Morphology of the earliest reconstructable tetrapod *Parmastega aelidae*

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The taxonomic diversity of Devonian tetrapods has increased dramatically in recent decades, but much of this diversity consists of tantalising fragments. The interpretative framework for the earliest stages of tetrapod evolution is still dominated by the near-complete *Ichthyostega* and *Acanthostega*, with supporting roles for the less complete but partly reconstructable *Ventastega* and *Tulerpeton*. All four are of late Famennian age, 10 million years younger than the earliest tetrapod fragments and nearly 30 million years younger than the oldest footprints. Here we describe a tetrapod from the earliest Famennian of Russia, *Parmastega aelidae* gen. et sp. nov., represented by three-dimensional material that allows reconstruction of almost the entire skull and dermal shoulder girdle. Its raised orbits, lateral line canals and weakly ossified postcranial skeleton suggest a largely aquatic, surface-cruising animal. In Bayesian and parsimony-based phylogenetic analyses the majority of trees place *Parmastega* as sister group to all other tetrapods.

The rate of discovery of Devonian tetrapods accelerated greatly during the late 20th and early 21st centuries. The description of *Ichthyostega* in 1932 was followed by *Acanthostega* in 1952, *Metaxygnathus* in 1977 and *Tulerpeton* in 1984; all other genera (*Hynerpeton*, *Ventastega*, *Elginerpeton*, *Obruchevichthys*, *Densignathus*,

Sinostega, *Jakubsonia*, *Ymeria*, *Webererpeton*, *Tutusius*, *Umzantsia*) have been described or identified as tetrapods since 1994[1-13]. Un-named Devonian tetrapod material has been described from Belgium[14,15] and the United States[16,17]. However, by far the most complete and scientifically influential Devonian tetrapod material is still that of *Ichthyostega* and *Acanthostega* from East Greenland[1,2,11,18-31], followed by *Ventastega* from Latvia[6,31,32] and *Tulerpeton* from Russia[4,33,34]. All other Devonian tetrapods are far less complete.

Ichthyostega, *Acanthostega*, *Ventastega* and *Tulerpeton* all date to the late Famennian, the last stage of the Devonian, when tetrapods had already been in existence for about 30 million years, judging by the trackway evidence[35,36], and had colonised both equatorial and polar environments[13]. The four genera are quite disparate, hinting at long evolutionary histories; the differences between *Ichthyostega* and *Acanthostega* are particularly striking, including braincase morphologies so different it seems improbable that one could be derived from the other[20].

The tetrapod material described here expands our understanding of the earliest stages of tetrapod evolution. It is securely dated to the earliest Famennian but is comparable to *Ventastega* in degree of completeness. Its source, the Sosnogorsk Formation of the southern part of Timan Ridge (Komi Republic, Russia)[37], straddles the Frasnian-Famennian boundary with vertebrate remains occurring in the Famennian part (Extended Data Fig. 1). It is thus only marginally younger than the fragmentary genera *Elginerpeton*, *Obruchevichthys* and *Webererpeton*, which are the oldest tetrapod body fossils[7,12]. The quality of the material, which consists of numerous isolated bones and some articulated skull regions, is excellent. Multiple examples of the same bone all show the same distinctive features (Extended Data Fig. 2), indicating that only a single tetrapod species is present, meaning that all the data can be pooled into one interpretation (Extended Data Fig. 3). The Sosnogorsk fossils thus give us the first detailed picture of an animal from the earliest part of the known tetrapod body fossil record.

Systematic palaeontology

Tetrapoda Jaekel, 1909

Parmastega aelidae gen. et sp. nov.

Remark. The term Tetrapoda is used here in its traditional, apomorphy-based sense of limbed vertebrates.

Etymology. The generic name derives from *parma*, a word in the Komi language describing the landscape of hills covered by coniferous forest, typical for South Timan, and Greek *stégi* meaning roof, understood here as skull roof. The specific name honours Associate Professor of Syktyvkar State University Dr. Aelida I. Popova (1929-2011), who first aroused PB's interest in natural sciences when he was a preschool boy.

Holotype. IG KSC 705/1, an articulated snout region (Fig. 1a-c).

Referred material. 106 individual bones or bone assemblies (Supplementary Table 1).

Locality and horizon. Sosnovskiy Geological Monument, right bank of the Izhma River opposite Sosnogorsk, Komi Republic, Russia; Sosnogorsk Formation, lowermost Famennian (Extended Data Fig. 1).

Diagnosis. A stem tetrapod diagnosed by the following unique combination of characters: dermal ornament of preorbital region developed into transverse parallel 'wave crests' with a spacing of a few millimetres; ornament present on dorsal blade of cleithrum and on anocleithrum; orbit strongly raised above skull roof, framed by an anterodorsal crest and a vertical anterior ridge carried on prefrontal; internasal fontanelle absent; median rostral paired; lacrimal excluded from orbit by prefrontal-jugal contact; intertemporal absent; pterygoids separated in midline by parasphenoid; interpterygoid vacuities absent; pterygoid dentition restricted to two lines of denticles, running anteriorly and anterolaterally from growth centre; ectopterygoid making large contribution to lateral wall of subtemporal fossa; middle part of otic capsule narrow, occupying approximately half of skull table width; posttemporal fossa wide, triangular; fang pair and row of marginal teeth on adsymphysial plate; middle part of prearticular with large muscle scar; interclavicle rounded with short posterior process.

Description

The material of *Parmastega* comprises the entire dermal skull apart from the preopercular and the posterior part of the quadratojugal, the entire ethmoid and dorsal part of the otoccipital braincase, the entire lower jaw, the dermal pectoral girdle (comprising, from dorsal to ventral, anocleithrum, cleithrum, clavicle and interclavicle) and the partly ossified scapulocoracoid (Figs 1-2). A total of 106

numbered specimens (Supplementary Table 1, 2), representing a minimum of 11 individuals, show a wide size range (Extended Data Figs 2, 4) but were all found within a small area of the site (Extended Data Fig. 1). Most specimens are isolated bones, but an articulated ethmoid (Fig. 1a-c) and several skull tables (Fig. 1d-g) are also present. The bones are three-dimensionally preserved in limestone, with little or no distortion, and have been freed from the matrix using dilute acetic acid (see Methods). Bones from the same individual can sometimes be identified by matching size and sutural fit (Extended Data Fig. 3). This allows us to reconstruct the skull, lower jaw and pectoral girdle with a high degree of confidence, excepting only the posterior part of the suspensorium (Fig. 3). Assuming proportions similar to *Acanthostega*[19], the maximum length of *Parmastega* was approximately 130 cm.

The skull shape is broadly similar to that of *Ventastega* and *Acanthostega*, although the orbits of *Parmastega* are raised higher above the skull table and the snout has a distinctly concave profile (Extended Data Fig. 4). The strongly raised orbits and relatively narrow snout are reminiscent of the elpistostegids *Elpistostege* and *Tiktaalik*[38,39]. However, the orbits are proportionately larger than in elpistostegids (Extended Data Fig. 5).

The dermal bone pattern of the skull roof and cheeks is, with a single exception, characteristic of Devonian tetrapods. There is no postrostral mosaic or internasal fontanelle. The median rostral is paired, as in *Acanthostega*, *Ventastega* and *Elpistostege*, but unlike *Ichthyostega* and *Elginerpeton* where it is single[7,18,26,32,38]. A tectal bone forms the dorsal margin of the naris, which lies very close to the jaw margin and faces ventrally; the ventral margin of the naris is formed by the maxilla as there is no lateral rostral. The lacrimal is excluded from the orbit by a long suture between the jugal and prefrontal. The latter is elongate and carries two bony crests, one forming the anterior part of the 'eyebrow' and the other an oblique ridge in front of the orbit, both more strongly developed in large specimens (Fig. 1m, 3a-c). The frontals are elongate with a distinct transverse ’step’ on the posterior part of the dorsal surface marking the transition from snout to skull table. Intertemporals are absent. The lateral margins of the supratemporal and tabular form a raised spiracular margin; the tabular horn has distinct dorsal and ventral components. A small part of the dorsal surface of the braincase is exposed posterior to the tabulars. The dermal ornament of the preorbital region includes areas of irregular transverse ripples (Fig. 1h, m; Extended Data Fig. 2), somewhat similar to the ornament of *Umzantsia*[13] but much

coarser; elsewhere it grades into conventional tetrapod 'starburst' ornament. Partly enclosed sensory line canals are well developed on the premaxilla, cheek bones and anterior part of the nasals, but are absent from the skull table (Fig. 1d).

Between the anterior suture for the jugal and the posterior suture for the preopercular, the ventral margin of the squamosal presents two distinct sutural margins that appear to be contacts for two bones (Fig. 1l). The posterior of these must be for the quadratojugal; given that the jugal lacks a posterior process, we tentatively infer that the anterior segment of the ventral margin contacts the maxilla (Fig. 3a). A squamosal-maxillary contact is characteristic for 'fish' members of the tetrapod stem group such as *Eusthenopteron*[40]; its presence in *Parmastega* is unique for tetrapods.

The palatal morphology of *Parmastega* is intermediate between those of elpistostegids and Devonian tetrapods. In the elpistostegids *Panderichtys* and *Tiktaalik*, the pterygoids are separated in the midline by a long denticulated parasphenoid[41,42]. The vomer has a transverse posterior margin, which in *Panderichthys* ends mesially in a short posterior process extending along the lateral margin of the parasphenoid[41]. This condition is broadly similar to that in *Eusthenopteron*[40]. By contrast, in *Ichthyostega*, *Acanthostega* and *Ventastega* the pterygoids meet in the midline, separating the parasphenoid from the vomers, and the most posterior point of the vomer is its posterolateral corner[6,18,23]. In *Parmastega* the parasphenoid separates the pterygoids, but is not denticulated anteriorly, and the vomeral morphology is intermediate (Fig. 1a, 3d). The pterygoid carries a longitudinal row or narrow band of denticles, and a shorter oblique band extending anterolaterally. Uniquely, the ectopterygoid extends posteriorly past its contact with the pterygoid to contribute to the lateral margin of the subtemporal fossa (Fig. 3d). This relationship is demonstrated by a sutural fit of three bones from one individual (Fig. 1p).

Two parts of the braincase are preserved: the ethmoid and part of the sphenoid in IG KSC 705/1 and the dorsal part of the otoccipital in IG KSC 705/17 (Fig. 1a,f-g). An ossified ethmoid is only shared with *Ichthyostega* among known Devonian tetrapods[18]. The otoccipital has a strongly developed prootic buttress, a narrow cranial cavity with small inner ears, and a posttemporal fossa bounded laterally by a crista parotica that extends onto the tabular horn. Its outline in ventral view resembles *Tiktaalik*[42] but is proportionately broader. Previously known Devonian tetrapod otoccipitals show two radically different morphologies. In *Acanthostega* and *Ventastega* the narrow posttemporal fossa is open laterally and the braincase occupies

almost the whole ventral surface of the skull table, whereas in *Ichthyostega* the narrow braincase is flanked by large cavities under the skull table that probably housed spiracular diverticula[20,24,25,32]. The otoccipital of *Parmastega* provides a plausible ancestral ground plan for both these morphologies (Extended Data Fig. 6).

The lower jaw is of typical tetrapod construction[30] but unusually slender and delicate (Fig. 2a-h, 3e). The only ossified parts of the Meckelian element are the articular and the symphysis. The prearticular carries very few denticles but bears a large ventral muscle scar on its middle part. Remarkably, the contact between the prearticular and the mesial lamina of the splenial is not a tight suture as in other known Devonian tetrapods[30] but a loose overlap that must have contained a ligamentous component and allowed a degree of flexibility. Fang pairs, positioned mesial to the tooth row, are present on the adsymphysial plate, dentary, and anterior and middle coronoids. Postsplenial and surangular pit lines are present. The dentary is splint-like and loosely attached.

The pectoral girdle is U-shaped in anterior view with the dorsal blades of the cleithra approximately parallel (Fig. 2i-o, 3a,c). The dorsal orientation of the anocleithrum, determined from well-preserved contact surfaces, makes the girdle surprisingly tall. Cleithrum and anocleithrum both carry dermal ornament, a characteristic otherwise absent in tetrapods except *Umzantsia*[13]. The clavicle is narrow and the interclavicle has a rounded corpus with a short posterior process (Fig. 2n,o); both bones somewhat resemble the corresponding elements in *Ichthyostega*[18], whereas *Acanthostega* and *Ventastega* have broader clavicles and kite-shaped interclavicles[29,32]. The scapulocoracoid is ossified in two parts: a dorsal scapular part coossified with the cleithrum (Fig. 3i), and a posterior coracoid ossification that carries the glenoid (Fig. 3p). As in *Ichthyostega*, *Elginerpeton* and *Hynerpeton*, the subscapular fossa is deep with a narrow apex; in *Acanthostega* and *Ventastega*, by constrast, the fossa is shallow and broad[5,18,29,32,43]. Limbs, pelvis, vertebrae and ribs are not preserved.

Phylogenetic analysis

The phylogenetic position of *Parmastega* was evaluated with maximum parsimony and Bayesian inference analyses applied to a data matrix of 26 taxa and 113 characters. A full account of the tree search settings and results is given in **Methods**;

character list and data matrix are provided in Supplementary Information files 2-4. Trees are shown in Extended Data Fig. 7.

The resolution of the strict consensus unweighted parsimony analysis was poor: all Devonian tetrapods including *Parmastega* formed a polytomy together with 'whatcheeriid-grade' Carboniferous taxa (Extended Data Fig. 7a). However, in 70% of the trees, *Parmastega* was the sister group to all other tetrapods. A range of different approaches (character reweighting by Rescaled Consistency Index and K values; calculation of agreement subtrees from consensus trees) was used to investigate the phylogenetic signal in the data set (Extended Data Fig. 7b-c,e-h). This revealed consistent patterns. If the position of *Parmastega* was resolved, it was always placed as the sister group to all other tetrapods; if *Ventastega* was resolved, it was placed immediately crownward to *Parmastega*. *Ichthyostega* was resolved crownward to *Acanthostega* in the Adams consensus of unweighted trees, but in the reweighted analyses *Acanthostega* was crownward to *Ichthyostega*. The Bayesian tree (Extended Data Fig. 7d) also recovered these positions for *Parmastega* and *Ventastega*, but failed to resolve *Ichthyostega* and *Acanthostega*.

Discussion

In essence, *Parmastega* is morphologically intermediate between the elpistostegids *Tiktaalik*, *Elpistostege* and *Panderichthys* on the one hand, and previously known Devonian tetrapods on the other. However, the mosaic of primitive and derived characters is not evenly distributed across the anatomy. The morphology of the lower jaw and the pectoral girdle is entirely tetrapod-like, as are the external dermal bone pattern of the snout region, the absence of gular plates, and the relative size of the orbits, whereas elpistostegid-like characteristics persist in the construction of the palate and the dermal ornamentation of the cleithrum and anocleithrum. This pattern hints at a sequence of evolutionary steps. Although no appendage bones are known, the morphology of the pectoral girdle strongly suggests that *Parmastega* possessed limbs rather than paired fins. Particularly significant is the scapulocoracoid, which forms the proximal attachment for many forelimb muscles and undergoes substantial shape change from elpistostegids[44,45] to tetrapods[5,18,29,32,34]. The scapulocoracoid of *Parmastega* conforms fully to the tetrapod pattern. The shape and construction of the lower jaw, and the absence of gular plates, suggest that gill ventilation and prey capture worked in the same way as in more crownward Devonian tetrapods. The

reconfiguration of the palate and the loss of dermal ornament on the shoulder girdle evidently lagged behind these transformations.

Until now, one of the most puzzling aspects of Devonian tetrapod anatomy has been the specialised ear region of *Ichthyostega*, which differs so much from those of other early tetrapods that it has been challenging to establish detailed homologies[18,20]. *Parmastega* partly resolves this problem by presenting a braincase morphology that is intermediate between *Ichthyostega* on the one hand and *Acanthostega* and *Ventastega* on the other, providing a plausible hypothetical ancestor for both patterns (Extended Data Fig. 6a). However, these transformations cannot be mapped parsimoniously onto the phylogeny, indicating the presence of non-trivial homoplasy either in the braincases or in other parts of the skeleton (Extended Data Fig. 6b).

The three-dimensional preservation and apparent absence of post-mortem transport makes the *Parmastega* fossils palaeobiologically informative. The environment of preservation, which was almost certainly also the living environment of *Parmastega*, was a coastal lagoon with brackish water and a rich fish fauna including the placoderm *Bothriolepis* and various sarcopterygians[46]. The concentration of the tetrapod remains to a small area of the site (Extended Data Fig. 1) suggests that *Parmastega* may have been a schooling animal. The vertebrate-bearing bed, Bed 40 (the "fish dolomite"), is composed of two consecutive tempestites; possibly a school of *Parmastega* was killed by the first storm event and their skeletons partly disarticulated by the second. Schooling behavior is also implied by the mass occurrence of *Acanthostega* on Stensiö Bjerg, East Greenland[47].

Raised orbits and a lack of lateral line canals on the skull table in *Parmastega* (Fig. 3a) suggests a surface-skimming position in the water, with emergent eyes, similar to crocodilians (Extended Data Fig. 8)[47]. The increase in orbit size across the fish-tetrapod transition has been linked to a shift from aquatic to aerial vision[48]; the relative orbit size of *Parmastega* falls well within the tetrapod range (Extended Data Fig. 5) and its eyes were thus probably adapted for use in air. Although all known Devonian tetrapods have dorsally positioned eyes, *Parmastega* shows the most extreme version of this condition (Extended Data Fig. 4). The nostrils of *Parmastega* face ventrally, indicating that the nose was not used for air-breathing while resting at the surface (Extended Data Fig. 8). We suggest that the dorsally placed spiracles took on this function, as previously argued for *Panderichthys*[49] and more crownward Devonian tetrapods[20, 50]. The lower jaw does not match the upper jaw in curvature,

either in lateral or ventral view (Extended Data Fig. 9a,d). This pattern is also seen in *Ventastega* (Extended Data Fig. 9b), *Acanthostega*[31] and *Ichthyostega*[18].

Surprisingly, the *Parmastega* material contains no vertebrae, ribs, pelvic girdles or limb bones. The lack of evidence for post-mortem transport, the partially ossified nature of the scapulocoracoid even in the largest individuals, and the preservation of the delicate isolated coracoid ossifications (Fig. 2i-l,p), suggests that this absence is not a taphonomic artefact but reflects a very lightly ossified or even cartilaginous axial and appendicular skeleton. *Ventastega* may also have had a lightly ossified postcranial skeleton[32]. *Acanthostega* and *Ichthyostega* became fully ossified as adults[2,18,19,21,27,29], but *Acanthostega* appears to have had a long juvenile stage with unossified endoskeleton[47]. Functionally, the poor ossification of *Parmastega* suggests little or no capacity for terrestrial locomotion. However, it contrasts strangely with the cranial morphology, which suggests that the eyes were habitually held above the surface of the water and thus implies some kind of engagement with the terrestrial environment. Even more puzzling is the fact that this poorly ossified postcranial skeleton is apomorphic: elpistostegids are well ossified, as are the majority of tetrapodomorph fishes[39,40].

Parmastega gives us the earliest detailed glimpse of a tetrapod: an aquatic, surface-skimming predator, just over a metre in length, living in a lagoon on a tropical coastal plain. It is phylogenetically least crownward of the non-fragmentary tetrapods, but is not necessarily representative of primitive conditions for the group. The slightly earlier *Elginerpeton*, which was also probably aquatic and even larger than *Parmastega* (Extended Data Fig. 3), had well ossified girdles and limb bones as well as a distinctive head shape with a narrow snout[7,30,43]. Moreover, the trackway record shows that tetrapods originated at least 20 million years before *Parmastega*[35,36], and the very existence of the trackways – which implies weight-bearing limbs, even if the prints were made in water – points to these forms having well ossified postcranial skeletons. Together with the evidence for significant morphological homoplasy among Devonian tetrapods, this hints at a tangled and still elusive early history for limbed vertebrates.

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Author contributions

PB initiated and directed the excavation program at Sosnogorsk that produced the material for the study. EL and PEA participated in excavations. PB carried out all preparation, consolidation and photography of specimens. PEA made the reconstructions of the skull, lower jaw and shoulder girdle. MR performed the phylogenetic analyses. PEA made Figures 1-3 and Extended Data Figures 2 and 3-9; PB made Extended Data Figures 1 and 3, as well as Tables 1 and 2. All authors participated in the interpretation of the material and the writing of the paper.

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Figure 1 | *Parmastega aelidae:* skull roof, cheek and palate. a-c, IG KSC 705/1, holotype of *Parmastega aelidae*; an articulated ethmosphenoid with associated prefrontal in ventral (**a**), dorsal (**b**) and lateral (**c**) views. The 10 mm scale bar of this specimen applies to the whole figure except **f-g**. **d-e**, 705/2, skull table in dorsal (**d**) and ventral (**e**) views. **f-g**, 705/17, skull table and partial braincase in ventral view. **g** is a false colour image identifying the components of the specimen. **h**, 705/18, right frontal, dorsal view. **i**, 705/19, left postorbital, external view. **j**, 705/20, left jugal, external view. **k**, 705/25, left lacrimal, lateral (top) and dorsal (bottom) views. **l**, 705/26, right squamosal, external view. **m**, 705/5, right prefrontal, external view. **n**, 705/4, left postfrontal, lateral (top) and dorsal (bottom) views. **o**, 705/28, right maxilla in internal (top), ventral (middle) and external (bottom) views. **p**, 705/29 (left dermopalatine), 705/30 (ectopterygoid) and 705/31 (pterygoid) in ventral view. **q**, 705/32, left dermopalatine in lateral (top) and ventral (bottom) views. cho, choana; fr, frontal; m.ro, median rostrals; na, nasal; pa, parietal; pi, pineal foramen; pmx, premaxilla; pp, postparietal; prf, prefrontal; psp, parasphenoid; socc, supraoccipital; su, supratemporal; ta, tabular; te, tectal; vo, vomer.

Figure 2 | *Parmastega aelidae:* lower jaw and pectoral girdle. a, IG KSC 705/21, right adsymphysial plate in mesial (bottom) and dorsal (top) views. **b**, 705/22, right anterior coronoid in mesial (bottom) and dorsal (top) views. **c**, 705/33, right middle coronoid in mesial (bottom) and dorsal (top) views. **d**, 705/36, left posterior coronoid in mesial (bottom) and dorsal (top) views. **e**, 705/37, articulated left splenial and adsymphysial plate in ventrolateral (top) and mesial (bottom) views. **f**, 705/34, articulated left postsplenial, angular and surangular in lateral view. **g**, 705/76, left

prearticular in mesial view. **h**, 705/67, right dentary in lateral (top), dorsal (middle) and mesial (bottom) views. **i-k**, 705/15, left cleithrum and partial scapulocoracoid in mesial (**i**), anterior (**j**) and lateral (**k**) views. **l**, 705/95 (right cleithrum) and 705/98 (anocleithrum) in lateral view. **m**, 705/98, right anocleithrum in lateral view. **n-o**, 705/92 (right clavicle) and 705/89 (interclavicle) in anterior (**n**) and ventral (**o**) views. **p**, 705/102, left coracoid in lateral view. **e-p** are shown to the same scale.

Figure 3 | *Parmastega aelidae:* reconstructions. a, skull, lower jaw and pectoral girdle of *Parmastega* in right lateral view. **b**, skull in dorsal view. **c**, skull and pectoral girdle in anterior view. **d**, skull in ventral view. **e**, right lower jaw ramus in mesial view. adsym, adsymphysial plate; an, anocleithrum; ang, angular; ant.cor, anterior coronoid; art, articular; cho, choana; cla, clavicle; clei, cleithrum; cor, coracoid; de, dentary; dpal, dermopalatine; ect, ectopterygoid; fr, frontal; gle, glenoid; ju, jugal; la, lacrimal; mid.cor, middle coronoid; m.ro, median rostrals; mx, maxilla; na, nasal; no, nostril; orb, orbit; ot.br, otoccipital braincase; pa, parietal; pi, pineal foramen; pmx, premaxilla; po, postorbital; pof, postfrontal; pospl, postsplenial; post.cor, posterior coronoid; pp, postparietal; prf, prefrontal; psp, parasphenoid; pter, pterygoid; qj, quadratojugal; scap, scapula; socc, supraoccipital; spl, splenial; sq, squamosal; su, supratemporal; suf, subtemporal fossa; sur, surangular; ta, tabular; te, tectal; vo, vomer. Vertical hatching indicates missing element with unknown outline, horizontal hatching damaged object with known outline. Scale of reconstruction determined by largest individual. **a-d** are shown to the same scale.

Methods

Preparation and illustration of specimens

The specimens were collected from the Sosnovskiy Geological Monument, right bank of the river Izhma opposite Sosnogorsk Town, Komi Republic, Russia, during a series of field seasons from 2002 to 2012. The bulk of the material was collected during the large-scale excavation in 2009-2012, when approximately 50 m^2 of the bone-bearing "fish dolomite" bed was dug out and then broken into small blocks using hammers, chisels, angle grinder, drill and portable jackhammer. Blocks containing parts of the same bone fragments glued together. The bones were freed from the limestone matrix using dilute (7-10 %) acetic acid alternating with drying and covering by consolidants PVB (before 2010) and Paraloid® B-72 (after 2010). The reconstructions of the skull and lower jaw were assembled by hand on the basis of photographs of individual bones, taken at appropriate angles. The pectoral girdle reconstruction was produced by sticking together the right anocleithrum, cleithrum, clavicle and interclavicle of one individual, making a three-dimensional virtual model of the assembly using photogrammetry (Agisoft PhotoScan), and importing this model into 3-matic (Materialise) where it was duplicated, mirrored and assembled into a complete girdle. The drawings of the girdle in Fig. 4 were traced directly from lateral and anterior projections of the model.

Phylogenetic analysis

The phylogenetic position of *Parmastega* was evaluated with maximum parsimony and Bayesian inference analyses applied to a data matrix of 26 taxa and 113 characters (Supplementary Files 1-3), based on a recent matrix published by Chen et

568 al.[51] with the addition of four new characters (nos. 7, 27, 28, 29). Prior to all analyses,
569 we explored the occurrence of possible "taxonomic equivalents"[52] by subjecting the
570 matrix to safe taxonomic reduction using the *Claddis* package[53] in the R environment
571 for statistical computing and graphics (https://cran.r-project.org). No taxon was
572 identified as being suitable for safe deletion.

573 For all parsimony analyses, we used PAUP* version 4.0a (build 164)[54] with
574 the following search settings. The "collapse branch" option was enforced for branches
575 possibly attaining a minimum length of zero. Tree searches employed a heuristic
576 option with tree bisection-reconnection branch swapping algorithm, saving no more
577 than a single tree of length greater than/equal to 1 step in each replicate, and using a
578 maximum of 5000 random step-wise taxon addition replicates while holding a single
579 tree in memory at each step. Following this initial round of tree searches, an
580 additional branch-swapping round was conducted on all trees saved in memory, this
581 time with the option of saving multiple trees in effect. This second round of tree
582 searches was repeated 10 times. No shorter or additional trees were found at the end
583 of this second round in any of the parsimony analyses. Three analyses were carried
584 out under maximum parsimony, each with the settings specified above.

585 In the first analysis, all characters were treated as unordered and of equal unit
586 weight. We obtained 23 shortest trees at 278 steps, with an ensemble consistency
587 index (C.I.) of 0.5 (0.4908 excluding 5 parsimony-uninformative characters), an
588 ensemble retention index (R.I.) of 0.6911, and an ensemble rescaled consistency
589 index (R.I.) of 0.3456. A permutation-tail probability test[55] using 1000 replicates
590 showed that the length of the shortest trees differed significantly from random ($p \sim$
591 0.001). The strict consensus (Fig. 5a) was poorly resolved. The Adams consensus
592 (Fig. 5b) had greater resolution, placing *Parmastega* and *Elginerpeton* as the joint

(unresolved) sister groups to all other tetrapods. The agreement subtree (a pruned topology including only those taxa for which all most parsimonious trees agree upon mutual relationships) included 18 out of the 26 original taxa (Extended Data Fig. 7a; deleted: *Acanthostega*; *Dendrerpeton*; *Densignathus*; *Elginerpeton*; *Greererpeton*; *Metaxygnathus*; *Ossinodus*; *Tantallognathus*). Node support value was evaluated via bootstrapping[56] and jackknifing[57] in PAUP*, in each case using 50% character resampling, and 50,000 random resampling replicates with the fast step-wise addition. In both cases, very few nodes receive support, namely post-*Panderichthys* taxa, post-elpistostegalian taxa, baphetids, and a clade of *Eoherpeton* plus *Proterogyrinus*.

In the second analysis, characters were re-weighted by the largest values of their rescaled consistency indexes from the initial analysis. PAUP* yielded a single tree (Fig. 5c) 112.3561 steps long, with C.I. = 0.6804 (0.6655 excluding uninformative characters), R.I. = 0.8297, and R.C. = 0.5645. This tree was 3 steps longer than the trees from the unweighted analysis and did not represent a significantly better fit for the data, in terms of tree length, than the unweighted trees, based upon Templeton, Kishino-Hasegawa, and Winning-sites tests in PAUP* The weighted analysis confirmed the status of *Parmastega* as the most basal tetrapod.

In the third analysis, we used implied weighting[58], experimenting with different integer values of Goloboff's constant of concavity K. We ran analyses with $1 \leq K \leq 10$ (e.g. ref. 59). For each K value, we saved all trees generated at the end of the analysis. The separate tree files obtained from all K-weighted analyses were stored in PAUP* after filtering out duplicated tree topologies. This process resulted in 5 K-weighted trees, which were summarised with a strict consensus (Extended Data Fig. 7b), an agreement subtree (Extended Data Fig. 7c), and an Adams consensus

(Extended Data Fig. 7d). The agreement subtree included 22 taxa (deleted: *Densignathus*; *Elginerpeton*; *Metaxygnathus*; *Ossinodus*).

For the Bayesian inference analysis, we employed MrBayes v. 3.2.6 (ref 60), with the following settings: variable coding; gamma-distributed rate model; 10^7 generations and four chains; discarding the first 25% of sampled trees. Convergence diagnostic was evaluated through inspection of the Potential Scale Reduction Factor values[61] output by MrBayes. These values approached or were identical to 1, indicating successfully convergent runs (Supplementary File 4). Credibility values for nodes in the Bayesian results (Fig. 5c) were moderate to strong for most nodes.

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Data Availability

In total, 132 specimens comprising 183 skeletal elements have been collected during the entire period of excavations (2002-2012). 106 specimens, all of them figured in Supplementary Table 1, have been deposited in the collection of the Institute of Geology, Komi Science Centre, Ural Branch of the Russian Academy of Sciences, Syktyvkar, Russia under the collection number IG KSC 705/ and are available for examination. Other specimens have been reserved for sharing with other museums. The LSID for *Parmastega* is urn:lsid:zoobank.org:act:76B5BB03-42FE-4F46-A284-F95E973CEE96.

Extended Data Figure 1 | The distribution of *Parmastega* at the Sosnogorsk fossil site. a-b, Maps of increasing resolution showing the location of Sosnogorsk within northwest Russia. The box around Ukhta and Sosnogorsk in **a** indicates the region shown in **b** In **b**, the brown belt extending from north to south indicates the outcrop of Famennian (D_3fm) deposits in the region, and the yellow arrow points to the Sosnogorsk fossil site (Sosnovskiy Geological Monument). **c**, Stratigraphic column through the Sosnogorsk Formation and part of the overlying marine Izhma Formation. Note the possible position of the Frasnian-Famennian boundary (D_3f / D_3fm) in the lower part of the Sosnogorsk Formation. The vertebrate-bearing part of the formation is shown in detail on the right, with the tetrapod-bearing level indicated with a red vertical bar. **d**, general view of outcrop #20 (Sosnovskiy Geological Monument) from the opposite bank of the Izhma River. 1 - limestone, 2 - dolomite, 3 - clay, 4 - nodular limestone, 5 - scree, 6 - landslide. D_3sn - Sosnogorsk Formation, D_3i**ž** - Izhma Formation. Distance A'-B' indicates the area of main excavation in 2010-2012. **e**, main excavation. Distance A-B indicates the area where all tetrapod bones were found during the excavation in 2012. The photo was taken on 2 August 2012. **f**, sketch-map of the main excavation, 2012, showing the distribution of tetrapod bones within the bed. The cluster numbers are indicated in orange.

Extended Data Figure 2 | Frontal bones of *Parmastega*. The figure shows all the complete and near-complete frontals of *Parmastega* (8 out of 9 known frontals), to scale, oriented with anterior at the top and aligned on the centre of radiation (horizontal line). Right frontals have been reversed so that all bones have the appearance of left frontals. From left to right the specimens are IG KSC 705/3

(reversed), 705/40, 705/44 (reversed), 705/43, 705/45, 705/18 (reversed), 705/42 and 705/41. Scale bar, 10mm.

Extended Data Figure 3 | Bone associations. a, **b**, diagrammatic images showing, in orange, associated bones of two individual skulls. **a**, the holotype, IG KSC 705/1. **b**, the largest individual, IG KSC 705/2 - 705/14 and 705/99. Note that in the lateral view of **b**, the preserved frontal and nasal are shown even though they are in fact on the other side of the skull. **c**, diagrammatic representation of the number of specimens of different bones in the sample.

Extended Data Figure 4 | Size and shape of Devonian tetrapods. Silhouette reconstructions, drawn to the same scale, of the heads of the known reconstructable Devonian tetrapods. The lower jaw of *Elginerpeton*, the largest known Devonian tetrapod (for which the skull cannot be reconstructed), is also included. All reconstructions except *Acanthostega* are assembled from more than one specimen; specimen numbers indicate the specimen used to determine the scale. The right-hand column shows the largest known individuals. The left-hand column shows the smallest individuals of *Parmastega* (all from Sosnogorsk) and *Ichthyostega* (based on the entire East Greenland collection, reviewed in ref. 64). Note similarity of size range despite very different nature of samples. *Ventastega* and *Acanthostega* show narrow size ranges, which are not illustrated. Reconstructions modified from the following sources: *Ichthyostega*, ref 19; *Acanthostega*, ref 31; *Ventastega*, ref 32; *Elginerpeton*, ref. 63.

Extended Data Figure 5 | relative orbit size. Plot of orbit length vs. skull length for a range of tetrapodomorph fishes, elpistostegids, Devonian tetrapods and post-Devonian tetrapods. Data taken from ref. 47, except *Parmastega*, which is based on the largest known individual (see Extended Data Fig. 3). Post-Devonian tetrapods from ref. 47 not included in our phylogenetic analysis are not shown. *Ac, Acanthostega; Ba b, Baphetes bohemicus; Ba k, B. kirkbyi; Ba l, B. lintonensis; Bal, Balanerpeton; Be, Beelarongia; Br, Bruehnopteron; Cab, Cabonnichthys; Can, Canowindra; Cl, Cladarosymblema; Cra, Crassigyrinus; Den, Dendrerpeton; Ed, Edenopteron; Elp, Elpistostege; Eoh, Eoherpeton; Eu, Eusthenopteron; Gog, Gogonasus; Goo, Gooloogongia; Gre, Greererpeton; Gy, Gyroptychius; He, Heddleichthys; Ich, Ichthyostega; Ko, Koharalepis; Man, Mandageria; Mar, Marsdenichthys; Meg, Megalocephalus; Oss, Ossinodus; Ost, Osteolepis; Pal, Palatinichthys; Pan, Panderichthys; Par, Parmastega; Ped, Pederpes; Pro, Proterogyrinus; Scr, Screbinodus; Sil, Silvanerpeton; Tik, Tiktaalik; Tin, Tinirau; Ven, Ventastega; Wha, Whatcheeria.*

Extended Data Figure 6 | Otoccipital morphologies of Devonian tetrapods. a, Comparative diagram of the otoccipial regions of *Parmastega*, *Ichthyostega* (new reconstruction, based on data from ref. 18, 20), *Ventastega* (modified from ref. 32) and *Acanthostega* (modified from ref. 20, semicircular canals modified from ref. 50) in ventral view. Note that the basiocipital-exoccipital complex is only preserved in *Ichthyostega* and *Acanthostega*; in these genera the inner ear is shown only on one side. Drawings are scaled to the same length from pineal region to posterior margin of otic capsule. The inner ear is represented by the grooves for the anterior and posterior oblique semicircular canals, except in *Ichthyostega* where it is represented by the

760 sacculus (modified from ref. 20). The braincases are arranged by morphological
761 similarity, so that a minimum number of transformations are required along each
762 branch. **b**, Consensus phylogeny from the analyses presented in this paper. The
763 phylogenetic topology does not match the similarity dendrogram.
764
765 **Extended Data Figure 7 | Phylogenetic analysis. a**, unweighted strict consensus
766 tree. **b**, unweighted Adams consensus tree. **c**, single tree resulting from reweighting
767 characters by Rescaled Consistency Index. **d**, Bayesian tree, with credibility values at
768 nodes. **e**, Maximum agreement subtree of unweighted parsimony analysis. **f**, Strict
769 consensus of K-weighted trees. **g**, Maximum agreement subtree of K-weighted
770 parsimony analysis. **h**, Adams consensus of all trees from all K-weighted analyses.
771
772 **Extended Data Figure 8 | *Parmastega* and caiman.** Comparison in left lateral view
773 of spectacled caiman (*Caiman crocodilus*) on the left and *Parmastega* on the right,
774 drawn to the same size, showing inferred similar cruising posture at the surface. Note
775 the different positions of the nostrils. The caiman image is based on a CT scan in the
776 Digimorph Archive (http://www.digimorph.org/specimens/Caiman_crocodilus/).
777
778 **Extended Data Figure 9 | fit of dentary against upper jaw. a**, dentary
779 of *Parmastega* (IG KSC 705-67) fitted against palatal reconstruction to show the
780 difference in curvature between the spade-shaped snout and the relatively straight
781 dentary. **b**, lateral view of skull reconstruction of *Parmastega* with closed mouth,
782 showing mismatch in curvature between upper and lower jaws. **c**, composite
783 reconstruction of *Ventastega*, superimposing lower jaw rami (from ref. 30) on skull
784 reconstruction (from ref. 32), showing shape relationship similar to **a**. Not to scale.

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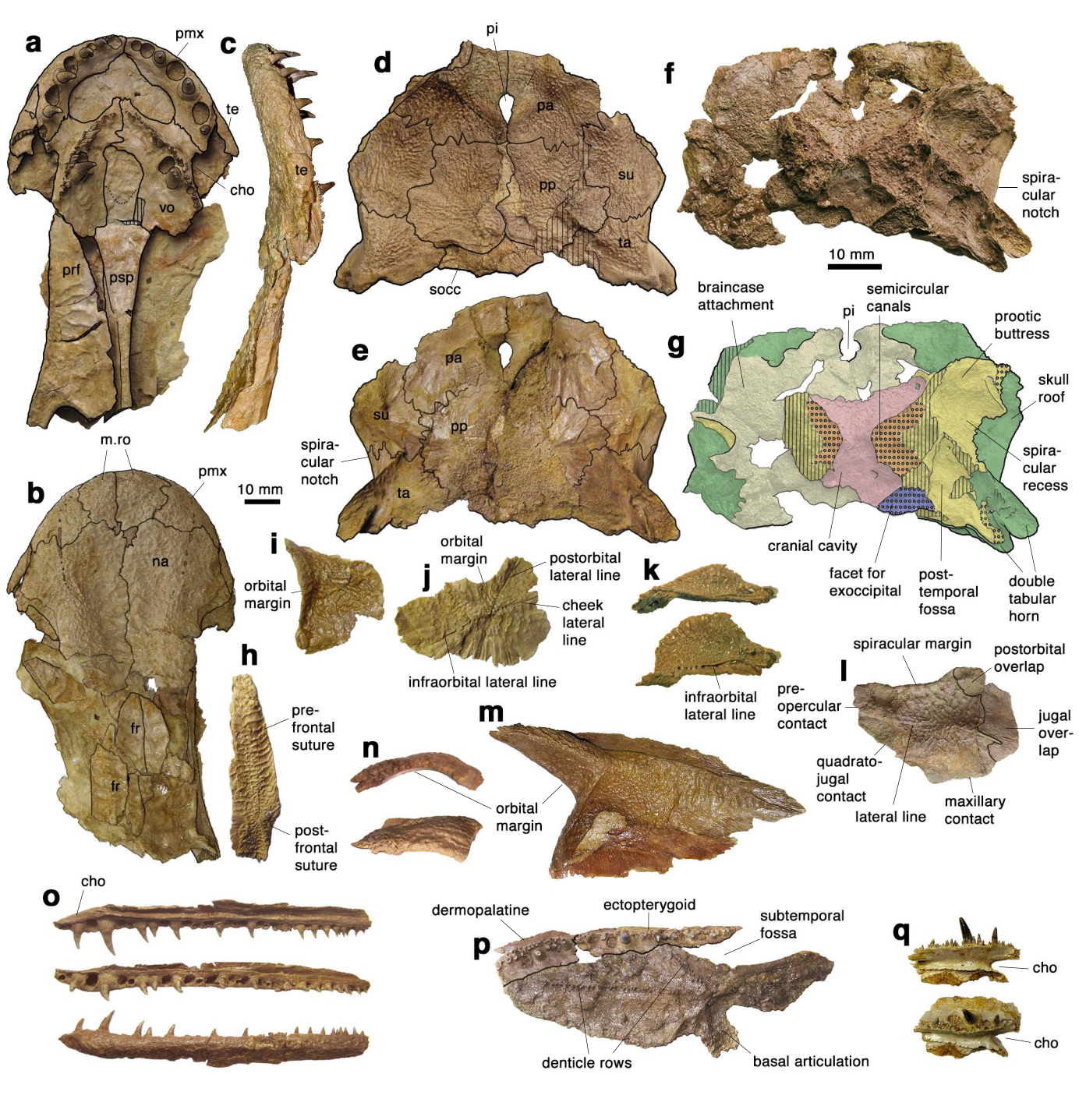
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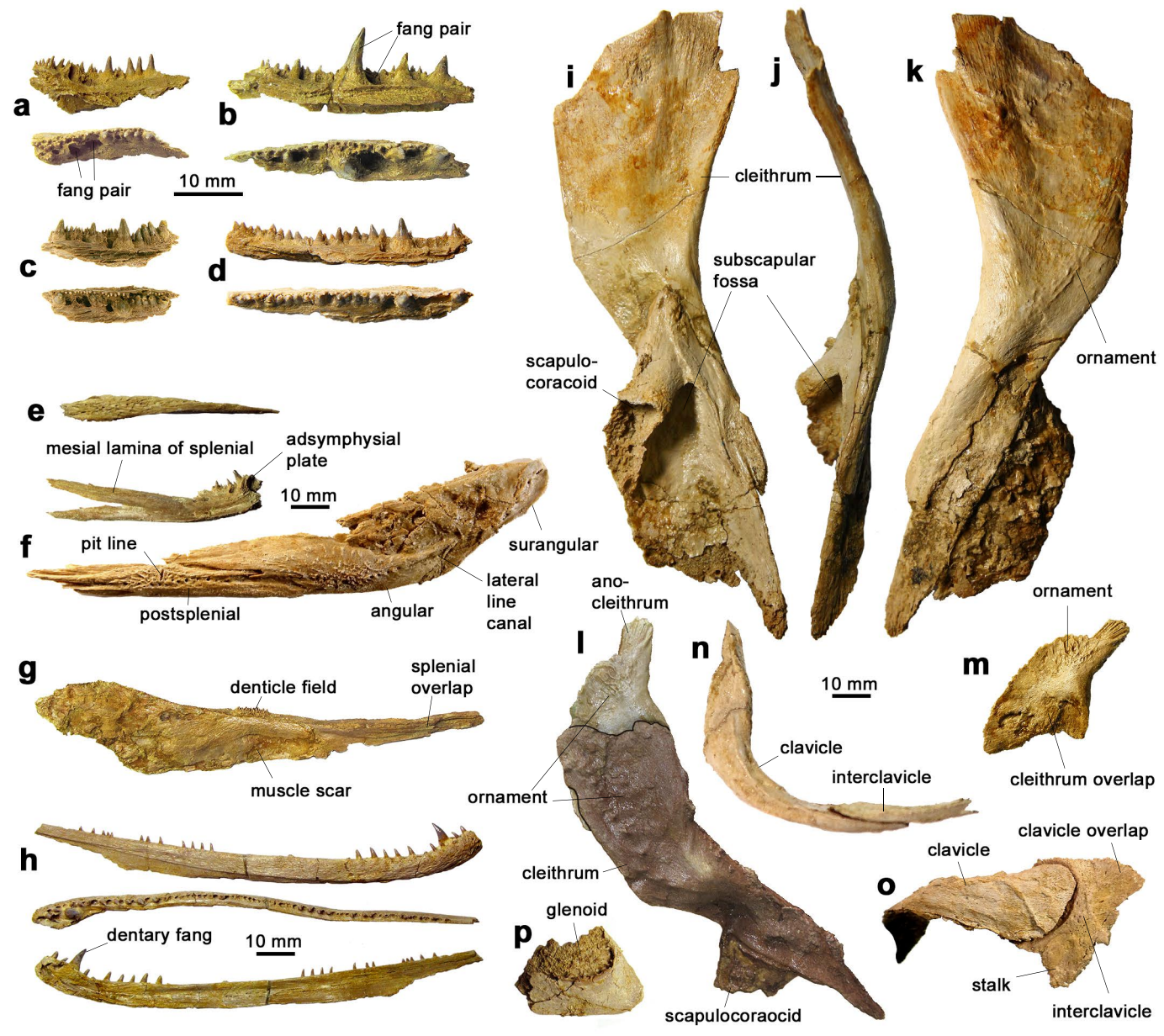
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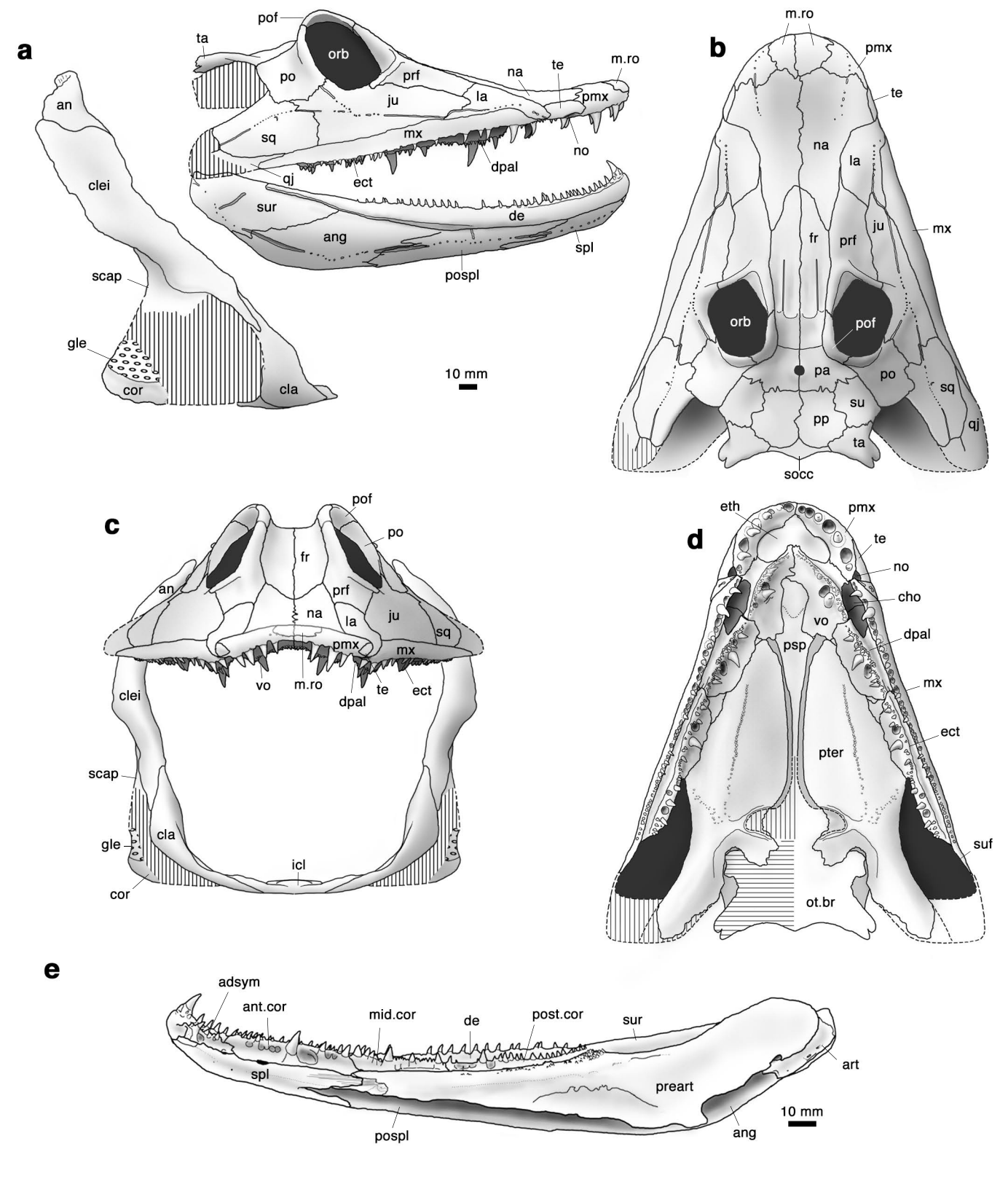
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