

**RAIBLIANIA CALLIGARISI GEN. N., SP. N., A NEW TANYSTROPHEID
(DIAPSIDA, TANYSTROPHEIDAE) FROM THE UPPER TRIASSIC (CARNIAN) OF
NORTHEASTERN ITALY**

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Abstract. Tetrapod remains are extremely rare in the early Carnian (Late Triassic) Calcare del Predil Formation on the Italian side of the Julian Alps (Friuli Venezia Giulia Autonomous Region), which yielded the Raibl fossil assemblage including the famous “Raibl ichthyofauna”. A new tanystropheid archosauromorph, *Raibliania calligarisi*, is here named based on a partial skeleton found in this formation along the Prasnig Brook. The new taxon is similar to *Tanystropheus*, sharing with it the very elongated cervical vertebrae, but is characterized by the presence of relatively large button-like teeth; apex of the neural spines not transversely thickened; articular facets on the upper corners of the neural spines of the dorsal vertebrae; short and distally pointed pleurapophyses of the second and last ‘lumbar’ vertebra; ilium with a long preacetabular process bearing a robust and transversely thick tuberosity and a medial ridge bordering the entire ventral part of the iliac blade; and pubis with a cranial process. Tanystropheids lived in the present day Alps and Prealps of Friuli Venezia Giulia Region from the late Anisian to the mid-late Norian and were an important component of the coastal reptile faunas, although they were less common than eusauroptrygians and placodonts during the early Carnian. Tanystropheids with extremely elongated cervical vertebrae are reported in this area from the upper Anisian to the lower Carnian.

INTRODUCTION

Today, the Cave del Predil village is in the territory of the Italian Republic, but it was part of the Austro-Hungarian Empire before the 1918, when its name was Raibl. It is located close to the border among Italy, Slovenia and Austria in the Tarvisio Municipality of Udine Province, Friuli Venezia Giulia Autonomous Region. The name “Raibl” is renowned worldwide as one of the historical localities for Triassic fish (Kner 1866, 1867, 1868; Hauer

1867; Griffith 1977) and flora (Bronn 1858; Schenk 1866-67; Stur 1885). Tetrapods are represented to date only by a caudal fragment of a vertebral column (MFSN 13228) that was tentatively referred to a thalattosaur by Dalla Vecchia (1994) and a few, still undescribed, fragmentary remains of uncertain affinities (Dalla Vecchia & Simonetto 2018). Here I report one of the still undescribed tetrapod remains collected in this historical fossil-bearing locality, MFSN 27532, which represents a new genus and species of tanystropheid archosauromorph. The affinity to the new taxon of MFSN 13228 is also discussed.

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TERMINOLOGY AND METHODS

If not specified otherwise, the terminology by Romer (1956) is used in this paper. “Cranial” and “caudal” were used instead of “anterior” and “posterior”. Proximal caudal vertebrae are considered those with pleurapophyses (sensu Wild 1973; the pleurapophyses are often reported as “caudal ribs” or “transverse processes” in the literature); middle caudals lack pleurapophyses, but have hemapophyses; distal caudals lack pleurapophyses and hemapophyses. The denominations of the laminae in the neural arches of the vertebrae are based on Wilson (2012); the use of “anterior” and “posterior” is maintained in these denominations. Measurements taken in the vertebrae are shown in Fig. 1. The preacetabular process or lobe is the projection of the iliac blade cranial to its connection with the acetabular portion of the ilium.

Most of the skeletal elements were still inside the rock when the holotype specimen of the new taxon was discovered and mechanical preparation (mainly by steel needles mounted on a support) was undertaken by the author under a Wild M3 binocular microscope at the MFSN during years 2006-2019.

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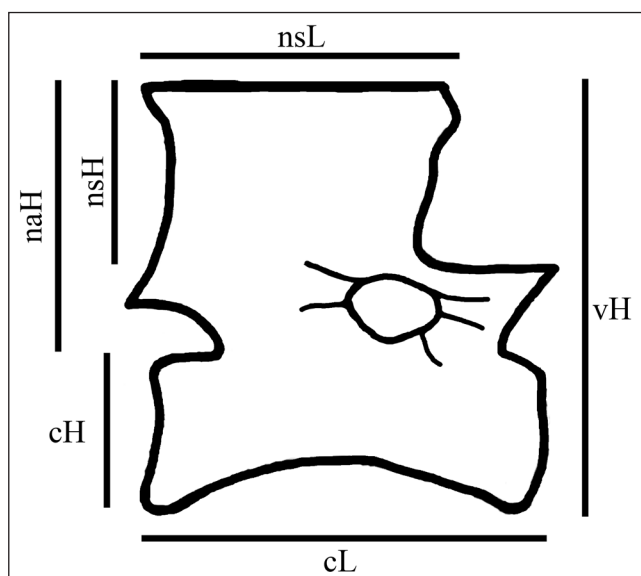


Fig. 1 - Measurements taken in the vertebrae of *Raiblia calligarisi* gen. n., sp. n. Abbreviations: cH, centrum height; cL, centrum length; naH, neural arch height; nsH, neural spine height; nsL, neural spine length; vH, total vertebral height.

GEOLOGICAL AND PALAEOONTOLOGICAL BACKGROUND

The Raibl fish-bearing beds were known in the 19th century literature as “Schwarze Schiefer” (Schenk 1866-67), “Fisch-Schiefer” (Hauer 1867) and “Bituminösen Schiefer” (Stur 1868). Assereto et al. (1968) included them in the Calcare del Predil (Predil

Limestone) corresponding to the “fish-bearing beds” and the “coral beds” of former authors (e.g., Suess 1867). The Predil Limestone crops out in the north-eastern corner of the Friuli Venezia Giulia Autonomous Region of Italy in the Italian portion of the Julian Alps and has a maximum thickness of 200 m. The Predil Limestone is composed mainly of well-bedded black limestone and marly limestone; bioclastic limestone with coral, echinoid, pelecypod, and gastropod remains occurs toward the top of the unit (Assereto et al. 1968). The Predil Limestone overlies and is laterally equivalent to the “Ladinian-Carnian dolomite” and is overlain by the Rio dal Lago Formation (Caggiati et al. 2018: fig. 2). It originated in a small marine basin with dysoxic to anoxic conditions at the bottom (Tintori 1992), which developed into and laterally to the carbonate platform of the “Ladinian-Carnian dolomite”.

According to Assereto et al. (1968), the Raibl fish association comes from the lower part of the Formation, which was dated to the early Carnian (early Julian) based on the presence of the ammonoids *Clionitites basileus* and *Trachyceras aon* (*Aon* Ammonoid Subzone). A recent study (Dal Corso et al. 2018) shows that the Predil Limestone spans the Carnian ammonoid zones 2 and 3 and part of zone 4 of Balini et al. (2010), corresponding to the *Trachyceras aon* and *Trachyceras aonoides* ammonoid subzones and the base of the *Austrotrachyceras austriacum* ammonoid Zone, i.e. most of the lower Carnian (Julian) (see also Caggiati et al. 2018).

The fossils in the “Raibl fish-bearing beds” include marine fishes (see Dalla Vecchia 2008b and references therein), terrestrial plants (Dobruskina et al. 2001; Kustatscher et al. 2011), decapod crustaceans (Bronn 1858; Audo et al. 2018), and other marine invertebrates (ammonoids and other cephalopods, rare pelecypods, gastropods and echinoids). The abundance of terrestrial plants and the comparatively high content of organic matter from continental sources (60% of the total; Tintori et al. 1985) suggest the presence of emergent areas close to the basins where the Predil Limestone was depositing. However, the absence of coeval terrigenous continental deposits in the region indicates that these areas were probably flat islands of the locally exposed Ladinian-Carnian carbonate platform (see Caggiati et al. 2017: fig. 2).

Although the fossils from the “Raibl fish-bearing beds” were historically reported in literature as coming from “Raibl” suggesting a provenance from

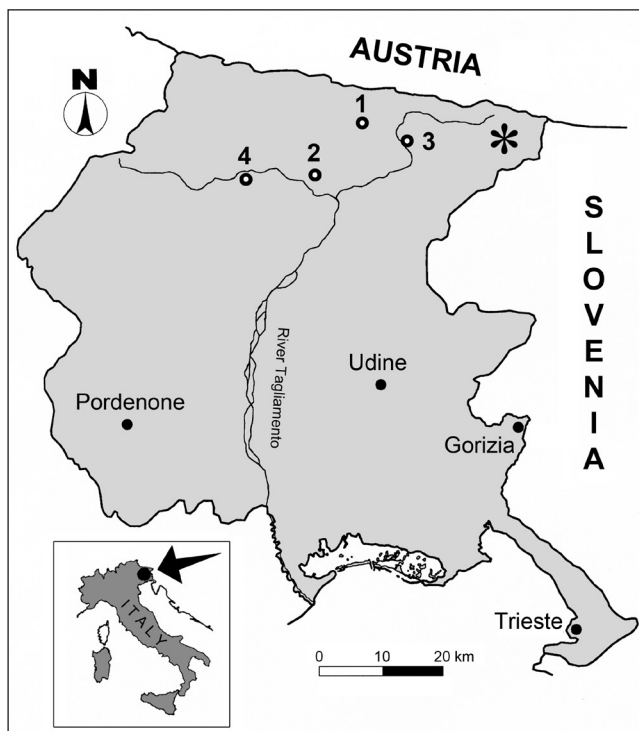


Fig. 2 - Location of the finding place of MFSN 27532 in the Friuli Venezia Giulia Autonomous Region of NE Italy (asterisk). The circles indicate the other localities mentioned in the text: 1, Aupa Valley (uppermost Anisian); 2, Fusesa (lower Carnian); 3, Dogna (lower Carnian); and 4, Preone and other localities of the Forni Dolomite Formation (middle-upper Norian).

the outskirts of the present-day Cave del Predil village, they actually came from several distinct outcrops of the Predil Limestone located along the Riofredo Valley, Prasnig Brook, Combattenti Brook and Klinken Brook, from the Saisera Valley to Cave del Predil village. The holotype of the new species here named (MFSN 27532) was found along the Prasnig Brook (which is reported in the Italian topographical map at scale 1:25,000 as “Canale Prasnig”, i.e. Prasnig Canal, although it is not an artificial waterway), about three kilometers WNW of Cave del Predil along the southern flank of Mount Cima del Cacciatore. The specimen MFSN 13228 comes from the Riofredo Brook, of which the Prasnig Brook is a left tributary. MFSN 13228 may be a limestone fragment which was transported by floodings from the Prasnig Brook to the Riofredo Brook.

The bones of MFSN 27532 are preserved inside a millimetric set of thinly laminated limestone (sub-millimetric lamination) in a limestone slab made of millimetre-thick alternance of thinly laminated sets and massive laminae.

Institutional Abbreviations: MCSN, Museo Cantonale di Scienze Naturali, Lugano, Switzerland; MFSN, Museo Friulano di Storia Naturale, Udine, Italy; MSNM, Museo Civico di Storia Naturale, Milano, Italy; PIMUZ, Paläontologisches Institut und Museum der Universität, Zürich, Switzerland.

SYSTEMATIC PALAEOLOGY

Diapsida Osborn, 1903

Archosauromorpha von Huene, 1946

Tanystropheidae Gervais, 1858

Raibliania gen. n.

Type species: *Raibliania calligarisi* sp. n.

Derivatio nominis: From Raibl, the old Austrian name of the Cave del Predil village, which is close to the finding site.

Diagnosis: medium-sized tanystropheid with very elongated cervical vertebrae and the following apomorphies: button-like teeth, at least locally (e.g., palate); apex of the dorsal, ‘lumbar’ and sacral neural spines not transversely thickened; articulation facet on the dorsocaudal corner of the neural spines and corresponding dorsocranial facet on the following vertebra in the dorsal vertebrae; pleurapophyses of the second ‘lumbar’ vertebra (last pre-sacral vertebra) that are much shorter than the pleurapophyses of the first ‘lumbar’ vertebra and tapers distally to a pointed end (like the last ‘lumbar’ of *Langobardisaurus pandolfii*, which, however, has five ‘lumbar’ vertebrae); ilium with comparatively long preacetabular process extending beyond the level of the cranial margin of the pubic peduncle and ending cranioventrally with a robust and transversely thick tuberosity; prominent and blunt medial ridge bordering the entire ventral part of the iliac blade from the cranioventral tuberosity to the caudal end of the postacetabular process; pubis with a cranial process.

Raibliania calligarisi gen. n., sp. n.

Figs. 3-9

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Derivatio nominis: In homage to the late Claudio Calligaris, who found the holotype specimen.

Holotype: MFSN 27532, partial skeleton.

Type Locality: Prasnig Brook, Tarvisio Municipality, Udine Province, Friuli Venezia Giulia Autonomous Region, Italy.

Horizon: Calcare del Predil (Predil Limestone), lower Carnian (Julian). The Prasnig Brook section of the Predil Limestone is referred to the *Trachyceras aon* and *Trachyceras aonoides* ammonoid subzones (Julian 1; Dal Corso et al. 2018).

Diagnosis: As for the genus.

Description

The holotype MFSN 27532 (Fig. 3) is a portion of an articulated skeleton including an isolated tooth crown, an incomplete cervical vertebra, a series of six dorsal, two ‘lumbar’, two sacral and one or two caudal vertebrae, several dorsal ribs, many in-

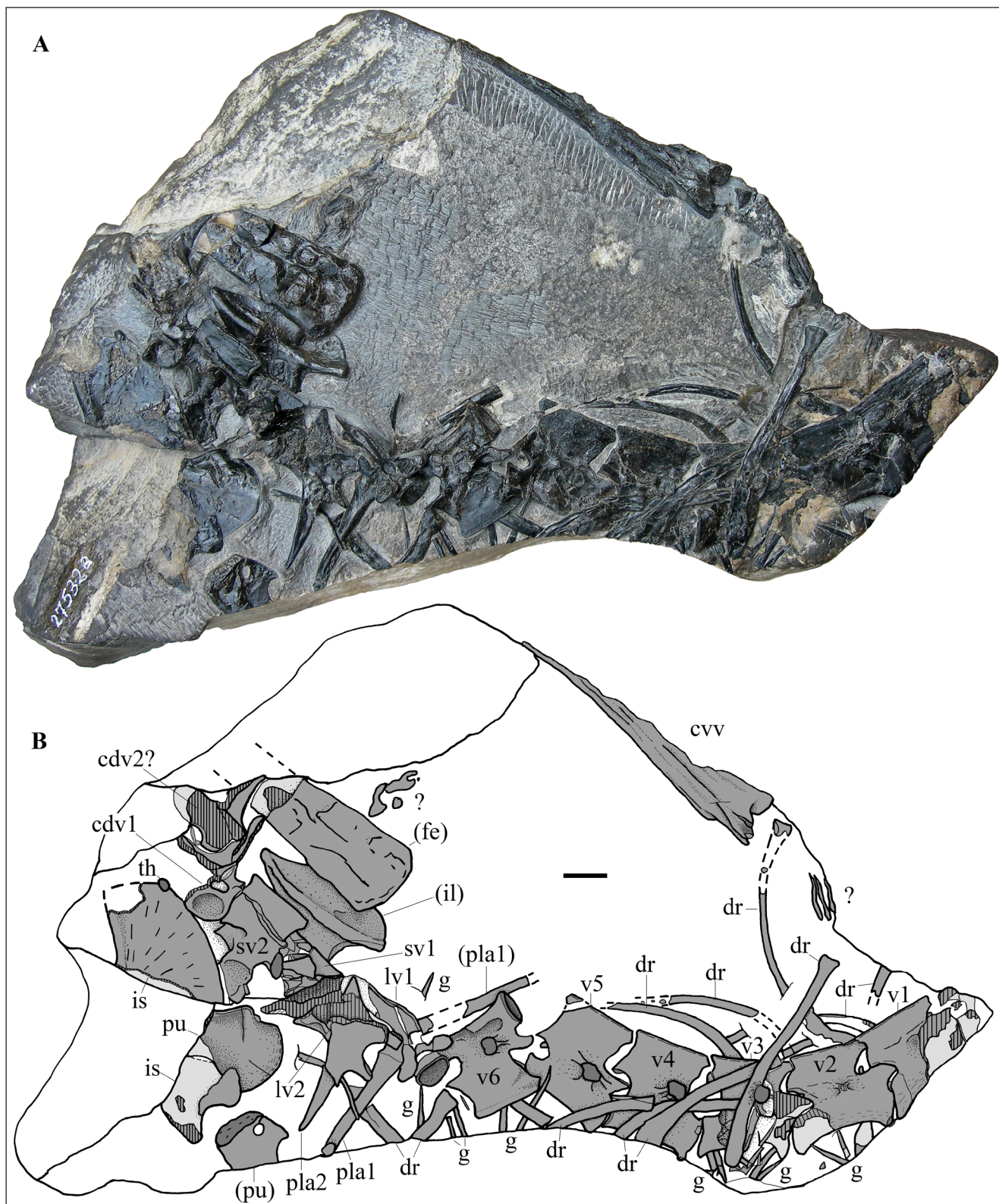


Fig. 3 - *Raiblibania calligaris* gen. n., sp. n., holotype (MFSN 27532). A) The specimen; B) Line drawing of the specimen. Abbreviations: cdv1-2, caudal vertebrae 1-2; cvv, cervical vertebra; dr, dorsal rib; fe, femur; g, gastrale; il, ilium; lv1-2, 'lumbar' vertebrae 1-2; pla1-2, pleurapophyses of the 'lumbar' vertebrae 1-2; pu, pubis; sv1-2, sacral vertebrae 1-2; th, tooth; v1-6, preserved vertebrae 1-6 ('mid'-'distal' dorsal vertebrae; progressive number). Elements in parentheses are from the left side. In B, the bone is gray, the impression of the bone is pale gray, the articular surfaces and the tooth are dark gray, and broken areas are indicated by the lined pattern. Scale bar equals 10 mm.

complete gastralia, a complete left ilium, two partial pubes, an incomplete ischium, a portion of the other ischium and the proximal part of the left femur.

Tooth

A button-like, elliptical element with a main axis of 2.8 mm and a shiny surface (Fig. 4) lays on the margin of the ischiadic fan in the distal part of the preserved portion of the skeleton. The exposed side is convex, whereas the opposite side is flat or concave. It is identified as a tooth because of its shape, size, and shiny black surface. The occurrence of a tooth in the pelvic region can be explained with the slight disarticulation of the skeleton and the caudal bending of the long neck, which would place the skull of the animal close to the caudal part of the animal's body (see Wild 1973, pl. 11; Olsen 1979, fig. 2). The tooth dropped out from its original position on the dentigerous bone, as it is commonly the case for teeth of *Tanystropheus longobardicus* (Bassani, 1886) (e.g., Wild 1973: pls. 5 and 18; Nosotti 2007: 11, figs. 3, 11, 47 and 48).

Only two fishes of the Raibl ichthyofauna have a durophagous or hemidurophagous dentition with button-like teeth (Kner 1866; Griffith 1977; Tintori 1990): the chondrichthyan *Paleobates* and the osteichthyan *Colobodus*. *Paleobates* is rare in the Raibl ichthyofauna and its teeth have a characteristically pitted surface (Dalla Vecchia 2008b). The palatal teeth of a colobodontid might resemble the tooth under discussion as for their shape (Sun et al. 2008: fig. 7D). However, colobodontids could reach a length of 1 metre and had comparatively small palatal teeth (Rusconi et al. 2007), thus the tooth of MFSN 27532 is too large to belong to a colobodontid. Only four fragmentary colobodontid specimens have been found in over 170 years of researches in the Predil Limestone (Kner 1866; Tintori 1990; Rusconi et al. 2007) and no fish bone is preserved in the slab to support the presence of a mixture of fish and reptile remains. Furthermore, the hemispherical teeth of the colobodontids have a circular outline rather than an elliptical one (Rusconi et al. 2007: fig. 5; Sun et al. 2008: fig. 7D).

The tooth may vaguely resemble a miniaturized placodont tooth plate. However, no placodont remains have ever been found in the basinal Predil Limestone in over 170 years of fossil collection that has yielded several hundred vertebrate specimens, nearly all belonging to fish. Instead, placodont re-

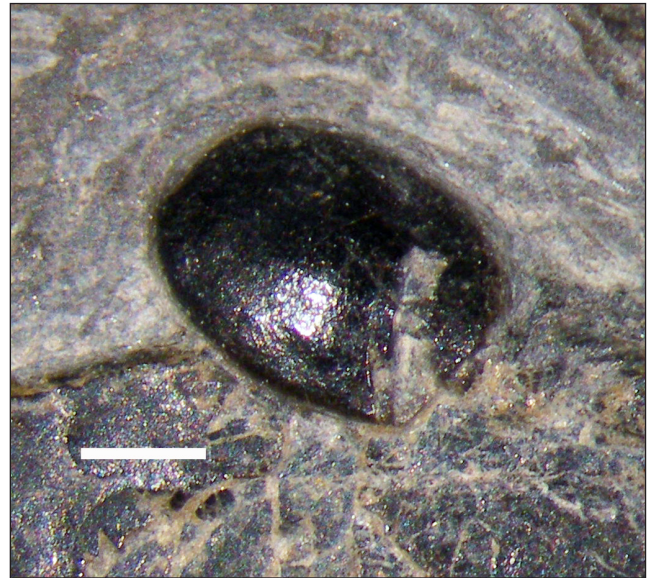


Fig. 4 - *Raibliania calligarisi* gen. n., sp. n., holotype (MFSN 27532), tooth crown. The isolated tooth lies on the margin of an ischiadic fan. Scale bar equals 1 mm.

mains are relatively common in the overlying shallow water Tor Formation, which is rich in thick-shelled bivalves (see below in the Discussion). Tooth plates of Carnian placodonts from northern Friuli are usually much larger than the tooth of MFSN 27532 and have flatter occlusal surfaces with large depressed facets (Dalla Vecchia 2008b: fig. 116A; Dalla Vecchia & Simonetto 2018: fig. 10A-F; pers. obs.).

Fossils are rare in the vertebrate-bearing part of the Predil Limestone. Only five specimens are listed as putative reptile remains by Dalla Vecchia & Simonetto (2018) from the Predil Limestone sample stored in the MFSN palaeontological collections and no other reptile remains are reported from other collections (Dalla Vecchia 2008b). The only documented cases of two or more associated vertebrate specimens on a single slab regard the fish *Peltopleurus* and mostly represent mass deaths (Dalla Vecchia 2008b; pers. obs.). Therefore, finding associate remains of two reptiles or a reptile and a fish on a limestone slab from the Predil Limestone is unlikely.

The slab MFSN 27532 is small in comparison with the size of the reptile it contains and preserves only part of its articulated skeleton. If the neck and the skull of the holotype of *Raibliania calligarisi* were associated to and had the same degree of articulation as the preserved part of the skeleton, comparison with similarly articulated skeletons

of *Tanystropheus longobardicus* (see Wild 1973: pls. 3, 8-9 and 13; Nosotti 2007: pls. I-IV) suggests that they would be out of the part of bed surface represented by the slab, although not very far from it. The dentigerous bones of MFSN 27532 are not preserved on the slab because of the small size of the latter.

One reviewer suggested that the purported tooth might be a coprolite. Coprolites have not been mentioned in the literature about the Predil Limestone (Tintori et al. 1985; Tintori 1990, 1992; Dalla Vecchia 2008b) and are very rare in the vertebrate-bearing beds of this formation. The inventory of the MFSN lists only three coprolites within a sample of at least 750 fossils from that part of the Predil Limestone (pers. obs.). One (MFSN 21941; 11 mm long and 7.7 mm wide) is a sub-spherical mass of amorphous phosphatic matter with an irregular surface and fish scales inside; the second (MFSN 49012; 10 mm long) is a rounded spot of black phosphatic matter with a lot of fish scales and bones exposed on its surface; the third (MFSN 49053; dimensions of the exposed portion are 7.5 x 8 mm) is an apparently lens-like and sub-circular mass of amorphous phosphatic matter that is only partly exposed. They are much larger than the purported tooth and have a different shape. Coprolites are more common (the inventory of the MFSN lists 67 coprolites in a sample of about 3700 specimens) in the basinal Forni Dolomite (Norian) of the close Carnic Prealps, which preserves a similar fossil association (i.e., terrestrial plants, decapod crustaceans, marine fishes and reptiles; Dalla Vecchia 2012). The shape of those coprolites is highly variable: cylindrical more or less thick, elongated and straight, ribbon-like more or less convoluted, elliptical and usually very flattened, and irregular sub-spherical (Dalla Vecchia 2008b: fig. 171; Dalla Vecchia 2012: 8.34). They are in most cases much larger than the purported tooth of MFSN 27532 and do not present its smooth and shiny surface and its cabochon-like shape.

The tanystropheid *Langobardisaurus pandolfii* from the Forni Dolomite has grinding tooth plates (Renesto & Dalla Vecchia 2000; Saller et al. 2013), thus the presence of this kind of dentition is not unexpected in a tanystropheid.

Therefore, the Occam's razor principle suggests that the tooth belongs to the animal whose bones it is associated with.

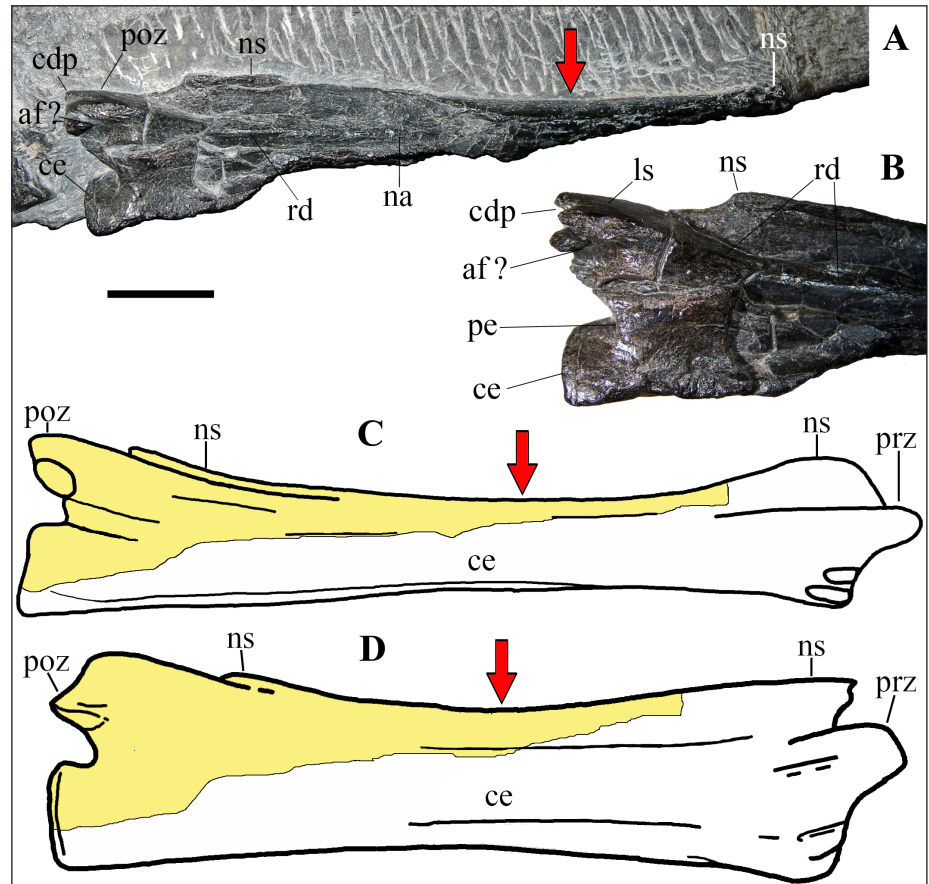
Axial Skeleton

The holotype preserves an incomplete cervical vertebra and a vertebral series composed of eight dorsal vertebrae, two sacral vertebrae and one or two proximal caudal vertebrae. The first five dorsal vertebrae of the series are preserved in anatomical articulation and in right lateral view. The following six vertebrae are slightly disarticulated and show different views, but are still aligned (Fig. 3).

Cervical vertebra. The cervical vertebra (Fig. 5A) is preserved along the margin of the slab. It lacks the cranial portion and most of the centrum (only a dorsal fragment of the caudal termination is preserved), but it is clearly extremely elongate. The preserved portion of the vertebra is 66 mm long. The vertebra is strongly compressed, suggesting that it was hollow inside like the cervicals of *Tanystropheus* (Peyer 1931; Wild 1973). The neural arch is low and long. The neural spine ("neural crest" of Rieppel et al. 2010: 1083) is dorsoventrally short, barely projecting and distinguishable from the neural arch, and has a concave dorsal margin like the cervical neural spines of *Tanystropheus* (Wild 1973: figs. 43, 47 and 97a; Dalla Vecchia 2006b: fig. 8A; Nosotti 2007: figs. 14 and 37). The caudal margin of the neural spine slopes caudoventrally. The postzygapophysis projects caudally slightly beyond the centrum. The dorsal side of the postzygapophysis is broad, shallowly convex and presents longitudinal striae (Fig. 5B) like in *Tanystropheus longobardicus* (see Nosotti 2007: fig. 57). There is a process that projects caudodorsally from the postzygapophysis (the "epipophysis" of Pritchard et al. 2015: e911186-3); it appears to be bifid, but this is probably due to damage. The articular facet of the postzygapophysis is difficult to locate with certainty because of the strong crushing of the neural arch; probably it faced ventrally or lateroventrally. The blunt dorso-lateral margin of the postzygapophysis continues along the lateral side of the neural arch as a thick ridge (Fig. 5B) like in *Tanystropheus longobardicus* (see Nosotti 2007: fig. 57).

Because of its position, the low degree of disarticulation of the preserved part of the skeleton and the usual backward bending of the long neck in articulated tanystropheid skeletons (e.g., Peyer 1931; Wild 1973; Olsen 1979; Renesto & Dalla Vecchia 2000; Nosotti 2007), the cervical vertebra is probably a distal element. It resembles the elongated cervical vertebrae of *Tanystropheus* (Peyer 1931; Wild

Fig. 5 - *Raiblibiana calligarisi* gen. n., sp. n., holotype (MFSN 27532), cervical vertebra. A) The preserved part of the vertebra; B) the caudal (distal) part of the vertebra and its structures; C) cervical vertebra ?10 of *Tanystropheus conspicuus* (redrawn from Wild 1973; not drawn to scale) with evidenced the portion of the vertebra preserved in A; D) cervical vertebra 11 of *Tanystropheus longobardicus* (redrawn from Wild 1973; not drawn to scale) with evidenced the portion of the vertebra preserved in A. The arrow points to the lowest point of the dorsally concave neural spine. Abbreviations: af, articular facet on the postzygapophysis; ce, centrum; cdp, caudodorsal process ("epiphysis") of the postzygapophysis; ls, longitudinal striae on the dorsal side of the postzygapophysis; ns, neural spine; pe, peduncle of the neural arch; poz, postzygapophysis; prz, prezygapophysis; rd, lateral ridge. The scale bar in A equals 10 mm.



1973; Dalla Vecchia 2000; Rieppel 2001; Renesto 2005; Nosotti 2007; Rieppel et al. 2010; see Fig. 5C-D). The cervical vertebrae 12 and 13 of *Tanystropheus* are much shorter than the preceding vertebrae (Wild 1973; Nosotti 2007; Rieppel et al. 2010) and the cervical of MFSN 27532 may be comparable with *Tanystropheus*' cervical vertebrae 10-11 (see Fig. 5). The neural arch of the cervical vertebra of MFSN 27532 is low, but it is comparatively higher than that of the cervical 10 of *Tanystropheus* (Wild 1973; Nosotti 2007; Fig. 5C) and more like that of the cervical 11 (Wild 1973: fig. 97a; see Fig. 5D).

Since the cranial and caudoventrally sloping part of the dorsally concave neural spine is preserved in the vertebra, comparison with the elongate cervicals of *Tanystropheus* suggests that only the cranial portion is missing (Fig. 5). This allows estimating the total length of the centrum based on the length of the preserved portion and the distance of the minimum height of the neural arch respect to the caudal end of the centrum. The total length of the cervical centrum of MFSN 27532 results to be 77.1 mm when compared to the cervical ?10 of *Tanystropheus conspicuus* v. Mayer, 1855 (Fig. 5C) and 81.8 mm when compared to the cervical 11 of *Ta-*

nystropheus longobardicus (Fig. 5D). These lengths are 3.50 and 3.72 times, respectively, the length of the preserved dorsal centrum 4; they are 3.85 and 4.09 times the length of the preserved dorsal centrum 6 (the last pre-'lumbar' centrum; see below). The ratios cervical 11/dorsal 10 centrum lengths (dorsal 10 is the last pre-'lumbar' vertebra in *Tanystropheus longobardicus*) are about 2.43, 3.50 and 5.00 in the small *Tanystropheus longobardicus* MSNM BES SC 1018, MSNM BES SC 265 and PIMUZ T/1277, respectively (Nosotti 2007; Wild 1980; for the differences between small and large *Tanystropheus longobardicus* specimens, see the Discussion section). The ratio of MFSN 27532 falls within the *Tanystropheus longobardicus*' ratios range.

Dorsal vertebrae sensu strictu. The segment of eight dorsal vertebrae probably does not represent the whole dorsal segment of the vertebral column, because *Tanystropheus longobardicus* has 12 dorsal vertebrae (including two 'lumbars' sensu Wild 1973; Nosotti 2007; Rieppel et al. 2010) and *Macrocnemus* and *Langobardisaurus* have 16-17 dorsal vertebrae (Rieppel 1989; Renesto 1994; Jiang et al. 2011; Saller et al. 2013). Therefore, the preserved segment lacks an unknown number of proximal dorsals, unless

the trunk of *Raibliania calligarisi* was apomorphically short.

The preserved segment of dorsal vertebrae can be divided into three regions. The first two preserved dorsals belong to the first region ('mid' dorsals), the third vertebra (which is partly covered by ribs and partly missing) may be transitional to the second region or belong to it, vertebrae 4 to 6 belong to the second region ('distal' dorsals), and the last two vertebrae are 'lumbar' vertebrae sensu Wild (1973).

The two 'mid' dorsals are preserved partly as bone and partly as the impression of the bone (Fig. 6A-B). They have been flattened by the sediment load. Only a few remains are preserved of a more cranial vertebra that is articulated with the one that is from here on reported as vertebra 1 of the series.

The centra of these vertebrae are elongate: length is 24 and 25 mm, respectively, height is about 9 mm (vertebra 2) and length/height ratio is 2.78. The total height of the vertebrae (21.5 mm) is lower than the length of the centra (total height/centrum length ratios are 0.90 and 0.86, respectively). The centrum is arched, with a deeply concave ventral margin and a convex dorsal margin. Probably, there is not a ventral keel (i.e., the ventral margin appears to be blunt). In lateral view, the caudal articular surface of the centrum of the vertebra 2 slants cranio-caudally, whereas the cranial one faces cranioventrally. Both articular surfaces are probably concave (they are not fully exposed). The lateral side of the centrum was flat or slightly depressed. The ventral third of the centrum presents thin and irregular longitudinal wrinkles on the surface.

The neural arch is relatively high (neural arch height/total vertebral height ratio is 0.56 and 0.54, respectively) and broad in lateral view. The pedicel is asymmetrically displaced cranially on the dorsal margin of the centrum, ending cranially at the cranial extremity of the centrum, whereas caudally it ends 4.5 mm ahead of the caudal extremity of the centrum. The neural spine is fan-shaped and subtrapezoidal with cranially and caudally projecting processes at the cranial and caudal dorsal corners of the spine and a flat dorsal surface. The cranial process is truncated and articulates on a corresponding caudoventral surface of the caudal process of the preceding vertebra. This spinal articulation is better observed in the following vertebrae 3-6 (Fig. 7). The spine is much flattened laterally and transversely

thin. Its apical portion is only imperceptibly thicker transversely than the rest. The narrow dorsal surface of the spine is ornate with small and transversely elongated papillae. The spine is much longer than high (spine length/height ratios are 3.23 and 2.73, respectively).

The transverse process is placed on the neural arch approximately at level of the zygapophysial surfaces and is displaced cranially with respect to the lateral midpoint of the arch, but is broken and nearly completely missing in both vertebrae. There are traces of two short and robust laminae (the "buttresses" of Nosotti 2007: 69) supporting the transverse process ventrally, one cranial and the other caudal. The strong crushing has possibly broken other laminae, whose existence cannot be excluded. There is no trace of a second articular surface for a dicephalous rib. The prezygapophysis and postzygapophysis are short and robust, and are directed cranially and caudally, respectively. The postzygapophysis is shorter than the prezygapophysis. The prezygapophysis ends slightly beyond the cranial end of the centrum, whereas the postzygapophysis ends at the caudal end. The articular facets of the prezygapophysis and postzygapophysis face dorsomedially and ventrolaterally, respectively. This orientation of the articular surfaces occurs also between vertebra 2 and 3. Like the small individuals of *Tanystropheus longobardicus* (see Nosotti 2007: fig. 60), the postzygapophysis is separated from the centrum by a deep notch, whereas there is no notch between the prezygapophysis and the centrum.

The 'distal' dorsal vertebrae (vertebrae 4-6 and probably 3) are similar to each other (Fig. 6A and C). Their total height is higher than the length of their centra (total height/centrum length ratios are 1.11, 1.15 and 1.15 in vertebrae 4-6, respectively). Their centra are slightly shorter than those of the 'mid' dorsals and decrease in length caudally, being 22.5, 22, 21.5 and about 20 mm long in vertebrae 3-6, respectively. Centra are elongate: height is 9.5-10 mm and length/height ratios range 2.37-2.00.

The morphology of the centra is like that of the 'mid' dorsals, but the centrum is slightly less arched in vertebrae 5 and 6. The caudal articular surface of the centrum slants cranio-caudally in lateral view in the vertebrae 3 and 4, but possibly not in the vertebra 5. Both articular surfaces are probably concave in all of the vertebrae; the only fully exposed is the cranial articular surface of the verte-

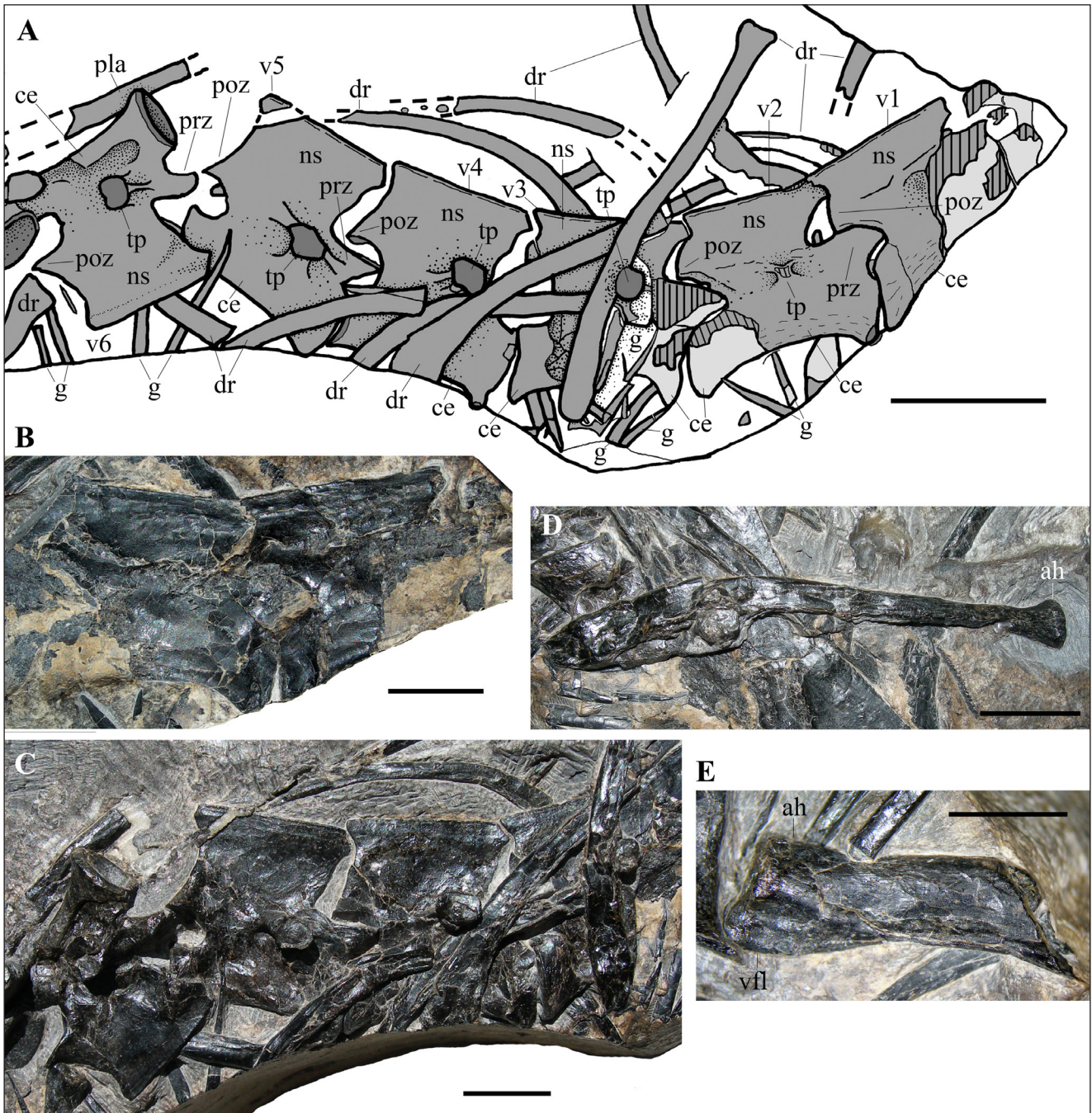


Fig. 6 - *Raibhania calligaris* gen. n., sp. n., holotype (MFSN 27532), dorsal vertebrae. Drawing of the preserved vertebrae 1 to 6 ('mid' and 'distal' dorsal vertebrae); B) the first two preserved dorsal vertebrae ('mid' dorsals); C) vertebrae 3-6 ('distal' dorsal vertebrae); D) the nearly complete mid-dorsal rib; E) the proximal portion of a distal dorsal rib. Abbreviations: ah, articular head of the dorsal rib; ce, vertebral centrum; dr, dorsal rib; g, gastrale; ns, neural spine; pla, pleurapophysis of the first 'lumbar' vertebra; poz, postzygapophysis; prz, prezygapophysis; tp, transverse process; v1-6, vertebrae 1-6 (progressive number); vfl, ventral flange of the head of the dorsal rib. In A, the bone is gray, the impression of the bone is pale gray, the articular surfaces are dark gray, and broken areas are indicated by the lined pattern. Scale bars equal 20 mm in A, 10 mm in B, C and D and 5 mm in E.

bra 6, which has a subcircular outline, is deeply concave and with thickened margins. The cranial and caudal articular portions of the centra are slightly expanded (trumpet-like), whereas the lateral side was originally slightly convex but is now depressed by crushing. Like the 'mid' dorsals, the surface of

the ventral third of the centrum presents thin and irregular longitudinal wrinkles.

The neural arches are similar to those of the 'mid' dorsals, but they are proportionally taller (neural arch height/total vertebral height ratio is 0.63, 0.66 and 0.64 in vertebrae 4-6, respectively). The

Fig. 7 - *Raibhania calligaris* gen. n., sp. n., holotype (MFSN 27532), neural spine articulations. Neural spines of the preserved vertebrae 3-5 ('distal' dorsal vertebrae), with the apical articulation between adjacent neural spines indicated by the arrow.



pedicel is displaced cranially on the dorsal margin of the centrum, but less than in the 'mid' dorsals. The neural spine is fan-shaped, laterally flattened and transversely thin, with cranially and caudally projecting processes at the top corners, and a flat dorsal surface like in the 'mid' dorsals. As in the latter, its apical portion is not transversely expanded and the apical surface is ornate with small elongated papillae. The articulation between the cranial and caudal processes of the neural spine is evident in all of the 'distal' dorsals (Fig. 7). The neural spine is proportionally taller than in the 'mid' dorsals and increases in height moving caudally (spine length/height ratio is 1.81, 1.68 and 1.63 in vertebrae 4-6, respectively).

The transverse processes are short, robust and laterally (laterocranially in the vertebra 5) directed. They are located high on the neural arch at the boundary between the neural spine and the pedicel (at level with the zygapophyses) and they are displaced on the cranial half of the neural arch. The single articular surface for the rib is elliptical to sub-circular, with the main axis oriented craniocaudally; in the vertebrae 4 and 5, this surface presents a ventral projection that could correspond with a ventral flange in the dorsal ribs (see below). There are one to three short and robust laminae (the "buttresses" of Nosotti 2007: 69) supporting the transverse process. Vertebra 3 has a sub-horizontal cranial lamina (probably a prezygodiapophyseal lamina) and a ventrocranial lamina (probably an anteroventral spinodiapophyseal lamina). The caudal and ventrocaudal margins of the transverse process are hindered by a dorsal rib and further laminae, if present, cannot be seen. Vertebra 4 has a caudal sub-horizontal lamina (a posterior spinodiapophyseal lamina) and a ventrocaudal lamina (posteroventral

spinodiapophyseal lamina). The cranial laminae, if present, are covered by a dorsal rib. Vertebra 5 has caudal and cranial sub-horizontal laminae (posterior spinodiapophyseal and prezygodiapophyseal laminae, respectively), the latter reaching the prezygapophysis laterally. There was possibly a single ventral lamina (ventral spinodiapophyseal lamina), but it is broken by crushing. Vertebra 6 has a sharp cranial sub-horizontal lamina reaching the base of the prezygapophysis laterally (prezygodiapophyseal lamina) and no caudal lamina. The ventral portion of the transverse process and the corresponding part of the centrum are damaged and laminae, if present, are not preserved.

The zygapophyses are short and robust. They are cranially directed and slightly splayed laterodorsally, as shown in vertebra 6. The zygapophyses end slightly beyond the extremities of the centra (vertebrae 4-6). The articular facets of the pre- and postzygapophyses face dorsomedially and ventrolaterally, respectively, but at a lower angle with respect to the 'mid' dorsals. In vertebrae 5-6 and in the following 'lumbar' vertebrae, the articular facets of the pre- and postzygapophyses face also slightly cranially and caudally, respectively. The zygapophyses are at the same level in the neural arch; the postzygapophysis is separated from the centrum by a deep notch.

Dorsal ribs. Remains of at least ten dorsal ribs are exposed. The dorsal ribs are slightly disarticulated and shifted from their original connection with the corresponding vertebrae. The most complete dorsal rib (Fig. 6D) is preserved at the transition between the 'mid' and 'distal' dorsal vertebrae, but could be from a more proximal position. It has a single articular head that is fan-like expanded. The shaft flares distally and tapers proximally, like in the

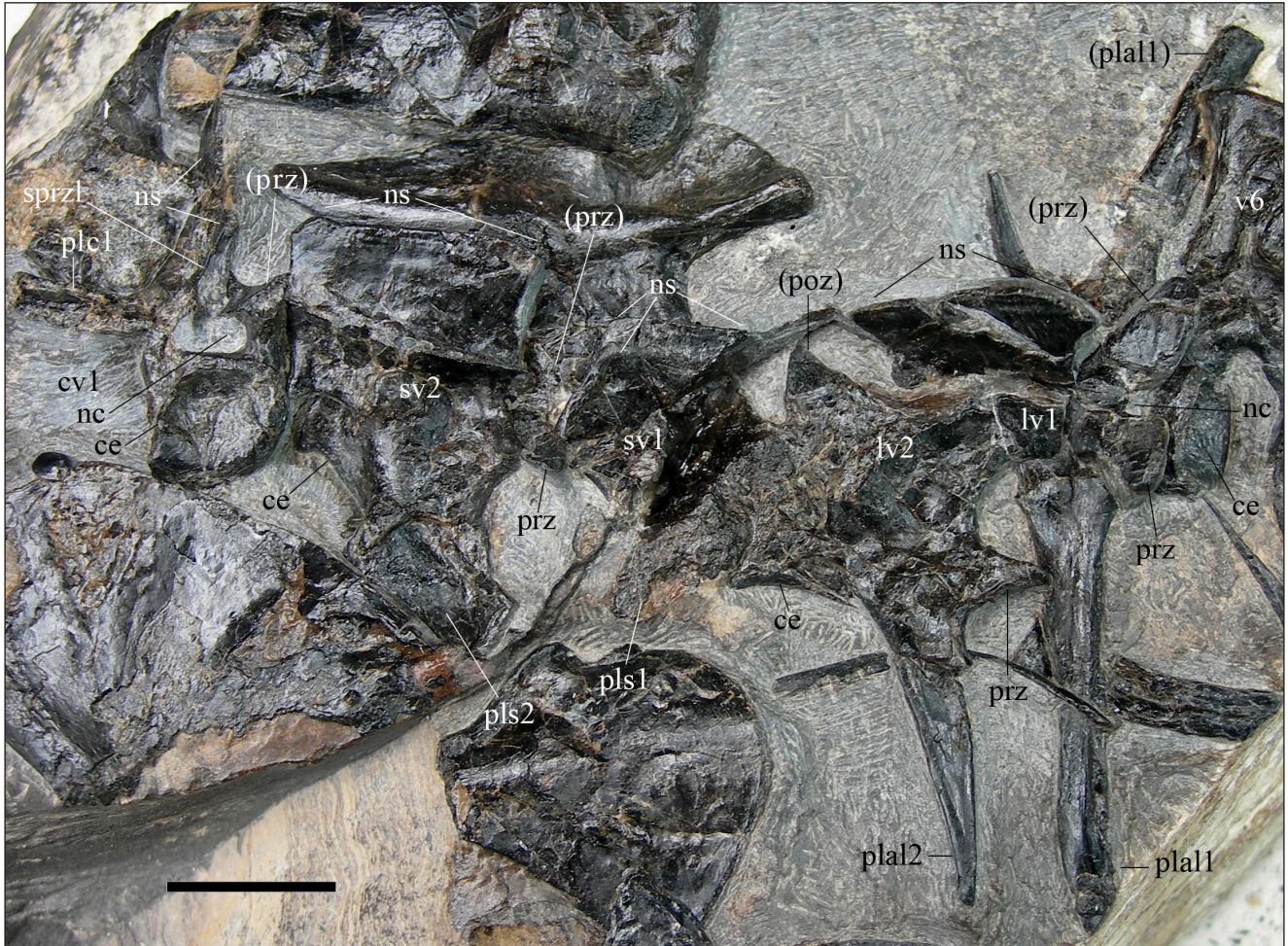


Fig. 8 - *Raiblibania calligarisi* gen. n., sp. n., holotype (MFSN 27532), 'lumbar', sacral and first caudal vertebrae. Abbreviations: ce, vertebral centrum; cv1, caudal vertebra 1; lv 1-2, 'lumbar' vertebrae 1-2; nc, neural canal; ns, neural spine; plc1, pleurapophysis of the caudal vertebra 1; plal1-2, pleurapophyses of the 'lumbar' vertebrae 1-2; pls1-2, pleurapophyses of the sacral vertebrae 1-2; poz, postzygapophysis; prz, prezygapophysis; sprzl, spinoprezygapophyseal lamina; sv1-2, sacral vertebrae 1-2; v6, vertebra 6 (last 'distal' dorsal vertebra). Structures in parentheses are from the left side. Scale bar equals 10 mm.

mid-dorsal ribs of *Tanystropheus longobardicus* figured by Wild (1973: fig. 35). The proximal articular head of the rib is preserved in craniocaudal view in other two ribs, which seem to be associated with the vertebrae 4 and 6 (the second and the last 'distal' dorsals, respectively). They have a single articular head, which is slightly expanded transversely and ventrodorsally and bear a robust ventral flange (Fig. 6E), possibly corresponding with the ventral projection of the articular surface for the rib on the transverse process. This flange resembles the "ventral process" in the dorsal ribs of the thalattosaur *Endennasaurus acutirostris* Renesto, 1992 (Renesto 1992: 415, fig. 4).

Lumbar' vertebrae. Vertebra 7 is partly exposed in craniodorsal and left lateral view (Fig. 8). It is like the preceding 'distal' dorsals, the main difference being the long pleurapophyses, which allow identifying it as a 'lumbar' vertebra. The cranial articular

face of the centrum is deeply concave and has a subcircular outline (the horizontal diameter is 8.7 mm long). The neural spine has the shape of the neural spine of the preceding dorsal, but its craniodorsal process does not appear to be truncated. Thin spinoprezygapophyseal laminae border a narrow and deep spinoprezygapophyseal fossa. The robust prezygapophyses are cranially directed and slightly splayed laterodorsally; they extend slightly beyond the extremities of the centrum. Their articular facets face dorsomedially.

Both pleurapophyses are damaged distally, but the right one is nearly complete. They are long (over 30 mm), narrow, straight and laterocranially directed. The shaft tapers in the proximal part, then its craniocaudal width remains constant. The distal portion is recurved cranially.

Vertebra 8 is the second 'lumbar' vertebra,

which is exposed in right lateral view, strongly crushed, broken and partly damaged (Fig. 8). The ventrocaudal part of the centrum, the rostral portion of the neural spine, the right prezygapophysis, the right pleurapophysis and the left postzygapophysis are the better preserved parts of this vertebra. The main difference with the preceding vertebra is the shorter (about 20 mm) and thorn-like pleurapophysis, which tapers distally to a point and is slightly curved caudally. The broken neural spine was possibly slightly shorter than the spines of the 'distal' dorsals, like the better preserved spine of the second sacral vertebra (see below).

Sacral vertebrae. Vertebra 9 is damaged because it is crossed by a fracture of the slab and most of it has been lost (Fig. 8). Its neural spine was broken into several pieces by compression. As it is placed between the second 'lumbar' and the second sacral (see below), this vertebra is identified as the first sacral. Its neural spine presents thin spinopostzygapophyseal laminae. Only a small proximal fragment and a partial impression are preserved of the right pleurapophysis.

Vertebra 10 is exposed in right laterodorsal view (Fig. 8). It is the sacral vertebra 2, because the right pleurapophysis (the robust rib is fused without suture with the transverse process) points lateroventrally and cranially (see cf. Wild 1973: figs. 55-56; Olsen 1979: fig. 2).

The neural spine is very thin transversely, fan-shaped but not as expanded apically as those of the 'distal' dorsals and slightly shorter (craniocaudal length is about 15.5 mm, against 19 mm of vertebra 4). The robust prezygapophyses are like those of the first 'lumbar' vertebra. The long right pleurapophysis is broken distally where it is crossed by a fracture of the slab. The pleurapophysis is craniocaudally waisted at midshaft and expanded distally. There is no trace of a pointed caudal process like that occurring in the second sacral rib of *Amotosaurus rotfeldensis* (see Fraser & Rieppel 2006); *Macrocnemus bassanii* (see Rieppel 1989) and *Langobardisaurus pandolfii* (see Renesto 1994). *Tanystropheus longobardicus* (see Ezcurra 2016) and *Tanytrachelos abynis* (see Olsen 1979; Smith 2011) also lack a caudal process of the second sacral pleurapophysis.

Caudal vertebrae. The vertebra 11, which follows the sacral vertebra 2, is set nearly vertically in the layer and shows the cranial and right lateral views (Fig. 8). Having straight pleurapophyses that

are laterocaudally directed from the upper part of the pedicel of the neural arch, it is the first caudal (cf. Wild 1973: figs. 57-59). The cranial articular facet of the centrum is deeply concave and has a subcircular outline. The partially preserved neural spine is tall (about 14.5 mm), squared and broad in lateral view and very thin transversely as in the preceding vertebrae. Thin spinoprezygapophyseal laminae border a deep spinoprezygapophyseal fossa. Only part of the robust left prezygapophysis is preserved; it bears a dorsomedially facing articular facet. The large neural canal is elliptical, slightly wider than high.

A very incompletely preserved bone just caudal to the first caudal vertebra could be the caudal vertebra 2, but the poor state of preservation prevents any statement about its morphology.

Gastralia

Many thin and straight bones with a sharply pointed extremity are preserved along the ventral margin of the series of dorsal vertebrae. They are identifiable as gastralia, although none is entirely preserved.

Pelvic girdle

All the preserved girdle bones are grouped close to the sacral vertebrae and plausibly belong to the pelvic girdle (Fig. 9A). The identification of these elements was based on comparison with the pelvic girdle elements of other tanystropheids (*Tanystropheus* [Wild 1973; Nosotti 2007], *Macrocnemus* [Rieppel 1989; Jaquier et al. 2017] and *Amotosaurus* [Fraser & Rieppel 2006]). Right and left pubes and ischia are partially preserved, whereas the left ilium is complete. The right ilium is missing. Pubes and ilia are disarticulated and drifted to the right side with respect to the vertebral column.

Ilium. The left ilium (Fig. 9B) is partly covered by the sacral vertebrae and the left femur. The iliac blade is 35 mm long. The caudally tapering postacetabular process is longer than the preacetabular process, but the latter is long compared with those of other tanystropheids (Rieppel 1989: figs. 1A and 4B; Wild 1973: fig. 93; Nosotti 2007: fig. 25; Fraser & Rieppel 2006: fig. 6A; Jaquier et al. 2017: fig. 8F) and probably extends cranially beyond the level of the cranial margin of the pubic peduncle. The preacetabular process ends cranioventrally with a short, robust and transversely (mediolaterally) thick

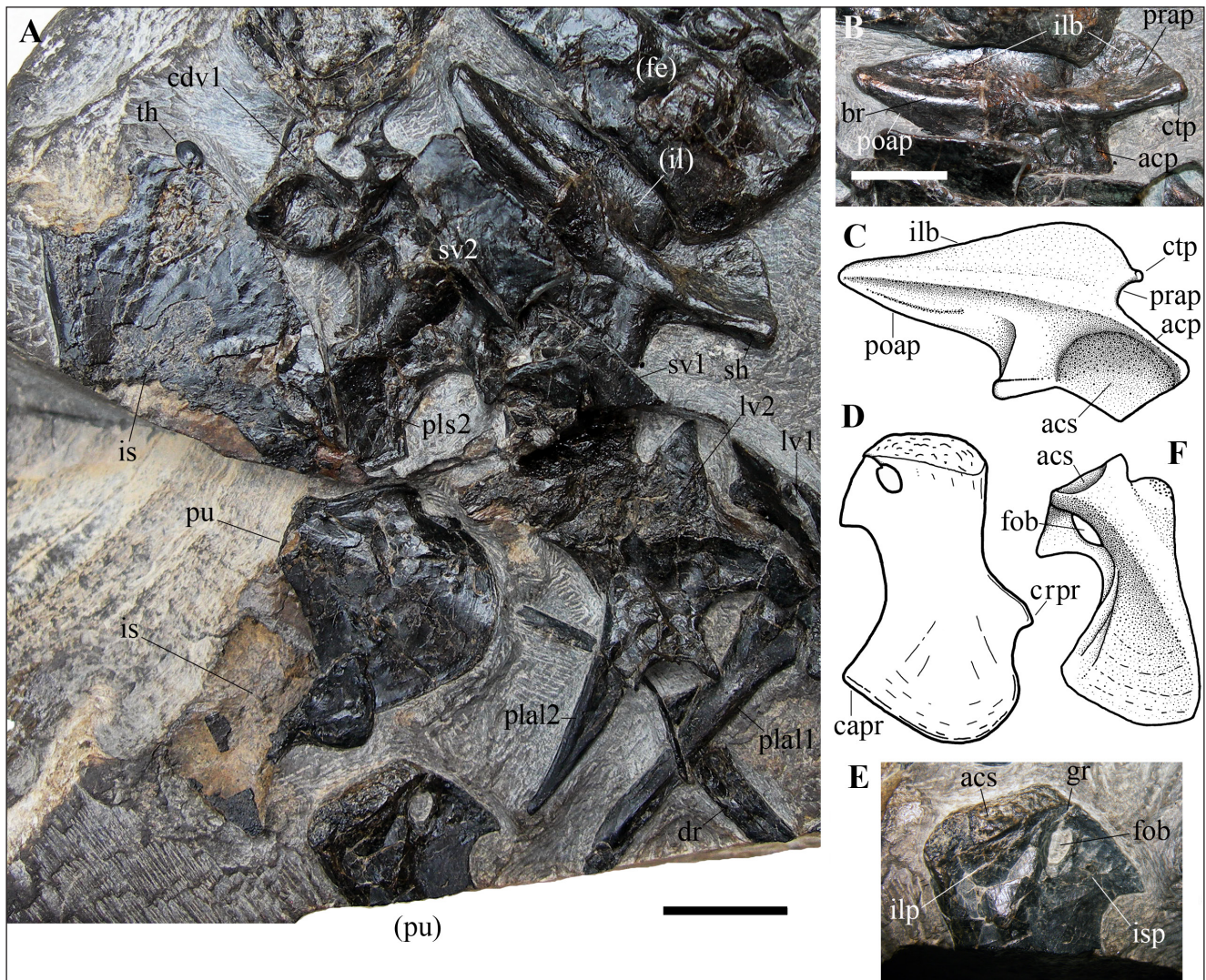


Fig. 9 - *Raiblibia calligarisi* gen. n., sp. n., holotype (MFSN 27532), pelvic girdle elements and comparison. A) the pelvic girdle of MFSN 27532; B) the left ilium of MFSN 27532 in medial view; C) drawing of the right ilium of a small individual of *Tanystropheus longobardicus*, lateral view; D) reconstruction of the right pubis of MFSN 27532 in ventrolateral view; E) reconstruction of the right pubis of a small individual of *Tanystropheus longobardicus* in ventrolateral view; F) particular of the proximal part of the left pubis of MFSN 27532 in ventrolateral view. Abbreviations: acp, acetabular portion of the ilium (pubic peduncle); acs, acetabular surface (contribution of each pelvic element to the acetabulum); br, blunt medial ridge along the ventral part of the iliac blade; cdv1, caudal vertebra1; capr, caudal process of the pubis; crpr, cranial process of the pubis; ctp, cranial tuberosity on the preacetabular process of ilium; dr, dorsal rib; fe, femur; fob, foramen obturatorium; gr, groove; il, ilium; ilb, iliac blade; ilp, iliac peduncle of pubis; is, ischium; isp, ischiadic peduncle of pubis; lv1-2, 'lumbar' vertebrae 1-2; pls2, pleurapophysis of the sacral vertebra 2; poap, postacetabular process of ilium; prap, preacetabular process of ilium; pu, pubis; sh, shelf; sv1-2, sacral vertebrae 1-2; th, tooth crown. Elements in parentheses are from the left side. C) and F) are redrawn from Nosotti (2007). Scale bar equals 10 mm.

tuberosity. This thickened part of the ilium continues caudally bordering the entire ventral margin of the medial side of the iliac blade as a blunt ridge. The ventral part of the preacetabular process is flat and shelf-like (Fig. 9A). The upper part of the iliac blade is sharp and its outline reminds that of *Tanystropheus longobardicus* (see Nosotti 2007: fig. 25; Fig. 9C). The acetabular portion is mostly covered by the sacral vertebrae. Only the dorsal part of the pubic peduncle is exposed; its cranial margin is more steep than in other tanystropheids (e.g., Riep-

pel 1989: fig. 4B; Wild 1973: fig. 93; Nosotti 2007: fig. 25).

Pubis. The slab contains the proximal portion of the left pubis in ventrolateral view and the distal portion of the right pubis in ventrolateral view. The cranial margin of the pubis is thick, whereas the caudal margin is blade-like. The outline of the complete pubis in ventrolateral view was obtained assembling the two preserved parts (Fig. 9D). The moderately expanded proximal end of the pubis shows a dorsolaterally facing and rough facet on

the thick iliac peduncle, which is the pubic contribution to the acetabulum (Fig. 9E). The proximal portion of the blade-like ischiadic peduncle is hook-like (with a caudal pointed process) as in some *Tanystropheus* specimens (Wild 1973: fig. 91k; Nosotti 2007: fig. 25; Fig. 9F) and probably bears most of the articular surface for the ischium (Fig. 9E). The obturator foramen is elliptical and large (the main axis is ca. 3 mm). It opens proximally at the boundary between the iliac and ischiadic peduncles. These peduncles are separated by a groove running from the proximal end of the obturator foramen to the articular margin of the pubis (Fig. 9E). The mid-shaft of the pubis is waisted, whereas the pubic apron is expanded and has a rounded distal margin. The ventrolateral surface of the pubic apron displays concentric striae. There is a moderately developed caudal process at the distocaudal corner and a hook-like cranial process just distal to midshaft (Fig. 9A and D). The margin of the cranial process is thickened.

Ischium. One ischium is close to the sacral vertebra 2 and the caudal vertebra 1; it preserves most of the broad and fan-shaped ischiadic blade (Fig. 9A). The surface of the blade displays thin radial striae. One margin (probably the caudal one) is straight and thick, whereas the remaining part of the preserved portion of the blade is very thin. The shape of the preserved part suggests the presence of a caudal process of the blade. The other ischium partly overlaps the right pubis and preserves part of the pubic peduncle and the impression of the cranial process of the ischiadic blade.

Because of the shape of pubis and ischium, there was a thyroid fenestra between these bones.

Hind limb

The preserved proximal part of the femur is straight and robust. It has been crushed by the sediment load. The shaft slightly tapers distally and the femoral head is not separated from the shaft by a neck (Figs. 3 and 9A). Its position respect to the left ilium suggests it is the left femur.

Discussion

The holotype and MFSN 13228

The specimen MFSN 13228, a series of three, partially preserved but articulated mid-caudal vertebrae (Fig. 10), is the only other reptile remain from the Predil Limestone to have been published

(Dalla Vecchia 1994). It was tentatively referred to a thalattosaur based on the resemblance with the Norian thalattosaur *Endennasaurus acutirostris* as for the elongation of the mid-caudal centra, tall neural spines and spatulate and long chevrons (Dalla Vecchia 1994). However, mid-caudals of *Endennasaurus acutirostris* do not have arched centra with a markedly concave ventral margin, centra are proportionally less elongated, cylindrical and not laterally concave, neural spines are proportionally lower and more backward sloping, and the articulation of the haemapophyses with the centra is different from that observed in MFSN 13228 (cf. Renesto 1992; Muller et al. 2005). Dalla Vecchia (1994) compared MFSN 13228 with the vertebrae of ichthyosaurs, placodonts, 'nothosaurs', drepanosaurids and thalattosaurids, but not with those of the tanystropheids. The successive discovery of MFSN 27532 in the Predil Limestone and in a place that is very close to the locality where MFSN 13228 was collected, suggests that a tanystropheid is a possible candidate for the latter.

To support strict relationships between MFSN 13228 and MFSN 27532 is the similar size (the centra of the dorsals of MFSN 27532 are 20-25 mm long, whereas those of the caudals of MFSN 13228 are 18-19 mm long), the elongation of the centra (length/height ratio is 1.63 in the caudals), and the arched centra with a markedly concave ventral margin and depressed lateral sides.

In *Tanystropheus*, the centra of the dorsal and caudal vertebrae have a similar elongation and both have a concave ventral margin as is the case with MFSN 27532 and MFSN 13228 (Peyer 1931: figs. 5-7; Wild 1973: fig. 62; Nosotti 2007: pl. II). Tanystropheids have elongate mid-caudal vertebrae with centra that are much longer than high (Pritchard et al. 2015; *Macrocnemus*, Premru 1991: figs. 2 and 16; Jaquier et al. 2017: fig. 1D; *Langobardisaurus*, Renesto & Dalla Vecchia 2000: fig. 1; *Tanytrachelos*, Olsen 1979; fig. 4B; Smith 2011: fig. 14). The hemapophyses of MFSN 13228 resemble the proximal hemapophyses of *Tanystropheus longobardicus* (see Wild 1973: fig. 37).

Consequently, MFSN 13228 might belong to *Raibliania calligarisi*. However, it is not considered here as a referred specimen of *Raibliania calligarisi*, because it was not associated with MFSN 27532 and the two specimens do not have overlapping elements.

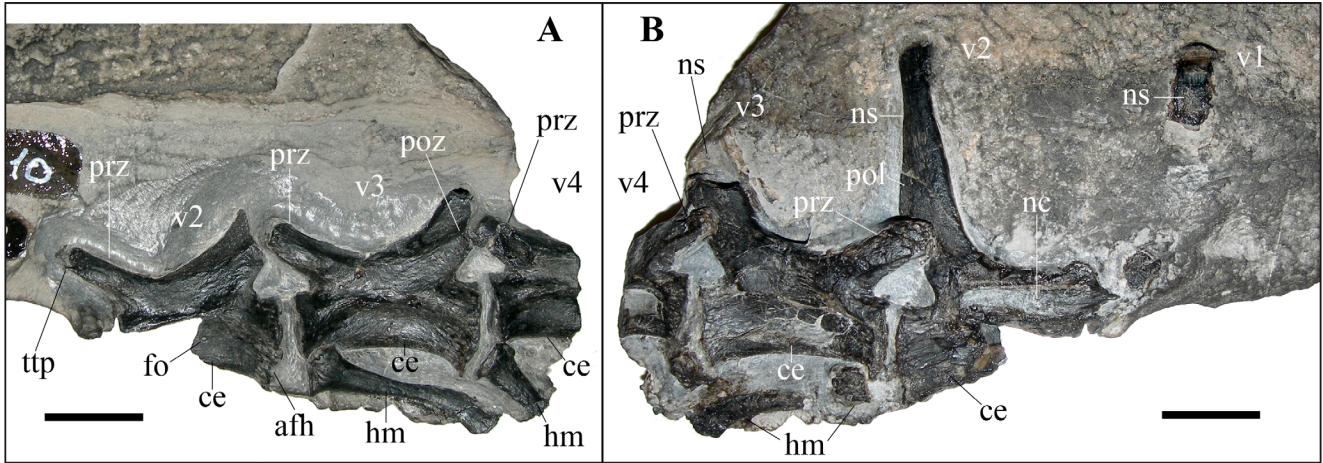


Fig. 10 - MFSN 13228, mid-caudal vertebrae. A) Left side of the specimen; B) right side of the specimen (partly weathered). Abbreviations: afh, articular facet for the hemapophysis on the centrum; ce, vertebral centrum; fo, foramen; hm, hemapophysis; nc, neural canal; ns, neural spine; pol, postspinal lamina; poz, postzygapophysis; prz, prezygapophysis; ttp, thorn-like terminal process of the prezygapophysis; v1-4, preserved vertebrae in proximodistal order. Scale bar equals 10 mm.

Size and ontogenetic stage

The specimen MSNM BES SC 265 of *Tanystropheus longobardicus* has dorsal vertebral centra that are 10-11 mm long and its estimated total body length is 110 mm; the specimen MSNM BES SC 1018 has dorsal vertebral centra that are 15.4-14.6 mm long and its estimated total body length is 140 mm (Nosotti 2007). Dorsal vertebral centra of MFSN 27532 are ~25 mm long. If the overall body structure of *Raibliania calligaris* were the same as that of *Tanystropheus longobardicus*, the scaled total body length of the holotype of *Raibliania calligaris* would be 2.3-2.6 m. Specimens of *Tanystropheus longobardicus* were grouped by Wild (1973) and Nosotti (2007) into two size-classes, one made of individuals with estimated total body length less than two metres (small size-class) and the other with total body length longer than two metres (large size-class). Based on the length of its dorsal vertebral centra, MFSN 27532 would fall in the lower range of the large size-class.

The neurocentral sutures are closed and obliterated in all of the MFSN 27532 vertebrae and also in MFSN 13228. In MFSN 27532, the ribs of the last two dorsal vertebrae and those of the second sacral vertebra are fused to the vertebra forming pleurapophyses. In MFSN 27532, the sacral vertebrae are unfused to each other, the pelvic bones are unfused to each other and the sacral pleurapophyses are unfused to the ilia, but this occurs also in the largest specimens of *Tanystropheus longobardicus* (see Wild 1973) and is probably independent from

the ontogenetic stage of the individual. Therefore, there is no macroscopic evidence supporting the osteological immaturity of the holotype of *Raibliania calligaris*.

Comparisons

Raibliania calligaris shows a strict resemblance with the tanystropheid *Tanystropheus*. Tanystropheidae is a clade of archosauromorph diapsids including also *Macrocnemus* species (uppermost Anisian-lowermost Ladinian, Italy and Switzerland; lower Ladinian, Switzerland; lowermost Carnian or uppermost Ladinian, Yunnan Province, China), *Amotosaurus rotfeldensis* Fraser & Rieppel, 2006 (lower Anisian, Germany), *Langobardisaurus pandolfii* Renesto, 1994 (middle-upper Norian, northern Italy and Austria), *Tanytrachelos abynis* Olsen, 1979 (lower Norian, eastern USA) and possibly the poorly known *Protanystropheus antiquus* (von Huene, 1907-08) (= *Tanystropheus antiquus*; from the lower Anisian of Poland and possibly from the lower Muschelkalk of Germany and the Netherlands) and *Augustaburiania vatagini* Sennikov, 2011 (Lower Triassic of European Russia) (Sennikov 2011; Pritchard et al. 2015; Ezcurra 2016).

Tanystropheid features. “Cervical vertebrae excessively [sic] elongated” and “neural spines of cervical vertebrae strongly elongated, very low” are diagnostic features of the Tanystropheidae according to Sennikov (2011: 91) and occur in *Raibliania calligaris*. According to Pritchard et al. (2015: e911186-12) “dorsal tip of [dorsal] neural spines

expanded into flattened platform”; “absence of dorsal intercentra”; and “prominent posterior process on ischium” are unambiguous synapomorphies of *Macrocnemus* + all other Tanystropheidae. “Fusion of ribs to transverse processes in posterior trunk region” and “dorsal neural spine expansion textured with transverse striations” are unambiguous synapomorphies of the clade (*Amotosaurus* + *Tanystropheus*) + (*Langobardisaurus* + *Tanytrachelos*) for Pritchard et al. (2015: e911186-12). The dorsal neural spines of *Raibliania calligarisi* are not expanded apically, but have a sort of “transverse striations”. “Cervical neural spine low at its anteroposterior midpoint, confluent with dorsal surface of neural canal” is the only unambiguous synapomorphy of the clade *Amotosaurus* + *Tanystropheus* according to Pritchard et al. (2015: e911186-12). “Iliac blade with strongly projecting anterior process” (see Pritchard et al 2015: fig. 15E-F and character 170 in the SI for a definition) is an unambiguous synapomorphy of *Langobardisaurus* + *Tanytrachelos* for Pritchard et al. (2015: e911186-12) and “straight proximal femoral shaft with limited sigmoid curvature” is also an apomorphy of derived tanystropheids (Pritchard et al. 2015: e911186-8).

“Epiphysis present in at least the third to fifth cervical vertebrae”, “length of the centrum versus height of the centrum in posterior dorsals = 1.48-2.04”, “dorsal vertebrae with fan-shaped neural spine in lateral view”, “thyroid fenestra between pubis and ischium” and “ischium with a posterior process that extends from the posterodorsal margin” are tanystropheid synapomorphies according to Ezcurra (2016: 284) and are present in *Raibliania calligarisi*. “Cervical neural spines dorsoventrally depressed at their anteroposterior midpoints, leaving them little more than midline dorsal ridges” is a synapomorphy of the clade *Amotosaurus rotfeldensis* + *Tanystropheus longobardicus* for Ezcurra (2016: 284). The very low neural spine is concave at its “anteroposterior” midpoint in MFSN 27532 (Fig. 5A).

Comparison with Tanystropheus. *Tanystropheus* is an iconic taxon because of the extreme lengthening of its neck through the exceptional elongation of its cervical vertebrae, which is not matched by any other living or extinct tetrapod (Wild 1973; Nosotti 2007; Li et al. 2004). The only preserved cervical vertebra of MFSN 27532 is evidently very elongated like the cervicals of *Tanystropheus longobardicus* and *Tanystropheus conspicuus* (see Fig. 5), although it is

probably not as elongated as their most elongated cervical vertebrae (cervicals 8-10; Nosotti 2007). As seen above, the centra of the cervicals 11 of the small-sized *Tanystropheus longobardicus* MNSM BES SC 265 and PIMUZ T/1277 are about 3.5 and 5 times, respectively, those of the respective last pre-lumbar vertebrae (dorsals 10), whereas the ratio based on the estimated length of the preserved cervical of MFSN 27532 and the length of the last pre-lumbar vertebra is intermediate (~4). Since only one cervical is preserved in MFSN 27532, further comparison with the neck of *Tanystropheus* is not possible.

Many papers have been published about the morphofunctional meaning of the outstanding neck of *Tanystropheus* and the palaeoecology of this bizarre reptile (Wild 1973; Tschanz 1988; Renesto 2005; Nosotti 2007; Jaquier & Scheyer 2017; Beadmore & Furrer 2017; Renesto & Saller 2018). Unfortunately, there are no works dedicated to a rigorous definition of the genus *Tanystropheus*. The diagnosis of *Tanystropheus* by Wild (1973: 148; amended by Wild 1980: 5) is a general description of the skeleton that does not distinguish between apomorphic and plesiomorphic features. Ezcurra (2016) diagnosed *Tanystropheus longobardicus*, but not the other named species and the genus *Tanystropheus* in his analysis of the phylogenetic relationships of basal archosauromorphs. Furthermore, Ezcurra’s analysis includes only three tanystropheid species: *Macrocnemus bassanii*, *Amotosaurus rotfeldensis* and *Tanystropheus longobardicus*. Apparently, Ezcurra (2016) considers *Tanystropheus conspicuus*, which is the type species according to Wild (1973: 148; contra Peyer 1931) as a synonym of *Tanystropheus longobardicus*. The diagnosis of *Tanystropheus longobardicus* by Ezcurra (2016: 25) is the following: “Large tanystropheid that differs from other archosauromorphs in the following combination of features: frontals flared laterally as wing-like structures above the orbits; large pineal foramen enclosed between frontals and parietals; ventrally flexed anterior end of dentary; strongly posteriorly developed retroarticular process of the lower jaw; conical and straight marginal tooth crowns with longitudinal ridges; 13 cervical vertebrae; length of the centra of the fourth and fifth cervical vertebrae at least 14 times their heights; distal end of second sacral rib not bifurcated; two ossified distal carpals; and manual digit IV composed of four phalanges”. This diagnosis does not allow establishing whether

MFSN 27532 belongs to *Tanystropheus longobardicus* or to a distinct taxon. However, this diagnosis does not consider the complex taxonomical history of *Tanystropheus* and the doubts still existing about the actual identity of *Tanystropheus longobardicus*. Detailed anatomical comparison is the only way to establish whether MFSN 27532 belongs to *Tanystropheus longobardicus*, to another tanystropheid species or to a distinct taxon.

Five species of *Tanystropheus* have been named to date: *Tanystropheus conspicuus* (middle Ladinian, Germany), *Tanystropheus longobardicus* (uppermost Anisian-lowermost Ladinian, NW Italy and Switzerland; possibly also from the uppermost Anisian of NE Italy [Dalla Vecchia 2006b] and the lowermost Carnian or uppermost Ladinian of Yunnan Province, China [Rieppel et al. 2010]); *Tanystropheus antiquus* von Huene, 1907-08 (lower Anisian of Poland and possibly from the Anisian of Germany and the Netherlands); *Tanystropheus biharicus* Jurcsák, 1975 (Anisian, NW Romania); *Tanystropheus meridensis* Wild, 1980 (lower Ladinian; Switzerland); *Tanystropheus fossai* Wild, 1980 (upper Norian, NW Italy), and *Tanystropheus haasi* Rieppel, 2001 (upper Anisian-lower Ladinian, Israel).

Tanystropheus antiquus is represented only by cervical vertebrae; its single diagnostic feature according to Fraser & Rieppel (2006: 869) is “neck vertebrae with central length less than three times the minimum height”, but these authors also consider that “referral of the material [of *Tanystropheus antiquus*] to the genus *Tanystropheus* must remain equivocal” (p. 870). This species has been subsequently transferred to the new genus *Protanystropheus* by Sennikov (2011), resulting in the new combination *Protanystropheus antiquus*.

Tanystropheus biharicus is based on fragmentary remains that Wild (1980: 12) has referred to *Tanystropheus* cf. *longobardicus*.

Tanystropheus meridensis has been referred to the small morph of *Tanystropheus longobardicus* (see below) by Fraser et al. (2004), Fraser & Rieppel (2006) and Nosotti (2007). As the holotype is represented by a skull and the first seven cervical vertebrae, comparison with *Raibliania calligarisi* is not possible, anyway.

Tanystropheus haasi is represented only by fragmentary vertebrae from the middle cervical region (Rieppel 2001), thus comparison with *Raibliania calligarisi* is limited. The deep groove separating the

centrum from the neural arch at the caudal end of the vertebrae and the other diagnostic features of *Tanystropheus haasi* (see Rieppel 2001: 274) would be barely visible in the crushed cervical of MFSN 27532, which, furthermore, is probably from the distal cervical region. Actually, Rieppel (2001) does not explain why those fragmentary vertebrae are referred to *Tanystropheus*.

Tanystropheus fossai is represented only by a single specimen made of four small cervical vertebrae (each about 35 mm long), supposedly from the distal part of the neck (possibly cervicals 7-10; Wild 1980), therefore comparison with *Raibliania calligarisi* is limited also in this case. The cervical vertebra of MFSN 27532 lacks the lateral wing-like crest in the caudal part of the centrum and the completely reduced neural spine, which are diagnostic characters of *Tanystropheus fossai* (see Wild 1980), but it is probably from a more caudal position respect to the preserved *Tanystropheus fossai* cervicals. Anyway, *Raibliania calligarisi* is much larger and older than *Tanystropheus fossai*. Renesto (2005) questioned the validity of *Tanystropheus fossai* and no tanystropheid apomorphies are apparent in the only specimen of this taxon according to Pritchard et al. (2015: e911186-15).

No satisfactory diagnosis of *Tanystropheus conspicuus* is available (see Wild 1973: 149), which is based on isolated bones (vertebrae, a humerus and a femur; Wild 1973: 150).

The most important *Tanystropheus* record is from the Besano Formation/Grenzbitumenzone (Anisian-Ladinian boundary) of Lombardy (NW Italy) and Tessin (Switzerland). As anticipated above, it is composed of two distinct size-classes of individuals. While Wild (1973) considered the small and large individuals as the juveniles and adults of *Tanystropheus longobardicus*, respectively, Fraser et al. (2004) suggested that they could represent two distinct species. The revision of *Tanystropheus* is beyond the scope of this paper, but it is necessary to highlight here that some morphological features support a taxonomic distinction between small and large-sized *Tanystropheus* individuals from the Grenzbitumenzone/Besano Formation and that the debate is not settled yet. Small individuals have an estimated body length ranging 53-190 cm (mean of 17 specimens: 113.3 cm; Wild 1973: tab. 1; Nosotti 2007) and are much smaller than the larger individuals, whose estimated body length ranges 210-535

cm (mean of 15 specimens: 312.3 cm; Wild 1973: tab. 1; Nosotti 2007: tab. 1). In the small individuals, the neural arches are fused to their centra without evident suture (Nosotti 2007). Fusion of centra and neural arches occurs during growth in archosauromorphs (e.g., Irmis 2007). Therefore, small individuals were plausibly not very young when they died, despite of their high size difference with the larger individuals. Larger individuals have only monocuspid marginal teeth, whereas small individuals have monocuspid and tricuspid marginal teeth (also *Lan-gobardisaurus pandolfii* has tricuspid marginal teeth; Renesto & Dalla Vecchia 2000). Total height/centrum length ratio and neural spine height/length ratio in the dorsal vertebrae are different in small and large individuals (Nosotti 2007). The obturator foramen opens caudally on the pubis in the small individuals (like in MFSN 27532), whereas the foramen is cranial in the large specimens (see Wild 1973: fig. 91; Nosotti 2007: fig. 25). The preacetabular process of ilium in lateromedial view is scarcely projecting cranially and blunt in small and large individuals according to Wild (1973: fig. 93), but Nosotti (2007: 33-34, fig. 25) has shown that at least some small individuals have a “short pre-acetabular process or tubercle” cranially on the ilium. Presence, shape and size of this tubercle have phylogenetic importance according to Pritchard et al. (2015: e911186-12) and Ezcurra (2016: 236).

The neotype of *Tanystropheus longobardicus* (PIMUZ T 2791) is a small individual (estimated total length is only 87 cm; Wild 1973: tab. 1), as also it was the holotype (see Bassani 1886; Peyer 1931, pl. 14), which was destroyed in the fire of the Natural History Museum of Milano during the Second World War. Therefore, the name *Tanystropheus longobardicus* would remain to the small-sized individuals with tricuspid teeth and the large-sized individuals would require a new name, in the case that large and small individuals belong to distinct species. For this reason, in this paper it is always specified, when possible, whether MFSN 27532 is compared with small-sized or large-sized specimens of *Tanystropheus longobardicus*.

The articular surfaces of the centra in the ‘mid’ and ‘distal’ dorsal vertebrae of MFSN 27532 are not vertical as in the mid-dorsals of the small individuals of *Tanystropheus longobardicus* (see Nosotti 2007: fig. 60B) as well as those of the large individuals (Rieppel et al. 2010: 1085). However, these ar-

ticular surfaces seem to be somewhat slanting also in the dorsals of *Tanystropheus conspicuus* (see Wild 1973: fig. 54a), thus this feature may distinguish only *Raibliania calligaris* from the specimens referred to *Tanystropheus longobardicus*.

The neural spines appreciably increase in height from ‘mid’- to ‘distal’ dorsal vertebrae in MFSN 27532 (Fig. 6A-C). Nosotti (2007) did not notice such increase in *Tanystropheus longobardicus*. This increase is not apparent in the reconstruction of the *Tanystropheus longobardicus* skeleton by Peyer (1931: pl. 4), but it was mentioned by Rieppel et al. (2010) and Renesto & Saller (2018), although it was not adequately figured in these papers.

Proportions are different in the dorsal vertebrae of *Raibliania calligaris* and *Tanystropheus longobardicus*. The presumed dorsals 4 and 11 (actually, dorsals 3 and 10; see Rieppel et al. 2010) of the small *Tanystropheus longobardicus* MSNM BES SC 1018 (Nosotti 2007: figs. 17-18) are both taller than long (total vertebral height/centrum length ratios are 1.16 and about 1.14, respectively), whereas the ‘mid’-dorsals of MFSN 27532 are longer than tall (total vertebral height/centrum length ratios are 0.90-0.86). In the mid-dorsals of *Tanystropheus conspicuus* and the large-sized *Tanystropheus longobardicus*, the total vertebral height is twice or more the length of the centrum (Wild 1973: fig. 54; Nosotti 2007: 68) and the neural spine is approximately as high as long or taller than long (Wild 1973: fig. 54; Nosotti 2007: 68).

Diagnostic features of *Raibliania calligaris*

MFSN 27532 presents features which allow distinguishing it from the others tanystropheids.

Button-like teeth. The premaxillary, maxillary and mandibular teeth of *Tanystropheus longobardicus* are characteristically conical, slender and pointed with apicobasal striations (Wild 1973; Dalla Vecchia 2006b: fig. 5B-C; Nosotti 2007). Small individuals of *Tanystropheus longobardicus* have also maxillary and mandibular tricuspid teeth (Wild 1973; Nosotti 2007). *Tanystropheus longobardicus* has also teeth in the pterygoids, palatines and vomers (Wild 1973; Nosotti 2007). According to Wild (1973: 13 and 48) the pterygoid teeth are all conical and comparatively smaller than that preserved in MFSN 27532. The palatine teeth could have a size comparable to that of MFSN 27532, but they are also conical (Nosotti 2007: 62). Vomerine teeth are described by Nosotti (2007: 21) as “tiny and pointed, with striated

enamel". Marginal teeth of *Macrocnemus* are conical and recurved (Ezcurra 2016; Jaquier et al. 2017), and also those, much smaller, on the palatal elements are slightly recurved (Jaquier et al. 2017: 14). The marginal teeth of *Amotosaurus* are conical and the palatal teeth are very small (the pterygoids, palatines and vomers are covered by a fine shagreen of denticles according to Fraser & Rieppel 2006) and have not been described in detail. Teeth of *Tanytrachelos* are "flattened, recurved, and have a single point" (Smith 2011: 14). Grinding tooth plates occur distally in the maxilla and mandible of *Langobardisaurus pandolfii* but their morphology is unlike that of the tooth under discussion (Renesto & Dalla Vecchia 2000: fig. 3; Saller et al. 2013: fig. 5).

Apex of the dorsal neural spines not transversely thickened. As seen above, "dorsal tip of [dorsal] neural spines expanded into flattened platform" is an unambiguous synapomorphy of the *Tanystropheidae* according to Pritchard et al. (2015). This apical expansion of the neural spine can be observed in *Tanystropheus conspicuus* (see Wild 1973: fig. 54). The apex of the neural spine in the reconstruction of a mid-dorsal of *Tanystropheus longobardicus* (small-sized specimen) by Nosotti (2007: fig. 60B) appears to be transversely thickened. The neural spines of the dorsal vertebrae of *Tanystropheus* cf. *T. longobardicus* from NE Italy (large-sized specimens) are transversely thicker apically than basally and the neural spine is proportionally thicker than in MFSN 27532 (pers. obs.). Instead, the neural spines of *Raibliania calligarisi* are transversely thin and is not appreciably expanded apically.

Articulation facet on the dorsocaudal corner of the neural spines and corresponding dorsocranial facet on the following vertebra in the dorsal vertebrae. There are no modified upper corners of the neural spine to allow articulation between contiguous neural spines in the dorsals of *Tanystropheus conspicuus* (see Wild 1973: fig. 54) and *Tanystropheus longobardicus* (see Wild 1973: pl. 1; Nosotti 2007: figs. 5, 60B and pl. II), small-sized *Tanystropheus* cf. *longobardicus* (see Renesto 2005: fig. 4) and large-sized *Tanystropheus* cf. *T. longobardicus* from NE Italy (Dalla Vecchia 2006b; pers. obs.).

The contact between the neural spines plausibly limited the movements of the vertebrae. The articular surfaces of the zygapophyses of MFSN 27532 are not sub-horizontal as those of the mid to distal dorsals of both the small and the large individuals of *Tanystropheus longobardicus* (see Nosotti

2007: 68; Rieppel et al. 2010: 1085; Renesto & Saller 2018: 25). In MFSN 27532, the inclined (dorsomedially-ventrolaterally facing) articular facets of the zygapophyses restricted the lateral bending of the thoracic vertebral column (Romer 1956) and could indicate a different locomotion style between *Raibliania calligarisi* and *Tanystropheus longobardicus*.

Pleurapophyses of the second 'lumbar' vertebra (last pre-sacral vertebra) that are much shorter than the pleurapophyses of the first 'lumbar' vertebra and tapers distally to a pointed end. The pleurapophyses of the second 'lumbar' vertebra seem to be shorter than those of the first 'lumbar' in *Tanystropheus longobardicus*, but they do not appear to be sharply pointed (see Wild 1973: pls. 1 and 7; Wild 1980: pl. 5; Nosotti 2007: pl. II). According to Nosotti (2007: 69), both 'lumbars' "bear long pleurapophyses" in the small-sized MSNM BES SC 265. According to Renesto (2005: 379), the small specimen MCSN 4451, referred to *Tanystropheus* cf. *T. longobardicus*, has "short but craniocaudally expanded transverse processes onto which is firmly sutured a short "lumbar" rib" in the last two dorsal vertebrae. In *Tanytrachelos abynis*, the pleurapophyses of the second 'lumbar' vertebra are like those of the first 'lumbar' and are distally truncated (see Olsen 1979: fig. 2). The last five dorsals of *Macrocnemus* are considered as 'lumbars' (Rieppel 1989); they bear short and straight ribs (Rieppel 1989), which are unfused to the transverse processes (Premru 1991; Pritchard et al. 2015: fig. 14C). According to Jaquier et al. (2017: 16), the penultimate dorsal vertebra of the *Macrocnemus bassanii* specimen PIMUZ T 2472 bears rather short "prong-like" ribs (see also Premru 1991: fig. 11), whereas those of the last dorsal vertebra are "only marginally longer, but expanded distally". The pleurapophyses of the last 'lumbar' vertebra of *Langobardisaurus pandolfii* are slightly shorter than those of the penultimate 'lumbar' vertebra, are tapering distally and probably pointed in the specimen MFSN 1921 (pers. obs.). However, *Langobardisaurus pandolfii* has a 'lumbar' region made of five dorsal vertebrae like *Macrocnemus* (Saller et al. 2013: 91).

Ilium with comparatively long preacetabular process extending beyond the level of the cranial margin of the pubic peduncle ending cranioventrally with a robust and transversely thick tuberosity. The preacetabular process is short, rounded and does not extend beyond the level of the cranial margin of the pubic peduncle in the ilia of *Tanystropheus longobardicus* (belonging to small and

large-sized individuals) figured by Wild (1973: fig. 93). The reconstruction of the ilium of a small-sized *Tanystropheus longobardicus* by Nosotti (2007: fig. 25) is like those figured by Wild (1973) but presents a small and cranially directed tuberosity on the cranial side of the preacetabular process (Fig. 9C), like that of *Macrocnemus bassanii* (see Rieppel 1989: fig. 4B). The presence of "strongly projecting anterior process" in the iliac blade is reported as an unambiguous synapomorphy of *Langobardisaurus* + *Tanytrachelos* by Pritchard et al. (2015: e911186-12). However, this process is not transversely thickened and lacks a ventral shelf in *Tanytrachelos abynis* (see Pritchard et al. 2015: fig. 15F) and the ilium is poorly preserved in all of the specimens of *Langobardisaurus pandolfii* (see Renesto 1994; pers. obs.). In *Amotosaurus rotfeldensis*, the preacetabular process is very short, rounded, not extending beyond the level of the cranial margin of the pubic peduncle in the ilium and lacks a tuberosity in the cranial side (Fraser & Rieppel 2006: fig. 6A).

Prominent and blunt medial ridge bordering the entire ventral part of the iliac blade from the cranioventral tuberosity to the caudal end of the postacetabular process. This ridge is not present in *Tanystropheus longobardicus* (see Peyer 1931: fig. 10; Wild 1980: pls. 4-5; Nosotti 2007: pl. II) and in the ilia referred to *Tanystropheus* cf. *T. longobardicus* from the uppermost Anisian of Aupa Valley (Fig. 2) stored at the MFSN (Dalla Vecchia 2006b: fig. 16; pers. obs.). The ridge probably lacks in *Macrocnemus bassanii* (see Rieppel 1989: fig. 1A) and possibly also in *Langobardisaurus pandolfii* (MFSN 1921, pers. obs.). Its presence or absence cannot be established in *Tanytrachelos abynis* (see Olsen 1979; Smith 2011) and *Amotosaurus rotfeldensis* (see Fraser & Rieppel 2006).

Pubis with a cranial process. The cranial margin of the pubes of *Tanystropheus longobardicus* figured by Peyer (1931: figs. 10-11), Wild (1973: fig. 91; belonging to small and large-sized individuals), Renesto (2005: pl. 2, fig. E, small-sized), Nosotti (2007: fig. 25, small-sized; Fig. 9F), and Renesto & Saller (2018: fig. 2, small-sized) lacks a cranial process. Also a pubis of a large-sized *Tanystropheus* from the Aupa Valley (MFSN 31868; Dalla Vecchia 2008b: fig. 61M) lacks a cranial process (pers. obs.). Furthermore, those pubes have mostly a 'cut' (i.e., not rounded) distal end, unlike MFSN 27532. The pubes of a *Macrocnemus* aff. *M. fuayensis* specimen from the Besano Formation of Switzerland figured

by Jaquier et al. (2017: fig. 8G) have a cranial process and a distal part rather similar to that of the pubis of *Raibhania calligarisi*, but the elements are distinctly stouter in the Swiss specimen. *Macrocnemus bassanii*, also from the Besano Formation, has a differently shaped pubis (see Rieppel 1989: fig. 4B). The pubes of *Amotosaurus rotfeldensis* (see Fraser & Rieppel 2006: fig. 6A) and *Tanytrachelos abynis* (see Smith 2011: fig. 7) do not have a cranial process.

The pubis of MFSN 27532 presents distinct iliac and ischiadic peduncles separated by a groove starting from the large obturator foramen and reaching the articular surface. The iliac and ischiadic peduncles of the pubes of *Tanystropheus longobardicus* figured by Wild (1973: fig. 91; belonging to small and large-sized individuals) and Peyer (1931: fig. 10) are not separated by a groove. Also the pubis of a large-sized *Tanystropheus* (MFSN 31868) from the Aupa Valley lacks a groove and a clear separation of the iliac and ischiadic processes (pers. obs.). The same occurs in *Macrocnemus* spp. (Rieppel 1989: fig. 4B; Jiang et al. 2011: fig. 6; Jaquier et al. 2017: fig. 8G) and *Amotosaurus rotfeldensis* (see Fraser & Rieppel 2006: fig. 6A). However, the reconstruction of the pubis of a small-sized individual of *Tanystropheus longobardicus* by Nosotti (2007: fig. 25) shows a large obturator foramen and a groove separating the iliac and ischiadic peduncles like the pubis of MFSN 27532, therefore this feature is not considered here as a diagnostic feature of *Raibhania calligarisi*.

If MFSN 13228 is from the tail of a specimen of *Raibhania calligarisi*, "craniocaudally narrow, tall and apically tapering neural spine of the mid-caudal vertebrae" and "small and thorn-like terminal process in the prezygapophysis of the mid-caudal vertebrae" (see Fig. 10) would be two further apomorphies of *Raibhania calligarisi* (see Wild 1973: fig. 62; Rieppel 1989: fig. 10; Renesto 1994: fig. 10; Renesto & Dalla Vecchia 2000: fig. 1; Nosotti 2007: fig. 6; Smith 2011: fig. 14; Sennikov 2011: figs 2i-k).

Tanystropheid diversity in the Triassic of northern Friuli

Abundant remains of a large-sized *Tanystropheus* (larger than *Raibhania calligarisi*) have been found in the uppermost Anisian (Illyrian; see Farabegoli et al. 1985; Fig. 11) Aupa Turbidites Formation of the Aupa Valley (Dalla Vecchia 2006b, 2008b; Dalla Vecchia & Simonetto 2018), about 25

km west of the locality where MFSN 27532 was found (Fig. 2). Those of *Tanystropheus* are the most common reptile remains in the marine Aupa Turbidites (Dalla Vecchia & Simonetto 2018), which include also a large nothosauroid, archosauriforms, and rare placodonts and ichthyopterygians (Dalla Vecchia 2006b; Dalla Vecchia & Simonetto 2018). Specimens from the Aupa Valley are roughly coeval with *Tanystropheus longobardicus* from the Besano Formation / Grenzbitumenzone of Switzerland and NW Italy, have been provisionally referred to *Tanystropheus* cf. *T. longobardicus* by Dalla Vecchia (2006b) and are over five million years older than *Raibliania calligaris* (see Cohen et al. 2013 for the geochronological information).

An about 130 mm-long cervical vertebra from the fossil-bearing locality of Fusea (about 38 km WSW of the type locality of *Raibliania calligaris*; Fig. 2) was referred by Dalla Vecchia (2000) to *Tanystropheus* cf. *longobardicus*. It has a tubular centrum without a neural crest at midcentral level and the neural arch with the neural spine is developed only at the caudal extremity of the centrum (the cranial extremity is missing; Dalla Vecchia 2000: fig. 4). A cyamodontoid placodont (possibly *Cyamodus*, see Rieppel & Nosotti 2002) and a large species of the nothosauroid *Nothosaurus* are the most common reptiles in the Fusea site (Rieppel & Dalla Vecchia 2001; Dalla Vecchia & Simonetto 2018). The fossil-bearing section occurs at the base of the Val Degano Formation just above a thick carbonate platform with evidences of emersions at its top (Dalla Vecchia 2000), which has been reported in the literature as Schlern Dolomite and considered as composed of the Ladinian Sciliar Dolomite and the Carnian Cassiana Dolomite (cf. Venturini & Fontana 2009). This section originated in a transitional depositional environment (e.g., a lagoon or a coastal marsh) subject to freshwater influence and oscillating salinity (Dalla Vecchia & Carnevale 2011). The basal beds of the Val Degano Formation yielded the conodont *Pseudofurnishius murcianus murcianus* (see Venturini 2009: 122) which has an uppermost Ladinian-lower Carnian range in the Alps (Plasencia et al. 2015); for this reason, Venturini (2009: 122) placed the Ladinian-Carnian boundary within the basal metres of the Val Degano Formation. However, the same conodont was found in the Rio di Terrarossa dolomite of the close (Fig. 2) Dogna Valley (Jadoul et al. 2002), which

has been considered as a lateral equivalent of the Conzen Formation by Caggiati et al. (2018, 2019) and lays above the thick carbonate platform that is reported as “Ladinian-Carnian dolomite” by Caggiati et al. (2018) (Fig. 11). The latter presents an unconformity at its top marked by a bauxite-bearing horizon (Jadoul et al. 2002) and corresponds to the Schlern Dolomite of Venturini & Fontana (2009). The Rio di Terrarossa dolomite has been dated to the late early Carnian (late Julian; Fig. 11) by Caggiati et al. (2018, 2019) based on ammonoid biostratigraphy and physical correlations. Correlation between the Fusea and Dogna sections, suggests now a late early Carnian age also for the Fusea fossil-bearing section, which was the first dating of the Fusea section reported in the literature (see Dalla Vecchia 2000). Consequently, the cervical vertebra from Fusea is much younger than the *Tanystropheus* cf. *longobardicus* of the Aupa Valley and slightly younger than *Raibliania calligaris*. It is now unclear whether the cervical from Fusea belongs to the large *Tanystropheus* species from the uppermost Anisian of the Aupa Valley, to *Raibliania calligaris* or to a distinct species. The study of the uppermost Anisian sample and the preparation of further Fusea bones possibly belonging to the same taxon, will hopefully clarify this aspect.

Tanystropheids are not reported in the Carnian reptile-bearing section of the Dogna area, located about 15 km WSW of the type locality of *Raibliania calligaris* (Fig. 2). This marine section represents a shallow water, carbonate-siliciclastic ramp sedimentary environment (Preto et al. 2005) set at the beginning of the Carnian Pluvial Episode (Dal Corso et al. 2018). It has yielded the cyamodontoid placodont *Protenodontosaurus italicus* (see Pinna 1990), the nothosauroid *Simosaurus* aff. *gailardoti* (see Dalla Vecchia 2008a), the pistosauroid *Bobosaurus forojuliensis* (see Dalla Vecchia 2006a), and relatively abundant remains of cyamodontoid placodonts and eosauroptrygians (Dalla Vecchia & Simonetto 2018). It was once correlated with the Rio del Lago Formation of the close Cave del Predil section, but it has recently been shown to correspond to the basal part of the Tor Formation (Caggiati et al. 2019) (Fig. 11). Therefore, its age is latest early Carnian (latest Julian) and it is slightly younger than the Fusea section. Despite to this small age difference, the two associations contain different genera and species of reptiles.

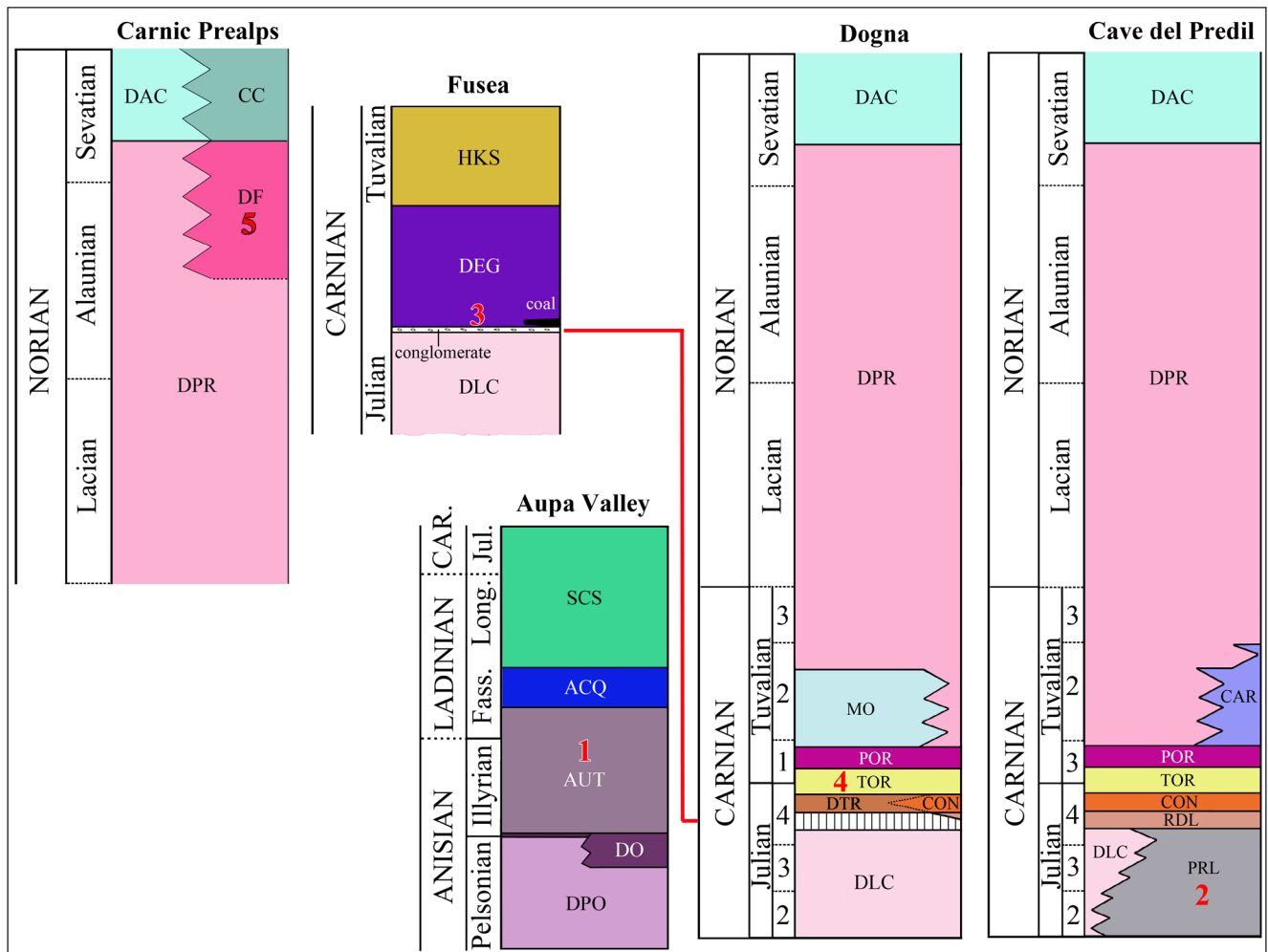


Fig. 11 - Chronostratigraphic scheme of the Triassic successions with tanystropheids and other reptiles in northern Friuli. The numbers indicate the stratigraphic position of the reptile-bearing localities mentioned in the text: 1, Aupa Valley, with *Tanystropheus* cf. *T. longobardicus*; 2, Cave del Predil (including the Prasnig Brook), with *Raibhania calligaris*; 3, Fucea, with a long-necked tanystropheid; 4, Dogna Valley and environs, without tanystropheids but with eusauropterigians and placodonts; and 5, localities of the northern side of the Carnic Prealps with the short-necked *Langobardisaurus pandolfii*. For the geographic location of the sites, see Fig. 2. Abbreviations: ACQ, Acquatona Formation; AUT, Aupa Turbidites Formation; CAR, Carnitza Formation; CC, Chiampomano Limestone; CNZ, Conzen Limestone; DAC, Dachstein Limestone; DEG, Val Degano Formation; DF, Forni Dolomite; DLC, Ladinian-Carnian dolomite; DO, Dont Formation; DPO, Popera dolomite; DPR, Main Dolomite (Dolomia Principale); HKS, Heiligkreuz Formation; MO, Monticello Member of the Main Dolomite; POR, Portella dolomite; PRL, Predil Limestone; RDL, Rio del Lago Formation; RTR, Rio di Terrarossa dolomite; SCS, San Cassiano Formation; TOR, Tor Formation. Black dotted lines indicate poor time constraints. Based on Dalla Vecchia (2008b) and Caggiati et al. (2018), modified.

Langobardisaurus pandolfii, a medium-sized tanystropheid with comparatively short cervical vertebrae with respect to *Tanystropheus* (Renesto & Dalla Vecchia 2000), occur in the much younger (middle-late Norian) fossil-bearing portion of the Forni Dolomite (Dolomia di Forni; Fig. 11) of the northern part of the close Carnic Prealps (Fig. 2). A second and diminutive tanystropheid taxon may be present in this unit (Dalla Vecchia 2012; pers. obs.). The Forni Dolomite represents the deposition in a relatively deep and anoxic marine basin bordered by the shallow carbonate platform of the Main Dolomite (Dolomia Principale; Dalla Vecchia 2012).

The tanystropheids probably lived together with the drepanosaurids and pterosaurs in the arid emergent parts of the carbonate platform and were transported into the marine basin after death (Dalla Vecchia 2012).

The palaeontological record shows that the tanystropheids populated this small area of the Alpine Region for nearly 35 million years (see Cohen et al. 2013 for the geochronological information). They were an important component of the local tetrapod faunas living in insular, coastal or shallow marine environments and appear to have been more diversified than previously supposed.

CONCLUSIONS

Raibliania calligaris is an early Carnian tanystropheid with a neck supported by very elongated vertebrae like the Anisian-Ladinian *Tanystropheus longobardicus*. It has a body size at the lower range of the large-sized *Tanystropheus longobardicus* specimens, but shows a stricter resemblance with the small-sized individuals referred to this species. It differs from the other tanystropheids in the possess of button-like teeth; in the relative lower transverse thickness of the neural spines of the mid-distal dorsal vertebrae (especially apically); in the apical articulation between the neural spines of the adjacent dorsal vertebrae; in the pleurapophyses of the second 'lumbar' vertebra, which are pointed and much shorter than those of the first 'lumbar' vertebra; in the ilium with a medial ridge bordering the entire ventral part of the iliac blade and a comparatively longer preacetabular process extending beyond the level of the cranial margin of the pubic peduncle, which bears a robust and transversely thick tuberosity; and in a pubis with a cranial process (like *Macrocnemus* aff. *M. fuayensis*).

The tanystropheids populated the present day northern Friuli for nearly 35 million years, were an important component of the local tetrapod faunas living in insular, coastal or shallow marine environments and were relatively well-diversified. The global geochronological range of the tanystropheids with extremely elongated neck vertebrae is from the late Anisian up to the late early Carnian or even up to the late Norian, if '*Tanystropheus fossai*' is considered. Tanystropheids did not reach the Triassic-Jurassic boundary. In the rest of the Mesozoic, a comparable elongation of the cervicals (low, ridge-like neural spines and the neural canal running inside the tubular and hollow vertebral centrum) was evolved only by azhdarchid pterosaurs (Martill et al. 1998; Witton & Naish 2008) about 100 million years later during the Late Cretaceous.

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