

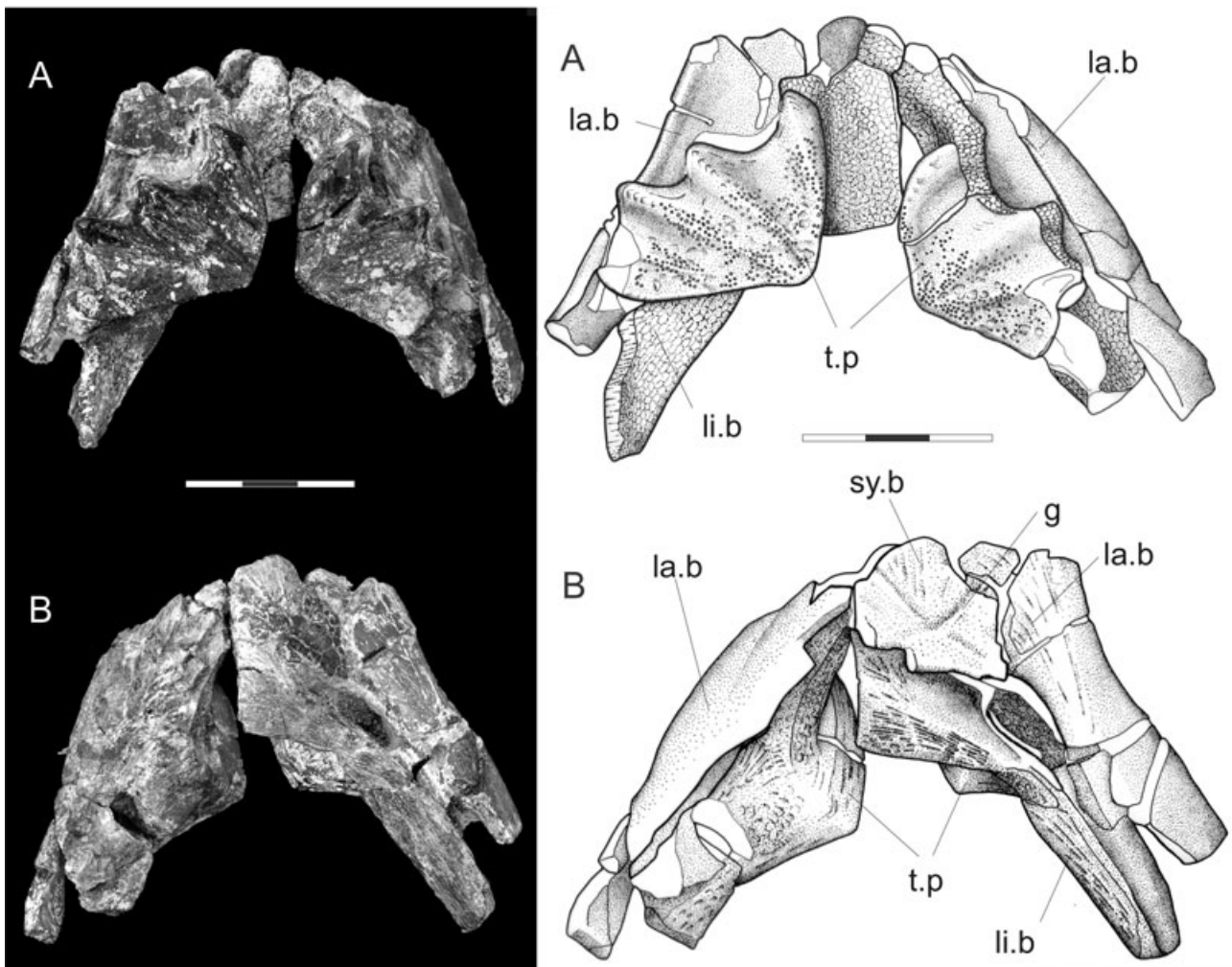


Figure 10. Photographs and drawings of the mandible of *Ferganoceratodus martini* sp. nov. (holotype, TF 7712) in occlusal (A) and ventral (B) views. Scale bars: 15 mm. Note that the drawings were made with both hemi-mandibles in a slightly shifted position, respectively, to the photographs.

labial ossification extends as a horizontal plate situated beneath the anterior extremity of the tooth plate. Although broken, it seems that the anterior tip of the ossification extended more anteriorly than the tooth plate itself. The lingual bone (Fig. 10, li.b) is a cancellous ossification and supports the lower tooth plate. The bone develops ventrolingually as a vertically curved plate that enclosed Meckel's cartilage. Posterodorsally, the bone formed the base of the coronoid process, but its participation in the process cannot be reconstructed. Anteriorly to the coronoid process, the dorsal part of the ossification twists to form an almost horizontal surface, on which is fused the tooth plate. Anteriorly to the tooth plate, the bone extends ventrally into a thin lamina, which meets its counterpart in a horizontal plane at the symphyseal level. The left paired symphyseal bone is preserved ventrally as a thin bony plate roughly triangular in shape (Fig. 10,

sy.b). It is very similar to the homologous bone in *Neoceratodus forsteri* (Jarvik, 1967: pl. 1).

The lower tooth plates are less complete than the upper ones, especially in their posterior part. They bear four ridges, and a fifth faint one was probably originally present. As for the upper tooth plates, the first three ridges are very sharp and the last one (or two) very shallow. Similarly, the surface of the plates shows a punctuated pattern of pits and the cutting labial margins of ridges bear denticles. The first notch is slightly broader and deeper than the second one, but not as much as in *Ferganoceratodus jurassicus*.

TOOTH PLATE MICROSTRUCTURE (FIG. 11)

Because the new species described herein is known by a single specimen, we did not prepare thin sections of the tooth plates for histological studies. However, we

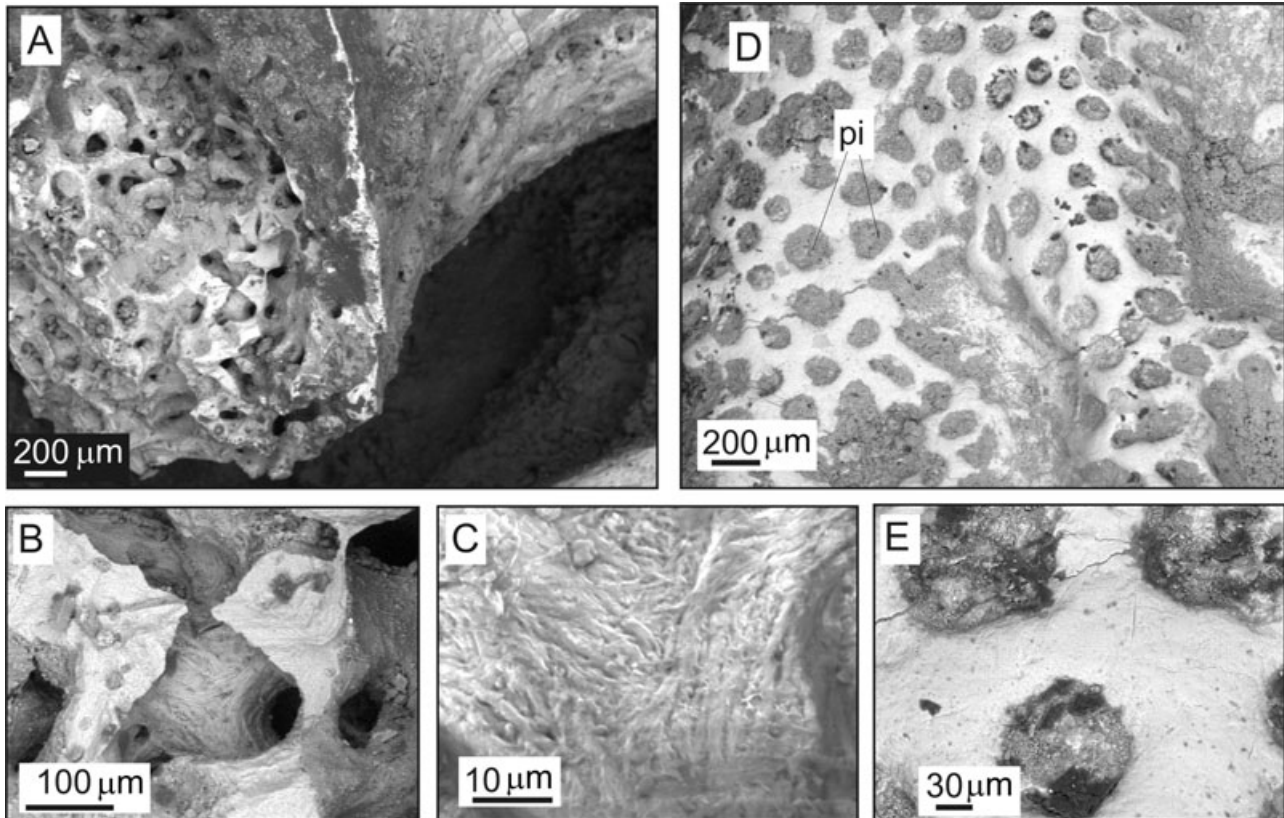


Figure 11. Tooth plate microstructure of *Ferganoceratodus martini* sp. nov. (holotype, TF 7712). A, limit between the tooth plate and the supporting bone, with the base of the pulp cavity (on the left). B, detail of the spongy bone forming the base of the pulp cavity. C, fibrous structure of the spongy bone. D, occlusal surface showing ridges and pits. E, detail of pits.

made SEM observations of the surface of the plate and of the base of the pulp cavity through a natural break in the lower right tooth plate (Fig. 11A).

The base of the pulp cavity is made up of spongy bone (Fig. 11B), as figured by for *Neoceratodus* in Günther (1871: pl. 33, fig. 2). The structure of the bone is also very similar to the middle part of the spongy bone of the hard snout (compare Figs 6B and 11B). At higher magnification, the mineralized tissue forming the spongy bone of the base of the pulp cavity shows a fibrous aspect (Fig. 11C).

The occlusal surface of all plates bears rounded crests and furrows produced by wear (Figs 7, 10). The whole surface is regularly covered with pits (Fig. 11D, E, pi) corresponding to pulp canals (Bemis & Northcutt, 1992). There is no trace of hypermineralized dentine free of denteons ('petrodentine' *sensu* Kemp, 2001).

SENSORY CANALS

In contrast to some post-Devonian lungfishes, the paths of the sensory canals are barely visible on the skull roof of TF 7712. The extrascapular commissure

is visible as a shallow groove crossing the posterior median bone, and extending in a very faint depression on the left posterior mediolateral ossification (Fig. 3A, g).

On the lower jaw, only the anterior tip of the mandibular sensory line canal and the mandibular commissure are visible as grooves on the left symphyseal bone (Fig. 10B, g), showing a triradiate pattern reminiscent of *Neoceratodus forsteri* (Jarvik, 1967).

SCALES (FIG. 12)

Posterior to the skull roof numerous fragments of scales have been found loose in the sediment. SEM observations of the pieces allows us to describe the surface and the section of the scales. Some fragments show on their external surface a reticulated pattern of ridges (Fig. 12B, r) separating deep grooves. The ridges radiate from centres and run almost parallel to each other, with some connecting bridges. The whole set of ridges are divided into several areas, separated from each other by a net of wider grooves (Fig. 12D, g). Other fragments show a very different ornamentation made up of a dense concentration of pointed and

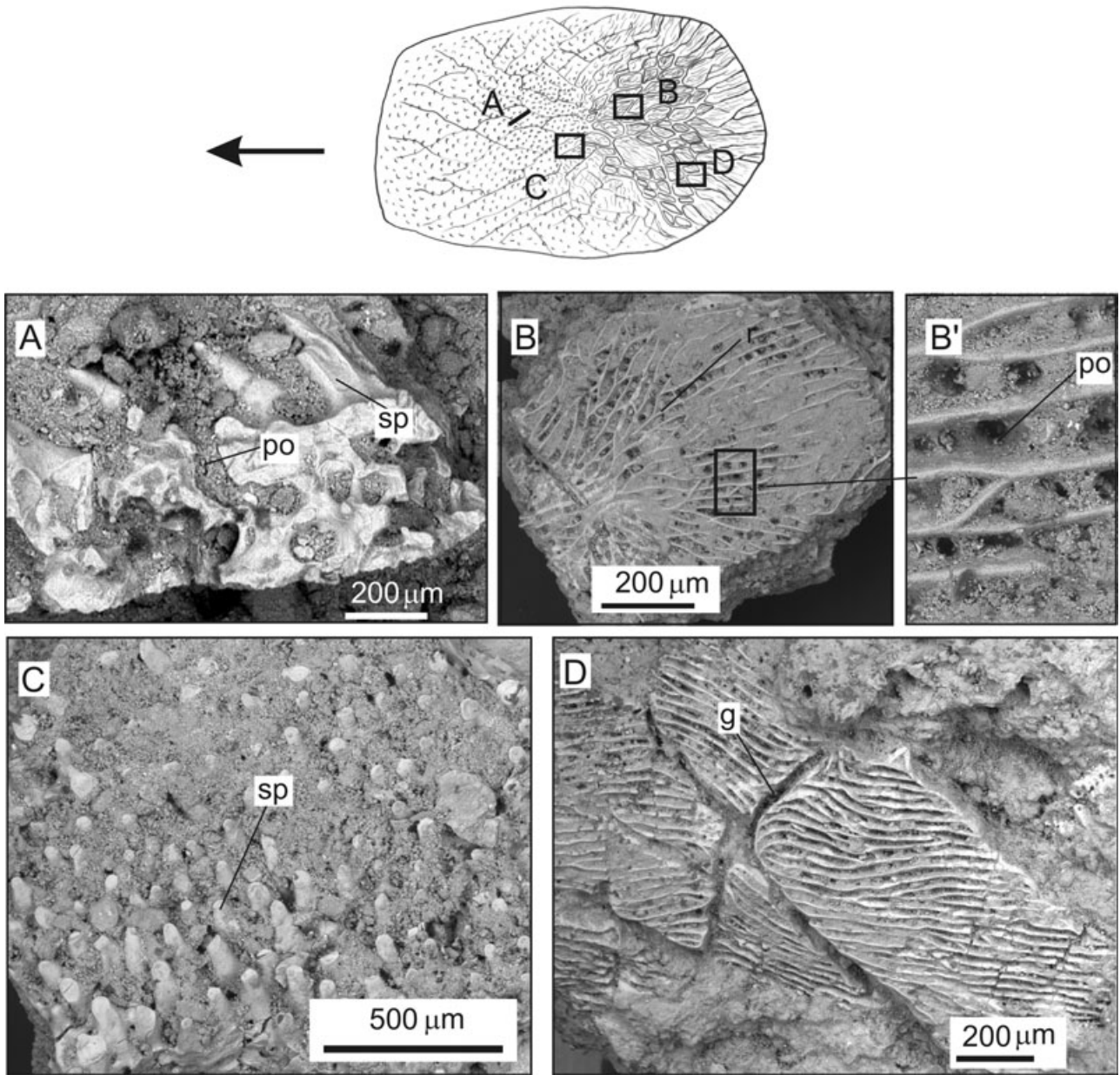


Figure 12. Reconstruction of a scale of *Ferganoceratodus martini* sp. nov. (top) with locations of the micrographs of details from the holotype (TF 7712) (A–D). Anterior region in section (A) and dorsal view (C), and posterior region (B and D). Arrow indicates anterior end.

slightly curved spines (Fig. 12A, C, sp). In section, the scale is formed by a complex network of interconnected cavities and canals, reminiscent of the spongy bone of the 'hard snout' (compare Figs 6B and 12A). Some of the canals open to the surface through pores (visible in section and in external view in the bottom of the grooves in Fig. 12A, po and Fig. 12B, po).

The morphology and the structure of the scale of *F. martini* are very similar to the structure described by Günther (1871) and Brien (1962) in *Neoceratodus*

forsteri. The area of the scale bearing the spines corresponds to the region of the scale covered by the preceding scale, while the area bearing the network of ridges corresponds to the posterior exposed portion. The preserved elements in TF 7712 correspond to the external-most denser and more mineralized layer of the scale of *Neoceratodus*. The deeper thick fibrous and lamellar layer of collagen, the isopedine layer, is missing in the fossil, probably because it was dissolved during the taphonomic process. The calcified super-

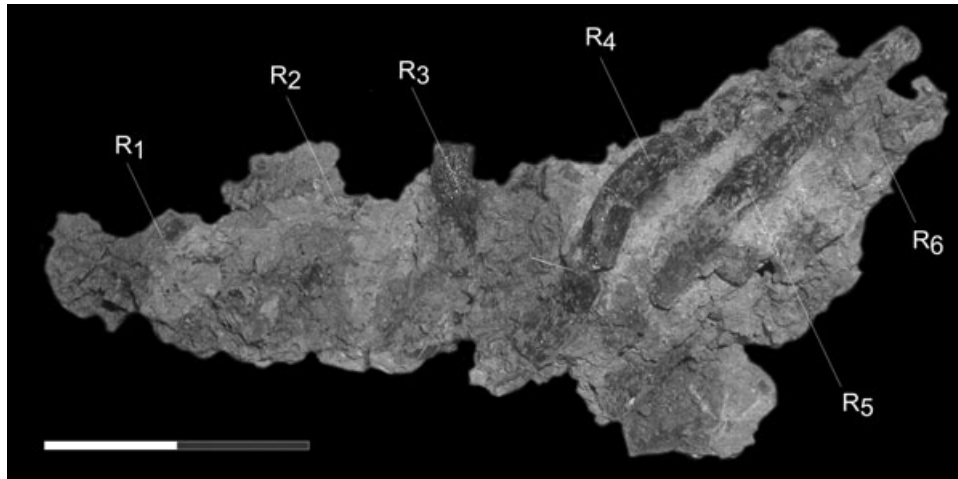


Figure 13. Anteriormost ribs of *Ferganoceratodus martini* sp. nov. (holotype, TF 7712) in ?dorsal view. Anterior extremity to the left. Scale bars: 20 mm.

ficial layer is described as a paving of thin plates resting on the isopedine in *Neoceratodus* (Brien, 1962: 95). These thin plates, separated from each other by the wide grooves, are present in TF 7712 as described above. The network of grooves is probably the reason for the very fragmentary state of preservation of the scales, which are not supported by the isopedine layer. Brien (1962) described several cross-sections of the superficial calcified layer, from the external margin of the scale toward its centre. Because the scale grows through apposition of new material at its lateral margin, the different sections described by Brien correspond to an ontogenetic series. The growth of the mineralized superficial layer proceeds from isolated trabeculae, which extend several lateral levels of mineralized connections, leading to a complex network of interconnected cavities. The latter pattern is reminiscent to the one described here in TF 7712.

VERTEBRAL ELEMENTS

Fragments of skeletal elements associated with the first vertebrae are preserved loose in the sediment behind the skull roof. Pieces of about six vertebral units are present, but the number is uncertain. The most obvious ossifications are sigmoid rods of bone lying parallel to each other (Fig. 13, R). They show no axis of symmetry and their proximal(?) portions are hollow and almost circular in section, while their distal(?) portions are filled and slightly flattened. Because of the sigmoid and asymmetrical shape, we regard these bones as ribs. Both extremities of all ribs are not preserved and we cannot observe if the proximal tips included remnants of the ventral arcuale as in Recent and some extinct forms (Arratia *et al.*, 2001: 162).

DISCUSSION

SYSTEMATIC AFFINITIES

Ferganoceratodus martini is included in the genus *Ferganoceratodus* because of the general pattern of the skull roof with two unpaired bones in the median series, two paired bones on the mediolateral series and probably two bones on the lateral series; the bones of the median series suture through a short contact; and the dental plates are of cutting type, with five diverging ridges on the upper plates and four diverging ridges on the lower plates, which are separated by deep notches.

Ferganoceratodus martini differs from *F. jurassicus* by the kind of suture between the posterior bone of the median series and the paired anterior bones of the mediolateral series, which is overlapping in the latter and vertical in the new species; the posterior bone of the mediolateral series has no median process; the lower tooth plates show a first notch not significantly deeper than the following ones and with an inner angle being higher than 90°.

Toothplates (Fig. 14)

Most of the Mesozoic lungfishes are known by isolated tooth plates only. This kind of material shows characters that allow systematic assignment. But we do not regard tooth plate characters as definite evidence in the search of phylogenetic relationships, except for a few character states defined below.

In Thailand several occurrences of isolated tooth plates have been recorded. An isolated plate has been described from the Late Triassic Huai Hin Lat Formation and was referred to '*Ceratodus*' cf. *szechuanensis* Young, 1942 by Martin & Ingavat (1982). Then, a

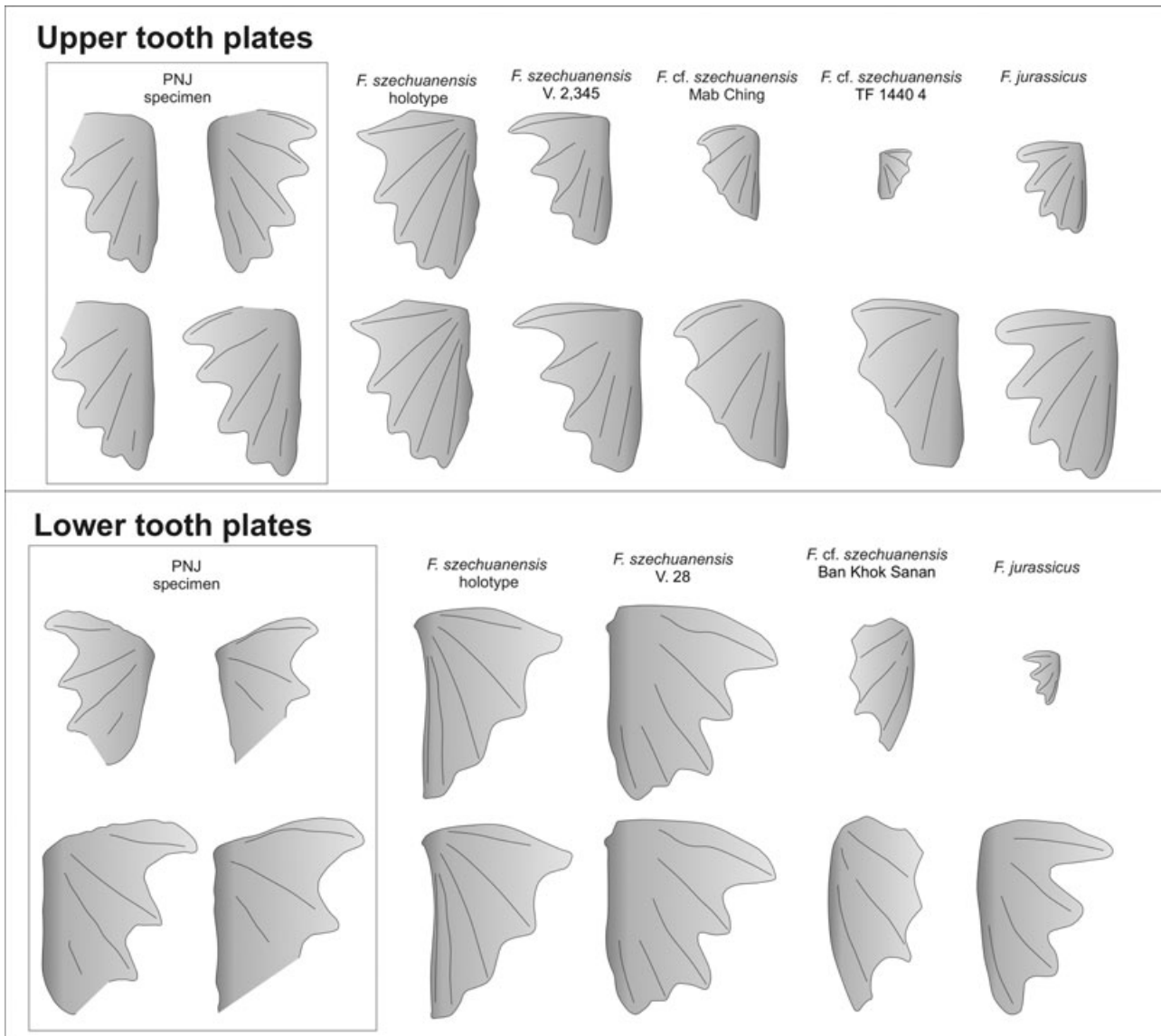


Figure 14. Upper and lower tooth plates of lungfishes from various Asian Mesozoic localities referred to *Ferganoceratodus*. The upper row shows the plates with their actual position (right or left side) and respective size; the lower row shows the plates adjusted to a similar size and position for comparison.

small complete tooth plate from Mab Ching in the southern peninsula of Thailand (Changwat Nakhon Si Thammarat Province), supposedly Middle Jurassic in age (Buffetaut, Tong & Suteethorn, 1994; Tong, Buffetaut & Suteethorn, 2002), and an incomplete tooth plate from Ban Khok Sanam, in the Phu Kradung Formation of north-eastern Thailand (Kalasin province), have been described by Martin *et al.* (1997). Both of them were referred to the same species as the Triassic one, and included in the genus *Ferganoceratodus* (Martin *et al.*, 1997). Based on the tooth plate morphology, *Ferganoceratodus jurassicus* differs from *F. szechuanensis* by the first notch of the tooth plate,

which is much deeper in the former species than in the latter. Except for this feature, the upper tooth plates are very similar in both species. A lower tooth plate from Sichuan referred to '*Ceratodus*' *szechuanensis* by Young (1942) has an inner angle less than 90° , while it is 115° in TF 7712 (Fig. 14). When adjusted to the same size (Fig. 14, lower row), all Asian tooth plates referred to the genus *Ferganoceratodus* are quite similar, if compared with tooth plates of other Mesozoic genera. Following the discovery of TF 7712, it is likely that the isolated Thai tooth plates from Mab Ching, Ban Khok Sanam and perhaps also from the Triassic Huai Hin Lat Formation, which were previously

referred to *F. szechuanensis*, actually belong to *F. martini* because their first notch is not as deep as in the holotype of *F. szechuanensis*. The discovery of associated bone remains and tooth plates at Phu Nam Jun confirms the previous assignment of isolated Thai tooth plates to the genus *Ferganoceratodus* and confirms that isolated tooth plates could be identified with accuracy.

Several other species based on isolated tooth plates have been referred to *Ferganoceratodus*. These are *F. concinnus* (Plieninger, 1844), from the Triassic of Germany, *F. sharategensis* (Krupina, 1994), from the Upper Jurassic of Mongolia (Martin *et al.*, 1997), and *F. madagascariensis* (Priem, 1924), from the Late Cretaceous of Malagasy (Martin, Barbieri & Cuny, 1999). However, we still regard with caution the assignment of these isolated tooth plates to *Ferganoceratodus*, especially because they come from much more distant locations (except the Mongolian one), and we await discoveries of more complete material before including these species into systematic, phylogenetic and palaeogeographical studies.

PHYLOGENETIC RELATIONSHIPS

Attempts have been made to resolve the phylogenetic relationships of post-Devonian taxa (Schultze, 1981 and Thomson, 1990 on the basis of cranial characters; Martin, 1982a on the basis of both cranial and dental characters) and of post-Devonian taxa together with Devonian taxa (Miles, 1977; Marshall, 1986; Schultze & Marshall, 1993; Schultze & Chorn, 1997 on the basis of both cranial and dental characters) or of Late Palaeozoic, Mesozoic and Cainozoic only (Schultze, 2004). All of these studies rest on parsimonious distributions of derived states of characters, and four of them included computer-based cladograms (Marshall, 1986; Schultze & Marshall, 1993; Schultze & Chorn, 1997; Schultze, 2004). The latter three analyses are the most complete, including 74, 47 and 56 characters, respectively. Many of the characters used in these studies are, however, defined as presence/absence of specific bones of the skull roof, implying the recognition of primary homologies that rest on assumptions of fusions and/or topographic invasions within the primitive ossification pattern. We consider that such recognitions are impossible or at best questionable in most Mesozoic taxa and, accordingly, we do not use most of the cranial characters as defined in these previous works.

An example of such difficulties is illustrated by the following two interpretations of bone patterns from the medial series of lungfish skull roofs. The supposed primitive condition in post-Palaeozoic lungfishes is the presence of a medial posterior ossification (AB-bone of Schultze, 1981, 2004; Kemp, 1998; central parietal of

Martin, 1981a; and B-bone of Thomson, 1990), which bears the posterior commissure; a paired (*Beltanodus*) or unpaired (*Microceratodus*, *Ptychoceratodus*, *Paraceratodus*, *Ceratodus*) ossification in the middle of the series (C-bone of Schultze, 1981; Kemp, 1998; frontal of Martin, 1981a; and D-bone of Thomson, 1990); and an anterior unpaired ossification (E-bone of Schultze, 1981; Kemp, 1998; rostral of Martin, 1981a; and F-bone of Thomson, 1990). Based on these patterns, Schultze (1981: figs 15–17) defined two trends in fusions, or topographic invasions, in the medial bone series of the more derived lungfishes: one led to the formation of a large anterior unit including the two anterior-most bones (EC-bone or central rostrifrontal), a trend occurring in parallel in *Arganodus atlantis* and *Ceratodus* (= '*Tellerodus*') *sturii*, and the other trend leading to the formation of a narrow elongated posterior unit including the two posteriormost bones (ABC-bone or central frontoparietal) in the sister genera *Asiatoceratodus* and *Neoceratodus* (Fig. 15A). This topology is found again in Schultze (2004), in which the presence of a composite ABC bone characterizes the node *Asiatoceratodus* and the two modern lineages. Kemp (1998), by contrast, questioned implicitly Schultze's interpretation by assigning *Arganodus atlantis* in the genus *Asiatoceratodus*, which she regarded as characterized by the presence of an EC-bone (Fig. 15B).

Both interpretations rest on similar patterns, but in each case the identification of bones is based on assumptions about the phylogenetic origin of the ossifications with no objective anatomical or ontogenetic evidence supporting them. As a consequence, both interpretations lead to two very different hypotheses of relationships. We have no objective reasons to choose between these two interpretations.

In the present study we avoid, as far as possible, the use of characters based on assumptions of fusions and/or topographic invasions of ossifications. We prefer to use fewer characters than in previous studies, but all characters are defined on the number of ossifications and topographical relationships between the bones only. These characters are basic features present in the ossification patterns of the skull roofs of all lungfishes under study (see 'Remark on nomenclature'). Possible secondary homologies (*sensu* Patterson, 1982) could eventually be determined a posteriori on the cladogram. We regard this approach as less subject to interpretations in the recognition of character states.

A constant feature within lungfish skull roofs is the presence of one median and one mediolateral series of bones (Romer, 1936). These series are regarded as primary homologies in the subsequent definition of characters (a way to test this assumption could be brought by the study of the ontogenetic development of these series in the modern forms).

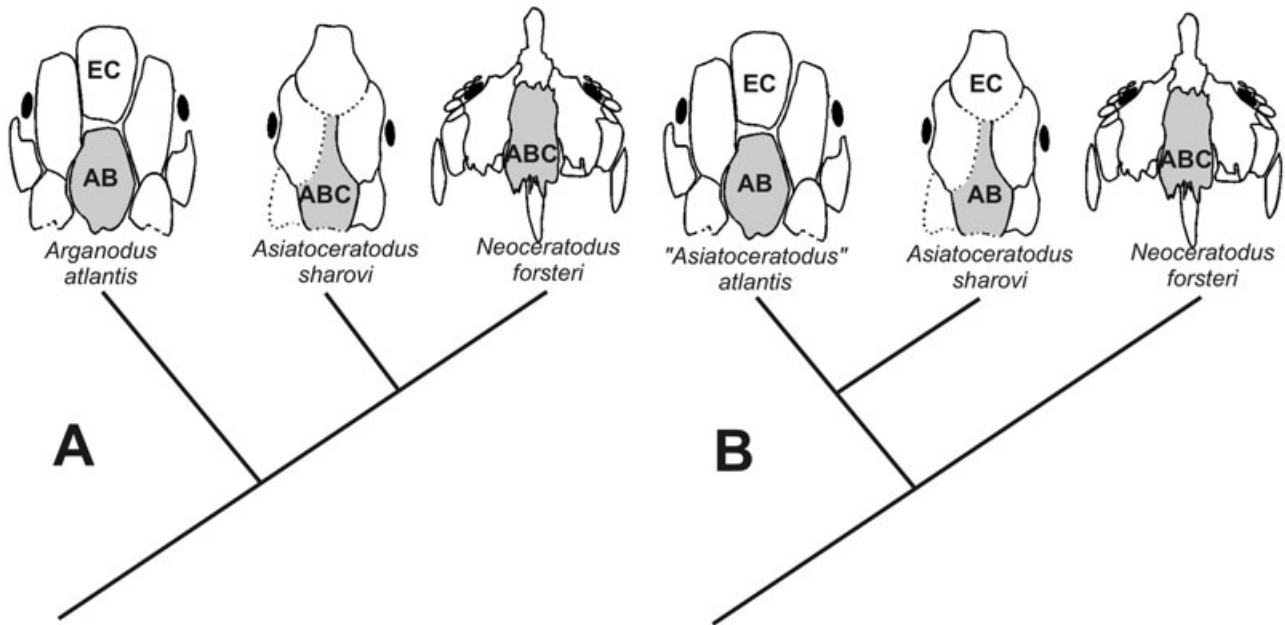


Figure 15. Relationships between *Arganodus atlantis*, *Asiatoceratodus sharovi* and *Neoceratodus forsteri* based on Schultze's (1981) interpretation of bone fusion (A) and relationships between 'Asiatoceratodus' (*Arganodus*) *atlantis*, *Asiatoceratodus sharovi* and *Neoceratodus forsteri* based on Kemp's (1998) interpretation of bone fusion (B).

Characters

Character 1: In the median ossification series of the skull roof, the primitive condition is the presence of more than three ossifications, or pairs of ossifications, such as observed in the Devonian *Dipterus* and the Permo-Carboniferous *Sagenodus* (state 0, Fig. 4). A first derived state is the presence of three ossifications or pairs of ossifications (state 1). A second derived state is the presence of only two ossifications (state 2) as observed in all known post-Triassic forms. The definition of this character does not include in the count the 'hard snout' ossification, which is present in *Dipterus* and TF 7712 at least.

Character 2: All Palaeozoic and some Mesozoic lungfishes have one or several ossifications of the medial series, which are paired (state 0, Fig. 4). The derived state is the presence in the medial series of unpaired ossifications only (state 1).

Two other characters related to the medial series are autapomorphic for some of the terminal taxa: they are not used in the analysis but are worth noting here. The first is the presence of a contact of the paired posterior mediolateral ossifications (generally regarded as the JLM-bones) in the midline in front of the posterior medial ossification (generally regarded as the ABC-bone), which covers it in part. This character is present in Lepidosirenidae (in the cladistic analysis below *Protopterus* is used as the single terminal taxon for the lepidosirenids). The median contact of the paired mediolateral ossifications is related

to muscle insertions on an emarginated skull, in relation to the very powerful bite of these fishes (Bemis, 1986). The second character on the medial series of ossifications is the presence of a fenestra in *Ptychoceratodus*. This fenestra is probably not related to muscle attachments as in lepidosirenids, because it lies dorsal to the brain cavity. According to Schultze's nomenclature (1981), the fenestra is located between the C- and E-bone, the position of the D-bone in Devonian lungfishes. The D-bone bears the pineal foramen in most Palaeozoic lungfishes (Campbell & Barwick, 1986). This pattern indicates that the fenestra in *Ptychoceratodus* was possibly related to the activity of the pineal organ, which is commonly exposed to exterior light in fishes and reptiles in order to adjust hormonal activity to the intensity and duration of daylight. Kemp (1996) proposed a reconstruction of the skull roof of '*Ptychoceratodus philippsi*', from South Africa and Australia, with a fenestra in the same location as in *P. serratus*. But, as Kemp mentioned herself in the text and showed in a figure of the actual specimen, the preservation is not good enough to suggest with confidence the presence of this fenestra.

Character 3: As for the medial series, we distinguish for the mediolateral series a primitive pattern with four or more bones (generally regarded as the I, J, K, L and supraorbital bones, state 0), a derived state with three ossifications (state 1), a second derived one with two ossifications (state 2) and a third state with a sin-

gle ossification (state 3, Fig. 4). In *Ceratodus sturii*, the posterior median bone is large and extends laterally to occupy the territory of the posterior ossifications of the mediolateral series in other Mesozoic lungfishes (Fig. 4). There is a single additional bone in each mediolateral series. We regard this condition as the state 2 of the character, i.e. the presence of two ossifications.

Character 4 (Fig. 16): Lungfishes with 'hard snout', i.e. heavily ossified nasal capsule and upper and lower lips, covered with cosmine (*Dipterus*, *Chirodipterus*) or

cosmine-free (*Griphognathus*, *Holodipterus*), are hitherto known in the Devonian only. In late Palaeozoic (Schultze & Chorn, 1997) and post-Palaeozoic (Kemp, 1998) lungfishes, the anterior extremity of the snout apparently lacks mineralized tissue. The pieces of 'hard snout' described here are the first evidence of an occurrence of mineralized snout, and/or lower lip, in a lungfish younger than Devonian in age. The absence of enameloid on both fragments may be due to (1) the absence of deposition of a superficial enameloid layer during the ontogeny of the fish, (2) wear during life or (3) chemical dissolution after the death of the animal.

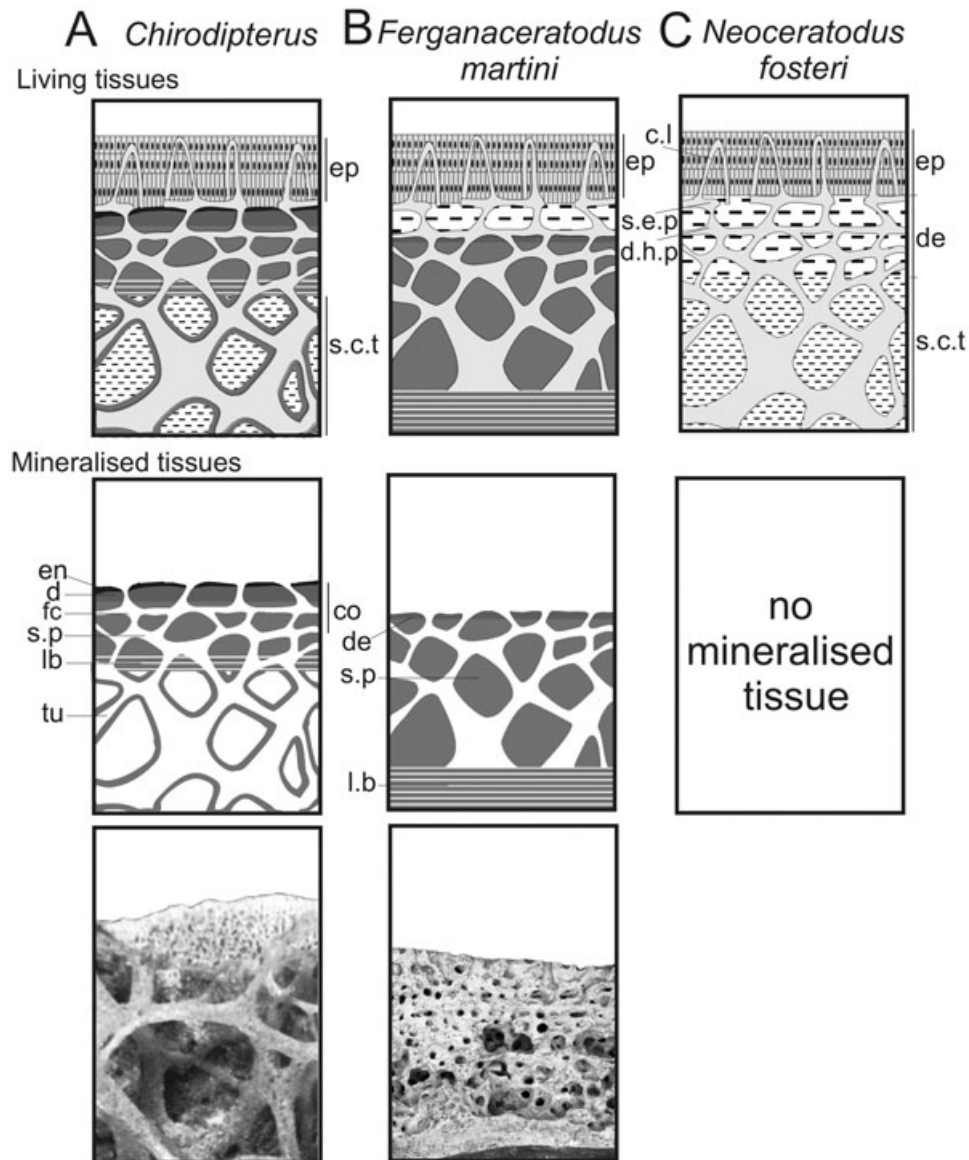


Figure 16. Schematic drawings and photographs showing three stages in the evolutionary trend of the 'hard snout' exemplified by *Chirodipterus*, *Ferganoceratodus martini* sp. nov. and *Neoceratodus forsteri*. The upper drawings show reconstructions of the structure in living fishes, the middle line drawings show the mineralized tissues as found in the fossil record and the lowest are photographs of actual specimens (*Chirodipterus* from Bemis & Northcutt, 1992: figure 24).

However, dissolution during the taphonomic process is unlikely because enameloid material is abundant and well preserved on the ganoid semionotiform fishes found in the same site (Cavin *et al.*, 2004). We rather suggest that the structure of the 'hard snout' of TF 7712 corresponds to a specific hard tissue of this fish, and its surface was neither worn nor dissolved. This structure, however, is difficult to interpret if we compare it to the complex tissues present in Devonian lungfishes. Moreover, the cavity network in the mineralization is proportionally much larger than the network observed in Devonian lungfishes, and we cannot distinguish a pore canal system differing from pulp cavities. Spongy bone with large pores irregular in size is present underneath the cosmine layer on dermal bones of *Chirodipterus*, and these pores may open to the surface where the cosmine layer naturally stops (Smith, 1977: pl. 9, fig. 79). The microstructure of the 'hard snout' of TF 7712 is very similar to the spongy bone without cosmine from *Chirodipterus*. Moreover, it matches well with *Chirodipterus* because of the arrangement of the chambers in continuous layers and the presence of flask-like cavities when observed in section. The average thickness of the two fragments described here, however, is more important than the dense mineralized tissue of the Devonian forms. In Devonian lungfishes, a network of rostral tubuli (*sensu* Bemis & Northcutt, 1992) lying underneath the rostral and symphyseal 'hard snout' is often present (Cheng, 1989). According to the general structure of the hard snout of *Chirodipterus*, and to the general evolutionary trend observed in lungfishes, we consider that part or the whole of the rostral and symphyseal mineralized tubuli of the Devonian lungfishes are here embedded in the basal spongy bone. Thus, the 'hard snout' of TF 7712 may be regarded as a mineralization of the deeper tissues of the dermis and the subcutaneous tissues, including at least in part the network of tubuli but excluding the superficial-most cosmine layer of the Devonian lungfishes. This trend would correspond to a sinking of the dermal bones within the dermis, which is a well-known phylogenetic trend in lungfishes. Schultze & Marshall (1993) mentioned that the snout of juvenile Devonian dipnoans is not ossified, indicating that the unossified snout of post-Devonian lungfish is a pedomorphic character.

The mineralized tissue described here is difficult to interpret in the light of the features of sarcopterygian cosmine as classically defined (Ørvig, 1969; Thomson, 1975). But the pattern is fully understandable if we follow the interpretation of cosmine proposed by Bemis & Northcutt (1992). These authors suggested (1) that the pore canal system of Palaeozoic lungfishes is homologous to the complex cutaneous vasculature of the living *Neoceratodus* and (2) that this system is exclusively involved in the deposition of the mineral-

ized tissue but has no electroreceptive or other functions related to the lateral line system. According to this pattern, pulp canal and pore canal do not belong to fundamentally different systems, but to different stages of a single system for deposition of mineralized tissue. According to this model, the network of rostral tubuli represents ossifications in the walls of endoskeletal canals containing blood vessels. In their paper, Bemis and Northcutt concluded the discussion by stating, 'it could be very interesting to examine the snout of very large specimens of *Neoceratodus*'. Through this proposition, they suggested that ossification in the snout could appear late in the ontogeny of *Neoceratodus*, thus verifying their hypothesis of homology between Devonian hard snout and the snout of *Neoceratodus*. Instead of a late ontogenetic state, the 'hard snout' described herein provides an 'intermediate' state from the fossil record between the cosmine-covered hard snout of the Devonian lungfishes and the capillary loops and associated structure present in *Neoceratodus*. The fossil provides support to Bemis and Northcutt's interpretation.

The interpretation expressed here is tentative pending new data. However, it appears to be the most parsimonious interpretation of these unusual pieces of mineralization.

According to these observations, we define the following character states: the primitive state is the presence of superficial cosmine or cosmine-like hard tissue in the snout (state 0); a first derived state is the presence of a deeper mineralization without superficial enamel (state 1) and a second derived state is the absence of hard tissue in the snout (state 2). For post-Devonian taxa, we coded the character only when articulated material is known, because one cannot show with confidence the presence/absence of 'hard snout' in taxa based on disarticulated remains only, i.e. *Arganodus*, *F. jurassicus* and *P. serridens*.

Character 5: Another independent character is defined on the gross dorsal snout morphology. Devonian lungfishes have a broad, heavily ossified snout region formed by a mosaic of small bones, some of them bearing the paired supraorbital sensory canals (state 0). This primitive condition is observed in *Dipterus* and in *Sagenodus*, although in the latter there is a single or double row of small anterior marginal bones only, but no elongate rostrum (Schultze & Chorn, 1997). Two derived states of this character are observed: one with the skull roof extending anteriorly as a rostrum formed by a single ossification bearing portions of the supraorbital sensory canals (state 1) and one with the skull roof anteriorly straight, or with a short rostrum, but which does not bear the supraorbital sensory canals (state 2). The first derived state is observed in *Gnathorhiza*, *Beltanodus*, *Microceratodus*

and *Neoceratodus*. In *N. forsteri*, the paired supraorbital canals do not mark the underlying bone, but their paths clearly lie over the rostral bone (Kemp, 1999). The second derived state is observed in *Arganodus*, *Asiatoceratodus*, *Ferganaceratodus*, *Gosfordia*, *Paraceratodus*, *Protopterus* and *Ptychoceratodus*. In dorsal view *Protopterus* apparently shows a rostrum (Fig. 4). In lateral view, however, the upper tooth plates are located close to the anterior margin of the anterior medial bone, indicating that the 'rostrum' is an artefact related to the narrowing of the skull roof and to the unique median contact of the paired mediolateral ossifications. Moreover, no trace of the paired supraorbital canals is visible on the anterior medial bone in *Protopterus*.

Character 6: The presence of a small free dermosphenotic (XK-bone) with a triradiate sensory canal pattern is the primitive condition in lungfishes (state 0). The absence of this small free bone, by fusion, topographic invasion or disappearance, is the derived state (state 1). The recognition of both states rests on the observation of the path of the sensory canals. Beltan (1968) suggested that the dermosphenotic is fused with the large bone bordering dorsally the orbit in *Beltanodus*. But the photograph of the single known specimen (Beltan, 1968: pl. L) shows that the ossification was probably free, as shown in the reconstruction given by Schultze (1981: 25). In *Ferganoceratodus jurassicus*, the pattern of ossifications (Nessov & Kaznyshkin, 1985: fig. 2a) and the reconstruction by Kaznyshkin (1993; Schultze, 2004) indicates that a free dermosphenotic was present.

Character 7: Primitively in dipnoans, the sensory canals are deeply buried in the bones (Campbell & Barwick, 1986; state 0). In most Mesozoic lungfishes, the paths of the sensory canals are still visible as ridges or grooves on the bones, but in the Recent taxa, the course of the canals fails to mark the bones, especially in the anterior part of the skull roof (Kemp, 1999). In *Gnathorhiza*, the situation is variable among species, with *G. bothrotreta* Berman, 1976b having some of its sensory canals at least enclosed in bone (Berman, 1976b), while they run in open channels in other species (Berman, 1976a). Accordingly, we define two derived states: sensory canals partly bone-enclosed (state 1) and sensory canal not bone-enclosed (state 2).

Character 8: Primitively, the parasphenoid in lungfishes is a small bone located under the oticooccipital region of the neurocranium (state 0). In most post-Devonian lungfishes, the parasphenoid extends anteriorly under the ethmosphenoid region, and develops posteriorly an elongated stem that reaches the poste-

rior margin of the skull roof (state 1). The derived condition allows an enlargement of the buccal cavity and may be linked with the capacity to gulp air (Campbell & Barwick, 1988).

Martin (1982a) recognized several characters in tooth plate morphology. We retain here the following two characters related to the upper tooth plates.

Character 9: The first ridge of the upper tooth plate is primitively longer or as long as the lingual margin (state 0), and secondarily shorter (state 1).

Character 10: There is primitively no contact between both upper tooth plates (state 0) and secondarily a contact (state 1). Campbell & Barwick (1988) suggested that the slot between upper plates, in the extinct and Recent dental plate lungfish types, used to be filled with the tongue pad, in order to seal tightly the buccal cavity when the fish swallowed air.

The presence of crushing ridges is an autapomorphic character of *Ceratodus*. The number of ridges is variable within a single species (Kemp, 1998: 56). The presence of parallel ridges lying perpendicular to the lingual margin varies with ontogeny.

We also consider here the following characters discussed elsewhere or defined here for the first time.

Character 11: No contact between both lower tooth plates of either side is the primitive state (state 0), a contact present is the derived one (state 1).

Character 12: The inner angle of the upper tooth plates, as defined by Martin (1984), is primitively greater than 90° (state 0) and secondarily less than 90° (state 1).

Character 13: Primitively, the scales of lungfishes are thick and covered with cosmine (Campbell & Barwick, 1986; Meinke, 1986; state 0). In one of the derived states, observed in *F. martini* and *Neoceratodus* among others, the superficial mineralized layer lacks an enameloid covering, but is still relatively thick and it contains a complex network of interconnected cavities (state 1). In a second derived state, present in *Protopterus* (Brien, 1962) and *Asiatoceratodus* (Vorobyeva, 1967) at least, the superficial mineralized layer lacks an enameloid covering and is very thin with no cavities (state 2). We suspect that the different states correspond to different stages of an ontogenetic series, and exemplified the paedomorphic trend detected in lungfish evolution by Bemis (1984).

Character 14: The course of mandibular canals is primitively parallel in two bones (state 0). In the studied set of taxa, two derived states are observed: the oral canal is in bone and the mandibular canal is in a gutter (state 1) or both canals lay superficial to the bone (state 2). This character was defined by Schultze & Chorn (1997). They defined a third derived state

(canals converging in one bone), but this is not present in any of the taxa compared here.

Terminal taxa (Fig. 4)

Arganodus atlantis Martin, 1979. Late Triassic of Morocco. Description from Martin (1981a) and Kemp (1998). The analysis below does not support the assignment of this species to *Asiatoceratodus* (Kemp, 1998).

Asiatoceratodus sharovi Vorobyeva, 1967. Early Triassic of the Fergana Basin, Kyrgyzstan. Description from Vorobyeva (1967) and discussion of characters in Schultze (1981) and Thomson (1990).

Beltanodus ambilibensis Schultze, 1981. Early Triassic of Madagascar. Description from Beltan (1968), Martin (1981b) and Schultze (1981).

Ceratodus sturii Teller, 1891. Late Triassic of Austria. We follow Kemp (1998) for the generic attribution of this species based on the crushing-type tooth plates. Description from Schultze (1981), Martin (1982b) and Kemp (1998).

Dipterus valenciennesi Sedgwick & Murchison, 1835. Old Red Sandstone (Middle Devonian) of UK. Description from White (1965) and direct observations.

Ferganoceratodus jurassicus Kaznyshkin & Nessov, 1985. Middle Jurassic of Kyrgyzstan. Description from Nessov & Kaznyshkin (1985), Kaznyshkin (1993) and direct observations.

Gnathorhiza spp. Cope, 1883. Carboniferous to Triassic of North America and Europe. Description from Olsen (1951) and Berman (1976a, b, 1979).

Gosfordia truncata Woodward, 1890. Early Triassic of New South Wales, Australia. Description from Woodward (1890), Ritchie (1981) and Kemp (1993).

Microceratodus angolensis (Teixeira, 1949). Early Triassic of Angola. Description from Schultze (1981) and Thomson (1990).

Neoceratodus de Castelneau, 1876. Early Cretaceous to Recent, various localities within the Southern Hemisphere. Description from Günther (1871), Kemp (1998, 1999), Bemis (1986) and Jarvik (1967).

Paraceratodus germaini Lehman *et al.*, 1959. Early Triassic from Madagascar. Description from Lehman *et al.* (1959) and Martin (1981b, 1982b).

Protopterus spp. Owen, 1839. Cretaceous to Recent, Africa. Description from Kemp (1998), Bemis (1986) and direct observations.

Ptychoceratodus serratus (Agassiz, 1838). Middle Triassic of Switzerland and Germany. Description from Schultze (1981) and Kemp (1998).

'*Ptychoceratodus philippsi*' (Agassiz, 1838). Early Triassic of South Africa and Australia. Kemp (1996) referred this material to the European species *Ptychoceratodus philippsi* (Agassiz, 1838). Martin *et al.* (1999), on the basis of differences in tooth plate mor-

phology, questioned this identification and referred the specimen to *Ptychoceratodus* sp.

Sagenodus spp. Owen, 1867. Permian and Carboniferous of Europe and North America. Description from Schultze & Chorn (1997).

The characters used in analyses and the data matrix are shown in appendices 1 and 2, respectively.

Other Mesozoic taxa not included in the analysis

Ariguna formosa (Wade, 1935) from the Early Triassic of New South Wales, Australia, is known by the holotype, an almost complete small specimen, and an isolated large scale tentatively referred to this species. The holotype has been described and figured by Wade (1935), White (1965), Martin (1982b), Kemp (1991, 1994) and Schultze (2004). This species has not been included in the phylogenetic analysis for two reasons. First, the descriptions and illustrations of the specimen are too different between authors to provide a reliable reconstruction on which we could base the coding of the characters. Direct observations of the type specimen (BMNH P.16828) did not allow us to accept one of the previous descriptions or to propose a new one. Second, because of the important difference in size between the small holotype and the large isolated scale referred to this species, the complete specimen is probably a juvenile (Kemp, 1994). The inclusion in the analysis of characters from a juvenile specimen may have distorting effects in the inference of the phylogenetic hypothesis, especially in a group where paedomorphosis may have played an important role.

Apheiodus anapes Kemp, 1993 from the Early Triassic of Queensland, Australia, is known by isolated tooth plates and isolated bones tentatively referred to a sagenodontid by Kemp (1993). *Namatozodia pitikanta* Kemp, 1993 also from the Early Triassic of Queensland, is known by a single tiny skull roof, 7 mm in length, referred to a sagenodontid (Kemp, 1993). These two species are known by material too incomplete to be included in our data matrix.

Metaceratodus Chapman, 1914 from the Cretaceous to the Pleistocene of Australia and from the Lower Cretaceous of South America is represented only by tooth plates and fragments of jaw bones (Kemp, 1997). Consequently it cannot be included in our analysis.

Previous studies (Fig. 17)

A few phylogenetic studies dealing with Mesozoic lungfishes have produced very different topologies. Moreover, they included different sets of terminal taxa, rendering any comparison difficult. Only a few similar interrelationships are commonly found in several analyses. Most of the studies found a sister-group rela-

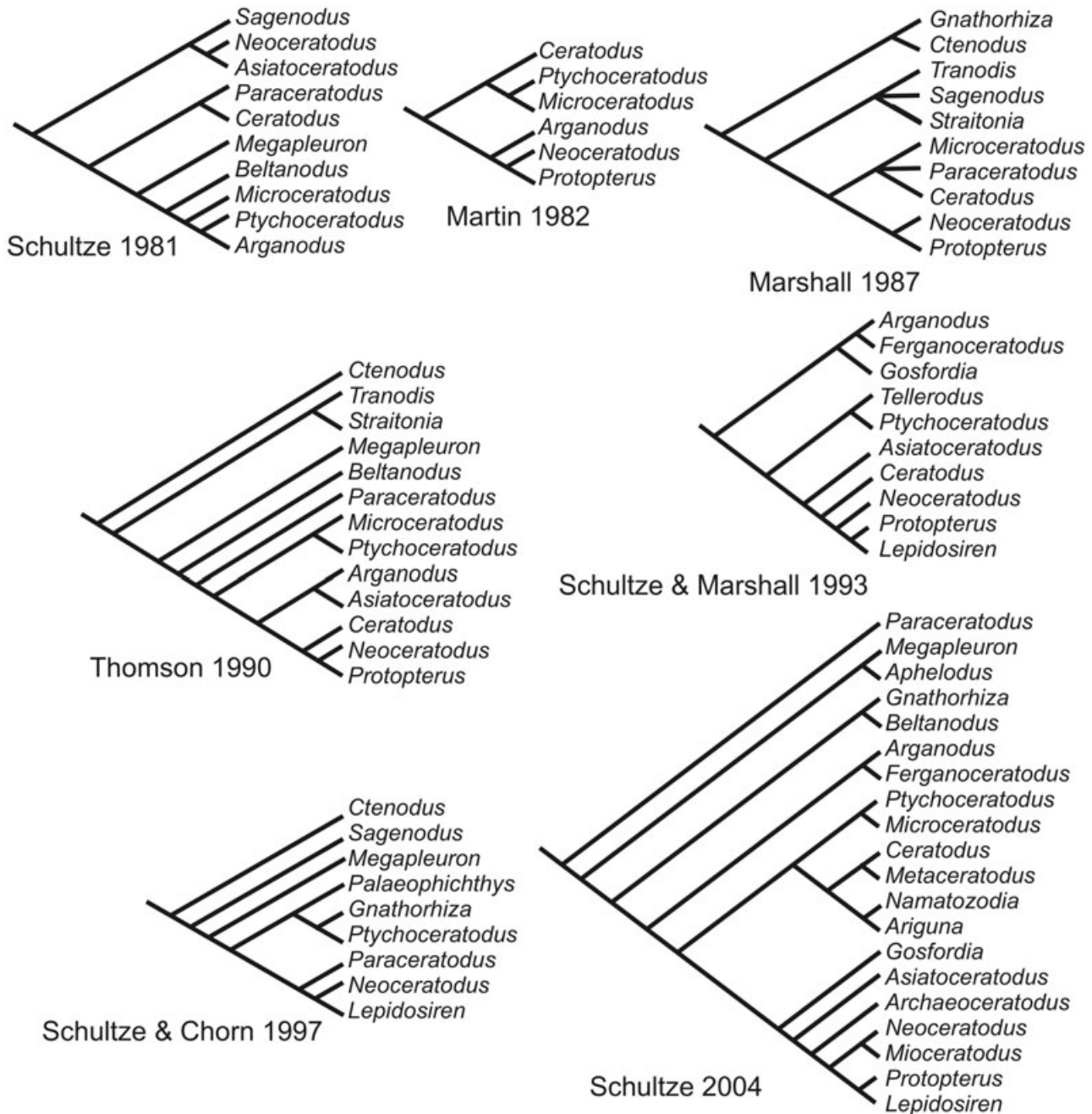


Figure 17. Previous hypotheses of phylogenetic relationships within the dipnoan taxa included in the present study.

tionship between the Recent *Neoceratodus* and the lepidosirenids (Martin, 1982a; Marshall, 1986; Thomson, 1990; Schultze & Marshall, 1993; Schultze & Chorn, 1997; Schultze, 2004), except Bertmar (1968), Schultze (1981) and Kaznyshkin (1993). According to Thomson (1990), this sister-group relationship rests on the presence in both clades of a single mediolateral ossification, but Kemp (1998) has shown that a supplementary small free I-bone is generally present in *Neoceratodus*,

although this bone is frequently lost in preparation and often fused with the JLM-bone. Martin (1982a) based the relationship between *Neoceratodus* and the lepidosirenids on the presence of fewer radiating ridges, but according to Kemp & Molnar (1981), a radiating pattern is present in juvenile *Neoceratodus*. Schultze & Chorn (1997) resolved the sister-group relationships on the basis of the presence of the occipital commissure in skin, bones C and Y combined with

neighbouring bones, no separate bone Z, no separate bone Y, parasphenoid with extremely long stalk, one infradentary, oral and mandibular sensory canals in skin and no bone I. In 2004, Schultze found an almost similar list of characters, plus two unique synapomorphies: ratio snout/cheek between 2.5 and 4, and no gular bone. However, these two characters are unknown in almost all the other taxa (except *Megapleuron* and *Gnathorhiza* for the ratio of the head).

Another common feature found in most previous phylogenies is a close relationship between *Ptychoceratodus* and *Microceratodus*. Martin (1982a), Thomson (1990) and Schultze (2004) proposed a direct sister-group relationship between both genera, and Schultze (1981) found the relationship (*Arganodus* + *Ptychoceratodus*) + *Microceratodus*. The characters involved in this relationship are the presence of three ossifications in mediolateral series (at least in one species of *Ptychoceratodus*) (Thomson, 1990), a large anterolateral bone regarded as a compound bone (Schultze, 1981), the presence of 4–6 radiating cutting ridges on tooth plates and a narrow median series between orbits (Martin, 1982a) or the presence of an unpaired C-bone and the supposed origin of the anterior bone of the mediolateral series [character 27 in Schultze (2001) and character 20 in Schultze (2004: missing in his list: 491)].

Asiatoceratodus is regarded as the sister-group of *Neoceratodus*, or of the neoceratodontids plus lepidosirenids, by Schultze (1981, 2004) on the basis of the median and lateral bone pattern, as the sister-group of *Arganodus* by Thomson (1990), and *Arganodus* is regarded as a junior synonym of *Asiatoceratodus* by Kemp (1998). Schultze (1981) resolved *Sagenodus* as the sister-group of (*Asiatoceratodus* + *Neoceratodus*) on the basis of a dermosphenotic supposedly formed by the fusion of X and K [this relationship is not found again in Schultze & Chorn (1997) and Schultze (2004)]. Schultze (1981) placed *Ceratodus sturii* (= '*Tellerodus*' *sturii*) as the sister-group of *Paraceratodus* on the basis of a broad posterior median bone, and Schultze (2004) resolved a family of Ptychoceratodontidae gathering six genera on the basis of two characters of the bone pattern of the skull roof. The pattern found by Schultze & Marshall (1993) cannot be discussed here, as a character list was not provided alongside their analysis.

RESULTS

We ran the data matrix (Appendix 2) using PAUP 4.0b10 with the heuristic tree-building routine and ACCTRAN optimization (using random addition sequence, 1000 replicates, ten trees held at each iteration, and tree bisection and reconnection branch-swapping). All characters were unweighted and

unordered. The result, using *Dipterus* as outgroup, gave 18 equally parsimonious trees (length = 29, CI = 0.759, RI = 0.825). The strict consensus tree is shown on the left-hand side of Figure 18, and supplementary information provided by the 50% majority rule tree is shown on the right. The node gathering all taxa above *Sagenodus* has a Bremer support of 2 while all other nodes have a Bremer support of 1 (Fig. 18). Our cladogram is characterized by a low level of homoplasy (CI and RI values are high), but with weakly supported nodes (very low Bremer support). The low Bremer support is explained by the low number of characters used, but the CI and RI values show that these are phylogenetically signal-laden. Another way to assess the phylogenetic signal of the data is to examine the distribution of lengths of all possible cladograms (Fig. 19). Because there are too many taxa to compute all possible cladograms with PAUP 4.0b10, we reduced the number of terminal taxa to 12 by eliminating three of the four taxa forming a polytomy in the first analysis (*Arganodus*, *Gosfordia* and *Ptychoceratodus*) and *Ferganoceratodus jurassicus*, which is very close to *F. martini*. The strict consensus cladogram of the six most parsimonious trees shows a pattern similar to the global cladogram (Fig. 19, frame). The mean length of the 654×10^6 trees is 44.95 steps (SD = 2.84), while the shortest tree is 27 steps long. The skewness statistic, g_1 , is -0.745 indicating a strong phylogenetic signal of the data.

The global cladogram, with 16 terminal taxa, displays mainly a pectinated pattern. Unsurprisingly, the Palaeozoic taxa (*Dipterus*, *Sagenodus* and *Gnathorhiza*) are located at the base of the cladogram (with *Beltanodus* in a unresolved trichotomy with *Gnathorhiza*), followed by *Microceratodus* from the Early Triassic of Angola. *Microceratodus* and the more derived lungfishes are characterized by the absence of paired bones in the medial series of the skull roof and the sensory canals are not bone-enclosed. The next node gathers *Neoceratodus* and the more derived lungfishes. The node is defined by the reduction from three to two ossifications in both the median and the mediolateral series. Within this clade, however, both characters show reversions: one in *Ptychoceratodus serratus* and *Paraceratodus germaini* for the median series, and in the same two species plus *Gosfordia truncata* for the mediolateral series. The sister-group of *Neoceratodus* gathers lungfishes with a generally straight anterior margin of the skull roof. An exception to this condition is the lepidosirenids, which have a tapered snout. But in these fishes the condition is not homologous to the plesiomorphic condition because the rostrum is formed by the narrowing of the anterior part of the skull roof rather than by the elongation of the anteriormost bone of the median series. The anteriormost bone of the median series in these

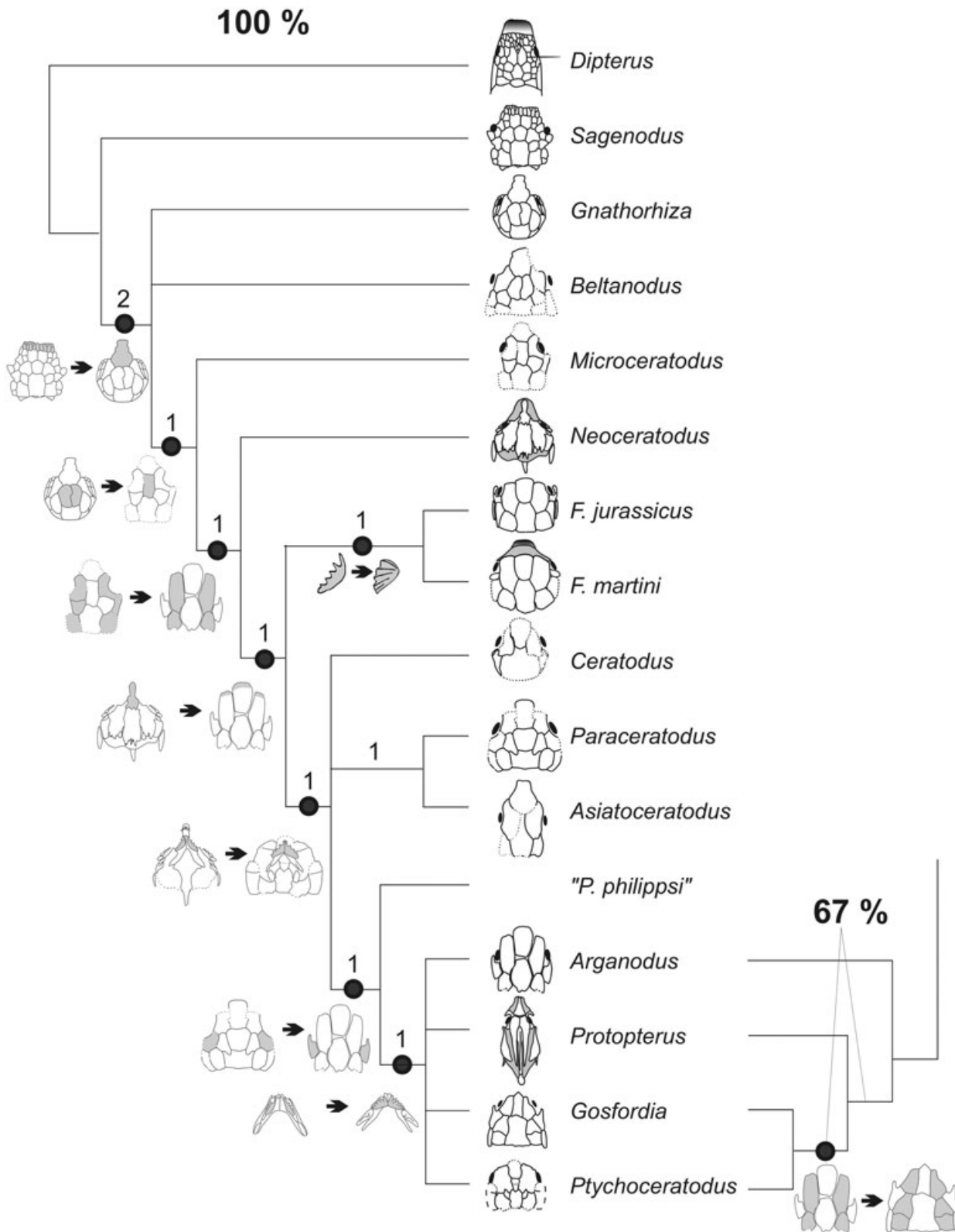


Figure 18. Strict consensus tree of 18 equally parsimonious trees using *Dipterus* as outgroup (length = 29, CI = 0.759, RI = 0.825). On the right are shown the differences in the relationship patterns within the 50% majority rule tree. The main synapomorphies are exemplified under their respective node and the Bremer support above the nodes.

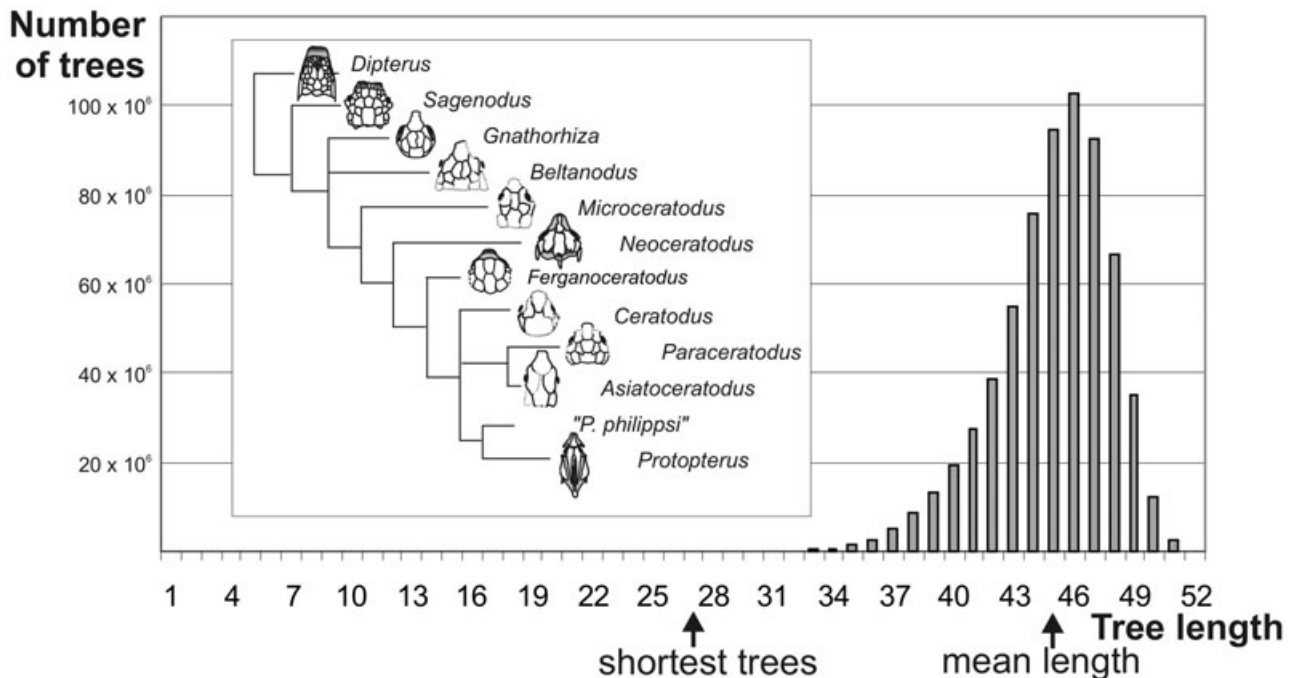


Figure 19. Histogram for the tree length distribution of all (nearly 654×10^6) possible trees using 12 terminal taxa and *Dipterus* as outgroup. The strict consensus tree of the 12 taxa is shown in the frame. The shortest tree length is 27 steps and the mean length of all trees is 44.95 steps (SD = 2.84). The skewness statistic, g_1 , is -0.745 , indicating a strong phylogenetic signal of the data.

fishes has a different topographic relationship with the surrounding bones because (1) it does not extend as far forwards of the palatine tooth plates as in more basal forms and (2) the posterior margin of the anteriormost bone is situated in front of the mediolateral ossifications (both in midline contact in that clade) rather than in between these ossifications as in all other lungfishes (Fig. 4). Within the sister-group of neoceratodontids, the basal most genus is *Ferganoceratodus*. It is characterized by several autapomorphies (see diagnosis in 'Systematic palaeontology'), but still has a gap between both upper tooth plates. However, this condition is known with confidence only in *F. martini*. In *F. jurassicus*, Kaznyshkin (1993) reconstructed the skull with the upper tooth plates in contact in the midline, but the material housed in Saint-Petersburg Museum shows no clear evidence of such a contact. The condition is coded with a '?' in our data matrix for that taxon.

Lungfishes more derived than *Ferganoceratodus* are characterized by a contact between palatine tooth plates and thin scales (the latter character, however, is unknown in several taxa). This node gathers three clades – *Ceratodus*, (*Paraceratodus* + *Asiatoceratodus*) and the more derived forms – in an unresolved trichotomy. Another possible synapomorphy at this node, not included in our analysis, is the presence of very thin

and elongated fins. This character is present in *Gosfordia* (Ritchie, 1981), lepidosirenids and apparently *Asiatoceratodus* (Vorobyeva, 1967). *Paraceratodus* has incompletely preserved paired fins, but these seem to be more completely ossified than in *Neoceratodus* (Lehman *et al.*, 1959) and thus incompatible with this character distribution. However, although *Paraceratodus* is resolved here as the sister group of *Asiatoceratodus*, this species is characterized by several reversals in the parsimonious analysis, and we regard its phylogenetic position as still uncertain. Most previous studies placed it in a much more basal position (Fig. 17).

The five most derived forms are gathered in a clade characterized by the absence of a free dermosphenotic. Within this group, '*Ptychoceratodus philippsi*' is resolved as the sister group of a clade comprising *Arganodus*, *Protopterus*, *Ptychoceratodus* and *Gosfordia*, which is characterized by both lower tooth plates in contact in the midline. In two-thirds of the most parsimonious trees, *Ptychoceratodus* and *Gosfordia* are sister taxa, on the basis of the reversion from two to three bones in the mediolateral series.

The cladogram is included into a temporal frame in Figure 20. Within this time-constraint pattern, the node between *Neoceratodus* and all other lungfishes is inferred to have occurred around the Palaeozoic–

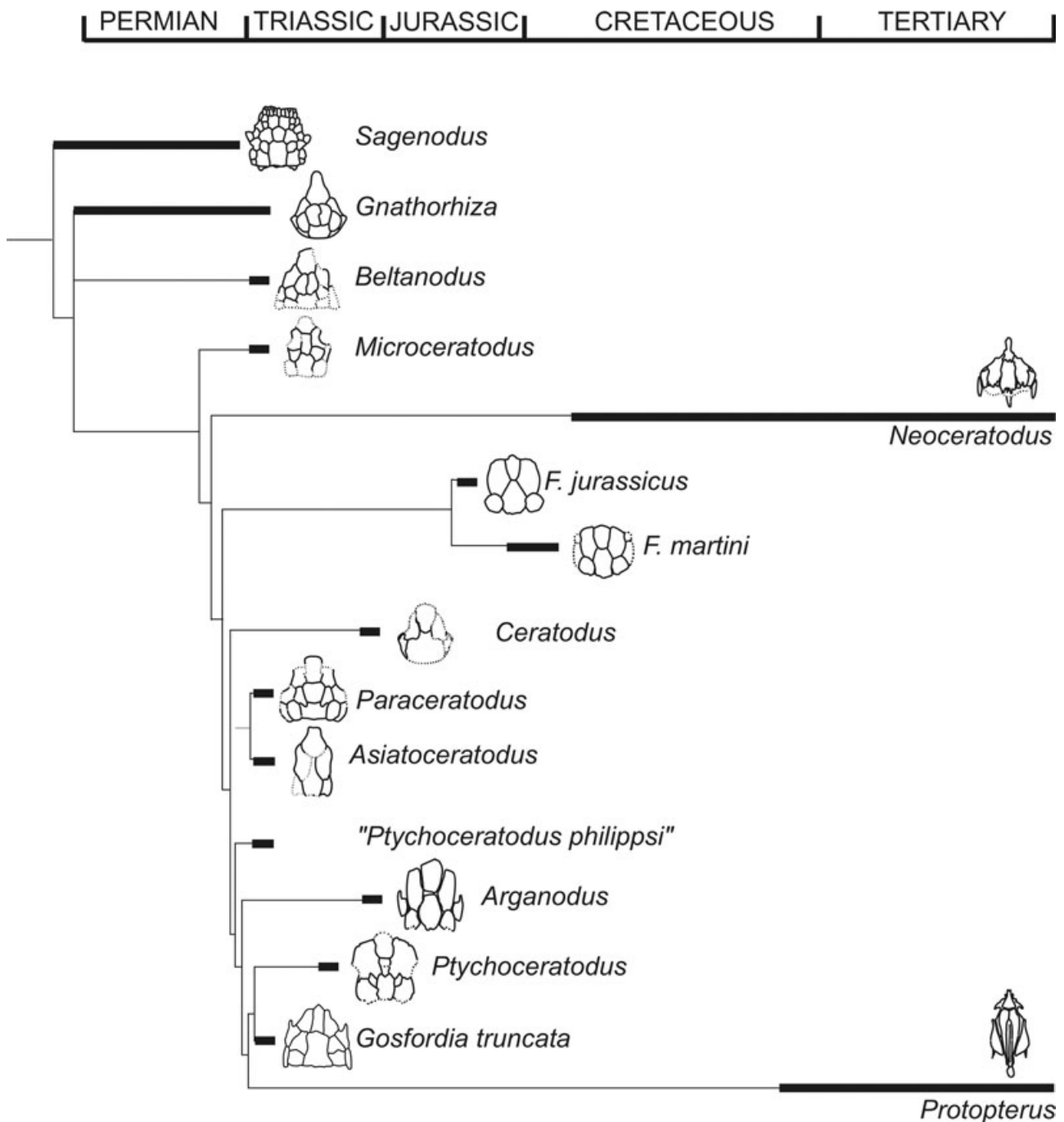


Figure 20. Plot of the phylogenetic tree against stratigraphy to show the correlation between stratigraphy and phylogeny.

Mesozoic boundary. It implies a ghost lineage for *Neoceratodus* of about 100 million years, which is not an especially long time-span if we consider the nature of the lungfish fossil record. The lineage represented by *Neoceratodus forsteri* as a terminal taxon in our analysis actually gathered other *Neoceratodus* species from the Early Cretaceous onwards, and possibly the genus *Mioceratodus* from the Miocene of Australia not

included here (Kemp, 1992, 1998; Schultze, 2004). The *Ferganoceratodus* lineage should also be dated to the Palaeozoic–Mesozoic boundary or the Early Triassic, but it is unknown in the fossil record of the Triassic and the Early Jurassic so far if we consider skull occurrence only. Most of the cladogenetic events as well as most of the observed occurrences are within the Triassic. The variation in the number of taxa over

time is roughly correlated with the amount of freshwater deposits (Schultze, 2004). However, we are unable so far to identify the Triassic peak of diversity as either a genuine biological radiation or as an artefact related to the nature of the sedimentary record. In Figure 20, *Protopterus* represents the terminal taxa for lepidosirenids, and *Lepidosiren* is not shown. *Protopterus* and *Lepidosiren* are sister-genera and they probably resulted from a vicariant event during the opening of the South Atlantic that split western Gondwana into South America and Africa during the Early Cretaceous.

The phylogenetic hypothesis proposed here differs from the previous analyses mentioned above (Fig. 17). The main difference with these hypotheses is the deep divergence we obtained here between the two Recent families.

PALAEOECOLOGY

Devonian lungfishes rapidly diversified into numerous taxa that lived, according to Campbell & Barwick (1986, 1988) and Schultze & Chorn (1997) either mainly or exclusively in marine environments, respectively. In the Lower Permian of Utah and New Mexico, high numbers of specimens of *Gnathorhiza* have been found fossilized in vertical burrows. This taphonomic feature is generally regarded as evidence of aestivation burrows and led most authors to suggest that these fishes had acquired a mode of life quite similar to the modern African *Protopterus*, which is able to survive during the dry season in a cocoon of mucus made up in mud where they breathe air (Fishman *et al.*, 1986). There are, however, alternative hypotheses proposing that these fishes were mainly marine dwellers and used borrows to escape the low tide (Schultze & Chorn, 1997). Here we distinguish between two issues regarding post-Palaeozoic lungfishes: (1) their possible exclusively freshwater mode of life and (2) their aestivation capability.

(1) Palaeoenvironment of post-Palaeozoic lungfishes

A review of the palaeoenvironmental data available for all Mesozoic and Cenozoic localities yielding lungfish remains is beyond the scope of the current paper, but we focus on the palaeoenvironmental conditions relating to the Phu Nam Jun site, as well as to other formations with a rich dipnoan fossil record.

Cavin *et al.* (2004) provided four lines of evidence to show that the fish carcasses in Phu Nam Jun are likely to have dried in the open air before burial. (1) The spatial distribution of the specimens is not random, but occurred in small areas as a result of concentrations of fishes in the last pools of water before the complete drainage of a former broader stretch of

water. (2) Many of the fish carcasses have rows of ganoid scales remaining articulated, but with the individual rows parting from each other, starting initially on the belly. In this case, the carcasses are often bent and the body twisted. These features occur in a similar way in carcasses of gars that dried in the open air along a shoreline at Smithers Lake, Texas (Weigelt, 1927). (3) So far only fish remains have been found at Phu Nam Jun, tetrapod remains being absent. This indicates that freshwater tetrapods (such as turtles or crocodylians) would have been able to escape a pond that was drying out, whereas fish could only be trapped and die. (4) The lungfish was found in a sandy pocket beneath the main fossiliferous layer. The latter point is discussed below. The complete drainage of shallow stretches of water is a common process in continental environments with a distinct dry season, such as flooded plains, deltas, rivers and isolated ponds, but is uncommon in marine environments, except in the intertidal zone. There are no sedimentary or fossil clues of an intertidal environment in Phu Nam Jun, but there is evidence of palaeosols indicating the settlement of a vegetation cover that is incompatible with a rhythmic tidal water covering. Accordingly, we are confident that *F. martini*, as well as the other fishes from Phu Nam Jun, lived in a freshwater environment.

Mention of the palaeoenvironment of some of the major Mesozoic localities that have yielded lungfish remains is worth noting here. The Triassic deposits that yielded *Asiatoceratodus* contain a rich flora and insect fauna indicating continental sediments deposited under arid conditions (Vorobyeva, 1967). The Triassic Cassange series in Angola that yielded *Microceratodus* also contains conchostracans, which are typical freshwater forms (Antunes & Schaeffer, 1990). *Paraceratodus* has been found in the middle part of the Sakamena Formation in Madagascar, which is composed of marls deposited in a lake or lagoon–marine environment (Pique *et al.*, 1999). The Middle Jurassic deposits that yielded *Ferganoceratodus jurassicus* also contain an assemblage of hybodont sharks, which are common freshwater dwellers in the Mesozoic, alongside ‘holostean’ fishes, ?urodeles, ?lizards, ?pterosaurs, crocodiles, dinosaurs and plesiosaurs. According to the fossil assemblage and to the sedimentology, the palaeoclimate was semi-arid and the fossiliferous accumulation occurred in a torrential turbid stream that sank in a body of brackish water (Nessov & Kaznyshkin, 1985). Most of the occurrences from the Cretaceous of Africa are from the ‘Continental intercalaire’ (Tabaste, 1963; Martin, 1984), which is a continental formation probably deposited in deltaic or fluvial environments (Russell & Paesler, 2003). The rare Late Cretaceous African occurrences from marine deposits are pro-

bably reworked as indicated by their state of preservation (Martin, 1984).

This rapid overview shows that the Phu Nam Jun depositional environment, as well as that of most other Mesozoic palaeoenvironments with lungfish remains, has evidence of freshwater conditions with, in some cases, possible weak marine influence. Because the reworking process is a one-way mechanism – from continental environments to marine environments – it is more parsimonious to regard most if not all these lungfishes as freshwater dwellers.

(2) *Aestivation capability*

Aestivation capability is observed today in *Protopterus* and *Lepidosiren* only. Both are sister-genera originating in the Early Cretaceous during the break up of West Gondwana (South America and Africa). *Neoceratodus* is able to survive long periods in aerial conditions provided that wet material is available (Kemp, 1986), but it does not possess the physiological machinery to aestivate. Consequently, the distribution of this peculiar character of modern lepidosirenids on a cladogram provides no information about aestivation capability in fossil forms. There is no trace of aestivation capability visible on body fossils, but the presence of lungfish remains within burrows, such the Permo-Triassic *Gnathorhiza*, is commonly regarded as evidence for this physiological adaptation to be present. If we accept this assumption we should assume, alongside the phylogeny resolved here, that either (1) the physiological machinery necessary to aestivate evolved several times during dipnoan history (in *Gnathorhiza* and in lepidosirenids at least) or (2) this capability is a synapomorphy at one level of the phylogeny, at the node *Gnathorhiza* + more derived forms for instance, and was lost in the *Neoceratodus* lineage at least. By contrast, if we reject this assumption we should regard the presence of lungfishes inside burrows as inconclusive evidence for aestivation capability. Schultze & Chorn (1997) support the latter hypothesis by claiming that *Gnathorhiza* occurs in burrows excavated in nearshore deposits and that this behaviour probably indicates an adaptation to survive in what was a tidal to supratidal area. Although the evidence for an ability to aestivate is not completely convincing for the Permian *Gnathorhiza*, the case is different for several of the Mesozoic forms. According to our phylogeny and to the freshwater habitats of Recent lungfishes, we postulate that all taxa situated between *Neoceratodus* and lepidosirenids, i.e. all Mesozoic taxa except *Gnathorhiza*, *Beltanodus* and *Microceratodus*, should have been freshwater dwellers, without positive indications to the contrary. Although Schultze (1995) regarded this argument as dubious because it is based on negative evidence, this

assumption is reinforced by the nature of the deposits of most of the localities yielding the fossils (see above). Most of the Mesozoic lungfish occurrences are preserved as isolated remains or as articulated specimens preserved flattened on one side. These provide few clues about their mode of life. The specimen described here, however, provides further information. The fossil fishes in Phu Nam Jun are located in a fossiliferous lens dipping about 15° to the south-east and containing between one and four layers of fish carcasses. The topmost specimens are generally poorly preserved and are often represented by isolated ganoid scales or rows of ganoid scales only, while the best-preserved specimens occur in the deeper layers. This feature is a clue that all the carcasses were deposited during a single event, after which the uppermost ones were destroyed at the interface with the atmosphere, while the deepest were protected within the sediment (a detailed taphonomic study is currently in progress). TF 7712 occurred in a peripheral location and was more deeply located according to the dip of the layer. During excavation, we did not observe the outline of a burrow, but the nature of the sediment surrounding the specimen differed from more distant sediment. These features may indicate that the lungfish was lying in a burrow during the accumulation of the fish carcasses. We suggest here that this indicates an aestivation behaviour during the dry season.

As a final comment on the palaeoecology of lungfishes, we note that aestivation is a loose term that encompasses different behaviours and physiological adaptations (Fishman *et al.*, 1986), and we do not assume here that *F. martini* had all the physiological machinery necessary to aestivate in such extreme and lengthy conditions as the Recent *Protopterus*. However, we suggest that *Ferganoceratodus*, as well as all lungfishes situated between *Ferganoceratodus* and the lepidosirenids in our phylogeny, were freshwater fishes adapted to survive dry spells in a burrow, whatever their exact physiology.

PALAEOBIOGEOGRAPHY

The palaeobiogeographical signal of the Mesozoic fossil record may be discussed only once the phylogenetic relationships and the palaeoecology of the taxa under concern are reasonably understood, which is assumed now to be the case.

When the phylogenetic tree is constrained into a palaeogeographical framework (Fig. 21), the main radiation of Mesozoic lungfishes is seen to have occurred in Pangea. The *Neoceratodus* lineage should also have originated on Pangea in the Late Permian – Early Triassic. This result contrasts with most other hypothesis of relationships that placed *Neoceratodus* as the sister group of lepidosirenids. A *Neoceratodus*–

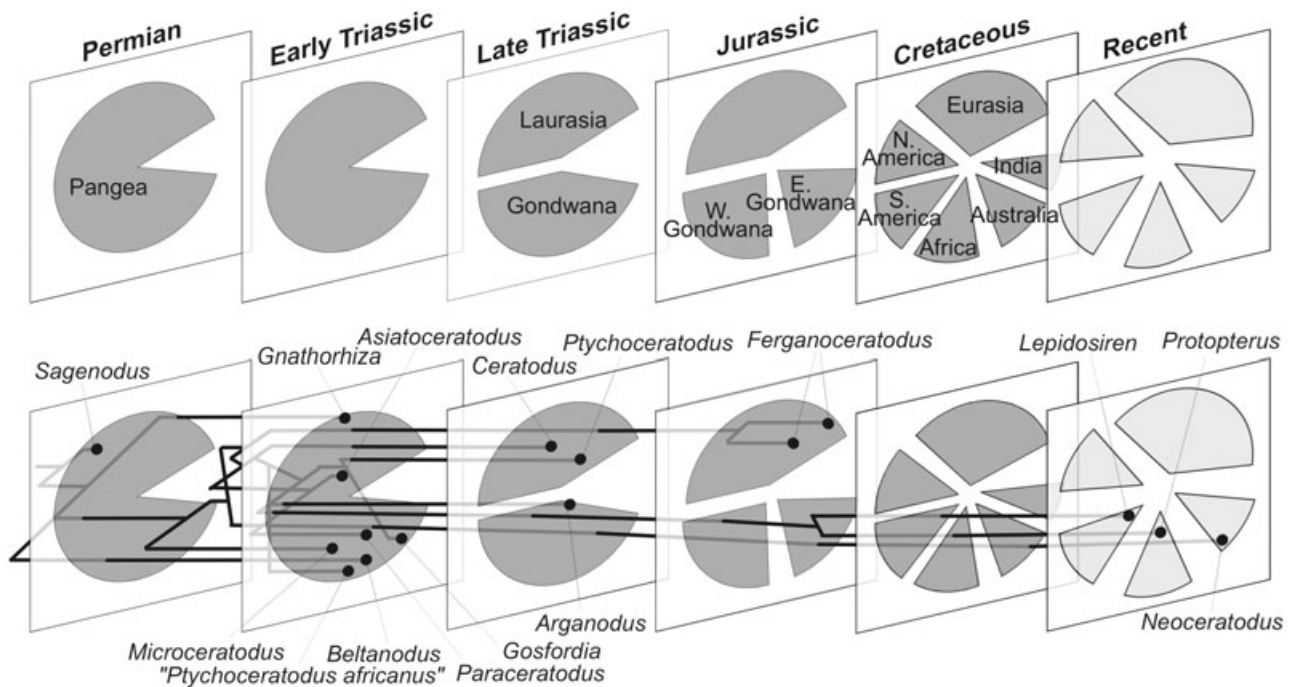


Figure 21. Plot of the phylogenetic tree against stratigraphy and palaeogeography. The upper row shows schematic evolution of the palaeogeographical pattern over time. The lower row shows the phylogenetic tree included in the palaeogeography. Vicariant events are favoured over dispersal events.

lepidosirenids sister-group relationship implies a vicariant event between the western Gondwanan lungfishes – *Protopterus* and *Lepidosiren* – and the eastern Gondwanan one – *Neoceratodus* – some time during the Jurassic. However, the presence of isolated tooth plates referable to *Neoceratodus* in the Early Cretaceous of Australia (Kemp & Molnar, 1981), Africa (Martin, 1984; Churcher, 1995; Churcher & De Iuliis, 2001) and South America (Martin, 1984; Gayet & Brito, 1989; Gallo & Azevedo, 1996) better supports the hypothesis of a widespread distribution of the representatives of the *Neoceratodus* lineage on Gondwana owing to an ancient origin of the group rather than a younger origin followed by dispersal events between Australia and western Gondwana via Antarctica.

Possible vicariant events are the cladogenetic event between *Asiatoceratodus* in Laurasia and *Paraceratodus* in Gondwana during the Early Triassic (but the sister-group relationships between the genera are weakly supported and questionable as mentioned above) and the cladogenetic event between *Ptychoceratodus serratus* in Laurasia and *Gosfordia* in Gondwana during the Early Triassic. A younger and better supported vicariant cladogenetic event is the separation of *Lepidosiren* and *Protopterus* during the fragmentation of western Gondwana into South America and Africa during the Early Cretaceous. There is

another possible sister-group relationship between both sides of the South Atlantic exemplified by *Aragnodus tiguidiensis* in the Early Cretaceous of North Africa (Martin, 1984) and *Aragnodus* sp. from the Albian–Cenomanian Itapecuru Group in Brazil [Dutra & Malabarba (2001) referred the material to *Asiatoceratodus* sp. by comparison with '*Asiatoceratodus*' *tiguidiensis*. However, we do not recognize here the synonymy of *Arganodus* with *Asiatoceratodus* proposed by Kemp (1998)]. But occurrences on both sides of the Atlantic are based on isolated tooth plates, and we await cranial material to confirm the hypothesis.

A speciation event between both species of *Ferganoceratodus* (based on skull materials) occurred on mainland Asia. The Indochina terrane, on which is located the Phu Num Jun site, has a Gondwanan origin and collided with mainland Asia with the closure of the Palaeotethys during the Late Palaeozoic (Metcalf, 1998; not shown on Fig. 21). The Thai lungfishes show no hint of Gondwanan relationships, but there is clear evidence of faunal continental dispersal between Central Asia (Kyrgyzstan, but also South China and Mongolia according to the isolated tooth plates) and south-east Asia during the Jurassic or earlier.

Paraceratodus and *Beltanodus* are two Madagascan lungfishes from the Early Triassic. They belong, however, to two very distinct lineages indicating that they are remnants of ancient Pangean faunas rather than

the result of a local diversification. In the same way, *Asiatoceratodus* and *Ferganoceratodus jurassicus* both have been found in the Fergana valley, from Lower Triassic and Middle Jurassic deposits, respectively, but they, too, belong to distinct lineages.

There are no strong discrepancies between the phylogenetic relationships and the palaeogeographical framework, such as the occurrence of very long ghost lineages. Moreover, no long faunal dispersals are required to explain the palaeobiogeographical pattern. This pattern of spatio-phylogenetic relationships is based on occurrences of reasonably complete specimens that generally include skull material and tooth plates. Isolated tooth plates are much more abundant and have often been referred to taxa discussed here. Some of this material may contradict the pattern proposed here if they are confirmed by more complete material in the future.

CONCLUSION

Non-dental remains of Mesozoic lungfishes are rare and any discoveries of cranial material will provide important information regarding the evolutionary history of these fishes. In particular, they bridge the wide gap between the relatively well-preserved Palaeozoic forms and the modern representatives. The new material described here is one of the pillars of the bridge. *F. martini* shows detailed anatomical characters of the skull roof, palate and lower jaw. It provides features that are either absent or unknown in other post-Palaeozoic lungfishes, such as the presence of a 'hard snout' with a structure intermediate between the cosmine-covered hard snout of some Devonian dipnoans and the soft, richly vascularized snout of *Neoceratodus*. The skull roof pattern described here leads us to question previous attempts to recognize homologous bones and scenarios of fusions or topographic invasions of ossifications among derived lungfishes. We chose to use a topographically based nomenclature in the description of the specimen and in the definition of the characters, which does not involve assumptions of fusion, fragmentation, loss, etc., in the establishment of primary homologies. The phylogenetic relationship we obtained shows good resolution and a low level of homoplasy, although all nodes are very weakly supported. When included within a spatiotemporal framework in an attempt to satisfy the 'chronobiogeographical' paradigm (Hunn & Upchurch, 2001), the cladogram becomes a tree, which is in good agreement with palaeogeographical reconstructions. No major dispersal events are necessary to explain the pattern, which is a rather satisfactory result for these sedentary fishes. The main feature of the tree is the deep and ancient split between the *Neoceratodus* lineage and a lineage comprising most of the Mesozoic forms

together with the lepidosirenids. This ancient split explains the wide distribution of representatives of the *Neoceratodus* lineage in Gondwanaland in the Cretaceous. Finally, the systematic assignment of the cranial material fits a former identification of the Thai lungfish based on isolated tooth plates, and confirms the use of tooth plates as diagnostic remains for dipnoans.

ACKNOWLEDGEMENTS

We are indebted to the head of Wat Buddhabut, Phra Sakda Thammaratho, for his help during the field trip. We thank all those who took part in the excavations at Phu Nam Jun and in the preparation of the specimen and A. Averianov (Saint Petersburg) for access to the collection. We thank Mr P. Crabb (Photographic Unit of NHM) for the photographs, Dr P. Taylor and Dr B. J. Williamson (NHM) for their help with the SEM, and Dr P. L. Forey (NHM) for his thorough reading of the manuscript and for his comments, as well as those of two anonymous referees. L.C.'s research was supported by a Marie Curie Individual Fellowship funded by the Swiss Federal Office for Education and Science (grant no. 02.0335). This work was supported by the Department of Mineral Resources, Bangkok, by the TRF-CNRS Special Programme for Biodiversity Research and Training (BRT/BIOTEC/NSTDA), Grant BRT R-245007, and by the Palaeontological Research and Educational Centre, Mahasarakham University.

REFERENCES

- Agassiz L. 1833–1843.** *Recherches sur les Poissons fossiles*, 5 volumes. Neuchâtel: Nicolet.
- Antunes MT, Schaeffer B. 1990.** Triassic fishes from the Cassange depression (R.P. de Angola). IV. – Synthesis and Discussion. *Ciências da Terra, Número Especial*: 33–39.
- Arratia G, Schultze H-P, Casciotta J. 2001.** Vertebral column and associated elements in Dipnoans and comparison with other fishes: development and homology. *Journal of Morphology* **250**: 101–172.
- de Beer G. 1937.** *The development of the vertebrate skull*. London: Oxford University Press.
- Beltan L. 1968.** La faune ichthyologique de l'Eotrias du N.W. de Madagascar: le neurocrâne. *Cahiers de paléontologie, éditions du CNRS*.
- Bemis WE. 1984.** Paedomorphosis and the evolution of the Dipnoi. *Paleobiology* **10**: 293–307.
- Bemis WE. 1986.** Feeding systems of living dipnoi: anatomy and function. In: Bemis WE, Buggren WW, Kemp NE, eds. *The biology and evolution of lungfishes*. *Journal of Morphology*, Centennial Supplement: 249–275.
- Bemis WE, Northcutt RG. 1992.** Skin and blood vessels of the snout of the Australian lungfish, *Neoceratodus forsteri*, and their significance for interpreting the cosmine of Devonian lungfishes. *Acta Zoologica (Stockholm)* **73**: 115–139.

- Berman DS. 1976a.** Cranial morphology of the Lower Permian lungfish *Gnathorhiza* (Osteichthyes: Dipnoi). *Journal of Paleontology* **60**: 1020–1033.
- Berman DS. 1976b.** Occurrence of *Gnathorhiza* (Osteichthyes: Dipnoi) in aestivation burrows in the Lower Permian of New Mexico with description of a new species. *Journal of Paleontology* **50**: 1034–1039.
- Berman DS. 1979.** *Gnathorhiza bothrotreta* (Osteichthyes: Dipnoi) from the Lower Permian Abo Formation of New Mexico. *Annals of the Carnegie Museum* **48**: 211–230.
- Bertmar G. 1968.** Phylogeny and evolution in lungfishes. *Acta Zoologica (Stockholm)* **49**: 1–13.
- Brien P. 1962.** Etude de la formation, de la structure des écailles de Dipneustes actuels et de leur comparaison avec les autres types d'écailles des Poissons. *Musée Royal d'Afrique Centrale-Tervuren, Belgique, Série 8 – Sciences Zoologiques* **108**: 54–128.
- Buffetaut E, Tong H, Suteethorn V. 1994.** First post-Triassic labyrinthodont amphibian in South East Asia: a temnospondyl intercentrum from the Jurassic of Thailand. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* **7**: 385–390.
- Campbell KSW, Barwick RE. 1986.** Paleozoic lungfishes – A review. In: Bemis WE, Buggren WW, Kemp NE, eds. *The biology and evolution of lungfishes. Journal of Morphology, Centennial Supplement*: 93–131.
- Campbell KSW, Barwick RE. 1988.** Geological and palaeontological information and phylogenetic hypotheses. *Geological Magazine* **125**: 207–227.
- de Castelnau F. 1876.** Mémoire sur les poissons appelés Barramundi par les aborigènes du nord-est de l'Australie. *Journal of Zoology* **5**: 129–136.
- Cavin L, Suteethorn V, Buffetaut E, Chitsing S, Lauprasert K, Le Loeuff J, Lutat P, Philippe M, Richter U, Tong H. 2004.** A new fish locality from the Continental Late Jurassic – Early Cretaceous of North-eastern Thailand. *Revue de Paléobiologie S.V.9*: 161–167.
- Cavin L, Suteethorn V, Khansubha S, Buffetaut E, Tong H. 2003.** A new Semionotid (Actinopterygii, Neopterygii) from the Late Jurassic – Early Cretaceous of Thailand. *Comptes Rendus Palévol* **2**: 291–297.
- Cavin L, Suteethorn VA. 2006.** A new Semionotiform (Actinopterygii, Neopterygii) from Upper Jurassic–Lower Cretaceous deposits of north-east Thailand with comments on the relationships of semionotiforms. *Palaeontology* **49**: 339–353.
- Chapman F. 1814.** On a new species of *Ceratodus* from the Cretaceous of New South Wales. *Proceedings of the Royal Society of Victoria* **27**: 25–27.
- Cheng H. 1989.** On the tubuli in Devonian Lungfishes. *Alcheringa* **13**: 153–166.
- Churcher CS. 1995.** Giant Cretaceous lungfish *Neoceratodus tuberculatus* from a deltaic environment in the Quseir (= Baris) Formation of Kharga oasis, Western desert of Egypt. *Journal of Vertebrate Paleontology* **15**: 845–849.
- Churcher CS, De Iuliis G. 2001.** A new species of *Protopterus* and a revision of *Ceratodus humei* (Dipnoi: Ceratodontiformes) from the Late Cretaceous Mut Formation of Eastern Dakhleh oasis, western desert of Egypt. *Palaeontology* **44**: 305–323.
- Dutra MFA, Malabarba MCSL. 2001.** Peixes do Albiano-Cenomaniano do Grupo Itapecuru no estado do Maranhao, Brasil. In: Rossetti DF, Goes AM, Truckenbrodt W, eds. *O Cretaceo na Bacia de Sao Luis-Grajau*. Meseu paraense Emilio Goeldi, 191–208.
- Fishman AP, Pack AI, Delaney RG, Galante RJ. 1986.** Estivation in *Protopterus*. In: Bemis WE, Buggren WW, Kemp NE, eds. *The biology and evolution of lungfishes. Journal of Morphology, Centennial Supplement*: 237–248.
- Fitzinger LJ. 1837.** Über *Lepidosiren*. *Archiv für Naturgeschichte* **2**: 232.
- Forey PL, Gardiner BG. 1981.** J. A. Moy–Thomas and his association with the British Museum (Natural History). *Bulletin of the British Museum (Natural History), Geology* **35**: 131–144.
- Gallo V, Azevedo SAK. 1996.** Um dipnoi da Formacao Brejo Santo, Eocretaceo da Chapada do Araripe, Ceara, Brasil. *Acta Geologica Leopoldensia* **19**: 43–58.
- Gayet M, Brito PM. 1989.** Ichtyofaune nouvelle du Crétacé supérieur du groupe Bauru (états de Sao Paulo et Minas Gerais, Brésil). *Geobios* **22**: 841–847.
- Günther A. 1871.** Description of *Ceratodus*, a genus of ganoid fishes, recently discovered in rivers of Queensland, Australia. *Philosophical Transactions of the Royal Society, London* **161**: 511–571.
- Hunn CG, Upchurch P. 2001.** The importance of time/space in diagnosing the causality of phylogenetic events: towards a 'chronobiogeographical' paradigm. *Systematic Biology* **50**: 391–407.
- Jain SL. 1968.** Vomerine teeth of *Ceratodus* from the Maleri Formation (Upper Triassic, Deccan, India). *Journal of Paleontology* **42**: 96–99.
- Jarvik E. 1967.** On the structure of the lower jaw in dipnoans: with a description of an early Devonian from Canada, *Melanognathus canadensis* gen. et sp. nov. *Journal of the Linnean Society (Zoology)* **47**: 155–183.
- Kaznyshkin MN. 1993.** On the phylogeny and systematics of dipnoan fishes Ceratodontoidei. In: Bogdanova TN, Khozatsky LI, eds. *Phylogenetical aspects of the Paleontology. Proceedings of the XXXV Session of All-Union Paleontological Society, Leningrad 1989*, 170–178 (in Russian).
- Kemp A. 1986.** The biology of the Australian lungfish, *Neoceratodus forsteri* (Kreffft 1870). In: Bemis WE, Buggren WW, Kemp NE, eds. *The biology and evolution of lungfishes. Journal of Morphology, Centennial Supplement*: 181–198.
- Kemp A. 1991.** Australian Mesozoic and Cainozoic lungfish. In: Rich PV, Thompson EM, eds. *The fossil vertebrate record of Australia*. Clayton, Victoria: Monash University Offset Printing Unit, 465–498.
- Kemp A. 1992.** New cranial remains of neoceratodonts (Osteichthyes: Dipnoi) from the Late Oligocene to Middle Miocene of Northern Australia, with comments on generic characters for Cenozoic dipnoans. *Journal of Vertebrate Paleontology* **12**: 284–293.
- Kemp A. 1993.** Problematic Triassic dipnoans from Australia. In: Lucas SG, Morales M, eds. *The nonmarine Triassic*. New

- Mexico Museum of Natural History and Science Bulletin, 223–227.
- Kemp A. 1994.** Australian Triassic lungfish skulls. *Journal of Paleontology* **68**: 647–654.
- Kemp A. 1996.** Triassic lungfish from Gondwana. In: Arratia G, Viohl G, eds. *Mesozoic fishes—systematics and paleoecology*. München: Verlag Dr Friedrich Pfeil, 409–416.
- Kemp A. 1997.** Four species of *Metaceratodus* (Osteichthyes: Dipnoi, Family Ceratodontidae) from Australian Mesozoic and Cenozoic deposits. *Journal of Vertebrate Paleontology* **17**: 26–33.
- Kemp A. 1998.** Skull structure in post-Paleozoic lungfish. *Journal of Vertebrate Paleontology* **18**: 43–63.
- Kemp A. 1999.** Sensory lines and rostral skull bones in lungfish of the family Neoceratodontidae (Osteichthyes: Dipnoi). *Alcheringa* **23**: 289–307.
- Kemp A. 2001.** Petrodentine in derived Dipnoan tooth plates. *Journal of Vertebrate Paleontology* **21**: 422–437.
- Kemp A, Molnar RE. 1981.** *Neoceratodus forsteri* from the Lower Cretaceous of New South Wales, Australia. *Journal of Paleontology* **55**: 211–217.
- Kreff G. 1870.** Description of a giant amphibian allied to the genus *Lepidosiren*, from the Wide Bay District, Queensland. *Proceedings of the Zoological Society of London* **1870**: 221–224.
- Krupina NI. 1994.** First finds of Dipnoans (Ceratodontida) from Mongolia. *Paleontological Journal* **28**: 93–99 (translated from Russian).
- Lehman J-P, Chateau C, Laurain M, Nauche M. 1959.** Paléontologie de Madagascar. XXVIII. – Les poissons de la Sakamena moyenne. *Annales de Paléontologie* **45**: 177–219.
- Marshall CR. 1986.** Lungfish, phylogeny and parsimony. In: Bemis WE, Buggren WW, Kemp NE, eds. *The biology and evolution of lungfishes*. *Journal of Morphology*, Centennial Supplement: 151–162.
- Martin M. 1979.** *Arganodus atlantis* et *Ceratodus arganensis*, deux nouveaux dipneustes du Trias supérieur marocain. *Comptes Rendus de l'Académie des Sciences, Paris* **289**: 89–92.
- Martin M. 1981a.** Les dipneustes et Actinistiens du Trias supérieur continental marocain. *Stuttgarter Beiträge zur Naturkunde, Serie B (Geologie und Paläontologie)* **69**: 1–29.
- Martin M. 1981b.** Les Dipneustes mésozoïques malgaches, leurs affinités et leurs intérêt paléobiogéographique. *Bulletin de la Société Géologique de France* **23**: 579–585.
- Martin M. 1982a.** Nouvelles données sur la phylogénie et la systématique des dipnoi postpaléozoïques. *Comptes Rendus de l'Académie des Sciences, Série II* **294**: 611–614.
- Martin M. 1982b.** Revision von *Tellerodus sturii* (Teller) 1891. *Verhandlungen der Geologischen Bundestalt* **2**: 21–31.
- Martin M. 1984.** Révision des Arganodontidés et des Néoceratodontidés (Dipnoi, Ceratodontiformes) du Crétacé africain. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlung* **169**: 225–260.
- Martin M, Barbieri L, Cuny G. 1999.** The Madagascar Ptychoceratodontids (Dipnoi). Systematic relationships and paleobiogeographical significance. *Oryctos* **2**: 3–16.
- Martin M, Buffetaut E, Tong H, Suteethorn V. 1997.** New Jurassic dipnoans from Thailand. *Geological Society of Denmark, On Line Series 1*: http://www.2dgf.dk/Publikationer/DGF_On_Line/Volume_1/newjur.htm.
- Martin M, Ingavat R. 1982.** First record of an Upper Triassic Ceratodontid (Dipnoi, Ceratodontiformes) in Thailand and its paleogeographical significance. *Geobios* **15**: 111–114.
- Meinke DK. 1986.** Biology and evolution of the dermal skeleton in lungfishes. In: Bemis WE, Buggren WW, Kemp NE, eds. *The biology and evolution of lungfishes*. *Journal of Morphology*, Centennial Supplement: 133–149.
- Metcalfe I. 1998.** Palaeozoic and Mesozoic geological evolution of the SE Asia region: multidisciplinary constraints and implications for biogeography. In: Hall R, Holloway JD, eds. *Biogeography and geological evolution of SE Asia*. Leiden, the Netherlands: Backhuys Publishers, 25–41.
- Miles RS. 1977.** Dipnoan (lungfish) skulls and the relationships of the group: a study based on new species from the Devonian of Australia. *Zoological Journal of the Linnean Society* **61**: 1–328.
- Müller J. 1845.** Über den Bau und die Grenzen der Ganoiden, und über das natürliche System der Fische. *Archiv für Naturgeschichte* **1845**: 91–142.
- Nessov LA, Kaznyshkin MN. 1985.** A lungfish and turtles from Upper Jurassic of Northern Fergana, Kirghiz SSR. *Vestnik Zoologii* **1**: 33–39.
- Olsen EC. 1951.** Fauna of Upper Vale and Choza: 1–5. *Fieldiana, Geology* **10**: 89–128.
- Ørvig T. 1969.** Cosmine and cosmine growth. *Lethaia* **2**: 241–260.
- Owen R. 1839.** A new species of the genus *Lepidosiren*. *Proceedings of the Linnean Society, London* **1**: 27–32.
- Owen R. 1867.** On the dental characters of genera and species, chiefly of fishes from the Lower Main seam and shales of coal, Northumberland. *Transactions of the Odontological Society of Great Britain* **5**: 323–376.
- Patterson C. 1982.** Morphological characters and homology. In: Joysey KA, Friday AE, eds. *Problems in phylogenetic reconstruction*. London: Academic Press, 21–74.
- Peyer B. 1959.** Über die Vomerzähne von *Ceratodus parvus* und über die verschiedenen Altersstadien seiner Zahnplatten. *Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich* **104**: 148–156.
- Philippe M, Suteethorn V, Lutat P, Buffetaut E, Cavin L, Cuny G, Barale G. 2004.** Stratigraphical and palaeobiogeographical significance of fossil wood from the Mesozoic Khorat Group of Thailand. *Geological Magazine* **141**: 319–328.
- Pique A, Laville E, Bignot G, Rabarimanana M, Thouin C. 1999.** The initiation and development of the Morondava Basin (Madagascar) from the Late Carboniferous to the Middle Jurassic: sedimentary, palaeontological and structural data. *Journal of African Earth Sciences* **28**: 931–948.
- Plieninger T. 1844.** In: Meyer H v, Plininger T, eds. *Beiträge zur Paläontologie Württemberg's, enthaltend die Fossilen Wierbelthierreste aus der Triasgebilden mit besonderer Rücksicht auf die Labyrinthodonten des Keupers*. Stuttgart, E Schweizerbart, 1–132.

- Priem F. 1924.** Paléontologie de Madagascar. XII. Les poissons fossiles. *Annales de Paléontologie* **13**: 1–28.
- Racey A, Goodall JGS, Love MA, Polachan S, Jones PD. 1994.** New age data for the Mesozoic Khorat Group of Northeast Thailand. In: Angsuwathana P, Wongwanich T, Tansathien W, Wongsomak S, Tulyatid J, eds. *Proceedings of the International Symposium on Stratigraphic Correlation of Southeast Asia*. Bangkok: DMR, 245–252.
- Racey A, Love MA, Canham AC, Goodall JGS, Polachan S, Jones PD. 1996.** Stratigraphy and reservoir potential of the Mesozoic Khorat Group, NE Thailand. Part 1: Stratigraphy and sedimentary evolution. *Journal of Petroleum Geology* **19**: 5–40.
- Reisz RR, Krupina NI, Smith MM. 2004.** Dental histology in *Ichnomyx karatajae* sp. nov., an Early Devonian Dipnoan from the Taymir Peninsula, Siberia, with a discussion on petrodentine. *Journal of Vertebrate Paleontology* **24**: 18–25.
- Ritchie A. 1981.** First complete specimen of the dipnoan *Gosfordia truncata* Woodward from the Triassic of New South Wales. *Records of the Australian Museum* **33**: 606–616.
- Romer AS. 1936.** The Dipnoan cranial roof. *American Journal of Science* **32**: 241–256.
- Romer AS. 1955.** Herpetichthyes, Amphibioidei, Choanichthyes, or Sarcopterygii? *Nature* **176**: 126.
- Rosen DE, Forey PL, Gardiner BG, Patterson C. 1981.** Lungfishes, tetrapods, paleontology and plesiomorphy. *Bulletin of the American Museum of Natural History* **167**: 163–275.
- Russell DA, Paesler MA. 2003.** Environments of Mid-Cretaceous Saharan dinosaurs. *Cretaceous Research* **24**: 569–588.
- Schultze H-P. 1981.** Das Schädeldach eines ceratodontiden Lungenfisches aus der Trias Süddeutschlands (Dipnoi, Pisces). *Stuttgarter Beiträge zur Naturkunde, Serie B (Geologie und Paläontologie)* **70**: 1–31.
- Schultze H-P. 1995.** Terrestrial biota in coastal marine deposits: fossil-Lagerstätten in the Pennsylvanian of Kansas, USA. *Palaeogeography, Palaeoclimatology, Palaeoecology* **119**: 255–273.
- Schultze H-P. 2001.** *Melanognathus*, a primitive dipnoan from the Lower Devonian of the Canadian Arctic and the interrelationships of Devonian Dipnoans. *Journal of Vertebrate Paleontology* **21**: 781–794.
- Schultze H-P. 2004.** Mesozoic sarcopterygians. In: Arratia G, Tintori A, eds. *Mesozoic fishes 3 – systematics, paleoenvironments and biodiversity*. München: Verlag Dr Friedrich Pfeil, 463–492.
- Schultze H-P, Chorn J. 1997.** The Permo-Carboniferous genus *Sagenodus* and the beginning of modern lungfish. *Contributions to Zoology* **67**: 9–70.
- Schultze H-P, Marshall CR. 1993.** Contrasting the use of functional complexes and isolated characters in lungfish evolution. In: Jell PA, ed. *Palaeontological studies in honour of Ken Campbell*. Association of Australasian Palaeontologists, 211–224.
- Sedgwick A, Murchison RI. 1835.** On the structure and relations of the deposits contained between the Primary rocks and the Oolitic series in the North of Scotland. *Transactions of the Geological Society of London* **2**: 125–160.
- Smith MM. 1977.** The microstructure of the dentition and dermal ornament of three dipnoans from the Devonian of Western Australia: a contribution towards dipnoan interrelations, and morphogenesis, growth and adaptation of the skeletal tissues. *Philosophical Transactions of the Royal Society, London* **281**: 29–72.
- Tabaste N. 1963.** Etude de restes de poissons du Crétacé saharien. *Mémoire IFAN, Mélanges Ichthyologiques* **68**: 437–485.
- Teixeira C. 1949.** La faune de poissons du Karroo de l'Angola et du Congo Belge. *Boletim do Museu e Laboratório Mineralógico e Geológico, Faculdade de Ciências da Universidade de Lisboa* **17**: 27–31.
- Teller F. 1891.** Über den Schadel eines fossilen Dipnoers, *Ceratodus sturii*, nov. spec. aus den Schichten der oberen Trias der Nordalpen. *Abhandlungen der Kaiserlich – Königlichen Geologischen Reichsanstalt* **15**: 1–39.
- Thomson KS. 1975.** On the biology of cosmine. *Peabody Museum of Natural History, Yale University* **40**: 1–58.
- Thomson KS. 1990.** Triassic fishes from the Cassange depression (R.P. de Angola). III.2.3-Sarcopterygii/Dipnoi. *Ciências da Terra, Número Especial*: 29–33.
- Thomson KS, Sutton M, Thomas B. 2003.** A larval Devonian lungfish. *Nature* **426**: 833–834.
- Tong H, Buffetaut E, Suteethorn V. 2002.** Middle Jurassic turtles from southern Thailand. *Geological Magazine* **139**: 687–697.
- Vorobyeva EI. 1967.** Triassic ceratod from South Fergana and remarks on the systematics and phylogeny of ceratodontids. *Paleontological Journal* **4**: 80–87.
- Wade RT. 1935.** The Triassic fishes of Brookvale, New South Wales. *British Museum (Natural History)*: 1–89.
- Weigelt J. 1927.** *Rezente Wirbeltierleichen und ihre paläobiologische*. Leipzig: Bedeutung-Verlag von Max Weg.
- White EI. 1965.** The head of *Dipterus valenciennesi* Sedgwick & Murchison. *Bulletin of the British Museum (Natural History), Geology* **11**: 1–45.
- Woodward AS. 1890.** The fossil fishes of the Hawkesbury Series at Gosford. *Memoirs of the Geological Survey of New South Wales Palaeontology* **4**: 1–55.
- Young CC. 1942.** Fossil vertebrates from Kuangyuan, N. Szechuan. *Bulletin of the Geological Society of China* **22**: 293–297.

APPENDIX 1

CHARACTERS USED IN ANALYSES

1. Median series with:
 0. more than 3 bones
 1. 3 bones or pairs of bones
 2. 2 bones
2. Paired bones in the median series:
 0. present
 1. absent
3. Mediolateral series with:
 0. 4 or more bones
 1. 3 bones
 2. 2 bones
 3. 1 bone
4. 'hard snout':
 0. present, with cosmine
 1. present, without cosmine
 2. absent
5. Skull roof:
 0. extending anteriorly as a mosaic of small bones bearing the supraorbital sensory canals
 1. extending anteriorly as a rostrum formed by a single bone bearing portions of the supraorbital canals
 2. anteriorly straight, or with a short rostrum without supraorbital sensory canal
6. Dermosphenotic:
 0. free
 1. fused or lacking
7. Sensory canals:
 0. deeply buried in the bones
 1. partly bone-enclosed
 2. above the bones (sometimes with grooves visible)
8. Parasphenoid:
 0. small bone located under the oticooccipital region
 1. extends anteriorly under the ethmosphenoid region, and develops posteriorly an elongated stem that reaches the posterior margin of the skull roof
9. First ridge of tooth plates:
 0. longer than or as long as the lingual margin
 1. shorter than the lingual margin
10. Contact between upper tooth plates:
 0. absent
 1. present
11. Contact between lower tooth plates:
 0. absent
 1. present
12. Internal angle of upper toothplates:
 0. $> 90^\circ$
 1. $\leq 90^\circ$
13. Scales:
 0. thick, with cosmine
 1. thick, without cosmine
 2. thin
14. Course of mandibular canals:
 0. parallel in two bones
 1. oral canal in bone, mandibular canal in gutter
 2. both above bone

APPENDIX 2

DATA MATRIX

	1	2	3	4	5	6	7	8	9	1	1	1	1	1
	1	2	3	4	5	6	7	8	9	0	1	2	3	4
<i>Arganodus atlantis</i>	2	1	2	?	2	1	2	1	1	1	1	0	?	2
<i>Asiatoceratodus sharovi</i>	2	1	2	?	2	?	2	?	0	1	0	0	2	?
<i>Beltanodus ambilobensis</i>	1	0	1	2	1	0	0	?	?	?	?	?	?	?
<i>Ceratodus sturii</i>	2	1	2	?	?	0	2	1	1	1	0	0	?	?
<i>Dipterus valenciennesi</i>	0	0	0	0	0	0	0	0	0	0	?	0	0	0
<i>Ferganoceratodus jurassicus</i>	2	1	2	?	2	0	2	?	1	?	?	1	?	?
<i>Ferganoceratodus martini</i>	2	1	2	1	2	0	2	1	1	0	0	1	1	2
<i>Gnathorhiza</i> spp.	1	0	1	2	1	1	1	?	0	0	?	0	1	1
<i>Gosfordia truncata</i>	2	1	1	2	2	1	2	1	?	?	?	?	2	2
<i>Microceratodus angolensis</i>	1	1	1	2	1	?	2	?	?	?	?	?	?	?
<i>Neoceratodus forsteri</i>	2	1	2	2	1	0	2	1	1	0	0	0	1	2
<i>Paraceratodus germanini</i>	1	1	0	2	2	0	2	?	0	1	?	?	?	?
<i>Protopterus</i> spp.	2	1	3	2	2	1	2	1	1	1	1	0	2	2
<i>Ptychoceratodus serratus</i>	1	1	1	2	2	1	2	?	1	1	1	0	?	2
' <i>Ptychoceratodus philippsi</i> '	1	1	2	?	2	1	2	?	1	1	0	?	?	?
<i>Sagenodus</i> spp.	0	0	0	2	0	0	0	1	0	0	0	0	1	1