

A Middle Triassic stem-turtle and the evolution of the turtle body plan

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The origin and early evolution of turtles have long been major contentious issues in vertebrate zoology^{1–11}. This is due to conflicting character evidence from molecules and morphology and a lack of transitional fossils from the critical time interval. The ~220-million-year-old stem-turtle *Odontochelys* from China¹² has a partly formed shell and many turtle-like features in its postcranial skeleton. Unlike the 214-million-year-old *Proganochelys* from Germany and Thailand, it retains marginal teeth and lacks a carapace. *Odontochelys* is separated by a large temporal gap from the ~260-million-year-old *Eunotosaurus* from South Africa, which has been hypothesized as the earliest stem-turtle^{4,5}. Here we report a new reptile, *Pappochelys*, that is structurally and chronologically intermediate between *Eunotosaurus* and *Odontochelys* and dates from the Middle Triassic period (~240 million years ago). The three taxa share anteroposteriorly broad trunk ribs that are T-shaped in cross-section and bear sculpturing, elongate dorsal vertebrae, and modified limb girdles. *Pappochelys* closely resembles *Odontochelys* in various features of the limb girdles. Unlike *Odontochelys*, it has a cuirass of robust paired gastralia in place of a plastron. *Pappochelys* provides new evidence that the plastron partly formed through serial fusion of gastralia^{3,13}. Its skull has small upper and ventrally open lower temporal fenestrae, supporting the hypothesis of diapsid affinities of turtles^{2,7–10,14,15}.

Turtles are readily diagnosed by the possession of a bony shell consisting of a dorsal carapace and a ventral plastron, which are linked by bony bridges on either side. In recent years embryological studies on extant turtles^{1,3} and recognition of stem-turtles^{4–6,12} have provided evidence about the stepwise acquisition of features of this unique body plan. The discovery of a new stem-turtle from the Middle Triassic (Ladinian) of Germany sheds new light on this evolutionary transition as well as on the long-contentious relationships of turtles to other amniotes.

Reptilia Laurenti, 1768

Pan-Testudines Joyce, Parham and Gauthier, 2004 (ref. 16)

Pappochelys gen. nov.

Etymology. *Pappos* (Greek): grandfather; *chelys* (Greek): turtle. Type species. *Pappochelys rosinae*.

Pappochelys rosinae sp. nov.

Etymology. In honour of I. Rosin, who prepared key specimens of the new taxon.

Holotype. Staatliches Museum für Naturkunde Stuttgart, SMNS 91360, incomplete, partly articulated postcranial skeleton (Fig. 1a, b).

Referred material. SMNS 90013, disarticulated skeleton with incomplete skull (Fig. 1c, d), and 18 additional specimens. See Supplementary Information for details.

Type locality. Schumann quarry, Eschenau, Vellberg municipality, Baden-Württemberg, Germany.

Type horizon. Top of Untere Graue Mergel, Lower Keuper (Erfurt Formation); late Middle Triassic (Ladinian: Longobardian). The fossils occur in a 5- to 15-cm-thick layer of dark grey lacustrine claystone, along

with fishes, temnospondyl stem-amphibians, and mostly terrestrial diapsid reptiles¹⁷. Despite extensive collecting in Lower Keuper strata for the past two centuries, not a single diagnostic bone of the new reptile was discovered until recently. Since 2006, the aforementioned fossils referable to this taxon have been recovered from the type locality.

Diagnosis. Small (estimated adult length ~20 cm); skull proportionately small, with short, deep temporal region; parietal with distinct occipital flange; jaw bones bearing teeth; squamosal and parietal bounding much of upper temporal fenestra; lower temporal opening

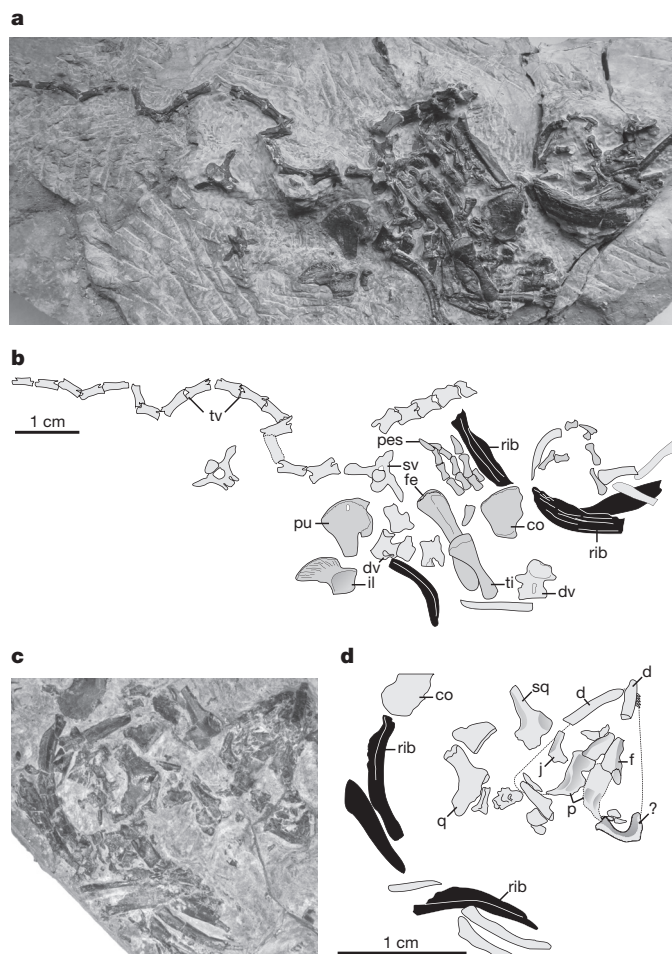


Figure 1 | *P. rosinae*. **a, b**, Articulated partial postcranial skeleton (SMNS 91360, holotype); **c, d**, disarticulated skeleton with incomplete skull (SMNS 90013). Photographs with explanatory outline drawings. Trunk ribs highlighted in black. Abbreviations: co, coracoid; d, dentary; dv, dorsal vertebra; f, frontal; fe, femur; il, ilium; j, jugal; p, parietal; pu, pubis; q, quadrate; sq, squamosal; sv, sacral vertebra; ti, tibia; tv, tail vertebra; question mark, unidentified cranial bone.

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open ventrally; trunk ribs anteroposteriorly broad, T-shaped in cross-section and with dorsal sculpturing; gastralia paired, robust, with ridged external surface; whip-like tail comprising some 50% of total length; scapula with tall, straight dorsal process and small 'acromial' flange; coracoid plate-like; ilium with long postacetabular process; pubis with thyroid foramen and distinct lateral process.

All specimens of the new taxon were mechanically prepared. Histological work on fossil bones employed standard techniques used for making petrographic thin-sections.

The skull of *Pappochelys* (Fig. 2c) has a large orbit and short, pointed snout and is triangular in dorsal view. Its broad cheek region has a small rounded upper and a ventrally open lower temporal fenestra. The configuration of the bones in the temporal region is consistent with that in diapsid reptiles.

The premaxilla, maxilla, and dentary bear teeth. The teeth are peg-like in the maxilla (Fig. 2a, b) and slightly inclined posteriorly in the anterior part of the dentary (Fig. 2i). In both upper and lower jaws, the more posterior teeth are smaller and somewhat more robust. The premaxilla bears four teeth, the maxilla up to 17, and the dentary at least 29. Tooth implantation appears to be subthecodont. The short maxilla has a large, posterodorsally directed facial process and a short anterior ramus. Its posterior process decreases in height posteriorly. The frontal (Extended Data Fig. 1g) is longer than the nasal and parietal. The parietal (Fig. 2d, Extended Data Fig. 1c, d) has a short posterolateral wing and distinctly offset occipital flange. There is no trace of a pineal foramen. The postorbital (Fig. 2e and Extended Data Fig. 1e) is short anteroposteriorly, with a rounded posterior and a long ventral process contacting the posterior margin of the dorsal process of the jugal. The postfrontal (Extended Data Fig. 1f) is triangular. The slender jugal (Fig. 2h and Extended Data Fig. 2) has an elongate, anterodorsally curving anterior process, a tapering dorsal process,

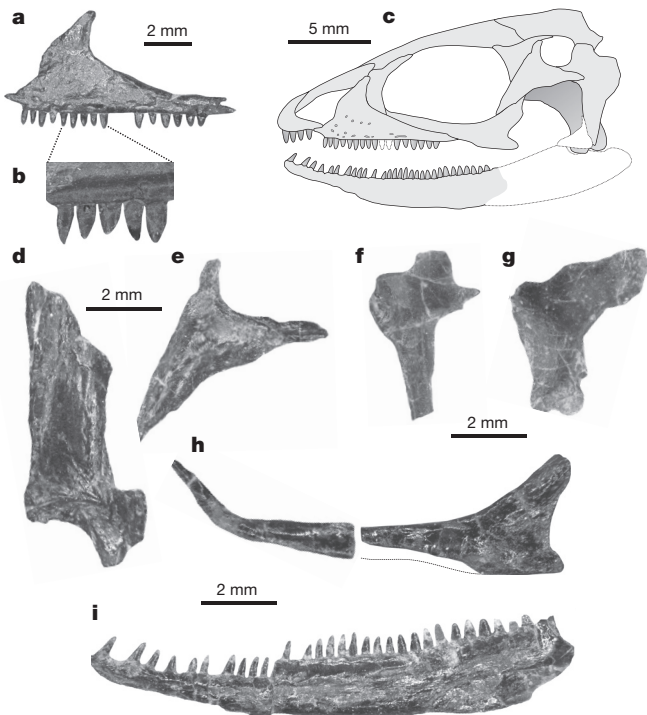


Figure 2 | Skull elements of *P. rosinae* (digitally extracted from surrounding matrix). **a, b**, Left maxilla (SMNS 91431; **a**, labial view; **b**, lingual view of marked section); **c**, skull reconstruction in lateral view, with preserved elements indicated in grey; **d**, right parietal (SMNS 91356); **e**, right postorbital (SMNS 91356); **f**, right squamosal (SMNS 90013); **g**, right quadrate (SMNS 90013); **h**, left jugal (SMNS 92066, broken into two segments and partly preserved as an impression); **i**, left dentary (SMNS 92066).

and a short posterior process that indicates a ventrally largely open lower temporal fenestra. The squamosal (Fig. 2f) has a long ventral process, tapering postorbital ramus, rounded posterior buttress, and median parietal process. The massive quadrate (Fig. 2g) has a slightly concave posterior margin. The palate is not clearly exposed in any available specimen. The dentary (Fig. 2i and Extended Data Fig. 2) is slender and curves anterodorsally. No other mandibular bones have been identified so far.

Cervical vertebrae (Fig. 3g) are elongate and low, with extensive postzygapophyses and low neural spines. The number of presacral vertebrae and relative lengths of the neck and trunk remain unknown. Dorsal vertebrae (Fig. 3h, i) have long cylindrical centra with nearly vertical rib facets at about midlength. The neural arch is fused to the centrum in adults, and the neural spine is low. There is no trace of neurals. Although the trunk region is disarticulated in all available specimens, the maximum number of trunk vertebrae did not exceed nine. The anteroposteriorly broad trunk ribs (Fig. 3a–d) each bear slightly asymmetrical anterior and posterior flanges and are distinctly T-shaped in cross-section. The confluent rib heads have a figure-eight shape in end view. The distal ends of the ribs are tapered. Undistorted

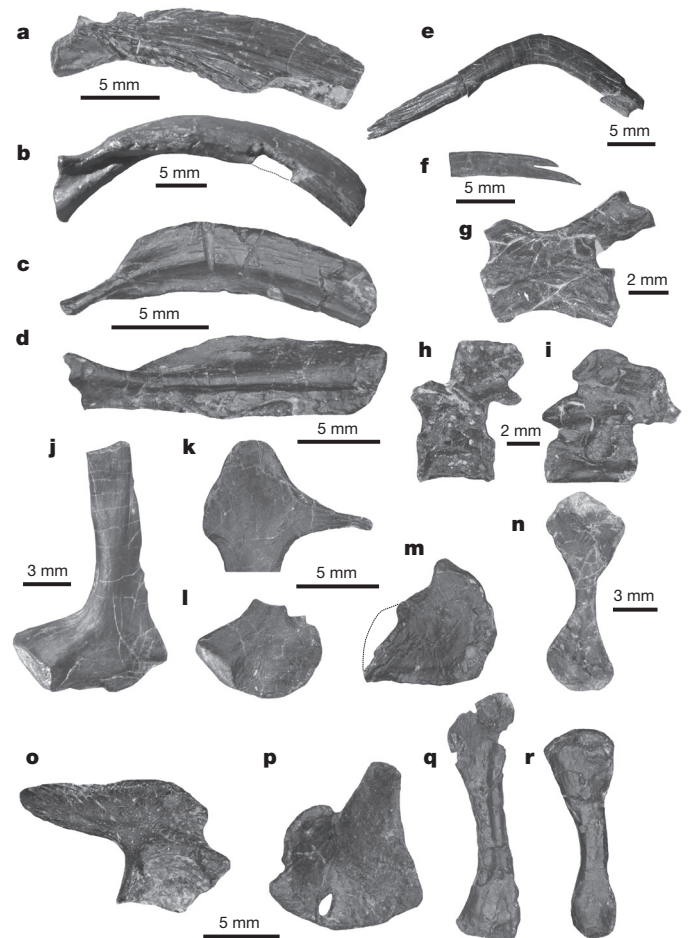


Figure 3 | Postcranial elements of *P. rosinae* (digitally extracted from surrounding matrix). **a**, Trunk rib in dorsal view (SMNS 92067); **b**, trunk rib in anterior view (SMNS 92068); **c, d**, trunk ribs in ventral view (**c**, SMNS 92063; **d**, SMNS 91360); **e**, gastralium (SMNS 91360); **f**, lateral ends of two fused gastralia (SMNS 91363); **g**, cervical vertebra (SMNS 91360); **h**, anterior dorsal vertebra (SMNS 91356); **i**, mid-dorsal vertebra (SMNS 91360); **j**, right scapula (SMNS 92044); **k**, incomplete interclavicle (SMNS 91895); **l**, proximal portion of right scapula (SMNS 91895); **m**, right coracoid (SMNS 91360); **n**, left humerus (SMNS 91113); **o**, right ilium (SMNS 91895); **p**, left pubis (SMNS 91360); **q**, right femur (SMNS 91356); **r**, left tibia (SMNS 91360).

ribs curve laterally, with the posterior flange being more extensive than the anterior one. Large ribs bear pronounced sculpturing on the dorsal surface, comprising ridges that may bear tubercles in places (Fig. 3a). This sculpturing suggests an intradermal origin of these structures⁵. Thin-sections of trunk ribs (Extended Data Fig. 4) show that they are rather compact and closely resemble those of *Eunotosaurus* in their histological structure⁵. The whip-like tail of *Pappochelys* comprises over 23 vertebrae with low neural arches and long, cylindrical centra (Fig. 1a, b).

The trunk has large paired gastralia (Fig. 3e and Extended Data Fig. 3). Individual elements are thick, with ridged surfaces and tapered ends. Successive gastralia occasionally fused to each other, as suggested by several particularly robust elements with forked distal ends (Fig. 3f). In ventral view, the anterior gastralia extend anterolaterally, whereas the reverse obtains on the posterior gastralia. None of the available fossils preserves undisturbed pairs of gastralia.

The scapula (Fig. 3j, l) has a tall, slender dorsal process, which was probably aligned vertically, and a short ‘acromial’ process. Its glenoid facet faces posterolaterally. The plate-like coracoid (Fig. 3m) has an anterolateral glenoid facet. The interclavicle (Fig. 3k) has a rounded anterior process, posterolaterally extending lateral processes contacting the clavicles, and a long, tapering posterior process. The robust humerus (Fig. 3n) has expanded articular ends. Radius and ulna are slender, and the manus has slender digits with long, narrow unguals.

The pelvis closely resembles those of *Odontochelys*¹² and *Proganochelys*¹⁸. However, the ischium remains separate from the pubis. The ilium (Fig. 3o) has a long postacetabular process with a strongly striated lateral surface and a straight dorsal margin. The pubis (Fig. 3p) has an oval thyroid foramen and a distinct lateral process. There is no trace of a hypoischium.

The hindlimb is only slightly longer than the forelimb. The S-shaped femur (Fig. 3q) has a distinct internal trochanter and an offset head.

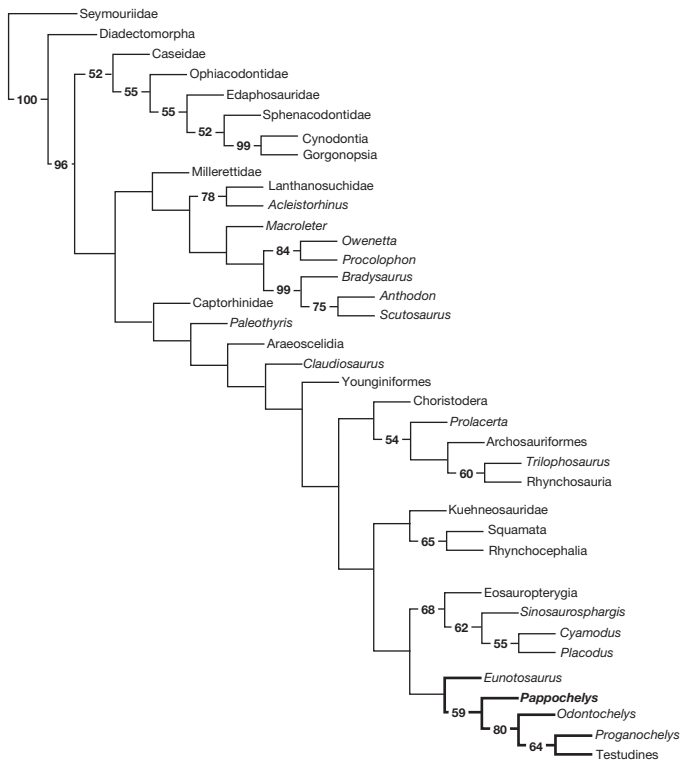


Figure 4 | Phylogenetic position of Pan-Testudines including *Pappochelys* among Amniota based on maximum parsimony analysis of the data matrix in ref. 5. Numbers at nodes indicate bootstrap percentages (only those >50) for each node. The tree has a length of 759 steps, a consistency index of 0.32, and a rescaled consistency index of 0.21.

The robust tibia (Fig. 3r) is much shorter than the femur. The pes is slightly larger than the manus.

Morphologically *Pappochelys* represents an intermediate stage between *Eunotosaurus*^{4,5,19} and *Odontochelys*¹². It shares the T-shaped cross-sectional outline of the broad trunk ribs with both taxa. Saurosphargid reptiles also have broad trunk ribs^{20,21}, but these differ from those of stem-turtles in being flatter (with the shaft not offset), straighter, single-headed, and uniform throughout the trunk region. By contrast, the thoracic ribs of *Pappochelys* and *Odontochelys* vary in shape with respect to their position, and some ribs have asymmetrical anterior and posterior flanges. Unlike *Eunotosaurus* and *Pappochelys*, *Odontochelys* has neurals and supports the hypothesis that the turtle carapace developed by outgrowth of intramembranous bone from the periosteum of the ribs and neural spines. *Odontochelys* also has a fully developed plastron whereas *Eunotosaurus* has paired gastralia⁴, as does *Pappochelys*. The gastralia, together with ventral elements of the shoulder girdle, formed the plastron in turtles^{3,13}. Although *Pappochelys* lacks a plastron, the typically thickened and sometimes two-ended gastralia indicate increased ossification in the ventral region and incipient fusion of successive elements in this taxon, supporting the hypothesis that the turtle plastron partly formed through their co-ossification^{3,13}. The lateral ends of the plastral elements in *Odontochelys* form spine-like projections¹² that resemble the distal ends of the gastralia in *Pappochelys* both in their alignment and in their striated surface texture.

The scapula and coracoid of *Pappochelys* closely resemble those of *Odontochelys* and the more derived *Proganochelys*. Compared with *Proganochelys*, the ‘acromial’ process of the scapula is short and forms a rounded anteromedial edge and the coracoid is not as expanded.

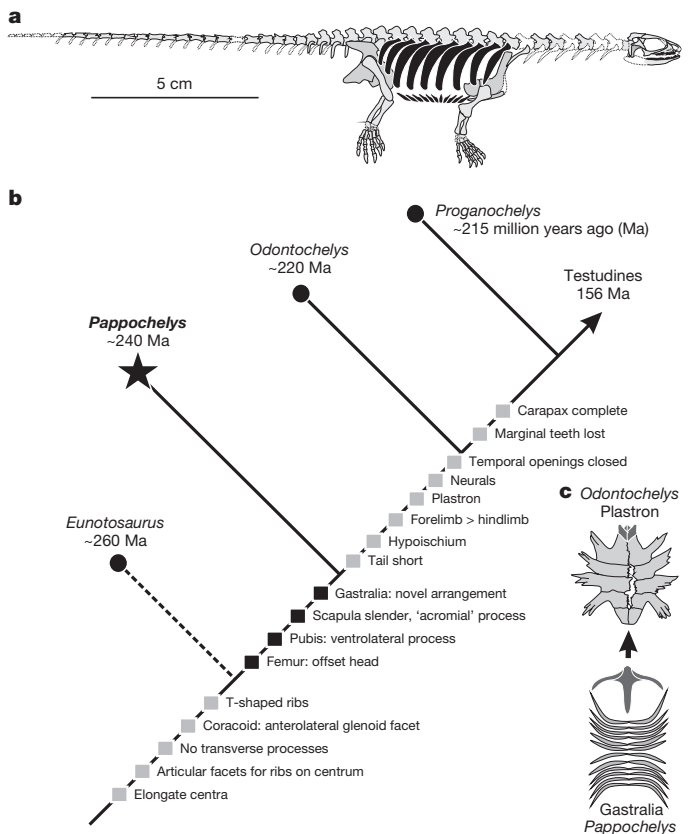


Figure 5 | Early evolution of the turtle body plan. a, Restoration of the skeleton of *Pappochelys* in lateral view (as yet unknown elements in white; preserved bones in grey; trunk ribs and gastralia highlighted in black); b, successive appearance of key features of the turtle body plan; c, plastron of *Odontochelys* and reconstructed ventral bones of the shoulder girdle and gastralia set in *Pappochelys* (elements of the shoulder girdle and their homologues are indicated in a darker shade of grey).

The pubis of *Pappochelys* has a distinct lateral process, as in *Odontochelys* and more derived turtles, where it contacts the plastron. The ilium closely resembles that of *Proganochelys* in outline.

The presence of two temporal openings on either side of the cranium in *Pappochelys* supports the hypothesis of diapsid affinities for turtles^{2,14,15}. The configuration of the squamosal, postorbital, and parietal closely resembles the condition in diapsid reptiles, whereas the small size of the upper temporal fenestra may suggest incipient reduction of that opening. A phylogenetic position of turtles within Diapsida has been consistently recovered by phylogenetic analyses based on molecular data (although most of the latter specifically place turtles with or close to archosaurs)^{7–10} but also by some morphologically based studies^{2,14,15}. Our phylogenetic analysis (Fig. 4 and Extended Data Figs 5 and 6; for detailed data see Supplementary Information) recovered Pan-Testudines as the sister-taxon to Sauropterygia, a clade of marine saurian reptiles, and this grouping as the sister-group to Lepidosauriformes as previously suggested in refs 2 and 14. Traditionally, palaeontologists interpreted turtles as primarily lacking temporal openings and accordingly assigned them a basal position among reptiles⁶. Similarly, the skull of *Eunotosaurus* was long considered 'anapsid' but, like *Pappochelys*, it has ventrally open lower temporal openings²². Furthermore, new research indicates that *Eunotosaurus* has upper temporal openings concealed by large supra-temporals²³.

Pappochelys is the most common reptile in the Vellberg lake deposit known so far, and is represented by various growth stages, which suggests that it either lived along the lakeshore or frequently entered the lake. Under a scenario that the turtle shell initially evolved in an aquatic setting², the plastron may have first developed as protection and 'bone ballast' for controlling buoyancy⁶. The thick gastralia and ribs in *Pappochelys* are consistent with aquatic or semi-aquatic habits. Although the oldest fully shelled turtles were probably terrestrial^{24,25}, *Odontochelys* apparently lived in deltaic or lagoonal settings along a coastline^{6,12}.

In summary, *Pappochelys* provides a new stage in the evolution of the turtle body plan (Fig. 5) and critical evidence for the diapsid relationships of turtles.

Online Content Methods, along with any additional Extended Data display items and Source Data, are available in the online version of the paper; references unique to these sections appear only in the online paper.

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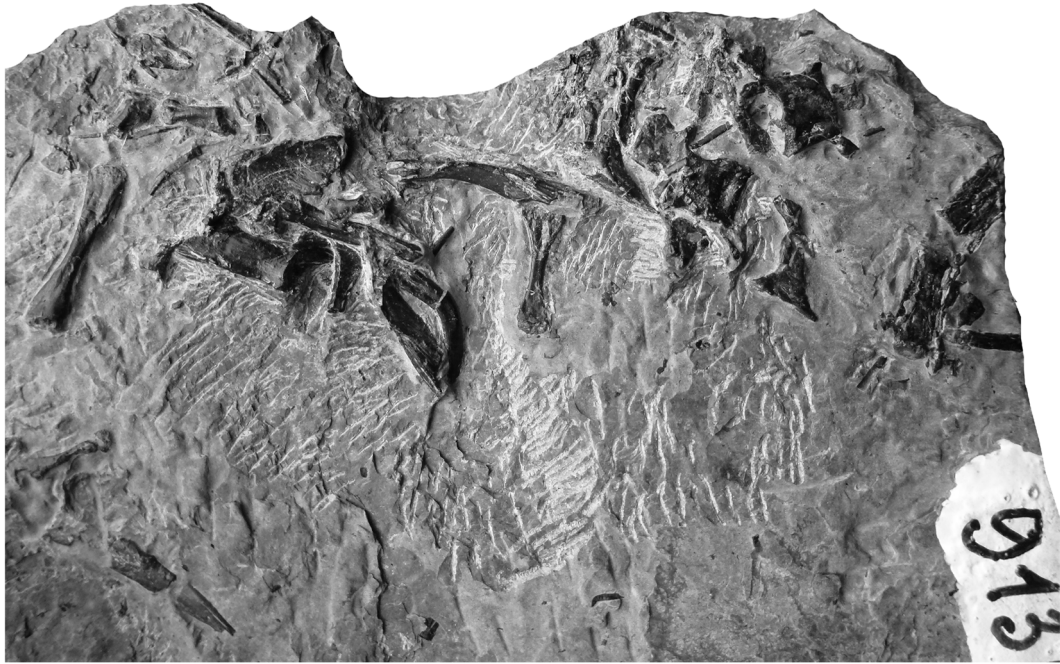
Supplementary Information is available in the online version of the paper.

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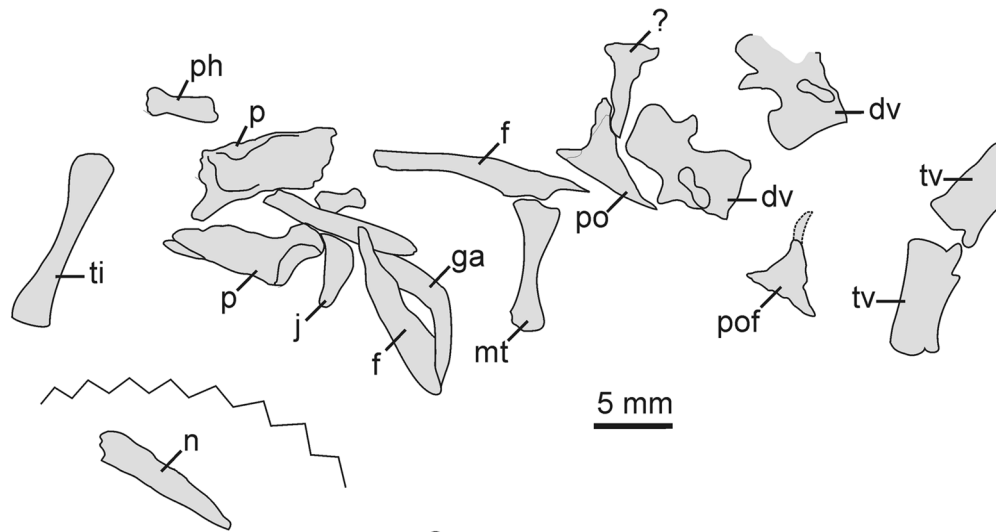
Author Contributions R.R.S. and H.-D.S. contributed equally to the research and the development of the manuscript; therefore their names are listed in alphabetical order.

Author Information *P. rosinae* is in the ZooBank database (<http://zoobank.org/>) with Life Science Identifier urn:lsid:zoobank.org:act:CDD54976-047F-43AA-80F4-9680DF78CD7B. Reprints and permissions information is available at www.nature.com/reprints. The authors declare no competing financial interests. Readers are welcome to comment on the online version of the paper. Correspondence and requests for materials should be addressed to R.R.S. (rainer.schoch@smns-bw.de) or H.-D.S. (suesh@si.edu).

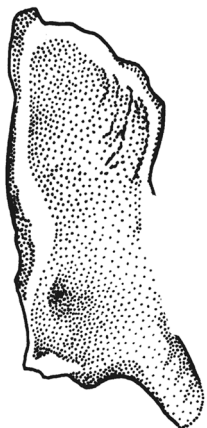
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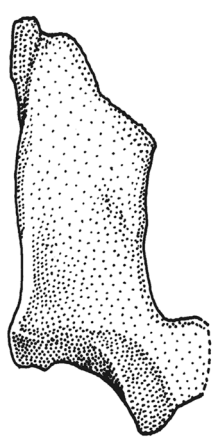
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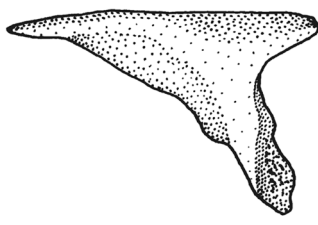
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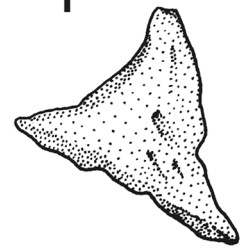
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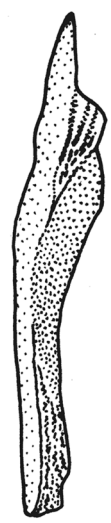
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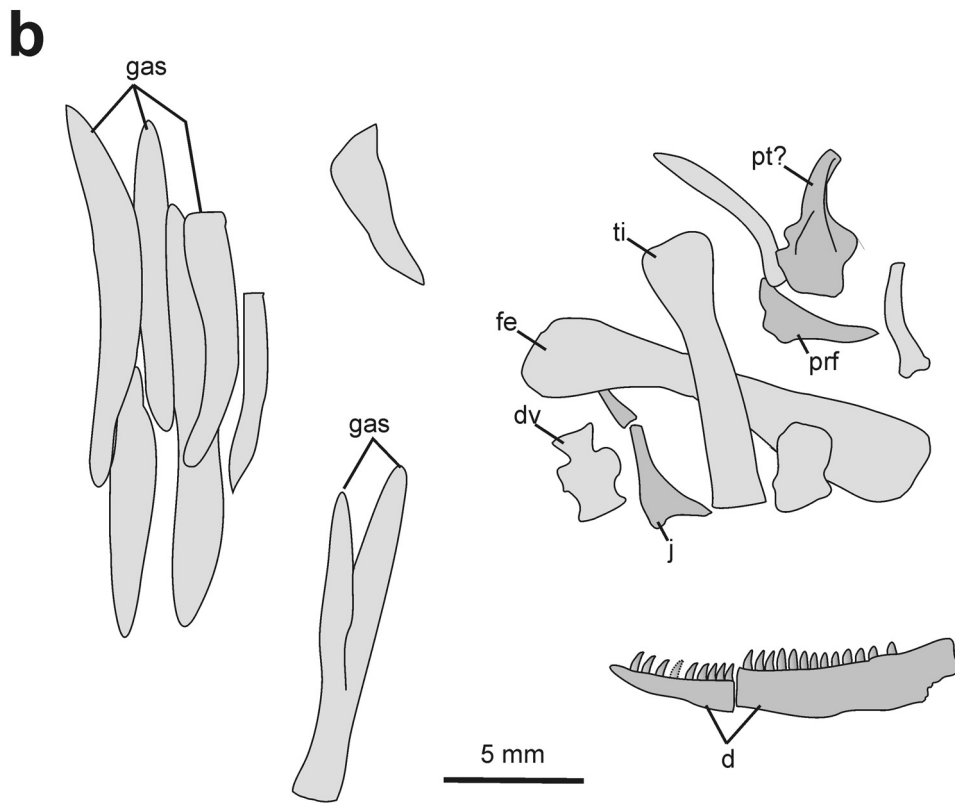
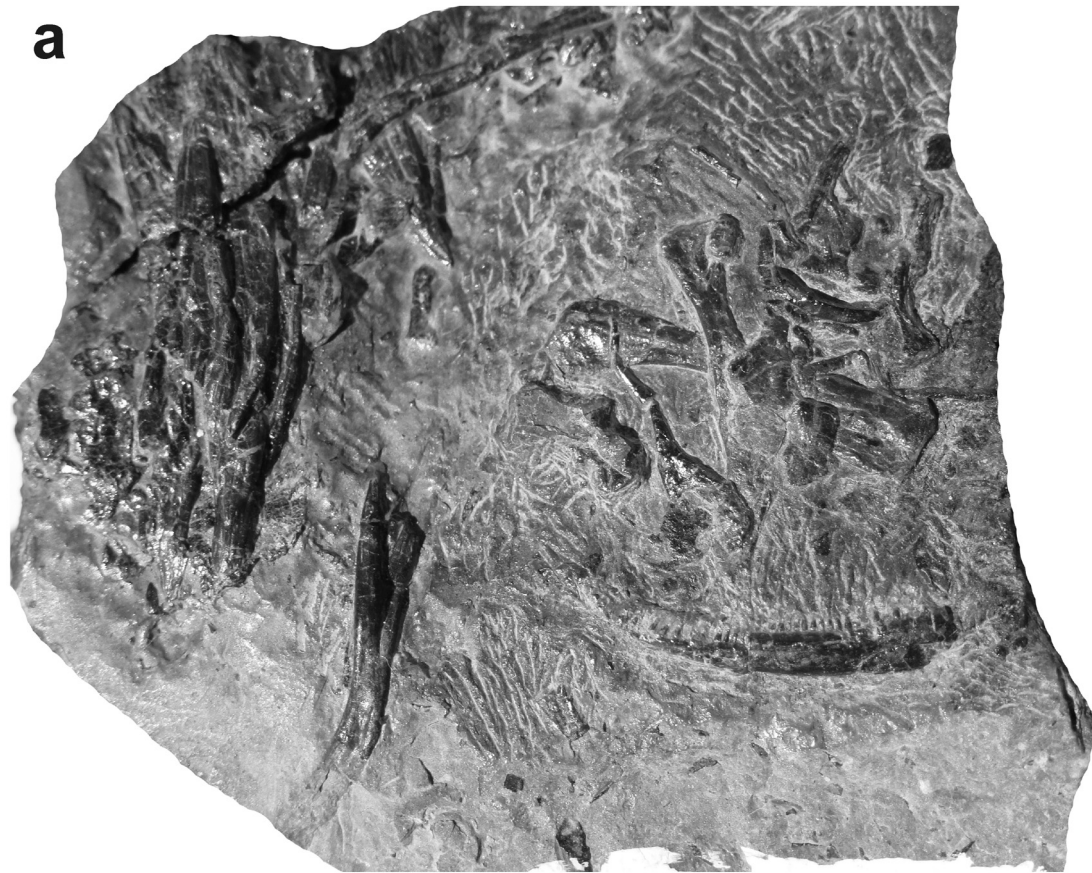


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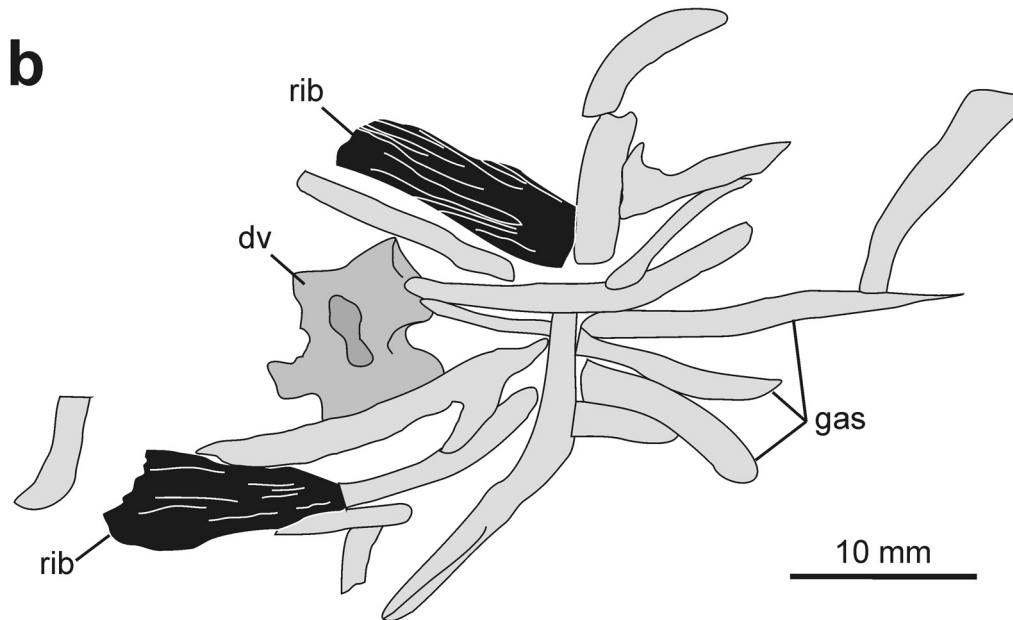
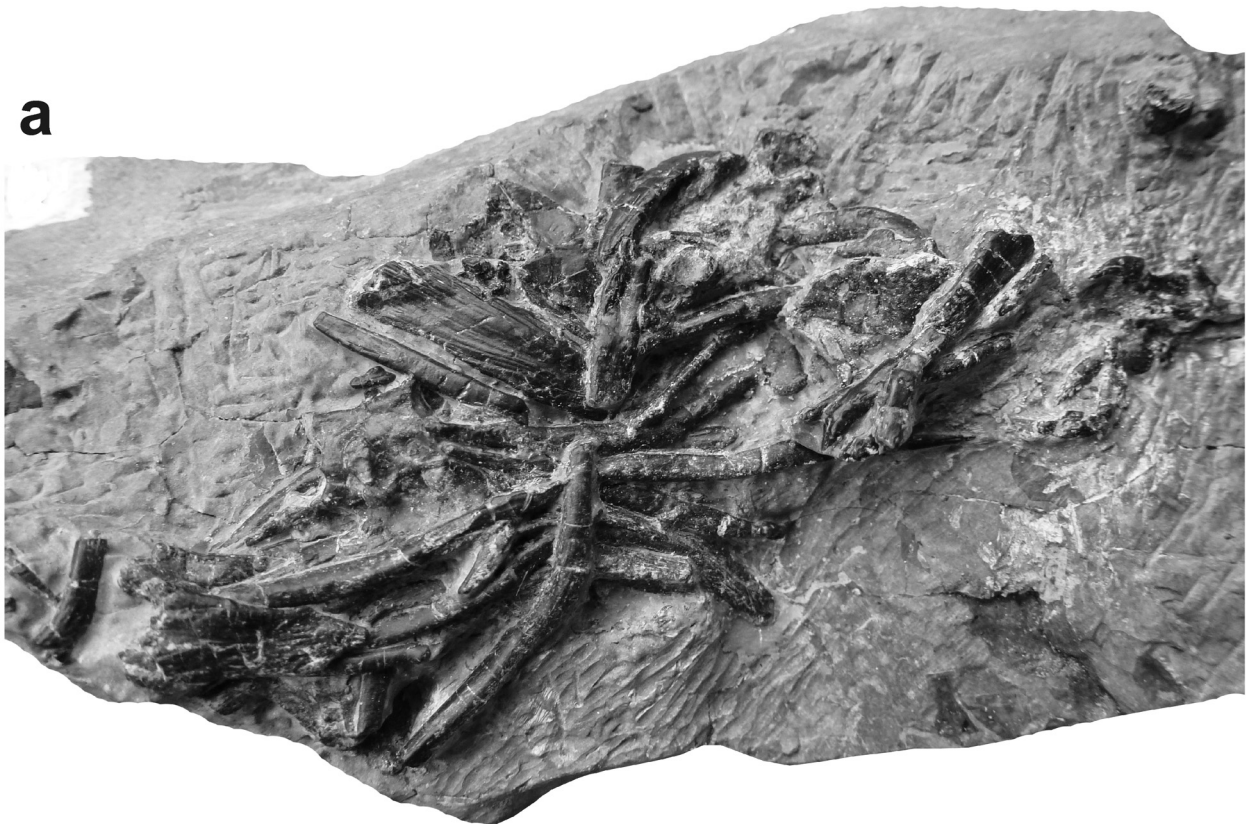
Extended Data Figure 1 | Cranial material of *P. rosinae*. **a, b**, Photograph and explanatory outline drawing of partial skull and postcranial skeleton of *P. rosinae* (SMNS 91356); **c**, left parietal in ventral view; **d**, right parietal in

dorsal view; **e**, left postorbital; **f**, left postfrontal; **g**, left frontal. Abbreviations: dv, dorsal vertebra; f, frontal; ga, gastralium; j, jugal; mt, metatarsal; n, nasal; p, parietal; ph, phalanx; po, postorbital; pof, postfrontal; ti, tibia; tv, tail vertebra.

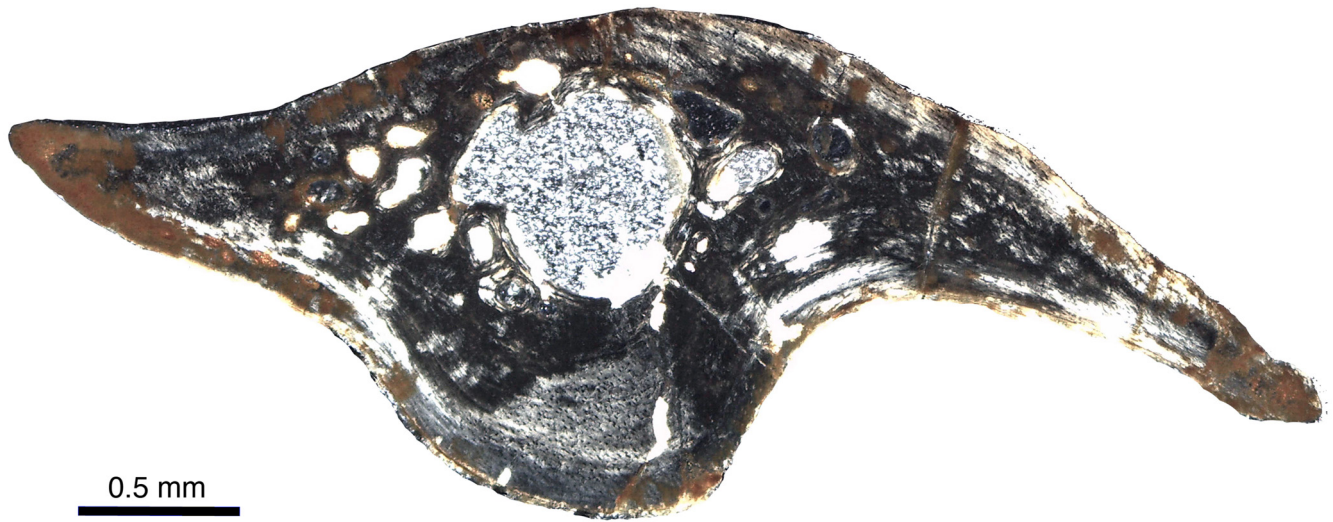


Extended Data Figure 2 | Skeletal remains of a very small individual of *P. rosinae*. **a, b**, Photograph (**a**) and explanatory outline drawing (**b**) of associated skeletal remains of a very small individual of *P. rosinae*

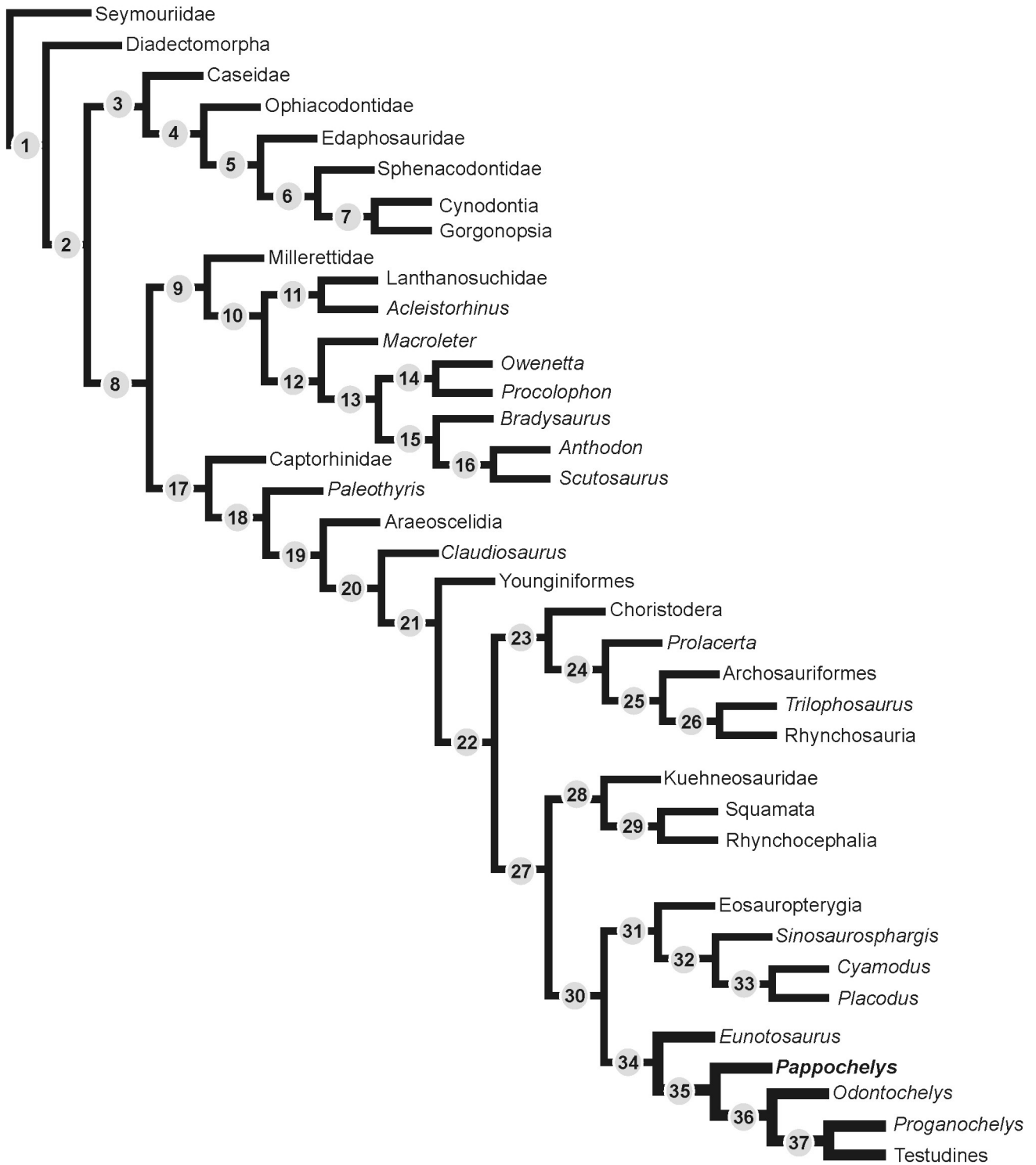
(SMNS 92066). Bones of the skull are shown in a darker shade of grey. Abbreviations: d, dentary; dv, dorsal vertebra; fe, femur; gas, gastralia; j, jugal; prf, prefrontal; pt?, possible pterygoid; ti, tibia.



Extended Data Figure 3 | Gastralia of *P. rosinae*. **a, b**, Photograph (**a**) and explanatory outline (**b**) of a set of gastralia elements and fragments of two trunk ribs (black) that are part of the incomplete, partly articulated postcranial skeleton SMNS 91360.



Extended Data Figure 4 | Transverse section through the broadened shaft of a left trunk rib.



Extended Data Figure 5 | Tree illustrating hypothesis of turtle relationships based on the Tree Analysis using New Technology (TNT) program. Individual nodes are numbered. For additional information refer to ‘Phylogenetic analysis’ section in Supplementary Information.



Extended Data Figure 6 | Tree illustrating hypothesis of turtle relationships based on Bayesian analysis. Numbers at individual nodes represent posterior probabilities. For additional information refer to 'Phylogenetic analysis' section in Supplementary Information.