Morphology and function of the palatal dentition in Choristodera

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Abstract

Choristoderes are a group of extinct freshwater reptiles that were distributed throughout Laurasia from the Middle Jurassic to the Miocene. They are inferred to have had a lifestyle similar to that of extant gavialid crocodiles, but they differed from crocodiles in retaining an extensive palatal dentition. All choristoderes had teeth on the vomers, palatines and pterygoids, and teeth are rarely present on the parasphenoid. Palatal teeth are conical, as in the marginal dentition, and form longitudinal and transverse rows. Detailed examination of different genera shows that the orientation of the palatal tooth crowns changes with their position on the palate, supporting the view that they are involved in intra-oral food transportation, presumably in combination with a fleshy tongue. Moreover, observed variation in palatal tooth shape and the width of palatal tooth batteries may provide additional clues about diet. The European *Simoedosaurus lemoinei* has sharper palatal teeth than its North American counterpart, *S. dakotensis*, suggesting a preference for softer prey – a conclusion consistent with the more gracile teeth and narrower snout.

Key words: *Champsosaurus*; function; morphology; palatal dentition; *Simoedosaurus*; subthecodont.

Introduction

Choristodera is an extinct (Middle Jurassic to Miocene) group of aquatic diapsid reptiles that typically occurred as part of a mesic Laurasian vertebrate assemblage (including fish, frogs, salamanders, turtles and crocodiles) in relatively warm, temperate climates (occasionally sub-tropical areas: Matsumoto & Evans, 2010). The group is characterized by a unique combination of characters, including a dorsoventrally depressed cordiform skull and conical subthecodont teeth.

Choristoderes are represented by three morphotypes (short-necked longirostrine, short-necked brevirostrine and long-necked brevirostrine). The short-necked longirostrine taxa form a monophyletic clade named Neochoristodera (*sensu* Evans & Hecht, 1993). The other morphotypes (short-necked brevirostrine and long-necked brevirostrine) fall into a paraphyletic set, informally named non-neochoristoderes, the earliest of which is *Cteniogenys*, a small lizard-like reptile known from the Middle–Late Jurassic of Euramerica (Britain, Portugal, USA; Evans, 1989,

1990, 1991; Chure & Evans, 1998). The long-necked taxa are all from the Early Cretaceous of Asia: *Hyphalosaurus* (*H. lingyuanensis*; *H. bitaigouensis*, China; Gao et al. 1999; Ji et al. 2004), *Shokawa ikoi* (Japan; Evans & Manabe, 1999) and probably *Khurendukhosaurus orlovi* (Mongolia and Russia; Sigogneau-Russell & Efimov, 1984; Efimov & Storrs, 2000; Skutschas, 2008). *Hyphalosaurus* is represented by nearly complete skulls, but many of these are dorsoventrally compressed and are rarely preserved in ventral view (Gao & Ksepka, 2008). The Japanese long-necked *Shokawa* is known from an articulated postcranial specimen and a few attributed jaw elements (Evans & Manabe, 1999). *Khurendukhosaurus* is known only from disarticulated postcranial elements and a few skull bones (basioccipital, exoccipital, maxilla, dentary; Skutschas, 2008). The short-necked brevirostrine morphotype has a wider geographical and chronological range: *Monjurosuchus splendens* (Gao et al. 2000; Gao & Li, 2007; Matsumoto et al. 2007) and *Philydrosaurus proseilus* (Gao & Fox, 2005; Gao et al. 2007, 2013) are from the Early Cretaceous of Asia (China and Japan), whereas the European *Lazarussuchus* (*L. inexpectatus*; Hecht, 1992; *L. dvoraki*; Evans & Klembara, 2005) is recorded from the Late Paleocene (France; Matsumoto et al. 2013) to Early Miocene (France, Czech Republic, Germany; Hecht, 1992; Evans & Klembara, 2005; Böhme, 2008). Neochoristodera (short-necked longirostrine type) is comprised of four genera of similar morphology – the Early Cretaceous *Tchoiria* (*T. namsarai*;

T. klauseni; Efimov, 1975; Ksepka et al. 2005) and *Ikechosaurus* (*I. magnus*; *I. sunailinae*; *I. gaoi*; *I. pijiagouensis*; Efimov, 1979; Sigogneau-Russell, 1981; Brinkman & Dong, 1993; Lü et al. 1999; Liu, 2004) from Asia (China, Mongolia), and the Late Cretaceous to Paleogene *Champsosaurus* (*C. laramiensis*, *C. ambulator*, *C. natator*, *C. lindoei*, *C. albertensis, C. dolloi, C. gigas, C. tenuis*; Erickson, 1972; Gao & Fox, 1998; Matsumoto, 2011) and *Simoedosaurus* (*S. lemoinei* and *S. dakotensis*; Gervais, 1877; Sigogneau-Russell, 1985; Erickson, 1987) from Europe and North America (Brown, 1905; Sigogneau-Russell & Russell, 1978).

The phylogenetic position of Choristodera within Reptilia remains problematic (Matsumoto et al. 2007, 2013), although many authors have placed the group somewhere on the diapsid stem (Evans, 1988; Gao & Fox, 1998; Rieppel & Reisz, 1999; Modesto & Sues, 2004). As with many phylogenetically problematic groups, they show a mixture of specialized and primitive traits. Among the latter is the presence of an extensive palatal dentition (Sigogneau-Russell, 1979, 1985), a feature generally considered plesiomorphic within amniotes where all major lineages show a crownward trend toward reduction or loss. Gao et al. (2007) recently presented a brief overview of palatal morphology in Choristodera, prompted by new specimens from the Early Cretaceous of China. They concluded that the choristoderan palate was uniquely modified from the basal diapsid condition in features such as the elongated vomers, posteriorly relocated choana and reduction of the interpterygoid vacuity, features probably linked to the aquatic lifestyle. However, details of palatal tooth morphology, replacement and function remain poorly understood, despite the recovery of many new specimens of both neochoristoderes and non-neochoristoderes. The aim in this review is to provide a detailed comparative study of the choristoderan palatal dentition and to relate it, where possible, to diet and/or feeding strategy.

Materials and methods

Of the 11 known choristodere genera, palatal elements are preserved in 9. Representatives of each were examined (Table 1) by stereomicroscopy, digital photographs and/or scanning electron microscopy (SEM), with some supplementary data taken from the literature. *Champsosaurus lindoei* (NMC 8920) was subjected to micro-computed tomography (CT) at the National Museum of Nature and Science, Tokyo, Japan, using TESCO, Microfocus CT TXS 320-ACTIS. The software Avizo 8.0 was used to visualize 3D images of the CT data. Palatal tooth patterns of choristoderes were plotted on a phylogenetic tree (Fig. 1) based on the bootstrap consensus tree of Matsumoto et al. (2013).

Abbreviations

Institutional

AMNH, American Museum Natural History, New York, USA; BMNH, The Natural History Museum, London, UK; IGM, Geological Institute of the Mongolian Academy of Sciences, Ulan Bataar, Mongolia; IRSNB, Institut Royal des Sciences naturelles de Belgique, Bruxelles, Belgium; IVPP V, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; LPMC, Liaoning Paleontological Museum of China; MNHN, Muséum National d'Histoire Naturelle, Paris, France; NMC, Canadian Museum of Nature, Ottawa, Canada; PIN, Paleontological Institute, Russian Academy of Sciences, Moscow, Russia; RTMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Canada; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; SMM, The Science Museum Minnesota, St Paul, Minnesota, USA.

Anatomical

ch, choana; D, dentary; Ept, ectopterygoid; F, frontal; Hy, hyoid; ip-v, interpterygoid vacuity; J, jugal; Mx, maxilla; P, parietal; Pal, palatine; Psh, parasphenoid; Pt, pterygoid; pt f, pterygoid foramen; pl f, palatal foramen; Po, postorbital; Prf, prefrontal; rtp, replacement tooth pit; sbt f, subtemporal fenestra; Sp, splenial; Vo, vomer.

Description

Structure of the marginal dentition in choristoderes

The marginal teeth of choristoderes are essentially homodont in both upper and lower jaws, and the implantation is subthecodont. Teeth are replaced by the erosion of a pit in the lingual surface of the old tooth base. However, there are minor differences between non-neochoristoderes and neochoristoderes in marginal tooth morphology. Teeth of non-neochoristoderes are relatively simple, and striated enamel covers the tooth crown but not the base (Fig. 2a,b). Furthermore, the crown is straight, allowing the teeth to be closely packed along the tooth row. In contrast, teeth of neochoristoderes are completely covered by striated enamel and there is enamel infolding at the base. In some neochoristoderes, such as *Simoedosaurus* and *Champsosaurus*, the anterior teeth are sharper and more slender than the posterior ones (Fig. 2d,e). The crown is labiolingually compressed and there are keels on each side of the tooth. The sharp tooth apex is curved either posteriorly or medially depending on tooth position (anterior–posterior, upper–lower jaws) and taxon. *Ikechosaurus* is unique among neochoristoderes in having straight tooth crowns and a lack of enamel over the tooth base, as in non-neochoristoderes, but it shows the basal dentine infolding of neochoristoderes (Matsumoto et al. 2014).

General structure of the palatal dentition in choristoderes

Non-neochoristoderes. The palatal dentition of neochoristoderes is relatively well known due to many specimens with nearly complete palatal elements, but this region is less known for non-neochoristoderes, due to poor preservation or a lack of relevant elements (Table 1). In many cases, description of the palatal dentition is based on, at most, a few specimens (e.g. *Hyphalosaurus*). The teeth are arranged

Table 1 List of specimens examined.

Genus	Species	Specimen number	Element	References
Cteniogenys	sp.	BMNH R11756–11758 uncataloged UCL specimens	Isolated palatine	Evans (1990), personal observation (RM)
	sp.	BMNH R11759	Isolated pterygoid	
Lazarussuchus	inexpectatus	Re 437	Preserves posterior palatine and anterior pterygoid tooth rows	Hecht (1992)
Monjurosuchus	sp.	IVPP V14261	Juvenile, complete palate	Personal observation (RM), Wang et al. (2005)
	splendens	IVPP V13761	Adult, partial pterygoid	
Philydrosaurus	proseilus	LPMC 021	Nearly complete palate pterygoid flange tooth row missing	Gao et al. (2007)
Hyphalosaurus	lingyuanensis	IVPP V11075	Mostly covered by matrix	Gao et al. (1999), personal observation (RM)
	baitaigouensis	LPMC no number	Nearly complete palatine and pterygoid	Gao & Ksepka (2008)
Ikechosaurus	sunailinae	IVPP V2774	Palatine	Sigogneau-Russell (1981)
	sunailinae	IVPP V9611-3	Complete palate	Brinkman & Dong (1993), personal observation (RM)
	sp.	IVPP V10596.1; IVPP V9611-2	Isolated parasphenoid; partial palatine and vomer	
Tchoiria	namsarai	PIN3386/1	Complete palate	Efimov (1975), Efimov & Storrs (2000)
	namsarai	HMNS 96720	Pterygoid flange missing	Personal observation (RM)
	klauseni	IGM 1/8	Pterygoid flange missing	Ksepka et al. (2005)
Champsosaurus	lindoei	RTMP 87.36.41; RTMP 94.163.01; NMC 8920	Complete palate, juvenile and subadult	Gao & Fox (1998), personal observation (RM)
	albertensis	RTMP 86.12.11	Pterygoid flange missing	Gao & Fox (1998), personal observation (RM)
	laramiensis	AMNH 982; 981	Complete palate	Brown (1905), personal observation (RM)
	ambulator	AMNH 983	Complete palate	Brown (1905)
	natator	NMC 8919	Pterygoid flange tooth row missing	Russell (1956), personal observation (RM)
	dolloi	IRSNB R21; IRSNB R 1568; IRSNB R 3662 MNHN BR 2020	Pterygoid flange missing Isolated vomer	Sigogneau-Russell (1979), personal observation
	gigas	SMMP 77.33.34	Complete palate	Erickson (1985), personal observation (RM)
	tenuis	SMM P79.14.1	Vomer, partial palatine	Erickson (1981), personal observation (RM)
	sp.	MNHN BR-9-P; RTMP 92.36.270; RTMP 91.50.104; RTMP 89.36.332	Complete palate; isolated palatine; isolated palatine; isolated vomer	Personal observation (RM)
Simoedosaurus	lemoinei	MNHN BR1935; MNHN BR728; MNHN BR9947; MNHN BR1-Gi-13	Pterygoid flange missing; Isolated palatine; isolated vomer; isolated pterygoid	Sigogneau-Russell & Russell (1978), personal observation (RM)
	dakotensis	SMM P76.10.1	Complete palate	Erickson (1987), personal observation (RM)
	sp.	SMNS 59026	Complete palate	Personal observation (RM)

as a series of longitudinal rows on the vomer, palatine and pterygoid, a pattern inherited from that of basal amniotes (R. Matsumoto and S. E. Evans, unpublished data). Although choristoderes were all essentially aquatic, there is no obvious aquatic specialization in the palatal dentition of basal taxa. The presence of a pterygoid flange tooth row is confirmed in neochoristoderes and *Cteniogenys* (Figs 1 and 3), but it remains uncertain in most non-neochoristoderes (e.g. Figs 1, 4 and 5: *Monjurosuchus, Philydrosauru*s, *Hyphalosaurus* and *Lazarussuchus*). In *Monjurosuchus* and *Phily-*

drosaurus, pterygoid flange teeth are obscured by poor preservation (Figs 1 and 5; Gao et al. 2007; RM personal observation). Gao et al. (2013) reported the pterygoid flange teeth to be absent in *Philydrosaurus*, based on a newly discovered juvenile specimen, but the flange is damaged. As in most diapsids, non-neochoristoderes generally lack parasphenoid and ectopterygoid teeth.

Neochoristoderes. Some species are represented by multiple specimens and examination has shown that palatal
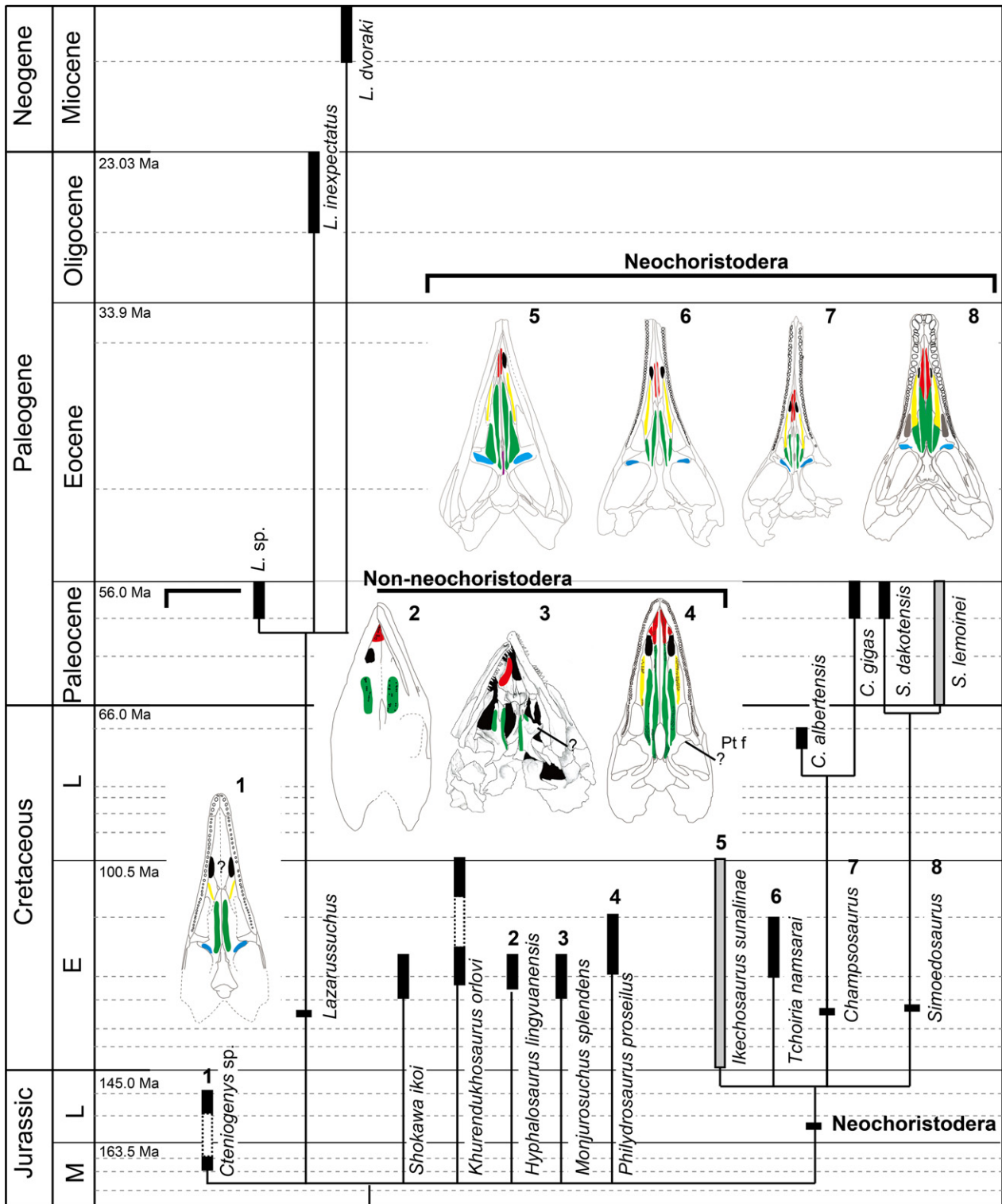
Fig. 1 Choristoderan phylogenetic tree with palatal tooth arrangement; phylogenetic tree based on Matsumoto et al. (2013). Dentition on each palatal element marked in a different color; red, vomerine teeth; yellow, palatine teeth; green, longitudinal pterygoid tooth row; blue, pterygoid flange tooth row.

features are consistent within species. As in non-neochoristoderes, neochoristoderes generally lack parasphenoid and ectopterygoid teeth, the exception being the Early Cretaceous *Ikechosaurus sunailinae* (Fig. 6: IVPP V9611-3; 10596.1), which has parasphenoid teeth. However, these were probably secondarily acquired as has been reported
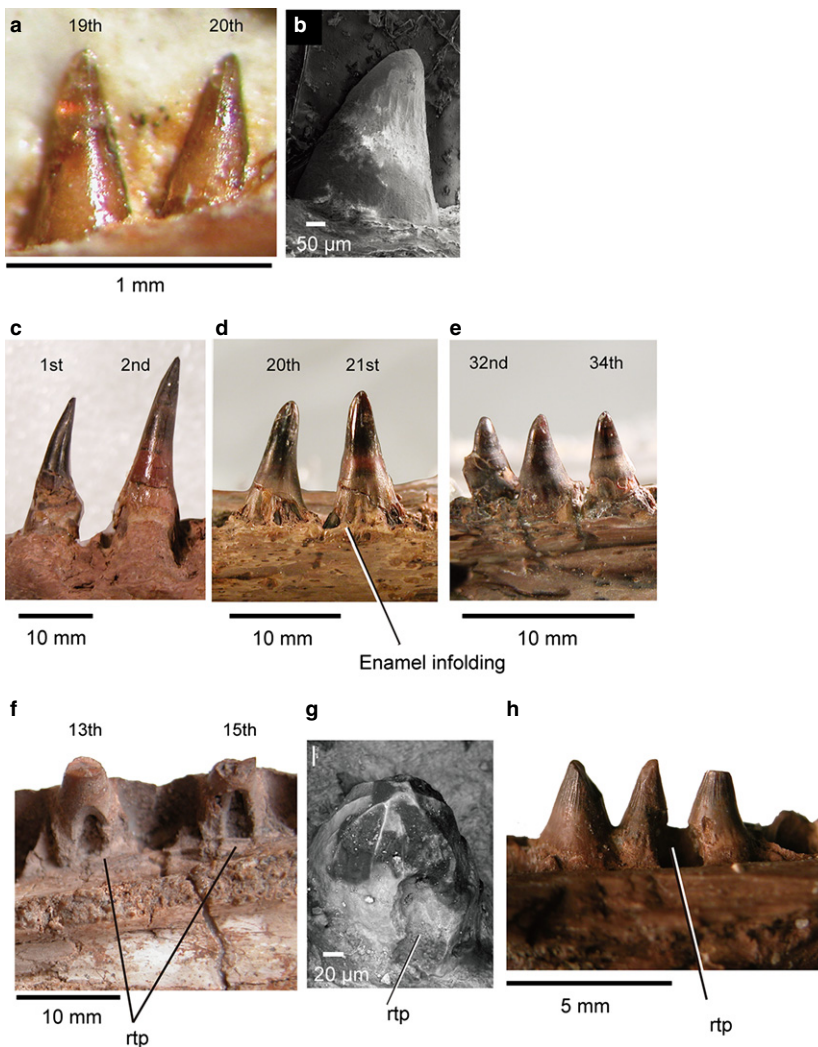
Fig. 2 Marginal and palatal tooth morphology: (a) juvenile *Monjurosuchus* sp. (IVPP V14261) dentary teeth in medial view; (b) *Cteniogenys* sp. dentary (UCL uncataloged) in lateral view, SEM; (c) *Champsosaurus giga*s (SMM P77.33.24) left dentary teeth in lateral view; (d, e) *Champsosaurus giga*s (SMM P77.33.24) right maxillary teeth in lateral view, image reflected for ease of comparison; (f) *Simoedosaurus lemoinei* (MNHN BR 1935) replacement maxillary teeth in medial view; (g) *Cteniogenys* sp. (BMNH R11759), right pterygoid tooth; (h) *Champsosaurus* sp. isolated right palatine teeth (RTMP 92.36.270) in medial view. Tooth position is uncertain in (b), (g), (h) due to incompleteness of specimens.

in Lepidosauromorpha (e.g. Kuehneosauridae; Evans, 2009). Lateral and medial tooth rows run longitudinally over the palate. The lateral row arises on the palatine, posterior to the choana, and runs onto the lateral side of the pterygoid, extending posterior to the end of the marginal tooth row. The row is generally continuous, but in some species it is interrupted by a gap at the palatine–pterygoid suture (e.g. *Tchoiria klauseni*; Ksepka et al. 2005). The medial row, on the other hand, begins on the vomer, anterior to the choana, runs along the medial side of the pterygoid, and terminates posterior to the interpterygoid vacuity. There is usually a toothless gap around the vomer–pterygoid suture. Both lateral and medial rows are generally single, except in a few *Champsosaurus* species (e.g. *C. gigas* and *C. dolloi*) where the pterygoid bears several rows (Fig. 7). However, the width of the tooth rows varies between species and between genera. In most species the longitudinal rows are fewer than 10 tooth positions across and the pterygoid flange tooth row has one–three tooth positions. However, in *Simoedosaurus* (Figs 8 and 9) and *Ikechosaurus* (Fig. 6) the longitudinal rows are generally more than 10 teeth across and the pterygoid flange tooth row may be 5–19 teeth across. These wide tooth batteries are a characteristic feature of *Simoedosaurus* and *Ikechosaurus*, so that the teeth cover most of the palatal surface (Figs 6, 8 and 9).

Naso-palatal trough. The medial and lateral longitudinal rows in neochoristoderes are separated by a distinct groove, the naso-palatal trough. Erickson (1985) suggested that this might be the functional equivalent of the secondary palate (by extending the nasal groove posteriorly). This structure is less obvious in non-neochoristoderes, but a newly discovered specimen of *Philydrosaurus* from the Early Cretaceous of China (Gao et al. 2007) appears to show some development of a trough extending posteriorly from the choana. However, due to the poor preservation of palatal elements in most non-neochoristoderes, the distribution and evolutionary history of the nasopalatal trough among non-neochoristoderes remains uncertain.
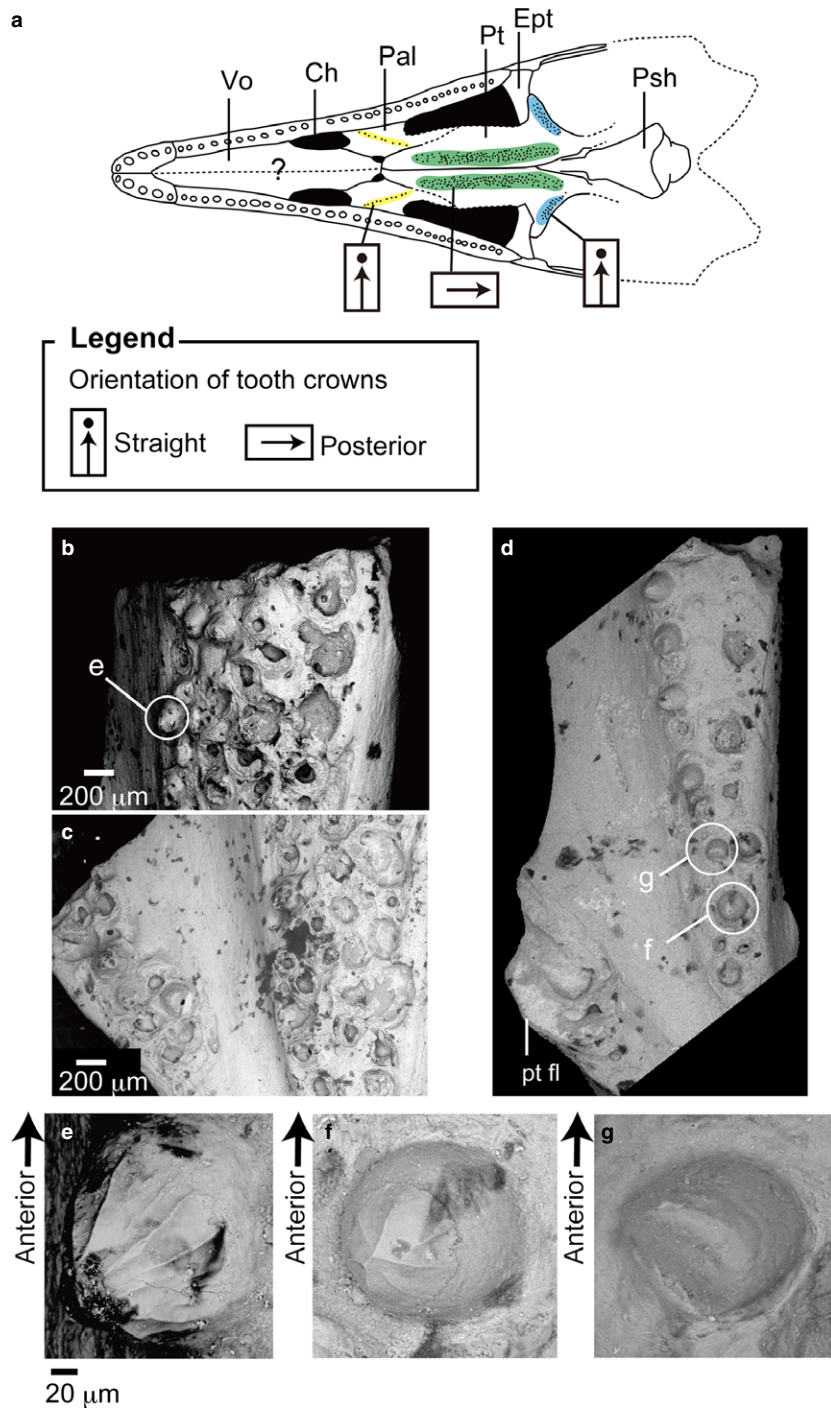
Fig. 3 Pterygoid teeth in *Cteniogenys* sp. (BMNH R11759) from the Middle Jurassic of Kirtlington, Oxfordshire, UK; (a) reconstructed skull in palatal view (Evans, 1990); color coding of the different regions of the palatal dentition are the same as in Fig. 2; (b) anterior longitudinal tooth row; (c) posterior pterygoid teeth; (d) isolated pterygoid from UCL uncataloged specimens (magnification × 50); (e) enlarged image of (b), worn tooth crown from the longitudinal pterygoid tooth row in medial view; (f) enlarged image of (d), complete crown on the longitudinal pterygoid tooth row in medial view (magnification × 500); (g) enlarged image of (d), posterior pterygoid tooth (magnification × 500).

Palatal tooth replacement

The marginal tooth replacement pattern is almost mirrored in the palatal dentition. Marginal tooth replacement has been described in *Cteniogenys* (Evans, 1990). Initially, the new tooth grows at the lingual side of the old tooth base. The new tooth attaches weakly to the base and erodes a pit in it (Fig. 2f). A similar replacement pattern can be recognized on one of the pterygoid teeth in *Cteniogenys*. The tooth shows an erosion pit made by a new tooth on the lingual side of the old tooth base (Fig. 2g). In contrast, in *Champsosaurus* (RTMP 92.36.270) the eroding pit straddles two old teeth (Fig. 2h), suggesting two original teeth were being replaced by a single larger tooth. A matching replacement pattern for marginal and palatal teeth was also reported in living squamates (Mahler & Kearney, 2006), although there is some variation in the position of the replacement (e.g. *Iguana* shows both lingual and labial replacement in different tooth rows; Mahler & Kearney, 2006).
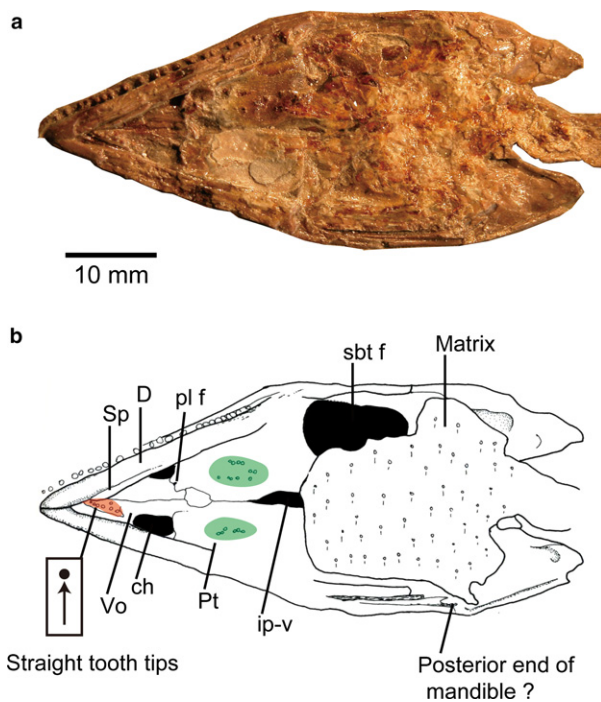
Fig. 4 *Hyphalosaurus lingyuanensis* holotype from the Early Cretaceous of the Yixian Formation of China (IVPP V11075): (a) photograph of the skull in palatal view; (b) line drawing of (a); color coding of the different regions of the palatal dentition are the same as in Fig. 2.

Palatal tooth platforms

Although there are differences of degree between species, the palatal tooth batteries of neochoristoderes sit on a bony platform that raises them above the level of the palatal surface. These platforms are particularly strongly developed anteriorly in *Champsosaurus* and *Simoedosaurus*, so that the palatine tooth bases lie almost level with, or even ventral to, the maxillary tooth bases (Fig. 10). Among non-neochoristoderes, a tooth platform is, at most, weakly developed in *Cteniogenys* (clearly recognized only in the longitudinal pterygoid row) and *Monjurosuchus*.

Tooth platforms may also be present along the posterior margin of the pterygoid flange but, in this case, the orientation of the tooth row also depends on that of the flange itself. The pterygoid flange is always angled forward in choristoderes, but the angulation is least in Neochoristodera (10–30 °; e.g. *Ikechosaurus*, IVPP V9611-3) and greatest in *Cteniogenys* (45 °; e.g. BMNH 11759) and *Monjurosuchus* (40 °; e.g. IVPP 14261), with *Philydrosaurus* midway between the two extremes (35 °; Gao et al. 2007; Supporting Information). In *Champsosaurus* and *Simoedosaurus*, the pterygoid flange also extends ventrally, due to the ectopterygoid contribution, and leans slightly anteroventrally, so that the pterygoid flange tooth tips face anteriorly (Figs 9f–h and 11h). Despite the uncertain relationship of the ectopterygoid and pterygoid, *Ikechosaurus* has an anteriorly facing pterygoid flange tooth platform (uncertain in *Tchoiria*). This is absent in *Cteniogenys* and *Monjurosuchus* (Figs 1, 3c and 5b), but unknown in other non-neochoristoderes.

Palatal tooth morphology, size and direction of tooth crowns

Individual palatal teeth (neochoristodere and non-neochoristodere) show the same morphology as the marginal teeth of non-neochoristoderes: they are conical, with enamel only partially covering the crown, and weakly developed ridges
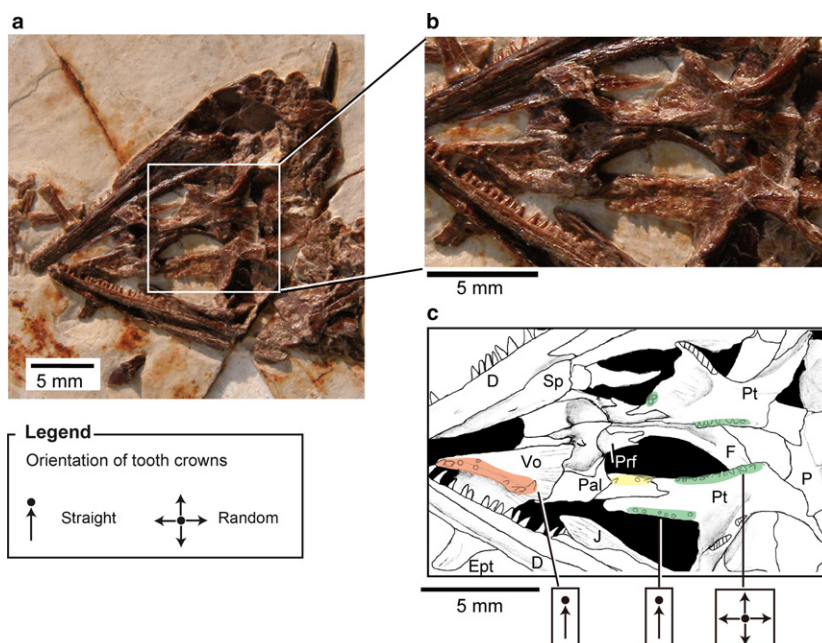

Fig. 5 (a) *Monjurosuchus* sp. (IVPP V14261) from the Early Cretaceous of China, skull in palatal view: (b) photographs of the skull, enlarged view of palatal tooth area in (a); (c) line drawing of (b); color coding of the different regions of the palatal dentition are the same as in Fig. 2.
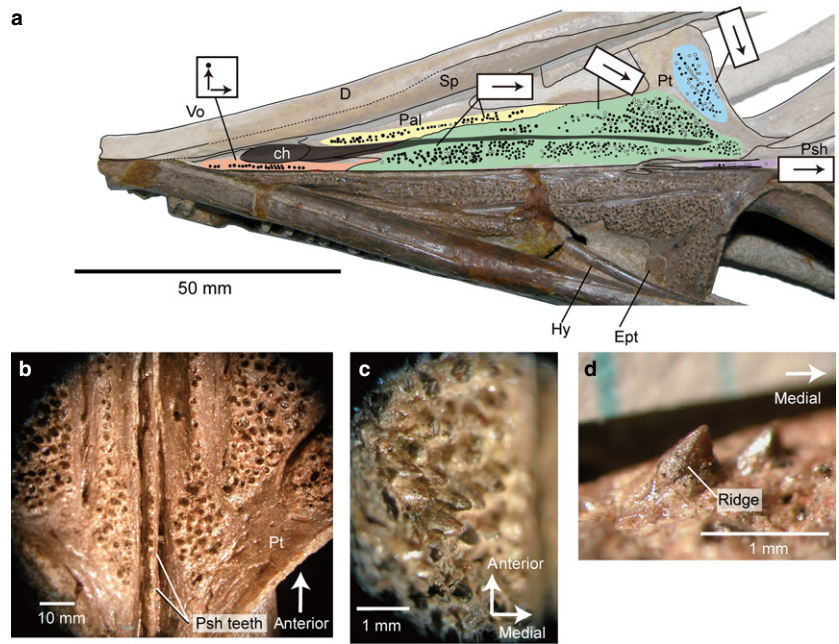
Fig. 6 *Ikechosaurus sunailinae* from the Early Cretaceous Chabu-Sumu locality, Inner Mongolia (IVPP V9611-3), skull in palatal view: (a) photograph and line drawing of the skull in ventral view. Black circles indicate alveoli of palatal teeth; white circles showing presence of the teeth; color coding of the different regions of the palatal dentition are the same as in Fig. 2; gray zone indicating nasopalatal trough; arrows on tooth row showing orientation of tooth crowns. (b) Enlarged image of pterygoid and parasphenoid regions; (c) enlarged image of the longitudinal pterygoid tooth row (posterior); (d) pterygoid flange teeth in posterior view (image inverted for comparison).
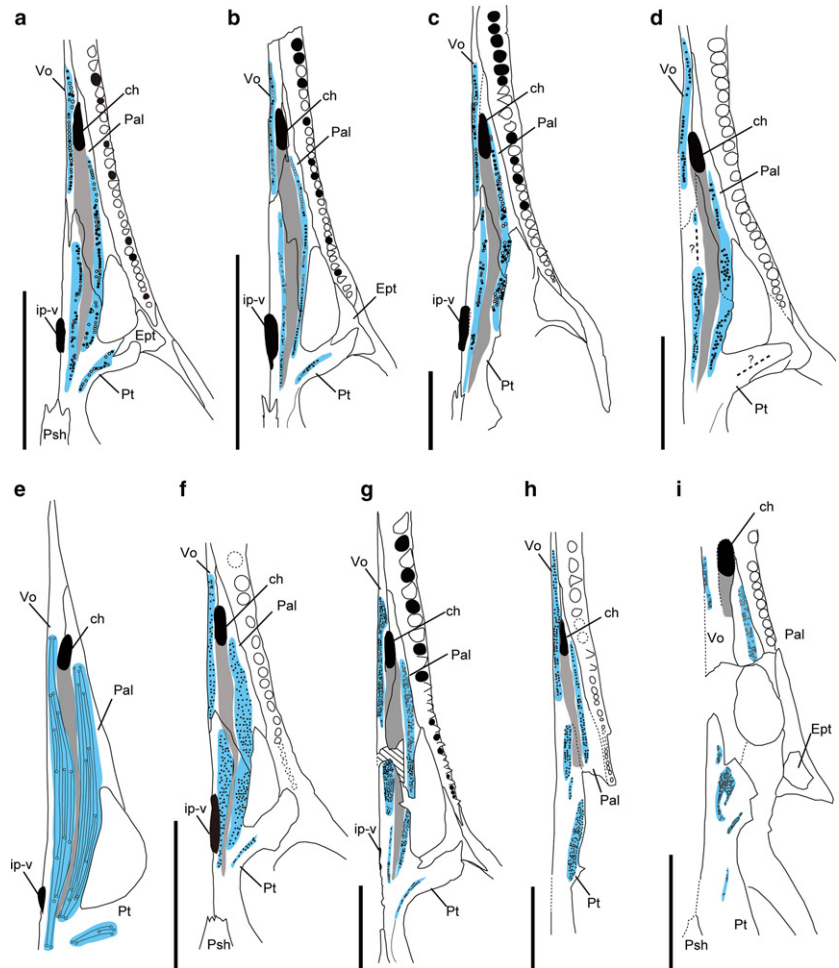

Fig. 7 Comparison of the palatal dentition in *Champsosaurus*; (a–d) from the Late Cretaceous; (e, f) from the Late Cretaceous and the Paleocene; (g–i) from the Paleocene. (a) Semi-adult *C. lindoei* (RTMP 87.36.41); (b) juvenile *C. lindoei* (RTMP 94.163.01); (c) *C. albertensis* (RTMP 86.12.11), pterygoid flange teeth incomplete; (d) *C. natator* (NMC8919) pterygoid flange teeth incomplete; (e) *C. ambulator* (modified from Sigogneau-Russell, 1979); (f) *C. laramiensis* (redrawn based on Brown, 1905 and Sigogneau-Russell, 1979); (g) *C. gigas* (SMM P77.33.24); (h) *C. dolloi* (IRSNB R21) pterygoid flange teeth incomplete; (i) *C. tenuis* (SMM P79.14.1) pterygoid flange teeth and pterygoid longitudinal tooth rows are incomplete. Scale bars: 50 mm, but scale is unknown in (e). Blue colored area marks the distribution of the palatal dentition, and gray colored area marks nasopalatal trough extending from the choana.

on the enamel surface (Fig. 2). All palatal teeth sit in shallow circular alveoli and lack basal enamel infolding.

In neochoristoderes the palatal teeth gradually become smaller from anterior to posterior ends of the longitudinal rows. In addition, the teeth on the lateral row are larger than those on the medial row. In the pterygoid flange row, teeth decrease in size from lateral to medial, but where the row is wide (*Simoedosaurus* and *Ikechosaurus*), the reduction is from anterolateral to posteromedial. This pattern differs in non-neochoristoderes. *Monjurosuchus* sp. (IVPP V14261) shows a reverse pattern on the pterygoid (longitudinal row), with the largest teeth in the medial row, and at its posterior end. In *Cteniogenys*, there is no significant size difference along either the longitudinal pterygoid row or the pterygoid flange row.

Kordikova (2002) reviewed palatal tooth morphology in choristoderes based on *Simoedosaurus* and *Champsosaurus*, and stated that the tooth crowns point sharply backward. However, detailed examination in several species of neochoristoderes, mainly *Champsosaurus* and *Simoedosaurus*, shows that the orientation of palatal tooth crowns changes with the position on the palate. In *Simoedosaurus*, the

European (Paleocene) *S. lemoinei* has anterior vomerine and palatine teeth that are blunt (Fig. 8c,f), with more posterior teeth becoming sharper and more backward pointed (Fig. 8e,g,i). In contrast, the shorter-snouted North American *S. dakotensis* is characterized by blunt palatal tooth crowns throughout the tooth row, with the crowns oriented vertically on the vomer and palatine, but varying posteriorly from straight to recurved (Fig. 9). SMM P76.10.1 is the only specimen of *S. dakotensis* that preserves a complete skull and palatal dentition. However, the marginal teeth are preserved in position with no trace of wear of the tooth crowns. It is therefore unlikely that the shape of the palatal tooth crowns is due to wear. The pterygoid flange tooth crowns curve medially in both species, but in *S. dakotensis* the teeth along the edge of the subtemporal fenestra point anteriorly.

Among the eight valid species of *Champsosaurus*, there is variation in the number and width of the longitudinal palatal tooth rows, and in the orientation of the tooth crowns. For example, although the Late Cretaceous *C. albertensis* (Fig. 12; RTMP86.12.11) and the Paleocene *C. gigas* (Fig. 11; SMM P77.33.24) have similar sized skulls, the
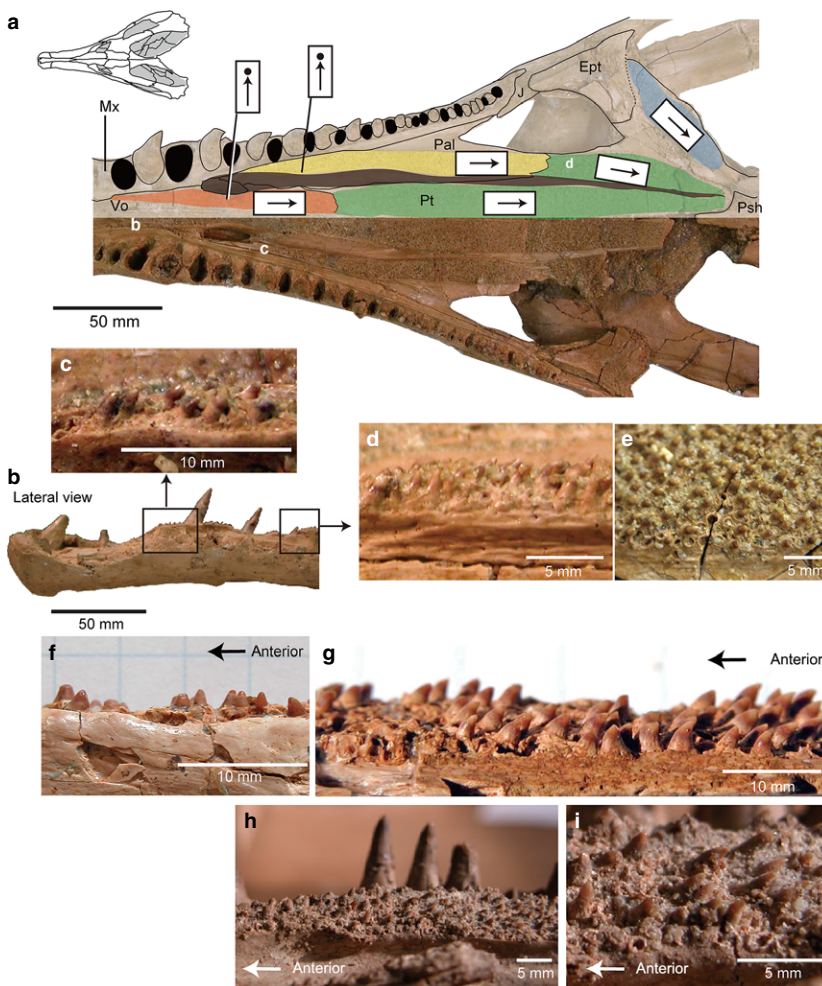

Fig. 8 Palatal dentition of *Simoedosaurus* sp. (SMNS 59026) (a–e) and *S. lemoinei* (f–i) from Mont Berru Reims, France: (a) photograph and line drawing of the skull (SMNS 59026) in palatal view; color coding of the different regions of the palatal dentition is the same as in Fig. 2; (b) lateral view of the snout (a); (c) enlarged image of anterior vomerine teeth of (b); (d) enlarged image of anterior palatine teeth of (b); (e) enlarged image of pterygoid teeth of (b) (reflected image); (f) isolated left vomer with teeth in lateral view, image inverted (MNHN BL9947); (g) isolated left palatine, image inverted (MNHN BR728); (h) posterior palatine dentition (MNHN BR 1935; neotype of *S. lemoinei*); (i) enlarged image of (h).
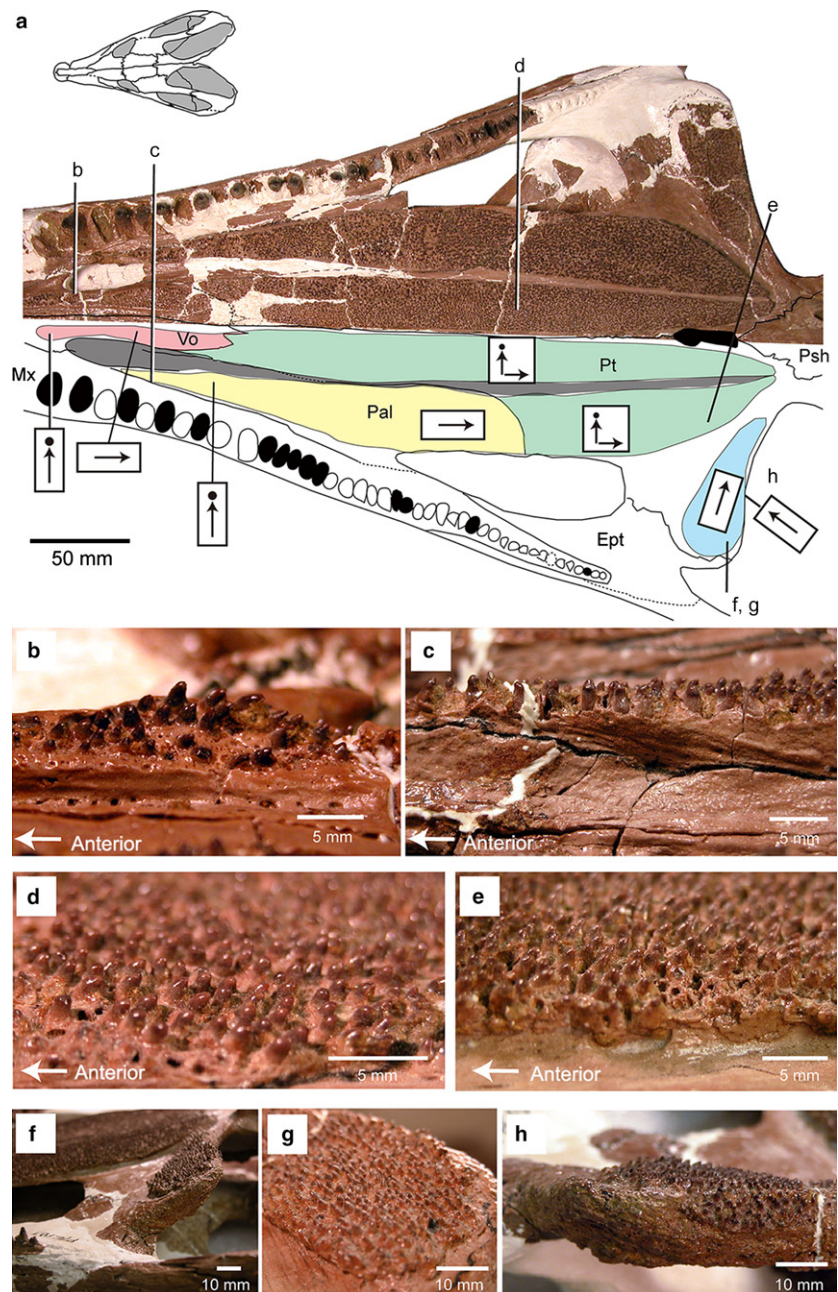
Fig. 9 *Simoedosaurus dakotensis* (SMM P76.10.1) from the Paleocene of western North Dakota (near top of Slope Formation), USA: (a) skull in palatal view, digital image above and line drawing below (the letters b–h correspond to the following close-up images below); color coding of the different regions of the palatal dentition is the same as in Fig. 2; (b) anterior vomerine teeth; (c) anterior palatine teeth; (d) posterior pterygoid, lateral tooth row; (e) posterior pterygoid, medial tooth row; (f) pterygoid flange in lateral view; (g) pterygoid flange in posterior view; (h) pterygoid flange teeth in lateral view.

palatal dentition is different. *C. albertensis* has either straight or randomly oriented crowns anteroposteriorly (Fig. 12), whereas in *C. gigas* the crowns are straight on anterior teeth (vomer and palatine) but curve sharply posteriorly in the pterygoid part of the rows (Fig. 11). In addition, *C. albertensis* has a relatively small number of large teeth in the longitudinal pterygoid row, whereas *C. gigas* has a larger number of small teeth. This seems to be a general difference between the Late Cretaceous (e.g. *C. lindoei*; *C. natotor*) and Paleocene species (e.g. *C. tenuis*; *C. dolloi*). Minor ontogenetic variation is also recognized in *Champsosaurus lindoei*, in which the width of longitudinal palatal tooth row seems to increase

slightly through ontogeny, from a single tooth wide in smaller individuals (Figs 7b and 12; RTMP 94.163.01: inner biquadrate width 50 mm) to double that in a larger individual (Fig. 7a; RTMP 87.36.41: inner biquadrate width 86 mm). However, *Champsosaurus* species are more consistent in the morphology of the pterygoid flange rows, which are usually one–two tooth positions wide with vertical tooth crowns (Fig. 7).

In the wide longitudinal tooth rows of the Early Cretaceous *Ikechosaurus*, the anterior (vomer and palatine) crowns are straight or point backward, but those on the pterygoid are first directed posteriorly and then gradually turn medially (Fig. 6a). The expansion of the palatal tooth
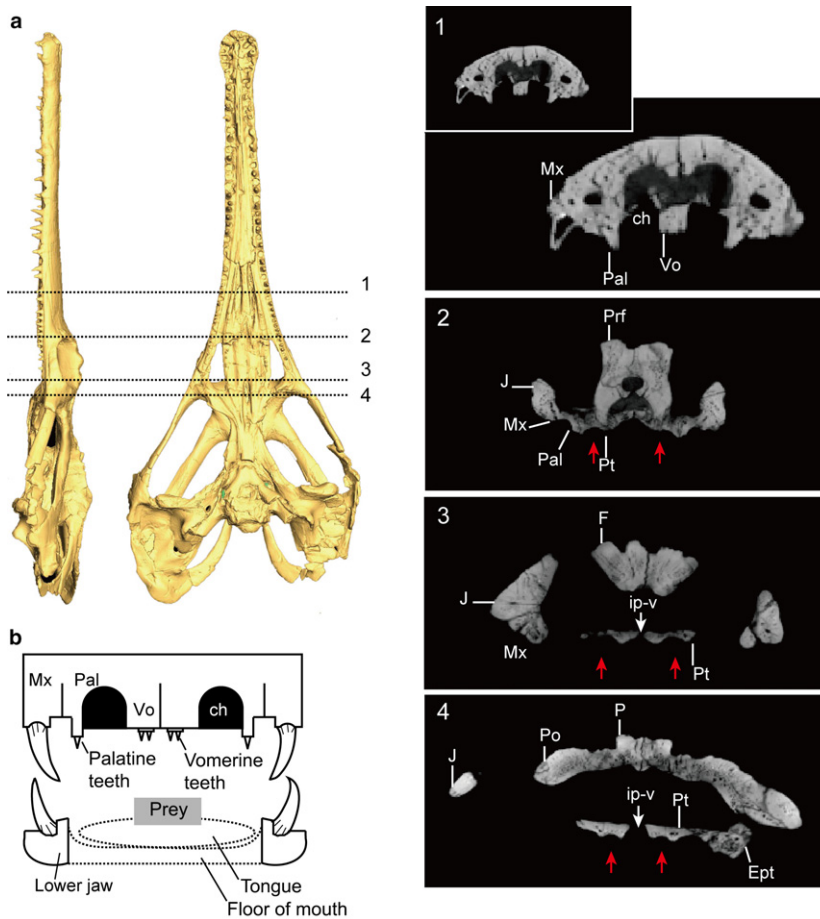
Fig. 10 (a) CT image of *Champsosaurus lindoei* (NMC 8920) without scale; the numbers on the skull corresponding to slice images 1–4. Red arrows showing nasopalatal trough. (b) Diagram of skull and lower jaw in anterior section (*Champsosaurus* as the model), the palatine teeth lie on the ridge, soft tissues are drawn in dashed-lines.

row is essentially similar to that of the Paleocene species *Simoedosaurus lemoinei* and *S. dakotensis*. However, unlike these *Simoedosaurus*, several well-preserved palatal teeth of *Ikechosaurus* show distinctive ridges on the sides (Fig. 6d). Interestingly within the extensive pterygoid tooth and pterygoid flange tooth rows, the teeth form antero-posteriorly and mediolaterally radiating lines, instead of having a random distribution as in *Simoedosaurus.* Furthermore, the parasphenoid tooth crowns incline posteriorly and, uniquely, the pterygoid flange teeth incline medially.

There are less available data on crown orientation in non-neochoristoderes due to poor palatal preservation (e.g. *Hyphalosaurus*; Fig. 4). The teeth of the anterior longitudinal row (vomer, palatine) are generally straight [*Hyphalosaurus, Monjurosuchus, Cteniogenys* (vomer unknown in *Cteniogenys*)], but the posterior teeth show some variation. In *Cteniogenys*, some worn teeth are retained in the sockets, stripped of their enamel, and with the tips smooth and flat (Fig. 3g). Originally, they were presumably conical and covered by enamel as shown in Fig. 3e,f. The tooth tips incline in random directions in the posterior part of the tooth row (pterygoid), but some terminal teeth are inclined posteriorly. In *Monjurosuchus*, the conical tooth tips are randomly oriented, posterior, anterior or vertical (Fig. 5). This orientation is recognized in at least two specimens

(IVPP V 13761, 14261), so is unlikely to be due simply to deformation.

Discussion

Evolutionary history of the palatal dentition in Choristodera

Tracing the evolutionary history of the choristoderan palatal dentition is complicated by a paucity of information on the palate of many non-neochoristoderes (poor preservation, specimen orientation), the absence of Triassic representatives (ghost lineage) and a lack of consensus on the interrelationship of non-neochoristoderes. However, a review of amniote palate morphology (R. Matsumoto and S. E. Evans, unpublished data) suggests that the primitive diapsid pattern consisted of longitudinal tooth rows on the vomer, palatine and pterygoid; a pterygoid flange row; and, probably, a tooth patch on the parasphenoid. This pattern would have been inherited by the common ancestor of all choristoderes and is broadly retained in the Jurassic *Cteniogenys* (Evans, 1990), albeit with an increase in width of the pterygoid tooth row and loss of the parasphenoid teeth. There was also a tendency to develop bony palatal ridges/platforms on the vomer, palatine and pterygoid to
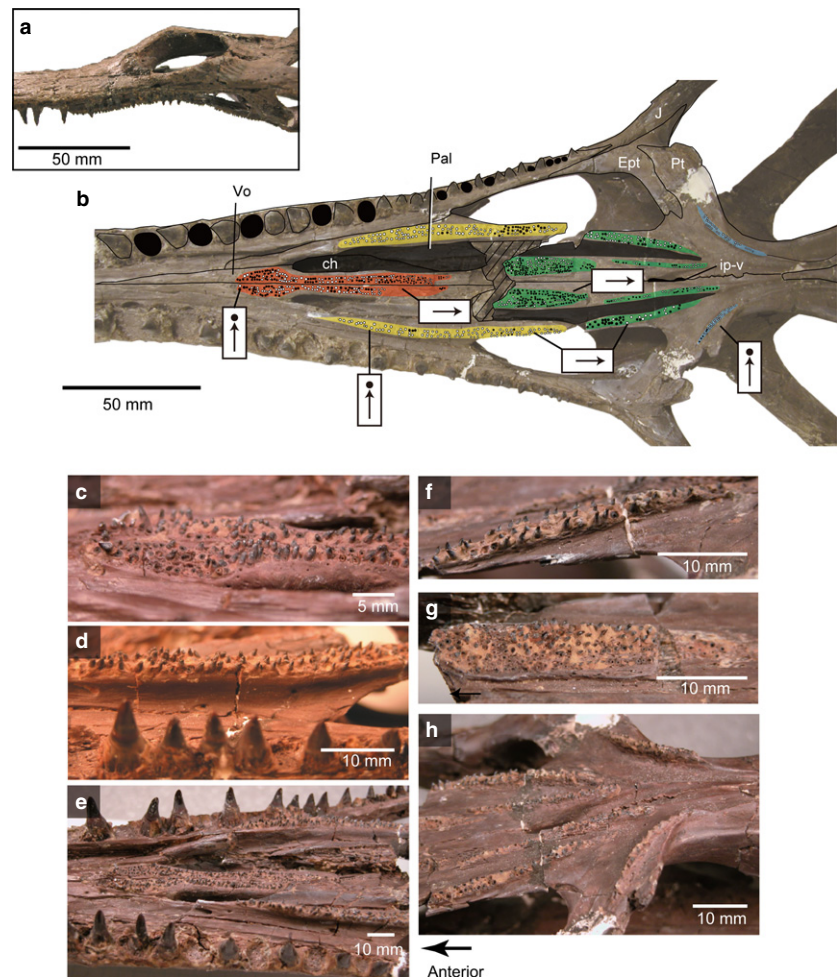
Fig. 11 *Champsosaurus gigas* (SMM P77.33.24) from the Paleocene of western North Dakota: (a) skull in lateral view; (b) line drawing and photograph of palatal dentition; (c) anterior vomerine teeth (reflected image); (d) palatine tooth row (reflected image); (e) anterior palatal dentition; (f) pterygoid, lateral tooth row; (g) pterygoid, medial tooth row; (h) pterygoid flange tooth row in lateral view. Black circles indicate alveoli of palatal teeth; color coding of the different regions of the palatal dentition is the same as in Fig. 2.

which the palatal teeth attached and which contribute to the formation of a nasopalatal trough. The latter feature is most obvious in *Champsosaurus* and *Simoedosaurus* (Figs 8–12) where it separates wide tooth batteries, and was thought to be a neochoristodere character. However, a weakly developed nasopalatal trough was recently reported in the non-neochoristodere *Philydrosaurus* (Gao et al. 2007). It is not present in *Cteniogenys* nor is it evident in a juvenile *Monjurosuchus* sp. (IVPP 14261) for which the palate is known. Additional specimens are required to understand the evolutionary history of the nasopalatal trough in choristoderes.

The function of the palatal dentition

Although there is variation in the choristoderan palatal dentition, the basic pattern can be summarized as follows. Medial and lateral longitudinal tooth rows, of variable width, run from the vomers to the pterygoids, supplemented by transverse pterygoid flange rows. The palatal tooth crowns on the vomer and palatine point straight down, while the more posterior (pterygoid) teeth point backward and/or medially (e.g. *Ikechosaurus*), often

with a reduction in size. The pterygoid flange teeth are straight or medially directed. This is especially clear in neochoristoderes *Ikechosaurus*, *Simoedosaurus* and *Champsosaurus* (*C. gigas*, juvenile *C. lindoei*). The anterior limit of the palatal dentition corresponds to the posterior limit of the lower jaw symphysis. Non-neochorisotoderes have a shorter symphysis and their anterior palatal teeth extend close to the premaxilla (unknown in *Cteniogenys*), whereas in the long-snouted neochoristoderes, with long symphyses, the palatal dentition begins further posteriorly. A mobile fleshy tongue, with both intrinsic and extrinsic musculature, is inferred to have been primitive for amniotes (Iwasaki, 2002), and seems to be correlated with the retention of a palatal dentition (lizards), or its replacement with analogous keratinized tubercles or ridges in the oral epithelium (crocodiles, turtles, mammals, birds). As suggested by Erickson (1985), therefore, a fleshy tongue probably worked with the palatal dentition in choristoderes during intra-oral transport of prey. The positional changes of palatal tooth orientation may correspond to the feeding stages categorized by Schwenk (2000): (1) prey capture; (2) ingestion; (3) intraoral transport; (4) swallowing.
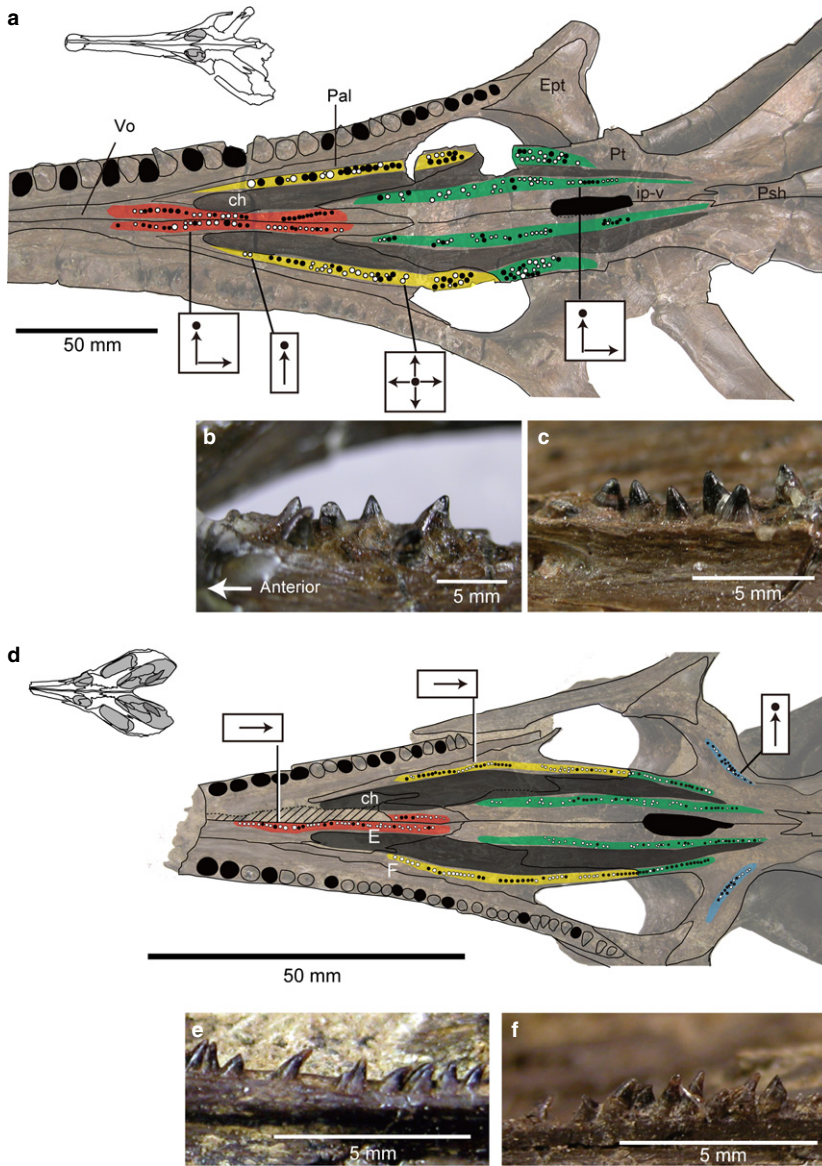
Fig. 12 Late Cretaceous *Champsosaurus*; (a–c) *C. albertensis* (RTMP 86.12.11) from the Horseshoe Canyon Formation at Drumheller, Canada; (a) photo and line drawing of *C. albertensis* in palatal view; (b) right vomerine teeth in lateral view; (c) right palatine teeth in medial view, reflected image. (d–f) *C. lindoei* (RTMP 94.163.01) from the Oldman Formation Alberta, Canada; (d) photo and line drawing of *C. lindoei* in palatal view; (e) right vomerine teeth in lateral view; (f) right anterior palatine teeth in lateral view. Black circles indicate alveoli of palatal teeth; color coding of the different regions of the palatal dentition is the same as in Fig. 2.
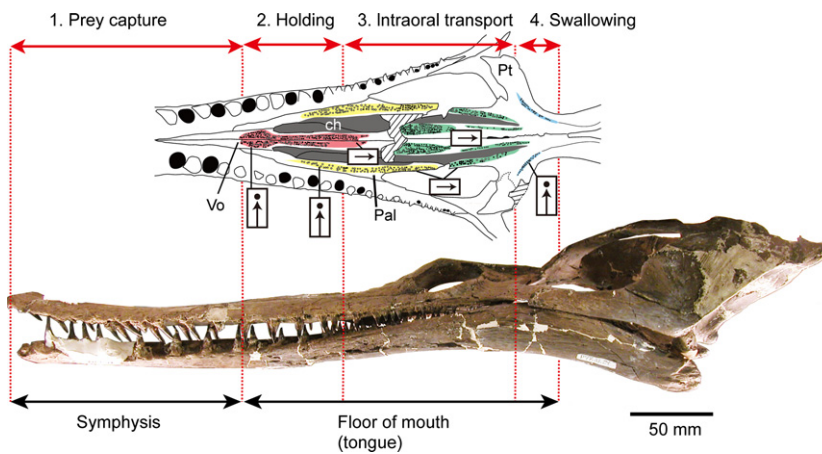

Fig. 13 Summary of the morphological variation in the palatal dentition of neochoristoderes corresponding to feeding stages; color coding of the different regions of the palatal dentition is the same as Fig. 2.

(1) Prey capture: mainly involves the anterior marginal teeth, the crowns of which are directed medially in neochoristoderes, but are generally straight in non-neochoristoderes.

(2) Ingestion: the straight anterior palatal teeth (on vomer and palatine) might have had a role in holding and reorienting the prey in combination with a fleshy tongue. In addition, in neochoristoderes, the ridges formed by the combination of raised palatal platforms and embedded teeth form a crest on the palatine medial to the marginal tooth row. This may help to hold prey where the larger marginal teeth are located (Fig. 13).

(3) Intraoral transport: the prey is manipulated by the tongue and pushed towards the back of the mouth with the posteriorly directed pterygoid teeth minimizing resistance against the tongue but preventing the prey from moving or sliding forward (Fig. 13).

(4) Swallowing: at the back of the mouth, the tooth crowns of the transverse pterygoid tooth row point medially. This may have helped to hold prey and avoid forward slippage while the tongue pushes food into the pharynx (pharyngeal packing). These pterygoid teeth are also level with the point at which the marginal tooth size is reduced. However, the posterior palatal teeth in some *Champsosaurus* (e.g. *C. albertensis*) are oriented randomly, perhaps to resist moving prey.

In the absence of muscular pharyngeal walls in reptiles (Schwenk, 2000), the pharynx itself then needs to be compressed externally (by neck muscles or neck flexion) in order to finally push the food item into the esophagus to initiate swallowing. With external constriction, there is a danger of the prey being squeezed back into the mouth instead of into the esophagus (Schwenk, 2000), and the posterior pterygoid teeth may help to resist this. The parasphenoid teeth in *Ikechosaurus* may have a similar function as the parasphenoid lies in the roof of the pharyngeal region. Their inferred redevelopment suggests that something has changed with respect to feeding strategy – in prey size, oral soft tissues or neck muscles – so that a firmer grip is required here.

Observed variation in palatal tooth shape and the width of palatal tooth batteries may also provide clues about diet. A study of the extant fish (*Cichlasoma*) found a correspondence between pharyngeal tooth morphology and diet: fish with pointed pharyngeal teeth showed a greater preference for soft prey than those with more robust rounded teeth (Trapani, 2003; Trapani et al. 2005). Relating this to choristoderes, the European *Simoedosaurus lemoinei* has sharper palatal teeth than its North American counterpart, *S. dakotensis*, suggesting a preference for softer prey – a conclusion consistent with the more gracile marginal teeth and narrower snout. Moreover, some *Champsosaurus* spe-

cies, before and after the K/Pg boundary, are differentiated by their palatal tooth morphology and arrangement. As noted above, the Cretaceous species *C. albertensis*, *C. lindoei*, *C. natator* tend to have fewer, larger pterygoid teeth than the Paleocene species *C. gigas* and *C. dolloi*. There are also differences in the snout length of these species. Paleocene species have slightly longer snouts and therefore higher marginal tooth count (59 in *C. dolloi*; 50 in *C. gigas*) than Cretaceous species (e.g. ~40 in *C. laramiensis*; 43 in *C. albertensis*). These differences could correlate with dietary change across the K/Pg boundary, reflecting the faunal and floral transformation associated with the major extinction event, as reported in mammals (Archibald & Bryant, 1990), birds (Longrich et al. 2011), insects (Labandeira et al. 2002), plants (Nichols & Johnson, 2008) and squamates (Longrich et al. 2012). Moreover, *Champsosaurus* and *Simoedosaurus*, having survived the extinction, seem to have co-occurred at some Paleocene localities (e.g. Mont-Berru, France; Fort Union Formation). They may have avoided competition by taking different prey, the long slender-snouted *Champsosaurus* feeding on schools of fish, like the extant *Gavialis*, and the wider-snouted *Simoedosaurus* taking single prey items as in broad-snouted modern crocodiles (Evans & Hecht, 1993; R. Matsumoto and S. E. Evans, unpublished data on neck anatomy). The morphology of the marginal teeth and their size (diameter and height) relative to the skull width (inner biquadrate width) are similar in both genera (Matsumoto, 2011), but *Simoedosaurus* has wider longitudinal and transverse palatal tooth rows, corresponding to the greater snout width. These shagreen teeth may have provided a more efficient gripping surface to hold large prey. The Early Cretaceous species *Ikechosaurus* is unique in having an elongated snout as in *Chamapsosaurus* (Matsumoto & Evans, 2010; Fig. 7) with a broad palatal tooth row as in *Simoedosaurus*. Remarkably, the marginal dentition of *Ikechosaurus* resembles that of non-neochoristoderes in that the exposed area of each tooth crown is short, probably due to soft-tissue cover at the tooth base (Matsumoto et al. 2014). The wider palatal gripping surfaces in this taxon might be necessary to supplement marginal dentition.

Thus, differences in the palatal dentition suggest that the neochoristoderan diet may have varied interspecifically. However, the evolutionary history of the palatal dentition remains incomplete, because palatal morphology as a whole is known only in a limited number of non-neochoristodere genera. Moreover, the question of diet and feeding strategy in this enigmatic group of reptiles needs to be approached from other perspectives, such as whole skull morphology and the structure of the marginal dentition.

Conclusions

(1) Choristodera show a modification of the primitive diapsid tooth arrangement, with one or two longitudinal rows and a transverse pterygoid row.

(2) Individual palatal teeth of neochoristoderes resemble the marginal teeth of non-neochoristoderes in being conical with striations on the enamel and in having a similar mode of tooth replacement.

(3) The width of the palatal tooth row, the sharpness of individual teeth and the orientation of the tooth tips show interspecific variation in *Champsosaurus* and *Simoedosaurus*.

(4) The sharpness of the palatal teeth differs between species and may reflect prey preference: sharp teeth for soft prey; blunt teeth for harder prey.

(5) Although the Late Cretaceous *C. albertensis* (RTMP86.12.11) and Paleocene *C. gigas* (SMM P77.33.24) have similar-sized skulls, they differ in the pattern of their palatal dentition. *C. albertensis* has fewer, larger palatal teeth, an arrangement that may be correlated with prey size and preference.

(6) The European *Simoedosaurus lemoinei* has sharper palatal teeth than its North American counterpart, *S. dakotensis*, a difference also reflected in the marginal dentition.

(7) The orientation of the palatal tooth tips changes antero-posteriorly across the palate in a manner consistent with the major stages of feeding: prey capture, ingestion, intraoral transport and swallowing.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Data S1. Summary of the palatal dentition in choristoderes.