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CARINTHIASUCHUS KANDUTSCHI, A NEW ARCHOSAUR (REPTILIA: DIAPSIDA) FROM THE TRIASSIC OF AUSTRIA

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Abstract. A partial skeleton of a small reptile with a distinctive maxilla, dentition, caudal vertebrae and osteoderms from the marine Partnach Formation (Ladinian-earliest Carnian) near Jadersdorf (Gitschtal, Hermagor) in the Gailtal Alps of Carinthia (Austria), represents a new archosaur taxon *Carinthiasuchus kandutschi* gen. n. sp. n.. It is diagnosed by autapomorphies in the anterior process and subnarial foramen of the maxilla, accessory articular processes in the neural arches of mid-distal caudal vertebrae, and shape and arrangement of the caudal osteoderms. It also shows a unique combination of features regarding the extent of the antorbital fossa in the maxilla and the morphology of its ventral edge, dentary shape, dentition, caudal vertebrae elongation and morphology. A segment of 16 mid-distal caudal vertebrae is one of the better articulated tail segments ever found in Triassic archosaurs, showing the arrangement of the dorsal osteoderms and the presence of accessory processes in the neural arches stiffening the posterior termination of the tail. Phylogenetic analysis recovered *Carinthiasuchus kandutschi* as a pseudosuchian in a basal position within the Poposauroidea. Absence of swimming adaptation in the tail and the presence of terrestrial plant remains in the same outcrop suggest terrestrial habits for this archosaur reptile.

INTRODUCTION

The osteological record of Anisian to Carnian (Middle to lower Upper Triassic) archosauriform reptiles is quite scanty from the Alpine Tethyan realm, i.e. the present day southeastern France, northern Italy, Switzerland, southern Germany, southern Austria, and north-western Slovenia (Charig et al. 1976; Dalla Vecchia & Avanzini 2002; Renesto et al. 2003; Nicosia et al. 2005; Dalla Vecchia 2008; Nesbitt et al. 2013). The better know taxon is the 'rauisuchian' *Ticinosuchus ferox* Krebs, 1965 from the Grenzbitumenzone/Besano Formation (upper Anisian) of Switzerland and Italy, which is represented by a nearly complete skeleton and two fragmentary remains (Krebs 1965; Lautenschlager & Desojo 2011). Other archosauriform remains are represented by the late Anisian *Heteropelta boboi* Dalla Vecchia, 2021 and by isolated skeletal elements and

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teeth from the Anisian and Carnian (Dalla Vecchia & Avanzini 2002; Renesto et al. 2003; Dalla Vecchia 2006, 2008; Petti et al. 2013; Dalla Vecchia & Simonetto 2018). The purported archosaur *Wachtlerosaurus ladinicus* Perner, 2018 from the Ladinian of N Italy is most probably a drepanosauromorph as suggested by its pectoral girdle (Perner 2018: fig. 3 at p. 4, fig. 2 at p. 5 and fig. 3 a p. 7; cf. Harris & Downs 2002: figs 1A-B and 2A-B).

The fossil record of the Poposauroidea from Europe is scarce: *Ctenosauriscus* from the uppermost Olenekian of N Germany (Butler et al. 2011), Ctenosauriscidae indet. from the lower Anisian of SW Germany (Butler et al. 2011), *Bromsgroveia* from the Ladinian of England (Galton 1985; Benton & Gower 2002), and a still undescribed small poposauroid from the uppermost Norian - lowermost Rhaetian of SW Poland (Niedźwiedzki et al. 2012).

Here we report on a new archosauriform taxon based on associate skeletal remains and teeth from the Ladinian or lowermost Carnian of the Gailtal Alps of SE Austria, which is recovered as a basal poposauroid in our phylogenetic analysis.

Institutional abbreviations – CM, Carnegie Museum, Pittsburgh, USA; **CPEZ**, Coleção Municipal, São Pedro do Sul; Brazil; **MFSN**, Museo Friulano di Storia Naturale, Udine, Italy; **Nockalm**, "Kärntens versteinerte Welten" Museum, Biosphärenzentrum Nokkalmhof, Kremsbrücke, Krems, Carinthia, Austria; **UFRGS**, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil.

Materials, terminology and methods

Nockalm 7030u is the only specimen of the new taxon. It is a thin slab of pale gray limestone containing part of a disarticulated skeleton, in particular a portion of the skull with partial mandibular rami, a concentration ('spot') of disarticulated elements of the caudal vertebral column and an articulated segment of the column from a more distal position of the tail. Most of the skeletal elements had already been affected by weathering when the fossil was discovered. The slab was broken into several fragments which were glued together. Nockalm 7030u is deposited at the "*Kärntens versteinerte Welten*" Museum an der Nockalmstrasse at Kremsbrücke, Krems, Carinthia, Austria, where it was prepared for exhibition. Further mechanical preparation by steel needles mounted on a support was undertaken under a Wild M3 binocular microscope during this study to expose small portions that were still covered by rock (e.g., the anterior process of the maxilla) or obscured by glue and paint.

Proximal caudal vertebrae are those with laterodorsal pleurapophyses (sensu Wild 1973) on the centrum; the middle caudal vertebrae are those without the pleurapophyses, but bearing a haemapophysis (chevron), whereas the distal caudal vertebrae lack a haemapophysis . The neural arch is composed of pedicels, zygapophyses, neural spine and accessory processes. Archosauriform taxonomy follows Nesbitt (2011). The term "paramedian osteoderms" is commonly reported in the descriptions of archosauriform reptiles, but it is used to indicate both a single longitudinal row of osteoderms and two rows. The meaning of the adjective "paramedian" given by the Merriam-Webster Medical Dictionary (https://www.merriam-webster.com/medical/paramedian) is "situated adjacent to the midline". Therefore, paramedian osteoderms are only those arranged into two parallel longitudinal rows that contact each other along the midline of the body.

Fig. 1 - Location of the finding locality of Nockalm7030u in Austria.

A phylogenetic analysis by parsimony was performed to test the phylogenetic affinity of the new taxon based on the data set of Desojo & Rauhut (2024). "Anterior" and "posterior" are used in the description of the specimen instead of "cranial" and "caudal" in order to avoid confusion with the original character formulations in the phylogenetic analysis.

Nomenclatural act

The electronic version of this article in Portable Document Format (PDF) will represent a published work according to the International Commission on Zoological Nomenclature (ICZN), and hence the new names contained in the electronic version are effectively published under that Code from the electronic edition alone. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the 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: LSIDurn:lsid:zoobank.org:pub:1860D140-D5FB-4C11-8112-9CD51D7295EE

The LSID for the genus name *Carinthiasuchus* gen. n.: LSIDurn:lsid:zoobank.org:act:46831516-91D8-4094-A45C-73318289857A

The LSID for the species name *Carinthiasuchus kandutschi* gen. n. sp. n.: LSIDurn:lsid:zoobank.org:act:252EC32E-EA71-4AE3-999B-F18AF84F51B1

LOCALITY, GEOLOGICAL SETTING AND ASSOCIATED FOSSILS

The specimen Nockalm 7030u was found by Georg Kandutsch NE of the village of Jadersdorf (Gitschtal, Hermagor) in the Gailtal Alps of SW Carinthia (Kärnten), SE Austria (Fig. 1). It

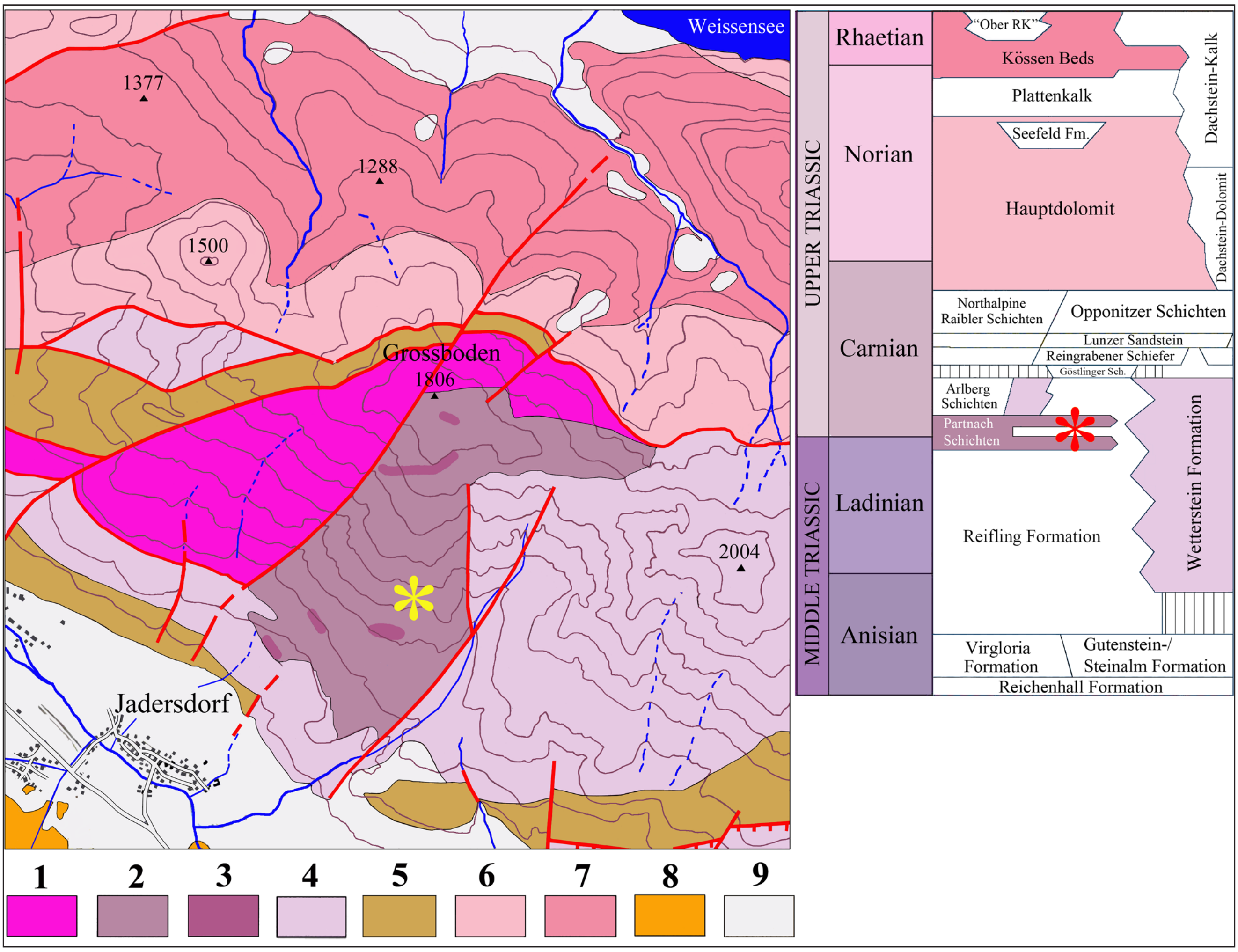

Fig. 2 - Geology of the finding area near Jadersdorf. Left: geological map based on Schönlaub et al. (1987 and 1989), modified; legend: 1) Muschelkalk (Anisian); 2) Partnach Formation, Partnach Plattenkalk (Ladinian); 3) Partnach Formation, tuff, tuffites and dacites (Ladinian); 4) Wetterstein Formation (lower Carnian); 5) Cardita Formation (Carnian); 6) Hauptdolomit (Norian); 7) Kössen Formation (Rhaetian); 8) Deformation Zone; and 9) Pleistocene-Present deposits. Right: stratigraphy of the Drau Range-North Karawanke-Arlberg-Bajuvaricum according to Piller et al. (2004).

was collected in an outcrop of thinly bedded dark limestones located between the localities Schwarzwaldgraben and Weißenbachgraben along the southern flank of the Mt. Großboden (Fig. 2). The geographic coordinates of the finding locality are 46° 40' 15"N 13° 20' 20"E. The zone belongs to the Drau Range of the Austro-alpine tectonic unit of the Eastern Alps. According to the sheet 199 - Hermagor of the Geological Map of the Austrian Republic at scale 1: 50.000 (Schönlaub et al. 1989), the specimen comes from the "*Dunkelgrauer Partnach-Plattenkalk*" (dark gray Partnach Plattenkalk) of the Partnach Formation (Fig. 2) which is dated to the Ladinian. According to the map, the Partnach Formation is a marine unit divided into three facies: tuffs, tuffites and dacites, the *Partnach-Schieferlage*, and the dark gray *Partnach Plattenkalk*. In the Austro-Alpine unit of the Northern Calcareous Alps of SE Austria, the Partnach Formation or Partnach Beds is middle-late Ladinian in age according to Janoschek & Matura (1980: tab. 5). Bechstädt (1978) introduced the lithostratigraphic name *Fellbacher Kalk* (Fellbach Limestone) for the well-bedded Ladinian limestone previously referred to as "*Plattenkalk*" or "*Partnachkalk*" in the Gailtal Alps. As there are marked differences between the original section of the Partnach Formation in the Northern Calcareous Alps of Germany (e.g., Tollmann, 1976) and the "*Dunkelgrauer Partnach-Plattenkalk*" of the Gailtal Alps, the name Fellbach Limestone has been preferred by Klein et al. (2025) for the fossil-bearing unit of the Drau Range. The Fellbach Limestone is considered Ladinian in

Fig. 3 - *Carinthiasuchus kandutschi,* gen. n. sp. n., Nockalm7030u, holotype. Scale bar equals 100 mm.

age by those authors in accordance with Bechstädt (1978), Warch (1984), and Tichy (1998). However, according to the Austrian Stratigraphic Chart 2004 (Piller et al. 2004), the Fellbach Formation results to crop out only in the Lienzer Dolomiten (i.e., WNW of the Drau Range) and is latest Anisian-Ladinian in age, whereas the Partnach Formation/*Partnach Schichten* of the Gailtal Alps (Drau Range), which is interbedded to the basin deposits of the Reifling Formation, is latest Ladinian-earliest Carnian in age (Fig. 2) and a lateral equivalent to the Abfaltersbach Formation in the *Lienzer Dolomiten*. As it can be seen in Fig. 2, Schönlaub et al. (1987, 1989) and Piller et al. (2004) do not always use the same lithostratigraphic units for the Drau Range.

Vertebrate remains are reported from several localities in the Gailtal Alps, all assigned to the Partnach Formation/Fellbach Limestone, but they do not include any archosauriform reptiles (Sieber 1955; Bachmayer & Warch 1959; Zapfe & König 1980; Wachtler 2018; Klein et al. 2025). The Partnach Plattenkalk/Fellbach Limestone in the finding outcrop presents abundant terrestrial plant remains, including the conifer *Voltzia*, and osteichthyan fishes (*Saurichthys* and a coelacanthiform; G. Kandutsch, pers. comm.). The two specimens of the new nothosaurid *Carinthiasaurus kandutschi* Klein, Furrer, Dojen, Lukeneder & Scheyer (2025) were found a few hundred metres WNW from the outcrop where the specimen Nockalm 7030u was collected (Kandutsch, pers. comm.).

SYSTEMATIC PALAEONTOLOGY

Reptilia Laurenti, 1768 sensu Modesto & Anderson, 2004
Diapsida Osborn, 1903
Archosauromorpha von Huene, 1946 sensu Dilkes, 1998
Archosauriformes Gauthier, Kluge & Rowe,1988
Archosauria Cope, 1869
Pseudosuchia Zittel, 1887-1890
Suchia Krebs, 1974 (sensu Nesbitt, 2011)
Paracrocodylomorpha Parrish, 1993
Poposauroidea Nopcsa, 1923

Carinthiasuchus kandutschi gen. n. sp. n.

Etymology: The genus is named after *Carinthia*, the Latin name of Kärnten, the southernmost federate state of Austria where the specimen was discovered and the Greek term *soúkhos* (*σούχος*) for crocodile. The species name is in honour of the discoverer of the holotype, Georg Kandutsch (Arriach/Hinterwinkl, Austria).

Holotype: Nockalm 7030u, part of the skull including the right maxilla with two teeth, part of the two mandibular rami, and parts of the mid-distal portion of the tail with osteoderms (Fig. 3).

Locality and stratigraphic horizon: Southern flank of Mt. Großboden NE of Jadersdorf in the Gitschtal close to Hermagor, Carinthia, SE Austria. *Partnach-Schichten/Fellbach Kalk*, Ladinian-lowermost Carnian.

Diagnosis. *Carinthiasuchus kandutschi* gen. n. sp. n. is an archosaur (see discussion) with the following apomorphies: short, straight and pointed anterior process of the maxilla with a dorsal articular facet and bordering dorsally a comparatively large subnarial foramen; accessory articular processes of the neural arches in the last middle and in the distal caudal vertebrae; paired and symmetrical paramedian osteoderms above the proximal mid-caudal vertebrae, drop-shaped, with coarse denticles along the margins posteriorly, with longitudinal median ridge dorsally but without sculpturing; single median row of elongated and lying 8-shaped osteoderms in the following mid-distal caudals with three osteoderms per vertebra, one above the middle of the vertebra and half on the anterior and posterior part of the neural arch, respectively. It also presents the following unique combination of character states: antorbital fossa extending laterally on the posterior process of the maxilla and not on the ascending one; ridge at the ventral margin of the antorbital fossa; heterodont maxillary teeth with symmetrical and labiolingually flattened crowns: lanceolate proximal crowns much higher than mesiodistally long and with small serrations along the cutting margins, distal crowns proportionally lower with coarser denticles along the distal cutting edge and small serrations along the mesial cutting edge; dentary teeth smaller than maxillary teeth; slender dentary with ≥23 teeth (in an immature individual); very elongated mid-distal caudal vertebrae (length/minimum height of the centra ranging 3.2-7.4 from the proximal mid-caudals to the distal caudals); low and squared neural spine of proximal mid-caudal vertebrae and placed on the posterior end of the neural arch; accessory laminar process on the neural arch in some mid-caudal vertebrae.

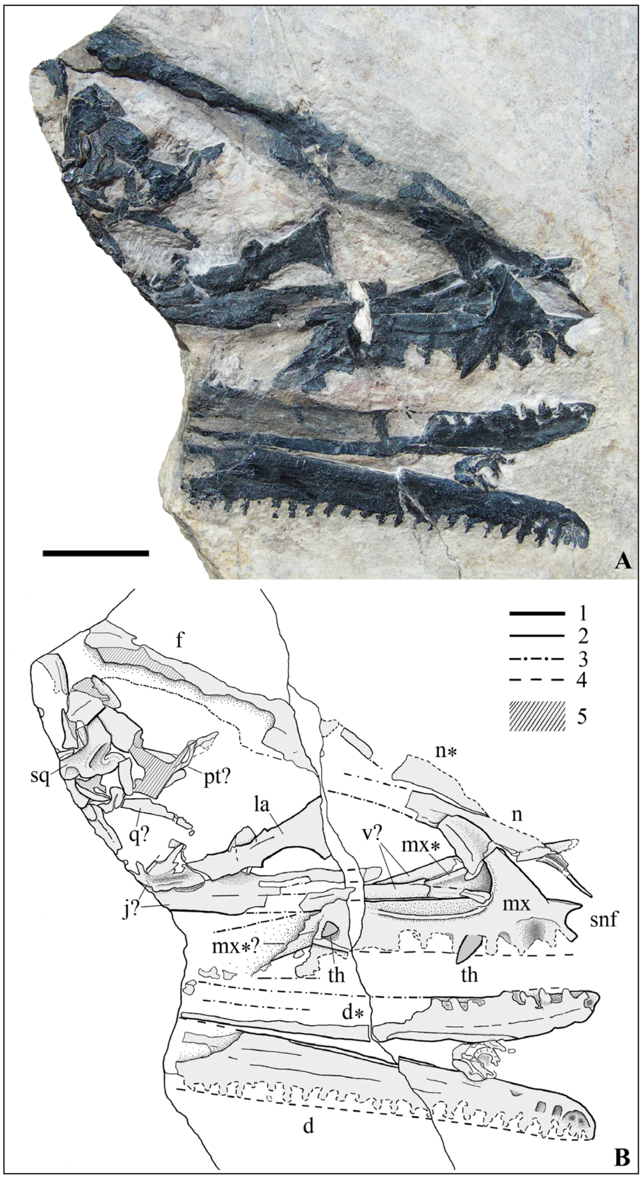

Fig. 4 - *Carinthiasuchus kandutschi*, gen. n. sp. n., Nockalm7030u, holotype, skull and mandible. (A) Photograph, (B) drawing (bone is gray and teeth darker gray). Abbreviations: d, dentary; f, frontal; j, jugal; la, lacrimal; mx, maxilla; n, nasal; pt, pterygoid; q, quadrate; snf, subnarial foramen; sq, squamosal; th, tooth; v, vomer; *, left element. Legenda: 1 = actual margin of the bone; 2 = broken margin of the bone; 3 = margin of the impression of the bone; 4 = probable margin of the skeletal element; 5 = broken surface of the skeletal element. Scale bar is 10 mm.

Description and comparisons

The preserved portions of the skeleton are distributed in three distinct parts of the slab because the skeleton disarticulated in sets that macerated separately and disarticulated at different rates on the sea bottom (Fig. 3). Part of the skull with the two mandibular rami is preserved close to the margin of the slab (upper left in Fig. 3). A slightly disarticulated proximal portion of the mid-caudal segment of the vertebral column occurs on the opposite right side of the slab. The third part is a mostly articulated mid-distal caudal segment of the vertebral column.

Skull. The skull is partly preserved and slightly disarticulated (Fig. 4). The premaxillae are missing and the portion of the skull posterior to the orbit was lost. Most of the cranial elements are strongly worn-out because they had been exposed to weathering for a long time. Therefore, the identification of most of them is tentative and based on their general outline and position in the skull respect to the right maxilla which is the better preserved element.

The right maxilla is exposed in lateral view overlapping and mostly concealing the left maxilla. It is triradiate with the ascending (dorsal) and poste-

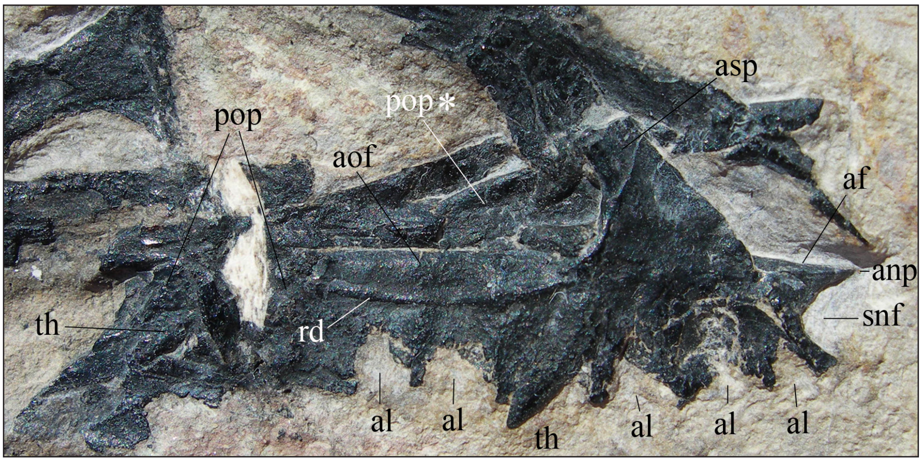

Fig. 5 - *Carinthiasuchus kandutschi*, gen. n. sp. n., Nockalm7030u, holotype, maxillae. The right maxilla is in lateral view, the left in medial view and mostly concealed. Abbreviations: af, articular facet on the anterior process; al, alveolus; anp, anterior process; aof, antorbital fossa (on the posterior process); asp, ascending process; pop, posterior process; rd, ridge; snf, subnarial foramen; th, tooth. For size, see figure 4.

rior (jugal) processes that are much larger than the anterior process. The posterior process is straight and rectangular, with a same height along the whole preserved portion. Its posterior termination is not clear because overlapping other bones and is possibly preserved just as impression; its minimum posterior extent is indicated by the most distal preserved tooth. An antorbital fossa extends on the dorsolateral side of the posterior process; its ventral margin is bordered by a blunt and thin but distinct ridge (Fig. 5). Only the basal part of the ascending process is preserved, which borders the antorbital fenestra anteriorly. The ascending process tapers dorsally and projects posterodorsally at an angle of 50°. The antorbital fossa does not extend on the ascending process. The short anterior process is straight and pointed with a nearly horizontal, dorsally facing and flat articular surface, plausibly for a corresponding articular facet on the posteroventral (maxillary) process of the premaxilla. An identification of this process as the palatal process present in many archosaurs (e.g. Gower 1999: fig. 4; Schoch 2011: fig. 4; França et al. 2013: fig. 5b, e, f, and i; Mastrantonio et al. 2019: figs. 5 and 6A) was rejected because the latter expands medially or anteromedially from the anteromedial edge of the maxilla on the medial side (Nesbitt 2011) and has an irregular shape, while the process is pointed and directed straight forward on the anterior side of the maxilla in Nockalm 7030u. Furthermore, the rough articular facet on the palatal process is for articulation with its antimere, thus it faces medially or anteromedially, not dorsally. The anterior process borders dorsally a broad and semicircular rostral notch on the anteroventral end of the maxilla. Notch and anterior process are on the same vertical plane and the notch was not produced by erosion. Even though the premaxilla is missing, that present on the maxilla is clearly the posterior half of a rounded opening that would extend on the premaxilla (cf. Nesbitt 2011: 63). Because the premaxilla is missing, it is not possible to immediately say whether the opening represents a subnarial foramen (Nesbitt 2011; subnarial fenestra sensu Parrish 1993) or a subnarial gap (Nesbitt 2011). A subnarial gap occurs in the non-archosaur archosauriform *Vancleavea campi* Long & Murry, 1995, in most crocodylomorphs, in some basal theropod dinosaurs and in the dinosaur *Heterodontosaurus tucki* Crompton & Charig, 1962 where it receives an enlarged dentary tooth (Nesbitt 2011). As there is no evidence of the presence of an enlarged dentary tooth in *Carinthiasuchus* at level of the rostral end of the maxilla (see below), and the gap should be walled by bone medially, it appears unlikely that the anterior notch of the new taxon corresponds to a subnarial gap.

The portion of the maxilla anterior to the anterior margin of the antorbital fenestra is much shorter than that behind the anterior margin of that opening.

The ventral margin of the right maxilla is strongly worn out showing the first six alveoli; the fourth alveolus preserves an erupting tooth. A second unerupted tooth occurs more distally, in correspondence of the maxillary tooth position 10 or 11.

The left maxilla is mostly concealed by the right one and by elements of the palate; only a portion of the posterior process can be distinguished, suggesting a slight counterclockwise rotation of the bone respect to the right element. A fragment of

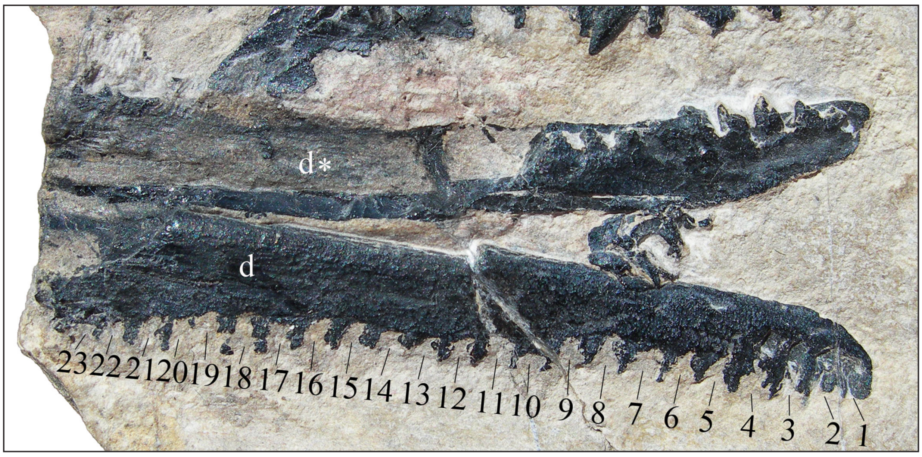

Fig. 6 - *Carinthiasuchus kandutschi,* gen. n. sp. n., Nockalm7030u, holotype, mandible. The two mandibular rami unfused at the symphysis and exposed in medial view. Abbreviations: 1-23, alveoli 1-23; d, dentary; *, left element. For size, see figure 4.

the posterior portion of the posterior process possibly crops out posterior to the preserved posterior portion of the right process.

If the parallel and aligned mandibular rami are in their anatomical position respect to the skull, the premaxilla was rather short, because the rami scarcely extend beyond the maxilla.

The two poorly preserved ribbon-like elements forming the anterodorsal margin of the skull are plausibly the nasals. The rostral termination of the right nasal is pointed and presents a groove, possibly for the articulation of the posterodorsal (nasal) process of the premaxilla.

The shape of the maxilla and the position of the nasals indicate the presence of a comparatively large and deep antorbital fenestra.

A thick bone at the posterodorsal margin of the preserved portion of the skull above the orbit represents plausibly the remains of the frontals and perhaps of the parietals; frontals and nasals form the dorsal margin of the skull.

A slender bone with an inverted L shape and a concave anterior margin is identified as the ?right lacrimal. It is detached from its articulation with maxillary, jugal and nasal and slightly rotated clockwise. It is dorsoventrally elongated and its anterior process seems to be anteroposteriorly short. Because of its shape, it probably overhung the posterodorsal part of the antorbital fenestra.

The jugals cannot be reliably identified, but are plausibly the elements in posterior continuity with the maxillae, testified by some small fragments of bone and faint impressions.

A spot of broken and apparently small-sized elements located below the frontoparietal plate in the orbital region may be made of the fragmentary prefrontals and postfrontals, remnants of the pterygoids and of a quadrate. Only one element can be confidently identified as a squamosal because it presents a notch that corresponds to the glenoid for the proximal head of the quadrate and a leaf-shaped process that departs near the glenoid and could be the postquadratic (posterior or posteroventral) process of squamosal; in that case, the bone could be identified as the right squamosal. Unfortunately, this bone is crushed and has been partly damaged during the preparation of the specimen, thus further details are not available.

Some ribbon-like elements extend medial and parallel to the posterior process of the maxillae. They are plausibly elements of the palate. The narrow ones at level of the antorbital fenestra may be the vomers.

Mandible. The mandibular rami are parallel, close to each other and unfused at the symphysis (Fig. 6). The left ramus appears to be exposed in dorsolingual view, while the right ramus rotated to the right of 180° showing its lingual side and is upside down. The right ramus, the most complete, bears alveoli up to the distal margin, thus it is composed only by the dentary; the posterior portion with the surangular, angular, prearticular and articular with the glenoid for the quadrate is missing. The distal termination of the dentary, bordering the external mandibular fenestra, is also missing. The dentary is straight and slender with nearly parallel dorsal and ventral margins; it expands slightly dorsoventrally at the distal end and tapers slightly to its rostral termination. The rostral termination of the left dentary is slightly bent dorsally, whereas the rostral end of the other dentary is straight, with a rectilinear dorsal margin and a curved ventral margin. Because of

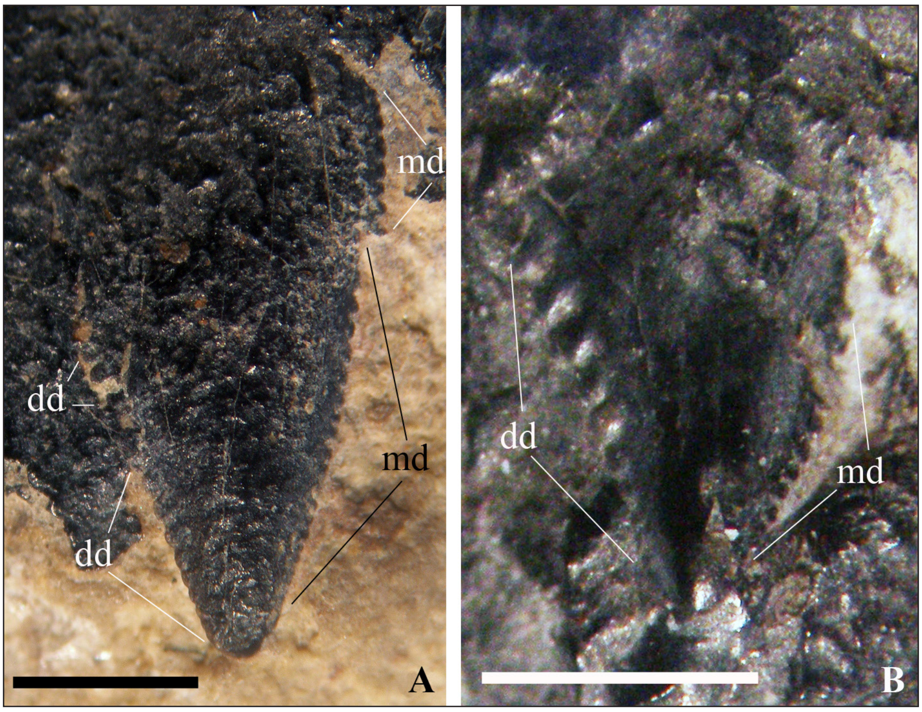

Fig. 7 - *Carinthiasuchus kandutschi*, gen. n. sp. n., Nockalm7030u, holotype, maxillary teeth. A) The mesial tooth; B) the distal tooth. Abbreviations: dd, distal denticles; md, mesial denticles. Scale bar is 1 mm.

erosion, there is no evidence of symphyseal structures, but the symphysis was probably very short. The rostral end is blunt.

The preserved portion of right ramus is 38.75 mm long. Height in the middle of the preserved portion is 5 mm (less that the height of the posterior process of the maxilla), whereas it is ca. 6 mm at the distal end. The length/height ratio with height measured around mid-dentary in the preserved portion of the element is 7.7. A distinct splenial cannot be distinguished; a thin distinct bone may be present at the ventral margin of the dentary; however, it may just be the result of the crushing. Interdental plates cannot be distinguished in the right dentary, but the alveolar margin is eroded. A shallow longitudinal depression midpoint in the distal half of the dentary may correspond to the Meckelian groove. There are at least 23 regularly-spaced empty alveoli corresponding to as many tooth positions. The inner part of the alveoli was exposed by the weathering of the mandibular walls. Tooth implantation was thecodont. Four fossae in the rostral end of the dentary are the deepest parts of the first four alveoli, perhaps corresponding to deeper-rooted and slightly larger first teeth. No dental plates can be distinguished, but this could be the result of erosion of the bone.

Only the rostral portion is preserved of the left dentary, with seven or eight empty alveoli; the posterior portion of the element is represented by a basal splint of bone and the impression of the remaining part. The tooth positions 3-5 appear to be somewhat different from the empty sectioned alveoli of the right ramus, probably because they still preserve remnants of the teeth and of the interdental plates that were lost or eroded in the other ramus.

Dentition. The mesial of the two preserved maxillary teeth (Fig. 7A) is just posterior to the ascending process and was not fully erupted with only the apical part out of the alveolus. It is not perpendicular to the main axis of the maxilla and the tooth was probably loose inside the alveolus because of putrefaction of the periodontal ligament. The crown is symmetrically lanceolate in labial view, labiolingually flattened and much apicobasally higher than mesiodistally long (~3.2 x 1.45 mm the exposed portion). The basal portion fades into the bone, thus it is impossible to know the total height of the crown and its maximum basal length. Both mesial and distal cutting margins are serrated with small rounded denticles that become smaller toward the apical part of the crown and are perpendicular to the crown margin. The mesial denticles are slightly smaller than the distal ones. There are about nine denticles per mm mesially at mid-crown; there are seven denticles per 0.5 mm apically on the mesial margin and five per 0.5 mm on the distal margin.

The distal and smaller tooth (Fig. 7B) was unerupted as it is totally preserved inside its alveo-

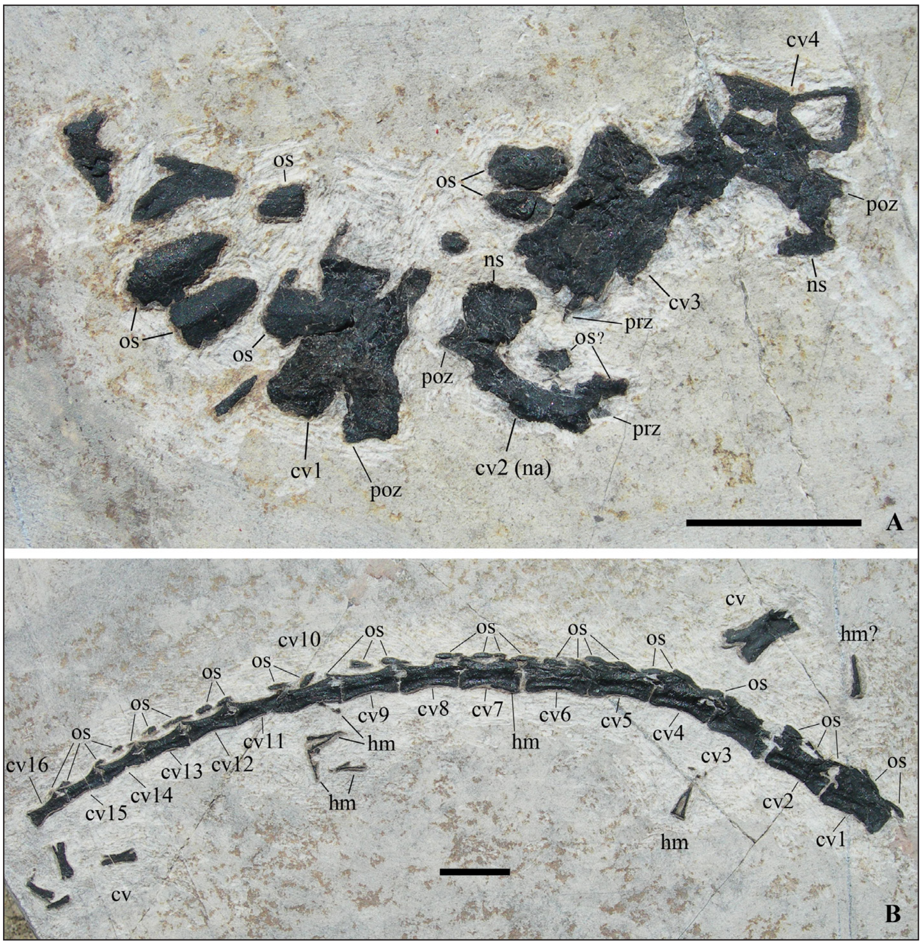

Fig. 8 - *Carinthiasuchus kandutschi,* gen. n. sp. n., Nockalm7030u, holotype. A) The 'spot' of disarticulated elements from the proximal part of the mid-tail; abbreviations: cv1-4, caudal vertebrae 1-4 (numbered in progressive order); na, neural arch; ns, neural spine; os, osteoderm; poz, postzygapophysis; prz, praezygapophysis. B) The row of mid-distal caudal vertebrae; abbreviations: cv1-16, caudal vertebrae 1-16 of the row (numbered in progressive order); cv, other disarticulated caudal vertebrae; hm, haemapophysis; os, osteoderm. The scale bars equal 10 mm. A high-resolution image of the row can be seen in the SI Fig. 1.

lus and its crown has been partially exposed by the weathering of the lateral wall of the posterior process of the maxilla. The basal portion fades into the bone, thus it is impossible to know the total height of the crown and its maximum basal length. The crown is triangular in labial view and nearly symmetrical, flattened labiolingually and apicobasally higher than mesiodistally long (1.8 x 1.5 mm the exposed portion). Denticles along the straight distal margin are markedly larger than those of the slightly arched mesial margin and markedly decrease in size toward the apical part of the crown; denticles of the mesial margin occur up to the basalmost preserved part. There are six denticles per 0.5 mm mesially and seven per mm distally. The larger distal denticles are rounded (not hooked or triangular), with comparatively deep interdenticle slits and are set at an angle with the crown margin.

The maxillary alveoli exposed in section (Fig. 5) have a maximum mesiodistal length (diameter) ~1.5 mm in the first alveolus, 2.5 mm in the alveolus 3, 2.7 mm in the alveolus 4 (that preserving the mesial erupting tooth inside), 2.4 mm in the alveolus 5, and ~1.75 mm in the alveolus 6.

The mandibular alveoli are regularly spaced (Fig. 6). Although alveoli 2, 7 and maybe 4 appear to be slightly larger than the others in the most complete ramus, there is no a marked difference in diameter among dentary alveoli. In that ramus, the sectioned alveoli have a maximum mesiodistal length (diameter) ranging 0.75-1.5 mm, but most of them are about 1 mm long. Although the apparent sizes of the alveoli are probably slightly increased by the erosion of the bone, they suggest that the mandibular teeth were sensibly smaller than the maxillary ones.

Alveoli appear to be inclined backward in the most complete ramus, but this may be caused by erosion. The first four alveoli corresponds to inner depressions in the dentary and possibly hosted symphysial teeth with deeper 'roots'.

Axial skeleton. The 'spot' of disarticulated elements of the vertebral column is composed of three vertebrae, a separate neural arch (all in lateral view), and at least 6-7 osteoderms. Other bone fragments occur 35 mm from these vertebrae including at least one incomplete osteoderm (see Fig. 3). The articulated mid-distal segment of the tail occurs 114 mm from the 'spot' and represents a more distal portion of the vertebral column.

Vertebrae. The most proximal preserved vertebrae are slightly disarticulated but still aligned; in Fig. 8A, they are numbered 1 to 4 in the presumed anteroposterior order (4 is the distalmost element) based on the slightly different lengths of the centra. They are strongly weathered and vertebra 4 is practically sectioned along the sagittal plane showing the hollow inner part of the centrum filled with sediment. These vertebrae do not present transverse processes or pleurapophyses, which would anyway have destroyed by weathering, if short. At least two (vertebra 4 and the isolated neural arch) preserve a neural spine, which was eroded in the other vertebrae. The centra are elongated (length 8.5-9.5 mm) and low (height at mid centrum is 2.5-3 mm); the ratio length/height at mid centrum is 3.2. The ventral margin of the centrum is concave in lateral view and the centrum is therefore lower in the middle than at the articular extremities. The low neural arch extends on most of the centrum and is slightly displaced anteriorly. The neural spine is placed at the posterior end of the neural arch; it is low and squared, slightly anteroposteriorly broader apically. The postzygapophysis is short and massive, whereas the praezygapophysis is slender and moderately projecting anteriorly; the zygapophyseal articular facet is probably horizontal. These vertebrae are associated to paired osteoderms (see below). For comparison with the row of articulated caudal vertebrae (size and shape of the centra and the relative positions of the two sets), those of the 'spot' are probably mid-caudal elements from a more proximal position.

The vertebral row is 120 mm long as a chord and is composed of 16 articulated vertebrae exposed in right lateral view. To facilitate the description, the vertebrae are numbered 1-16 in anteroposterior direction (see Fig. 8B). This segment is better preserved than the remains of the 'spot', although it is also weathered and crossed by fractures. A disarticulated vertebra in right lateral view and close to the vertebrae 3 and 4 of the row is obviously from a more proximal position, although it is slightly shorter than the first vertebra of the row. Four very small and disarticulated vertebrae occur close to the last (16th) vertebra of the row and are the most distal preserved elements. Therefore, the vertebrae belonging to this distinct segment of the vertebral column are 21. The articulated vertebrae are associated with a dorsal row of osteoderms still is situ. There are also four or five disarticulated haemapophyses plus two that are associated with the vertebrae 6 and 9 of the vertebral row.

The vertebral centra range 9.8-4.5 mm in length, which diminishes moving distally. The shape of the centra is like that of the more proximal elements of the 'spot' but the centra of the vertebral row are more elongated, the ratio length/height at mid centrum being 4.45, 4.5, and 5 in the vertebrae 1, 2 and 9 of the row and 7.4 in the smaller, complete distal vertebra (that of Fig. 9G).

The neural arches of the articulated vertebrae are low, extend on most of the centrum and have a peculiar morphology. The first vertebra of the row has a low and rounded neural spine extending on the posterior part of the arch and the osteoderms lie on it (Fig. 9B). The neural spine of the following vertebra seems to be different, but its anterior part is probably damaged; the posterior portion appears to have a flat top and an osteoderm lies on it (Fig. 9B). The neural spine of the vertebra 4 is low and rounded like that of vertebra 1; also in this case, an osteoderm lies on it (Fig. 9C). The spine of vertebra 5 is different because apparently it has a concave dorsal surface that gives it the outline of a volcanic cone; the anterior part of an osteoderm fits in the depression (Fig. 9D). The morphology of the neural arch changes with vertebra 7 or possibly with vertebra 6 which, however, is worse preserved than 7. The neural spine appears to be represented by just a small process above the postzygapophysis and

Fig. 9 - *Carinthiasuchus kandutschi*, gen. n. sp. n., Nockalm7030u, holotype, mid-distal caudal vertebrae of the 'row'. A) the proximal isolated vertebra; B) vertebrae 1 and 2 of the row; C) vertebrae 3-5, D) vertebrae 4-5, E) vertebrae 7-9; F) vertebrae 11-13; G) the most complete of the distal disarticulated vertebrae; H) vertebra 7 and its accessory laminar process/accessory neural spine; I) detail of the articulation between the neural arches of the vertebrae 8 and 9; J) detail of the articulation between the neural arches of the vertebrae 11 and 12. Abbreviations: alp, accessory laminar process/accessory neural spine; apn, anterior process of the neural arch; ce, centrum; cv1-12, vertebrae 1-12 of the row; hmf, haemapophysial facet on the centrum; ns, neural spine; os, osteoderm; poz, postzygapophysis; ppn, posterior process of the neural arch; prz, praezygapophysis; su, suture. The red asterisks mark the better preserved lying 8-shape osteoderms. Scale bar is 10 mm in B, 1 mm in I, and 5 mm in the other figures.

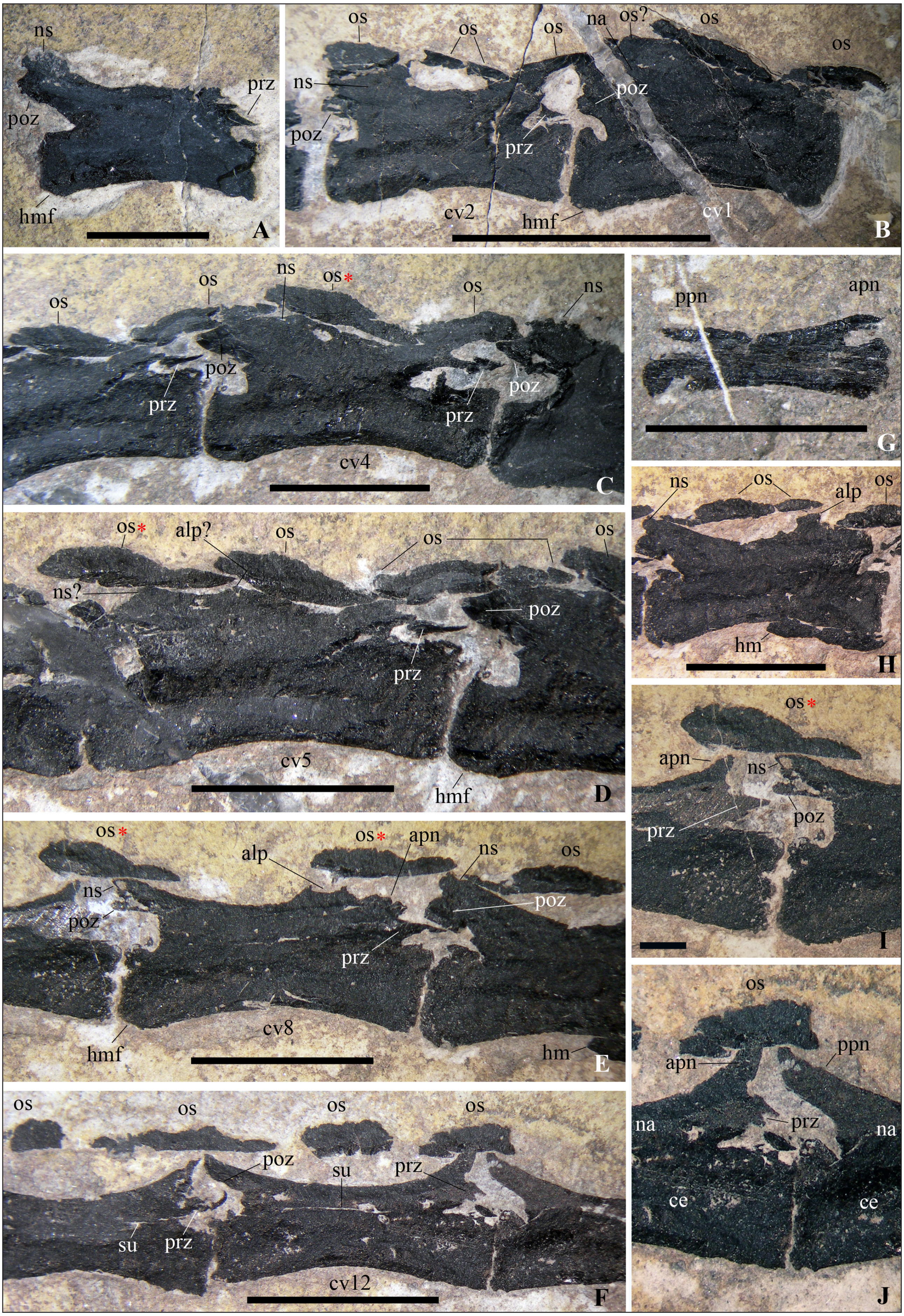
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Figure 9

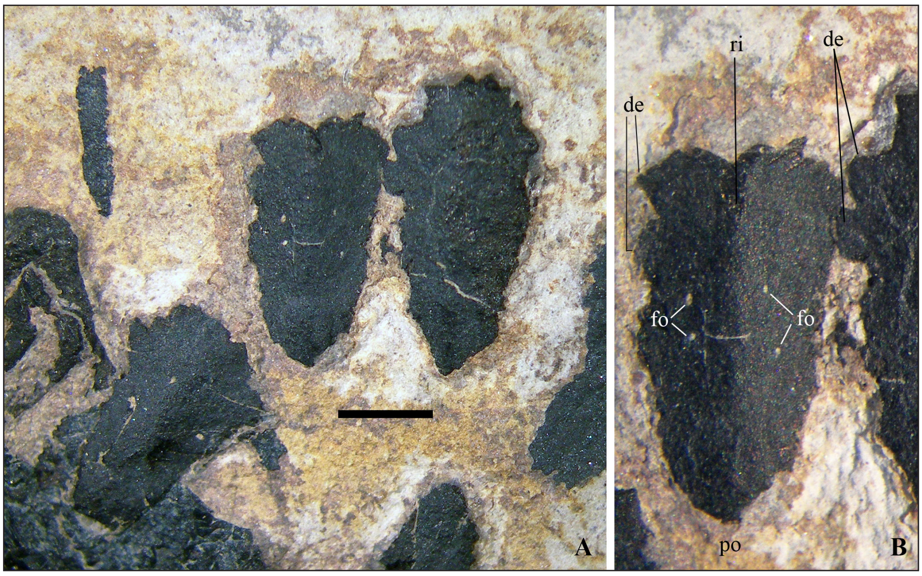
there is a larger accessory dorsal process in a more anterior position on the top of the neural arch (Fig. 9H). In vertebra 7, the process is damaged, but in vertebra 8 is better preserved and has the outline of a volcanic cone like the neural spine of vertebra 5, but it is much smaller (Fig. 9E). The neural spine of vertebra 8 is a small process set just above the postzygapophysis like in vertebra 8, thus the anterior dorsal process can be identified as an accessory laminar process sensu Nesbitt (2011: 118; accessory neural spine of Lautenschlager & Desojo 2011). It is possible that the posterior point of the volcanic cone-like neural spine of vertebra 5 is the actual neural spine and the anterior point is an accessory laminar process (see Krebs 1965: fig. 25); a forward migration of the accessory laminar process and its separation from the neural spine is observed in *Ticinosuchus* (Krebs 1965: figs. 25-26).

In vertebrae 7 and 8, the postzygapophysis and the neural spine seem to be at the end of a slender posterior posterodorsally directed process of the neural arch (Fig. 9E). The prezygapophysis of vertebra 8 articulated with the postzygapophysis of vertebra 7. A further process occurs between the accessory laminar process and the prezygapophysis of vertebra 8; it is anterodorsally directed above the distinct prezygapophysis. In vertebra 8, the process is partially eroded, but it can be fully appreciated in the following vertebrae. This process may occur also in the preceding vertebrae 4-6, but it is incompletely preserved. In vertebra 9, this anterior process articulates with the neural spine of the preceding vertebra when the distinct zygapophyses of the two vertebrae are articulated (Fig. 9I). Posterior to vertebra 9, there seems to be no neural spine. The dorsal side of the neural arch is concave and there are two finger-like processes at the two extremities (Fig. 9F). The anterior process is anterodorsally directed and overhangs the distinct praezygapophysis, whereas the posterior process is posterodorsally directed and bears the postzygapophysial facet on its posteroventral side (Fig. 9F and J). The anterior process articulates on the posterior process of the preceding vertebra and the articular facet is nearly vertical (Fig. 9J). In the last disarticulated distal vertebrae (Fig. 9G), there seem to be only these processes and no separate zygapophyses as, for example, in vertebrae 12 and 13. These anterior and posterior processes of the neural arch made the tail stiffer, probably reducing lateral and vertical movements between the adjacent vertebrae; they also served as support for the osteoderms (Fig. 9F).

Haemapophyses. The four scattered haemapophyses are Y-shaped with simple, rod like haemal spines (Fig. 8B). The pedicels are as long as the spine or longer. Three haemapophyses close to each other are rather small (~5 mm high) suggesting that they disarticulated from the distal part of the mid-caudal vertebral row. The largest and plausibly most proximal chevron (it occurs at level of caudal 3 of the row) is 6.5 mm high but the spine is incomplete distally; it has pedicels that are bridged proximally by a bony lamina. A further element may occur between the first two vertebrae of the row and the close isolated vertebra. Two haemapophysis are *in situ* (Fig. 8B) associated with the vertebrae 6-7 and 9-10. The presence of the disarticulated haemapophyses close to the vertebral row, their size and the association of one of them with the vertebrae 9 and 10 indicate that at least the first ten elements of the row are middle caudals.

Osteoderms. Osteoderms are associated with all preserved caudal vertebrae. Those in the 'spot' of disarticulated mid-caudal elements are clearly paired, although disarticulated from their original position above the vertebrae (Fig. 8A). One complete osteoderm is paired to one that is damaged at the broader extremity (Fig. 10). Another nearly complete is close to the latter, lies above the centrum of the vertebra 1 in Fig. 8A and was possibly paired with another close and partly preserved osteoderm. Two paired and damaged osteoderms are close to the centrum of the vertebra 3 (Fig. 8A). A fragmentary osteoderm is possibly preserved near the isolated neural arch. Other bone fragments preserved in this 'spot' are probably incomplete osteoderms. The complete and nearly complete osteoderms are exposed in dorsal view. At least one osteoderm missing the extremities is preserved in the group of bone fragments placed 35 mm from the main one (see Fig. 3). These small bones have all approximately the same size and are longer than wide; the complete one is 6.4 mm long and 3.2 mm wide at maximum. They are drop-shaped and symmetrical when complete, with irregular margins and relatively large marginal 'denticles', mainly in the broader, presumably posterior, half (Fig. 10). The dorsal surface is not pitted and is not even coarsely rough or crossed by radial striae and grooves; it is pierced by small neurovascular

Fig. 10 - *Carinthiasuchus kandutschi*, gen. n. sp. n., Nockalm7030u, holotype, osteoderms. (A) The three better preserved osteoderms of the proximal mid-tail vertebrae in dorsal view. B) Detail of the osteoderm. Abbreviations: de, marginal denticles; fo, neurovascular foramen; po, pointed and probably anterior extremity of the osteoderm; ri, longitudinal median ridge. Scale bar is 2 mm.



foramina (four and paired, in the osteoderm of Fig. 10B). The osteoderms are arched in a way to form a blunt and median longitudinal ridge dorsally. There is no distinct anterior process, but one extremity of the osteoderm (plausibly the anterior one) is somewhat pointed. Those paired osteoderm are probably paramedian pairs along a single paramedian row despite they are symmetrical. Because of their size and the length of the corresponding vertebral centra, there were two or three pairs of paramedian scutes per vertebra.

The osteoderms of the articulated vertebral row are still closely associated to their vertebrae dorsally and apparently form a single median row (Figs. 8B and 9B-F). They occur up to the last vertebra of the string; at least 29 can be identified, but some have been destroyed by weathering and/or preparation. There are three osteoderms per vertebra: one lies above the middle of the vertebra, half of an anterior one above the anterior zygapophyseal articulation and associated processes, and half of a posterior one above the posterior zygapophyseal articulation and associated processes (see Fig. 9). In the middle caudal vertebrae from a more proximal position, the posterior osteoderm lays on the low neural spine. Osteoderms contact each other in the vertebrae 4 and 5 but they do not overlap. They are all narrow and anteroposteriorly elongated. Because of their shape, they probably rotated to show their dorsoventral side; Their length seems to diminish in those associated to the distal caudal vertebrae and also the shape seems to become more irregular backward (Fig. 9F and J), but those distal elements are mostly damaged, thus this change may be apparent. The better preserved and mostly complete osteoderms occur in the vertebrae 4-9 of the row (Fig. 9C-E, H-I). They are 4-5.7 mm long. They have an overall shape of a lying 8 composed by a larger (posterior) and a smaller (anterior) portions, both lanceolate in the exposed view (Fig. 9C-E, H-I). It is possible that the point of the anterior narrower portion was overlapped by the posterior broader portion of the preceding osteoderm. The surface has often a spongy and finely striated aspect and there seems to be a thin and irregular longitudinal ridge, at least on the broader portion of the osteoderm. These elements may be the results of the cossification of two adjacent osteoderms as it appears in the osteoderm above vertebra 7, where the two portions are close to each other but separated (Fig. 9C-E, H-I).

PHYLOGENETIC ANALYSIS

Carinthiasuchus kandutschi gen. n. sp. n. is unambiguously referable to the Archosauriformes based on the combination of antorbital fenestra, teeth with serrated cutting margins and thecodont implantation, and osteoderms (Nesbitt 2011). In order to test the affinities of *Carinthiasuchus kandutschi* gen. n. sp. n. among the archosauriforms, we included it in the data set of Desojo & Rauhut (2024), which is an updated version of the phylogenetic matrix of Nesbitt (2011) focusing on that clade. The matrix is reported in the SI. The dataset was analysed using equally weighted parsimony in TNT 1.6 (Goloboff & Morales 2023). All analyses were performed setting maxtree = 50.000. We performed 1000 'Traditional search' runs using default settings, then explored the tree islands stored in the RAM during the first search round. Nodal support was calculated replicating the analysis and saving all trees up to 10 steps longer than the shortest topologies. The reduced strict consensus of the most parsimonious trees found was produced in TNT pruning *a posteriori* six "wildcard" terminal taxa (i.e., *Pagosvenator candelariensis* Lacerda, de França & Schultz, 2018, CM 73372, CPEZ 239b, UFRGS PV0629 T, UFRGS PV152 T, and UFRGS PV156 T, see Desojo & Rauhut 2024). The analysis found 39.312 shortest trees of 1712 steps each (Consistency Index excluding uninformative characters = 0.3101; Retention Index = 0.7360). The reduced strict consensus of the shortest trees found (Fig. 11) broadly agrees with the topology discussed by Desojo & Rauhut (2024). In all shortest trees, *Carinthiasuchus kandutschi* is placed among an early-diverging branch of the pseudosuchian clade Poposauroidea, as sister taxon of *Qianosuchus mixtus* Li Wu, Cheng, Sato & Wang, 2006 from the Anisian of China (Li et al. 2006). The nodal support of this node is low (Bremer support = 1) due to the very fragmentary nature of Nockalm 7030u. Yet, *Carinthiasuchus kandutschi* is unambiguously excluded from the most derived poposauroid clade including *Arizonasaurus babbitti* Welles, 1947, *Xilousuchus sapingensis* Wu, 1981 and shuvosaurids because it retains the plesiomorphic combination of both maxillary and dentary teeth with the presence of osteoderms (Nesbitt 2011). We tested three alternative placements of *Carinthiasuchus kandutschi* among Pseudosuchia re-running the analysis in TNT and enforcing the sister taxon relationships of the former with, alternatively, three pseudosuchians from Europe: i.e., *Ticinosuchus ferox*, *Batrachotomus kupferzellensis* Gower, 1999 (upper Ladinian, Germany), and *Polonosuchus silesiacus* Sulej, 2005 (upper Carnian, Poland). The shortest topologies found under these constraint tests were, respectively, five, three, and eight steps longer than the shortest trees found with no topological constraints. These results suggest that alternative placements of the new taxon among early-diverging suchians, outside Poposauroidea, are suboptimal explanations of the available data, yet a rauisuchian affinitity for *Carinthiasuchus* is less likely.

Discussion

The skeletal remains preserved on the slab clearly belong to the same individual, because they are closely associated, have sizes compatible with the provenance from a single individual, they were found in a lithostratigraphic unit where reptile remains are uncommon, and they represent the first evidence of archosaur reptiles in it.

Size and ontogenetic stage

The skull of Nockalm 7030u was not much longer than the 53 mm preserved. Considering a short premaxilla, the estimated skull length is ~65 mm. For comparison, the estimated skull length of *Ticinosuchus ferox* is 260 mm (Krebs 1965) and that of *Batrachotomus kupferzellensis* is approximately 400-500 mm (Gower 1999). The small size and the lack of fusion of the skull elements and of the mandibular rami at the symphysis suggest that the individual was immature. Although the neural arches in the distal and at least in part of the mid-caudals appear to be fused to their centra, some elements present sutural lines (Fig. 9E-F) and the lack of fusion in at least one of the vertebrae of the 'spot' is evidenced by the isolated neural arch (Fig. 8A). This also supports the immaturity of the individual. Therefore, the adult of *Carinthiasuchus kandutschi* was probably somewhat larger than the only known individual.

Maxilla. Antorbital fenestra and antorbital fossa are plesiomorphic features for the Archosauriformes, but the participation to the antorbital fossa of the elements bordering the antorbital fenestra varies within the clade. According to Nesbitt (2011: 96) the fossa could be, alternatively, restricted (1) to the lacrimal; (2) to the lacrimal and the dorsal process of the maxilla; or (3) it can be present on the lacrimal, dorsal process of the maxilla and the dorsal margin of the posterior process of the maxilla (the ventral border of the antorbital fenestra). In Nockalm 7030u, the fossa occurs on the dorsal margin of the posterior process of the maxilla but not on the dorsal (ascending) process of that bone, thus *Carinthiasuchus kandutschi* does not fall in any of the states identified by Nesbitt (2011). However, the late Early Triassic poposauroid *Xilousuchus sapingensis* from China (Nesbitt et al. 2011: figs 2 and 3C) and *Arizonasaurus babitti* from the Anisian of SW USA (Nesbitt 2005: fig. 3) present the antor-

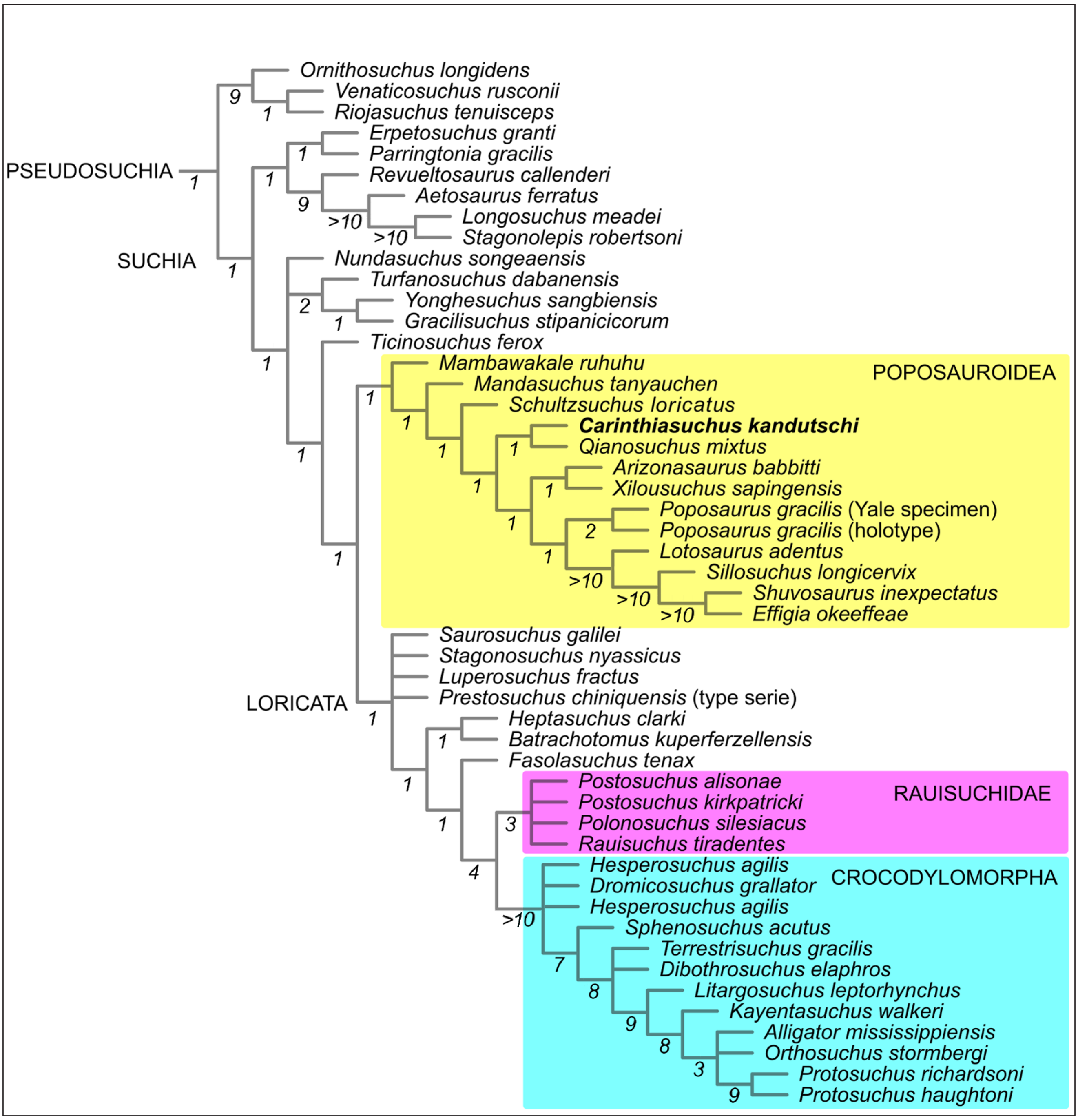


Fig. 11 - *Carinthiasuchus kandutschi,* gen. n. sp. n., phylogenetic relationships. Reduced strict consensus of the shortest trees found by the phylogenetic analysis after a posteriori pruning of six "wildcard" terminal taxa (see text). Number at nodes indicate the Bremer support values. This is the pseudosuchian portion of the tree; the whole tree is in the SI (SI Fig. 2)

bital fossa on the posterior process of the maxilla but not on the basal part of the ascending process and the antorbital fossa forms higher in the ascending process. Since only the base of the ascending process of *Carinthiasuchus kandutschi* maxilla is preserved, the development of the antorbital fossa in the new taxon may potentially be the same as in those poposauroids. This peculiar configuration of the antorbital fossa could thus represent an additional synapomorphy linking *Carinthiasuchus kandutschi* with some early-diverging poposauroids.

A "bulbous" distinct ridge (Nesbitt 2011: 65) bordering the antorbital fossa ventrally on the posterior process of the maxilla is a synapomorphy of the rauisuchid *Postosuchus kirkpatricki* Chatterjee, 1985 (Norian, SW USA) and *Polonosuchus silesiacus*, whereas the ridge is "sharp" in the aetosaur *Stagonolepis robertsoni* Agassiz, 1844, *Revueltosaurus callen-*

deri Hunt, 1989, the poposauroid *Lotosaurus adentus* Zhang, 1975 and *Effigia okeefeae* Nesbitt & Norell, 2006 and some basal dinosaur (ibidem). In *Xilousuchus sapingensis* and *Qianosuchus mixtus*, no ridge separates the antorbital fossa from the rest of the lateral face of the maxilla (Nesbitt 2011; Nesbitt et al. 2011). Furthermore, *Carinthiasuchus kandutschi* lacks the slot on the anterolateral surface of the maxilla for the posterior process of the premaxilla which is synapomorphic of the Poposauroidea.

An anterior process on the maxilla bordering a subnarial foramen is observed in *Batrachotomus* (Gower 1999: figs. 2A, 3A, and 4-5), but it is smaller and lacks a dorsally-facing articular surface. A process and notch occur also in the maxilla of an unnamed archosaur coeval with *Batrachotomus* (Schoch 2011: figs. 3 and 4a-b), but the notch is lateral to the process rather than below. *Heptasuchus clarki* Dawley, Zawiskie & Cosgriff, 1979 (sister taxon of *Batrachotomus*) has a short triangular anterior process on the maxilla and a comparatively large subnarial foramen like *Carinthiasuchus kandutschi* in the reconstruction by Dawley et al. (1979: fig. 2), but it is different in the reconstruction by Nesbitt et al. (2020: fig. 3).

Shape and size of the anterior process of *Carinthiasuchus kandutschi* are comparable to those of the crocodylomorph *Dromicosuchus grallator* Sues, Olsen, Carter & Scott, 2003, which, however, contacts the nasal and borders the subnarial gap (Irmis 2013: fig. 4a). According to Nesbitt (2011), the presence of a subnarial foramen between the maxilla and the premaxilla occurs in many other archosaurs, i.e. *Qianosuchus mixtus*, *Fasolasuchus tenax* Bonaparte, 1981*, Rauisuchus tiradentes* von Huene, 1942*, Postosuchus kirkpatricki* and *Polonosuchus silesiacus*, *Hesperosuchus* "*agilis*" Colbert, 1952, *Kayentasuchus walkeri* Clark & Sues, 2002, and *Protosuchus*. The border of the foramen is present on the maxilla but not on the premaxilla in *Erythrosuchus africanus* Broom, 1905, *Lotosaurus adentus*, *Effigia okeefeae*, and *Shuvosaurus inexpectatus* Chatterjee, 1993. In all these taxa, the foramen is comparatively smaller than the notch present in Nockalm 7030u.

A small anterior process and notch occur also in the maxilla of the small non-archosaur archosauriform *Polymorphodon adorfi* Sues, Schoch, Sobral & Irmis, 2020 from the Ladinian of Germany, but the notch is much smaller than in *Carinthiasuchus kandutschi* (Sues et al. 2020: fig. 3B).

Dentary. Although the exact height/length ratio of the dentary of *Carinthiasuchus kandutschi* cannot be calculated because the bone is incomplete distally, the dentary of the Austrian taxon is more slender than that of most pseudosuchians (Nesbitt 2011: figs 8, 11-12). For example, the ratio (calculated on the entire dentary) is 6.1 in *Ticinosuchus* according to the reconstruction by Krebs (1965) and 6.3 in *Batrachotomus* according to the reconstruction by Gower (1999). Closer is the ratio of the entire dentary of *Qianosuchus* based on Li et al. (2006; fig. 2B; 7.9), while those of the Norian-Rhaetian crocodylomorphs *Dromicosuchus grallator* (see Nesbitt 2011: fig. 12E) and *Terrestrisuchus gracilis* Crush, 1984 (Crush 1984: fig. 5) are higher (8.5 and 17, respectively).

The dentary of *Carinthiasuchus kandutschi* bears also an unusually high number of teeth (Nesbitt 2011: figs 8, 11-12). *Ticinosuchus* has 16 dentary teeth in the reconstruction by Krebs (1965); *Batrachotomus* has 13 in the reconstruction by Gower (1999) and other loricatans have usually 14-15 teeth. Crush (1984: 142) reconstructed a total number of 24 teeth for the dentary of *Terrestrisuchus gracilis* but commented that "this may be slightly more than were originally present".

Teeth. Serrated labiolingually flattened crowns in the maxillary and dentary teeth are a plesiomorphic feature within the Archosauriformes (Nesbitt 2011). Serrated archosauriform teeth are plesiomorphically blade-like and slightly recurved distally, with a convex mesial cutting margin and a straight or concave distal cutting margin. The finder of the specimen soon noticed that the posterior maxillary crown of Nockalm 7030u resembles the denticulated and symmetrical posterior maxillary crowns of the Triassic pterosaur *Austriadactylus cristatus* Dalla Vecchia, Wild, Hopf & Reitner, 2002 (see Dalla Vecchia et al. 2002: fig. 3C; Dalla Vecchia 2014: fig. 4.1.17), but the new Austrian specimen is obviously not a pterosaur. The non-archosaur archosauriform *Polymorphodon adorfi* has a distinctly heterodont dentition in the maxilla and dentary (Sues et al. 2020). Unlike *Carinthiasuchus kandutschi*, the anterior maxillary crowns are slightly recurved (Sues et al. 2020: figs 4A and 7) and the marginal denticles of the German taxon are hook-shaped; furthermore, denticles appear to be comparatively smaller than in the distal maxillary crown of the Austrian taxon, if the serration is the same in the posterior maxillary teeth as in the anterior maxillary and dentary teeth (Sues et al. 2020: figs 3B-C and 4).

A variety of isolated serrated teeth of archosauriform reptiles are known from the Middle - lower Upper Triassic sites of the Alps (e.g., Dalla

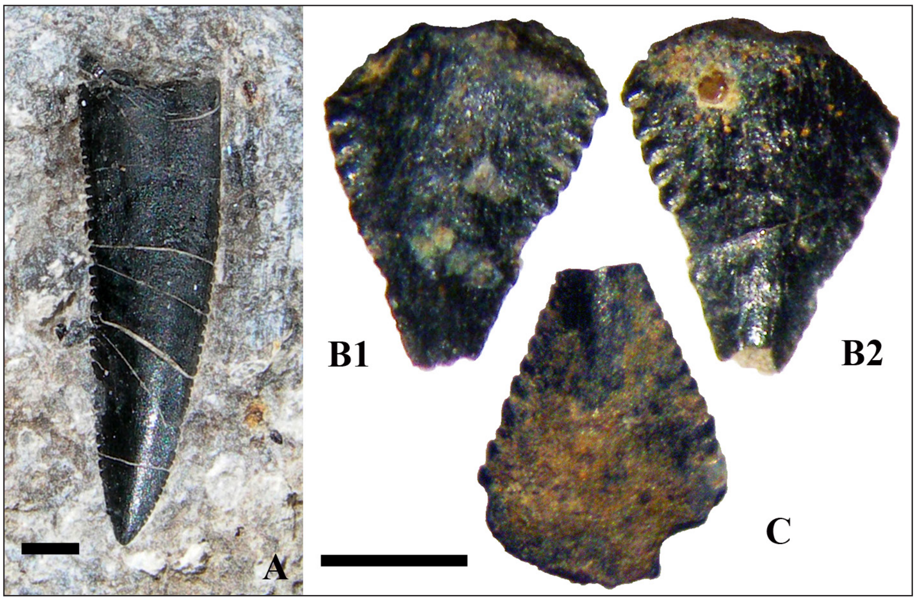


Fig. 12 - Archosauriform tooth crowns from the lower Carnian of Fusea (Italy) in labiolingual views. A) MFSN 31609; B1-2) MFSN provetta Z1 (no number), labial and lingual views (or vice versa); C) MFSN provetta K17. The scale bar is 1 mm in A and 0.5 mm in B and C.

Vecchia & Avanzini 2002; Renesto et al. 2003; Dalla Vecchia 2008; FMDV, pers. obs.), but skeletons with a corresponding in situ dentition are unreported. Isolated small and serrated teeth with labiolingually compressed, symmetrical or nearly symmetrical crowns occur from the lower Carnian of the Fusea site in the Carnian Alps of Italy (Dalla Vecchia 2008; FMDV, pers. obs.). The Fusea site (Udine Province, Friuli Venezia Giulia Autonomous Region) is located about 40 km SW of the Jadersdorf site. Those mostly still undescribed teeth indicate the existence of a variety of small-sized archosauriform reptiles that are testified only by teeth. One tooth has a very tall and mesiodistally narrow crown with finely serrated cutting margins (Fig. 12A) like the anterior maxillary tooth of *Carinthiasuchus kandutschi*; more common are the lower, mesiodistally broader and symmetrical crowns with coarser denticles (Fig. 12B-C) resembling the distal maxillary tooth of the new taxon, although mesial and distal denticles do not show a marked difference in size and are comparatively smaller. Other tooth crown types from Fusea site are figured in Dalla Vecchia (2008: figs 93 and 95). Archosauriforms with a serrated dentition unlike that plesiomorphic for the clade may have been common along the western Tethyan coasts during Middle-early Late Triassic times.

Caudal vertebrae. Articulated tails are rare in the fossil record of Triassic archosaurs. The holotype of *Ticinosuchus ferox* has a nearly complete and slightly disarticulated vertebral column made of 55 caudals (Krebs 1965; Lautenschlager & Desojo 2011), 21 of which are considered as proximal elements. Also *Decuriasuchus quartacolonia* de França, Ferigolo & Langer, 2011 (Ladinian, Brazil) has about 50 vertebrae in the tail (França et al. 2011: fig. 1). The poposauroid *Qianosuchus mixtus* has 23 proximal caudal vertebrae and at least 22 more distal elements, for an estimated total of >50 vertebrae in its fairly long tail (Li et al. 2006).

Thus, the 25 caudals preserved in Nockalm 7030u plausibly represent most of the distal half of the tail. The presence of a chevron associated with vertebra 9 of the row suggests that at least 14 of the total 25 vertebrae are mid-caudals and only 11 are potentially distal caudals, but some distal elements are surely missing.

The rauisuchid *Rauisuchus tiradentes* (Carnian, Brazil) has comparatively elongated "posterior" caudals, but the length/height at mid centrum ratio is only 2.27 in the specimen figured by Lautenschlager & Rauhut (2014: fig 11C). The elongate distal caudal vertebrae of *Postosuchus kirkpatricki*, which lack a neural spine as the posterior vertebrae of the 'row', have a maximum ratio of about 3.7 (Weinbaum 2013: fig. 7c). The basal poposauroid *Schultzsuchus loricatus* Desojo & Rauhut, 2024 (Ladinian, Brazil) has elongated distal caudals, but the ratio is only 2.6 (Desojo & Rauhut 2024: fig. 4l). Instead, the derived poposauroid *Shuvosaurus inexpectatus* (Norian, SW USA) presents a mid caudal vertebra with a ratio 3.67 but distal caudals with a ratio over 10 (Nesbitt & Chatterjee 2024: figs. 25e-f and 26i-j and o-p), which are therefore even more elongate than those of *Carinthiasuchus kandutschi*.

An accessory laminar process (sensu Nesbitt

2011) is found in the anteroventral portion of the ventral half of the neural spines of the mid-caudal vertebrae in the phytosaur *Smilosuchus*, the ornithosuchid *Ornithosuchus, Qianosuchus mixtus*, "rauisuchoids" (*Ticinosuchus ferox*, *Rauisuchus tiradentes*, *Polonosuchus silesiacus*, *Decuriasuchus quartacolonia* and *Batrachotomus kupferzellensis*), crocodylomorphs (*Saltoposuchus* and *Terrestrisuchus*), and some theropod dinosaurs (Lautenschlager & Desojo 2011; Nesbitt 2011). In *Ticinosuchus ferox*, the accessory process starts at the sixth caudal and can be traced up to the 35th to 40th vertebrae. In *Qianosuchus mixtus*, the process occurs in only 10 mid-caudal vertebrae; in *Decuriasuchus quartacolonia*, it occurs in the "mid-portion of the tail" (França et al. 2011: 392). In *Ticinosuchus ferox* (see Krebs 1965: figs. 25-26), *Qianosuchus mixtus* (cf. Nesbitt 2011) and *Decuriasuchus quartacolonia* (see França et al. 2011: figs 1 and 3d and f), which preserve nearly complete and articulated tails, the accessory process lie more distally on the neural spine of the anterior caudal vertebrae than they do on the more posterior caudal vertebrae, i.e. the accessory process migrates anteriorly and is neatly separated from the neural spine in the distal mid-caudals. The volcanic cone-like process present in a few mid-caudals of *Carinthiasuchus kandutschi* are unlike those present in the vertebrae figured by Lautenschlager & Desojo (2011: fig. 9), but the change in morphology with position along the column corresponds. However, unlike Nockalm 7030u, these accessory processes are usually associated with tall neural spines and are lower than the spines. Unlike the other archosaurs with tall caudal spines, these processes are evidently related to the support of the overlying osteoderms in *Carinthiasuchus kandutschi*.

The accessory articular processes of the neural arches observed in *Carinthiasuchus kandutschi* are not reported in any Triassic archosauriform (e.g., Colbert & Mook 1951; Krebs 1965; Crush 1984; Li et al. 2006; Nesbitt et al. 2009; Nesbitt 2011; França et al. 2011; Weinbaum 2013; Lautenschlager & Rauhut 2014; Ezcurra 2016; Li et al. 2016; Nesbitt & Chatterjee 2024).

Unlike *Qianosuchus*, *Carinthiasuchus kandutschi* does not show any swimming adaptation in the tail (i.e., tall neural spines and chevrons) and was probably a land dweller. Despite that the Partnach Formation is considered a marine lithostratigraphic unit, the presence of terrestrial plant remains in the same outcrop as Nockalm 7030u indicates the existence of a close emergent land. Therefore, *Carinthiasuchus kandutschi* lived on that emergent land and the only know individual was transported to sea like the few known specimens of *Ticinosuchus ferox* in the Grenzbitumenzone/Besano Formation (Röhl et al. 2001; Rieppel 2019).

Osteoderms. Among the archosauriforms, *Vancleavea*, the proterochampsians *Chanaresuchus* and *Tropidosuchus*, *Euparkeria*, phytosaurs, and most crocodylian-line archosaurs bear osteoderms dorsal to the neural spines of the vertebrae (Nesbitt 2011). Pseudosuchian clades are generally characterized by osteoderms (Scheyer & Desojo 2011), but poposauroids lack osteoderms with the exclusion of the basal *Qianosuchus mixtus*, *Schultzsuchus loricatus* and *Mandasuchus tanyauchen* Butler, Nesbitt, Charig, Gower & Barrett, 2017 (?Middle Triassic, Tanzania). *Qianosuchus*, however, does not have osteoderms in the tail (Li et al. 2006) and it is unclear whether *Mandasuchus* had caudal osteoderms or not (Butler et al. 2017). Since the tails of Triassic archosaurs are rarely found articulated, the morphology and arrangement of the caudal osteoderms is practically unknown. Partial exception is *Ticinosuchus ferox*, as seen above; the caudal osteoderms of the new taxon are unlike those of the Swiss archosaur which are pentagonal or "arrowhead-shaped" (Lautenschlager & Desojo 2014: 360) and overlapping in a single row along the anterior to mid-caudal segment of the tail (Krebs 1965: fig. 63; Lautenschlager & Desojo 2014). The outline of the most proximal preserved caudal osteoderms of the new taxon (Fig. 10) resembles that of the osteoderm of *Batrachotomus kupferzellensis* tentatively referred as caudal by Gower & Schoch (2009: fig. 7JK), which, however, is flat, less elongated, and without a median longitudinal ridge and lateral denticles. The most proximal preserved caudal osteoderms of *Carinthiasuchus kandutschi* are somewhat similar to the drop-shaped symmetrical osteoderm of the rauisuchian '*Prestosuchus' chiniquensis* von Huene, 1938 (Ladinian, Brazil) figured by Scheyer & Desojo (2011: pl. 1, fig. 5) and the supposedly caudal, symmetrical and leaf-shaped, osteoderms of *Rauisuchus tiradentes* (see Lautenschlager & Rauhut 2014: fig. 16D), which, however, present radial ridges on the external surface and lack lateral denticles. The presumed caudal osteoderms of the loricatan *Fasolasuchus tenax* (Norian, Argentina) differ from those of *Carinthiasuchus kandutschi* in the bifid and narrower extremity and the absence of lateral denticles (Bonaparte 1981: fig. 20A). *Schultzsuchus loricatus* has putative caudal osteoderms that are stouter than those of *Rauisuchus tiradentes* and "almost symmetric ...triangular, almost heart shaped, with a centrally placed anterior articular projection and a marked ventral concavity posteriorly on the basal surface" (Desojo & Rauhut 2024: 990). Furthermore, they have "smooth ridges radiating laterally from an anteroposterior low central protuberance" (*ibidem*). Thus, they are unlike those of *Carinthiasuchus kandutschi*.

The rauisuchian *Decuriasuchus quartacolonia* has a median row of osteoderms on the back of the tail (one pair per vertebra), and scattered smaller osteoderms along the ventral surface of the tail (França et al. 2013). *Ticinosuchus ferox* has also a single median row of osteoderms dorsally in the whole tail (excluded the terminal caudals) and ventrally in the proximal half of the tail (Krebs 1965: 118, pl. 3). The presence of a single row of dorsal osteoderms in the tail is supposed also for *Postosuchus alisonae* Peyer, Carter, Sues, Novak & Olsen, 2008 (see Peyer et al. 2008: 373), *Saurosuchus galilei* Reig, 1959 (Sill 1974: 349), and *Fasolasuchus tenax* (see Bonaparte 1981: 74), but this is deduced by the symmetrical shape of few scattered elements. *Carinthiasuchus kandutschi* is distinguished by the presence of paired and symmetrical paramedian osteoderms above the proximal mid-caudal vertebrae. Two paramedian rows of caudal scutes are reported in *Polonosuchus silesiacus* by Szulej (2005: 79), but this is wrongly considered the 'normal' condition in 'rauisuchians' by Szulej (2005). Those purported caudal scutes are asymmetrical (Szulej 2005: fig. 4H-L). The basal crocodylomorph *Protosuchus richardsoni* Brown, 1933 (Lower Jurassic, SW USA) has a single paramedian row of paired symmetrical osteoderms along the whole dorsal side of the tail, but the lateral and ventral sides are covered by smaller osteoderms "so that the tail is completely encased in armor plates" (Colbert & Mook 1951: 166); a single paramedian row of paired symmetrical osteoderms in the tail presumably occurred also in some Triassic basal crocodylomorphs like, for example, *Dromicosuchus grallator* (see Sues et al. 2003: 336 and fig. 5).

Elongated and lying 8-shaped osteoderms like those associated to the mid-distal caudals of Nockalm 7030u are unreported within the Triassic archosauriforms (Walker 1964; Krebs 1965; Sill 1974; Peyer et al. 2008; Nesbitt et al. 2009; Gower & Schoch 2009; França et al. 2011; Scheyer & Desojo 2011; Li et al. 2016; Parker et al. 2022; Desojo & Rauhut 2024).

Unlike *Ticinosuchus ferox* (see Krebs 1965) and *Decuriasuchus quartacolonia* (see França et al. 2011), there is no evidence of ventral osteoderms in Nockalm 7030u, but this may be due to disarticulation, as suggested by the dislocation and dispersal of the haemapophyses.

CONCLUSIONS

Carinthiasuchus kandutschi is a new archosaur, one of the very few from the Middle-lower Upper Triassic of the Alpine realm. The phylogenetic analysis recovered it as a pseudosuchian in a basal position within the Poposauroidea. The only European poposauroids, the late Olenekian *Ctenosauriscus koeneni* (Huene, 1902) and the Anisian *Bromsgroveia walkeri* Galton, 1985, belong to the sail-backed Ctenosauriscidae. Although the lack of both pelvis and dorsal vertebrae in Nockalm 7030u prevents any direct comparison of *Carinthiasuchus kandutschi* with these taxa (Butler et al. 2011), the new Austrian taxon is provisionally excluded from Ctenosauriscidae based on the presence in the holotype of features optimized as plesiomorphic states among the later-diverging poposauroid node including Ctenosauriscidae (e.g., marginal dentition and osteoderms; Nesbitt 2011; our study). The discovery of *Carinthiasuchus*, despite its fragmentary status, is thus significant in expanding both the geographic and stratigraphic distribution of the poposauroids in Europe and their diversity. The new taxon is represented by a small immature individual characterised by features in the maxilla, dentary, dentition, elongation of mid-distal caudal vertebrae and presence of accessory processes in their neural arches, and shape and arrangement of the caudal osteoderms. It was probably a terrestrial dweller living in emergent areas along the western margin of the Tethys Ocean.

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