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European origin of placodont marine reptiles and the evolution of crushing dentition in Placodontia

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Sauropterygia was the most successful marine reptile radiation in history, spanning almost the entire Mesozoic and exploiting a wide range of habitats and ecological niches. Here we report a new, exceptionally preserved skull of a juvenile stem placodont from the early Middle Triassic of the Netherlands, thus indicating a western Tethyan (European) origin for Placodontia, the most basal group of sauropterygians. A single row of teeth on an enlarged palatine supports this close relationship, although these are small and pointed instead of broad and flat, as is the case in placodonts, which demonstrate the strongest adaptation to a durophagous diet known in any reptile. Peg-like, slightly procumbent premaxillary teeth and an 'L-shaped' jugal also confirm a close relationship to basal placodonts. The new taxon provides insight into the evolution of placodont dentition, representing a transitional morphology between the plesiomorphic diapsid condition of palatal denticles and the specialized crushing teeth of placodonts.

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Sauropterygia is the most diverse group of marine reptiles known^{1,2}, with a variety of morphologies, ecologies and life history strategies that included the armoured, durophagous placodonts³, the predatory, shallow marine pachypleurosaurs and nothosaurs⁴, and the obligate swimming, viviparous plesiosaurs⁵. The group spanned around 180 myr, from the upper Lower Triassic to the Cretaceous–Palaeogene boundary (~245–65.5 mya^{6,7}). Despite a global geological distribution and extensive fossil record (at least in Europe and Asia), it is still unclear where the clade originated, especially in the light of new discoveries from China⁸. Indeed, recent studies on pachypleurosaur phylogeny have suggested that despite the basal-most placodont being from Europe⁹, the clade may have originated in the Eastern Tethys^{10,11}.

Here we present a new fossil skull of a juvenile sauropterygian from early Middle Triassic deposits of Winterswijk, the Netherlands. The fossil displays a suite of morphological characters identifying it as a stem placodont, emphasizing the role of the western Tethys (present day Europe and western Middle East) as a Middle Triassic marine reptile biodiversity hotspot (over 60 species, see compilation in Kelley *et al.*¹²). Although the skull lacks a heavily specialized dentition adapted for crushing hard-shelled prey, features such as an elongated palatine bone carrying a single row of pointed teeth strongly support that the new taxon is not only basal to all placodonts but, combined with its early stratigraphic age, also implies that the clade originated in Europe, spreading eastwards to the Eastern Tethys.

Although the placodonts have been studied since the 1830s¹³, the evolutionary origin of their highly specialized durophagous dentition has, until now, remained unknown. The new fossil thus provides the unique opportunity to describe, for the first time, the dentition of a stem placodont, and enables us to pinpoint the developmental changes necessary to create the transition from a generalized piercing dentition with interlocking conical teeth to the extreme form of crushing dentition found in these reptiles.

Results

Systematic palaeontology. Sauropterygia Owen, 1860; Placodontiformes tax. nov.; *Palatodonta bleekeri* gen. et sp. nov.

Etymology. *Palato-*, from the Latin ‘palatum’, meaning of the palatine bone; *-donta*, from the ancient Greek ‘odon’, meaning tooth; *bleekeri*, after the discoverer, Remco Bleeker, Goor, the Netherlands.

Holotype. TW480000470 (Fig. 1; Supplementary Figs S1 and S2), Twentse Welle Museum, Enschede, the Netherlands.

Locality and horizon. Vossenveld Formation¹⁴, Lower Muschelkalk (early Anisian), Winterswijk, the Netherlands. The horizon corresponds to layer 9 of Oosterink¹⁵.

Diagnosis. Premaxilla large with distinct, narrow caudal process running between external nares and containing four blunt, peg-like, slightly procumbent teeth; a single row with at least 10 narrow, pointed teeth on the palatine; maxilla excluded from orbit and containing at least six pointed teeth; parietal with distinct caudolateral bulge located near dorsal margin of upper temporal fenestra; upper temporal fenestra laterally placed; jugal distinctly open L-shaped (boomerang-shaped); postorbital with distinct caudal process; quadratojugal absent; and excavated cheek region.

Description. The type and only known specimen is of a juvenile individual and has a high, blunt-snouted skull preserved in right

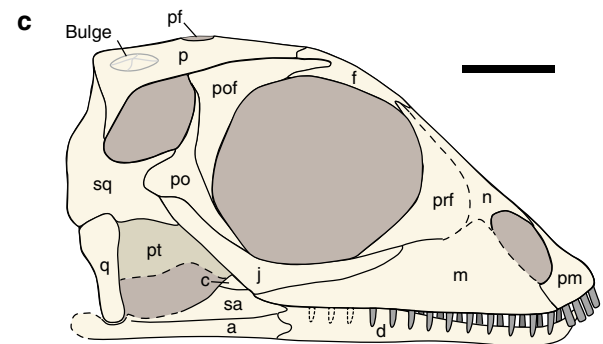
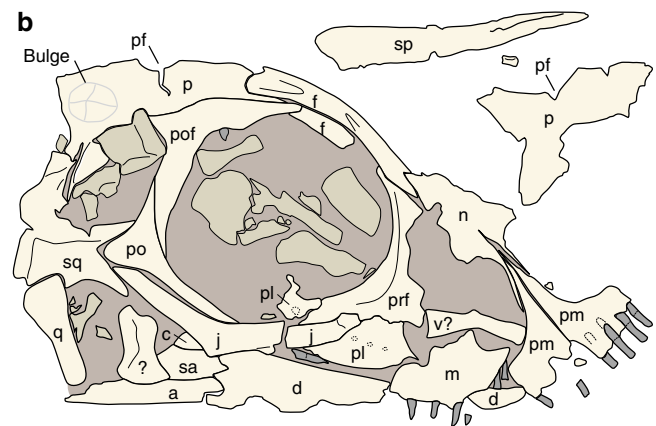
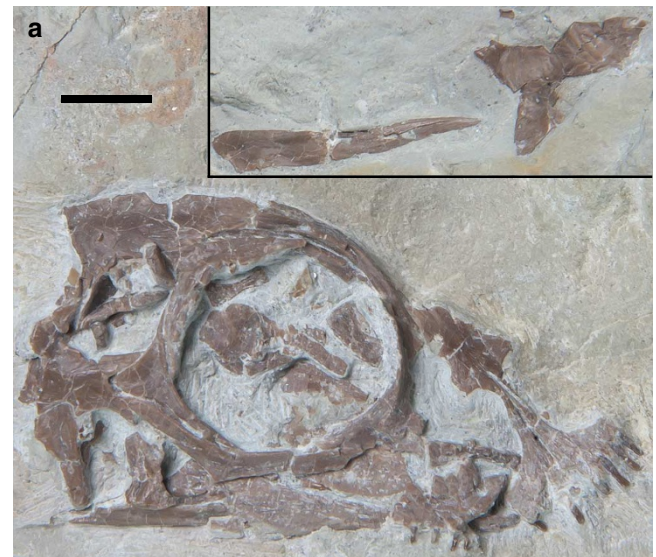


Figure 1 | *Palatodonta bleekeri* genus et species nova holotype (TW480000470). (a) Right lateral view of the specimen with disarticulated elements inset. (b) Labelled interpretation. (c) Reconstruction in lateral view. a, angular; c, coronoid; d, dentary; f, frontal; j, jugal; m, maxilla; n, nasal; p, parietal; pf, pineal foramen; pl, palatine; pm, premaxilla; po, postorbital; pof, postfrontal; prf, prefrontal; pt, pterygoid; q, quadrate; sa, surangular; sp, splenial; sq, squamosal; v, vomer. Scale bar, 3 mm.

lateral view, with the exception of the right parietal, the premaxillae and nasals, which are preserved in dorsal view (Fig. 1; for a detailed morphological description, see Supplementary Note 1 and Supplementary Movie). The left parietal and left splenial are disarticulated, and preserved in a position just dorsal to the skull itself. The posterior part of the maxilla was removed during preparation, and extended caudally to meet the

jugal, containing at least six pointed teeth (Supplementary Figs S1 and S2a). *Palatodonta* can be identified as a sauropterygian, as the premaxilla forms most of the snout rostral to external nares; a lacrimal being absent; an upper temporal fenestra and a lower temporal fenestra that open ventrally; a suborbital fenestra being absent; and teeth on the pterygoid flange being absent.

Several disarticulated elements that do not belong to the skull are preserved in this specimen, mostly within the orbit. We speculate that they are mostly from the postcranium, some of which are phalanges. In addition, a disarticulated tooth is visible between the mandible and jugal, probably originating from the right dentary, but may have been from the palatine or maxilla (Supplementary Fig. S2c). However, its robust appearance would indicate a caudal position in the skull as, in the dentary at least, posterior teeth are generally more massive (Fig. 2a,e). Another disarticulated tooth is visible at the dorsal margin of the orbit, in contact with the postfrontal. The teeth are heterogeneous, with different tooth-bearing elements displaying different tooth morphologies (Supplementary Fig. S2). The premaxillary teeth are blunt, peg-like, procumbent and have long roots, roughly equal to the length of the crowns. They are somewhat similar in morphology to that of the basal placodont *Placodus*, which would have used these teeth to pick up sessile, hard-shelled prey from the sea floor¹⁶. In fact, several placodont taxa exhibit procumbent, elongate teeth on the premaxilla, that is, *Paraplacodus*, *Placodus*, *Protenodontosaurus* and, to a lesser degree, *Cyamodus hildegardis*⁴. However, unlike *Placodus*, the premaxillary teeth of which are almost always disarticulated from the skull owing to a presumed fibrous attachment in the large alveolar spaces, the equivalent teeth in *Palatodonta* are articulated and firmly rooted within the bone¹⁶. All other teeth in *Palatodonta* are of extremely different morphology to those of placodonts, and are more similar to the expected plesiomorphic condition in that they are narrow and pointed instead of flattened and rounded (Supplementary Fig. S2).

Despite these differences, the skull of *Palatodonta* shows several similarities to the basal-most placodont *Paraplacodus*. The lower temporal fossa is open ventrally, with a highly excavated cheek region, the jugal is loosely 'L-shaped' and the quadrate is a simple bar, sutured dorsally to the squamosal. However, *Palatodonta* differs from other placodonts, with the exception of *Placodus*, in that the maxilla is excluded from the orbit and the jugal directly contacts the squamosal.

Additional micro-computed tomography (μ CT) scanning provided insight into structures that were not visible on the outer surface of the slab. This revealed that only the right half of the skull was preserved and the left half was lost before fossilization. Using the μ CT data, it was possible to reconstruct the entire right mandible, a large portion of the right palatine carrying a row of 10 pointed teeth, a large bone fragment interpreted as the right pterygoid, part of the basisphenoid and a variety of other, less diagnostic elements that most likely pertain to the braincase and the postcranium (Fig. 2).

The morphology of the palatine is particularly noteworthy, as it shares the condition of having a single row of teeth with the placodonts, although these are narrow and pointed in *Palatodonta*, instead of the round and flat shape typical for placodonts (Supplementary Fig. S3). In addition, the portion of the basisphenoid appears to be the hypophyseal pit, as it has a clear pair of foramina that we identify as the internal cerebral carotid foramina, similar to those seen in the placodonts *Placodus* and *Placochelys*^{17,18} and is consistent with the plesiomorphic condition seen in the basal diapsid *Youngina*¹⁹. There are two ascending processes lateral to the cerebral carotid foramina, similar to those present in *Placodus*¹⁷. The pterygoid is arched and edentulous, comparable to the condition seen in placodonts, providing a flange at the caudolateral margin of the palate.

Phylogenetic analysis. A phylogenetic analysis (see Methods and Supplementary Note 2 for Bremer and Bootstrap support and

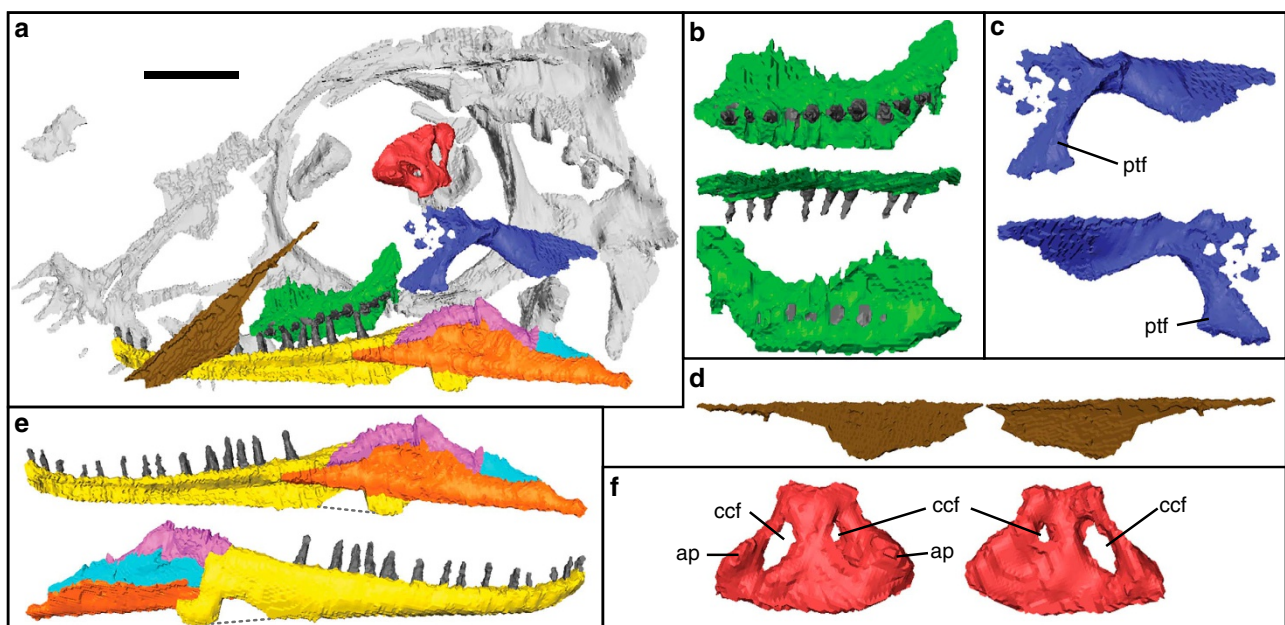


Figure 2 | Three-dimensional reconstruction of μ CT data showing obscured elements. (a) Skull interior with obscured elements highlighted. red, basisphenoid; dark blue, pterygoid; green, palatine; brown, right splenial; yellow, dentary; pink, coronoid; light blue, surangular; orange, angular. (b) Palatine in ventral (top), lateral (middle) and dorsal (bottom) views. (c) Pterygoid in medial (top) and lateral (bottom) views. (d) Right splenial in lateral (left) and medial (right) views. (e) Right mandible in medial (top) and lateral (bottom) views. (f) Basisphenoid in dorsal (left) and ventral (right) views. ap, ascending process; ccf, cerebral carotid foramen; ptf, pterygoid flange. Scale bar, 3 mm, **b-f** not to scale.

Supplementary Note 3 for character description) revealed *Palatodonta* to be sister taxon to Placodontia, supported by a single unambiguous synapomorphy (no. 51, pterygoids are generally shorter in this group compared with the palatines) and moderate bootstrap and Bremer support values (Fig. 3; Supplementary Fig. S4; see Methods section below). On the other hand, the new taxon is clearly separated from Placodontia by missing two unambiguous synapomorphies, that is, the complete lack of durophagous

dentition (no. 63) and having more than three premaxillary teeth (no. 64) (Fig. 4).

The first search run on the matrix included all taxa, which yielded three most parsimonious trees (MPTs), with the shortest tree length of 566 steps (Consistency index (CI) = 0.334, Retention index (RI) = 0.659, Rescaled consistency index (RC) = 0.220 and Homoplasy index (HI) = 0.666). The strict consensus tree (Fig. 3; Supplementary Fig. S5a) recovered a sistergroup relationship between archosauromorph taxa and the lepidosaur lineage, but a monophyletic Lepidosauromorpha (that is, Lepidosauria plus Sauropterygia) was not supported. Instead, there is a basal grade including ichthyosaurs, thalattosaurs and several other diapsid taxa leading to Sauropterygia. The proposed Placodontiformes taxon nov. is sister to a monophyletic Eosauropterygia. It is noteworthy that the pistosauroid clade, which includes the plesiosaurs, was found to be the sister taxon to the remaining eosauropterygians. Note the basal position of turtles

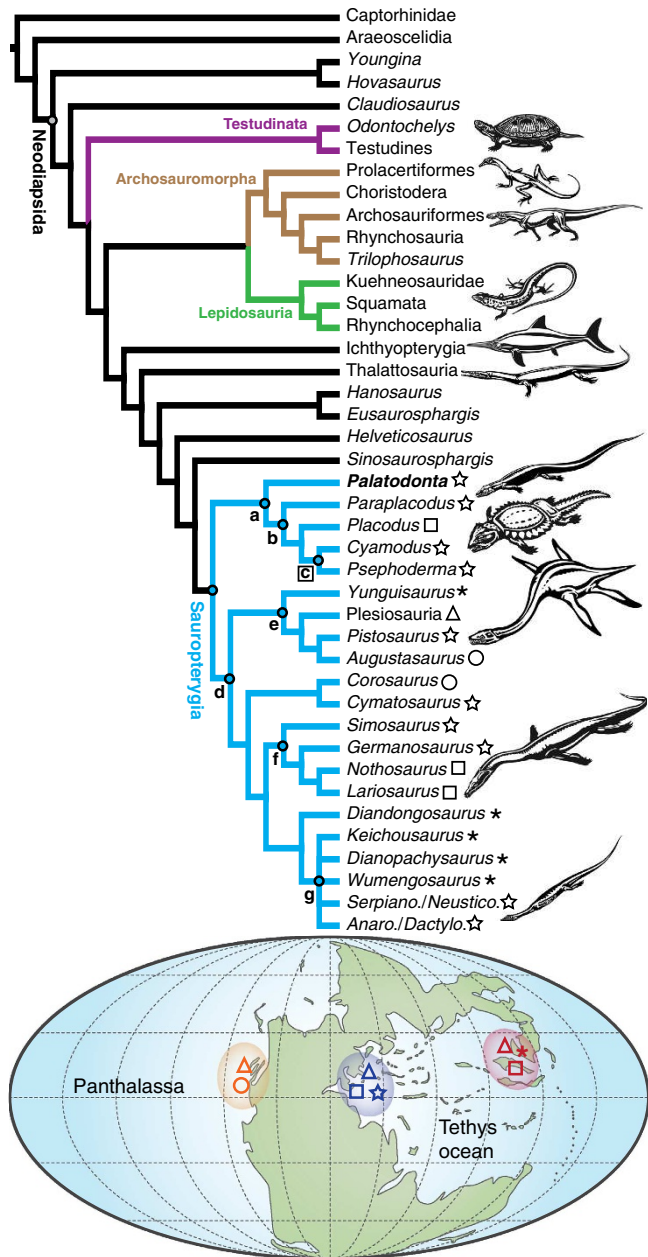


Figure 3 | Strict consensus tree showing the relationships of Sauropterygia within Diapsida combined with their geographic distribution. All scores equal 100, apart from those shown (tree description shown in Methods; Supplementary Fig. S5). (a) Placodontiformes (new taxon). (b) Placodontia. (c) Cyamodontioidea. (d) Eosauropterygia. (e) Pistosauroida. (f) Nothosauroida. (g) Pachypleurosauria. Taxa are indicated by symbols on a simplified map of the Middle Triassic (adapted from Blakey⁵⁷ and McKie and Williams⁵⁸) with the eastern Tethyan province (red), western Tethyan province (dark blue) and eastern Panthalassic province (orange) highlighted.

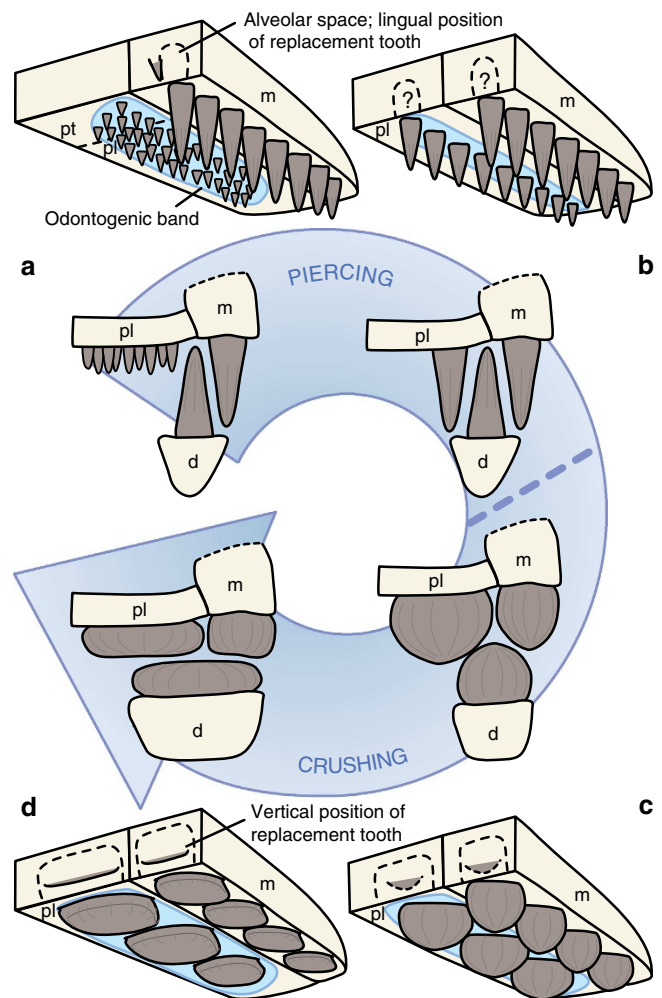


Figure 4 | Diagrammatic representation of tooth development of four taxa depicting the evolution from a pointed piercing dentition to a flattened crushing one. (a) Generalized stem neodiapsid showing the plesiomorphic condition of denticles on the palate. (b) *Palatodonta bleekeri* gen. et sp. nov., with a single row of pointed teeth on the palatine, maxilla and dentary. (c) The basal placodont *Paraplacodus*, with rounded teeth, more adapted for a crushing diet. (d) Typical dentition of *Placodus* and cyamodontoid placodonts, showing highly flattened and enlarged crushing teeth. Note that mode of tooth replacement is not known in *Palatodonta*. In *Paraplacodus*, vertical tooth replacement is inferred by presence of dentary replacement teeth in PIMUZ T2805. Abbreviations as in Fig. 1.

(*Odontochelys* and Testudines). The 50% majority rule consensus tree (Supplementary Fig. S5b) differs from the strict consensus only in the resolution within pachypleurosaurs.

The second search run on the matrix excluded Ichthyopterygia, yielding 85 MPTs, with the shortest tree length of 549 steps (CI = 0.344, RI = 0.666, RC = 0.229 and HI = 0.656). In comparison with the strict consensus tree in the first search run (Supplementary Fig. S5a), the exclusion of Ichthyopterygia led to a polytomy consisting of the archosaur and lepidosaur lineages, the turtles and the more highly nested diapsids (thalattosaurs to sauropterygians). The resolution is lower in Sauropterygia in the strict consensus compared with the first search run as well. In the 50% majority rule consensus (Supplementary Fig. S6b), *Corosaurus* is recovered as sister taxon to all remaining eosauroptrygians, followed by the pistosauroid clade, with *Cymatosaurus* moving onto the stem of the latter.

The third run of the matrix excluded Ichthyopterygia and turtles (*Odontochelys* and Testudines), yielding 502 MPTs with the shortest tree length of 499 steps (CI = 0.355, RI = 0.673, RC = 0.239 and HI = 0.645). For this analysis, the number of trees retained was successively raised to 30 to acquire the shortest tree. Further increase to a 1,000 replicates and 100 retained trees per analysis led to the same topology of the strict consensus tree but differed in that all archosauromorph taxa were found in one polytomy in the 50% majority rule tree. This analysis yielded a poorly resolved strict consensus tree (Supplementary Fig. S7a) with polytomies in several sections of the cladogram. Especially, the resolution among the archosaur and lepidosaur lineages collapsed completely. The 50% majority rule consensus (Supplementary Fig. S7b) is somewhat better resolved, with sauropterygian ingroup relationships largely mirroring those shown in Supplementary Fig. S6b.

In the fourth analysis (with options set to 1,000 replicates and 100 trees retained), the all-zero ancestor, as well as Ichthyopterygia and turtles, were removed, and Captorhinidae and Araeoscelidia served as outgroups instead. Forty-seven MPTs were found with the shortest tree length of 520 (CI = 0.358, RI = 0.662, RC = 0.237 and HI = 0.642). Results were overall comparable to the outcome of the third run as indicated by the strict consensus (Supplementary Fig. S8), with relationships among Sauropterygia being slightly better resolved. Note that in this analysis, *Cymatosaurus* again moved onto the plesiosaur stem.

For the fifth analysis, the matrix was pruned to include only Sauropterygia as ingroup and *Sinosauropsphargis* as outgroup. Three MPTs were found with the shortest tree length of 315 (CI = 0.483, RI = 0.609, RC = 0.294 and HI = 0.517). Similar to the results of the first search run, a sistergroup relationship between *Corosaurus* and *Cymatosaurus* was recovered, but now this clade is sister to all remaining eosauroptrygians. Ingroup relationships of the latter are not well resolved as indicated by polytomies in both the strict consensus (Supplementary Fig. S9a) and the 50% majority rule tree (Supplementary Fig. S9b).

Discussion

Palatodonta is clearly a juvenile specimen, owing to its small size (20.5 mm in length; see Supplementary Table S1 for a full list of measurements), relatively large orbit and lack of extensive bone fusion. Thus, its suitability for phylogenetic analysis was investigated using osteological comparisons with modern reptilian hatchlings and adults (turtles, non-varanoid squamate lizards and crocodylians). This lead us to the interpretation that, although overall proportions change during ontogeny and sutures might become obliterated with age, the suture patterns of this juvenile generally reflect the adult condition of the new species (see Bhullar *et al.*²⁰). This is also supported by observations in

pachypleurosaurs, which also do not change cranial bone configuration through ontogeny^{21–23}.

Palatodonta shares with the basal-most placodont *Parapalacodus* the distinctly open L-shaped jugal, as well as a ventrally open lower temporal fossa and excavated cheek region. The former character also appears convergently in *Claudiosaurus* and in some pachypleurosaurs, whereas the latter is a plesiomorphic condition for sauropterygians in general. The loss of the lower temporal fossa and closure of the cheek region is secondarily developed only among the more highly nested placodonts (*Placodus* and cyamodontoids^{18,24}), the fusion of nasals found in the new skull is present only in some *Cyamodus* spp. so far, whereas the condition remains debatable in *Parapalacodus*.

Palatodonta is not a juvenile of any known placodont because juvenile specimens of *Parapalacodus* (Paläontologisches Institut und Museum Universität Zürich (PIMUZ) T2805) and the armoured cyamodontoid *Cyamodus* (PIMUZ T2797) show that, despite being of similar size, crushing dentition is already fully formed very early during ontogeny (Supplementary Fig. S3). Previous research shows that it is tooth formula that changes through placodont ontogeny, not shape²⁵.

Although *Palatodonta* shares several characters with *Parapalacodus*, the presence of pointed palatal teeth suggests that *Palatodonta* is a stem representative with a very different lifestyle and diet to crown group Placodontia. We hypothesize that the comb-like arrangement of blunt, peg-like premaxillary teeth in *Palatodonta* (Supplementary Fig. S2b) were used for sifting through soft sediments on the shallow ocean floor to root out small, soft prey items, whereas the more massive equivalent teeth in *Parapalacodus* and *Placodus* served to pluck hard-shelled prey from hardgrounds³.

The palatine dentition in *Palatodonta* represents an intermediate condition between the denticles/teeth of stem neodiapsids²⁶, and the flattened, enlarged palatal crushing teeth seen in placodonts⁴ (Fig. 4, Supplementary Note 1). An evidence-based scenario for this morphological transformation of dentition can thus be formulated.

In many Permian diapsid reptiles, clusters of small denticles or teeth are present on the vomer, palatine and pterygoid bones (Fig. 4a), thus an odontogenic band (a place of residence of stem cells active in tooth formation²⁷) acting as precursor to dental lamina formation (Richman and Handrigan²⁸ and references therein) is assumed to be present in these ancient reptiles. In particular, the expression of *Shh* (Sonic hedgehog) and transcription factor *Pitx2* (pituitary homeobox 2) as part of a gene network with others (for example, *Wnt*- and *Bmp*-related pathways), must have had a critical role in palatal tooth formation^{28,29}. These conserved pathways and proteins are not only important, for example, in patterning the central nervous system, in limb bud formation and internal organogenesis³⁰, but are also known to be active in tooth development from fish to mammals³¹.

Compared with their Permian ancestors, the palatine of Placodontiformes increased in length and size relative to the vomer and the pterygoid, forming most of the palate, with the dentition of *Palatodonta* consisting of single row of conical palatine teeth similar to those of the maxillary tooth row (Fig. 4b). As indicated by studies of modern snakes³², a rostral and caudal truncation of the developmental field or a suppression of growth factors by antagonistic morphogens²⁸ could have been responsible for the suppression of palatal teeth in the vomeral and pterygoidal regions in that taxon (Fig. 4a,b).

The dental formula was further modified in crown group Placodontia to be suited to a durophagous diet by reducing the number of ankylosed thecodont teeth¹⁶ and allowing them to become larger and successively flattened (Fig. 4c,d), whereas at the same time, increasing the alveolar dimensions in the skull bones and the mandible. We can assume that the enamel

(=dental) organ forming placodont teeth was enlarged and flattened in the more derived placodonts in comparison with modern reptiles²⁸, probably filling most of the dental alveolar space, to generate the broad, sheet-like initial enamel secretion forming the top layer of the plate- or bean-shaped crushing teeth (including replacement teeth; Fig. 4). One means to achieve a size increase in teeth in mammals³³ is the suppression of apoptosis during early development (that is, suppressing *p21*, a cyclin-dependent kinase inhibitor), a mechanism associated with pathological macrodontia (anomalous enlargement of teeth). However, differences in apoptosis between reptile and mammal teeth are known, with apoptosis affecting the stellate reticulum in the former but occurring at the inner enamel epithelia in the latter²⁸. A considerable increase in enamel organ dimension could then have caused a displacement of the successional dental lamina, so that tooth replacement became vertical (Fig. 4d) and not lingual to the functional tooth¹⁶.

Although there is a general consensus that Sauropterygia are well nested within Diapsida^{4,34}, the exact relationships within and among groups are still debated. Our results indicate that pachypleurosaurs, together with nothosaurs, are highly nested within Sauropterygia (Fig. 3; Supplementary Fig. S4; Supplementary Notes 2 and 3). In contrast, it was previously widely accepted that the small- to medium-sized Pachypleurosauria represented the most plesiomorphic clade within Eosauropterygia, and palaeobiogeographic hypotheses favoured an origination of the whole group in the Eastern Tethyan realm¹¹. This was supported, for example, by the occurrence of *Keichousaurus yuananensis* from the Jialingjiang Formation, Hubei Province, China, which is either late Early Triassic or early Middle Triassic in age^{4,35}. New, yet to be described, sauropterygian material has recently been found in the Early Triassic (Spathian, Olenekian) of Chaohu, Anhui Province, however³⁶. Given the fact that the geologically oldest eosauropterygians outside of Asia (*Corosaurus* from North America and Sauropterygia indet. from Europe⁴) also occur in the late Early Triassic, however, the western Tethys or the eastern Panthalassic ocean could potentially have been the site of origin for the clade as well (Fig. 3; Supplementary Fig. S4). Despite this, a robust node in all phylogenetic analyses conducted (see Supplementary Figs S5–S10) indicates that Placodontiformes originated in the Western Tethys, and from there diversified and migrated into the Eastern faunal province.

Methods

μCT scanning. Scanning was carried out with a Phoenix v tome x s (GE Phoenix X-ray; 240 kV) at the Steinmann Institute, University of Bonn, Germany, with a voltage of 170 kV and a current of 150 μA. A total of 1,501 images were taken without beam filtration, each with an exposure time of 667 ms, resulting in a voxel size of 0.055 mm. Stacks of digital CT images were produced with the VGStudio MAX 2.0 software (Volume Graphics) and served as the base for virtual three-dimensional reconstructions of the bony structures by means of the manual segmentation function of the software Avizo version 6.2.1.

Phylogenetic analysis. Analyses were run in PAUP 4.0b10 for Microsoft Windows 95/NT³⁷ using PaupUP³⁸ version 1.0.3.1. Trees resulting from the analyses were transformed using Mesquite³⁹ and the Adobe Photoshop Creative Suite. All analyses were run under parsimony setting using the heuristic search option, with all 140 characters being unordered and not weighted in any way. Furthermore, all characters were found to be parsimony-informative, no aspect of the tree topology was enforced and the ingroup was set to be monophyletic.

The character matrix used herein is based on the matrix of Liu *et al.*¹¹, which is itself based mainly on Rieppel *et al.*⁴⁰ (in return this matrix was based on Rieppel⁴¹). The original characters (7) and (120) were removed by Liu *et al.*¹¹ because they were found uninformative in their analysis, whereas two new characters (1) and (61) were added from Rieppel and Lin¹⁰. Note that the re-shuffling of characters by Liu *et al.*¹¹, in contrast to the matrices used by Li *et al.*⁴², Shang *et al.*⁴³ or Wu *et al.*⁴⁴, is also adopted herein.

From the matrix used by Liu *et al.*¹¹, several character definitions of the matrix were modified and three new characters (138–140) have been introduced. On the

other hand, a few of the original taxa used have been re-scored (*Cyamodus*, *Placodus*, *Wumengosaurus* and Younginiformes). Instead of Younginiformes, *Hovasaurus boulei*⁴⁵ (scoring followed mainly Currie⁴⁶ and Bickelmann *et al.*⁴⁷, as well as personal observation of specimens in the PIMUZ collections) and *Youngina capensis*⁴⁸ (scoring followed Smith and Evans⁴⁹ and Bickelmann *et al.*⁴⁷) are used as terminal taxa, because the group was recently found to be paraphyletic⁴⁷.

On the other hand, several sauropterygian taxa new to the Liu *et al.*¹¹ matrix (*Diandongosaurus acutidentatus*, *Paraplagodus broilii*, *Psephoderma alpinum*; *Yunguisaurus liae* and *Palatodonta*; this paper), as well as thalattosaurs (scoring after Müller^{50–52}, Müller *et al.*⁵³, Liu and Rieppel⁵⁴, Li *et al.*⁴² and personal observations of specimens in the PIMUZ collections), the stem turtle *Odontochelys semitestacea*⁵⁵, Ichthyopterygia and four additional neodiapsid taxa (*Eusaurosphargis dalsassoi*, *Sinosaurusphargis yunguisensis*, *Hanosaurus hupehensis* and *Helveticosaurus zollingeri*) have been added. The new matrix thus comprises 42 taxa (43 for those that include a hypothetical all-zero ancestor) and 140 informative characters in total. For the present study, less well-known or highly fragmentary Chinese sauropterygian taxa such as *Chinchenia*, *Kwangisaurus*, *Sanchiaosaurus*^{34,41,44} and *Largocephalosaurus*⁵⁶ were not included.

Bootstrapping and Bremer support. A first bootstrap analysis (based on 1,000 replicates) was performed on the matrix used in the first search run. This analysis shows a loss of resolution in large parts of the tree. However, the newly proposed Placodontiformes has a value of 78% (Supplementary Fig. S10a), with a Bremer support score of 3 for the clade. A second bootstrap analysis (again based on 1,000 replicates) was run on the data set of the third run (Ichthyopterygia and turtles removed), which also showed high support (75%) for Placodontiformes, while Bremer support score for the taxon remained at 3 (Supplementary Fig. S10b). Apart from these slightly different bootstrap values, the general topologies of the two trees did not change, with the exception of the all-zero ancestor and Captothinidae forming a basal polytomy in Supplementary Fig. S10a, instead of a resolved grade in Supplementary Fig. S10b. The third bootstrap analysis (Supplementary Fig. S10c; also with 1,000 replicates) was performed on the pruned data set of the fifth analysis (Supplementary Fig. S9a). Here the bootstrap support and topology was generally similar to the previous analyses, although support for Placodontiformes is much higher at 91%, and *Wumengosaurus* now forms a clade with the European pachypleurosaurs (Supplementary Fig. S10c). Once again, the node Placodontiformes had a Bremer support score of 3.

Nomenclatural acts. This published work and the nomenclatural act it contains have been registered in ZooBank, the proposed online registration system for the International Code of Zoological Nomenclature (ICZN). The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix 'http://zoobank.org/'. The LSID for this publication is: urn:lsid:zoobank.org:pub:2CC51C4F-03F2-4647-9829-99646F6DA78E.

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Author contributions

J.M.N. and T.M.S. wrote the manuscript and prepared the figures. N.K. and J.M.N. conducted the morphological description of outwardly visible structures. N.K. carried out the CT scanning. T.M.S. and J.M.N. performed the phylogenetic analysis. J.M.N. created the three-dimensional reconstruction and conducted the morphological description of the concealed elements.

Additional information

Supplementary Information accompanies this paper at <http://www.nature.com/naturecommunications>

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Erratum: European origin of placodont marine reptiles and the evolution of crushing dentition in Placodontia

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The file containing Supplementary Data 1 was inadvertently omitted during production of this article and should have been referred to in the 'Phylogenetic analysis' section of the Methods, as follows: 'The character matrix used herein (Supplementary Data 1) is based on the matrix of Liu *et al.*¹¹'. Supplementary Data 1 is now available to download from the HTML version of this Erratum.