

# Morphology and systematics of the Pennsylvanian amphibian *Platyrhinops lyelli* (Amphibia: Temnospondyli)

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**ABSTRACT:** The morphology of the amphibamid temnospondyl amphibian *Platyrhinops lyelli* from the Middle Pennsylvanian of Linton, Ohio is reassessed from previously described and undescribed specimens. Newly reported or newly significant features include the presence of bicuspid marginal teeth, anteriorly widened frontals, elongate choanae, a broad rhomboidal sphenethmoid and a pair of flattened blade-like ceratohyals. One specimen shows an unusual distribution of tooth sizes along the premaxillaries. No derived characters can be found to justify reference of the species *lyelli* to the genus *Amphibamus* as represented by its type species *A. grandiceps*, but *Platyrhinops* does belong to the ‘*Amphibamus* branch’ of the Amphibamidae.

**KEY WORDS:** Amphibamidae, Carboniferous, dentition, Dissorophoidea, Ohio

*Platyrhinops lyelli* is based on a small number of amphibian specimens from the mid-Pennsylvanian locality of Linton, Ohio, USA. It belongs to the clade of temnospondyl amphibians known as the Dissorophoidea – more specifically, the Family Amphibamidae – which have long been part of the debate over the origin of modern amphibians. Recent work has focused on this family, with several new taxa having been described in the past few years. Inclusion of *Platyrhinops lyelli* in this debate has relied on old or incomplete descriptions: this paper aims to clarify its anatomy so that it can more accurately be included in ongoing cladistic, systematic and morphological studies.

For many years, *Platyrhinops lyelli* was considered congeneric with *Amphibamus grandiceps*, a small temnospondyl from the Late Carboniferous of Mazon Creek, Illinois. Both have a history of being perceived as frog-like and being possible early relatives of frogs. From its first description, *Platyrhinops* (as ‘*Pelion*’) was noted as remarkably frog-like by Wyman (1858), Cope (1868) and Moodie (1916). Under the generic name ‘*Miobatrachus*’, *Amphibamus grandiceps* was more specifically implicated in the origin of modern amphibians by Watson (1940), who pointed out many potential similarities between it and anurans. Reig (1964) suggested ‘branchiosaurs’, a group of poorly known larval temnospondyls, as lissamphibian ancestors. Branchiosaurs and amphibamids, then and now, are considered as closely related (e.g. Schoch & Milner 2008). Carroll (1964) and Estes (1965) agreed that dissorophoids, and *Amphibamus grandiceps* in particular, were close to the ancestors of lissamphibians. At the time, the inter- and intra- relationships of the dissorophids as a family remained unresolved.

Bolt (1969) described the small dissorophoid temnospondyl *Doleserpeton* from the Early Permian of Oklahoma, and erected the monotypic family Doleserpetonidae for it. This animal not only had pedicellate teeth but they were bicuspid: these were lissamphibian-like features. Later, Bolt (1974) described morphological features of *Amphibamus*, *Tersomius* and other dissorophids, separating them from the Doleserpetonidae. Bolt (1979) described bicuspid and possibly pedi-

cellate teeth in *A. grandiceps*, concluding that it was a juvenile dissorophid.

In the context of lissamphibian origins, Truab & Cloutier (1991) distinguished four families of dissorophoids; one family in particular – the Dissorophidae – included the genera *Doleserpeton*, *Tersomius* and *Amphibamus*, amongst others. The other three families were the Trematopidae, the Micromelerpetontidae and the Branchiosauridae. The latter two families are those containing the mainly paedomorphic forms generally known as branchiosaurs.

Milner (1993) and Clack & Milner (1994) attempted to clarify the systematic position of some of the dissorophoid taxa and recognised that *Amphibamus grandiceps* and *A. lyelli* did not share any characters that could unite them in a single genus. They placed the species *lyelli* within the next available generic name (see synonymy history below), *Platyrhinops*. They reinstated the Family Amphibamidae for *Doleserpeton*, *Tersomius*, *Amphibamus* and *Platyrhinops*. Milner (1993) placed Amphibamidae, Branchiosauridae and Lissamphibia in an unresolved trichotomy, with the Dissorophidae, Micromelerpetontidae and Trematopidae, in that order, as successive stem-ward families.

Since then, many anatomical and phylogenetic studies of the dissorophoids have been undertaken, resulting in a growing consensus over the content and intra- and inter-relationships of the Amphibamidae, especially with respect to their closeness to modern amphibians. This work is summarised below in section 8.

## Institutional abbreviations

AMNH – American Museum of Natural History, New York, USA

BMNH – Department of Palaeontology, Natural History Museum (previously British Museum (Natural History)), London, UK

CM – Carnegie Museum, Pittsburgh, USA

FMNH – Field Museum of Natural History, Chicago, USA



MB – Museum für Naturkunde, Humboldt Universität, Berlin, Germany

MCZ – Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA

USNM – National Museum of Natural History, Washington D.C., USA

YPM – Peabody Museum, Yale University, New Haven, USA

## 1. Systematic history of the *Platyrhinops* material

*Platyrhinops lyelli* has a complex synonymy, the holotype and some of the referred specimens having long and distinct taxonomic histories. In the following brief account, the pre-1964 histories of five of the most significant specimens are reviewed separately in the interest of clarity, followed by an integrated history of subsequent research.

Following the description of *Baphetes planiceps* by Owen in 1854, the second Carboniferous amphibian specimen to be recognised as such was a skeleton collected by Dr John V. Lauderdale in 1857 from the mine dump at Linton, Ohio. The type specimen of *Colosteus scutellatus* had in fact been described earlier, in 1856, but as a fish (see Hook 1983 for details). Lauderdale's specimen was reported as a 'batrachian reptile' by Wyman in late 1857. Although only poorly visible in ventral aspect, it was immediately observed to be frog-like in general appearance and initially named *Raniceps lyelli* by Wyman in 1858. However, because the genus *Raniceps* was preoccupied, a new generic name *Pelion* was created for it by Cope in 1868. The main slab of the holotype specimen (AMNH 6841) bore an almost complete skeleton of a small amphibian visible in ventral aspect and it was immediately recognised as strikingly frog-like in its possession of elongate limbs and a broad, rounded skull with large palatal vacuities. Wyman (1858), Cope (1868, 1875) and Moodie (1916) all commented on its frog-like appearance, and Moodie went so far as to place it in the Order Salientia. Cope (1875) and later authors placed it in its own family, the Peliontidae. While the specimen was unprepared, it was only poorly visible in ventral aspect and its skull roof was unknown. This led to an unfortunate and extremely confusing phase in the systematic history of this material. In 1930, Romer referred a series of Linton amphibians to *Pelion lyelli* and described *Pelion* largely from these referred specimens. They were all basal dvinosaurs now placed in the genus *Isodectes* (Sequeira 1998) (then called *Saurerpeton*), and so *Pelion* as described by Romer (1930, 1947) apparently combined an *Isodectes* (= *Saurerpeton*)-like skull with the long limbs of the *Pelion* holotype. Steen (1931) referred one of the British Museum's Linton specimens to *Pelion lyelli* and was followed in this by Watson (1956); however, Steen's specimen is also a basal dvinosaurian of the genus *Isodectes* (Milner & Sequeira in prep.).

A second specimen entered the literature in 1874, when Cope made a sculptured fragment of skull (AMNH 2566) the holotype of *Tuditonus mordax*, *Tuditonus* being a poorly defined 'catch-all' genus at that time. Cope correctly identified the material as a snout region but Moodie (1909a, 1916) misinterpreted the sculptured nasals as the skull table of a horned nectridean and referred the specimen to *Diceratosaurus punctolineatus*. Romer (1930) and Steen (1931) reverted to Cope's correct interpretation.

The third specimen to be described was an incomplete postcranial skeleton from Linton (AMNH 2002) described by Cope (1877) as the holotype and only specimen of *Ichthyocanthus platypus*. In the absence of a skull, the systematic position of this specimen was persistently enigmatic for over a century and it was variously identified as a rhachitome (Cope 1888,

Romer 1947), an embolomere (Romer 1930 as ?*Leptophractus lancifer* Romer, 1963), a lepospondyl (Moodie 1916) and even doubtfully as a captorhinomorph (Romer 1966).

In the early twentieth century, the Linton material was extensively reviewed by Moodie, who described a fourth specimen, another incomplete postcranial skeleton (USNM 4461), as an example of the nectridean *Diceratosaurus punctolineatus* (Moodie 1909b, 1916).

In 1931, Steen transferred the type of '*Tuditonus*' *mordax* and a newly described well-preserved skull (BMNH R.2670) to a new genus *Platyrhinops*. At the time, no other good skull of *Platyrhinops* was known from Linton and the type material had just been confused with *Saurerpeton* by Romer, so Steen's *Platyrhinops mordax* was more correctly recognised as a primitive dissorophid quite distinct from *Pelion lyelli* (Romer 1947; Gregory 1950).

Thus, by 1947, the type of *Pelion lyelli* was confusingly associated with basal dvinosaurian material, most other specimens were variously misidentified or undetermined, and only Steen's skull of *Platyrhinops* was relatively correctly assigned to the Dissorophidae. One consequence of this confusion was that the Linton material had ceased to be seriously considered in relation to the origin of Lissamphibia. When Watson (1940) and Romer (1947) had emphasised the derived, possibly frog-like features of *Amphibamus grandiceps* (as '*Miobatrachus romeri*') from Mazon Creek, no consideration was given to the contemporaneous Linton material. In 1950, Gregory argued that *Amphibamus grandiceps* was more primitive and less frog-like than Watson had suggested, and that although its relationship to frogs was plausible, there were no positive features to support it. The resemblances noted by other authors were argued by Gregory to be similarities associated with small size.

The acid-etching of the holotype of *Pelion lyelli* by Dr Donald Baird in the 1950s revealed a skull roof like that of the small Permian dissorophid *Tersomius*, and it was immediately clear that none of Romer's referred material belonged with the holotype. As a result of the preparation of this and other specimens, Carroll (1964) established the concept of *lyelli* as an early and primitive dissorophid. He demonstrated that there were four Linton specimens that could be correctly associated with the holotype, none of which had previously been referred to *lyelli*. The newly-prepared skull roof of the holotype bore an obvious resemblance to that of *Amphibamus grandiceps* from the contemporaneous locality of Mazon Creek (Watson 1940; Gregory 1950) and Carroll transferred *lyelli* to the genus *Amphibamus*, establishing the binomen which was used for the next 30 years. Carroll was able to recognise both the Cope and Steen *Platyrhinops mordax* specimens as large individuals of *A. lyelli*, together with USNM 4461 and a hitherto undescribed palate MCZ 1277, both of which had also been acid-etched by Baird. Carroll followed Gregory in laying emphasis on the primitive features of *Amphibamus* with respect to dissorophids, and made no mention of any possible resemblance to lissamphibians. Estes (1965), however, was impressed by the similarity between the palate construction of the Linton *Amphibamus* and those of primitive frogs and salamanders, and argued that it strengthened the case for a temnospondyl–lissamphibian relationship. The case for dissorophoid relationship to lissamphibians was taken up by Bolt, who discovered bicuspid pedicellate teeth in the genera *Doleserpeton* (Bolt 1969), *Tersomius* (Bolt 1977) and in *Amphibamus grandiceps* from Mazon Creek (Bolt 1979). Bolt (1979) also suggested that *Amphibamus grandiceps* from Mazon Creek and *Amphibamus lyelli* from Linton might prove to be conspecific, if studied comparatively.

Subsequently, an unreported Linton specimen from the collections of the Museum für Naturkunde, Berlin was described as a small specimen of *Amphibamus lyelli* by Milner (1982) who argued that it showed distinct differences from *A. grandiceps*, and that the two species could not be used to construct a single growth series. The holotype of Cope's *Ichthyacanthus platypus* was finally recognised as a large individual of *A. lyelli* and described as such by Hook & Baird (1984). A few years later, Daly (1994) redescribed the postcranial skeleton of *A. lyelli* as part of her revision of the Amphibamidae, and Clack & Milner (1994) gave a preliminary account of the work presented herein. In the process of their redescription, the present authors failed to identify any derived characters shared by *Amphibamus lyelli* and *Amphibamus grandiceps* that would define the genus *Amphibamus*; in a simple iterative cladistic analysis, they concluded that *Amphibamus grandiceps* and *Doleserpeton annectens* were more closely related to each other than either was to *Amphibamus lyelli*. '*A. lyelli*' is therefore transferred to the distinct and definable genus *Platyrrhinops*, the most senior valid genus applicable to Linton material (Clack & Milner 1994). Subsequent computer analyses of amphibamid relationships (Schoch & Rubidge 2005; Ruta & Bolt 2006; Huttenlocker *et al.* 2007; Anderson *et al.* 2008a, b; Fröbisch & Reisz 2008) have all confirmed Clack & Milner's 1994 conclusion. In 1994, Clack & Milner also referred amphibamid material from Nýřany in the Czech Republic to *Platyrrhinops* cf. *P. lyelli*. That material will be described in a separate publication as a distinct species of *Platyrrhinops*.

*Platyrrhinops lyelli* has become recognised as an early amphibamid in the Linton fauna, represented by seven specimens with diverse systematic histories. However, three further undescribed specimens exist, whilst some of the reported material has never been described in detail. These specimens contain much new information about the structure, ontogeny and variation of the skull and, to a lesser extent, the postcranial skeleton of *P. lyelli*. Using latex peels of almost all specimens of *P. lyelli*, a comprehensive redescription of the skull and postcrania through the preserved size range has been attempted. There is only a little to add to the descriptions of the postcranial skeleton by Carroll (1964), Hook & Baird (1984), and Daly (1994), and the account of the postcranial skeleton is intended as a supplement to their publications, with emphasis on the skeleton of small individuals.

## 2. Material and methods

The following description is based primarily on study of peels of the following specimens of *P. lyelli*. These are in approximate order of decreasing size: USNM 4461, a large articulated postcranial skeleton showing about 18 presacral vertebrae, parts of the pectoral girdle and one manus, left ilium, left hind limb lacking pes; MCZ 1277, a large skull and mandibles in ventral aspect, midline length about 60 mm, snout–quadrate length about 77 mm; BMNH R.2670, a slightly sheared skull with disrupted lower jaws, of midline length about 49 mm, snout–quadrate length about 59 mm, also a clavicle; MB Am.23/48, counterparts of a large skull and mandibles, slightly disarticulated, midline length about 50 mm, snout–quadrate length about 59 mm; CM 44757, an incomplete large skull in dorsal aspect, showing the skull table and right suspensorium in dorsal view with part of the right palate and maxilla in ventral view; AMNH 6841, holotype specimen, almost complete articulated skeleton and skull in dorsal view, lacking only a few phalanges from each limb and parts of the left pectoral girdle (a peel of the original (ventral) surface prior to etching

by Baird shows no additional details), skull midline length about 25 mm, snout–quadrate length about 32 mm; MB Am.331a,b, counterparts of a skull and anterior postcranium, showing about 15 presacral vertebrae, left pectoral limb and girdle, midline skull length about 18 mm, snout–quadrate length about 20 mm, also includes some well-preserved features which are believed to be size-independent (e.g. sclerotic ring and palatal sutures); CM 23057, counterparts of the smallest known skull, midline length about 13 mm, snout–quadrate length about 16 mm. AMNH 2002 and AMNH 2566 were not studied at first-hand. Peels of three *Amphibamus grandiceps* specimens – YPM 794 and 795, FMNH 2000 – were also used for comparison.

Peels were coated with ammonium chloride for study and initial drawing with a camera lucida, followed by additional rendering using Adobe Photoshop and a Wacom graphix pad. Denticulated fields have in most cases been rendered by mechanical texture. The angle of the cheeks in the skull reconstructions was determined partly by modelling the skull roof and palate in paper and curving the cheeks downwards until a satisfactory fit between the palate and the braincase was achieved, and partly by comparison with three dimensional skulls of *Tersomius* and *Broiliellus* from the Texas Red-Beds (Carroll 1964). Photographs were taken by Mr P. Crabb (NHM, London).

## 3. Systematic palaeontology

Family Amphibamidae Moodie, 1910  
(=Peliontidae Cope, 1865, Micropholidae Watson, 1919,  
Miobatrachidae Watson, 1940,  
Doleserpetontidae Bolt, 1969)

**Diagnosis.** Small amphibious-terrestrial dissorophoids growing to a maximum known skull length of 60 mm (*Platyrrhinops lyelli*). Synapomorphies (Schoch & Rubidge 2005; Huttenlocker *et al.* 2007; Fröbisch & Reisz 2008) include: long premaxillary alary process extending beyond posterior border of external naris, palatine and ectopterygoid reduced to narrow struts not wider than adjoining maxilla; pleurocentra at least approach each other on ventral side, frequently fused to form a larger element; thoracic ribs very short simple rods; humerus shaft elongate and rod-like; humerus head with small, usually poorly ossified condyles, slightly broadened proximal head region and reduced deltopectoral buttress; cleithrum forming simple rod with no head. Included genera are *Amphibamus*, *Doleserpeton*, *Eoscopus*, *Georgenthalia*, *Gerobatrachus*, *Micropholis*, *Pasawioops*, *Platyrrhinops*, *Plemmyradytes* and *Tersomius*. From the Pennsylvanian and Lower Permian of Europe and North America and the Lower Triassic of South Africa.

**Systematic note.** The analysis by Schoch and Rubidge (2005) placed the genus *Micropholis* within the Amphibamidae. Subsequent analyses have found a closer relationship between *Amphibamus* and Branchiosauridae than between *Amphibamus* and *Micropholis* (Schoch & Milner 2008; Fröbisch & Reisz 2008; Fröbisch & Schoch 2009a; Ruta 2009). The *Amphibamus*-clade amphibamids and branchiosaurids appear to be more closely related to each other than either is to the *Micropholis*-clade amphibamids (e.g. see also Ruta & Bolt 2006) and most of the above diagnosis does also apply to the Branchiosauridae. This might ultimately be resolved systematically either by making the Branchiosauridae a subfamily of the Amphibamidae, or alternatively reducing the Amphibamidae to forms more closely related to *Amphibamus* than to *Apateton* and reestablishing the Micropholididae for the

'*Micropholis* branch' (*Micropholis*, *Tersomius* and *Pasawioops*) of amphibamids. A more comprehensive combined analysis of both amphibamid and branchiosaurid genera would be a necessary prerequisite before adopting either of these alternatives.

Genus *Platyrhinops* Steen, 1931

(= *Raniceps* Wyman, 1858a non Oken, 1817,  
*Pelion* Wyman in Cope, 1868 non Kirby, 1858)

**Type and only species.** *Raniceps lyelli* Wyman, 1858.

**Diagnosis.** As for the only species.

*Platyrhinops lyelli* (Wyman) Clack & Milner, 1994  
Figs 1–9

#### Synonymy.

- 1857 'batrachian reptile' Wyman, p. 172.  
1858 *Raniceps lyelli* Wyman, p. 160, fig. 1.  
1868 *Pelion lyelli* (Wyman); Wyman, in Cope p. 211.  
1874 *Tuditamus mordax* Cope, p. 274.  
1875 *Pelion lyellii* (Wyman); Cope, p. 390, pl. 26, fig. 1.  
1875 *Tuditamus mordax* Cope; Cope, p. 395.  
1877 *Ichthyacanthus platypus* Cope, p. 574.  
1888 *Eryops platypus* Cope; Cope, p. 289, unnumbered text-fig.  
1909a *Diceratosaurus punctolineatus* (Cope); Moodie, p. 356,  
pl. 64, fig. 2 non Cope 1875.  
1909b *Diceratosaurus punctolineatus* (Cope); Moodie, p. 25 non  
Cope 1875.  
1915 *Ichthyacanthus platypus* Cope; Moodie, p. 509, fig. 2.  
1916 *Pelion lyelli* (Wyman); Moodie, p. 72, fig. 17, pl. 24,  
fig. 1.  
1916 *Diceratosaurus punctolineatus* (Cope); Moodie, p. 118,  
120, pl. 16, fig. 5, Pl. 22, fig. 5 non Cope 1875.  
1916 *Ichthyacanthus platypus* Cope; Moodie, p. 172, pl. 23,  
fig. 1.  
1930 *Pelion lyelli* (Wyman); Romer, p. 94, non figs 4–6, (*partim*  
Carroll 1964).  
1930 '*Tuditamus*' *mordax* Cope; Romer, p. 118.  
1930 ?*Leptophractus lancifer* (Newberry); Romer, p. 129, non  
Newberry 1856.  
1931 *Platyrhinops mordax* (Cope); Steen, p. 865 figs 11–13,  
pl. 3, figs 1,2.  
1947 *Ichthyacanthus platypus* Cope; Romer, p. 107.  
1947 *Pelion lyelli* (Wyman); Romer, p. 116 non fig. 22, (*partim*  
Carroll 1964).  
1947 *Platyrhinops mordax* (Cope); Romer, p. 162, fig. 29.  
1950 *Platyrhinops mordax* (Cope); Gregory, p. 855.  
1963 *Ichthyacanthus* (sic) *platypus* Cope; Romer, p. 441.  
1964 *Amphibamus lyelli* (Wyman); Carroll, p. 227, figs 21–24,  
pl. 2.  
1970 *Ichthyacanthus platypus* Cope; Panchen, p. 65.  
1979 *Amphibamus lyelli* (Wyman); Bolt, p. 535, fig. 4.  
1982 *Amphibamus lyelli* (Wyman); Milner, p. 645, text-fig. 3C,  
D.  
1984 *Amphibamus lyelli* (Wyman); Hook & Baird, p. 697, fig. 1.  
1989 *Amphibamus lyelli* (Wyman); Carroll, fig. 7B.  
1994 *Amphibamus lyelli* (Wyman); Daly, p. 24, figs 24–25.  
1994 *Amphibamus lyelli* (Wyman); Hook & Baird, p. 151.  
1994 *Platyrhinops lyelli* (Wyman); Clack & Milner, p. 185,  
fig. 1.  
1999 *Amphibamus lyelli* (Wyman); Carroll *et al.*, figs 4A, C.  
2004 *Platyrhinops lyelli* (Wyman); Schoch & Milner, fig. 2c.  
2005 *Platyrhinops lyelli* (Wyman); Schoch & Rubidge, p. 514.  
2007 *Platyrhinops lyelli* (Wyman); Huttenlocker *et al.*, table 1.  
2008b *Platyrhinops lyelli* (Wyman); Anderson *et al.*, table 2.

**Diagnosis.** Amphibamid characterised by the following autapomorphies: widened medial region of skull in adult manifested by greatly enlarged interorbital width made up of expanded anterior region of frontals and posterior region of postfrontals, together with wide rhomboidal sphenethmoid with anterolateral extensions, and wide cultriform process; gastralia poorly ossified in large specimens and unossified in small specimens. The extreme length of the phalanges is a possible autapomorphy, although its distribution is poorly known.

Synapomorphies with a limited distribution include: abbreviated skull table significantly wider than long (also in *Amphibamus*, *Doleserpeton*, *Georgenthalia* and *Gerobatrachus*); presence of a parasphenoid denticle field extending along cultriform process (also in *Amphibamus*, *Pasawioops* and *Micropholis*); absence of an intervomerine pit (shared with *Amphibamus* and *Doleserpeton*) and bicuspid marginal teeth (also in *Amphibamus*, *Doleserpeton* and *Tersomius*).

Apparent primitive features not found in many amphibamids are: retention of a prefrontal-postfrontal suture (shared with *Amphibamus* uniquely among the known amphibamids); retention of a palatine-pterygoid suture excluding the ectopterygoid from the margin of the interpterygoid vacuity (shared with *Amphibamus* and *Eoscopus*); single pairs of vomerine fangs (no second vomerine fangs as in *Eoscopus* and *Tersomius*); retention of a presacral column of 25–26 vertebrae, similar to those of *Eoscopus* (24) and *Doleserpeton* (24) but longer than those of *Amphibamus* (18), *Gerobatrachus* (17) and *Micropholis* (18).

**Holotype.** AMNH 6841 (*ex* Columbia University 7909G), J. S. Newberry Collection, collected by J. V. Lauderdale in 1857. Counterparts of an almost complete articulated medium-size skeleton. Holotype of *Raniceps lyelli* Wyman, 1858. Figured by Wyman 1858, fig. 1, Cope 1875, pl. 26, fig. 1, Moodie 1916, fig. 17 and pl. 24, fig. 1 as *Pelion lyelli*, Carroll 1964, figs 21, 23 and plate 2 as *Amphibamus lyelli*; Fig. 1.

**Horizon.** Cannel coal below coal seam identified as the Upper Freeport Coal, Allegheny Group, late Middle Pennsylvanian.

**Locality.** Mine dump from coal mines originally owned by the Ohio Diamond Coal Company, Linton, Saline Township, Jefferson County, Ohio (see Hook & Ferm 1985; Hook & Baird 1986 for further data and sources).

#### Referred material.

AMNH 2002 (*ex* Columbia University 7954G), collected by J. S. Newberry. Holotype of *Ichthyacanthus platypus* Cope, 1877. Figured by Moodie 1915, fig. 2, 1916 pl. 23, fig. 1 as *I. platypus*, Hook & Baird 1984, fig. 1 as *Amphibamus lyelli*, vertebrae figured by Carroll 1989, fig. 7B, Carroll *et al.* 1999, fig. 4C as *Amphibamus lyelli*. Counterparts of large posterior trunk and hind limbs in articulation.

AMNH 2566. Holotype of *Tuditamus mordax* Cope, 1874. Figured by Moodie 1909a, pl. 64, fig. 2, 1916 pl. 22, fig. 5 as *Diceratosaurus punctolineatus*. Large anterior palate.

BMNH R.2670, J. W. Davies Collection, purchased by BM(NH) in April 1895. Figured by Steen 1931, text-figs 11–13, pl. 3, figs 1, 2 as *Platyrhinops mordax* (Fig. 2).

CM 23057, collected by R. Lund in 1972. Figured for the first time in this present work (Fig. 3).

CM 44757, G. A. McComas Collection. Figured for the first time in this present work (Fig. 4).

MB Am.331a–b (*ex* MB 1888-1456a/b). Figured by Milner 1982, text-figs 3C, D as *Amphibamus lyelli* under its previous specimen number. MB 331a figured by Carroll *et al.* 1999, fig. 4A as Redpath Museum cast 14493 (Fig. 5).

MB Am.23/48. Fig. 6. A reconstruction based on this specimen was made by Schoch & Milner (2004 fig. 2C) as MB Am.19 (a previous temporary catalogue number).

MCZ 1277, C. M. Wheatley Collection. Determined by D. Baird 1957. Figured by Carroll 1964 figs 21C, 22B–D as *Amphibamus lyelli* (Fig. 7).

USNM 4461, R. D. Laco Collection, collected by T. Stock in 1888. Determined by D. Baird 1960. Figured by Moodie 1916, pl. 16, fig. 5 as *Diceratosaurus punctolineatus*, by Carroll 1964, fig. 24 and by Daly 1994, figs 24–25 as *Amphibamus lyelli* (Fig. 1c).

## 4. Description

### 4.1. Dermal skull roof

The dermal sculpture comprises an even reticulate ridge, or honeycomb pattern, on most dermal bones. There is some elongation of the sculpture pattern at certain sutural borders, where more rapid growth is presumably taking place. This is most noticeable on either side of the common frontal suture, and on either side of the parietal-supratemporal suture (BMNH 2670, Fig. 2b). On the premaxilla and maxilla, the reticulate ridges tend to be shallow and organised in vertical rows down to the tooth-row. There are no superficial ridges on the dermal skull roof as in many dissorophids, and the only obvious thickening of the bone appears to be along a line from the back of the orbit to the otic notch. This line represents the angle between the skull-table and the cheek. The postorbital, supratemporal and squamosal all appear to have been thickened along the line of this angle, thus rendering it relatively crush-resistant and somewhat prominent in the crushed specimens (e.g. BMNH R.2670, Fig. 2b). In the smaller specimens, skulls have been flattened, suggesting that such ridges had yet to form, and they contrast with the even smaller, but still three-dimensional form of the *Amphibamus grandiceps* skulls. No specimen of *Platyrhinops* shows any vestige of lateral-line pits or sulci, and these are presumed to be absent in the large specimens.

The number and position of the dermal bones in the skull is in most respects typical for temnospondyls. The only paired ossifications that are absent are the intertemporals, but they are only found in more primitive grades of temnospondyls and only occur as occasional aberrations in dissorophoids. The skull outline of *Platyrhinops* is generally broader in relation to length than in *Amphibamus*, with a more rounded snout. This is the case even in small specimens where the interorbital region has not widened. In the largest example, MCZ 1277, the outline of the skull in ventral view appears more elongated, but this is based on the mandible configuration and the skull itself may have been crushed somewhat (Fig. 7).

**4.1.1. Premaxilla.** The premaxillae have a moderately deep, interdigitating, common medial suture and laterally form the anterior border of the external nares. Each bears a broad triangular alary process extending back into a triangular slot on the leading edge of each nasal. In BMNH R.2670 (Fig. 2a), the slot is visible on the left nasal and the process of the right premaxilla is visible on the edge of the specimen. The lateral faces of the process are straight in BMNH R.2670 (Fig. 2a) but in the holotype (Fig. 1a), the lateral face is shallowly concave. There is no clear evidence for or against the presence of an internarial pit (as in *Doleserpeton*) or ossification (as in some *Tersomius*), but it has been restored without either as in *Amphibamus*.

**4.1.2. Maxilla.** The maxilla is best seen in MB Am.23 (Fig. 6a, c). Anteriorly it contacts the premaxilla by a narrow bar extending below the external naris. Behind this is a broad convex pars facialis with a convex dorsal edge ahead of the orbit. It passes along the edge of the orbit as a low shelf and it is this element that forms the ventrolateral orbit margin, rather

than a posterior extension of the lacrimal (Carroll 1964) or a possible lateral extension of the palatine (LEP, Bolt 1969). It narrows to a point posteriorly, substantially bordering the quadratojugal and excluding the jugal from the skull margin. In CM 44757 (Fig. 4), the medial face of the maxilla bears a medial groove which receives the lateral margins of the palatine and ectopterygoid. Judging from CM 44757, the palatine extends a process lateral to the choana, which appears to extend to the vomer and thus exclude the maxilla from the choanal margin. However, it is not entirely clear from the peel whether the apex of this process is formed from a ridge of the maxilla, a continuation of the palatine, or an artefact of the peel.

**4.1.3. Lacrimal.** The lacrimal extends broadly from the external naris to the orbit. In the holotype (Fig. 1a), BMNH R.2670 (Fig. 2a) and MB Am.48 (Fig. 6b), the lacrimal borders the anterolateral orbit margin broadly. In the holotype and BMNH R.2670, the lacrimal terminates posterolaterally as a point partway along the orbit margin. It does not contact the jugal. In the small MB Am.331 (Fig. 5c), the left lacrimal is visible in palatal aspect through the left choana and appears to bear a single unbranched lacrimal duct.

**4.1.4. Septomaxilla.** Because of the crushing or absence of the nasal region in all specimens, no septomaxilla is visible on any specimen. Carroll (1964) reported a septomaxilla in *Tersomius*. Daly (1994) could not recognise a septomaxilla in any of her specimens of *Eoscopus*, but did figure septomaxillae in specimens of *Tersomius* cf. *T. texensis* (Daly 1994, fig. 29). It is possible that septomaxillae were present in all amphibamids, but may have been situated almost entirely internally within the external naris and hence difficult to observe in intact skulls. A parallel to this is the presence of septomaxillae in *Trimerorhachis insignis*. Case (1935) described a suite of specimens of this form without seeing a septomaxilla, yet several crushed specimens (MCZ 1546) from the Williams Ranch locality in Texas show the presence of septomaxillae.

**4.1.5. Nasal.** The nasals are large rectangular bones, about equal to the frontals in length or slightly longer. Each bears a triangular slot in the anterior margin for reception of the alary process of the premaxilla. None of the large specimens has the anterior region of the nasals sufficiently well preserved for the margin of the external naris or the presence of an internasal foramen to be ascertained. There is considerable asymmetry in the nasal-frontal suture of some specimens such as BMNH R.2670 (Fig. 2a) and the holotype (Fig. 1a) where there is a long common suture between the left nasal and the right frontal, separating widely the right nasal and left frontal. In the smaller example, MB Am.331, the right nasal is significantly longer than the left (Fig. 5a).

**4.1.6. Prefrontal.** The prefrontal forms the anteromedial margin of the orbit. It is a roughly triangular shape, sutures broadly with the lacrimal, nasal and frontal, and narrowly with the postfrontal. It extends ahead of the frontal for about half its length.

**4.1.7. Postfrontal.** The postfrontal forms the postero-medial margin of the orbit. It makes a narrow contact with the prefrontal. The suture with the postorbital is variable, being narrow in MB Am.48 (Fig. 6b) but broad in the holotype (Fig. 1a) and BMNH R.2670 (Fig. 2a). The postfrontal is very variable in shape, but is generally narrow anteriorly and considerably expanded posteriorly. The posterior region widens relative to the anterior width with ontogeny. Anderson *et al.* (2008b) followed by Fröbisch & Reisz (2008) use postfrontal shape (their character 48) as a taxonomically useful character, assigning the state ‘postfrontal narrow and sickle-shaped’ to *Platyrhinops*. In fact, this state characterises the small specimens but not the larger ones (e.g. Figs 2a, 4a, 6a)

and this character requires some size-linked qualification of the states if it is to be of any real value. The same ontogenetic change may be seen in *Apateon* as recently figured by Fröbisch & Schoch (2009b, fig. 3a, b).

**4.1.8. Postorbital.** The postorbital forms the posterior margin of the orbit. It varies in shape during ontogeny, but does not extend back to form a wedge between the supratemporal and squamosal as in many temnospondyls. A similar condition is reported in the newly described *Cacops morrisoni* by Reisz, Schoch & Anderson (2009) and may prove to be a widespread dissorhoid feature. In small specimens, the postorbital is a shallow crescent-shaped bone with a narrow contact with the supratemporal. In the large BMNH R.2670, it is a rhomboid element almost as long as wide. In the holotype (Fig. 1) and BMNH R.2670 (Fig. 2), it extends finger-like processes between the orbit margin and the postfrontal and jugal.

**4.1.9. Jugal.** The jugal forms the posterolateral margin of the orbit. Anteriorly it extends to a fine point wedged between the orbit and the dorsal edge of the maxillary. This point extends about half way forward along the orbit on the right sides of the holotype (Fig. 1a) and BMNH R.2670 (Fig. 2a). Posteriorly the jugal expands to form a major area of the cheek. It sutures with the posterior end of the maxillary, the latter bone excluding it from the skull margin.

**4.1.10. Lateral exposure of palatine (LEP).** This is present in many amphibamids and might be predicted to be present in *Platyrhinops*. In most specimens this area of the skull is either absent or badly crushed. On the right side of BMNH R.2670 (Fig. 2a) is a structure which resembles a dorsal palatine exposure, but close examination and careful matching with the counterpart convinces us that it is a fragment of coronoid crushed up into the orbit margin and wedged between the jugal and the lacrimal. The presence of a lateral exposure of the palatine remains to be demonstrated.

**4.1.11. Frontal.** The frontals are anteroposteriorly elongate, roughly rectangular bones. They are excluded from the orbit margin by the prefrontal-postfrontal connection. In all the larger specimens, the frontals widen anteriorly and the anterior width is about one and half times the posterior width. The anterior suture of the frontals with the nasals is very asymmetrical, as described above. Anderson *et al.* 2008b (not followed by Fröbisch & Reisz 2008) uses as his character 50 the anterior widening of the frontals to describe the condition in several amphibamids. However, no other amphibamid genus shows any approach to the degree of overall widening found in *Platyrhinops* and this remains a characteristic of this genus.

**4.1.12. Parietal.** The parietals are large rectangular bones with a slightly narrower anterior region where they are wedged between postfrontals. The pineal foramen is situated slightly anterior to the middle of the interparietal suture. CM 44757 (Fig. 4a, b) has a well-preserved circular pineal foramen with a raised rim covered in fine pitting. In MB Am.48 (Fig. 6b, d), the pineal foramen is a wide oval and the margin is less prominent. The interparietal suture is sometimes prominently interdigitated posterior to the pineal foramen (Figs 1a, 2a). This phenomenon is a feature of many early tetrapod skulls, seen also for example in *Acanthostega* (Clack 2002a). The sutural lamina that underlies the frontals can be seen in CM 44757 and conforms with that seen in other temnospondyls (Kathe 1999).

**4.1.13. Supratemporal.** The supratemporal is a squarish bone with similar length and width. It broadly enters the margin of the tympanic notch between the tabular and the squamosal, and forms most of the dorsal margin of the notch. In CM 44757 (Fig. 4a, b) the notch is crushed laterally and the supratemporal possesses a semilunar flange extending between

the squamosal and the tabular. The supratemporal changes in shape slightly in larger specimens (particularly BMNH R.2670, Fig. 2a), growing backwards at the posterolateral corner and thus contributing to the backward extension of the posterolateral corner of the tabular in large skulls.

**4.1.14. Postparietal.** The postparietals are short, wide rectangular bones. Their shape is somewhat variable. In MB Am.48 (Fig. 6b) each postparietal has a slight convexity on the posteromedial edge and a slight concavity on the posterolateral edge. In BMNH R.2670 (Fig. 2a), the concavity is more pronounced and lateral to it the postparietal is deflected backwards as part of the tabular extension. In most specimens, the postparietals possess unornamented triangular posterior flanges extending down to the exoccipitals.

**4.1.15. Tabular.** The tabulars are small bones forming the posterolateral corners of the skull table. They vary from a square to a wide rectangular shape and most bear a backwardly directed posterolateral point. In MB Am.48 (Fig. 6b), BMNH R.2670 (Fig. 2a) and CM 44757 (Fig. 4c), the tabular extends onto the occipital surface. In the latter specimen there seems to be an unornamented component to the lateral corner of the tabular, approximating to a small 'tabular horn' (Fig. 4c). Our high fidelity peel of MB Am.331a reveals that both tabulars are in fact present (Fig. 5a), *contra* Milner (1982). They are also present in CM 23057 (Fig. 3a).

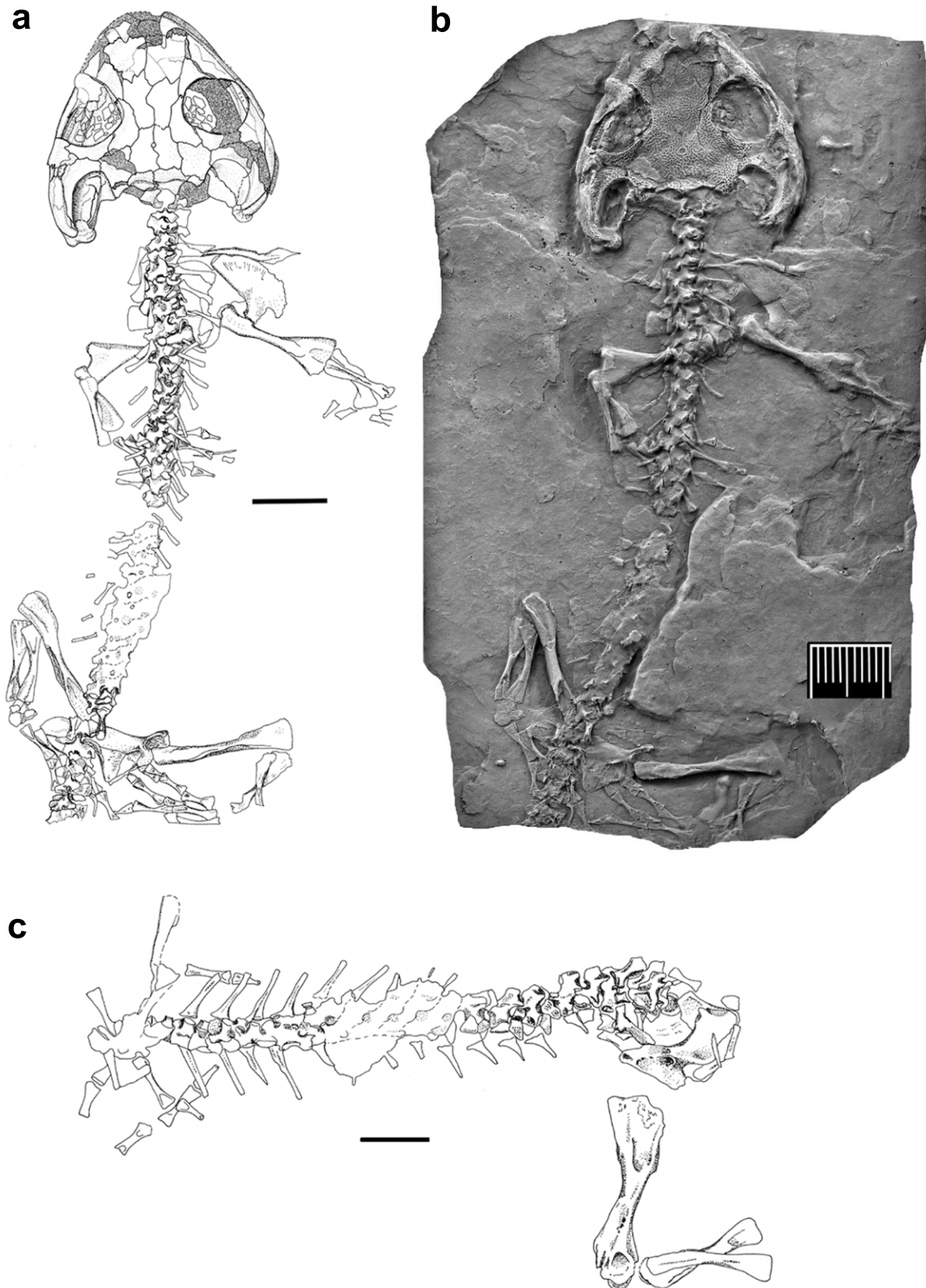
**4.1.16. Squamosal.** The squamosal is a large narrow crescent-shaped bone bordering much of the large tympanic notch. The posterior ramus is very long and narrow and seems to be variable in its backward extension. In the left side of the holotype (Fig. 1a) and in CM 44757 (Fig. 4a), the posterior ramus is very long and almost reaches the dorsal process of the quadrate. In the holotype (right side) the posteromedial extension of the quadratojugal appears to occupy more of the cheek surface between the squamosal and the quadrate. The squamosal also makes a major contribution to the inner faces of the tympanic notch. Dorsally it partly underlies the supratemporal. On the anterior and ventral inner faces of the notch, the squamosal forms a large smooth surface of bone, along with a small portion of the quadratojugal and a dorsal exposure of the quadrate ramus of the pterygoid. Because of crushing in all specimens it is not possible to see the slot for the stapes on these specimens.

**4.1.17. Quadratojugal.** The quadratojugals are large, massive bones forming the posteroventral corners of the cheeks. Each quadratojugal carries a posteromedial extension behind the squamosal. This extension is partly ornamented and overlies the quadrate. In CM 44757, the extension wraps around both sides of the base of the dorsal process of the quadrate (Fig. 4a). Also in CM 44757, the posteroventral margin of the quadratojugal is slightly expanded and heavily sculptured (Fig. 4d).

## 4.2. Palate

Much of the palate is difficult to observe in large specimens of *P. lyelli* because of the persistent presence of platelets of denticle-bearing bone displaced over the palate, together with the presence of a suture-obscuring shagreen of denticles over the ventral surface of the lateral palatal ossifications. The palatal sutures are described from MB Am.23 (Fig. 6a, c) with some reference to the small MB Am.331b (Fig. 5c, d) but some have to be inferred. The palatal dentition is discussed in a later section.

**4.2.1. Vomer.** The vomers are large plates of bone at the anterior of the palate. Their posterior width is one and a half times their anterior width. They suture with the premaxillae anteriorly, with the palatines posterolaterally and contact the parasphenoid cultriform process posteromedially, but it is not

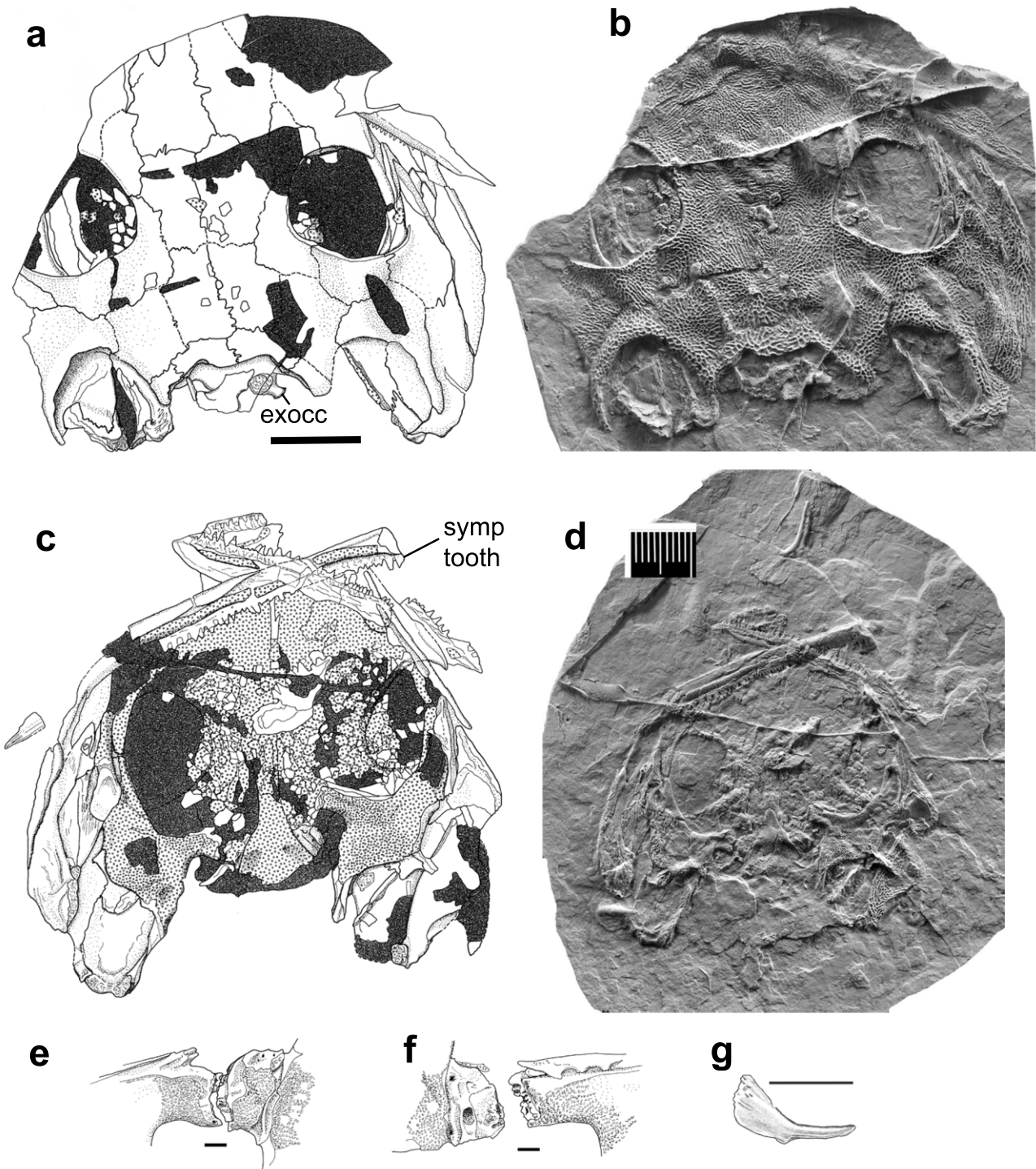


**Figure 1** *Platyrrhinops lyelli* (Wyman): (a) AMNH 6841, interpretive drawing of holotype skeleton in dorsal aspect; (b) AMNH 6841, photograph of holotype skeleton in dorsal aspect; (c) USNM 4461, drawing of postcranial skeleton in dorsal (anterior) and left lateral (posterior) aspects. Scale bars=10mm.

clear whether this contact is sutural or not. There is no evidence for the presence of an intervomerine pit. The vomers and their surroundings are best seen in MB Am.23 (Fig. 6). In this specimen an undulating vomer-palatine suture can be seen near the posterior end of the choana. The choana has an unusual shape in *P. lyelli*, in that it is long and narrow with the

straight vomerine margin running parallel with the anterior maxilla. A similar shape occurs in the armoured dissorophid *Broiliellus brevis* (Carroll 1964, fig.10).

**4.2.2. Palatine.** The palatine contacts the ectopterygoid and pterygoid narrowly. It enters the interpterygoid vacuity margin broadly as a result of the posterior withdrawal of the



**Figure 2** *Platyrrhinops lyelli* (Wyman), BMNH R.2670: (a) interpretive drawing of skull in dorsal aspect; (b) photograph of skull in dorsal aspect; (c) interpretive drawing of skull in ventral aspect; (d) photograph of skull in ventral aspect, with the clavicle shown at the top; (e, f) basiptyergoid-basisphenoid articulations; (g) drawing of the clavicle. Abbreviations: exocc=exoccipital; symp tooth=symphyseal tooth. Scale bars: (a–d) = 10mm; (e, f) = 1mm; (g) = 10mm.

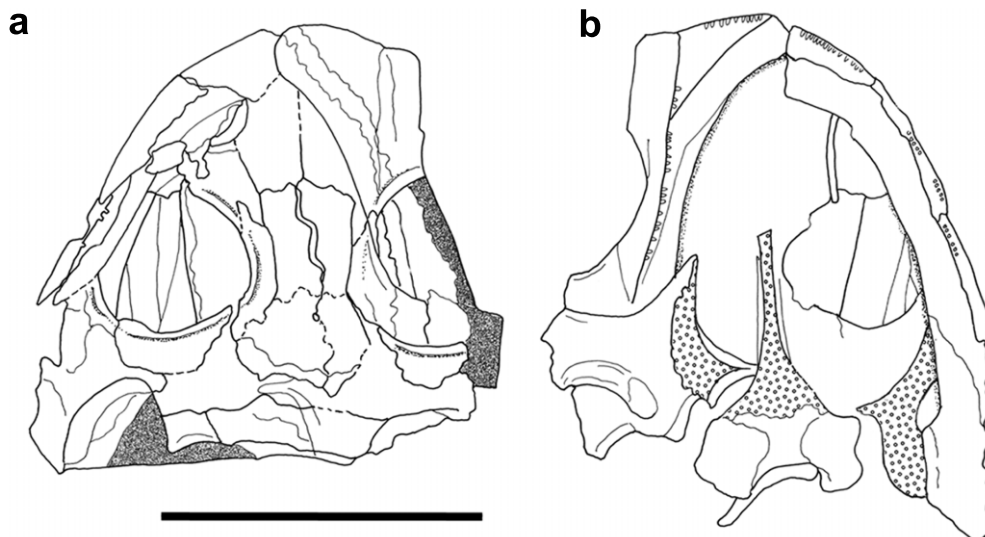
palatine ramus of the pterygoid. The posterior two-thirds of the palatine is slender. Anterolaterally it extends a slender process between the posterior region of the choana and the maxillary (CM 44757, Fig. 4d). The maxilla appears to be entirely excluded from the choanal margin (see section 4.1.2.).

**4.2.3. Ectopterygoid.** The ectopterygoid is an anteroposteriorly elongate rectangular bone, narrowly suturing anteriorly with the palatine, and broadly suturing medially with the pterygoid and laterally with the maxilla (eg. MB Am.23, Fig. 6a). Its posterior edge borders the subtemporal fossa, but its

anteromedial corner is excluded from the border of the interptyergoid vacuity by the palatine-ptyergoid suture. In small amphibamids such as *Amphibamus* and *Doleserpeton*, the ectopterygoid is small or absent, and *Platyrrhinops* is primitive in this respect.

**4.2.4. Pterygoid.** The pterygoid is of characteristic temnospondyl triradiate construction. The palatine ramus is short and broad, with the palatine/ptyergoid suture at mid-orbit level (BMNH R.2670, Fig. 2). From the palatine ramus, the pterygoid broadens to a posteromedially curved central area. Schoch & Milner (2004, fig. 2C) and Schoch & Rubidge





**Figure 3** Small skull probably *Platyrrhinops lyelli* (Wyman), CM 23057 in (a) dorsal aspect; (b) ventral aspect. Scale bar = 10mm.

(2005) recorded *Platyrrhinops* as having only a pterygoid–ectopterygoid contact, but this is clearly not so and was based on MB Am.23, in which the lateral palatal series is less well preserved than in BMNH R.2670. This was incorporated in later analyses and will need to be corrected in future analyses. Ectopterygoid entry into the interpterygoid vacuity margin appears to be restricted to *Amphibamus* and *Doleserpeton*. The pterygoid bears a rounded flange which forms the antero-medial border of the subtemporal fossa. The flange is large as in all large dissorophoids and was probably vertically orientated in the uncrushed skull. Medial to the central region of the pterygoid is the stout rod-like basiptyergoid process, about twice as long as wide (BMNH R.2670, Fig. 2e, f). The quadrate ramus of the pterygoid is an elongate triangular ramus terminating in a point slightly ahead of the articulatory surface of the quadrate. It twists from the horizontal to the vertical plane posteriorly, and so the posterior region tends to be crushed. In dorsal aspect the quadrate ramus forms the medial region of the ventral face of the otic notch and sutures broadly with the squamosal (BMNH R.2670, Fig. 2a).

**4.2.5. Quadrate.** The quadrate is a large structure forming the jaw hinge at the posterolateral corner of the cheek region. It is best seen in both aspects on the right side of BMNH R.2670 (Fig. 2a, c). The articulatory surface consists of a waisted bar of bone in which the lateral condyle is laterally elongate, while the medial condyle is anteromedially elongate, and puts forward a slender triangular flange of bone in an anteromedial direction. This flange sutures with the quadrate ramus of the pterygoid and the posterior region of the squamosal inside the otic notch. The posterodorsal process of the quadrate found in *Doleserpeton* and *Amphibamus grandiceps* by Bolt (1977, 1979) can also be seen in specimens BMNH 2670 (Fig. 2a, b) and CM 44757 (Fig. 4a, b).

**4.2.6. Parasphenoid.** In large specimens, the cultriform process of the parasphenoid is slender but its sutural relationship with the vomers is not known. It broadens sharply at the posterior end of the interpterygoid vacuity to a large, roughly rectangular basal plate. The basal plate is slightly broader posteriorly and its posterior edge bears anteroposterior fluting (MB Am.23, Fig. 6a, c). In the larger specimens, the ventral surface of the basal plate is denticle-covered and so surface features are not readily visible: in the largest specimen, MCZ 1277, the denticle field is continuous across the basal articulation (Fig. 7a, b). In BMNH R.2670 (Fig. 2c, d), it bears a pair of distinct pits in the expected position of the carotid artery

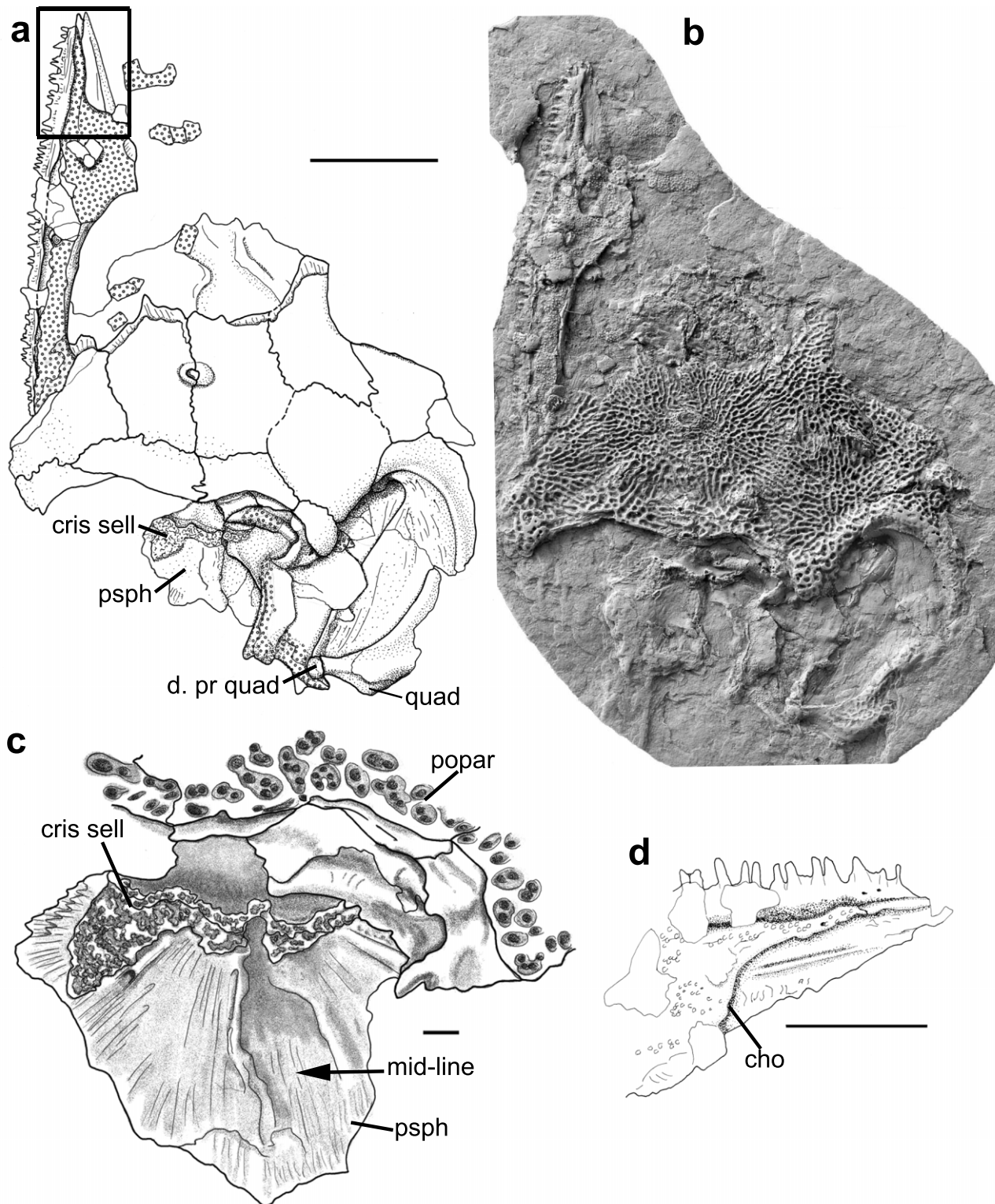
foramina, but the foramina themselves are not visible. In the small MB Am.331 (Fig. 5c, d), a pair of deep grooves on either side of the base of the cultriform process may represent the carotid foramina. The dorsal surface is described in the following section on the braincase.

### 4.3. Braincase and occiput

A few features of the braincase and occipital regions can be seen and inferences may be made about other structures, one of which appears to be peculiar to *Platyrrhinops*.

**4.3.1. Sphenethmoid.** The ventral aspect of the sphenethmoid is not directly visible in any specimen, but in MCZ 1277 (Fig. 7a, b) its complete shape may be discerned in relief under the sheets of palatal denticles over the interpterygoid vacuities. It appears to be a very broad rhomboidal shape ('shovel-shaped') with the anterior edge about twice the width of the posterior edge and the sides therefore diverging anteriorly. In most temnospondyls, the sphenethmoid, where visible, is either parallel-sided and narrow or diamond-shaped and widest in the middle. The only other described temnospondyl that has a sphenethmoid which is widest at or near its anterior edge is the clearly unrelated Upper Permian *Saharastega moradiensis* recently described by Damiani *et al.* (2006). This shape is probably associated with the unusually short wide shape of the skull of large *Platyrrhinops lyelli* and the great interorbital width in these specimens. CM 44757 shows the apparent dorsal view of the sphenethmoid, anterior to the preserved parts of the skull table, with the dorsal margins that would have contacted the skull roof assuming a lyre-shaped pattern. The lateral margins are not clear, but it appears to have the broad shape seen in MCZ 1277. However, no further details are determinable.

**4.3.2. Parabasisphenoid.** CM 44757 shows a dorsal view of the parabasisphenoid, in which the depression for the pituitary vein, the crista sellaris, the internal surface of the basiptyergoid process and the foramen usually interpreted as for the internal carotid (Shishkin 1968; Schoch 1999) are visible (Fig. 4a–c). The sutural contact surface of the parasphenoid for the basal articulation is represented on the right side. BMNH R.2670 shows the basal articulation on each side, both of which are somewhat disarticulated (Fig. 2e, f). The basiptyergoid process shows a system of ridges, grooves and foramina that can be seen where the covering of denticulated plates has been lost. The sutural surfaces between the endoskeletal elements of the basal processes each side of the articulation can also be made

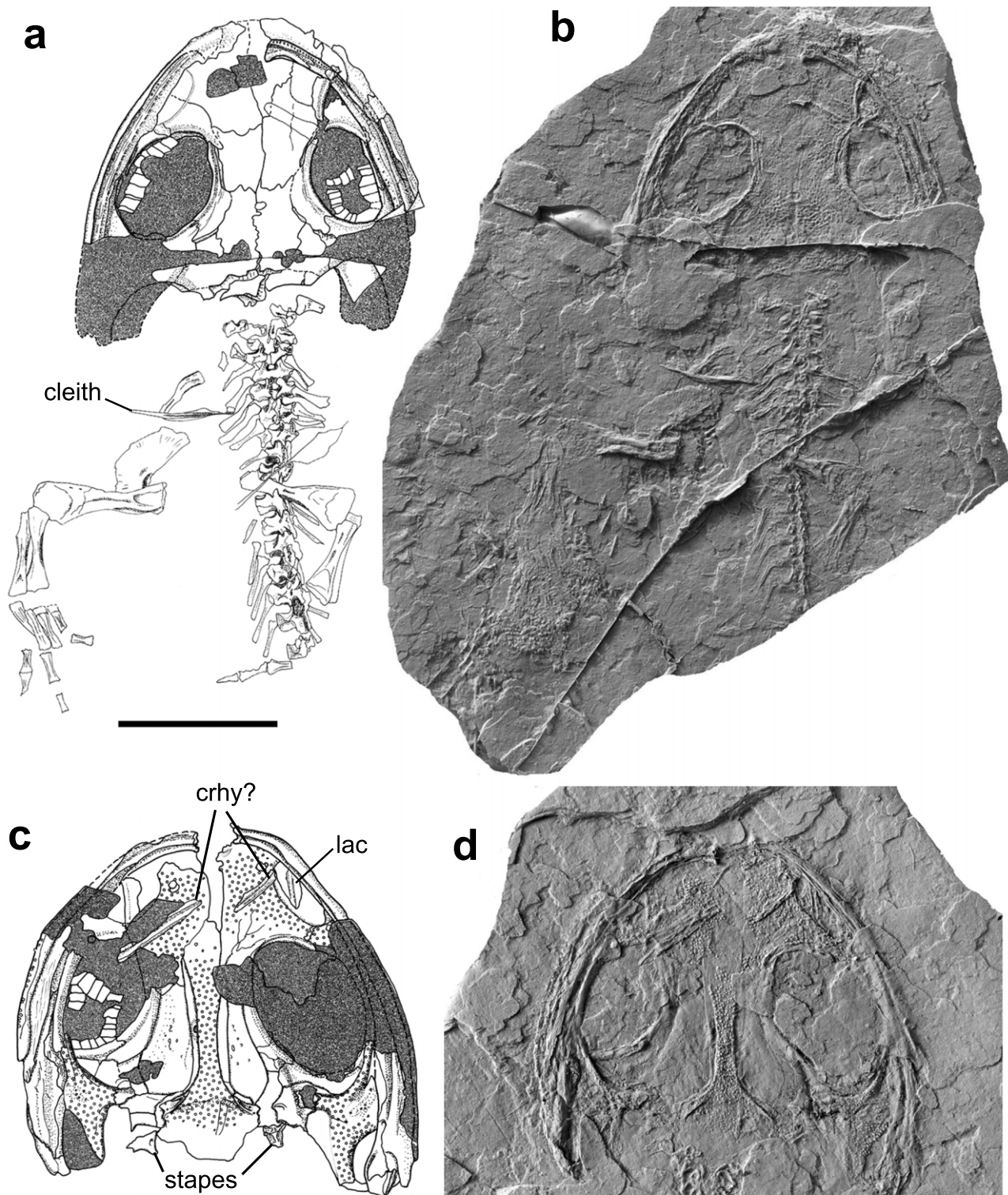


**Figure 4** *Platyrrhinops lyelli* (Wyman), CM 44757: (a) interpretive drawing of skull fragment (inset, see (d) for enlargement); (b) photograph of skull fragment; (c) basal plate of parasphenoid in dorsal aspect; (d) palatine forming lateral choanal margin. Abbreviations: cho=choanal margin; cris sell=crista sellares; d. pr quad.=dorsal process of quadrate; popar=postparietal; psph=parasphenoid; quad=boss on surface of quadrate. Scale bars: (a, b, d)=10mm; (c)=1mm.

out, showing that the junction was an immobile one, as it seems to have been in *Amphibamus*, *Doleserpeton* and *Tersomius* (Bolt 1977, 1979).

**4.3.3. Opisthotic and exoccipital.** CM 44757 shows what may be the occipital exposure of the right opisthotic and part of the exoccipital, though details are difficult to make out. In the holotype specimen, a pair of ossifications immediately

behind the postparietals appear to be the displaced exoccipitals. Each appears to have a posteriorly directed articular condyle, ahead of which the bone curves in a semicircular loop to the vicinity of the postparietal. There is also a lateral flange to each bone representing the articulation with the opisthotic. In the dorsal counterpart of BMNH R.2670 (Fig. 2a), the right exoccipital is visible.



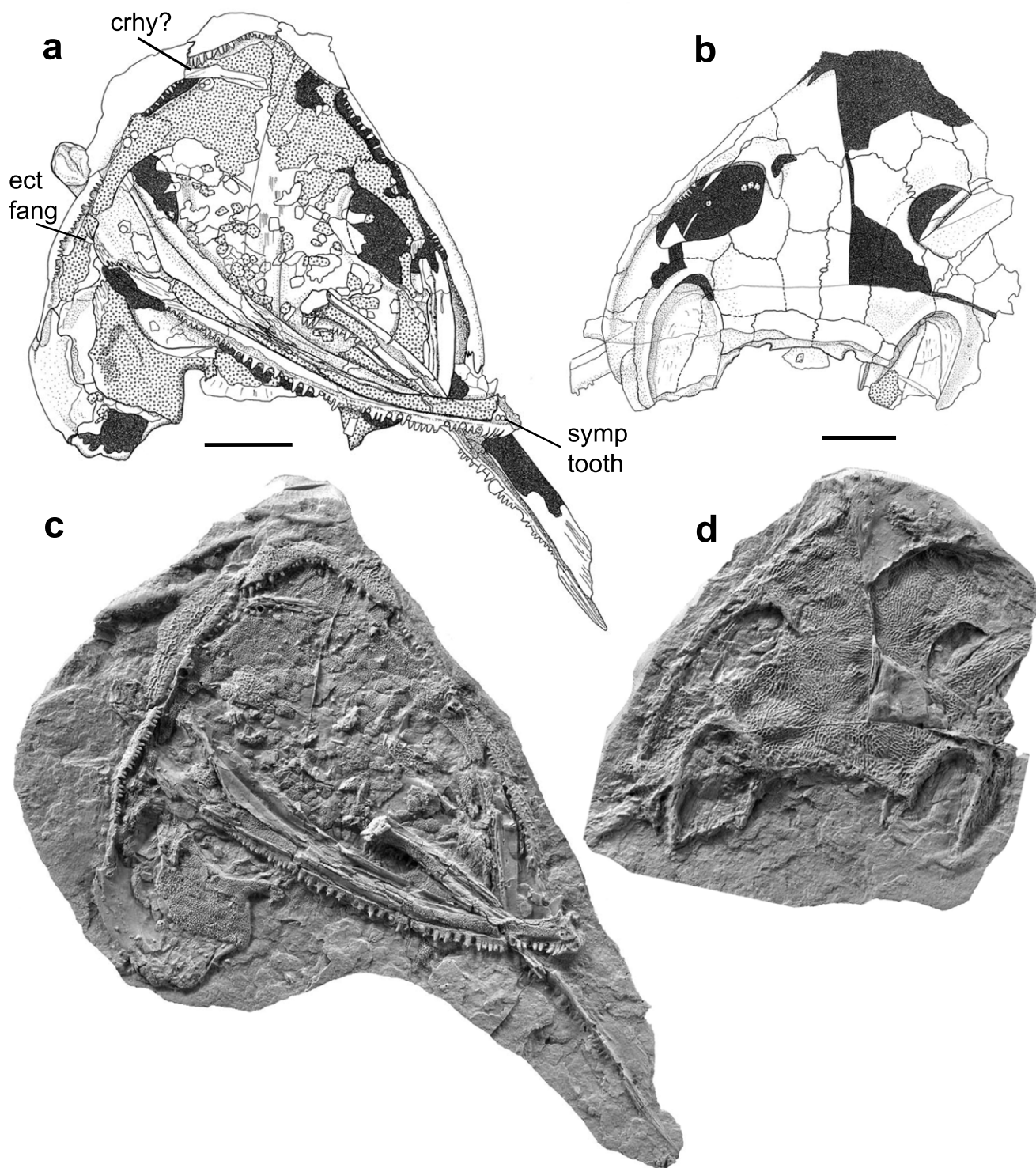
**Figure 5** *Platyrrhinops lyelli* (Wyman), MB Am.331a–b: (a) interpretive drawing of dorsal aspect; (b) photograph in dorsal aspect; (c) interpretive drawing in ventral aspect; (d) photograph in ventral aspect. Abbreviations: cleith=cleithrum; crhy?=possible ceratohyal; lac=lacrimal. Scale bars=10mm.

#### 4.4. Mandible

The mandible of *Platyrrhinops lyelli* is best visible in medial aspect in MB Am.23 (Fig. 6a, c) and BMNH R.2670 (Fig. 2c, d) and in lateral aspect in MCZ 1277 (Fig. 7). It is very similar in shape to that of *Tersomius* as figured by Carroll (1964, fig. 8A–D). The number of coronoids is not determinable, but if it is assumed to be three (as in all other temnospondyls in which the number can be determined) then the number (ten) and position of the elements in the mandible is typical for temnospondyls.

**4.4.1. Dentary.** The dentary forms the outer face of the mandible for much of the anterior two-thirds of the mandible length. At its posterior end, the dentary narrows to a point at the level of the tooth row (MCZ 1277 (Fig. 7) and BMNH R.2670 (Fig. 2c).

**4.4.2. Coronoids.** The coronoid series is represented by denticle-covered bones and the sutures between the elements cannot be certainly distinguished. There are divisions in the coronoid row but they may simply be cracks. If the denticle-covered area is assumed to represent the coronoids, then they



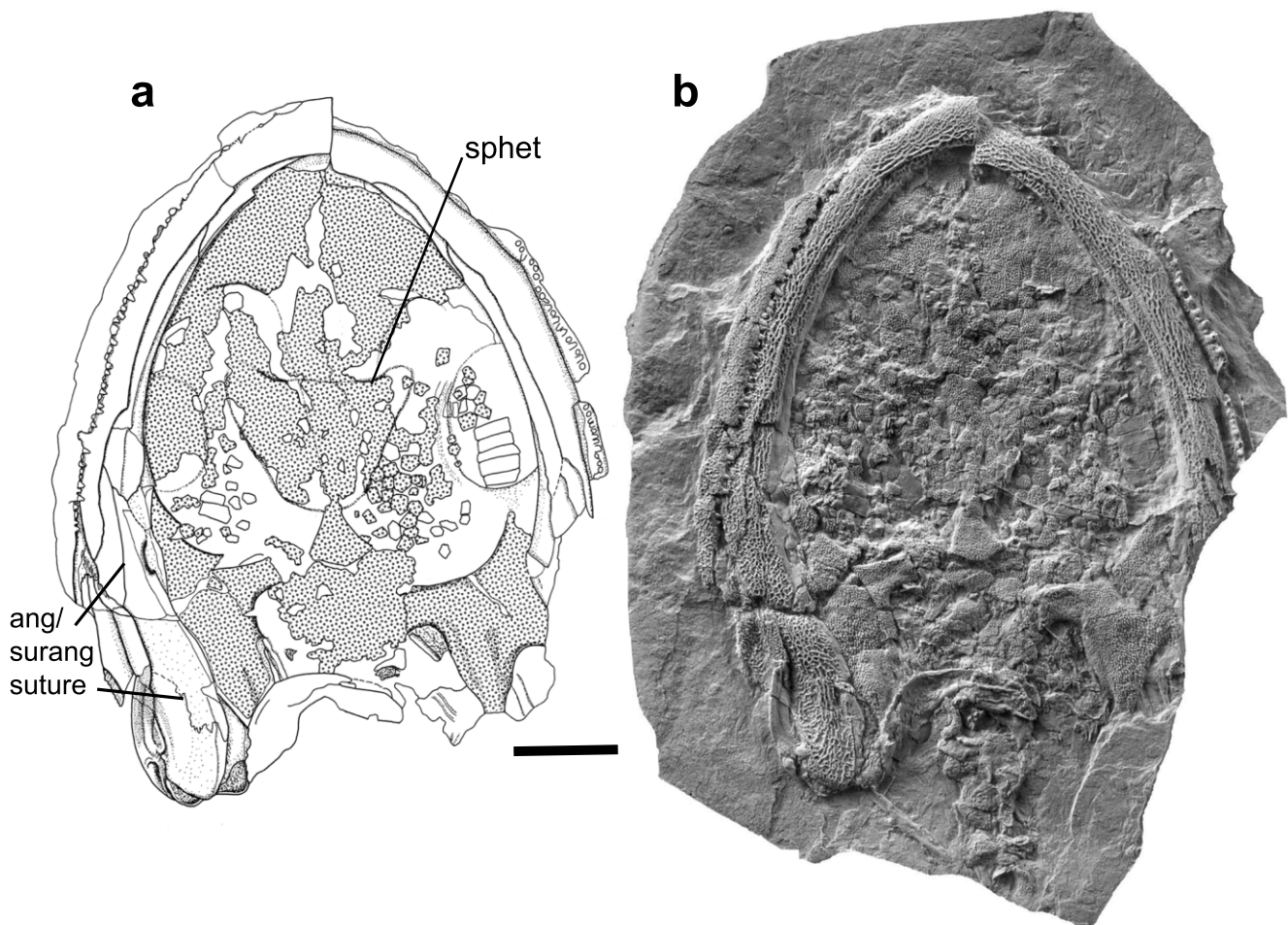
**Figure 6** *Platyrrhinops lyelli* (Wyman): (a) MB Am.23, interpretive drawing of skull in ventral aspect; (b) MB Am.48, interpretive drawing of skull in dorsal aspect; (c) MB Am.23, photograph of skull in ventral aspect; (d) MB Am.48, photograph of skull in dorsal aspect. Abbreviations: crhy?=possible ceratohyal; ect fang=ectopterygoid fang; symp tooth=symphyseal tooth. Scale bars=10mm.

extend along the mesial edge of the dentary from the mandibular symphysis back to the mandibular fossa. The posterior coronoid forms an elevated process at the anterolateral edge of the mandibular fossa, the medial face of which is also denticle-covered at the anterior end (BMNH R.2670, Fig. 2c).

**4.4.3. Splenial.** The splenial forms the ventral face of the anterior mandible and is wedged below the anterior coronoid and the dentary. The splenials are visible in ventral aspect in MCZ 1277 (Fig. 7) where they extend back about one quarter of the length of the mandible. They do not extend as far forward as the symphysis, so fail to make contact with each

other. Posteriorly, the splenial suture with the postsplenial is long and oblique [BMNH R.2670, (Fig. 2c); MB Am.23, (Fig. 6a); MCZ 1277 (Fig. 7a)].

**4.4.4. Postsplenial.** The postsplenial forms the ventral face of the anterior middle region of the mandible and wedges below the middle coronoid series and the dentary. Contact between the postsplenial and the middle coronoid is found in many temnospondyls, but not most other tetrapods. It may constitute a synapomorphy at some level, though this remains to be investigated. The postsplenials are visible in ventral aspect in MCZ 1277 (Fig. 7) and in medial aspect in MB



**Figure 7** *Platyrrhinops lyelli* (Wyman), MCZ 1277: (a) interpretive drawing of large skull and mandibles in ventral aspect; (b) photograph of large skull and mandibles in ventral aspect. Abbreviations: ang/surang suture=angular/surangular suture; sphet=sphenethmoid. Scale bar = 10mm.

Am.23 (Fig. 6a). In both specimens, they are about half as long again as the splenials. They suture with the splenials anteriorly and with the angulars and the surangulars posteriorly.

**4.4.5. Angular.** The angular is a large bone forming the posteroventral region of the mandible. It is best visible in MCZ 1277 (Fig. 7) and appears to be of typical temnospondyl configuration. It wraps under the ventral face of the mandible and borders the prearticular. The two bones surround the small inframeckelian fossa and the ventral margin of this fossa can be seen on the edge of the angular in MCZ 1277.

**4.4.6. Surangular.** The surangular forms the dorsolateral face of the mandible and the lateral border of the mandibular fossa. It is the one element in the mandible of *P. lyelli* which appears to have an unusual configuration. In MCZ 1277 (Fig. 7) and in BMNH R.2670 (Fig. 2) (morphological right sides) it appears to extend forwards to drive a long wedge between the angular and the dentary. Primitively, as in *Tersomius* and many other temnospondyls, the angular and dentary have a broad sutural contact and there is only a very short anterior wedge of the surangular. In the right mandible of the palatal counterpart of BMNH R.2670 (Fig. 2c), the surangular forms the posterior region of the coronoid process. Carroll (1964) suggested that the surangular and angular were almost invariably co-ossified, but we find a distinct suture between them in MCZ 1277 (Fig. 7), even though this is the largest specimen.

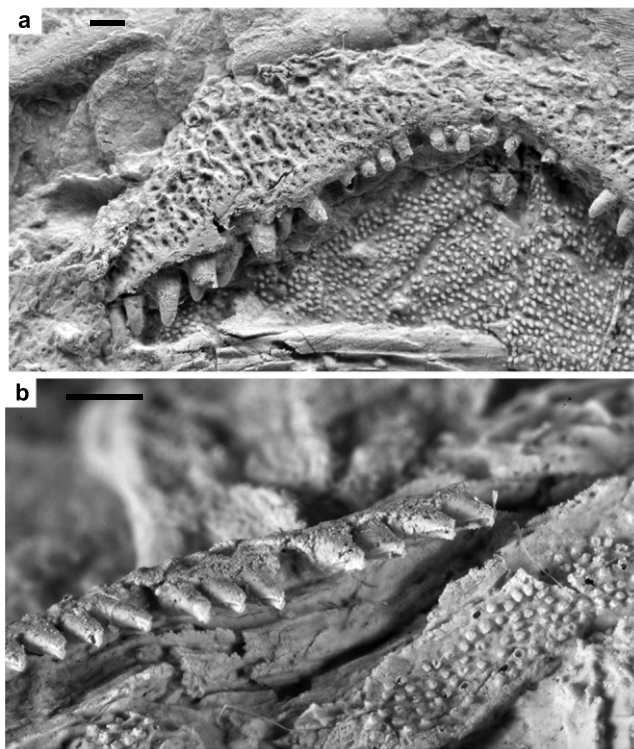
**4.4.7. Prearticular.** The prearticular forms the medial face of the posterior region of the mandible. Its anterior region is visible on the right mandible of MB Am.23 (Fig. 6a, c), where

it forms the medial border of the mandibular fenestra, but is crushed posteriorly so the inframeckelian fossa is not visible.

**4.4.8. Articular.** The articular is visible as a poorly defined block of bone forming the hinge at the posterodorsal corner of the jaw. In the right mandible of MB Am.23 it is visible in dorsal aspect as a rhomboidal surface with an anteroposterior medial groove.

## 4.5. Dentition

**4.5.1. Marginal dentition and tooth replacement.** Palatal fangs and larger marginal teeth all show folding of the enamel at the base of their crowns, implying a labyrinthodont structure. In the following discussion, all dental counts refer to teeth + replacement spaces. The premaxillae of MB Am.23 (Figs 6a, 8a) each bear 17–18 marginal teeth. These teeth are not of uniform size and are of a configuration which has not to our knowledge been reported in any other temnospondyl. There are three distinct sizes of tooth on each premaxillary tooth-row, comprising a medial series of small teeth, a pair of medium teeth and an outer series of large teeth (Fig. 8a). On the left premaxilla, the numbers are 6:2:9 and on the right 8:2:7 (+1?). It is not clear whether this represents a static configuration or if a juvenile dentition is in the process of replacement by an ontogenetically later dentition. The only other large specimen with a visible premaxillary dentition is BMNH R.2670 (Fig. 2c), in which the incompletely exposed right premaxilla bears at least 14 teeth of apparently uniform size. Our count contrasts with that of Carroll (1964), who estimated 21 premaxillary teeth, based



**Figure 8** *Platyrrhinops lyelli* (Wyman), MB Am.23: (a) right premaxilla showing smaller medial marginal teeth and larger lateral marginal teeth; (b) sequence of marginal teeth on right maxilla, showing several examples of bicuspid crowns. Scale bars=1mm.

largely on MCZ 1277. Our peel of this specimen shows very few premaxillary teeth sufficiently well preserved to count.

The maxillae of MB Am.23 (Fig. 6a, c) have spaces for 57 teeth (left) and 61 teeth (right). In CM 44757, (Fig. 4a, b), the right maxilla is estimated to have space for 64 teeth, although there is a short gap in the middle which makes the estimate approximate. MCZ 1277 (Fig. 7) has space for 54+ teeth on the right maxillary. Carroll (1964) estimated a count of 55 maxillary teeth for *Platyrrhinops*, a little lower than ours. Our estimates for the total number of teeth in the upper row vary between 74 and 79, similar to the conclusion reached by Milner (1982) and Carroll (1964), who both estimated about 76. Carroll (1964) previously noted the greater number of upper row teeth in *P. lyelli* as compared with *A. grandiceps*.

The dentaries of MB Am.23 (Fig. 6a, c) and BMNH R.2670 (Fig. 2c) bear two pairs of symphyseal fangs on each side of the symphysis just below the marginal tooth-row. In MB Am.23 the dentary has space for 66–68 marginal teeth. If our estimates of tooth count are correct, they suggest a greater number of upper than lower teeth, the implication being that dentary teeth are larger than maxillary and premaxillary teeth, on average. Only one specimen (MB Am.23/48) preserves examples of both rows, and bears out that inference. Differences in size between upper and lower jaw teeth are not uncommon in early tetrapods, with dentary teeth sometimes being smaller (eg. *Ichthyostega* (Jarvik 1996), *Acanthostega* Clack 2002b) and sometimes larger (eg. *Greerpeton* (Smithson 1982), *Balanerpeton* (Milner & Sequeira 1994)). The significance of the difference is unclear.

An important feature that high fidelity silastomer peels have revealed is that dentary, maxillary and premaxillary teeth are bicuspid, particularly well shown in MB Am.23/48 (Fig. 8b) but also present in MCZ 1277. Unfortunately the preservation does not allow us to say whether this is true of the smaller premaxillary teeth of these specimens. We are unable to determine the situation in the teeth of smaller skulls, so cannot

determine the ontogeny of this type of dentition. There is no evidence of pedicely in any specimen.

**4.5.2. Palatal fangs, denticles and dermal platelets.** *P. lyelli* has the typical temnospondyl condition of a single fang+replacement pit on each of the vomers, palatines and ectopterygoids. They are best seen in MB Am.23 (Fig. 6a, c). The vomerine fang-pit pair is posteromedial to the anteromedial corner of the elongate choana. There are no other vomerine fang-pairs, in contrast to the condition in *Tersomius* and *Eoscopus*. Schoch & Milner (2004, fig. 2C) reconstructed the vomers with several scattered teeth as well as the fang pairs, but these appear to be broken crowns of marginal teeth scattered across the vomers in the specimen used in the reconstruction. The palatine fang-pit pair (also in CM 44757, Fig. 4a, b) is posterolateral to the posterior margin of the choana and about one-third of a choana-length from it. The ectopterygoid fang-pit pair is near the anterior end of the ectopterygoid and can be seen on the right side of MB Am.23 (Fig. 6a) and BMNH 2670 (Fig. 2c), where the ectopterygoid is somewhat displaced. In contrast to Milner's (1982) observations of the small specimen MB Am.331, further examination has revealed that it does possess both vomerine and palatine fang pairs (Fig. 5c). *A. grandiceps*, by contrast, possesses a row of somewhat enlarged teeth, rather than simple fang pairs on each of the marginal palatal bones.

The vomers, palatines, ectopterygoids, pterygoids and parasphenoid all bear a dense covering of palatal denticles in medium-large specimens. The denticles are simple, unicuspid and of even size and density over most of the palatal elements. However, on the central region of the pterygoids and the pterygoid flanges, the denticles are slightly larger and very densely packed. They also reveal directional changes that are probably not accounted for by simple crushing. The denticles also extend well down the medial face of the quadrate ramus of the pterygoid. In all specimens, large numbers of denticle-bearing platelets of bone are associated with the palatal region. In MCZ 1277, they are still more or less *in situ* and form a sheet of denticle-bearing bone across the entire area of the interpterygoid vacuities, obscuring the underlying bones entirely (Fig. 7).

In the right mandibles of MB Am.23 (Fig. 6) and BMNH R.2670 (Fig. 2), the coronoid series bears denticles along its entire length from the mandibular symphysis back to the edge of the mandibular fossa.

#### 4.6. Other skeletal structures of the head

**4.6.1. Stapes and hyobranchial system.** None of the large specimens has a recognisable stapes, but both stapes are present in the small MB Am.331 and the left stapes is visible in both counterparts (Fig. 5a, c). The stapes comprises an undivided footplate, perforated by the stapedia foramen, and the ossified proximal region of a shaft. The shaft is narrowing where ossification ceases distally and, if it were extended further in cartilage, would be considered a rod-like stapes as found in *Doleserpeton* (Bolt & Lombard 1985, fig. 2).

No obvious ceratobranchial elements are preserved *in situ*, nor do any specimens bear ceratobranchial ossicles or gill-rakers. However, two specimens bear structures in the palatal/intermandibular region which appear to be modified hyobranchial elements. In the small MB Am.331b, there are two linear ossifications lying free across the underside of the vomers (Fig. 5c, d). These linear structures are respectively 5 mm and 3 mm in length and could represent either two distinct elements or one broken element. Each is flattened, with a shallow linear groove running along the exposed surface. The bone is smooth and there is no trace of sculpture, striation or

denticles on the surface. A similar structure is present superimposed on the right vomer of the much larger skull MB Am.23 (Fig. 6a, c). The skull is about 60 mm long and the linear ossification is over 10 mm long, with one end obscured by an overlapping maxilla. The ossification is again a smooth flattened bone with a linear groove along at least part of its length. There appears to be a small lateral expansion partway along the bone but this may be an artefact of crushing.

As these enigmatic structures are visible in two specimens, in a similar position, they are presumably not a chance superposition of an exotic bone from elsewhere, but represent a rarely preserved structure of the palate or intermandibular region. The most plausible identity for these elements is that they are ceratohyals, retained into the adult and modified in relation to tongue movement. They appear different in shape and position from the hyobranchials described in *Pasawioops* (Fröbisch & Reisz 2008). Large flattened ceratohyals have not been reported previously in metamorphosed temnospondyls, but the homologous structures, similarly flattened, do occur in some lissamphibians. In some terrestrial urodeles, such as the Salamandridae, the ceratohyals are modified as flattened oval plates of bone situated just behind the symphyseal region, with their long axes at about 45° to the anteroposterior axis (Francis 1934). These structures are discussed further below.

**4.6.2. Sclerotic ossicles and palpebral dermal plates.** Sclerotic ossicles were present in *P. lyelli*, although none of the large specimens has a complete ring preserved *in situ*. Two sclerotic plates are visible in the left orbit of AMNH 6841 (Fig. 1a) and a few are present in the region of both orbits in MCZ 1277 (Fig. 7a). Each plate is of elongate rectangular shape and about three times as long as wide. One of the smaller specimens – MB Am.331 (Fig. 5a, b) – has a nearly complete ring of about 25 sclerotic ossicles in the right orbit, and *P. lyelli* may be assumed to have possessed a typical temnospondyl sclerotic ring of 25–30 ossicles. Incompletely preserved rings are also present in *A. grandiceps*.

Two specimens, the holotype AMNH 6841 (Fig. 1a, b) and BMNH R.2670 (Fig. 2a, b), also bear a series of palpebral ossifications in association with the orbits. These structures are known in three-dimensionally preserved dissorophoid skulls such as that of *Tersomius texensis* figured by Carroll (1964, fig. 2), and are clearly situated within an upper eyelid. The palpebral ossifications are a series of loosely arranged irregular dermal platelets in the medial region of the orbit, as seen in crushed specimens. These platelets have larger shallower sculpture pits than the dermal bones of the skull roof, and each platelet has the suggestion of a thickened rim around it. In both orbits of AMNH 6841 and in the left orbit of BMNH R.2670, the palpebral ossifications are nearly undisturbed, and 11–14 well-defined platelets are evident.

Reconstructions of the skull and mandible of a large, presumably adult, individual are presented in Figure 9.

#### 4.7. Postcranial skeleton

Only a few aspects of the postcranial skeleton are described and discussed in the following paragraphs, which are intended to supplement the descriptions of Carroll (1964), Hook & Baird (1984) and Daly (1994). The new specimens that formed the stimulus for this redescription are largely cranial, and of the newly presented material, only MB Am.331 bears any significant postcranium. A few observations of anatomical and systematic significance can, however be usefully made.

**4.7.1. Vertebrae.** As noted by Carroll (1964 p. 234), AMNH 6841 has 25–26 presacral and one sacral vertebra. No other Linton specimen has a complete presacral column, but the incomplete specimens are consistent with this column length. AMNH 2002 bears at least 17 caudals which show a

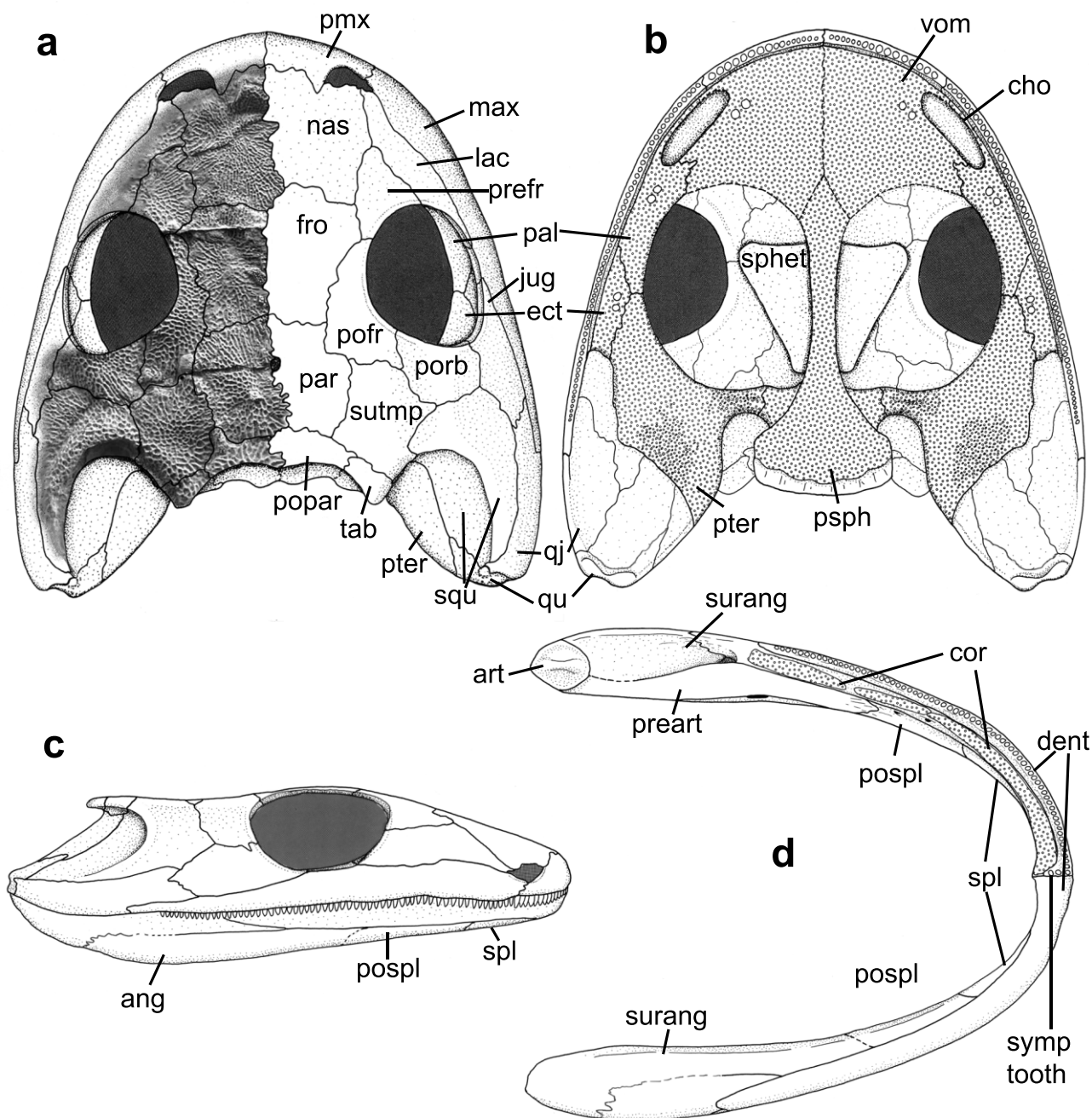
marked decline in size (Hook & Baird 1984) and suggest that the tail was about as long as the trunk. The tail was clearly not deep along most of its length.

The trunk vertebrae have been described as typically rha-chitinous by all authors up to and including Clack & Milner (1994), with the implication that the pleurocentra were small, laterally situated structures. Clack and Milner argued that *Platyrhinops* differed from all other amphibamids in retaining primitive small pleurocentra. However, Daly (1994, p. 29, fig. 24) has shown that in USNM 4461, the posterior trunk pleurocentra are ventrally expanded and probably met broadly in the midline. As these are the only clearly observable trunk pleurocentra in any Linton *Platyrhinops* available to us, it must be assumed that *Platyrhinops* was a typical amphibamid in possessing enlarged pleurocentra. On the other hand, in redescribing AMNH 2002, Hook & Baird (1984) did not note the presence of enlarged pleurocentra, even though this is by far the largest preserved specimen. The situation in this specimen is ambiguous, because the centra are dispersed.

In AMNH 6841, the anterior vertebral column is preserved crushed in lateral view, and it can be seen that the fourth vertebra has a distinctly lower neural arch than those around it. None of the neural arches is tall, so the distinction is not great, but neural arch 4 is only about three-quarters of the height of the others (Fig. 1a, b). This is similar to the situation in *Trimerorhachis sandovalensis* (Berman & Reisz 1980, p. 468 and fig. 7), and is a less pronounced form of the condition seen in *Eryops* (Moulton 1974, p. 29 and text-fig. 1) and *Sclerocephalus* (Boy 1988, p. 122 and Abb. 7), in which the fourth trunk vertebrae have a very reduced neural spine, in contrast to the tall neural spines of the third and fifth vertebrae. Few articulated anterior vertebral columns of temnospondyls are figured in the literature and the extent of this character is unknown. It is also present in the basal tetrapod *Acanthostega gunnari* from the Upper Devonian of Greenland (Coates 1996) and so may be a primitive tetrapod feature retained in a range of Palaeozoic temnospondyls.

**4.7.2. Ribs.** Little can be added to the description of the ribs given by Carroll (1964), except that the cervical flanges seen in the holotype are already present in the small specimen MB Am.331 (Fig. 5a, b).

**4.7.3. Appendicular skeleton.** A few modifications can be made to the description given by Carroll (1964). The scapulo-coracoid is quite well preserved in the holotype, and has a fimbriated anterior edge, alongside which lie the cleithrum and clavicle (Fig. 1a, b). The posterior edge of the scapulo-coracoid is thickened and curves posteriorly to produce the glenoid buttress, though the glenoid itself cannot be seen. The quality of our peel does not allow us to confirm the presence of an interclavicle in the holotype. The cleithrum appears as a very short almost cylindrical element, but some of it may be obscured. The clavicle has a rather narrow ventral plate, here preserved in internal view. Another, well preserved, clavicle exposed in internal view is present on BMNH R.2670, which shows a rather more expanded ventral plate, grooved where it would have contacted the interclavicle, and pierced by nutrient foramina (Fig. 2d, g). The stem is grooved for reception of the scapular blade. The expansion of the ventral plate may be growth-related, as BMNH R.2670 has a skull length approximately twice the length of that of the holotype, or it may simply be better exposed. MB Am.331 also preserves a scapulo-coracoid, of a similar shape to that of the holotype, but with less curvature to the glenoid buttress (Fig. 5a, b). A possible cleithrum or poorly preserved clavicle is also present but adds little detail. A certain amount of variation occurs in the shape of the ilium and its dorsal blade, but this could be a result of



**Figure 9** *Platyrrhinops lyelli* (Wyman): Reconstruction of skull of large specimen in (a) dorsal aspect, ornamentation adapted from BMNH R.2670. Note that the premaxilla/nasal suture on the left hand side does not follow that in the fossil, because the latter is crushed and elevated posteriorly in this region; (b) ventral aspect; (c) right lateral aspect; (d) mandibles in dorsal aspect (above) and ventral aspect (below). Abbreviations: ang=angular; art=articular; cho=choanal margin; cor=coronoids; dent=dentary; ect=ectopterygoid; fro=frontal; jug=jugal; lac=lacrimal; max=maxilla; nas=nasal; pal=palatine; par=parietal; pmx=premaxilla; pofr=postfrontal; popar=postparietal; porb=postorbital; pospl=postsplenial; preart=prearticular; prefr=prefrontal; psph=parasphenoid; pter=pterygoid; qj=quadratojugal; qu=quadrate; sphet=sphenethmoid; spl=splenial; squ=squamosal; surang=surangular; sutmp=supratemporal; symp=symphyseal; tab=tabular; vom=vomer.

differential preservation. However, variation in iliac morphology is also seen in some other early tetrapods such as *Ichthyostega* (Jarvik 1996).

Little can be added to the description of the limbs given by Carroll (1964) based on the holotype. As noted by Carroll, the length of the limbs in general is greater compared to vertebral column length than that in many other temnospondyls, such as its close relative *Amphibamus grandiceps* and in *Eryops* (Carroll 1964). The humerus is also longer relative to midline skull length than in *Dendrerpeton* (based on figures from Holmes *et al.* 1998), and *Eoscopus* (from Daly 1994). In the only specimens of *Platyrrhinops* that preserve both the skull and

the humerus, the latter is slightly shorter relative to midline skull length in the smaller specimen MB Am.331 compared with the holotype, but this is perhaps not surprising given typical ontogenetic scaling effects in which the head in vertebrates is usually comparatively larger in juvenile animals.

#### 4.8. Dermal scales

Most articulated Palaeozoic temnospondyls bear a chevron-like arrangement of heavily ossified gastralia on the abdomen and many bear dorsal osteoderms as well. Articulated tetrapods from Linton are no exception and in a small sample of any one species, well-preserved individuals may be expected to



bear gastralia. *Platyrrhinops* is therefore striking in that dermal scales are not visible in small and medium-size articulated specimens such as MB Am.331 (16 mm skull), AMNH 6841 (25 mm skull) and USNM 4461 (Fig. 1c). Milner (1982) commented that this species was characterised by a total lack of dermal scales, but Hook & Baird (1984) were able to show that AMNH 2002, a large postcranial fragment (estimated skull length 60 mm), bore some chevrons of small, slender, poorly ossified gastralia. If, as seems likely, attribution to *P. lyelli* is correct, then the taxon must be accurately characterised not by the absence of all dermal scales but by the presence of poorly ossified gastralia in large specimens and the apparent absence of dorsal osteoderms in all specimens.

## 5. Ontogeny and variation

The discovery of the tiny skull CM 23057 now allows a better comparison of similarly sized skulls of *A. grandiceps* and *P. lyelli*, and further information can be added to the comparisons made by Milner (1982). It also allows comparisons with growth series now documented in some detail by Schoch and colleagues for other temnospondyl taxa, in particular the eryopoids *Onchiodon* (Witzmann 2005) and *Sclerocephalus* (Schoch 2003) and the zatracheid *Acanthostomatops* (Witzmann & Schoch 2006). Zatracheids may be closely related to dissozophoids (see Witzmann & Schoch 2006).

CM 23057 (Fig. 3), with a midline skull length of 13 mm, is only slightly larger than the two best preserved skulls of *A. grandiceps* at 10 mm and 10.4 mm respectively. CM 23057 is already larger than most of the described series of skulls of the branchiosaur *Apateon*, in which progressive ossification of the dermal skull bones has been documented. A full set of dermal bones is preserved in CM 23057, including the tabulars, and by the same size, even the slowest-ossifying branchiosaurids have also a full complement of dermal bones (Schoch 2002a). Widening of the interorbital region, consequent mainly upon widening of the pre- and post-frontals, recorded in *Acanthostomatops* (Witzmann & Schoch 2006) is also seen in *P. lyelli*, as well as in some of the branchiosaurid taxa such as *Melanerpeton* (Schoch 2004), and may be a more widely distributed character.

Significant differences in ossification patterns can be detected between *P. lyelli* and *Amphibamus* as compared with *Onchiodon* (Witzmann 2005). For example, the stapes is present in the 10 mm skull of *Amphibamus* and the 18 mm skull of *P. lyelli*, as compared with *Onchiodon* in which its first appearances is recorded in a skull of nearly 30 mm skull length. In this, *Amphibamus* is more comparable to *Apateon*, in which the stapes ossifies first at about 9 mm skull length (Schoch 2004). In other aspects, *Platyrrhinops* appears to follow the sequence in *Onchiodon*. Palatal platelets bearing ossicles appear to be absent in the smallest *P. lyelli* skull (CM 23057, Fig. 3), to form an incomplete sheet in skulls between 25 and 50 mm, but to be more extensive in the largest skull at a midline length of 60 mm. In *Onchiodon*, likewise, they first appear at 25 mm skull length (Witzmann 2005).

Comparing CM 23057 to MB Am.331 suggests a widening of the cultriform process and its associated denticle field during growth. It is difficult to be certain whether this is a continuous trend, because in the larger specimens the cultriform denticle field is either obscured or confluent with the denticle platelets of the palate. At 13 mm skull length, the width of the cultriform process is similar to that of *A. grandiceps*. By 60 mm skull length, the denticle field completely sheathes the basal articulation and the parasphenoid plate. The anteroposterior length of the basal articulation increases with skull length, though the

increase is hard to quantify. Because of the limited preservation of CM 23057, it is not possible to compare the palatal dentition of a small *P. lyelli* specimen to *A. grandiceps* at a similar size. Therefore, it is not possible to say whether possession of a row of small teeth on the marginal palatal bones of the latter is a juvenile formula that might be replaced by the single fang pair as seen in *P. lyelli*.

Dermal sculpture of the skull bones increases in depth and definition with skull length in *P. lyelli*. Up to 18 mm skull length, sculpture is very faint, if present at all. At 25 mm, it is conspicuous on most skull bones, though it shows elongated pits at the bone margins. By 50 mm, the sculpture is almost entirely reticulate and continuous over the whole skull and lower jaw. In comparison, in the 10 mm skull of *A. grandiceps*, the sculpture is already conspicuous and almost entirely reticulate.

*P. lyelli* and *Amphibamus* resemble *Onchiodon* in having the sclerotic plates, dermal and endoskeletal shoulder girdle, and the ilium ossify early in development. This is probably the primitive condition, as is early ossification of the skull roof (Schoch 2002b). By contrast, in *P. lyelli*, centra are present in an animal of 25 mm skull length, whereas in *Onchiodon*, they ossify first at about 45 mm skull length. In *A. grandiceps*, both sets of centra are represented in animals as small as 10 mm skull length (Bolt 1979).

In MB Am.331 (18 mm skull length), the left radius, ulna, metacarpals and phalanges are clearly preserved in articulation, but no carpals are ossified. In AMNH 6841 (25 mm skull length), no ossified carpals are present, as noted by Carroll (1964, p. 238), but five very poorly ossified tarsals are present in the left pes (Carroll 1964, p. 240, fig. 1). In AMNH 2002, the fore-limbs are not present but the hind limbs bear well-ossified tarsals, although their configuration is not clear (Hook & Baird 1984, p. 700).

*Amphibamus* and *P. lyelli* appear to differ in the appearance of certain appendicular elements. *Amphibamus* already has a well ossified ischium and probably a pubis at 10.4 mm skull length (YPM 794, pers. obs.), whereas *P. lyelli* still lacks these bones at 25 mm skull length. The rest of the postcranial skeleton of *Amphibamus* is better ossified than in *P. lyelli*, and considerably more so than in *Acanthostomatops*, in which the ischium does not appear until a skull length of between 30 and 35 mm (Witzmann & Schoch 2006). However, *Amphibamus* lacks ossified carpals and tarsals.

There has been no attempt at a diagrammatic summary of the ontogenetic changes in *Platyrrhinops lyelli* as it is felt that the small sample size (eight critically relevant specimens) and incompleteness of material means that ontogenetic changes cannot be sequenced with much precision, in particular in the gap between skulls of 25 mm and 50 mm midline skull length (msl in the following text). Such changes that can be sequenced require considerable qualification and are as follows:

1. At 18 mm msl (MB Am.331), the stapes body is ossified (probably unossified at 13 mm msl in CM23057), and the cultriform process has widened (still narrow in the 13 mm msl CM23057).
2. At 25 mm msl (AMNH 6841), heavy dermal ossification of the skull has developed in the form of striate/reticulate pitting of the dermal bones and a partial cover of palatal osteoderms (light pitting and no osteoderms in MB Am.331). The centra have ossified (unossified in MB Am.331) and the tarsals are partly ossified (unknown in smaller specimens). The carpals, pubes and ischia are still unossified at this size.
3. By 50–55 mm msl (BMNH R.2670, MB Am 23/48, MCZ1277 and by estimate USNM 4461), several changes

have occurred, but their sequence during the doubling of size from the previous specimen is unknown. Progressive ossification of dermal elements has resulted in fully reticulate pitting of the dermal bones (BMNH R.2670 and MB Am. 23/48) and a full covering of tooth-bearing platelets over the palate (MCZ 1277). The proportional widening of the central region of the skull has occurred both on the skull roof (BMNH R.2670, MB Am 23/48) and the sphenethmoid (MCZ1277). The pubis and ischium have ossified and the tarsals are fully ossified (USNM 4461). The ossification point of the carpals is unknown.

4. At an approximate msl of 60–70 mm (AMNH 2002), poorly ossified gastralia appear; these are certainly absent in USNM 4461 (estimated msl 50 mm).

In the light of the new information about ossification sequences in temnospondyls, it is now possible to give fresh consideration to the ontogenetic status of taxa such as *P. lyelli* and *Amphibamus*. Bolt (1977, 1979) claimed that known specimens of both *Amphibamus* and *Doleserpeton* were juvenile, though post-metamorphic, individuals, and suggested that *Amphibamus* might well represent a juvenile form of *P. lyelli* and that the two were possibly conspecific. Based on the more recently discovered specimen of *P. lyelli*, MB Am 331 (as MB Am 1888–1456), Milner (1982) showed this not to be the case. The studies for this present paper have served to emphasise this, with the discovery of further differences in morphology related to similar-sized individuals. For example, the skull bones of *Amphibamus* show more developed dermal sculpture than those of *P. lyelli* of similar size (also noted by Bolt 1979). Milner (1982) pointed out the differential in width between postfrontals of the 18 mm skull of *P. lyelli* and those of *Amphibamus*. Though exhibiting only relatively simple non-interdigitating sutures, *Amphibamus* skulls retained more of their three-dimensionality at 10 mm than *P. lyelli* did at 13 mm or even 18 mm, implying a more robust construction, less susceptible to compression. The maintenance of three-dimensionality is also evident in the many uncrushed elements in the postcranium of *Amphibamus* specimens, again perhaps implying more robust ossification; though in both cases, it could be argued that the effect is a product of taphonomic circumstances. More compellingly, the more complete ossification of the postcranium, detailed above, suggests that at 10 mm skull length or only very slightly more, *Amphibamus* had a more fully developed pelvis than *P. lyelli* at 25 mm skull length. Though it retained a few juvenile characters at a comparably small size, *Amphibamus* was much more fully ossified and probably therefore ontogenetically ‘older’ than *P. lyelli*, and certainly could not have ‘metamorphosed’ into the larger adults of *P. lyelli* (contra Bolt 1979 and cf. Milner 1982).

## 6. Morphology and lifestyle of *Platyrhinops*

*Platyrhinops* has generally been perceived as an amphibious to terrestrial member of the Westphalian swamp fauna. Carroll (1964, p. 240) interpreted it as relatively terrestrial with large feet for moving on soft boggy substratum. DeMar (1968, p. 1240) however described it as semiaquatic, although this adjective seems to have been used as a relative term in comparison with Permian armoured dissorophids, and was largely based on a general assessment of the associated faunas.

Carroll (1964) commented on the lack of lateral line canals, the length of the limbs, the reduction of the dermal shoulder girdle, and the almost complete ossification of the skeleton as supporting his suggestion of an animal that did not habitually live in the water. While this is true, several of these features in *Platyrhinops* (and *Amphibamus*) suggest similarities to modern

amphibians, in particular, anurans. The lack of lateral line canals does not preclude lack of any lateral line organs. Modern amphibians also lack lateral line canals as such, though tadpoles and aquatic adults retain patches of neuromasts in the skin (Fritzsche 1989). The large orbits, coupled with the size of the sclerotic rings and presence of palpebral cups, suggest protuberant eyes. The large, flattish head with wide mouth and slender jaws, coupled with enlarged palatal vacuities and tiny ribs, suggest the animals were buccal pumpers (Janis & Keller 2001). The small size and lack of ventral gastralia in *P. lyelli* suggest that cutaneous gas exchange was likely. Both these modes of breathing have been suggested as primitive for tetrapods, but lissamphibians and their stem group specialised in them (Clack 1992, 2002b).

Evidence from the hyobranchial skeleton suggests the presence of a frog-like ear and a frog-like extensible tongue. The structures interpreted as ceratohyals in *Platyrhinops* deserve some comment. In some terrestrial urodeles such as the Salamandridae, the ceratohyals are modified as flattened oval plates of bone situated just behind the symphyseal region, with their long axes at about 45° to the anteroposterior axis (Francis 1934). The *musculares subhyoideus* arise from the posterior ends of the ceratohyals and insert on an aponeurosis of the *m. intermandibularis*. Contraction of the *m. subhyoideus* causes movement of the ceratohyals, which results in tongue elevation (Duellman & Trueb 1986). In ambystomatids and plethodontids, the ceratohyals are also flat and elongate, but are situated along the lingual side of each jaw margin with their long axes anteroposteriorly directed, and are not concerned with tongue movement, the *m. subhyoideus* being absent (Duellman & Trueb 1986). In frogs, the anterior hyoid cornua or hyale associated with tongue movement are also modified ceratohyals (Duellman & Trueb 1986, table 13.1).

These structures in *Platyrhinops* may thus represent a primitive version of the tongue-elevating system found in salamanders and frogs. The presence of denticles over the roof of the mouth and along the cultriform process in *Platyrhinops* is also consistent with the presence of a manipulative tongue. This has implications, not only for the interpretation of the lifestyle of *Platyrhinops*, but also for the possible relationship between amphibamids and lissamphibians.

An ossified hyobranchial skeleton, present in juveniles of the zatracheid *Acanthostomatops*, has been shown to be mostly resorbed in the adult animal. However, some of the larger specimens do appear to retain ossified ceratohyals, which Witzmann & Schoch (2006) suggested were associated with the presence of a manipulative tongue, and as suggested here also in *Platyrhinops*. The presence of denticles over the roof of the mouth and along the cultriform process in *Platyrhinops* is also consistent with the presence of a manipulative tongue, and the increased area of denticulation in larger individuals may reflect changes to feeding habits with age and growth. The differentiated premaxillary dentition of MB Am 23/48 may also indicate age-related changes to feeding strategies.

Branchiosaurids (the sister-taxon of the ‘*Amphibamus* branch’ amphibamids), *Micropholis* (the type of the ‘*Micropholis* branch’ amphibamids) and micromelerpetontids (probably primitive dissorophoids) all retain a hyobranchial skeleton in which the ceratohyals are ossified only as a central segment of a rod-like element (Boy 1985, fig. 4; Boy & Sues 2000, figs 6, 7) and this appears to be the generalised condition for dissorophoids, at least outside the ‘*Amphibamus* branch’ of the amphibamids. This suggests that the situation in *Platyrhinops* is a derived characteristic of a fairly restricted group of amphibamids and possibly occurring only in adults, not juveniles.

The length of the presacral vertebral column in *Platyrhinops*, at about 25, is common in early terrestrial tetrapods. Coupled with the long limbs and large feet, it suggests an animal in which limb extension rather than axial bending was more significant in locomotion. The large feet, if webbed, could also have provided the main propulsion in swimming, as well as spreading the load when traversing boggy ground as Carroll (1964) suggested.

## 7. Inferences from palaeoenvironment and assemblage at Linton

The *Platyrhinops lyelli* specimens described above are all derived from the sapropelic coal that underlies the Upper Freeport Coal locally at Linton, Ohio. The vertebrate-bearing horizon is a very local structure and was originally an abandoned channel in a meandering river in a fluviodeltaic system (Hook & Ferm 1985, 1988). The abandoned channel appears to have formed an ox-bow lake which was about 300 m wide (Hook & Ferm 1985) and in which a sapropelic peat was laid down in an anaerobic hypolimnion (Hook & Hower 1988).

*Platyrhinops* specimens occur at a low frequency in the Linton assemblage. At Linton, at least 900 tetrapod specimens have been collected (Hook & Baird 1986, fig. 4), most of which are clearly aquatic forms, such as the colosteid *Colosteus*, the temnospondyl *Isodectes* (= *Saurerpeton*) and the nectridean *Sauroplorea*. Of the 900 tetrapod specimens, ten are certainly *Platyrhinops* (the material listed in this present work). Thus, *Platyrhinops* specimens represent 1.1 per cent of the tetrapod assemblage. The genus is clearly not an abundant element in the assemblage but, equally, the presence of ten specimens of different sizes suggests a local form regularly dying in the lake and hence perhaps a lake-margin inhabitant throughout its terrestrial life-history. The relatively good preservation of many of the specimens suggests that they were not transported. Of the ten specimens, five (AMNH 6841, AMNH 2002, MB Am.331, MCZ 1277 and USNM 4461) were articulated skeletons when buried. A further three (BMNH R.2670, CM 23057, and MB Am.23/48) are isolated skulls with mandibles, on slabs which are sufficiently restricted that one cannot determine whether the postcranium was originally present or not. Only two specimens (AMNH 2566, CM 44757) are comprised of disarticulated skull elements. Each of the specimens showing an articulated vertebral column is disrupted around the abdominal region. The two most complete show evidence of some dissolution or other cause of loss of detail around this region, the other two have lost either the anterior or posterior parts of the entire animal. This probably relates to the decay of internal organs and the subsequent disintegration of the body at this point. In conclusion, *Platyrhinops lyelli* appears to have been a lake-margin inhabitant, living and feeding above the air-water interface throughout its post-metamorphic life with occasional individuals of all sizes dying in the lake and being buried on the lake-bed.

## 8. Systematic position of *Platyrhinops* within the Amphibamidae

Among the earliest major cladistic analyses to include not only amphibamids but *Platyrhinops* itself was that by Ruta *et al.* (2003) (see also Ruta & Coates 2007). In at least some trees, they recovered a sister-group relationship between *Amphibamus* and *Doleserpeton*, with *Platyrhinops* and the more recently described *Eoscopus* (Daly 1994) clustering in a clade with, but more basal than, a number of branchiosaurids. *Tersomius* was deliberately excluded from the study by Ruta *et al.*

(2003) because of doubts about its validity as a monophyletic taxon.

In recent years, several new amphibamid taxa have been described: *Plemmyradytes* (Huttenlocker *et al.* 2007), *Georgenthalia* (Anderson *et al.* 2008a), *Gerobatrachus* (Anderson *et al.* 2008b) and *Pasawioops* (Fröbisch & Reisz 2008), and one dissorophoid taxon has been redescribed and assigned to the Amphibamidae, namely *Micropholis* (Schoch & Rubidge 2005). Some consensus is emerging as to their internal relationships. *Amphibamus* and *Doleserpeton* always emerge as closely related, either as sister-taxa, or with *Amphibamus* as sister to the lissamphibian-like *Gerobatrachus*, with *Doleserpeton* at the next node. *Platyrhinops* emerges at the next node, corroborating the separation of this genus from *Amphibamus*, as suggested by Clack & Milner (1994). The genera *Plemmyradytes*, *Eoscopus* and *Georgenthalia* occupy the next three nodes respectively in Fröbisch & Reisz (2008), in contrast to Huttenlocker *et al.* (2007), in which *Plemmyradytes* appeared as more closely related to *Micropholis*, *Tersomius* and *Eoscopus*. In most of these analyses, *Micromelerpeton* appears well below the Amphibamidae (e.g. Fröbisch & Reisz (2008), Fröbisch & Schoch (2009b)) a view endorsed by the present authors, though Anderson *et al.* (2008a) included *Micromelerpeton* within their definition of the family.

Most of these recent analyses have recovered a dichotomy within the Amphibamidae, with *Amphibamus*, *Doleserpeton* and *Platyrhinops* on one branch (the 'Amphibamus branch', and *Tersomius* and *Micropholis* (the 'Micropholis branch') on the other. *Plemmyradytes* and *Eoscopus* were placed on the 'Micropholis branch' by Huttenlocker *et al.* (2007), whereas these two genera were placed, with *Georgenthalia*, on the 'Amphibamus branch' by Fröbisch & Reisz (2008). They placed *Pasawioops* as the sister-taxon to *Micropholis*.

Following these analyses, those of Schoch & Milner (2008) and Fröbisch & Schoch (2009a) have found a closer relationship between *Amphibamus* and Branchiosauridae than between *Amphibamus* and *Micropholis*. The 'Amphibamus branch' amphibamids and the branchiosaurids appear to be more closely related to each other than either is to the 'Micropholis branch' amphibamids, and most of the diagnosis for Amphibamidae does also apply to the Branchiosauridae, certainly if allowance is made for the paedomorphic nature of many branchiosaurids. We are moving toward a situation where the branchiosaurids are effectively a paedomorphic subgroup of the amphibamids (see the authors' comments under Systematic Note above).

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