The dipnoan buccal pump reconstructed in 3D and implications for air breathing in Devonian lungfishes

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Abstract.—Lungfishes are known for, and indeed take their name from, their bimodal respiratory abilities. All three extant genera can use their lungs to extract oxygen from the atmosphere, although their reliance upon this capability differs among taxa. Lungs are considered primitive for the Osteichthyes, however the distinctive buccal pump mode of air gulping exhibited by extant lungfishes appears to be a specialization. It is associated with a number of derived skeletal characters (cranial ribs, long parasphenoid stalk, midline gap between palatal tooth plates) that first appeared during the Devonian. These have been described individually, but in no Devonian lungfish has their three-dimensional (3D) spatial relationship been reconstructed and analyzed. Here we present the 3D morphology of *Rhinodipterus*, a Mid-Late Devonian lungfish from Australia and Europe, based on synchrotron tomography and conventional microtomography scans.

Unlike less crownward contemporaneous lungfishes such as *Griphognathus* and *Chirodipterus*, *Rhinodipterus* has a full set of skeletal buccal pump components that can be directly compared to those of extant lungfishes, suggesting that it made more extensive use of air breathing than other Gogo or Bergisch Gladbach genera. This is interesting in relation to the environmental context as Gogo and Bergisch Gladbach are both marine, contrasting with the frequently hypoxic tropical to subtropical fresh water environments inhabited by modern lungfishes. The evolution of buccal pump-supported lung ventilation was evidently not necessarily associated with a transition to non-marine habitats.

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Introduction

Dipnoans, or lungfishes, as their name suggests, are a group of fish with bimodal respiratory abilities. Not only do they extract oxygen from the water through their gills, but all extant taxa actively swim to the surface to gulp air, although their reliance upon this behavior varies among species, *Neoceratodus* being a facultative air breather whilst *Lepidosiren* and *Protopterus* are obligate air breathers (Johansen et al. 1967, Bishop and Foxon 1968, McMahon 1969, Burggren and Johansen 1986). Dipnoans possess 'true' lungs in the sense that they arise embryonically from the digestive tract ventrally and lie ventral to it. Also, they are associated with a circulatory system that returns blood directly to the heart by means of a pulmonary vein, and they are usually paired. In comparison, gas bladders such as those of many actinopterygians (including gar, bowfin and some teleosts) arise from the digestive canal either laterally or dorsally, lie dorsal to it, and appear to lack specialized pulmonary circulation (Coolidge et al. 2007). Although many people associate lungs with tetrapods, lungs are in fact thought to have evolved very early in the gnathostome lineage; they were probably secondarily lost in chondrichthyans, meaning that their presence in sarcopterygians and actinopterygians would be a retention of a primitive condition (Liem 1988, Perry et al. 2001).

Lungfishes are not the only fish with 'true' lungs; for example they are also found in the polypterids, or bichirs (Bartsch 1997, Graham et al. 2014). Lungs are considered to be

primitive for all osteichthyans, and they may have been either lost or modified into a gas bladder within the actinopterygian lineage (Liem 1988, Perry et al. 2001) and in coelacanths (Millot and Anthony 1958). In fact, recent work (Longo et al. 2013) has shown that the bowfin *Amia* retains pulmonary arteries, and suggests that the pulmonary circulation is homologous across all osteichthyans. While two-stroke pumping is also present in tetrapods, the specific two-stroke buccal pump style of air gulping seen in extant lungfishes is unique to this group and is thought to have arisen during the Devonian (Thomson 1969, Campbell and Barwick 1988, Long 1993, Clack 2007, Clement and Long 2010). The two-stroke buccal pump involves mixing of fresh and spent air in the expanding mouth, before compression forces the mixture into the lungs (with the excess expelled through the mouth or nares). This is distinct from a four-stoke buccal pump where old air is bought into the mouth and expelled before taking in new, fresh air to then compress into the lungs (Brainerd 1994, Kardong 2006).

The mechanics of the dipnoan air breathing buccal pump was studied in detail half a century ago (Grigg 1965, Johansen et al. 1967, Bishop and Foxon 1968, McMahon 1969). There are numerous soft tissue adaptations relating to the specialized circulation and respiratory systems of lungfishes, in the heart and lung for example, in addition to those skeletal elements involved (Burggren and Johansen 1986). McMahon (1969) observed using X-ray cinematography that the pectoral girdle, ceratohyal and cranial ribs are activated during respiratory cycles in *Protopterus*. Similarly, the muscles attaching to the cranial rib were shown to be electromyographically stimulated during both expansion and compression of the buccal cavity (McMahon 1969). Moreover, based upon their observations of *Lepidosiren*, Bishop and Foxon (1968) emphasized the essential role of the tongue in the dipnoan buccal pump; it is vital to seal the buccal cavity by pressing the tongue against the roof of the mouth before forcing air down into the lungs.

Due to the scarcity of preserved soft tissue, we must rely on osteological features associated with buccal pump air breathing as indicators of this behavior in extinct forms. A number of characters considered important for buccal pump air gulping have been identified in several fossil lungfishes. These include an elongated parasphenoid stem (thought to enlarge the buccal cavity so as to hold a larger air bubble), tooth plates with an abrupt posterior edge and slot for the tongue pad (to create an effective seal), and a mobile pectoral girdle and hyoid arch indicated by large areas for muscle attachments (to allow even greater expansion of this region) (Campbell and Barwick 1988). Thomson (1969) recognized that reduced ossification of the cheek and operculogular series would allow greater lateral expansion of the buccal cavity, also the importance of cranial ribs in anchoring the pectoral girdle during hyoid depression and their likely role in air gulping in fossil lungfishes has been discussed (Long 1993), and Long and Clement (2009) interpreted curved pleural ribs as a possible adaptation for enlarged lungs in air breathing forms. However, others (Pardo et al. 2014) have alternatively interpreted the presence of cranial ribs and elongation of the parasphenoid in relation to a change in diet from durophagous to more omnivorous feeding, and not necessarily related to air gulping.

Initially, many researchers theorized that the transition to freshwater environments, which are commonly less oxygenated than marine waters (Graham 1997), drove the evolution of vertebrate air breathing (Thomson 1969, Graham et al. 1978) during a time of low global oxygen levels (Clack 2007, Berner 2009, Dahl et al. 2010). Indeed, most lungfish fossils that have been considered as 'air breathers' have been found in freshwater or marginal deposits, and the best-preserved marine lungfishes usually lack those features considered salient (Miles 1977, Campbell and Barwick 1988). The exceptions include *Scaumenacia* and *Fleurantia* from the Late Devonian Escuminac Bay (Miguasha) fauna (Cloutier 1996), and *Rhinodipterus*.

Rhinodipterus is a Mid-Late Devonian genus originally known from deposits throughout Europe (Gross 1956, Ørvig 1961, White 1962, Krupina 1995), including the early Frasnian marine Bergisch Gladbach locality in Germany. The most recently described species, *Rhinodipterus kimberleyensis* (Clement 2012), hails from the

shallow tropical reef deposits of the early Frasnian Gogo Formation, north Western Australia. This genus has previously been discussed in relation to the evolution of buccal pump air breathing in lungfishes, with particular emphasis on its marine origin (Clement and Long 2010). One of our specimens, a skull from the Gogo Formation of Western Australia, is a perfectly undistorted partial cranium; the other, from Bergisch Gladbach in Germany, is slightly flattened but includes the skull, and an articulated anterior vertebral column and shoulder girdle. *Rhinodipterus* is one of the most crownward fossil lungfishes with a solidly ossified braincase and anterior axial elements, which allows the spatial relationships of buccal pump components to be reconstructed.

As Bergisch Gladbach and the Gogo Formation both yield three-dimensional skeletal material that is often exceptionally preserved, the use of micro computed tomography and synchrotron tomography to analyze these specimens enables new insights into the anatomy of lungfishes, which is fundamental for interpreting their evolutionary relationships. The aim of the present study is to further our understanding of the anatomy of this genus from three-dimensional scan data of both *Rhinodipterus ulrichi* and *Rhinodipterus kimberleyensis,* and to use this new data to reconstruct the most complete dipnoan buccal pump complex in three dimensions to date.

Material And Methods

Rhinodipterus ulrichi, Ørvig 1961 (NRM P6609a) is from the latest Givetian/earliest Frasnian lagoonal Bergisch Gladbach area, Germany (Ørvig 1961, Jessen 1973, Friedman and Coates 2005). The specimen is a partially mechanically prepared three-dimensional specimen, which has suffered some slight lateral compression. NRM P6609a was scanned using propagation phase contrast X-ray synchrotron microtomography (PPC-SRμCT) at beamline ID19, European Synchrotron Radiation Facility (ESRF), France, with an isotropic voxel size of 30 microns. In order to reach optimal contrast, the specimen was scanned with 4 meters between the sample

and the detector to obtain propagation phase contrast. It was also scanned using the attenuation protocol (Sanchez et al. 2013) with the sample immersed in a plastic tube filled with aluminum balls, in order to work at relatively low energy using a filtered white beam. The average detected energy of the polychromatic beam resulting from the filters, detector properties and transmission through the sample and aluminum balls was 90 keV. 4000 projections of 0.1 s each over 360 degrees were used in half-acquisition mode (center of rotation on the side of the field of view) in order to reach a lateral reconstructed field of view of 80 mm. Two columns of 30 scans each were necessary to cover the full length of the specimen. Each scan was reconstructed independently and all the slices were concatenated at the end of the processing to produce the final reconstructed volume. The synchrotron data has been deposited onto and can be accessed from the ESRF public database at http://paleo.esrf.fr.

Rhinodipterus kimberleyensis, Clement 2012 (WAM 09.6.149) is from the early Frasnian Gogo Formation (Playford 1980, Playford et al. 2009). This specimen is uncrushed, undistorted and was acid-prepared in dilute acetic acid. WAM 09.6.149 was scanned at the Australian National University (ANU) High Resolution X-ray Computed Tomography facility (Sakellariou et al. 2004), with a scan resolution of 55.5 microns.

Three-dimensional modeling and segmentation of both specimens was completed using either VGStudio Max, version 2.2 (Volume Graphics Inc., Germany) or Mimics v.15.01 (Materialise Medical Co, Belgium). Stereolithographs (STL) were then imported into 3-matic 8.0 (Materialise Medical Co, Belgium) and combined to create a hypothetical *Rhinodipterus* buccal pump complex with elements from the two individuals scanned (see animation in Supplementary Appendix). As *R. ulrichi* had suffered some lateral compression during preservation, this specimen was scaled and expanded using the warp tool (3-matic 8.0) to match the dimensions of the undistorted *R. kimberleyensis* specimen, using the width across the quadrate-articular joint as a reference point. While both specimens were of similar scale in skull length (*R. kimberleyensis* ≈ 52 mm,

R. ulrichi 62 mm), the skull width was approximately two-thirds of the length in the undistorted specimen, while it was only one-third for *R. ulrichi*. Some elements were already preserved in natural articulation (such as the cranial rib and occipital neural arch), while the pectoral girdle elements were positioned accordingly by comparison with extant taxa (Criswell 2015). Furthermore, paired elements have been mirrored to complete both left and right sides.

Phylogenetic analysis was conducted using the 'comprehensive character matrix (S1)' of Pardo et al. (Pardo et al. 2014), containing 38 taxa and 150 characters, but with 15 character states corrected for *Rhinodipterus* (3, 26, 37, 39, 41, 48, 49, 52, 67, 72, 81 and 115 for *R. kimberleyensis;* 16, 36 and 38 indicate changes in scoring for *R. ulrichi*). The corrected character matrix and justification for corrected codings can be found in Supplementary Information at http://dx.doi.org/10.5061/dryad.57f3t. The maximum parsimony analysis was conducted using PAUP*4.0b10 (Swofford 2001) using the heuristic search setting with stepwise addition with random addition sequence, and a total of 1000 replications. All characters were assigned equal weight. Bootstrap analysis of 1000 replicates using fast stepwise addition was conducted to assess node support. Bayesian inference was assessed using MrBayes v.3.2.4 (Ronquist et al. 2012), with prior settings for standard morphological analyses retained. A 50% majority-rule consensus tree was generated with posterior probabilities greater than fifty percent retained.

Institutional abbreviations: ANU, Australian National University, Canberra, Australia; ESRF, European Synchrotron Radiation Facility, Grenoble, France; NRM, Naturhistoriska Riksmuseet, Stockholm, Sweden; WAM, West Australian Museum, Perth, Australia.

Systematic Background And New Features

The systematic background of *Rhinodipterus* is as follows: Osteichthyes (Huxley 1880); Sarcopterygii (Romer 1955); Dipnomorpha (Ahlberg 1991); Dipnoi (Müller 1844); Rhinodipteridae (Campbell and Barwick 1990); and *Rhinodipterus* (Gross 1956).

Following our work on *Rhinodipterus* for the current paper, we wish to propose a slightly amended diagnosis for *Rhinodipterus kimberleyensis* (Clement 2012): Amended diagnosis. *Rhinodipterus* sp. with parasphenoid stalk strongly waisted; pterygoid tooth plates with seven tooth rows; prearticular tooth plates with six tooth rows; symphysis length 50 percent of total mandible length; ceratohyal with pronounced lateral crest and distinct ventral notch; sacculolagenar pouch with notch on ventral margin.

The original diagnosis (Clement 2012) is mostly confirmed, except the author wishes to remove 'pectoral girdle with horizontal dorsal edge' from the species diagnosis. Although it remains to be confirmed, it is unlikely that the shoulder girdle of *R. kimberleyensis* differs so greatly from that of *R. ulrichi*, and instead was probably interpreted erroneously in the original diagnosis. Also note that "few or no lateral line pores on J bone" has been removed from the diagnosis as these have been shown to vary with age and between individuals of the same species and are unlikely to be a useful diagnostic character (e.g., see White 1965).

Rhinodipterus kimberleyensis, Gogo, Australia.— The original description of *R. kimberleyensis* WAM 09.6.149 (Clement 2012) is confirmed, however additional information concerning the skull and neurocranium will be discussed below. Much more detail can be gleaned from *R. kimberleyensis* compared to that of *R. ulrichi* NRM P6609a due to its lack of crushing and better preservation. The posterior occipital region is obscured in the *R. kimberleyensis* specimen by disarticulated scales and other bones, however the use of tomographic data has now enabled its description (Fig. 1A-D).

Compared to the other long-snouted lungfishes from Gogo, the outline of the neurocranium of *R. kimberleyensis* in posterior view appears taller than that of *Griphognathus* (Miles 1977), more akin to that of *Robinsondipterus* (Long 2010: Fig. 3C). The dorsolateral cristae (Fig. 1B,D) are prominent, robust, and diverge at 45 degrees from each other. The median crista is less obvious, and as in *R. ulrichi*, does not continue as far anteriorly as the dorsolateral cristae. There is heavy roughening on the dorsolateral cristae bone surface that may represent muscle attachment
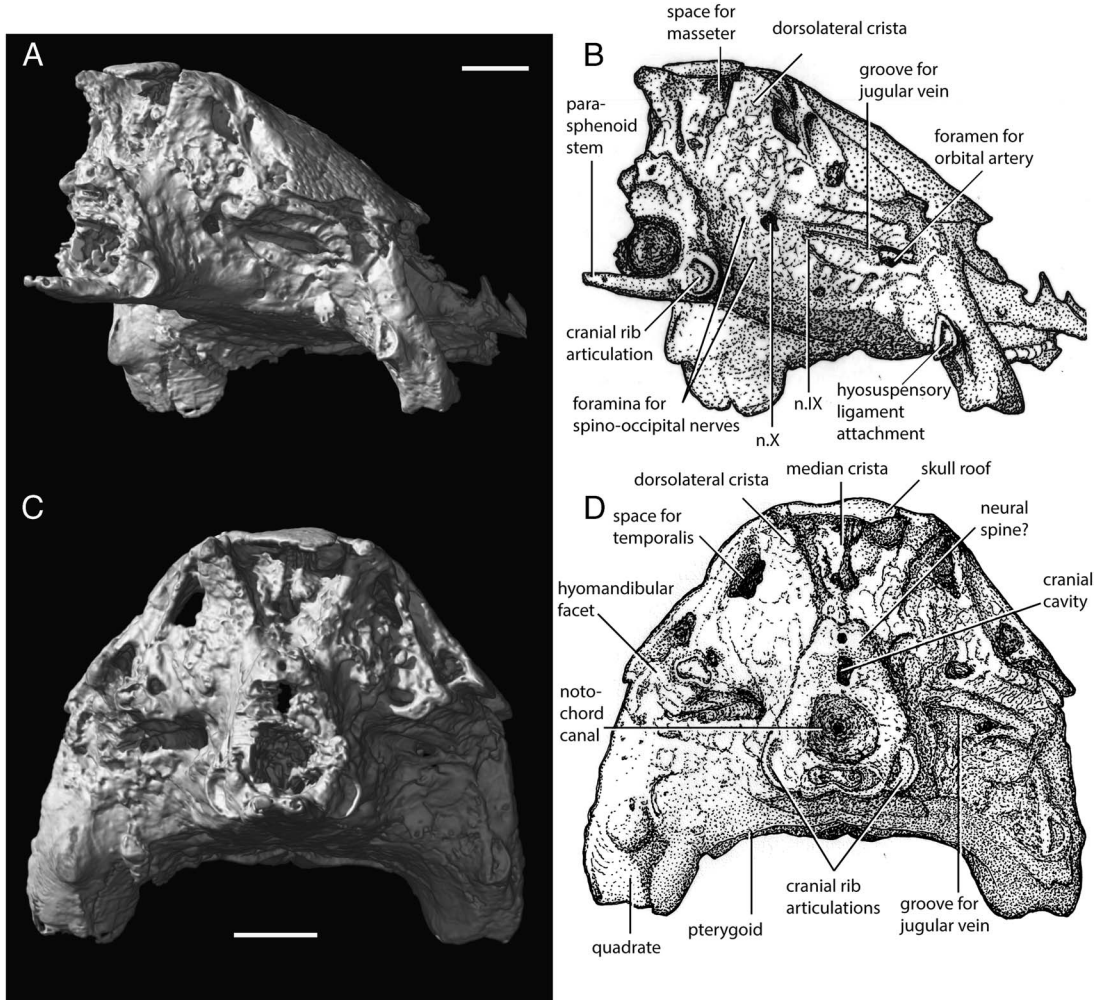
FIGURE 1. *Rhinodipterus kimberleyensis* (WAM 09.6.149) skull in (A, B) posterolateral view. C, D, Posterior view.

scars for the adductor mandibulae. There are single articulations for each hyomandibular facet in contrast to *Robinsondipterus* (Long 2010: Fig. 3), which has separate ventral and dorsal portions. The attachments for the hyosuspensory ligaments lie further ventrally as well-defined, rounded depressions filled with periosteal bone. Posteriorly, the most striking feature is that of the large, rounded articulations for cranial ribs (Fig. 1C,D). They are kidney-shaped with distinct lateral rims, protruding ventrolaterally from the occiput with their lower extent in line with the parasphenoid. The parasphenoid tip is bifuricated posteriorly. The buccohypophyseal opening does not extend through the parasphenoid,

and is only visible as an indentation on the dorsal side.

Rhinodipterus lacks ossified vertebral disc centra like those in *Griphognathus* (Schultze 1975). Instead, similar to many other Devonian taxa including *Chirodipterus* and *Dipterus*, *Rhinodipterus* had a large and essentially unconstricted notochord. The anteriormost part is represented by a large notochordal tunnel that is circular in cross-section, pierces the occiput, and passes forwards ventral to the hindbrain cavity and inner ears (Clement and Ahlberg 2014). In occipital view, the foramen magnum (the posterior opening of the cranial cavity) is smaller than the notochordal tunnel opening, and is oval in outline (Fig. 1C,D).

The foramen for the vagus nerve (X) lies on the side wall of the neurocranium ventral to the dorsolateral cristae, and anteriorly there is a smaller foramen for the glossopharyngeal nerve (IX). A broad, deep 'fluted' groove is visible on both sides of the specimen similar to that in *Griphognathus*, *Holodipterus* (Miles 1977) and *Robinsondipterus* (Long 2010), extending from in front of the foramen for glossopharyngeal nerve (IX) anteriorly towards the robust quadrate bones, and presumably formed a muscle attachment point. Ventral to this, the groove for the jugular vein can be seen, terminating in an opening to carry the vein forwards internally, close to the foramen for the orbital artery. Several small foramina are visible posteriorly on the lateral face of the occiput for the spino-occipital nerves (Fig. 1A,B).

The tooth plates of *R. kimberleyensis* have already been described (Clement 2012), however some further details are herein included. There are six clear tooth rows present with the beginning of a seventh on each pterygoid tooth plate, and the angle between the first and last row is 64 degrees. The length of the hypermineralized dentine area (excluding the smooth dentine medial extension and posterior lip) is 10.5 mm, while the width is 5.5 mm. The number of teeth per row is difficult to determine accurately as the proximal area of each row convalesces into a common, smoothed dentine pad. Distally there are between three to five distinct denticles in each row.

Rhinodipterus ulrichi, Bergisch Gladbach, Germany.—An articulated head plus anterior body of *Rhinodipterus ulrichi* (Ørvig 1961) (NRM P6609a) was synchrotron scanned using propagation phase contrast synchrotron microtomography (PPC-SRµCT) and three dimensionally rendered (Fig. 2). The specimen has undergone slight lateral compression during fossilization; the right side remains the more complete. The lower jaw, operculum, cheek and paired fin elements are not preserved. The original description of *R. ulrichi* (Ørvig 1961) with additions about the postcranial skeleton from (Schultze 1975) is confirmed, with some further comments and other features described herein.

The occipital region has separate cavities for the large notochordal canal and smaller cranial cavity identifiable posteriorly (Fig. 3A,B). The cranial rib articulation surfaces are present, the right one still remains in articulation with the rib. The articulations are broad, rounded structures forming the posteroventral margin of the neurocranium. The median crista, both dorsolateral cristae and some remnants of lateral cristae are present (Fig. 3A–C). The median crista appears discontinuous, not reaching as far anteriorly as the dorsolateral cristae; a similar condition is found in *Orlovichthys*, 'holodontids', *Griphognathus* and *Chirodipterus* (Friedman 2007). There is contact between the visceral surface of the skull roof and the median crista, and both dorsolateral cristae. The quadrate bones are thick and robust. Some evidence of the inner ear is preserved, most probably representing the cavities for the sinus superior. It is not possible to make out the semicircular canals and these were most likely either crushed or not well preserved.

The orbitotemporal region of the braincase is not well preserved and was perhaps partly cartilaginous in life. However, in its most anterior part the cranial cavity outline is visible and carries a small, rounded protuberance dorsally that corresponds to where a pineal eminence would lie (Fig. 3E). The skull roof is solid in this region and there is no evidence of an open pineal foramen. The ethmoid region is better preserved; two separate cavities for the olfactory canals can be identified, although these seem to have collapsed in places. There appears to have been considerable ossification in the snout anteriorly, probably representing crushed rostral tubuli.

In *R. ulrichi*, the parasphenoid is broad and rectangular in outline (Fig. 2D), and does not extend past the occiput as far posteriorly as in the Australian species. In lateral profile the pterygoids are more strongly flexed than in *R. kimberleyensis*, however this may have resulted from the compression of the specimen during preservation. Only the pterygoid tooth plates are preserved in NRM P6609a; these carry six rows of teeth with the beginnings of a seventh as per the holotype (Ørvig 1961) and *R. kimberleyensis* (Clement 2012). The characteristic elongate anteromedial extensions, and the stout, triangular posterior tooth plate extensions are clearly observable in
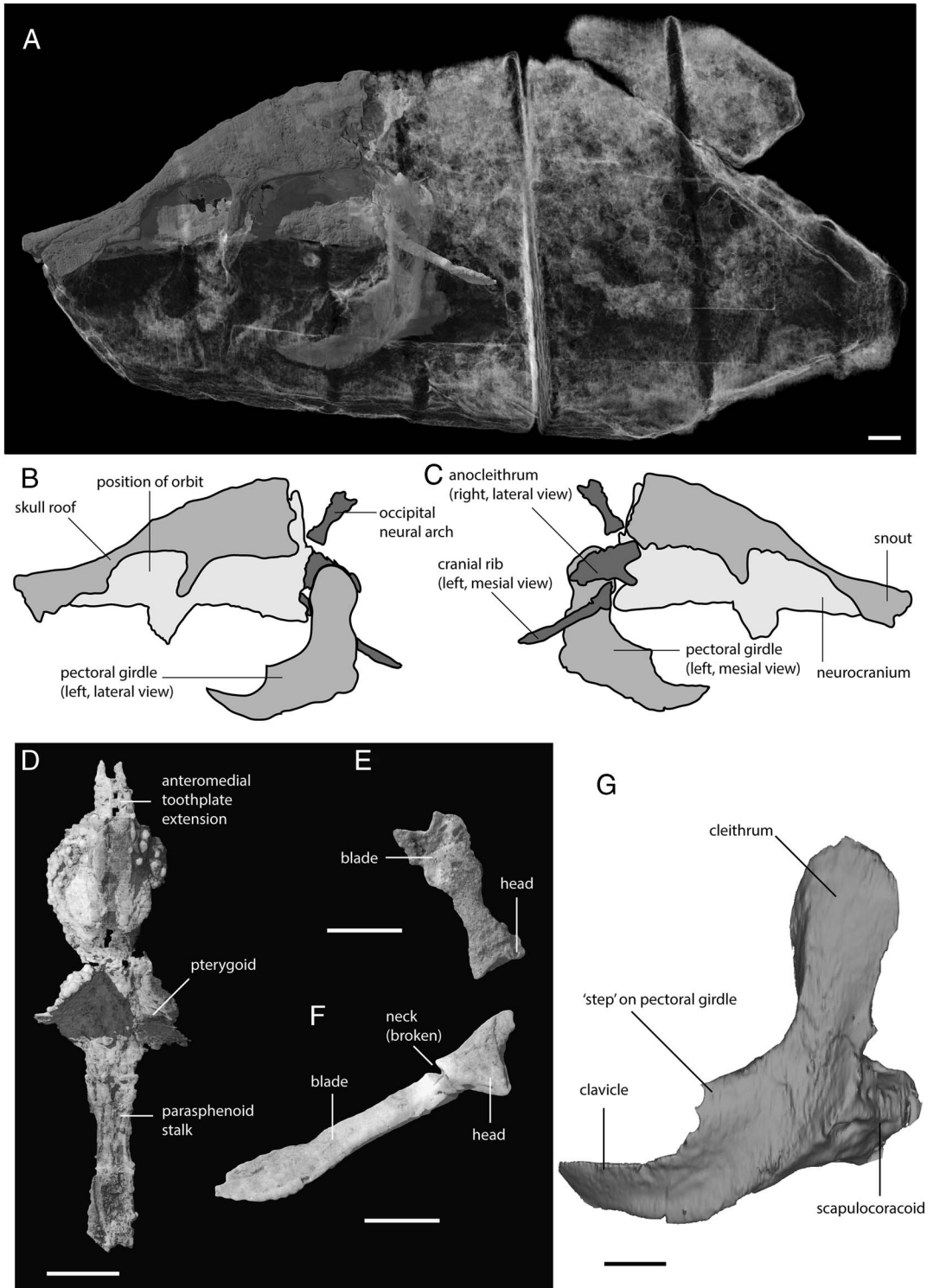
FIGURE 2. *Rhinodipterus ulrichi* (NRM P6609a). A, Whole specimen rendering with matrix transparent. B, C, Schematic drawing showing spatial relationships of various elements in left and right lateral view. D, Parasphenoid and tooth plates in ventral view. E, Occipital neural arch in medial view. F, Cranial rib in medial view. G, Pectoral girdle in lateral view. All scale bars represent 5 mm.
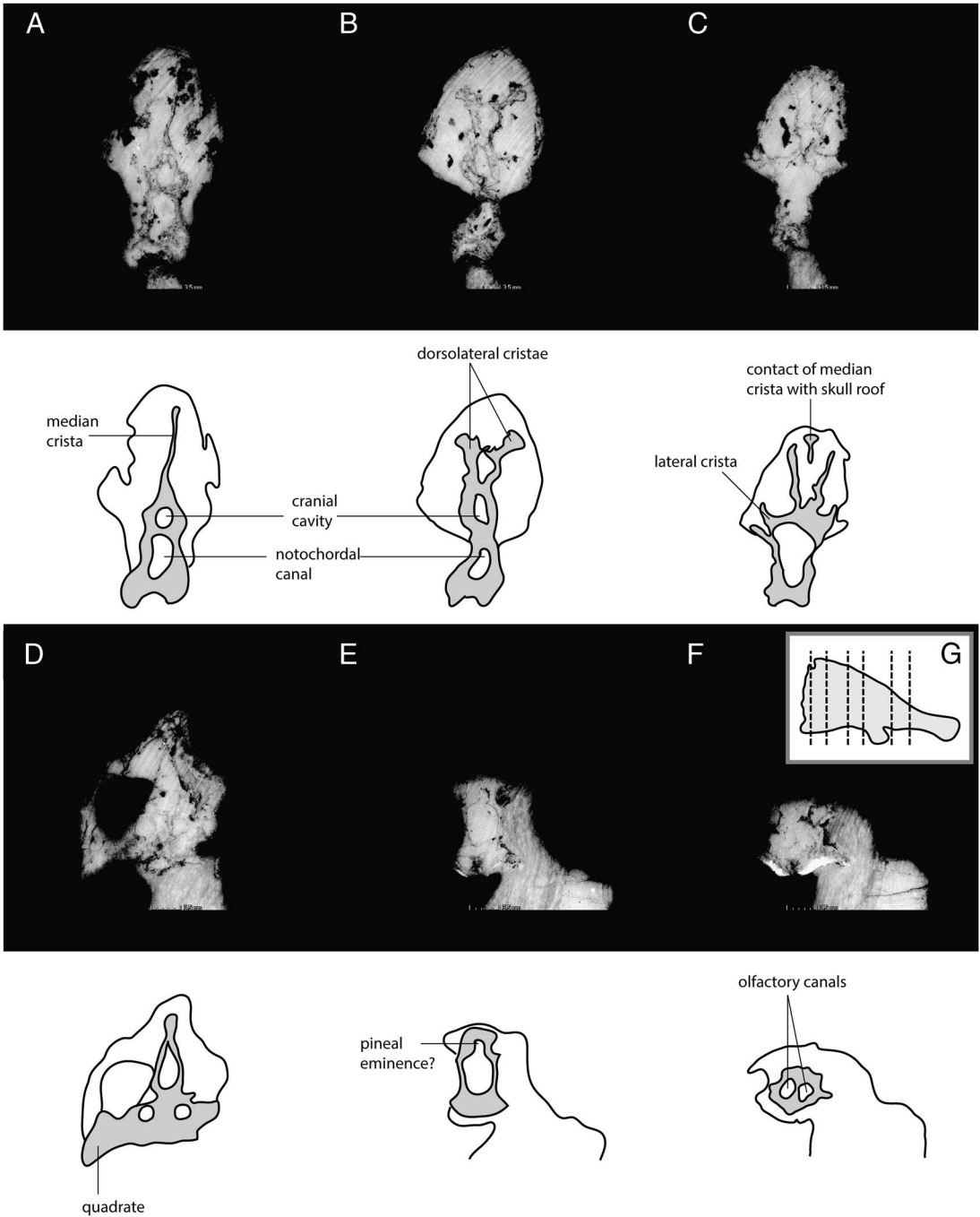
FIGURE 3. A–F, *Rhinodipterus ulrichi* (NRM P6609a) skull and neurocranium in progressive transverse sections moving anteriorly. G, Diagram illustrating positions of slices A–F.

both specimens. The angle between the most mesial and lateral rows is 68 degrees, similar to *R. kimberleyensis* with 64 degrees. There are between two to four discrete denticles distally in each tooth row. The width to length ratio of the tooth plate as well as the tooth row angles have likely been affected by the lateral compression of the specimen.

Cranial ribs were first described in *Rhinodipterus* by Schultze (1975), however here we present the first example with them preserved *in situ* in natural articulation. In *R. ulrichi* NRM P6609a one right rib is preserved (Fig. 2F). There is a break in the bone neck meaning the posterior blade has shifted out of position slightly. However, the bone's relationship with the neurocranium, size, orientation and morphology can be determined from the scan data. The bone angles posterventrally approximately 30° from the horizontal plane of the parasphenoid, similar to extant genera (Goodrich 1958). The cranial rib measures more than 20 mm in length, and is significantly larger than the pleural ribs. The head is a robust, expanded structure measuring 5mm at its widest point. The rib has a narrow neck, and the flattened shaft broadens posteriorly to form a smoothly rounded distal margin. Schultze (1975) figured two different morphologies for the cranial ribs in *R. ulrichi*. In two diagrams (Schultze 1975: Fig. 2A,B) he figures either one or two cranial ribs carrying a well-developed median process in association with another smooth bone lacking this process. No evidence of such a median process can be seen in NRM P6609a. Furthermore, a squat, robust occipital neural arch is well-preserved in articulation with the rear of the neurocranium (Fig. 2E). This bone is shorter than the cranial rib, at just 12 mm in length. The head is bulky and triangular in shape, there follows a stout neck, and the posterior portion of the bone flattens out into a broad blade.

The right dermal shoulder girdle of *R. ulrichi* NRM P6609a represents the first complete shoulder girdle described for this genus (Fig. 2G). It is a robust, well-preserved structure and comprises the clavicle, cleithrum and partial scapulocoracoid. The left anocleithrum is also present. It is less well preserved than that of *R. kimberleyensis*, but nevertheless carries the same two anterior projections and posterior blade-like region as the Australian species. Like *R. kimberleyensis*, the angle between the anterodorsal projection and the corpus of the anocleithrum is smooth, creating an almost completely flat dorsal margin. The anocleithrum of *Rhinodipterus*

most resembles that of *Andreyevichthys* in outline and orientation of the anterodorsal projection (Friedman 2010).

The cleithrum of *R. ulrichi* is high and broad, widening near the rounded dorsal margin. The posterior edge is mostly straight, with a broad, smoothed posteroventral corner. A strong ridge runs down the cleithrum towards the clavicle, but it disappears in the posterior region of the clavicle. The boundary between the cleithrum and clavicle bones is indistinct. The clavicle of *R. ulrichi* is scythe-like anteriorly with a convex ventral margin and pointed tip. The large step on the clavicle anteromedial margin separates the anterior ramus and broad corpus, similarly to that of *Griphognathus, Soederberghia* and *Rhynchodipterus* (Friedman 2010). The cleithrum ridge only appears on the posterior portion of the bone, rather than extending to the tip as in *Scaumenacia* for example. Portions of the scapulocoracoid are preserved in *R. ulrichi*; it is a sturdy, tripodal structure similar to that of *R. kimberleyensis*, but it is difficult to differentiate the bone margins accurately in the scan data. It appears that the shoulder girdle did not bear surface ornamentation.

In many respects the pectoral girdle most closely resembles that of *Griphognathus*. Both genera have a tall, broad cleithrum with straight posterior margin, and a clavicle with large dorsal step and pointed anterior end. It is not as slender as those of *Robinsondipterus* (Long 2010: Fig. 9) and *Scaumenacia* (Friedman 2010: Fig. 8). However the cleithrum bears a more prominent ridge and its dorsal edge is more rounded in *Rhinodipterus*. In light of the newly described *R. ulrichi* shoulder girdle material, we wish to amend the description *contra* Clement (2012) of a "pectoral girdle with horizontal edge" in *R. kimberleyensis*. Only a partial shoulder girdle is known in *R. kimberleyensis*, and the new data from NRM P6609a suggests that this structure was interpreted erroneously in the original description.

Rhinodipterus buccal pump complex.—Both *R. ulrichi* and *R. kimberleyensis* possess cranial ribs, an elongate parasphenoid, a slot between tooth plates with an abrupt posterior margin, and a pectoral girdle with large areas for muscle attachment. In addition, *R. kimberleyensis* has

posteriorly rounded ceratohyals with large areas for muscle attachment (Clement 2012), and curved pleural ribs are known in *R. ulrichi* (Schultze 1975). The relative scarcity of dermal cheek and operculogular elements known for this genus may indicate decreased ossification in this area.

Figure 4 shows the most complete buccal pump complex reconstructed in three dimensions (see also electronic supplementary material at http://dx.doi.org/10.5061/dryad.57f3t). Three elements (pectoral girdle, cranial rib and occipital neural arch) have been modeled from *R. ulrichi*, and three others (skull, mandible and anocleithrum) from *R. kimberleyensis*. Both the cranial ribs and occipital neural arches articulate with the rear of the braincase, but the cranial ribs diverge from the midline at a greater angle. The occipital neural arches extend upwards in a posterodorsal direction, while the cranial ribs have a more acute posteroventral orientation. The posterior extent of the cranial ribs reaches the level of the scapulocoracoid posteroventral corner. The clavicle lies further ventrally than the mandible, and the cleithrum reaches as far dorsally as the articulation for the occipital neural arches. The anterodorsal processes of the anocleithra articulate with the rear of the skull roof, and lie medial to the cleithrum. The posterior margin of the anocleithra extends further than the cleithrum, but not so far as the scapulocoracoid.

Discussion

Buccal pump complex in Rhinodipterus.— *Rhinodipterus* from Bergisch Gladbach and Gogo Formation are closely related (see section *b* below) and provide valuable information in relation to the functional complex of the dipnoan buccal pump (Bishop and Foxon 1968, Thomson 1969, Burggren and Johansen 1986). Most workers hypothesize that dipnoan buccal pump air breathing evolved during the Devonian, concurrently with but independently of the tetrapods (Clack 2007, Clement and Long 2010), while others suggest it was a feature of post-Devonian dipnoans (Pardo et al. 2014). To help clarify when dipnoan air breathing appeared, we shall herein discuss those features in *Rhinodipterus* considered salient in the dipnoan air breathing buccal pump (Thomson 1969, Campbell and Barwick 1988, Long 1993, Long and Clement 2009).

Both the pectoral girdle and hyoid arch move significantly in extant lungfishes during air breathing behavior (Bishop and Foxon 1968, McMahon 1969), mostly during the inspiration phase, but also when forcing air down into the lungs. Robust pectoral and hyoid elements with large spaces for muscle attachment have greater mobility, and the large, rounded ends of ceratohyals like those in *Rhinodipterus* (see Clement 2012: Fig. 6A–D) indicate a greater potential for rotation. We note that many elements of a buccal pump functional system could be utilized during either suction feeding or active aerial respiration. Indeed, there is similar movement of the hyoid arch and pectoral girdle during buccal pump activity during both air gulping and suction feeding behaviors in the extant taxa (Bemis 1986). We propose there was potential for comparable movement of these elements in some of the earlier fossil forms such as *Rhinodipterus* also. It is therefore reasonable to deduce the highly mobile pectoral girdle and hyoid arch in this taxon could have contributed to both behaviors from as early as the Middle Devonian.

Campbell and Barwick (1988) discussed the elongation of the parasphenoid stem (in conjunction with the relative forward movement of the jaw articulation) and concluded that these changes would have considerably increased the size of the buccal cavity allowing the animal to hold a larger air bubble within the mouth. However, others (Pardo et al. 2014) have alternatively interpreted the presence of cranial ribs and elongation of the parasphenoid in relation to a change in diet from durophagous to more omnivorous feeding, and not necessarily related to air gulping.

Cranial ribs are paired bones that articulate with the rear of the braincase in all extant lungfishes (Goodrich 1958), and Long (1993) has previously discussed their significance in fossil forms. Muscles attaching to the cranial ribs are activated during both expansion and compression of the buccal cavity in extant lungfishes during aerial respiration (McMahon 1969,
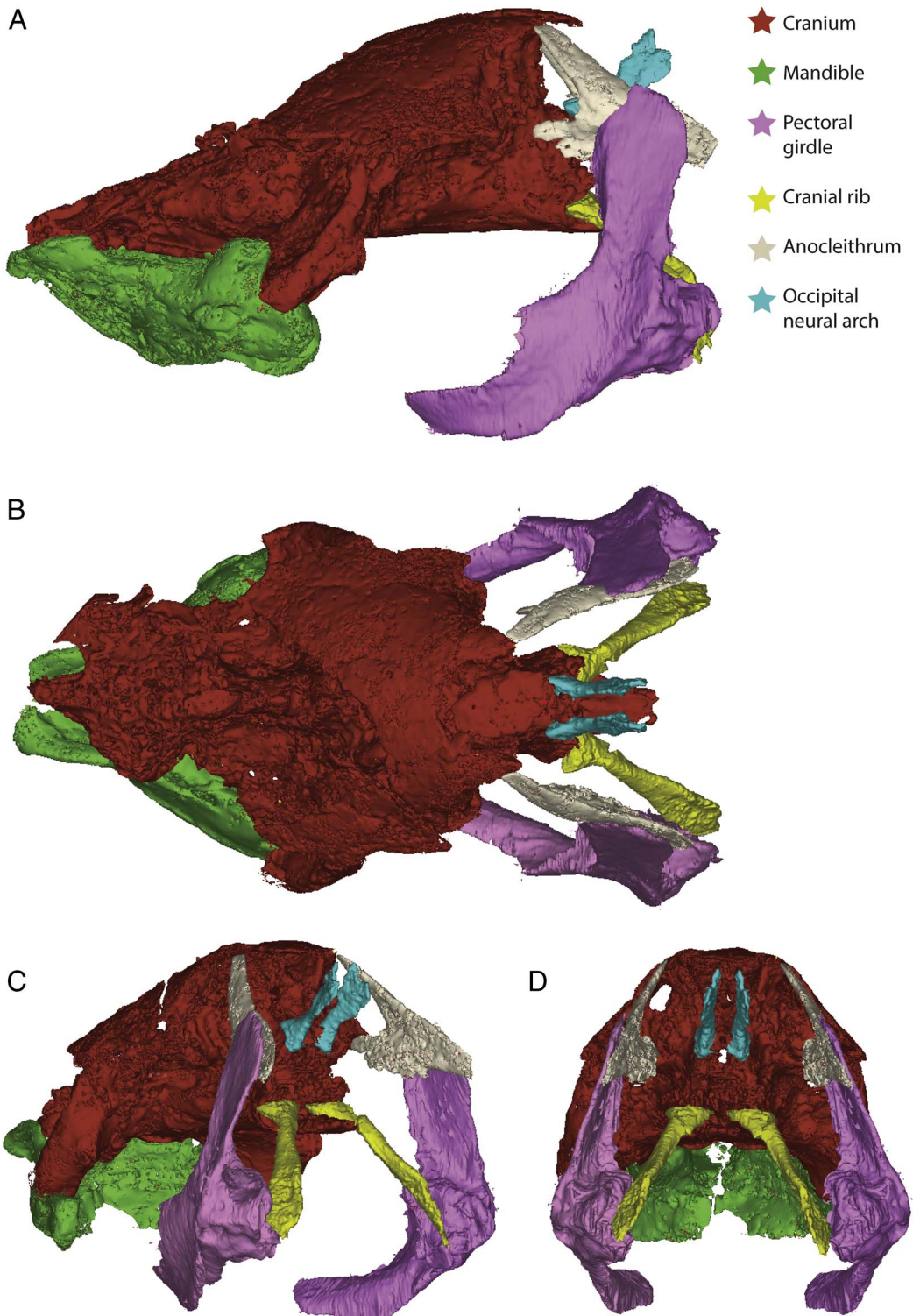
FIGURE 4. Reconstruction of the dipnoan buccal pump complex in 3D, using combined elements from *R. kimberleyensis* WAM 09.6.149 (skull, mandible, anocleithrum), and *R. ulrichi* NRM P6609a (pectoral girdle, occipital, cranial rib). A, left lateral view. B, Dorsal view (anterior to the left). C, Left posterolateral view. D, Posterior view.

Bemis 1986). The anterior muscles that cross from the cranial ribs to the pectoral girdle likely play an important role in anchoring the pectoral girdle during hyoid depression. This action may be performed during suction feeding, but also activated during head raising such as when an animal comes to the surface to breathe (McMahon 1969, Long 1993); this contrasts with the arching of the trunk and downward head angle seen during typical feeding behavior (Bemis 1986).

Thomson (1969) recognized the reduction in size and ossification of the cheek and opercular elements in lungfishes over time and attributed this to a gradual increased reliance on aerial respiration in this group (cf., aquatic respiration). His reasoning followed the premise that with decreased ossification, this region is capable of greater lateral expansion and therefore the animal is able to hold a greater volume of air within the buccal cavity. While much skull roof material is known for *Rhinodipterus*, the cheek elements are considerably less commonly preserved, perhaps due to decreased ossification in this area. We cannot however, definitively comment on the relative reduction in these cheek elements in *Rhinodipterus* with respect to aerial respiration.

In a recent paper, Pardo et al. (2014) argue that a number of features involved in the buccal pump complex of *Rhinodipterus* (as discussed by Clement 2012) are not necessarily related to air breathing but more generally to a change in diet. Their argument that a gap between the pterygoid tooth plates is common in Devonian lungfishes, and that it always accepts the prearticular tooth plates during occlusion, is problematic on two counts. Firstly, many Devonian lungfishes do not possess a pronounced gap between the tooth plates. They either have no gap at all, for example as in *Dipnorhynchus* (Campbell and Barwick 2000), or have only a very narrow one, such as '*Chirodipterus*' *australis* (Miles 1977). Secondly, the morphology of the lower jaws—not only in *Rhinodipterus* but in Devonian lungfishes in general—show without a doubt that the medial most tooth rows of the prearticular tooth plate could never fit into the gap between the pterygoid tooth plates.

A sizeable gap is retained here during occlusion, most probably to accommodate a soft tissue tongue pad to create a seal during air breathing as earlier hypothesized (Campbell and Barwick 1988). Such a pad has been shown to have a vital role in the air breathing behavior of extant forms (Bishop and Foxon 1968, McMahon 1969). The tongue in extant lungfishes lacks intrinsic musculature and does not seem to play a role in the transport of food within the mouth, which is instead achieved hydraulically (Bemis 1986).

The suite of characters discussed here (Fig. 4) is comparable with those of extant taxa (Criswell 2015) and suggests that, at least biomechanically, *Rhinodipterus* would have been capable of buccal pump air gulping. Naturally, without being able to observe these structures in action, we cannot prove that this was its sole or principal function. However, anatomical evidence from *Rhinodipterus* and other taxa (*Howidipterus*, *Barwickia*, Long 1993 and possibly also *Dipterus* Campbell and Barwick 1988; Trewin and Ahlberg 1995) lend support to the hypothesis that buccal pump aerial respiration evolved in lungfishes in the Middle Devonian. This also coincides with the probable appearance of tetrapods based on trackway evidence, and, presumably, their air breathing capabilities (Clack 2007, Niedźwiedzki et al. 2010). The appearance of air breathing in tetrapods is thought to have been concurrent, but independent from that in the Dipnoi (Clement and Long 2010).

Clement and Long (2010) suggested that in contrast to a transition into a freshwater setting, a global oxygen decrease during the Devonian (Berner 2006) drove the appearance of air gulping in lungfishes. However, more recent work suggests that the Devonian oxygen dip was not as extreme as first modeled (Berner 2009). While it is known that the Gogo reef environment was at times euxinic (anoxic in the presence of hydrogen sulfide), this occurred at depth and it is thought that the near-surface waters were better oxygenated (Melendez et al. 2013). The capacity to supplement oxygen through aerial respiration could have provided a strong adaptive advantage to those with the ability to do so during periods of aquatic hypoxia, and no doubt played an

essential role in shaping the evolutionary history of some lungfishes.

While most extant air breathing fish occur in freshwater environments (Graham 1997), *Rhinodipterus* strengthens the idea that the evolution of dipnoan buccal pump-supported lung ventilation was not necessarily associated with a transition to non-marine habitats, and demonstrates that an effective buccal pump evolved in Devonian dipnoans well before the Permian origin suggested by Pardo et al. (2014). Rather than relying on aerial respiration exclusively, a relevant functional analog might instead be the extant tarpon, a primitive marine teleost that uses air breathing to boost its metabolic rate and endure temporarily hypoxic environments (Geiger et al. 2000). Indeed, in many extant fishes (including *Neoceratodus*) activity is a stronger stimulus for air breathing than aquatic hypoxia (Johansen et al. 1967). The evolution of buccal pump air breathing in lungfishes provides a scenario that does not require being tied to either specific environmental condition.

Phylogenetic position of Rhinodipterus.— Recent work by Pardo et al. (2014) describing the Permian lungfish, *Persephonichthys* from Nebraska, USA, includes a phylogenetic analysis that recovers *Rhinodipterus* as polyphyletic, with *R. ulrichi* placed far more basally than '*R*'. *kimberleyensis*. The matrix used (Qiao and Zhu 2009) incorporates 150 characters and 38 taxa, but was modified by Pardo et al. (2014) to include *R. kimberleyensis*. However, upon closer inspection of the scoring we find a number of significant errors (these are detailed in the Supplementary Appendix, alongside the corrected character matrix). Having found 15 errors within the scoring for the two *Rhinodipterus* species alone, we hesitate to accept the result of Pardo et al. (2014) that this genus is polyphyletic, at least with respect to *R. kimberleyensis* and *R. ulrichi*. Upon running their character matrix with characters 3, 16*, 26, 36*, 37, 38*, 39, 41, 48, 49, 52, 67, 72, 81 and 115 corrected as detailed above (* indicates changes in scoring for *R. ulrichi*, all others refer to *R. kimberleyensis*), we find that the position of *R. kimberleyensis* is drastically different in our analysis. *R. kimberleyensis* is recovered as the sister taxon to *R. ulrichi* with bootstrap support of 73% (Fig. 5), a very significant figure considering the overall bootstrap support is low (with the exception of outgroup support). *Rhinodipterus* spp. sit crownward of *Dipterus* and a 'Chirodipterid' clade ('*C*.' *australis*, '*C*.' *liangchengi*, *Pillararhynchus*, *Sorbitorhynchus*, *Adololopas*), but below *Chirodipterus wildungensis* and a number of other Late and post-Devonian lungfish. We do not by any means claim to have resolved Devonian lungfish phylogeny, but we do feel justified in rejecting the claim that *Rhinodipterus* is polyphyletic (Pardo et al. 2014). Instead, we accept that *R. kimberleyensis* and *R. ulrichi* are in fact sister taxa. It is clear that resolving Devonian lungfish phylogeny requires much more work and is beyond the scope of this paper.

Conclusions

Using tomographic data we have reconstructed the most nearly complete dipnoan buccal pump complex in three dimensions, using elements from both *R. kimberleyensis* and *R. ulrichi*. *Rhinodipterus* possessed many of the features considered salient for dipnoan buccal pump air gulping and is argued to have been able to utilize this ability better than the other dipnoans from Gogo or Bergisch Gladbach. The presence of *Rhinodipterus* in marine waters lends support to the hypothesis that the evolution of buccal pump air gulping in dipnoans is not necessarily tied to freshwater environments. Instead, dipnoan air gulping perhaps evolved as a means to endure temporarily hypoxic conditions, like the extant Australian lungfish or the primitive marine teleost, *Megalops*.

Moreover, we have presented new anatomical information for both *Rhinodipterus kimberleyensis* Clement, 2012 and *Rhinodipterus ulrichi* Ørvig, 1961 including an amended diagnosis for *R. kimberleyensis*. We have also shed light on neurocranial anatomy and anterior axial elements, including the first cranial rib preserved in articulation. Furthermore, a corrected character matrix lends support to the close relationship of *R. ulrichi* and *R. kimberleyensis*, and we reject
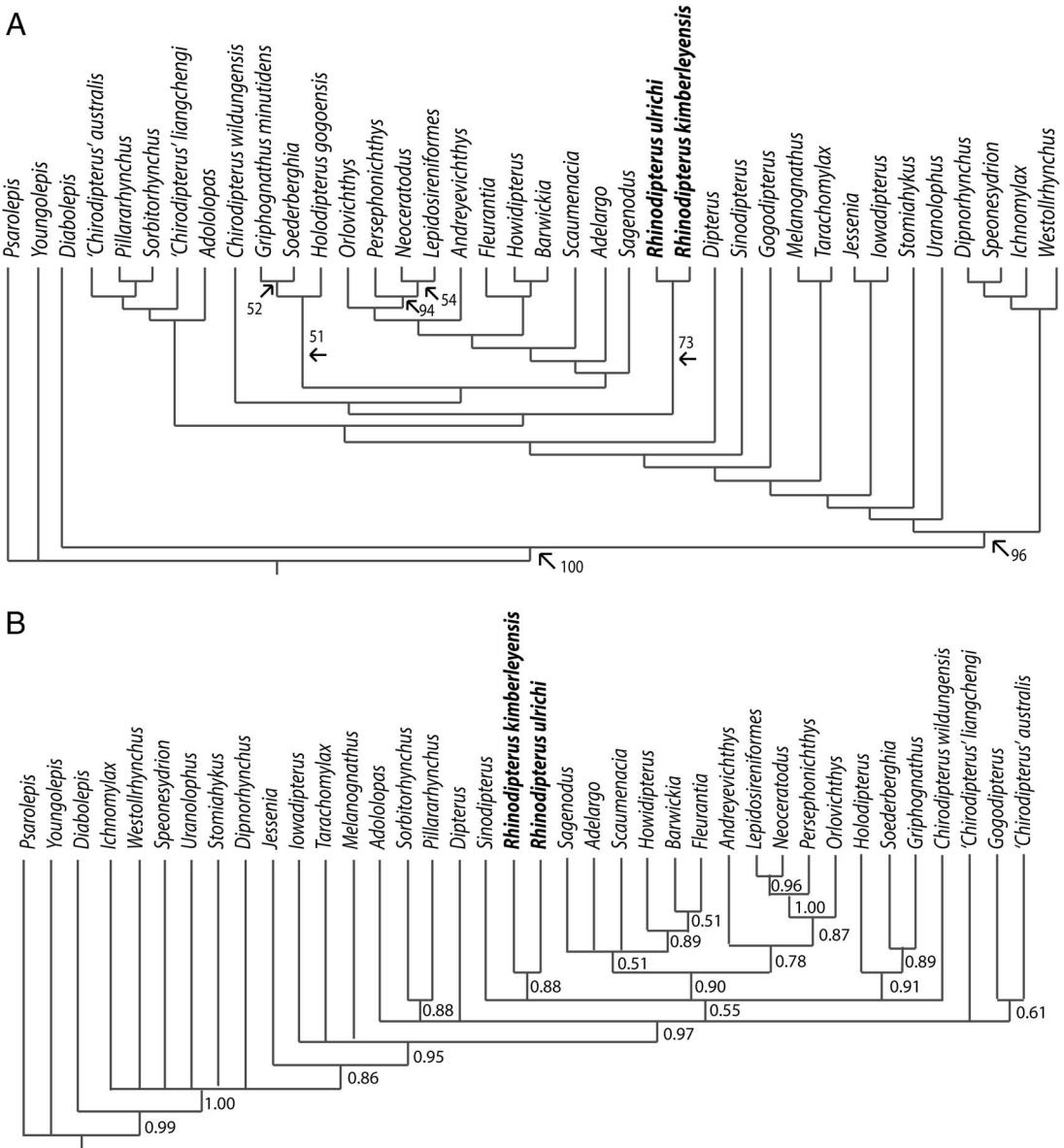
FIGURE 5. A, Phylogenetic relationships of lungfishes based on maximum parsimony analysis of the matrix of Pardo et al. (2014) containing 15 corrected characters for *Rhinodipterus* spp., with bootstrap support values >50% indicated, (Tree length = 501 steps, Consistency Index = 0.3713, Rescaled Consistency Index = 0.2350); B, Bayesian inference 50% majority-rule consensus tree showing posterior probabilities >50%.

the hypothesis of some earlier authors that *Rhinodipterus* is polyphyletic.

Acknowledgments

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