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Unique method of tooth replacement in durophagous placodont marine reptiles, with new data on the dentition of Chinese taxa

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Abstract

The placodonts of the Triassic period (~252–201 mya) represent one of the earliest and most extreme specialisations to a durophagous diet of any known reptile group. Exceptionally enlarged crushing tooth plates on the maxilla, dentary and palatine cooperated to form functional crushing areas in the buccal cavity. However, the extreme size of these teeth, combined with the unusual way they occluded, constrained how replacement occurred. Using an extensive micro-computed tomographic dataset of 11 specimens that span all geographic regions and placodont morphotypes, tooth replacement patterns were investigated. In addition, the previously undescribed dental morphologies and formulae of Chinese taxa are described for the first time and incorporated into the analysis. Placodonts have a unique tooth replacement pattern and results follow a phylogenetic trend. The plesiomorphic *Placodus* species show many replacement teeth at various stages of growth, with little or no discernible pattern. On the other hand, the more derived cyamodontoids tend to have fewer replacement teeth growing at any one time, replacing teeth unilaterally and/or in functional units, thus maintaining at least one functional crushing area at all times. The highly derived placochelyids have fewer teeth and, as a result, only have one or two replacement teeth in the upper jaw. This supports previous suggestions that these taxa had an alternative diet to other placodonts. Importantly, all specimens show at least one replacement tooth growing at the most posterior palatine tooth plates, indicating increased wear at this point and thus the most efficient functional crushing area.

Key words: durophagy; Placodontia; tooth replacement; Triassic marine reptiles.

Introduction

Placodontia are a clade of Triassic sauropterygian marine reptiles that inhabited the margins of the Tethys Ocean in present day Europe, Middle East and China (Hagdorn & Rieppel, 1999; Li, 2000; Rieppel, 2000; Li & Rieppel, 2002; Jiang et al. 2008; Zhao et al. 2008; Scheyer et al. 2012). The clade is composed of two main groups: the more plesiomorphic, non-armoured 'placodontoid' genera (*Paraplacodus* and *Placodus*), and the more derived, heavily armoured Cyamodontoidea. They are characterised by their highly specialised crushing dentition which, when combined with features such as an akinetic skull, robust braincase and heavily reinforced cranial bones, represent one of the most extreme examples of reptilian durophagy known (Sander, 1999; Rieppel, 2000; Neenan & Scheyer, 2012). Placodont teeth are extremely enlarged, and are located on the palatine, as well as the marginal tooth-bearing elements, i.e. maxilla, dentary and, in most cases, premaxilla. It has recently been shown that placodont palatine dentition originally evolved for feeding on soft prey, and was later adapted for crushing (Neenan et al. 2013). Placodont dentitions have been extensively studied (Jaekel, 1907; Peyer, 1931; Kuhn-Schnyder, 1959; Vogt, 1983; Mazin, 1989; Rieppel, 1995, 2000; Sander, 1999; Neenan et al. 2013), with sauropterygian tooth replacement and implantation being described in detail by Rieppel (2001). However, this study only utilised one placodont taxon, *Placodus gigas*, in the form of four

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fragmentary specimens and some cross-sections [not computed tomography (CT)] of the skull and dentary. While this did shed light on the process of placodont dental replacement, it did not reveal data on replacement patterns, nor was it conclusive for all placodont taxa. Indeed, four new taxa have been described from China since: *Sinocyamodus xinpuensis* (Li, 2000); *Psephochelys polyosteoderma* (Li & Rieppel, 2002); *Placodus inexpectatus* (Jiang et al. 2008); and *Glyphoderma kangi* (Zhao et al. 2008).

The inclusion of these relatively new Chinese taxa in this study is vital, owing to our comparatively poor understanding of their morphology (including dentition), and for obtaining a complete record of placodont tooth evolution on both the eastern and western margins of the Tethys Ocean (i.e. present-day South China and Europe/Middle East). We thus provide in this paper a description of the dentition of these taxa (with the exception of *Glyphoderma*, see below), as well as including them in the tooth replacement analysis.

Tooth replacement in reptiles

Reptiles generally replace teeth constantly throughout life (polyphyodonty) and, as a consequence, show replacement teeth in several stages of development within the jaw/skull (Owen, 1840–1845). Teeth are implanted in various ways (Edmund, 1960, 1969), with the ancestral condition of subthecodonty (socketed teeth with some ankylosis by cementum) being present in parareptiles and some early synapsids, such as pelycosaurs. Most lizards and snakes show pleurodont attachment (ankylosed to the inner side of the labial wall of the tooth-bearing bone), while many marine reptiles, most archosaurs and mammals exhibit thecodont implantation (the tooth sits in a deep socket and is affixed by uncalcified connective tissue). Teeth are replaced in an alternating manner, i.e. even numbered teeth are coordinated in one wave of replacement from posterior to anterior, while the odd numbered teeth do the same but at roughly the opposite phase of replacement. These waves of replacement, first described by Woerdeman (1921), are known as Zahnreihen and are a phenomenon that has been confirmed subsequently (in adult specimens at least) for fossil and extant taxa by several authors (e.g. Edmund, 1960, 1969; Hopson, 1980; DeMar & Bolt, 1981; de Ricqlès & Bolt, 1983; Kieser et al. 1993; Small, 1997; Delgado et al. 2003), but see a review by Whitlock & Richman (2013) for other hypotheses. In most reptiles, replacement teeth develop directly lingually to the corresponding functional teeth and lie in resorption pits at the bases of the latter, whereupon the attachment is resorbed, the functional tooth is lost and the replacement tooth takes its place. This can be seen clearly in squamates such as *Iguana* (termed the 'iguanid' method), but also occurs in crocodilians (Edmund, 1960, 1969) and ichthyosaurs (Maxwell et al. 2012). There are exceptions to this, however, such as in varanid and anguimorph lizards (McDowell & Bogert, 1954; Edmund, 1960; Cooper, 1966; Rieppel, 1978) where the replacement tooth grows in an apparently interdental position, posterior and lingual to the functional tooth (termed the 'varanid' method by Edmund, 1960); and in some agamid lizards that show both acrodont and pleurodont tooth attachment (Cooper et al. 1970). In squamates with palatal dentition, such as many iguanids, lacertids, anguids and snakes, palatal teeth are usually replaced in the same way as marginal ones, but the replacement tooth is situated labially rather than lingually (Mahler & Kearney, 2006).

In sauropterygians such as *Nothosaurus* and *Simosaurus*, tooth replacement occurs in a similar way to other reptiles, i.e. in waves of Zahnreihen. Unique to Sauropterygia, however, replacement teeth grow in distinct alveolar spaces located disto-lingual to each functional tooth (Burckhardt, 1895; Edinger, 1921; Rieppel, 2001). Here, once a replacement tooth reaches full size, the bone separating the alveolus from the functional tooth is resorbed, and the replacement migrates horizontally and labially. The ankylosed base of the old functional tooth is resorbed, thus expelling it, and the new replacement tooth takes its place. Placodonts are the exception to this general rule, however. Despite their polyphyodont condition, it has already been suggested that they might not replace their teeth in an alternating order (Rieppel, 2001) and, owing to the extreme size of the functional teeth, spatial constraints prevent horizontal tooth replacement. This issue is overcome by instead utilising a vertical mode of replacement, with new teeth growing directly below the functional ones in a large alveolar space (Fig. 1; Jaekel, 1907; Vogt, 1983; Rieppel, 2001).

Placodont teeth act together in groups to create functional 'crushing areas' (*sensu*; Mazin & Pinna, 1993); regions between palatine, maxillary and dentary tooth plates that generate maximum force in order to crush hard-shelled prey. However, if placodonts replaced their teeth like most other reptiles/sauropterygians, i.e. in alternating waves, these 'areas' would potentially be rendered inert, preventing the animal from efficiently feeding. We therefore hypothesise that placodonts modified the plesiomorphic condition of alternate tooth replacement to compensate for this feeding strategy. Because replacement teeth are not usually visible in external view in placodonts, as they are located under the functional teeth, a large dataset of 11 micro (μ)-CT scans, including all placodont morphotypes, was used to reveal *in situ* replacement teeth at their various stages of development.

Materials and methods

The skulls of all valid placodont species, including at least one specimen of each, were scanned using μCT, with the exception of *Placochelys placodonta*, a specimen of which the authors were unable to obtain. *Paraplacodus broilii*, *Cyamodus hildegardis*, *Henodus*

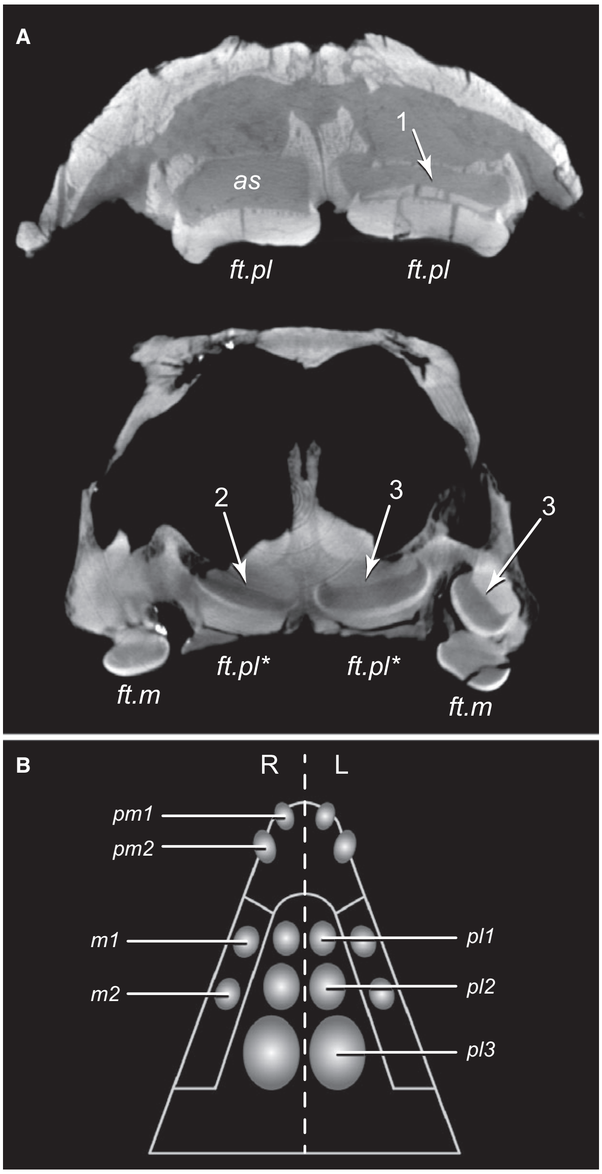

Fig. 1 Visualisation of the tooth replacement stages (A) and dental formula nomenclature (B) used in this paper. (a) Coronal sections revealing replacement teeth in the armoured placodont *Psephoderma alpinum* PIMUZ A/III 1491 (top), and the unarmoured *Placodus gigas* BSP 1968 I 75 (bottom). Stage 1, the replacement tooth is little more than a thin layer of enamel and does not resemble a functional tooth. Stage 2, the replacement tooth begins to resemble a functional tooth, but has not reached full size. Stage 3, the replacement tooth has reached approximately full size and is ready to replace the functional one. (b) Schematic representation of a placodont palate to demonstrate the dental nomenclature used in this paper. as, alveolar space; ft.m, maxillary functional tooth; ft.pl, palatine functional tooth; ft.pl*, broken palatine functional tooth; m1 and m2, 1st and 2nd maxillary teeth; pl1–pl3, 1st to 3rd palatine teeth; pm1 and pm2, 1st and 2nd premaxillary teeth.

chelyops and the Chinese *Glyphoderma kangi* were excluded from this study owing to excessive scan artefacts and/or poor state of preservation that prevented the observation of replacement teeth. However, it should be noted that *Henodus* is not considered to be durophagous but rather a filter feeder (Rieppel, 2002). Details of the specimens used herein, as well as the scan parameters, are provided in Table 1. All German specimens were scanned at Giesserei Technologie Aalen, Hochschule Aalen, Germany with a Wälischmiller RayScan 200; all Chinese specimens at the Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, P. R. China with a specially constructed 2D scanner commissioned by the IVPP; *Protenodontosaurus* was scanned at the 'Abdus Salam' International Centre for Theoretical Physics, Trieste, Italy with a special machine of their own construction, described by Tuniz et al. (2013); and *Psephoderma* was scanned at the Steinmann-Institute for Geology, Mineralogy and Palaeontology, University of Bonn, Germany using a Phoenix v tome x s. μCT slice data were reconstructed into 3D volumes using the manual segmentation function of Avizo 6.2. Replacement teeth were identified by the presence of enamel which, owing to its high density, made them relatively simple to locate and segment.

Replacement teeth were categorised into three stages of development (Fig. 1A), based mostly on the state of growth of the enamel cap, as dentine is not always visible in our scan data. Stage 1 replacement teeth are at the earliest stage and are much smaller than functional teeth, consisting mainly of a thin enamel layer with very little or no dentine. Stage 2 replacement teeth resemble a functional tooth more closely, but have not yet reached full size, having a thinner enamel cap and less dentine than a functional tooth. Finally, stage 3 replacement teeth are approximately full size, with fully developed enamel and dentine components, and are ready to erupt and become functional.

Owing to the frequent mention of specific teeth in the current paper, they will be referred to throughout the text in the following manner: right or left side of the skull (R or L), followed by the tooth-bearing element (pm, premaxilla; m, maxilla; pl, palatine; d, dentary), and then by the number of the tooth position, where 1 is the most anterior (palatal dentition) or mesial (marginal dentition; Fig. 1B). For example, the second palatine tooth on the right side will be referred to as Rpl2.

Institutional abbreviations used in this paper are: BSP; Bayerische Staatssammlung fur Paläontologie und Historische Geologie, Munich, Germany; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, P. R. China; MFSN, Museo Friulano di Storia Naturale di Udine, Italy; PIMUZ, Palaeontological Institute and Museum, University of Zurich, Switzerland; SMNS; Staatliches Museum für Naturkunde Stuttgart, Germany; UMO, Urwelt-Museum Oberfranken, Bayreuth, Germany.

Results

All specimens scanned revealed replacement teeth at varying stages of growth (Figs 1 and 2, and Figs S1–S11), and in all cases a maximum of one replacement tooth is present per functional tooth, with the exception of *Cyamodus kuhnschnyderi*, which has two replacement teeth for Rpm1 (Fig. S3b).

All *Placodus* specimens show multiple replacement teeth at various stages of growth (Figs 1 and 2, and Figs S1, S2 and S9). The UMO BT 13 specimen of *Placodus gigas* is missing all premaxillary teeth, a common state of preservation in this taxon owing to these teeth being attached by soft tissue (Rieppel, 2001), as well as Rm4. Because the latter shows no sign of a replacement tooth, it is assumed that it

Table 1 Information regarding the taxa included in this study.

Taxon	Specimen number	Locality and stratum	μCT slice thickness, mm	μCT voltage, kV	μCT current, μA
Placodus gigas Agassiz (1833)	UMO BT 13	Hegnabrunn, Bavaria, Germany. Upper Muschelkalk, Anisian, Middle Triassic	0.227	210	130
Placodus gigas Agassiz (1833)	BSP 1968 I 75	Near Bayreuth, Bavaria, Germany. Upper Muschelkalk, Anisian, Middle Triassic	0.192	210	120
Placodus inexpectatus Jiang et al. (2008)	IVPP V 14996 new specimen	Yangjuan Village, Guizhou Province, China. Falang Formation, Anisian, Middle Triassic	0.200	190	100
Sinocyamodus xinpuensis Li (2000)	IVPP V 11872 holotype	Guanling, Guizhou Province, China. Guanling Formation, Carnian, Upper Triassic	0.194	190	100
Cyamodus kuhnschnyderi Nosotti & Pinna (1993)	SMNS 15855 holotype	Tiefenbach, Baden-Württemberg, Germany. Upper Muschelkalk, lower Ladinian, Middle Triassic	0.227	210	120
Cyamodus muensteri Agassiz (1839)	BSP AS VII 1210 holotype	Near Bayreuth, Bavaria, Germany. Upper Muschelkalk, Anisian, Middle Triassic	0.139	215	150
Cyamodus rostratus Münster (1839)	UMO BT 748 holotype	Near Bayreuth, Bavaria, Germany. Upper Muschelkalk, Anisian, Middle Triassic	0.155	210	120
Protenodontosaurus italicus Pinna (1990)	MFSN 1819GP holotype	Chiout Zuguin, Udine, Italy. Carnian, Upper Triassic	0.040	149	201
Macroplacus raeticus Schubert-Klempnauer (1975)	BSP 1967 I 324 holotype	Hinterstein, Bavaria, Germany. Kössen Formation, Rhaetian, Upper Triassic	0.213	210	120
Psephoderma alpinum Meyer (1858)	PIMUZ A/III 1491 new specimen	Schesaplana Mountain, Switzerland. Rhaetian, Upper Triassic	0.166	130	130
Psephochelys polyosteoderma Li & Rieppel (2002)	IVPP V 12442 holotype	Xinpu, Guizhou Province, China. Falang Formation, Carnian, Upper Triassic	0.200	190	100

is missing due to taphonomic reasons. All other teeth are preserved and are paired with a replacement tooth, with the exception of Lpl2. BSP 1968 I 75 is missing part of the rostrum, and consequently the premaxillary and first maxillary teeth have not been preserved. Similar to UMO BT 13, the m4 is missing, but on the left side rather than the right, and has no replacement. However, unlike the other two *Placodus* specimens, all palatine teeth have a replacement tooth that is at least at stage 2, and only has one maxillary tooth with a replacement tooth present. *Placodus inexpectatus* is the Chinese representative of the genus (Figs 2b and 3) and, similar to its European counterpart, appears to also easily lose the premaxillary teeth during fossilisation, although one is still preserved *in situ*. All other teeth are preserved in the skull, despite the heavily damaged right side. Similar to UMO BT 13, all maxillary teeth save one have a replacement tooth at some stage of growth. Palatine tooth plates 1 and 3 on both sides have replacement teeth; however, neither pl2 has one. The mandible of *Placodus inexpectatus* shows a much more homogeneous pattern of tooth replacement, in that three of the four anterior teeth (Ld1, Rd1, Rd2) have replacement teeth at stage 2, the second and third dentary tooth plates of both sides (Ld4, Ld5, Rd4, Rd5) have stage 3 replacement teeth, and the first and fourth tooth plates have no detectable replacement teeth (Ld3, Ld6, Rd3, Rd6). It should be noted, however, that extensive damage on the right side of the skull as well as poor preservation below Ld6 could account for the lack of observed replacement teeth here (Fig. S9). The only missing tooth in the mandible is Ld4, which has a stage 3 replacement tooth. Thus, the functional tooth may have been lost prior to death.

Three of the four valid species of *Cyamodus* were included (Rieppel, 2000; Fig. 2a, and Figs S3–S5), *C. hildegardis* only being excluded due to its poor state of preservation. *Cyamodus kuhnschnyderi* is unique among our sample of taxa in that Rpm1 has two replacement teeth: a stage 3 immediately followed by a stage 1. With the exception of

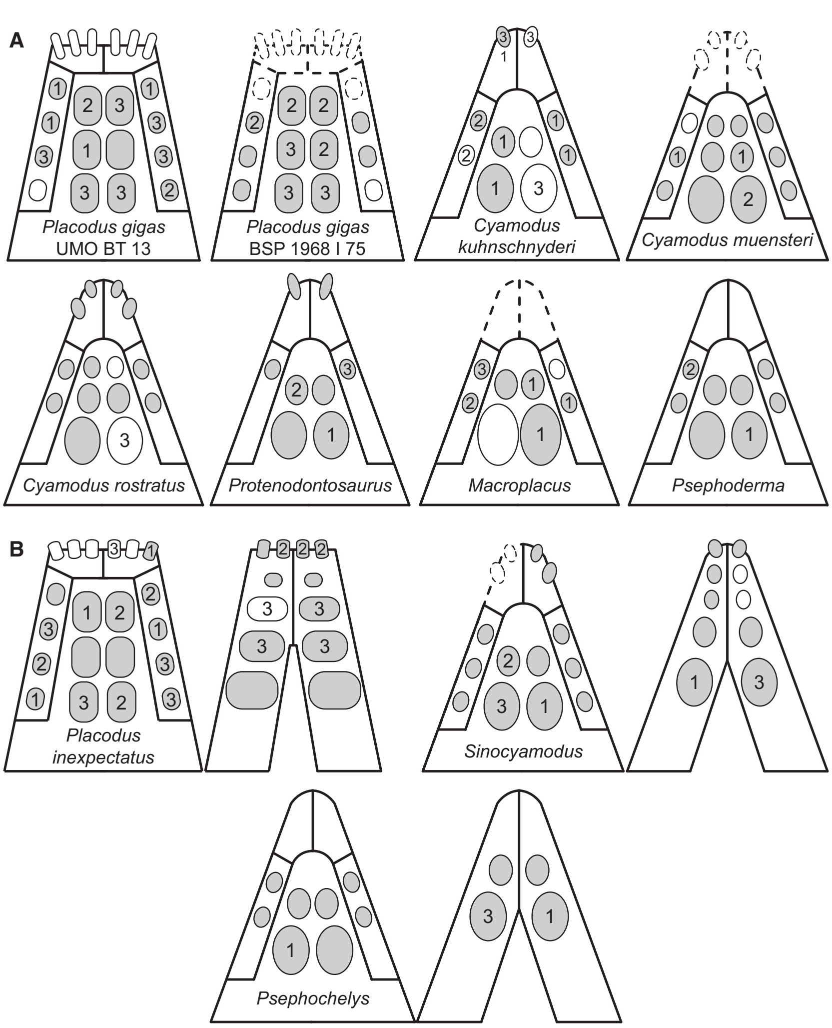

Fig. 2 Simplified reconstructions of placodont skulls and mandibles showing functional dentition and replacement tooth stages. (a) Palatal view of European placodont skulls. (b) Palatal view of Chinese placodont skulls with dorsal view of each corresponding mandible. Preserved teeth are shown in grey and missing teeth in white. Dashed lines indicate broken parts of specimens that have not been preserved. The numbers indicate tooth replacement stages and correspond to Fig. 1.

Lpl1, all teeth in the skull have corresponding replacement teeth in all phases of development. In total, four teeth are missing in this specimen (Lpm1, Rm2, Lp1 and 2), with only Lpm1 and Lpl2 exhibiting a stage 3 replacement tooth. This skull also features a fairly uniform replacement pattern with all teeth in a specific element being at the same stage, with the exception of the left palatine. The holotype of *Cyamodus muensteri* is damaged and extensively reconstructed, with the rostrum and all premaxillary teeth missing. Rm1 is also missing and lacks a replacement tooth. Of the preserved teeth, only Rm2, Lpl2 and Lpl3 have replacement teeth, all at either stage 1 or 2 of growth. *Cyamodus rostratus* contains even fewer replacement teeth, with only one stage 3 being present (Lpl3), the corresponding functional tooth of which is missing and may have been in the process of replacement before death. The dentition of *Sinocyamodus* (Figs 2b and 4, and Fig. S10) supports a close relationship with *Cyamodus* (see below). The right premaxilla is missing in this specimen, but all other teeth in the skull are present. The dentary is missing two teeth (Rd2 and 3), neither of which have replacement teeth. The majority of teeth have no replacement, with the exceptions being Rpl1, Rpl2, Lpl2, Rd5 and Ld5. Importantly, the pl2 and their corresponding d5 teeth are at exactly the same stage of replacement (stage 1 on the left and stage 3 on the right).

Protenodontosaurus is characterised by its uniquely elongated and procumbent premaxillary teeth, as well as the presence of only one tooth on each maxilla (Fig. 2a, and Fig. S6). All functional teeth are preserved in this specimen, with only three featuring replacement teeth (Lm1, Rpl1, Lpl2).

Macroplacus (Fig. 2a, and Fig. S7) shares many features with the placochelyid taxa *Placochelys*, *Psephoderma* and *Psephochelys* (and possibly *Glyphoderma*); however, the lack of a preserved rostrum prevents certain assignment into this clade, which is characterised by edentulous rostra. This taxon features enormous pl2 teeth, by far the largest of any placodont, although the right one is missing and lacks a replacement tooth (as is Lm1). This was probably lost due to taphonomic factors. However, the remaining Lpl2 forms a functional unit with the surrounding Lpl1 and Lm2 teeth, all of which have a replacement tooth at stage 1 of growth, thus indicating a degree of modularity in this taxon.

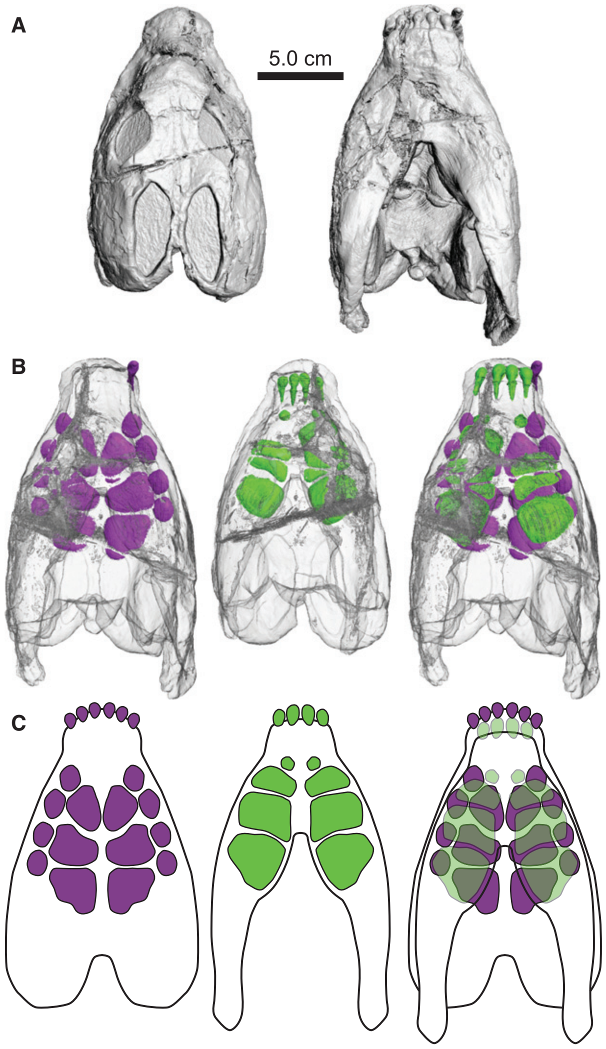

Fig. 3 The skull and functional dentition of the Chinese placodont *Placodus inexpectatus* IVPP V 14996. (a) Surface renderings of the skull in dorsal (left) and palatal (right) views. (b) Transparent surfaces revealing the dentition of the skull in palatal view (left), the dentary in dorsal view (middle) and occluding in palatal view (right). (c) Reconstructions of the complete dentition that correspond to (b). Purple, teeth in upper jaw (premaxilla, maxilla and palatine); green, teeth in dentary.

Psephoderma represents the only European placochelyid in our sample, and is characterised by two tooth plates on the maxilla and palatine, with a long, narrow edentulous rostrum (Fig. 2a, and Fig. S8). While all functional teeth have been preserved in this specimen, only two have replacement teeth (Rm1 and Lpl2). A similar condition can be found in the Chinese placochelyid, *Psephochelys* (Figs 2b and 5, and Fig. S11), which shares the same tooth formula as *Psephoderma*. In contrast, however, there is only one replacement tooth in the skull (Rpl2) and two in the dentary (Ld2 and Rd2). Rpl2 and the corresponding Rd2 both have stage 1 replacement teeth, whereas Ld2 has a stage 3, while its palatine counterpart has none.

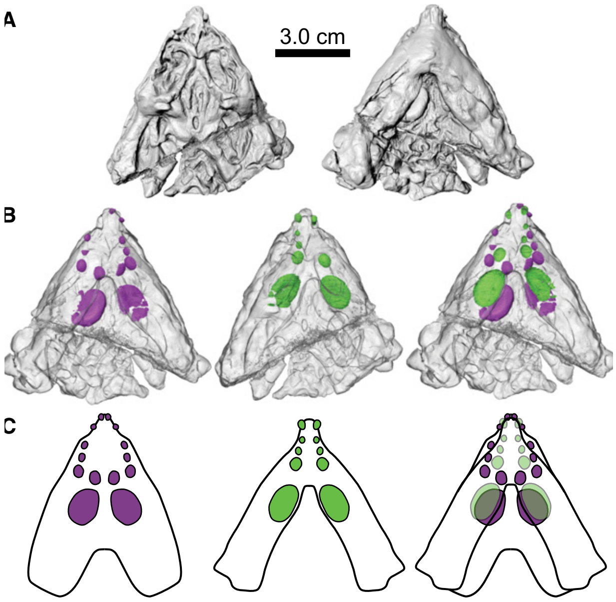

Fig. 4 The skull and functional dentition of the Chinese placodont *Sinocyamodus xinpuensis* IVPP V 11872. (a) Surface renderings of the skull in dorsal (left) and palatal (right) views. (b) Transparent surfaces revealing the dentition of the skull in palatal view (left), the dentary in dorsal view (middle) and occluding in palatal view (right). (c) Reconstructions of the complete dentition that correspond to (b). Colour scheme as in Fig. 3.

The dentition of Chinese placodonts

The dentitions of Chinese placodonts have not previously been described in any detail owing to the fact that specimens are usually embedded in a block of matrix and/or the mandibles are still articulated with the skull, thus obscuring the teeth. However, our μCT scans have revealed them for the first time, providing valuable morphological data for future comparative and phylogenetic analyses (Figs 3–5). A new specimen of *Placodus* (IVPP V 14996) is almost certainly synonymous with the holotype specimen of *Placodus inexpectatus* described by Jiang et al. (2008), and is a solitary skull with articulated jaw that is three-dimensionally preserved (Fig. 3, and Fig. S9). There is a large crack running through the entire specimen which, in dorsal view, begins below the right orbit and travels posteriorly past the posterior margin of the left orbit, also passing through the right and left pl3 and Rd6. There is also a smaller crack that runs anterior to the orbits and through both pl1 and d5 teeth. Our μCT data show the entire right side of the skull to be damaged, including most of the teeth. However, almost all of the teeth are preserved, with the exception of the premaxillary ones, which are all missing apart from Lpm3. The dentition of *Placodus inexpectatus* is very similar to that of its European counterpart, *Placodus gigas*, in that there are three premaxillary, four maxillary (although this ranges from three to five in *Placodus gigas*, but four is by far the most common condition; see Rieppel, 1995 for an

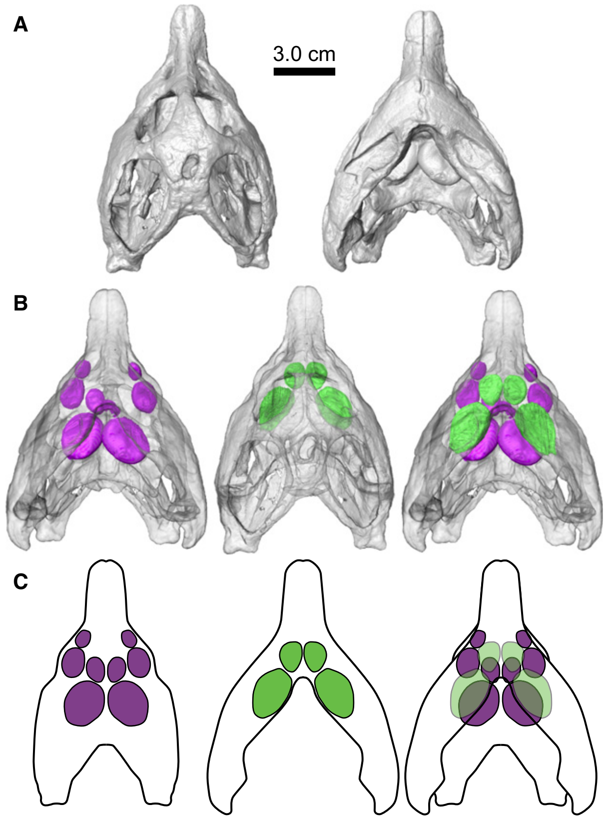

Fig. 5 The skull and functional dentition of the Chinese placodont *Psephochelys polyosteoderma* IVPP V 12442. (a) Surface renderings of the skull in dorsal (left) and palatal (right) views. (b) Transparent surfaces revealing the dentition of the skull in palatal view (left), the dentary in dorsal view (middle) and occluding in palatal view (right). (c) Reconstructions of the complete dentition that correspond to (b). Colour scheme as in Fig. 3.

overview), three palatine and two anterior, procumbent dentary teeth. However, the anterior premaxillary and dentary teeth are much shorter and more rounded than those of *Placodus gigas*, indicating a possible functional difference. These teeth also feature extended roots that are over double the length of the crown. In addition, there are four tooth plates on the dentary in *Placodus inexpectatus*, whereas only three is the most common condition found in *Placodus gigas*, although some specimens do exhibit four (Rieppel, 1995). This 'extra' tooth in *Placodus inexpectatus*, as well as in a minority of *Placodus gigas* jaws, is the anteriormost crushing tooth, and is much smaller and rounder than the others (Fig. S9d), occluding slightly anterior to the first maxillary and palatine teeth of the skull (Fig. 3b,c). The dentary crushing plates are also somewhat larger than those on the palatine, and are located slightly more labially. This allows them to not only occlude with the palatine teeth, but with the maxillary ones too, forming functional crushing areas.

The holotype specimen of *Sinocyamodus* (IVPP V 11872) was described by Li (2000) and consists of an almost complete skeleton prepared in dorsal view. The skull and articulated mandible (which have been prepared out of the slab) are three-dimensionally preserved but somewhat crushed, with several cervical vertebrae still being attached (Fig. 4, and Fig. S10). Both pl2 and the left d5 teeth have been damaged due to the crushing, but do not appear to have moved. A large crack runs through the anterior of the right upper temporal fossa and through the posterior of the left one, although this does not contact the teeth. A large part of the right premaxilla is missing, as are its associated teeth, and Rd2 and 3 have also been lost. The functional teeth of *Sinocyamodus* are numerous, generally small and widely spaced. There are two blunt and rounded premaxillary, three maxillary, two palatine and five dentary teeth. With the exception of the posteriormost tooth plates, none of the teeth occlude to create functional crushing areas, but fit alongside one another. The tooth formula is similar to that of the subadult *Cyamodus hildegardis* specimen PIMUZ T 2796 (Fig. S12; Kuhn-Schnyder, 1959) which, when combined with the small size of the specimen, would suggest that this animal was not yet fully grown. The lack of functional crushing areas in both specimens may also indicate a softer diet at earlier ontogenetic stages in these placodonts.

The holotype specimen of *Psephochelys* was first described by Li & Rieppel (2002), and consists of an exquisitely preserved skull with articulated jaw and some postcranial material including the dorsal armour, gastralia, parts of the shoulder and pelvic girdle, and a few vertebrae. The skull is almost complete, with only some posterior elements of the braincase missing. However, the right palatine teeth have taphonomically shifted ventrally, with Rpl1 having rotated as well. This could account for the lack of replacement teeth in this element. Like the European placodonts *Placochelys* and *Psephoderma*, *Psephochelys* lacks any anterior teeth in the premaxilla or dentary, and was thus suggested by Li & Rieppel (2002) to form a clade with these genera (Placochelyidae). All of its teeth are enlarged crushing plates, with the maxilla, palatine and dentary each bearing two teeth (Fig. 5, and Fig. S11).

Discussion

Our results follow a clear phylogenetic trend (Fig. 6), with notably different patterns of tooth replacement being observed between the more plesiomorphic 'placodontoids' (i.e. *Placodus*) and the derived cyamodontoid taxa. However, we acknowledge at this point that the results are based on a limited sample, because in many cases only a single specimen per species is known or available, and thus we were unable to test for intraspecific variation.

The basal *Placodus gigas* and *Placodus inexpectatus* show many replacement teeth at various stages of growth, with little or no discernable pattern (Fig. 2). Indeed, teeth of the various tooth-bearing elements are not replaced in functional units, and no maintenance of functional crushing

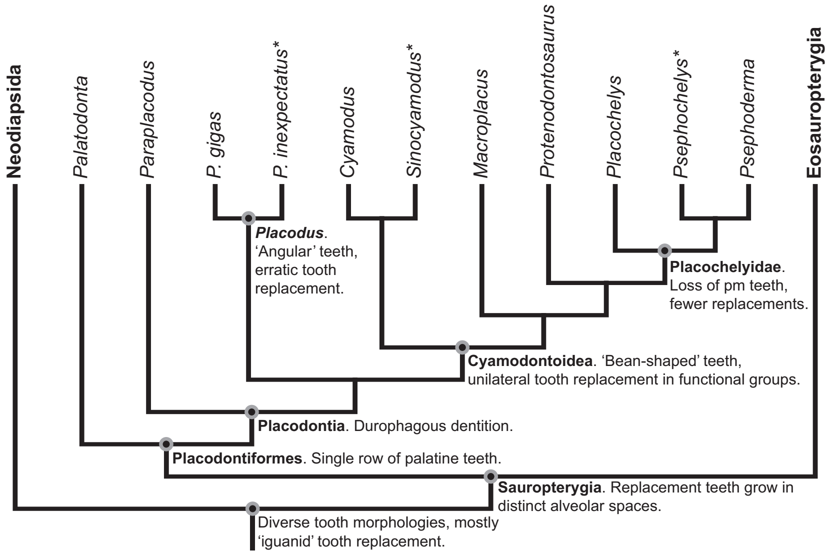

Fig. 6 Composite phylogeny of placodont relationships with the evolution of dental formula, morphology and replacement highlighted. Based on Rieppel (2000), Jiang et al. (2008) and Neenan et al. (2013). The phylogenetic position of *Placodus inexpectatus* was recovered by Jiang et al. (2008), whereas the positions of *Sinocyamodus* and *Psephochelys* are hypothetical, based on dental and gross morphological features provided in this paper as well as previously published data (Li, 2000; Li & Rieppel, 2002). Asterisked taxa are Chinese, all other placodonts are from Europe. pm, premaxilla.

areas is apparent. However, most, if not all, of the palatine tooth plates always have replacement teeth, with the posteriormost ones always featuring at least one at stage 3 of growth. The skull of both species of *Placodus* is particularly robust, reinforced with pachyostotic bone, a highly ossified and load-bearing braincase, with evidence of massive jaw musculature (Rieppel, 2002; Neenan & Scheyer, 2012). The frequent replacement of the palatine teeth, combined with this skull morphology suggests that these teeth were being subjected to high strains, and would indicate that *Placodus* was eating particularly tough food items. It is also important to note that despite the apparently disordered replacement pattern of the teeth in the upper jaw, the dentary teeth in *Placodus inexpectatus* show a highly organised bilateral pattern of replacement, with teeth on each element corresponding to their opposite number (with the exception of d2), a condition seen in some lizards (e.g. *Anguis*; Cooper, 1966). Why tooth replacement in the dentary should follow such a clear bilateral pattern while the condition of the upper jaw is so unpredictable is unclear.

The three species of *Cyamodus* as well as *Sinocyamodus* have the most teeth of the cyamodontoid taxa, and also show the most variation in tooth replacement (Fig. 2). The skulls of *C. muensteri* and *C. rostratus* are quite damaged, and many of the replacement teeth appear to be missing. However, *C. kuhnschnyderi* not only has a wealth of replacement teeth, but shows a high degree of modularity and uniformity in that each tooth-bearing element has a replacement tooth at the same stage of growth, with the exception of the left palatine that is probably missing a replacement tooth (Fig. S3). This is the only example in our sample that grows replacement teeth in this fashion; however, the palatine teeth are at opposite phases of replacement, meaning that a functional crushing area is preserved at all times. This is also the case for *Sinocyamodus*, which only has a few replacement teeth. However, a clear pattern is visible at the posteriormost palatine and dentary teeth, which correlate to each other in terms of replacement tooth stage. The advantage of having a mandible in this specimen has revealed that, in cyamodontoids at least, corresponding teeth of the upper and lower jaws are replaced in unison on individual sides in order to preserve functional crushing areas. This is also the case in *Psephochelys*, although damage to the left palatine teeth means that this pattern is only visible for the right half of the skull.

Macroplacus exhibits a strong pattern in that it clearly replaces its teeth in unilateral functional units. The left palatine teeth worked in unison with Lm2 (Lm1 is missing in this specimen along with its replacement tooth) and the corresponding dentary tooth/teeth to form functional crushing areas, and were all replaced at the same time. During replacement, the equivalent unit on the right side would have been used for feeding.

Placochelyid placodonts such as *Psephoderma* and *Psephochelys* lack anterior dentition (i.e. premaxillary and anterior dentary teeth), and it has been suggested that, instead of feeding on epibenthic sessile prey like most placodonts, they would have fed on endobenthic non-sessile hard-shelled invertebrates (Pinna & Nosotti, 1989; Mazin & Pinna, 1993; Rieppel, 2002). The elongate rostra of these taxa would have been used to probe sediments to find buried prey items, much like extant eagle rays, and possibly would have fed more on crustaceans than bivalve molluscs (Stefani et al. 1992). Our results support these predictions. The number of replacement teeth in *Psephoderma* and *Psephochelys* is heavily reduced, with very little tooth replacement occurring anterior to the posteriormost palatine and dentary tooth plates (Fig. 2). Like other placodonts, it is likely that the majority of crushing occurred at this point, thus requiring more replacement.

Some specimens exhibit replacement teeth that are inverted or strongly angled: *Placodus gigas* (Figs S1a–d and S2a);

C. kuhnschnyderi (Fig. S3a,c); and *C. muensteri* (Fig. S4a). Because the majority of placodont replacement teeth grow in a horizontal or near-horizontal position, we suggest that these occurrences are purely taphonomic in origin. As previously mentioned, replacement teeth grow in a large alveolar space, so it is logical to assume that as the tissues in this space decomposed, some teeth may have moved from their original positions.

All placodont specimens share one characteristic in common: at least one replacement tooth is always present for the posteriormost palatine and dentary tooth plates (with the exception of the posterior dentary teeth of *Placodus inexpectatus*, which are probably missing due to poor preservation). We suggest that this is the case for functional reasons. Rieppel (2002) used morphological and biomechanical analyses to determine the feeding methods of placodonts. He found that in both *Placodus* and cyamodontoids (with the exception of *Henodus*), the position of the coronoid process compared with the mandibular articulation and reconstructed jaw musculature would have placed the most efficient centre of crushing at the posterior tooth plates. It is logical then that these teeth would be subjected to increased stresses and wear, requiring constant replacement. It is also worth noting that large alveolar spaces directly below functional teeth that are experiencing high crushing loads represent a structural weakness. Future research planned by JMN and TMS aims to clarify how stress and strain is distributed though the placodont skull despite this.

A characteristic common to all cyamodontoid placodonts is that tooth replacement is always unilateral (apart from the premaxillae of *C. kuhnschnyderi*). This is once again for functional reasons, preserving functional crushing areas on at least one side of the mouth.

Chinese taxa

The dental morphology of the Chinese taxa has provided valuable data for future comparative and phylogenetic analyses. While no comprehensive placodont phylogeny exists (this work is currently in preparation elsewhere), we can draw some conclusions regarding the phylogenetic position of these taxa (Fig. 6). Judging by tooth shape, formula and replacement patterns, *Placodus inexpectatus* is confirmed as a separate species to the European *Placodus gigas*, in agreement with the phylogenetic analysis of Jiang et al. (2008). The procumbent anterior teeth of the premaxilla and dentary are much shorter and more bulbous in *Placodus inexpectatus*, indicating a dietary and/or functional difference between the two taxa. Tooth formula and shape also indicate a close relationship between the European *Cyamodus* and *Sinocyamodus*. The *Sinocyamodus* holotype is also interpreted to be a subadult, judging by its small size, the similar tooth formula to a subadult *C. hildegardis* (Fig. S12) and the low number of replacement teeth (Fig. 2b). The small teeth that do not occlude (with the exception of the pl2 and corresponding d5 teeth) indicate that juvenile placodonts may have consumed softer prey before adulthood. In agreement with Li & Rieppel (2002), tooth formula and replacement patterns also support the placement of *Psephochelys* within the Placochelyidae, owing to its striking similarity with *Psephoderma*.

Tooth replacement rates

While we have demonstrated the patterns of placodont tooth replacement in this paper, the rate at which this occurred remains unclear. It has been observed that in many extant reptiles replacement teeth require approximately 3 months to grow (e.g. *Heloderma*, *Iguana* and *Varanus*; Edmund, 1969). However, it is important to note that they also tend to replace their teeth at progressively slower rates as they age (Cooper, 1966; Cooper et al. 1970; Kline & Cullum, 1984), especially in *Alligator* (Erickson, 1996). Owing to the posterior–anterior replacement pattern seen in most reptiles, this can mean that posterior teeth are replaced at a slower rate than anterior ones, or can even stop being replaced altogether, as seen in agamid lizards (Cooper et al. 1970). Placodonts appear to have the opposite condition, however, with cyamodontoid specimens frequently lacking anterior replacement teeth, but always having posterior ones. This is probably due to the method of feeding employed, as the posterior teeth are experiencing the most stress and thus wear. It is also possible that placodonts simply stopped replacing teeth after a certain age, at least in the anterior part of the mouth. Heterodontosaurid dinosaurs for example, which had a high degree of tooth wear, are known to completely stop tooth replacement in mature individuals (Hopson, 1975, 1980). In addition, it has recently been shown that sauropod dinosaurs show strong interspecific variation in tooth replacement rates, depending on the feeding method employed (D'Emic et al. 2013), which could also be the case for placodonts – particularly when explaining the differences observed between the 'placodontoid' and cyamodontoid taxa.

Concluding remarks

Placodonts have a unique and highly specialised dentition for duraphagous feeding, and the methods of tooth replacement required for this are equally unique. By combining evidence gleaned from individual specimens in our sample, we can show that placodonts did not replace their teeth in Zahnreihen waves as is the case with most reptiles. In *Placodus*, a diet of particularly hard-shelled prey caused increased wear, especially in the posterior dentition. As a consequence, tooth replacement was relatively frequent and occurred in no discernable pattern. However, in the more derived cyamodontoids, multiple teeth worked in unison as efficient functional units on opposite sides of the skull, and were replaced together and unilaterally in order to maintain this functionality. The highly-derived placochelyids show very little tooth replacement anterior to the posteriormost crushing plates, thus suggesting a slightly softer diet, i.e. crustaceans.

Tooth formula, shape and replacement patterns can also be used to make phylogenetic conclusions regarding the Chinese placodonts, pending future analyses (Fig. 6). *Placodus inexpectatus* is supported as a member of the genus *Placodus,* while *Sinocyamodus* shares similarities with *Cyamodus*, and *Psephochelys* closely resembles *Psephoderma*.

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Author contributions

TMS and JMN designed the research. JMN carried out the segmentation, analysis and wrote the manuscript. OR and CL provided expert knowledge and insight. CL enabled and supported scanning of the Chinese material at the IVPP. GM made the specimen of *Protenodontosaurs* available for scanning and transported it to Trieste, where FB and CT carried out the scan.

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Supporting Information

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

Fig. S1 Coronal slices in anterior view through six planes in the skull of *Placodus gigas* UMO BT 13, showing replacement teeth at various stages of growth (red).

Fig. S2 Coronal slices in anterior view through three planes in the skull of *Placodus gigas* BSP 1968 I 75, showing replacement teeth at various stages of growth (red).

Fig. S3 Coronal slices in anterior view through six planes in the holotype skull of *Cyamodus kuhnschnyderi* SMNS 15855, showing replacement teeth at various stages of growth (red).

Fig. S4 Coronal slices in anterior view through three planes in the holotype skull of *Cyamodus muensteri* BSP AS VII 1210, showing replacement teeth (red).

Fig. S5 Coronal slice in anterior view through the holotype skull of *Cyamodus rostratus* UMO BT 748, showing replacement tooth (red).

Fig. S6 Coronal slices in anterior view through three planes in the holotype skull of *Protenodontosaurus italicus* MFSN 1819GP, showing replacement teeth at various stages of growth (red).

Fig. S7 Coronal slices in anterior view through four planes in the holotype skull of *Macroplacus raeticus* BSP 1967 I 324, showing replacement teeth at various stages of growth (red).

Fig. S8 Coronal slices in anterior view through two planes in the new skull of *Psephoderma alpinum* PIMUZ A/III 1491, showing replacement teeth (red).

Fig. S9 Coronal slices in anterior view through eight planes in the skull of the Chinese placodont *Placodus inexpectatus* IVPP V 14996, showing replacement teeth at various stages of growth.

Fig. S10 Coronal slices in anterior view through three planes in the holotype skull of the Chinese placodont *Sinocyamodus xinpuensis* IVPP V 11872, showing replacement teeth at various stages of growth.

Fig. S11 Coronal slice in anterior view through the holotype skull of the Chinese placodont *Psephochelys polyosteoderma* IVPP V 12442, showing replacement teeth.

Fig. S12 Reconstruction of the dentition of a subadult specimen of *Cyamodus hildegardis* PIMUZ T 2796, showing the dentition of the skull in palatal view (top left), the dentary in dorsal view (top right) and tooth occlusion in palatal view (bottom).