

## A taxonomic revision of the genus *Tanystropheus* (Archosauromorpha, Tanystropheidae)

Stephan N.F. Spiekman and Torsten M. Scheyer

### ABSTRACT

*Tanystropheus* represents one of the most characteristic genera of Triassic reptiles and is typified by easily recognizable, hyperelongate cervical vertebrae. First described in 1852, isolated cervical vertebrae and other remains have been referred to the genus and various species have been erected and rejected based on this material. This has resulted in a complicated and convoluted taxonomic history of the genus and confusion as to the validity of species and the referral of specimens. With the exception of the well-represented *T. longobardicus*, the five other species of *Tanystropheus* are known from isolated elements or a single, partial specimen. Here, we provide a complete overview of the taxonomic history and a revision of the genus based on first hand observations of the type material of most of the species. From this, we conclude that *T. conspicuus* and *T. haasi* should be considered nomina dubia and that *T. meridensis* constitutes a junior synonym to *T. longobardicus*. Furthermore, *T. longobardicus* can be subdivided into two discrete morphotypes that might represent separate species. However, a more detailed study is required to test this hypothesis. Finally, *T. fossai* is considered distinctly different from the other *Tanystropheus* taxa and is therefore referred to a separate genus, *Sclerostropheus*.

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## INTRODUCTION

*Tanystropheus* represents one of the most enigmatic tetrapod taxa of the Triassic due to its unique morphology and palaeobiology. Its most striking aspect is its extremely long neck, which consists of a relatively small number (13, see Rieppel et al., 2010) of bizarrely elongated cervical vertebrae with reduced neural spines. This type of cervical vertebrae is unique among tetrapods and easily recognizable.

For almost a century the genus *Tanystropheus* von Meyer, 1852, was only known from a number of these elongate vertebrae from the Upper and Lower Muschelkalk of Central Europe (Meyer, 1855; Huene, 1907-1908). Their position along the vertebral column was unclear, and they were tentatively interpreted as caudal vertebrae. They were only recognized as cervical vertebrae following the discovery of largely complete and articulated skeletons from the Besano Formation of Monte San Giorgio on the border between Switzerland and Italy (former Grenzbitumenzone, Anisian-Ladinian boundary, Middle Triassic; Stockar, 2010) (Peyer, 1931).

Based on these more complete specimens, it was originally proposed that the genus *Tanystropheus* was closely related to Sauropterygia (Peyer, 1931), but subsequent authors placed it in either “Prolacertiformes” or “Protosauria”; two clades roughly encompassing the same taxa (e.g., *Prolacerta broomi*, *Protosaurus speneri*, and *Macrocnemus* spp.) characterized by the presence of elongated cervical vertebrae (e.g., Camp, 1945a; Camp, 1945b; Wild, 1980a; Benton, 1985; Chatterjee, 1986; Evans, 1988; Benton and Allen, 1997; Jalil, 1997; Dilkes, 1998). Although originally considered to belong to Lepidosauromorpha (Wild, 1973), “Prolacertiformes/Protosauria” were grouped within Archosauromorpha by Gow (1975), a placement which was later supported by Benton (1985) and Evans (1988) and is now firmly established. However, recent analyses strongly indicate “Prolacertiformes/Protosauria” to be polyphyletic within Archosauromorpha, generally distinguishing a monophyletic Tanystropheidae from other “protosaurus” like *Prolacerta broomi* and *Protosaurus speneri* (Dilkes, 1998; Rieppel et al., 2003; Pritchard et al., 2015; Ezcurra, 2016; Spiekman, 2018).

The genus *Tanystropheus* is currently represented by six species. Out of these species, only *T. longobardicus* from the Besano Formation of Monte San Giorgio is represented by various articulated and largely complete specimens, including

skull material (Wild, 1973; Nosotti, 2007). Recently, a nearly complete skeleton from the latest Ladinian or earliest Carnian of southwestern China could not be distinguished from the *T. longobardicus* specimens from the European Besano Formation, and was identified as *T. cf. longobardicus*, implying the possibility of a Tethys-wide distribution for this species (Rieppel et al., 2010). Other species are comprised of either a number of isolated remains (*T. conspicuus*, *T. antiquus*, and *T. haasi*) or a single incomplete specimen (*T. meridensis*, *T. fossai*) (Meyer, 1855; Huene, 1905, 1907-1908; Wild, 1973, 1980a; Rieppel, 2001; Fraser and Rieppel, 2006; Sennikov, 2011; Skawiński et al., 2017). Additionally, isolated remains from Europe, the Middle East, Asia, and North America have been attributed to the genus but have not been determined to the species level (Vickers-Rich et al., 1999; Dalla Vecchia, 2000; Rieppel, 2001; Dalla Vecchia and Avanzini, 2002; Dalla Vecchia, 2005; Li, 2007; Sues and Olsen, 2015).

Here we provide a review of the long and convoluted taxonomic history of the genus *Tanystropheus* and revise its taxonomy based on firsthand observations, including observations of the type material of *T. conspicuus*, *T. longobardicus*, *T. meridensis*, and *T. fossai*, and a cast of the holotype of *T. haasi*.

### Taxonomic History of *Tanystropheus*

The genus *Tanystropheus* was erected on the basis of eight isolated, elongate bones from the Upper Muschelkalk of Bindlach near Bayreuth, Germany, and an incomplete specimen from the lowermost Keuper of Upper Silesia (Laryszów, Poland), which were identified as reptilian vertebrae and assigned to *Tanystropheus conspicuus* by Meyer (1855). He pointed out that these bones had previously been described by Count Georg zu Münster, who had interpreted them as limb bones of a saurian reptile, which he had named “*Macrocelosaurus*”. However, since this work has been lost and this genus name has fallen into disuse (*nomen oblitum*), the genus name *Tanystropheus* has received precedence (Wild, 1973, p. 148; Melville, 1981).

A number of isolated remains from the Chinle Formation (Late Triassic) of northwestern New Mexico, USA, were assigned to three new species: *Tanystropheus bauri*, *Tanystropheus willistoni*, and *Tanystropheus longicollis* (Cope, 1887). However, additional findings showed distinct differences with *T. conspicuus* from the Upper Muschelkalk, and this material was soon after re-

assigned to a new genus of dinosaur, *Coelophysis* (Cope, 1889).

Later, additional elongate vertebrae from various localities were described (reported on in Huene (1905) and described in more detail in Huene (1907-1908); Supplementary Table 1). A number of these specimens from the Upper Muschelkalk were assigned to *Tanystropheus conspicuus*, whilst two additional species of *Tanystropheus* were erected. A number of elongate vertebrae from the Gogolin beds (Lower Muschelkalk) near Gogolin and Krappitz in Silesia, Poland, were identified as being similar to *T. conspicuus* and assigned to *T. antiquus* and a vertebra from the Norian of Stuttgart-Heslach, Germany, was assigned to *T. posthumus*. However, subsequent findings of *Tanystropheus* later indicated that this latter species did not belong to this genus (Peyer, 1931). Currently, this specimen is considered an otherwise indeterminable caudal vertebra of a theropod dinosaur, and the taxon "*Tanystropheus posthumus*" is considered a *nomen dubium* (Rauhut and Hungerbühler, 2000). The *T. antiquus* material from the Gogolin beds was recently preliminarily revised, and these specimens are considered to be of early Anisian and possibly latest Olenekian age (Skawiński et al., 2017).

More than 75 years after the initial description of the isolated remains of *Tanystropheus conspicuus*, excavations at the Besano Formation at Monte San Giorgio revealed largely complete and articulated specimens that could be referred to *Tanystropheus* (Peyer, 1930, 1931). Previously, the identity of the elongate vertebrae of *Tanystropheus* had been unclear, and they had been suggested to be caudal vertebrae (Meyer, 1855; Huene, 1907-1908). The articulated nature of the specimens described by Peyer (1931) clarified that they undeniably represented hyper-elongated cervical vertebrae. Furthermore, cranial remains within this material showed distinct tricuspid marginal dentition. The presence of these tricuspid teeth, as well as the elongate cervical vertebrae, was identical to that present in a now lost specimen from the same locality that had previously been described and interpreted as a pterosaur, *Tribelesodon longobardicus*, in which the cervical vertebrae had been misidentified as elongated phalanges due to a lack of comparative material (Bassani, 1886; Nopsca, 1923). Peyer (1931) assigned this specimen and the newly discovered material to *Tanystropheus longobardicus*.

Following the description of the articulated *Tanystropheus longobardicus* specimens, isolated

**TABLE 1.** Tooth counts of relevant *Tanystropheus* specimens from Monte San Giorgio. Specimens assigned to the small morphotype are indicated by an asterisk. Abbreviations: ia, inapplicable; mx, maxilla; pmx, premaxilla.

	Pmx. tooth count	Maxilla tooth count	Mx.		Dentary position first tricuspid	Pterygoid tooth count	Palatine tooth count	Vomer tooth count
			position first tricuspid	How tricuspid				
PIMUZ T 2819	6	?	ia	ia	ia	0	?	?
PIMUZ T 2790	6	15	ia	ia	ia	0	?	15
PIMUZ T 2787	?	?	ia	ia	ia	0	0	12
PIMUZ T 2792 (cast of SNSB-BSPG 1953 XV 2)	?	?	ia	ia	?	?	?	5 or 6
PIMUZ T 2482*	6?	?	7	rather bulbous	12?	?	5	?
PIMUZ T 2795*	?	?	?	at least a bit	?	around 12	at least 3	7
MSNM BES SC 265*	6	?	4 or 5	distinctly	around 7th	?	?	present
MSNM BES SC 1018*	6	15	1st to 3rd	distinctly	around 5th	12 sensu Nosotti (2007)	at least 3	at least 3
PIMUZ T 2484*	?	15	around 5th	distinctly	beyond 10th	around 13	6	?
PIMUZ T 2779*	?	?	?	distinctly	?	?	?	10
PIMUZ T 3901*	6	?	3 or 4	distinctly	beyond 4th	?	?	?
PIMUZ T 1277*	?	?	?	distinctly	around 5th	?	?	?

remains from other localities, mainly part of the Upper and Lower Muschelkalk of Europe, were re-evaluated and elements other than elongate cervicals were identified to likely belong to the genus *Tanystropheus* (Huene, 1931). Among this material was a vertebra from the Erfurt Formation (Lettenkeuper, middle Ladinian) of Gaildorf, Germany, that was originally described by Plieninger (1846) and, together with other fragmented remains, including a partial upper jaw including teeth, was assigned to "*Zanclodon laevis*", thus predating *T. conspicuus* by Meyer (1855). However all the material assigned to "*Z. laevis*" apart from the upper jaw fragment has been lost, and this jaw fragment has thus been assigned as the lectotype of the taxon, which differs distinctly from that of *Tanystropheus* spp. (Wild, 1973). "*Z. laevis*" was also briefly discussed, and its taxonomic history summarized by Schoch (2011), who also figured the type specimen and identified it as an archosauriform. Additionally, among the material discussed, specimens previously assigned to "*Thecodontosaurus latespinatus*", "*Thecodontosaurus primus*", and "*Procerosaurus cruralis*" were also considered to very likely belong to the genus *Tanystropheus* (Huene, 1931; see also the synonymy lists for *T. conspicuus* and *T. antiquus* by Wild, 1973, p. 148-149, 151). However, the assignment of "*Thecodontosaurus primus*" to the genus was recently questioned, and a detailed revision of this material is required to establish its affinities (Skawiński et al., 2017).

Tanystropheid remains from the Upper Buntsandstein (Röt Formation, early Anisian; Menning and Hendrich, 2016) of the Black Forest, Germany, which slightly predates the Lower Muschelkalk, were described and assigned to *Tanystropheus longobardicus* and *Macrocnemus bassanii* (Ortlam, 1966). This material was initially re-assigned to *T. antiquus* (Wild, 1980a). However, Wild subsequently considered this material to differ from *Tanystropheus* spp. to such a degree that it belonged to a different genus, but did not formally re-assign this material (Wild, 1987). Later, the Buntsandstein specimens were assigned to a new genus and species, *Amotosaurus rotfeldensis*, whilst *T. antiquus* was tentatively maintained as a valid taxon representing material from the Lower Muschelkalk (Fraser and Rieppel, 2006).

In the initial description of *Tanystropheus longobardicus* no detailed comparison with *T. conspicuus* and *T. antiquus* from the Germanic Basin was provided in expectation of further preparation and additional finds from excavations at Monte San

Giorgio (Peyer, 1931). This comparison was eventually provided in an extensive monograph on *T. longobardicus* following the availability of more specimens (Wild, 1973). Therein, *T. conspicuus* was distinguished from *T. longobardicus* based on comparatively wider rib attachment sites and a concavity on the anterior end of the neural spine of the cervical vertebrae. Although these minor differences were considered not to be sufficient to define a species, the distinction between the two taxa was maintained in expectation of additional specimens from the Upper Muschelkalk that would allow for a more complete comparison. Although never providing a formal revision, Wild later considered *T. conspicuus* to very likely be indistinguishable from *T. longobardicus* (Wild, 1980a, 1980b, 1987). *Tanystropheus antiquus* showed more disparity from *T. longobardicus* in having distinctly shorter cervical vertebrae with more pronounced neural spines and zygapophyses (Wild, 1973), as was also pointed out previously in comparison to *T. conspicuus* (Huene, 1907-1908). Additionally, the monograph provided a systematic palaeontology section, including a synonymy list and overview of the occurrence for each of the three species in detail (Wild, 1973). From this, it followed that *T. conspicuus* occurred in the Upper Muschelkalk (late Anisian-early Ladinian; Menning and Hendrich, 2016) of Germany (area surrounding Bayreuth, Bindlach, Crailsheim, Schloss Stetten, Erfurt, and Göttingen) and France (Lunéville; although Peyer, 1931, did not consider this specimen, a vertebra, to belong to *Tanystropheus*), and in the Lettenkeuper (middle Ladinian; Menning and Hendrich, 2016) of Germany (Gaildorf, Crailsheim, and Helmstedt). The single specimen from the Upper Muschelkalk of Laryszów assigned to *T. conspicuus* by Meyer (1855) was not included in this list. The material assigned to *T. conspicuus* comprises isolated cervical, dorsal, sacral, and caudal vertebrae, as well as an isolated humerus and femora (Wild, 1973). Since the original description by Meyer (1855) provided a syntype of nine cervicals, one of these, U-MO BT 740 (Meyer, 1855, plate 30, figure 2), was assigned as the lectotype of the species. The material assigned to *T. antiquus* comprised a number of isolated cervical and dorsal vertebrae and a femur, which originated from the Lower Muschelkalk of Krappitz and Gogolin in Silesia, Poland, and near Jena and Rüdendorf near Berlin, Germany (Wild, 1973). Later an isolated cervical vertebra from the Lower Muschelkalk of Winterswijk (Vossenveld Formation), the Netherlands, was also assigned to the species (Wild and

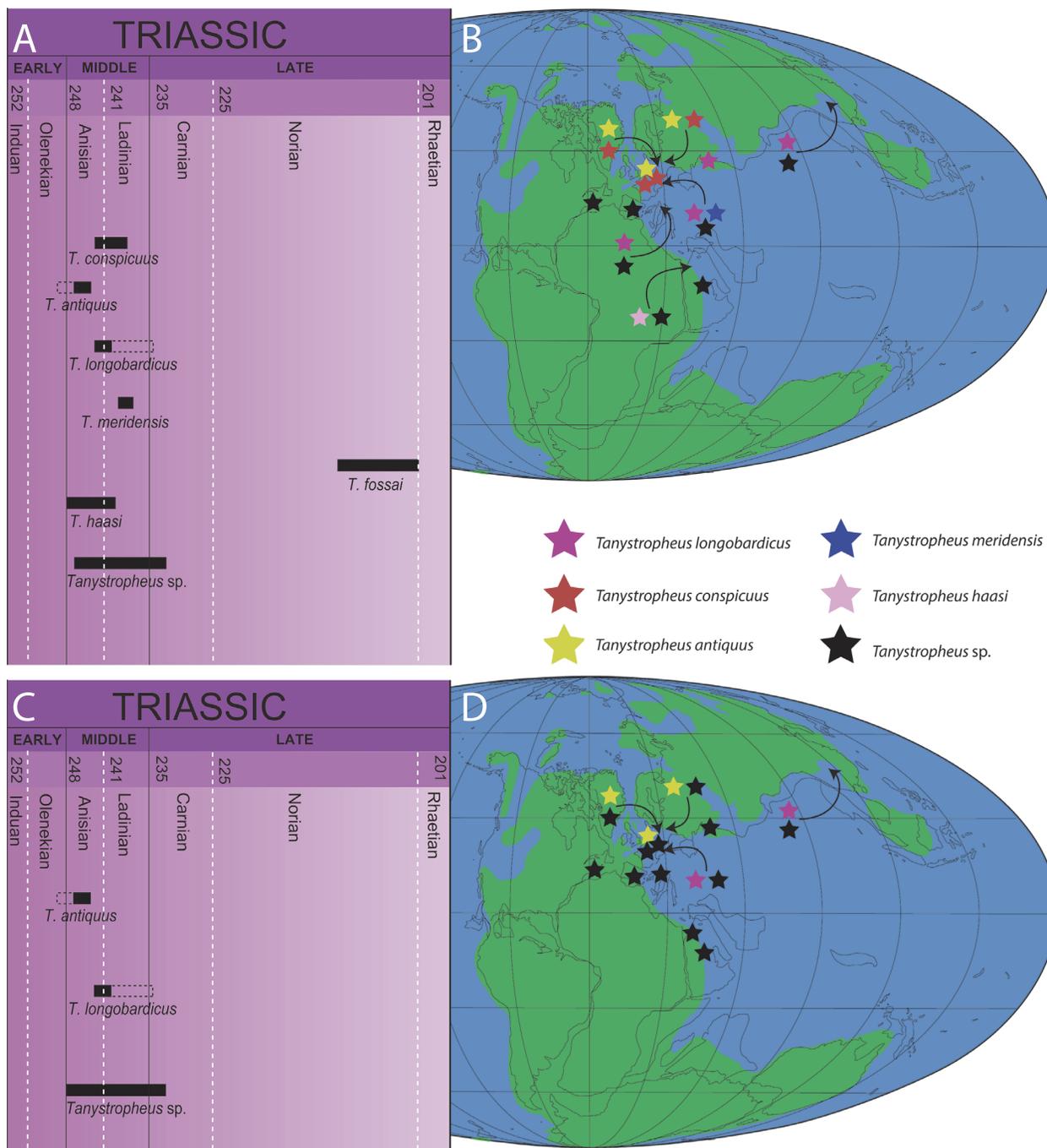
Oosterink, 1984) and recently more tanystropheid material from this locality was described and discussed (Spiekman et al., 2019). The assignment of specimens from Schattenmühle near Bonndorf in the Black Forest and Diedesheim near Mosbach (both Germany) to *T. antiquus* was considered uncertain (Wild, 1973). SMNS 16687 (no. 7 in Huene 1907-1908, p. 225, plate 93, figure 1) was established as the lectotype, since Wild (1973), as well as Fraser and Rieppel (2006), thought that the majority of the other specimens belonging to the syntype were very likely destroyed during the Second World War. However, it was recently reported that these specimens still exist (Skawiński et al., 2017). The specimens assigned to *T. longobardicus* were restricted to the Besano Formation of Monte San Giorgio and the Buntsandstein material assigned to the species by Ortlam (1966; Wild, 1973), which as mentioned before was soon after reassigned to *T. antiquus* and later to *Amotosaurus rotfeldensis* (Fraser and Rieppel, 2006). Because the holotype, a specimen originally assigned to *Tribesodon longobardicus* (Bassani, 1886), was unfortunately destroyed in the Second World War (specimen figured in Arthaber, 1922, figure 3a), PIMUZ T 2791, the main specimen (“Hauptfund”) of the description by Peyer (1931), was established as the neotype of *T. longobardicus* (Wild, 1973).

Additionally, the presence of another species of *Tanystropheus* from Makhtesh Ramon (Anisian-Ladinian) of Israel was also briefly noted on, based on material which was first reported on by Peyer (1955). However, this new species was not erected therein, since the material was projected to be worked on by Georg Haas and identified preliminarily as *Tanystropheus* sp. (Wild, 1973). This material was eventually described and assigned to the species *Tanystropheus haasi* (Rieppel, 2001). It comprises posterior ends of two mid-cervical vertebrae, as well as a number of highly fragmentary specimens assigned to the same species based on their similar size. In the diagnosis, *T. haasi* was distinguished from other *Tanystropheus* species based on the presence of a distinct horizontal groove that separated the vertebral centrum from the neural arch, the presence of thickened margins of the articulation facets of the postzygapophyses, the presence of a straight posterior margin of the postzygapophyseal trough, which is located at the level of the articulation facet of the centrum, and the presence of a long posterior process of the neural spine that overlies the postzygapophyseal trough. Additional specimens from the same locality were referred to two different morphotypes, with

one being distinctly larger and the other being distinctly smaller than *T. haasi*. The larger morphotype is represented by the posterior end of a posterior cervical vertebra (cervical vertebra 11 or 12) and various highly fragmented specimens, referred to *Tanystropheus* sp. The best-preserved specimen was estimated to be approximately 40% larger than the known 11<sup>th</sup> cervical of *T. conspicuus* (based on Wild, 1973). It was described as being different from *T. haasi* and any other species of *Tanystropheus* in possessing a distinct recess in the posterior margin of the postzygapophyseal trough and a horizontally oriented postzygapophysis in which the articulation facet faces ventrally rather than ventrolaterally. It additionally differed from *T. haasi* in possessing an oval posterior opening of the postzygapophyseal canal, which is circular in *T. haasi*. The smaller morphotype was considered to be very similar to *T. conspicuus* and is represented by a number of fragmentary cervical vertebrae, with two specimens that consist of the anterior end of the vertebral centrum being the most diagnostic. The material assigned to this morphotype does not show overlapping diagnostic morphology with the *T. haasi* material nor with that of the larger morphotype from Makhtesh Ramon. Furthermore, a handful of vertebrae remains referred to the genus *Tanystropheus* have also been described from the Jilh Formation of Saudi Arabia (dated to the Middle Triassic), which has been considered closely related to that of Makhtesh Ramon (Vickers-Rich et al., 1999). However, this *Tanystropheus* material was not identified to the species level.

A new species, *Tanystropheus biharicus*, was erected based on a single isolated cervical from the Anisian of Romania (Jurcsák, 1975), and later additional fragmentary remains were attributed to this species (Jurcsák, 1976, 1978, 1982). However, Wild (1980a) found the holotype to be indistinguishable from both *T. longobardicus* and *T. conspicuus*, and it was reassigned to *T. cf. longobardicus*.

In the same study, additional previously undescribed *Tanystropheus* specimens were presented, and two more species were erected, *Tanystropheus meridensis* and *Tanystropheus fossai* (Wild, 1980a). *Tanystropheus meridensis* is known from a single specimen, PIMUZ T 3901, that originates from the Cassina beds of the Meride Limestone at Monte San Giorgio (early middle Ladinian), which are slightly younger than the Besano Formation from which the *T. longobardicus* specimens originate (Stockar, 2010; Figure 1). The species con-



**FIGURE 1.** The (A, C) spatial and (B, D) temporal distribution of the various species of *Tanystropheus* based on the taxonomic assignments prior to this study (A-B) and following the findings of this study (C-D). Map modified from Smith et al. (1994).

sists of a small specimen preserving a complete yet heavily crushed skull and the first seven cervical vertebrae. It was described as differing from *T. longobardicus* in the absence of palatal teeth, the quadrate being comparatively taller and more curved, the presence of paired parietals, and having slightly more elongate cervical vertebrae. Addi-

tionally, a single, incomplete tricuspid tooth from the lower Lettenkeuper near Hall in Baden-Württemberg was identified as *T. cf. meridensis* (Wild, 1980a). Later an additional specimen, MCSN 5562, was described from the Cascina or Cava Inferiore beds of the Meride Limestone of Monte San Giorgio, which are very slightly older than the

Cassina beds in which PIMUZ T 3901 was found, yet younger than the Besano Formation (Stockar, 2010). Because the skull and anterior part of the cervical column is missing in this specimen, a direct comparison with PIMUZ T 3901 is impossible. However, this specimen showed no distinct differences from the *T. longobardicus* specimens and was identified either as *T. cf. longobardicus* (Renesto, 2005) or *T. longobardicus* (Nosotti, 2007). Although *T. meridensis* has not formally been revised, the species has been considered synonymous and indistinguishable from the small specimens of *T. longobardicus* (Fraser et al., 2004; Nosotti, 2007). However, it was considered possible that two taxa are represented among the *Tanystropheus* specimens of Monte San Giorgio, with the small specimens forming a distinct separate morphotype from the large sized specimens, meaning that these differences are attributable to specific variation rather than ontogenetic variation (Fraser et al., 2004).

*Tanystropheus fossai* has also been described on the basis of a single specimen (MCSNB 4035), which constitutes four largely articulated cervical vertebrae and associated cervical ribs (Wild, 1980a). This specimen originates from the late Norian of Lombardy, Italy, and thus represents the latest occurrence of the genus (Wild, 1980a; Renesto and Dalla Vecchia, 2018; Figure 1). This specimen was distinguished from other species of *Tanystropheus* based on distinct laterally projecting crests on the lateral surface of the cervical centra and the presence of bifurcated cervical ribs. The assignment of *T. fossai* to *Tanystropheus* was corroborated (Dalla Vecchia, 2000), although similarities between these vertebrae and the caudal vertebrae of certain Triassic pterosaurs was also pointed out. However, the presence of thin and hyperelongate ribs occurring parallel to the vertebral column precludes their identification as caudal vertebrae. Another study found the vertebrae of *T. fossai* to lack any unequivocally diagnostic characters for the assignment to the genus and stated that they are markedly shorter proportionally than those of other *Tanystropheus* species (Renesto, 2005).

Two further specimens were described, a partial right coracoid from the Upper Muschelkalk of Siles in Andalusia, Spain, and a poorly preserved, fragmentary dorsal vertebra from the late Ladinian of Seiser Alm in South Tyrol, Italy. They were identified as *Tanystropheus* sp. indet. and ?*Tanystropheus* sp. indet., respectively, expanding the

geographic distribution of the genus known at that time (Wild, 1980a).

A complete isolated femur from the S-charl Formation (late Anisian to early Ladinian) of Piz Ravigliel near Davos, canton Graubünden, Switzerland was briefly described and assigned to *Tanystropheus* sp. by Eichenberger (1986).

A number of isolated *Tanystropheus* remains from northern Italy have been described and assigned to *Tanystropheus* sp. and *Tanystropheus cf. longobardicus* (Dalla Vecchia, 2000; Dalla Vecchia and Avanzini, 2002; Dalla Vecchia, 2005). An isolated proximal caudal (MFSN 25761) and the proximal half of a thoracic rib, missing the articular head, were found in close association in a single block. The vertebra shares many similarities and has been assigned to the genus *Tanystropheus*, but, although it was considered different from the caudal vertebrae of *T. conspicuus* and *T. longobardicus*, it was not assigned on the species level because the material was considered too incomplete (Dalla Vecchia, 2000). Although the rib is undiagnostic, it is indistinguishable from the ribs of *Tanystropheus*, and because of its close association with the caudal vertebra, it has been suggested that it could belong to the same individual. The block contains four other unidentifiable bones. It was recovered as an isolated block and thus cannot be assigned to a specific locality, and it could have an earliest Triassic to Norian age (Dalla Vecchia, 2000). An additional specimen from layer E of the Fusesa site in Friuli, Italy, which is most likely of early Carnian age, constitutes the posterior half of a cervical vertebra. Although it was described as being most similar to the middle to posterior cervical vertebrae of *T. longobardicus*, it was not formally assigned to the species and identified as *Tanystropheus* sp. (Dalla Vecchia, 2000). An additional specimen, the posterior part of a small cervical vertebra, was described from the Ladinian of the Mendel Pass in South Tyrol, Italy (Dalla Vecchia and Avanzini, 2002). It was not identified on the species level, and attributed to *Tanystropheus* sp. Another 30 *Tanystropheus* specimens were described from the late Anisian deposits of the Aupa Valley, Friuli, Italy (Dalla Vecchia, 2005). Among these remains are virtually complete cervical, dorsal, sacral, and caudal vertebrae, as well as several isolated teeth, a complete left clavicle, and a right ilium. This material might differ from other *Tanystropheus* species on the basis of the absence of the neural spine on the posterior end of the neural arch in the cervical vertebrae and the wide transverse process of the dorsal vertebrae, but

was otherwise considered very similar to *T. longobardicus*, and the material was therefore referred to *T. cf. T. longobardicus* (Dalla Vecchia, 2005).

Since the 2000s, many new discoveries from the Middle to Late Triassic of southwestern China (Guizhou and Yunnan Provinces) have revealed a rich fauna of marine vertebrates, including several tanystropheid taxa; e.g., *Dinocephalosaurus orientalis*, *Macrocnemus fuyuanensis*, *Tanystropheus* sp., and *T. cf. T. longobardicus* (Li et al., 2004; Li, 2007; Li et al., 2007; Rieppel et al., 2008; Rieppel et al., 2010; Jiang et al., 2011), as well as potentially *Fuyansaurus acutirostris* and *Pectodens zhenyuensis* (Fraser et al., 2013; Li et al., 2017). These findings greatly enlarged the known geographic range of the clade to the eastern part of the Triassic Tethys Ocean, including that of *Tanystropheus* spp., which were previously only known from its western margin (Li et al., 2007; Rieppel et al., 2010; Jaquier et al., 2017). Two *Tanystropheus* specimens from China are currently described, both comprising postcranial skeletons lacking the skulls and originating from the Zhuganpo Member of the Falang Formation (latest Ladinian to earliest Carnian) near Xingyi, Guizhou Province, China. The smaller specimen, IVPP V 14472, was interpreted as a juvenile specimen and comprises the posterior part of the cervical column, the trunk, the pectoral and pelvic girdles, the forelimbs, and a femur. It was considered to be very similar to *T. longobardicus* and identified as *Tanystropheus* sp. (Li, 2007). The larger specimen, GMPKU-P-1527, possesses a largely complete postcranial skeleton, including most of the cervical series, a complete trunk series and most of the tail, parts of both sides of the pectoral girdle, a complete right forelimb, parts of both pelvic girdles, and most of the right hind limb with the exception of the foot. It was found to be very similar to the large specimens of *T. longobardicus* known from the Besano Formation, with the only possible minor differences being the somewhat larger size of the chevron bones and the lack of slight swellings on the cervical ribs (Rieppel et al., 2010), which were observed in PIMUZ T 2819 (PIMUZ T 2189 therein). Although no distinct differences with *T. longobardicus* were found, the specimen was referred to *T. cf. T. longobardicus* because the authors considered the absence of a skull to preclude a sufficiently detailed comparison to the European large-sized *T. longobardicus* specimens. Nevertheless, these findings indicate a very close association between the faunas from both ends of the Tethys Ocean, as has also been established for other marine reptile

clades; e.g., Sauropterygia (Li, 2006; Jiang et al., 2008; Wang et al., 2019) and Ichthyopterygia (Jiang et al., 2006). Furthermore, even for the genus *Macrocnemus*, a taxon generally considered to be terrestrial, a very close association has been established for specimens occurring at both sides of the Tethys (Jaquier et al., 2017).

Tanystropheid remains from the Donskaya Luka locality (Lipovskaya Formation, late Olenekian) of the Ilovinsky District, southwestern Russia, were described and considered most closely related to *Tanystropheus antiquus* and *Amotosaurus rotfeldensis* (Sennikov, 2011). These remains were assigned to a new genus and species, *Augustaburiania vatagini*. This taxon is comprised of isolated specimens, and the material attributed to it consists of a number of isolated cervical and anterior dorsal vertebrae, partial sacral vertebra, caudal vertebrae, humeral fragments, femora, and a proximal fragment of a tibia. It might represent the earliest occurrence of Tanystropheidae, although recently described isolated archosauromorph remains from the Sanga do Cabral Formation of Brazil (Induan–early Olenekian) predate *Au. vatagini* and likely also belong to the clade (De Oliveira et al., 2018). Additionally, Sennikov (2011) re-evaluated *T. antiquus* and it was considered to differ sufficiently from the other *Tanystropheus* species to merit assignment to a separate genus, and it was re-assigned to *Protanystropheus antiquus*. However, most of the type material of this species was not included in this diagnosis, nor in that of Wild (1973) or Fraser and Rieppel (2006), as it was still considered lost at the time. Although a full revision of the taxon was refrained from, initial observation of the original material by Huene (1905, 1907–1908) led to the consideration that *T. antiquus* is a valid taxon, giving it preference over *P. antiquus* (Skawiński et al., 2017). However, this preliminary interpretation only covered the specimens from the Gogolin Formation, and the taxonomic status of the *T. antiquus* specimens from Germany and the Netherlands was considered to be uncertain until a detailed revision of original material from the Gogolin Formation is completed. Additionally, the existence of new material assigned to *T. conspicuus*, which originated from the lowermost Keuper (Ladinian) of Laryszów in Upper Silesia, Poland, was also briefly noted on. This is the same locality from which a specimen included in the original description of *T. conspicuus* by Meyer (1855) also derived (Skawiński et al., 2017).

A virtually complete and strongly elongated cervical vertebra was described from the Economy Member of the Wolfville Formation of Carrs Brook in Nova Scotia, south-eastern Canada, which is of Anisian to Carnian age (Sues and Olsen, 2015). Although only represented by a single isolated element, its size and shape does correspond to that of *Tanystropheus* spp. and is more similar to that of *T. longobardicus*, *T. conspicuus*, and *T. haasi*, than that of *T. antiquus* or *T. fossai*. It was identified as cf. *Tanystropheus* sp. It represents the first occurrence of *Tanystropheus* from North America.

In summary, prior to this study, a total of six species of *Tanystropheus* were acknowledged, namely *T. conspicuus*, *T. antiquus*, *T. longobardicus*, *T. meridensis*, *T. fossai*, and *T. haasi*. However, of these taxa, the validity of *T. meridensis* has been strongly disputed, whereas *T. conspicuus* has also been considered indistinguishable from *T. longobardicus*. Furthermore, the assignment of *T. antiquus* and *T. fossai* to the genus *Tanystropheus* has also been questioned, although *T. antiquus* is currently tentatively accepted as belonging to this genus. Additional specimens attributable to the genus *Tanystropheus* have been described from the Jilh Formation of Saudi Arabia (Middle Triassic), Makhtesh Ramon in Israel (Anisian-Ladinian), the Economy Member of the Wolfville Formation of south-eastern Canada (Middle to earliest Late Triassic), the Zhuganpo Member of the Falang Formation (latest Ladinian to earliest Carnian) of Guizhou Province, southern China, the earliest to Late Triassic of northern Italy, with the majority of specimens coming from the late Anisian, and the Upper Muschelkalk of Siles in Andalusia, Spain (Anisian-Ladinian) (Supplementary Table 1; Figure 1).

## MATERIAL AND METHODS

This study includes all figured and referenced material of *Tanystropheus*, with critical taxa (*T. longobardicus*, *T. fossai*, *T. meridensis*, *T. conspicuus*) having been studied personally and some more fragmentary additional material taken from the literature.

### Institutional Abbreviations

BSPG, Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; GMPKU, Geological Museum of Peking University, Beijing, China; HUJ-Pal, Paleontological Collections of the Department of Evolution, Systematics and Ecology of the Hebrew University of Jerusalem, Jerusalem, Israel; IVPP, Institute of Vertebrate Paleontology

and Paleoanthropology, Beijing, China; MFSN, Museo Friulano di Scienze Naturali, Udine, Italy; MCSN, Museo Cantonale di Scienze Naturali di Lugano, Lugano, Switzerland; MCSNB, Museo Civico di Scienze Naturali "E. Caffi" Bergamo, Bergamo, Italy; MGUWr, Geological Museum, Institute of Geological Sciences, University of Wrocław, Wrocław, Poland; MSNM, Museo di Storia Naturale, Milan, Italy; PIMUZ, Paläontologisches Institut und Museum der Universität Zürich, Zurich, Switzerland; PIN, Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; U-MO, Umwelt-Museum Oberfranken, Bayreuth, Germany; YPM, Yale Peabody Museum, New Haven, Connecticut, USA.

## RESULTS

### Revision of the Various *Tanystropheus* Taxa and Specimens

***Tanystropheus antiquus*.** The recent rediscovery of specimens used in the description in Huene (1907-1908) for *Tanystropheus antiquus* invalidates the diagnoses for this species in Wild (1973) and Fraser and Rieppel (2006), as well as that of Sennikov (2011) for *Protanystropheus antiquus* encompassing the same material, since all of these considered most of the original material to be lost and therefore did not include it (Skawiński et al., 2017). Based on observations of this original material, *T. antiquus* was considered to be a valid species and *P. antiquus* was rejected. However, in anticipation of a more detailed revision of these specimens and other tanystropheid material from Poland, an emended diagnosis for the species was not provided (Skawiński et al., 2017; Szczygielski, personal commun., 2019). Therefore, we currently consider only the cervical vertebrae from the Gogolin Formation that have previously been identified as *T. antiquus* in Huene (1907-1908) to belong to this species. Until the revision of this material has been completed, it can preliminarily be distinguished from other *Tanystropheus* species based on the neck vertebrae having a centrum length of less than three times their minimum height (i.e., having comparably shorter cervical vertebrae than other *Tanystropheus* species; sensu Fraser and Rieppel, 2006). We agree with Fraser and Rieppel (2006) that the other cervical vertebrae found in the Lower Muschelkalk of Europe (i.e., Vossenveld Formation of Winterswijk, the Netherlands, Schaumkalk Formation of Rüdersdorf and Isserstedt) likely can also be attributed to this

species, as their morphology corresponds to the preliminary diagnosis, and identify this material here as *T. cf. T. antiquus* (following Spiekman et al., 2019). Material with tanystropheid affinities from these localities other than cervical vertebrae, including the femur (MGUWr 3894s) from the Gogolin Formation, can currently not be assigned to this species, as its preliminary diagnosis only applies to cervical vertebrae, and are identified here as *Tanystropheus* sp. These remains could be considered, however, if the revision of the Polish tanystropheid material also includes non-cervical material. The specimens from the Lower Muschelkalk of Bonndorf and Diedesheim, Germany, and the vertebra from Podloer Bruch near Gogolin are here considered indeterminable due to lack of diagnostic features and assigned to ?Archosauromorpha indet.

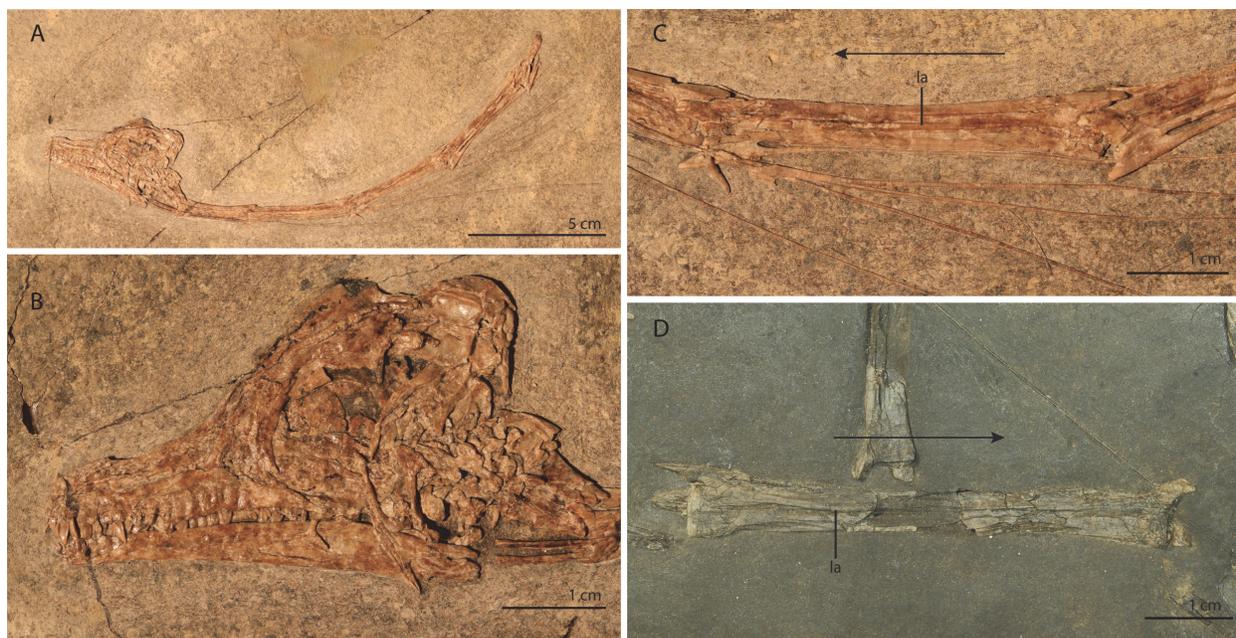
***Tanystropheus meridensis.*** *Tanystropheus meridensis* was described based on a single specimen, PIMUZ T 3901 (Figure 2A-C). This specimen from the Meride Limestone is of Ladinian age in contrast to the Anisian-Ladinian boundary age of the specimens of the Besano Formation previously assigned to *T. longobardicus*, and the former was considered to represent a slightly more derived form than the latter (Wild, 1980a). In this regard, it is relevant that a small-sized skeleton missing the skull and anterior part of the cervical column subsequently found in slightly older deposits of the Meride Limestone could not be distinguished from specimens referred to *T. longobardicus* and was identified as *T. cf. longobardicus* (Renesto, 2005). This was later corroborated, and the specimen was even considered to be identifiable to *T. longobardicus* (Nosotti, 2007). Although never formally reassigned, *T. meridensis* was considered to be indistinguishable from *T. longobardicus* in Fraser et al. (2004) and Nosotti (2007), with the holotype having been studied in detail in the latter. A new interpretation of some of the skull bones was provided therein, and it was compared to the small-sized specimens assigned to *T. longobardicus* housed in the collections of PIMUZ and MSNM, most notably MSNM BES SC 1018.

*Tanystropheus meridensis* was distinguished based on the following combination of characters in the diagnosis of Wild (1980a): Skull morphology as in *T. longobardicus* with the exception of the following: presence of paired parietals, a probably edentulous palatine, and a quadrate that is more elongate and has a more concave posterior margin; a premaxilla bearing five single cusped teeth; a maxilla bearing three single cusped teeth and 12

tricuspid teeth; a lower jaw with three large single cusped and 16(?) tricuspid teeth; all teeth bear sharpened ridges, mainly on their anterior and posterior edge; cervical vertebrae similar to *T. longobardicus*, but slightly more elongate; fourth to sixth cervicals bearing a long horizontal lamina on the lateral margin of their centrum with a foramen positioned ventral to this lamina.

Re-analysis of PIMUZ T 3901 reveals that this diagnosis is problematic and results in the conclusion that *Tanystropheus meridensis* is indeed indistinguishable from the material previously assigned to *T. longobardicus* and should thus be considered synonymous with the latter, as will be demonstrated in the following. The parietals of PIMUZ T 3901 were considered to be unfused in Wild (1980a). However, the parietals were reinterpreted in Nosotti (2007), in which the element indicated as the right parietal in Wild (1980a) was identified as representing both parietals and the left parietal of Wild (1980a) was not identified. Personal observation (by SNFS and TMS) did not allow for a confident identification of these bones, and neither interpretation can be excluded (Figure 2B). This would imply that the fusion of the parietals cannot be assessed unambiguously, which invalidates this character as being diagnostic for *T. meridensis*. In any case, the fusion of the parietals can be considered a poor diagnostic character, as it is highly dependent on the ontogenetic stage of the specimen. The absence of teeth on the palatine would differentiate PIMUZ T 3901 from small specimens identified as *T. longobardicus*, although the palatines of larger specimens assigned to *T. longobardicus* are edentulous. The palatine of PIMUZ T 3901 indicated in Wild (1980a) was not identified as such in Nosotti (2007), in which that element was not identified due to the poor preservation of the skull in that region. Personal observation of this element (by SNFS) does not reveal the presence of any teeth or alveoli on this element, but also reveals no features that would identify this bone as a palatine (Figure 2B). Therefore as in Nosotti (2007), we consider the presence of the palatine and the presence of teeth on the palatine to be indeterminable in PIMUZ T 3901.

The quadrate was considered to be a diagnostic element for *Tanystropheus meridensis* that, apart from the characters in the diagnosis, additionally differed from that of the quadrate of *T. longobardicus* in having a wider pterygoid ramus and a convexity on its anterior margin (Wild, 1980a). The wider pterygoid ramus in *T. meridensis* was interpreted to represent a more derived state, since



**FIGURE 2.** Photographs of (A) PIMUZ T 3901, the former holotype of *Tanystropheus meridensis*; (B) a detail of the skull of PIMUZ T 3901 in left lateral view; (C) a detail of the fifth cervical vertebra of PIMUZ T 3901 in left lateral view; and (D) a detail of a partially broken cervical vertebra of PIMUZ T 2484 referred to the small morphotype of *T. longobardicus* in right lateroventral view. The arrows are pointing anteriorly. Abbreviations: la, lamina.

*Macrocnemus bassanii*, which was regarded to be a more basal taxon of the “prolacertiform” lineage, also was considered to bear a shorter pterygoid ramus. The pterygoid ramus of *M. bassanii* is indeed much shorter than that of *T. longobardicus* (personal observation SNFS). However, the pterygoid ramus cannot be identified in the figures presented in Wild (1980a), and personal observation (by SNFS) reveals that the quadrate is badly broken, strongly hampering any unambiguous observation of this element (Figure 2B). Nevertheless, the structure that was likely interpreted as the anterior convexity in Wild (1980a) could represent a part of the compressed pterygoid ramus, and it is not noticeably wider than that of PIMUZ T 2484. In Nosotti (2007), the shape of the left quadrate of MSNM BES SC 1018, a small-sized specimen of *T. longobardicus*, which was not available to Wild, was considered to be the closest in morphology to that of PIMUZ T 3901 among the PIMUZ material. This specimen is preserved under roughly the same angle as in PIMUZ T 3901. In any case, the strong compression of the specimen precludes any definitive statement on this aspect of the quadrate or its taller size and concave posterior margin mentioned in the diagnosis for *T. meridensis* in Wild (1980a). We therefore corroborate the assessment in Nosotti (2007) that the quadrate of PIMUZ T

3901 is indistinguishable from the quadrate of that present in the material previously assigned to *T. longobardicus*.

A detailed overview of the ontogenetic variation of *Tanystropheus longobardicus*, including the transition from a partially tricuspid marginal dentition to a dentition consisting of solely single cusped teeth, was presented by Wild (1973, p. 124-126). Regardless of whether the presented variation is related to ontogeny, this indicates that the number of tricuspid compared to single cusped teeth is variable among the small morphotype of *T. longobardicus*, and the dentition of PIMUZ T 3901 does not show a larger deviation than is shown within these specimens (Wild, 1973; Table 1; see also the section “The small and large morphotype of *Tanystropheus* from Monte San Giorgio: Two taxa or ontogenetic variation?” below). The presence of cutting edges described by Wild (1980a) is corroborated. However, similar edges are also found in specimens attributed to *T. longobardicus* (e.g., MSNM BES SC 1018), and they likely represent a feature related to tooth wear (see Njau and Blumenshine, 2006 for similar wear of crocodylian teeth).

Wild (1980a) stated that the cervical vertebrae of PIMUZ T 3901 were slightly longer than those of specimens of similar size previously attributed to

*Tanystropheus longobardicus* and that this provided additional support for the hypothesis that *T. meridensis* was more derived than *T. longobardicus*. The support for this claim appears to be absent, however; since the graph provided by Wild (1980a, figure 7) shows the second to sixth cervical vertebra preserved in PIMUZ T 3901 to be virtually identical in size to the corresponding vertebrae in the similarly sized specimen PIMUZ T 2795, well within the margin of deviation one can expect to be attributable to intraspecific variation. This latter specimen was previously assigned to *T. longobardicus* (Wild, 1973).

Finally, PIMUZ T 3901 was considered to differ from *Tanystropheus longobardicus* in bearing a long horizontal lamina on the lateral margin of the centrum with a foramen positioned directly below it in the fourth to sixth cervical (Wild, 1980a). The foramina cannot be observed and likely were misidentified cracks that occur throughout the specimen. The laminae are pronounced and clearly discernible, but these are similar to those visible in other small-sized species attributed to *T. longobardicus* (e.g., PIMUZ T 2484; Figure 2C and D).

A comparison of PIMUZ T 3901 with small-sized specimens attributed to *Tanystropheus longobardicus* is difficult because all specimens are heavily compressed. Nevertheless a comparison based mainly on PIMUZ T 2791, PIMUZ T 2484, and MSNM BES SC 1018 reveals no distinct differences with PIMUZ T 3901. Based on this, in addition to the refuted diagnosis of Wild (1980a) and

the observations of previous studies (Fraser et al., 2004; Nosotti, 2007), *T. meridensis* is considered morphologically indistinguishable from small-sized specimens previously assigned to *T. longobardicus*. As such we propose *Tanystropheus meridensis* Wild 1980 to represent a junior synonym of *Tanystropheus longobardicus* Bassani 1886.

**The small and large morphotype of *Tanystropheus* from Monte San Giorgio: Two taxa or ontogenetic variation?**

The specimens of *Tanystropheus* from Monte San Giorgio can be divided into two morphotypes, a small morphotype partially bearing tricuspid marginal dentition and a large morphotype bearing only single cusped dentition. A summary of the characters that distinguish the two morphotypes is presented in Table 2, and the relevant specimens of both morphotypes are listed in Tables 1, 3, and 4, in which the specimens assigned to the small morphotype are indicated by an asterisk at the end of their respective specimen number. The distinction between the two morphotypes was already noted in the original description of the material (Peyer, 1931). However, at the time it was not determined whether these morphotypes represented distinct species or different ontogenetic stages of the same species in expectation of additional *Tanystropheus* findings from Monte San Giorgio. The variation observed in the Monte San Giorgio material was extensively described in Wild (1973, p. 124-140). The main differences that were recognized therein between the two morphotypes concerned the absence or presence of tricuspid

**TABLE 2.** An overview of the morphological differences between the large and small morphotype identified among the *Tanystropheus* specimens from Monte San Giorgio.

	Large morphotype	Small morphotype
Tricuspid marginal dentition	Absent	Present on the maxilla and dentary
Prenarial process of the premaxilla	Absent or incipient	Small but present
Postnarial process of the premaxilla	Absent	Long
Vomer	Wide with dentition on the outer margin	Narrow with a single straight tooth row
Pterygoid	Edentulous and wide anteriorly	Tooth bearing and tapering anteriorly
Palatine	Edentulous and plate-like	Tooth bearing and narrow
Parietal	Long anterolateral and posterolateral processes and narrow in between these processes	Wide with short anterolateral and posterolateral processes
Paroccipital process of the opisthotic	Long and slowly reduces in height distally	Very short and expanding distally
Distinct "keel" on the anterior end of the dentary	Present	Absent, dentary slightly downturned anteriorly
Dorsal vertebrae	Relatively short with high neural spine	Relatively long with low neural spine

**TABLE 3.** The lengths of the maxilla, dentary tooth row, and premaxillary body of each relevant *Tanystropheus* specimen from Monte San Giorgio and the relative size of each specimen based on these measurements. Specimens assigned to the small morphotype are indicated by an asterisk. Abbreviations: ia, inapplicable.

	Maxilla length (in mm)	Dentary length	Premaxilla main body (in mm)	Relative size maxilla (in %)	Relative size dentary (in %)	Relative size premaxilla (in %)	Mean relative skull size estimate (in %)	Femur length (in mm)	Relative size femur (in %)
PIMUZ T 2819	74.6	113.83	35.6	100	100	100	100	?	ia
PIMUZ T 2790	46.2	81.52	34.13	61.93029	71.62	95.87079	76.47	?	ia
PIMUZ T 2787	43.8?	71.65	30	58.71314	62.94	84.26966	68.64	148.03	100
PIMUZ T 2792 (cast of SNSB-BSPG 1953 XV 2)	40.87?	57.93?	16.04	54.78552	50.89?	45.05618	50.24	106.25	71.78
PIMUZ T 2482*	27.2	35.58	11.83	36.46113	31.26	33.23034	33.65	?	?
MSNM BES SC 265*	24.9	33.8	11	33.37802	29.69	30.89888	31.32	71	47.91/48.84
MSNM BES SC 1018*	24.2	30.3	35.6	32.43968	31.27	26.96629	30.23	70.92/72.3	54.21
PIMUZ T 2795*	?	?	10.75	?	?	30.19663	30.19663	80.25	47.96
PIMUZ T 1277*	?	34.04	?	?	29.9	?	29.9	?	56.45
PIMUZ T 2484*	23.55	32.44	10.47	31.56836	28.5	29.41011	29.83	57.89	?
PIMUZ T 2779*	?	30.88?	9.07	?	27.13?	25.47753	26.3	?	39.11
PIMUZ T 3901*	20.39	30.06	7.8	27.33244	26.41	21.91011	25.22	83.56	?

marginal dentition, the number of teeth in the premaxilla and maxilla, the relative size of the orbits, the relative length of the maxillae, the shape of the premaxillae, frontals, parietals, and quadrates, and the shape of the bones of the palatal region and their dentition. It was concluded that there was a gradual transition in these characters from the small morphotype to the large morphotype, and therefore they were considered to represent a juvenile and adult form of the same species, respectively.

However, it has subsequently been suggested that the lack of a long postnarial process and distinct tricuspid dentition in the large morphotype, which are present in the small morphotype, does indeed indicate that the two morphotypes represent two different species (Fraser et al., 2004; but see also Renesto, 2005). We identified the differences between the two morphotypes and document herein in detail how the variation is distributed

between the specimens from Monte San Giorgio to establish whether there is a gradual transition from the smaller morphotype to the larger morphotype as the specimens increase in size. If this is the case, this would be a strong indication that the observed differences represent ontogenetic variation. If no gradual transition between the two morphotypes can be observed, this would be an indication that they represent different species. In order to trace these characters through the growth series we ordered the specimens based on their relative size. Because the considered characters consist largely of cranial characters and most relevant specimens do not preserve the limbs, and because most of the considered skulls are disarticulated, relative size was based on the mean of the length of the tooth-bearing margin of the premaxilla, the maxilla, and the dentary (Table 3).

Most of these characters can only be assessed qualitatively, but the relative size of the

**TABLE 4.** The measurements and ratios used to establish the relative size of the prenarial and postnarial processes of the premaxilla and the dentary keel of each relevant *Tanystropheus* specimen from Monte San Giorgio. Specimens assigned to the small morphotype are indicated by an asterisk. Abbreviations: de., dentary; ia, inapplicable; pmx., premaxilla; po. p., postnarial process; pre. p., prenarial process.

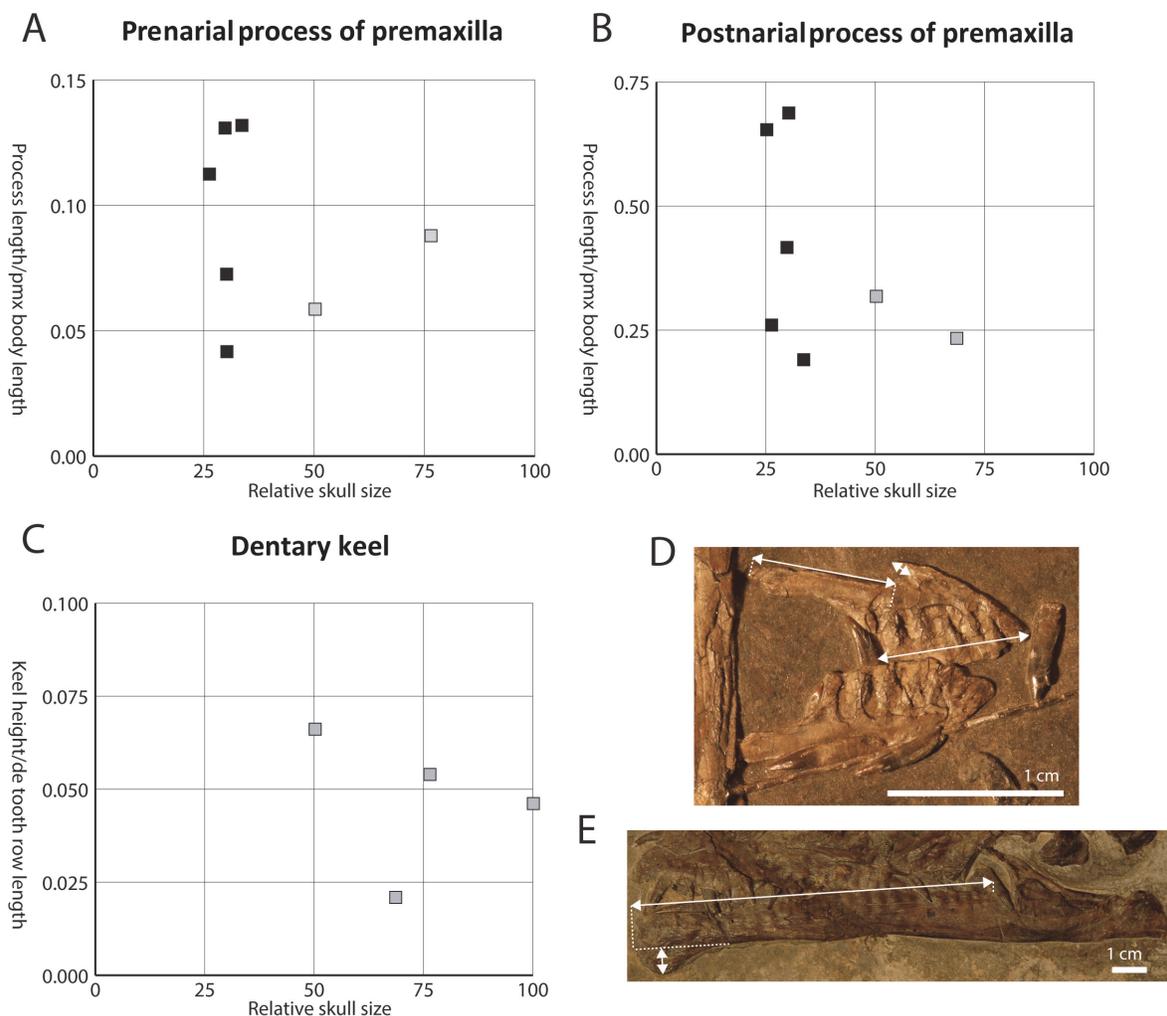
	Pmx. pre. p. length (in mm)	Pmx. po. p. length (in mm)	Dentary keel height (in mm)	Pmx. pre. p./ pmx. main body	Pmx. po. p./ pmx. main body	De. keel/de. tooth margin
PIMUZ T 2819	?	ia	4.8	?	ia	0.046602
PIMUZ T 2790	3	ia	4.4	0.087899	ia	0.095238
PIMUZ T 2787	ia	7	1.5?	ia	0.233333	0.022422
PIMUZ T 2792 (cast of SNSB-BSPG 1953 XV 2)	0.94	5.1	3.83	0.058603	0.317955	0.075142
PIMUZ T 2482*	1.56?	2.25	ia	0.131868	0.190194	ia
PIMUZ T 2795*	0.78?	?	?	0.072558	?	?
MSNM BES SC 265*	?	?	ia	?	?	ia
MSNM BES SC 1018*	0.4	6.6	ia	0.041667	0.6875	ia
PIMUZ T 2484*	1.37	4.36	ia	0.13085	0.416428	ia
PIMUZ T 2779*	1.02	2.36	?	0.112459	0.260198	?
PIMUZ T 3901*	?	5.1	ia	?	0.653846	ia
PIMUZ T 1277*	?	?	ia	?	?	ia

prenarial and postnarial processes of the premaxilla and the relative size of the dentary keel were calculated for each specimen (Figure 3 and Table 4). These results indicate that the size of the prenarial and postnarial processes of the premaxilla vary strongly in size in the smaller morphotype. In the larger morphotype, these processes are either absent or very small (PIMUZ T 2790 for the prenarial process and PIMUZ T 2787 and PIMUZ T 2792 for the postnarial process). When looking at the size of the dentary keel it becomes evident that this structure is absent in all specimens of the small morphotype, whereas the relative size of the keel in the large morphotype does not appear to increase with overall size.

The amount of marginal teeth and the distribution of tricuspid dentition in relation to ontogeny was discussed in detail in p. 124-126 of Wild (1973) in which it was found that a gradual transition occurs from the smallest to the largest specimens of *Tanystropheus* from Monte San Giorgio. In the smallest specimens, all the maxillary teeth and the dentary teeth with which they articulate are tricuspid, whereas the premaxillary teeth and the dentary teeth articulating with these are pointed single-cusped teeth. As the specimens become larger, the tricuspid dentition was described as being progressively replaced by single-cusped teeth from anterior to posterior until the entire marginal dentition is made up of single-cusped teeth in

the largest specimens, which were considered to be sexually mature, thus indicating that the difference in dentition can be attributed to ontogenetic variation rather than a taxonomic distinction (Wild, 1973, figure 80). Our findings, which include the specimens considered in Wild (1973), as well as PIMUZ T 1277, PIMUZ T 3901 (previously the holotype of *T. meridensis*), MSNM BES SC 265, and MSNM BES SC 1018, are presented in Table 1. We found that all the specimens in which the tooth count could be established with certainty bore six premaxillary teeth and 15 maxillary teeth, in contrast to Wild (1973), in which the tooth count of these elements was considered to increase with the size of the specimens. We found the position of the anteriormost tricuspid tooth to vary in the specimens bearing tricuspid dentition, ranging from the first or second tooth position on the maxilla (MSNM BES SC 1018) to the seventh (PIMUZ T 2482) counted from anterior in specimens that are roughly subequal in size (Table 3). The presence of tricuspid teeth on the posterior end of the dentary was documented in PIMUZ T 2792 (Wild, 1973). This observation could not be corroborated, and we were also not able to observe any tricuspid tooth in any of the other specimens attributed to the large morphotype.

The shape of the parietal varies strongly among the observed specimens. The most consistent difference between the small and large mor-



**FIGURE 3.** Graphs visualizing the data presented in Table 4 scaled against the relative skull size estimated of each specimen; (A) the ratio of the length of the prenarial process of the premaxilla divided by the length of the premaxillary body (=premaxillary tooth row); (B) the ratio of the length of the postnarial process of the premaxilla divided by the length of the premaxillary body; (C) the ratio of the height of the dentary keel divided by the length of the tooth row of the dentary; (D) the premaxillae of PIMUZ T 2484 indicating the measurements taken for establishing the relative length of the prenarial and postnarial processes of the premaxilla; (E) the left dentary of PIMUZ T 2819 indicating the measurements taken for establishing the relative height of the dentary keel. The black squares represent specimens assigned to the small morphotype and the grey squares represent specimens assigned to the large morphotype. Abbreviations: de, dentary; pmx, premaxilla.

photype is that the parietal is very wide and flat and does not bear a distinct supratemporal fossa in the small morphotype (Figure 4A). The parietal of the large morphotype has a much narrower intertemporal region of the parietal because of a strongly ventrally slanting supratemporal fossa. Furthermore, a distinct sagittal crest runs along the midline of the parietal in the large morphotype that diverges laterally on each side of the parietal lateral to the pineal foramen (Figure 4B). Additionally the parietal of PIMUZ T 2819 bears conspicuous anterolateral processes, which are absent in the

smaller specimens. These processes are also absent in PIMUZ T 2787, another specimen belonging to the large morphotype. However, because the articulating parietal and frontals are preserved in ventral view, it is possible that the anterolateral processes are covered by the frontals ventrally. Although it is preserved in dorsal view, it is even possible that the parietal of PIMUZ T 2484 bears anterolateral processes, but that these were covered by the postfrontals, which cannot be identified with certainty in PIMUZ T 2819 and might have been lost or displaced. The presence of the



**FIGURE 4.** Elements exhibiting morphological variation in various specimens of *Tanystropheus* from Monte San Giorgio; (A) various elements of PIMUZ T 2484; (B) the parietal of PIMUZ T 2819 in dorsal view; (C) various elements of PIMUZ T 2482; (D) a pterygoid of PIMUZ T 2787; (E) the partial braincase of PIMUZ T 2819; (F) the skull of MSNM BES SC 1018 in left lateroventral view; (G) various elements of PIMUZ T 2787. Abbreviations: de, dentary; mx, maxilla; pa, parietal; pal, palatine; pmx, premaxilla; pop, paroccipital process; pt, pterygoid; vo, vomer.

anterolateral processes of the parietal therefore remains unclear in *Tanystropheus* from Monte San Giorgio with the exception of PIMUZ T 2819. The difference of the shape of the parietal between the small and the large morphotype could be attributed to ontogenetic differences, as it is strongly variable through ontogeny in extant non-avian sauropsids. In *Varanus panoptes* for instance, the parietal of the juvenile is also much wider and lacking the ventrally slanting supratemporal fossae seen in the adult (Werneburg et al., 2015, supplementary material).

The most striking differences between the two morphotypes are seen in the palatal region, namely in the shape of the vomer, palatine, pterygoid, and their dentition. They differ in the presence of teeth on the pterygoid and palatine in the small morphotype, which are absent in the large morphotype, and on the vomer the dentition is larger and more recurved in the large morphotype than in the small morphotype (Figure 4, Table 1). The number of teeth in the vomer also differs in specimens belonging to the large morphotype, namely between PIMUZ T 2790 and PIMUZ T 2787 (Table 1). The tooth rows of both specimens are fully preserved, and their tooth count could therefore be established with certainty. Similarly, the tooth count of the vomer of the small specimen PIMUZ T 2779 could also unambiguously be determined. In specimens PIMUZ T 2792 and PIMUZ T 2795 observation was somewhat hampered by poor superficial preservation of the vomers, and their tooth count could be up to three teeth more than documented in Table 1. Nevertheless, it appears that the tooth count of the vomer varied in both morphotypes, and it is likely neither a taxonomically nor ontogenetically diagnostic character, since palatal tooth count has been shown to be intraspecifically variable in a number of extant palatal teeth-bearing squamates (Mahler and Kearney, 2006). The tooth count of the palatine could only be established with certainty in PIMUZ T 2484 and PIMUZ T 2482 of the small morphotype (Figure 4A and C). As stated above, in the large morphotype palatine teeth are absent (PIMUZ T 2787; Figure 4G). In PIMUZ T 2484, the tooth count is six, whereas it is five in that of the somewhat larger specimen PIMUZ T 2482. The pterygoid teeth are absent in the large morphotype (PIMUZ T 2787; Figure 4D). For the small morphotype the amount of pterygoid teeth can be counted in PIMUZ T 2795 (around 12), PIMUZ T 2484 (around 13; Figure 4A), and MSNM BES SC 1018 (around 12; Figure 4F). However, a definitive tooth count is hard to establish because

the alveoli are very small, but the amount of pterygoid teeth is likely subject to intraspecific variation. Furthermore, these three specimens of the small morphotype are very similar in relative size and therefore do not allow for an assessment of the tooth count in disparate ontogenetic stages within the small morphotype (Table 3).

The vomer of the large morphotype is very wide anteriorly and thus forms a wide contact with the premaxilla and has a similar curvature as this bone (Figure 4G). It only allowed for the presence of a narrow choana laterally. The tooth row extends along the outer margin of the bone, and the vomerine teeth are quite large and recurved. The vomer of the small morphotype on the other hand is an anteroposteriorly straight bone (Figure 4C), similar to, but considerably shorter relatively, than the vomer of *Macrocnemus* spp. (Jaquier et al., 2017). The vomerine tooth row is straight and bears small teeth. The right vomer is fully preserved in ventral view in the smallest specimen belonging to the large morphotype (PIMUZ T 2792) and both vomers are preserved in articulation and in ventral view in the second to largest specimen of the small morphotype (PIMUZ T 2795). The difference in calculated relative estimated skull size between these two specimens is 20.4% (Table 3). Nevertheless, the vomer of PIMUZ T 2792 is indistinguishable from the vomers of larger specimens PIMUZ T 2787 and PIMUZ T 2790, and the vomers of PIMUZ T 2795 are indistinguishable from those of the smaller specimen PIMUZ T 2779. It seems unlikely that a gradual transition occurred from the morphology seen in the small morphotype to that seen in the large morphotype in the growth trajectory in between PIMUZ T 2795 and PIMUZ T 2792, and, therefore, this character appears to support a taxonomic distinction between the two morphotypes.

The palatine is well-preserved in PIMUZ T 2787 among the specimens of the large morphotype and in PIMUZ T 2484, PIMUZ T 2482, and MSNM BES SC 1018, with a likely partial palatine present in PIMUZ T 2795, among the specimens of the small morphotype (Figure 4A and G). Apart from being edentulous, the palatine of the large morphotype is different in being wider and more posteriorly extended with a smaller lateral extension articulating with the maxilla. Among the specimens of the small morphotype, there is a distinct difference in the size of the alveoli, which are comparatively very large in PIMUZ T 2484. In MSNM BES SC 1018, they are still larger than the alveoli on the pterygoid but comparatively smaller than

those of PIMUZ T 2484. They are smaller still in PIMUZ T 2482 and PIMUZ T 2795, if the element in the latter specimen is indeed a palatine and not a fragment of the pterygoid. According to the relative size estimates, these four specimens are very similar in overall size (Table 3). Therefore, it appears that the observed variation is related to intraspecific variation independent of ontogeny. The shape of the palatine of PIMUZ T 2484 and PIMUZ T 2482, the two specimens of the small morphotype preserving a complete palatine, is indistinguishable. The overall shape of the palatines of the small morphotype is strongly distinct from that of the large morphotype. This and the presence of teeth on the palatine, which are absent in the large morphotype, form clear distinctions between the two morphotypes that appear unlikely to be solely attributable to ontogenetic or any other form of intraspecific variation.

The pterygoid of the large morphotype is characterized by a wide anterior portion or palatal ramus that is somewhat rounded anteriorly. This element is best preserved in PIMUZ T 2787 (Figure 4D). The pterygoid of the small morphotype has a much narrower palatal ramus that tapers to an end anteriorly, best preserved in PIMUZ T 2484 (Figure 4A). PIMUZ T 2792, the smallest specimen attributable to the large morphotype, preserves a single pterygoid, either the left pterygoid in dorsal view or the right in ventral view. It is incomplete, missing most of the quadrate ramus and part of the transverse flange. Furthermore, part of the palatal ramus is broken as indicated by its irregular medial margin, and therefore its morphology cannot unambiguously be observed. No teeth or alveoli can be observed on this element but it cannot be established whether it is preserved in dorsal or ventral view.

The ectopterygoid has been tentatively identified in PIMUZ T 2795 and PIMUZ T 2787 (Wild, 1973). Its morphology is poorly known, and the elements identified as such are similar in the two specimens.

The preservation of the opisthotic including the paroccipital process can only be observed in PIMUZ T 2484 among the specimens of the small morphotype and in PIMUZ T 2819 among the large morphotype specimens (Figure 4A and E). The difference between the two morphotypes is striking. However, none of the larger specimens belonging to the small morphotype or smaller specimens of the large morphotype preserve this element, and therefore there is no possibility of observing the morphology in the more intermediately-sized speci-

mens. The shape of the braincase, including the opisthotic and its paroccipital process are known to change drastically in shape in extant diapsids. In *Alligator mississippiensis* and *Varanus panoptes* for instance, the paroccipital process becomes distinctly longer and narrower with age (Dufeau and Witmer, 2015, supplementary material; Werneburg et al., 2015, supplementary material), thus showing a similar disparity in shape from a juvenile to adult as seen in the small and large morphotype of *Tanystropheus* from Monte San Giorgio.

In the axial skeleton minor variation was mentioned (Wild, 1973). The cervical vertebrae were described as transitioning from a crescent-shaped cross section in the smaller specimens to a more triangular cross section in the larger specimens. Additionally the neural spines of the cervical vertebrae were considered to increase somewhat in relative size through ontogeny. No particular intraspecific variation was noted on in the dorsal column. The amount of caudal vertebrae bearing pleurapophyses was considered to increase with size, ranging from eight or nine in PIMUZ T 2791 to around 14 in PIMUZ T 2818. Due to the crushing of the specimens we were not able to observe the cross sectional shape of the cervical vertebrae in the material from Monte San Giorgio in detail. The isolated three-dimensional elements from the Upper Muschelkalk attributed to *Tanystropheus conspicuus* all represent specimens of the size range of the large morphotype, and therefore the presence of ontogenetic variation within that material cannot be confidently established.

Although not specifically discussed in Wild (1973), variation can be observed in the dorsal vertebrae of the *Tanystropheus* material from Monte San Giorgio in the relative height of the neural spine and length of the centrum, as well as the occurrence of laminae. Only PIMUZ T 2817 and PIMUZ T 2818 among the specimens of the large morphotype preserve an articulated dorsal column. In the former, apart from the anteriormost dorsal vertebrae, all dorsal vertebrae are partially broken, whereas in the latter, the specimen is heavily crushed and many characters of the dorsal vertebrae are obscured. Isolated dorsal vertebrae are also preserved in PIMUZ T 2787 and PIMUZ T 2792. Due to the isolated nature of these vertebrae, however, it is not possible to establish the exact position of each element in the vertebral column. Additionally the dorsal vertebral column is also complete in the Chinese specimen GMPKU-P-1527, which does not possess a skull but its size fits well within the size range of the large morpho-

type. However, its dorsal vertebrae are either covered by matrix or overlying ribs, or are only visible in ventral view. The dorsal part of the vertebral column is similarly disarticulated or heavily crushed in specimens of the small morphotype. The dorsal vertebrae can at least be partially counted and observed in MSNM BES SC 265 and PIMUZ T 1277. Although aspects of the dorsal column have been described for *Tanystropheus* from Monte San Giorgio (Wild, 1973; Renesto, 2005; Nosotti, 2007), no distinct differences between the large and small morphotype can be observed, and a comparison throughout the growth series is not possible.

The number of caudals bearing pleurapophyses in the specimens listed in Wild (1973, p. 136) could not be established with certainty due to the elements being poorly visible or too disarticulated. However, the number of pleurapophyses bearing caudals could be established in MSNM BES SC 265, a specimen of the small morphotype not available to Wild (Nosotti, 2007). The first eight caudals unambiguously bear pleurapophyses. Furthermore, in another specimen of the small morphotype, PIMUZ T 1277, at least six caudals bear pleurapophyses (Wild, 1980a). None of the specimens of the large morphotype from Monte San Giorgio allow for an exact count of caudal vertebrae bearing pleurapophyses. However, in the large Chinese specimen, GMPKU-P-1527, pleurapophyses can also be found in the first eight caudals (Rieppel et al., 2010). Although cranial material is absent in this specimen, its postcranial skeleton is morphologically indistinguishable from the large morphotype from Monte San Giorgio. Based on a comparison between these available specimens, we do not observe any distinct difference in this character between the two morphotypes as was suggested in Wild (1973).

Differences in the appendicular skeleton were documented in the shape of the pectoral and pelvic girdle elements (Wild, 1973). These differences all relate to proportional shape changes that do not appear to bear any taxonomic signal (see Wild, 1973, figures 89-93; personal observation SNFS and TMS). Similarly, variation among the limb elements is also minor and relates to the curvature of these elements (see Wild, 1973, figures 94-96; personal observation SNFS and TMS). We therefore consider these differences to be minor and easily attributable to ontogenetic variation, and they are, therefore, not considered to distinguish the two morphotypes.

In summary, the presence of prenarial and postnarial processes of the premaxillae is largely

restricted to specimens of the small morphotype, and they are absent or very small in the large morphotype and the dentary keel present in the large morphotype is completely absent in the small morphotype (Table 2; Figure 3). A comparison of the relative size of the processes of the premaxilla in the small morphotype, and the dentary keel in the large morphotype reveals that much variation occurs in these characters that is apparently independent of size, indicating that it is likely not linked to ontogeny. We did not find any variation in the number of premaxillary and maxillary teeth within and between the two morphotypes in contrast to Wild (1973; see Table 1). We were also not able to identify the presence of tricuspid teeth in PIMUZ T 2792 or any of the other specimens attributed to the large morphotype. We did find the position of the anteriormost tricuspid tooth on the maxilla to vary in specimens of the small morphotype, but apparently independent of size. Distinct differences are observed between the two morphotypes in the shape of the parietal and paroccipital process of the opisthotic (Table 2; Figure 4A-B and E). However, these differences could be the result of ontogenetic variation as observed in extant sauropsids. The palatal regions differ between the two morphotypes with the large morphotype having an anteriorly rounded vomer with large teeth and a narrow straight vomer with relatively much smaller teeth being present in the small morphotype (Figure 4C and G). The relatively small size difference between PIMUZ T 2792 and PIMUZ T 2795 but their very differently shaped vomers indicates that this difference is unlikely to be attributable to ontogeny. The palatine of the large morphotype differs from that of the small morphotype in being edentulous, wider, and more posteriorly extended with a relatively smaller lateral extension articulating with the maxilla (Figure 4A, C, and G). The size difference between the single specimen of the large morphotype preserving the palatine and the specimens of the small morphotype preserving the palatine is large. Nevertheless, the difference between the two morphotypes is disparate to such an extent that it seems unlikely that it is attributable to ontogeny. The pterygoid of the large morphotype differs from the small morphotype in being edentulous and with a wide and rounded palatal process (Figure 4A and D). Here, too, the size difference between the specimens of both morphotypes is large, but their morphology is similarly disparate that it seems unlikely that it is the result of ontogenetic variation. Tooth count is likely variable on all tooth-bearing palatal elements in both morpho-

types independent of ontogeny (Table 1). However, the absence or presence of dentition on certain palatal elements is specific to each morphotype. In the postcranial skeleton, no consistent differences between the two morphotypes could be found.

The consistently observed differences in the shape of the premaxilla, dentary, and palatal elements are distinct and would represent a highly unusual ontogenetic transformation in *Tanystropheus* among sauropsids. Furthermore this transformation would have to occur in a relatively short part of the growth trajectory (between 33.7% and 50.24% of the maximum skull size estimated for *Tanystropheus* from Monte San Giorgio based on PIMUZ T 2819; Table 3). However, to unambiguously establish whether the two morphotypes represent different species based on a comparison of external morphology would require an overlapping size range between the two, which is not the case with the specimens currently known. Therefore, to establish whether the two morphotypes represent two distinct species requires additional study beyond a purely external morphological comparison, and we plan to use histological data and microtomographic scans to address this outstanding issue. Therefore, in the current study we are able to clearly separate two morphotypes in the *Tanystropheus* material from Monte San Giorgio. However, we find that it is currently not possible to exclude the possibility that the two morphotypes represent an ontogenetic series of the same taxon, and we therefore maintain the identification of the two morphotypes to *T. longobardicus*.

***Tanystropheus conspicuus* and *Tanystropheus haasi*.** With the exception of a single undescribed dentary attributed to *Tanystropheus conspicuus* (SMNS 56289), both *T. conspicuus* and *T. haasi* are known from limited isolated postcranial material and are distinguished from other *Tanystropheus* species based on the morphology of their cervical vertebrae. These are similar in overall shape and size to those of the large morphotype of *T. longobardicus*, but can be easily distinguished from *T. antiquus* based on their relative length and are considerably larger than the cervical vertebrae known for the small morphotype of *T. longobardicus* and *T. fossai*. In order to assess the taxonomic validity of these taxa, the morphology of the cervical vertebrae of *T. conspicuus* and *T. haasi* is discussed here in detail and compared to each other and those of the large morphotype of *T. longobardicus*.

The diagnostic features of *Tanystropheus conspicuus* are currently unclear. *T. conspicuus* was distin-

guished from *T. longobardicus* based on the somewhat wider rib attachment sites and the bifurcating anterior end of the neural spine of the cervical vertebrae (Wild, 1973). This diagnosis was considered insufficient but maintained in expectation of the discovery of additional *T. conspicuus* material. The taxonomic status of *T. conspicuus* was later commented on in Wild (1980b), p. 204: “[...] and the probable identity of *T. longobardicus* and *T. conspicuus* from the Upper Muschelkalk (which at [the] moment cannot be proved, because of the lack of skull finds of the latter species). So in the Upper Muschelkalk only skeletal elements of adult specimens are found, never of juvenile ones. The preservation of juvenile skeletons of *T. longobardicus* in the Grenzbitumenzone is caused by the vicinity of the land during development of this basin [...]” The latter remark refers to the hypothesis that the small morphotype of *Tanystropheus* from Monte San Giorgio (*T. longobardicus*) was terrestrial (Wild, 1973), a view which has been disputed by various studies (e.g., Cox, 1975; Tschanz, 1986; Nosotti, 2007). Regardless, the material ascribed to *T. conspicuus*, although being represented only by isolated elements, largely cervical vertebrae, was considered to be indistinguishable from the large morphotype of *Tanystropheus* from Monte San Giorgio. The study was concluded with the following: “If it can be shown that the Upper Muschelkalk species *T. conspicuus* is identical with *T. longobardicus*, then this species would be a typical and widespread faunal element in the Tethyan and epicontinental Middle Triassic. New finds, which are under study, might confirm this assumption.” (Wild, 1980a, p. 205). However, no new material of *T. conspicuus* has been published on since, with the exception of the briefly mentioned fragmentary remains from Poland (Skawiński et al., 2017). In addition, GMPKU-P-1527 from the latest Ladinian or earliest Carnian of southwestern China could not be distinguished from the large morphotype of *T. longobardicus* (personal observation SNFS and TMS), and was identified as *T. cf. T. longobardicus* by Rieppel et al. (2010), indicating that at least one species of *Tanystropheus* occurred widespread throughout the Tethys. Regardless it is possible that multiple species of *Tanystropheus* co-occurred in the same habitat, as has been suggested for the fauna of Makhtesh Ramon (Rieppel, 2001) and would be the case if the small and large morphotype of *T. longobardicus* from Monte San Giorgio represent two separate species. Furthermore and crucially, the difference between or synonymy of *T. conspicuus* and the large morphotype

of *T. longobardicus* cannot and should not be focused on temporal or spatial occurrence, but mainly on morphology (see also Simpson, 1951).

*Tanystropheus haasi* was distinguished within the genus *Tanystropheus* on the basis of 1) the presence of a deep horizontal groove directly dorsal to the centrum at the posterior end of the middle cervical vertebrae; 2) the presence of thickened margins of the articulation facets of the postzygapophyses; 3) a straight posterior margin of the postzygapophyseal trough; 4) which is furthermore located far posteriorly, namely dorsal to the posterior articulation surface of the centrum; 5) the presence of a long pointed posterior process of the neural spine that overlies the postzygapophyseal trough (Rieppel, 2001).

We document the morphological variation between and within the cervical vertebrae of *Tanystropheus conspicuus* and *T. haasi* consisting of the diagnostic characters of *T. haasi* as well as additionally observed variation among and within these morphotypes, an overview of which is provided in Supplementary Table 2. The main findings are discussed below and subsequently compared to the cervical vertebrae of the large morphotype of *T. longobardicus*. Four cervical vertebrae that were included in the original description of *T. conspicuus* by Meyer (1855, plate 30) were studied firsthand, including U-MO BT 740 (Figure 5), the specimen identified as the lectotype of the species in Wild (1973), in addition to four other cervical vertebrae assigned to *T. conspicuus* housed in the U-MO (Figure 6). *Tanystropheus haasi* was studied by firsthand observation of a cast of the holotype of *T. haasi* (PIMUZ A/III 726, cast of HJ-Pal. TR 1; Figure 7), and the additional material attributed to the species based on Rieppel (2001). When discussing these characters, it is important to consider that apart from the relative length, the morphology of the cervical vertebrae varies distinctly depending on the position of each vertebra within the cervical column, particularly at the anterior and posterior ends of each vertebra. This variation was described in detail for the three-dimensionally preserved cervical vertebrae of *T. conspicuus*, and based on this variation, the position in the cervical column of the various cervical vertebrae was assigned (Wild, 1973). However, this identification is inconclusive since all *T. conspicuus* vertebrae are preserved in isolation, thus not allowing the establishment of the exact position of each vertebra in the cervical column.

1) A horizontal groove is absent in the majority of the cervical vertebrae from the Upper Muschel-

kalk of Bindlacher Berg. However, specimens U-MO BT 732, U-MO BT 738, and U-MO BT 736 exhibit a larger excavation directly dorsal to the centrum than the other studied specimens, similar but somewhat less pronounced to that observed in PIMUZ A/III 726 and described for *Tanystropheus haasi* (Rieppel, 2001). 2) Distinct and wide, flat articulation surfaces directed lateroventrally can be observed in the majority of the studied specimens. But no distinct thickening of the articulation facets of the postzygapophyses could be observed. Similarly we consider the only preserved articulation facet of the left postzygapophysis of PIMUZ A/III 726 to not be distinctly thickened, but to be comparable in thickness and width to that of the cervical vertebrae from the Upper Muschelkalk of Bindlacher Berg. 3) In the studied specimens, a notch on the posterior margin of the postzygapophyseal trough could be observed in U-MO BT 734, U-MO BT 740, U-MO BT 736, and U-MO BT 738, whereas this margin was straight in U-MO BT 733, U-MO BT 739, and U-MO BT 732. In PIMUZ A/III 726 the posterior margin of the postzygapophyseal trough could not be observed since it is broken off posteriorly. 4) The posterior margin of the postzygapophyseal trough was located directly dorsal to the posteriormost end of the centrum in U-MO BT 733 and U-MO BT 734, whereas it is anterior to the posteriormost end of the centrum in the other studied specimens. In PIMUZ A/III 726 the posterior extent of the postzygapophyseal trough is located somewhat posterior to the posterior end of the centrum on its right side where it is complete. 5) A large posterior process of the neural spine as shown in Figure 4A of Rieppel (2001) cannot be observed in any of the studied *T. conspicuus* specimens. However, it is important to note that both the anterior and posterior ends of the neural spines are broken in virtually all of the specimens. In U-MO BT 736 the neural spine is not very distinct posteriorly, but it slightly protrudes over the postzygapophyseal trough. In PIMUZ A/III 726 the neural spine similarly protrudes very slightly over the postzygapophyseal trough, but it is much less expanded than in HJ-Pal. TR 1447.

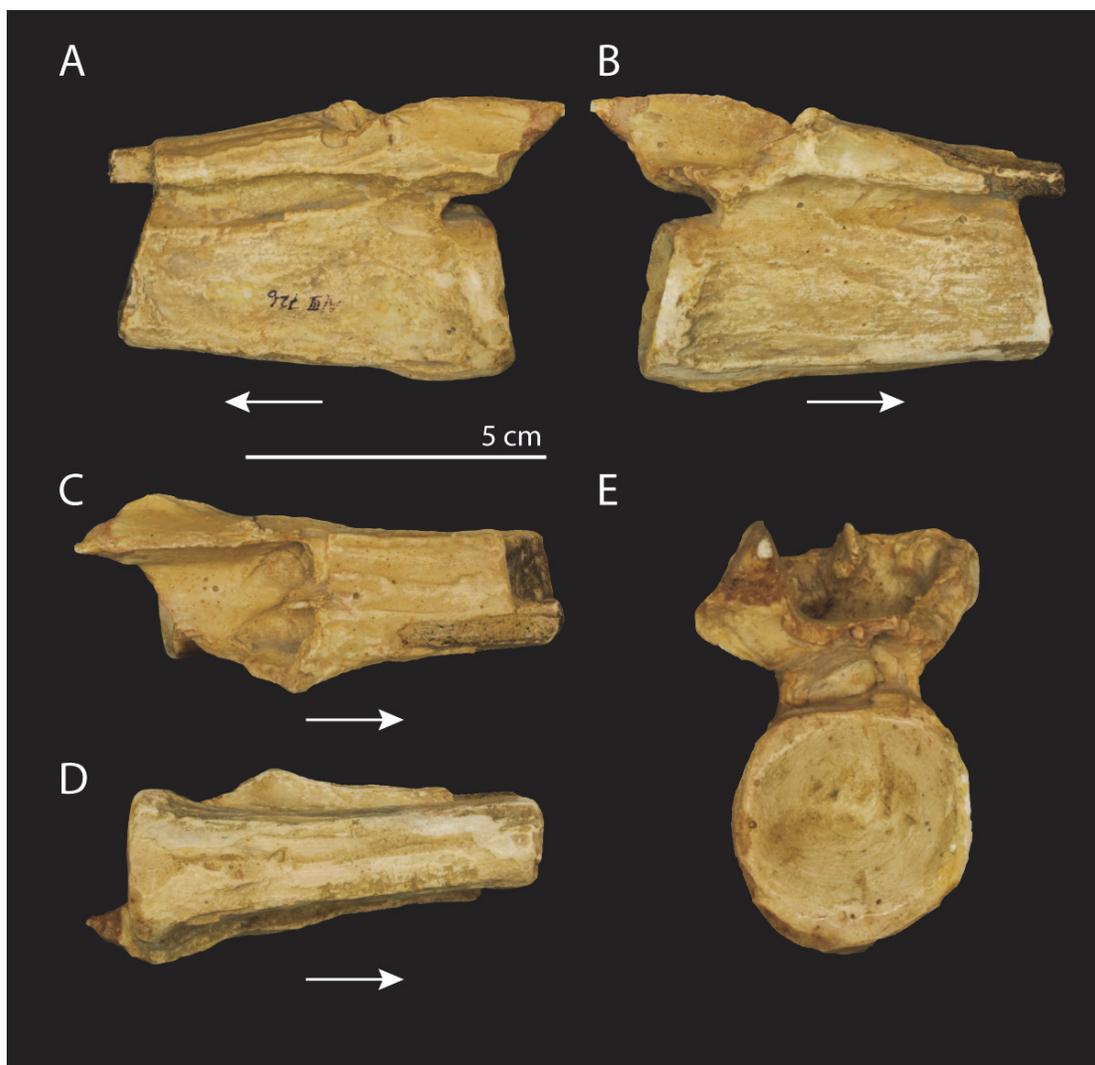
Additional variation in the cervical vertebrae could be found in the presence of the ventral foramen (foramina venae vertebralis sensu Wild, 1973, 1987; Figure 5D), the anteroposterior length of the postzygapophyseal canal, the height of the posterior opening of the neural canal, the depth of the excavation of the articular ends of the cervical centra, the shape of the articular ends of the cervical centra, how distinct the ventral keel is pronounced,



**FIGURE 5.** The isolated cervical vertebra U-MO BT 740, assigned as the lectotype of *Tanytropheus conspicuus* by Wild (1973) in (A) left lateral view; (B) right lateral view; (C) dorsal view; (D) ventral view; (E) anterior view; (F) posterior view; and (G) oblique posterodorsal view of the posterior end. The numbers refer to the following morphological characters of the cervical vertebrae (not inferring absence or presence, which is discussed in the text): (1) presence or absence of a deep horizontal groove directly dorsal to the centrum at the posterior end of the vertebrae; (2) presence or absence of thickened margins of the articulation facets of the postzygapophyses; (3) presence or absence of a straight posterior margin of the postzygapophyseal trough; (4) degree of posterior extension of the postzygapophyseal trough; (5) presence or absence of a long pointed posterior process of the neural spine that overlies the postzygapophyseal trough. The arrows are pointing anteriorly.



**FIGURE 6.** Isolated cervical vertebrae of *Tanystropheus conspicuus* from the Upper Muschelkalk of Bindlacher Berg housed in the U-MO; (A) U-MO BT 732 in right lateral view; (B) U-MO BT 733 in right lateral view; (C) U-MO BT 736 in right lateral view; (D) U-MO BT 737 in left lateral view; (E) U-MO BT 739 in left lateral view; (F) the preserved anterior and posterior ends of U-MO BT 738 in left lateral view; (G) the preserved posterior end of U-MO BT 734 in left lateral view. The arrows are directed anteriorly.



**FIGURE 7.** The cast of the holotype of *Tanystropheus haasi* (PIMUZ A III 726, cast of HUU-Pal. TR 1), the posterior part of a mid-cervical vertebra; in (A) left lateral; (B) right lateral; (C) dorsal; (D) ventral; and (E) posterior view. The arrows are pointing anteriorly.

and the dorsal extension of the neural spine. In U-MO BT 736 and U-MO BT 737 a distinct dorsal convexity of the neural spine can be observed slightly posterior to the mid-length of both vertebrae (Figure 5C-D). In other observed specimens, the neural spine is not markedly expanded here and straight. This character cannot be observed in PIMUZ A/III 726 since the majority of the vertebra is not preserved.

Overall, the observed variation in the *Tanystropheus conspicuus* material indicates that most of the features indicated as diagnostic for *T. haasi* fall within the range of intraspecific variation for *T. conspicuus*. However the horizontal groove dorsal to the posterior end of the centrum is less distinct in the specimens of *T. conspicuus* in which

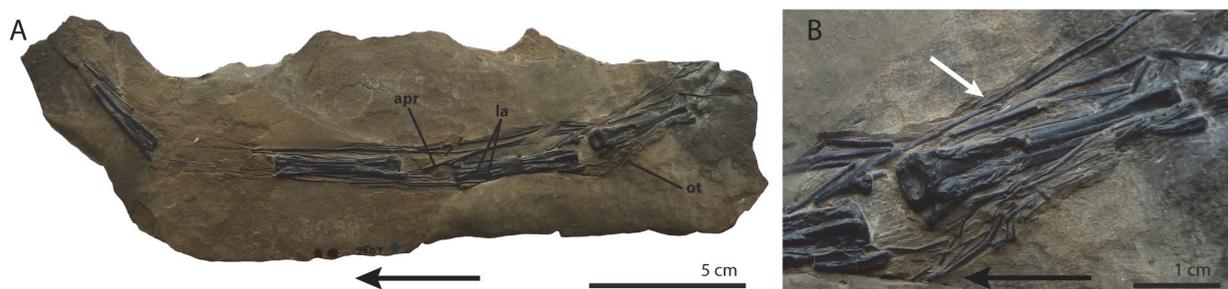
it is present than observed in *T. haasi*. Furthermore, the distinctly expanded posterior end of the neural spine overhanging the postzygapophyseal trough as described for HUU-Pal. TR 1447 could not be observed for *T. conspicuus*, or in the cast PIMUZ A/III 726 of *T. haasi*. Our findings indicate that much variation occurs in the morphology of the cervical vertebrae of *T. conspicuus*, and that this variation overlaps with much of the morphology considered diagnostic for *T. haasi*. This comparison highlights the difficulty of differentiating species of tanystropheids on the basis of isolated cervical vertebrae alone, as much variation occurs along the cervical column and intraspecifically.

The majority of the characters discussed above cannot be observed in *Tanystropheus lon-*

*gobardicus* because the specimens attributed to this species of both the large and small morphotype were strongly flattened during fossilisation or because the cervical vertebrae are still in articulation with each other and therefore the pre- and postzygapophyseal regions are largely obscured. This therefore hampers a detailed comparison. The size and shape of the vertebral centra, neural spines, and zygapophyses that can be observed for the large morphotype of *T. longobardicus* are indistinguishable from *T. conspicuus* and *T. haasi*. Additionally, other isolated material assigned to *T. conspicuus*, comprising dorsal, sacral, and caudal vertebrae, as well as a humerus and femora, also cannot be distinguished from this taxon (Wild, 1973; personal observation SNFS). However, because only a very limited comparison is possible, and skull material, which is likely more diagnostic, is completely lacking for both taxa, an unambiguous taxonomic identification of *T. conspicuus* and *T. haasi* is not possible. Therefore we propose to consider both taxa as nomina dubia.

***Tanystropheus fossai*.** The only known specimen of *Tanystropheus fossai*, MCSNB 4035, consists of four articulated cervical vertebrae and associated cervical ribs and originates from the late Norian of northern Italy (Figure 8). It was interpreted to be a juvenile individual and distinguished from other species of *Tanystropheus* based on the absence of a neural spine and the presence of wing-like laterally projected crests on the posterior end of the centrum of the cervical vertebrae (Wild, 1980a). It cannot be determined whether the specimen represents a juvenile based solely on cervical vertebrae and ribs. Nevertheless we concur that the absence of the neural spine and laterally projected crests on the posterior ends of the centra of the cervical vertebrae represent diagnostic features not present in other tanystropheids. Additionally

MCSNB 4035 also differs from other *Tanystropheus* taxa in having an elongated anterior free-ending process of the cervical ribs. Furthermore, dorsal to the vertebrae, a number of elongate and thin elements are preserved, which are clearly thinner than the cervical ribs preserved ventral to the vertebrae. Although figured, these elements were not commented on in Wild (1980a). They likely represent ossified tendons, similar to those present in many dinosaurian taxa (Organ and Adams 2005), but previously unknown for tanystropheids. Finally, as was also described in Wild (1980a), some of the cervical ribs appear to bifurcate (Figure 8B). It was unclear to Wild (1980a) whether these bifurcations represented a taxonomic feature or pathology. However, since no similar cases of bifurcating cervical ribs are known among amniotes, they most likely represent a pathological anomaly. Another possibility is that the apparent bifurcation of the ribs is formed by ossified tendons running parallel and attaching to the cervical ribs. The seemingly abundant presence of these tendons dorsal to the vertebrae possibly support this hypothesis. Regardless, we think it unlikely for these bifurcations to represent a taxonomic feature and therefore do not consider it a diagnostic character for the taxon. The relative length of the centra of the mid-cervical vertebrae is in correspondence with that found within the genus *Tanystropheus*, with the centrum being approximately 11 times longer than its minimum height in the second preserved vertebra from anterior (length 40.4 mm; height: 3.6 mm). This is in contrast to the observation presented in Renesto (2005), in which the cervical vertebrae of MCSNB 4035 were described as being considerably shorter than those of other *Tanystropheus* species. Although not identified as such, the morphology of the vertebrae of MCSNB 4035 was also likened to the caudal vertebrae of certain Triassic pterosaurs



**FIGURE 8.** MCSNB 4035, the holotype and only known specimen of *Sclerostropheus fossai*; (A) the complete specimen; (B) a close up of a single vertebra including its corresponding cervical rib. The black arrows indicate the anterior direction and the white arrow indicates the apparent bifurcation of the cervical rib. Abbreviations: apr, anterior process of the cervical rib; la, lamina; ot, ossified tendons.

(Dalla Vecchia, 2000). However, it can be excluded that they indeed represent caudal vertebrae based on the associated cervical ribs. The articulation surfaces of the vertebrae appear to be amphicoelous.

Since the first identification of *Tanystropheus fossai*, many additional tanystropheid taxa with elongated cervical vertebrae have been described; e.g., *Langobardisaurus pandolfii*, *Dinocephalosaurus orientalis*, and *Fuyansaurus acutirostris* (Renesto, 1994; Renesto and Dalla Vecchia, 2000; Li, 2003; Rieppel et al., 2008; Fraser et al., 2013). Most of the diagnostic features of *T. fossai* cannot be observed in these taxa. However, the extended anterior free-ending process of the cervical ribs present in *T. fossai* can also be observed in *D. orientalis*, as well as in *Pectodens zhenyuensis*, a long-necked diapsid of possibly tanystropheid affinity (Rieppel et al., 2008; Li et al., 2017). Although only known from a single, fragmentary specimen, we consider MCSNB 4035 to show distinct morphological disparity from known *Tanystropheus* taxa as to merit its assignment to a separate genus. This interpretation is additionally supported by the large temporal gap between MCSNB 4035 and the known *Tanystropheus* taxa (Figure 1) and the taxonomic diversity of long-necked tanystropheid taxa. We therefore reassign MCSNB 4035 to *Sclerostropheus fossai* (gen. nov.).

#### **Specimens not identified on the species level.**

The isolated element PIMUZ A/III 771 from Piz Ravigliel represents a complete, mediolaterally crushed, right femur with a total length of 190 mm (Figure 9). It is strongly sigmoidal and bears a distinct crest-like medial trochanter that is confluent with the femoral shaft distally. This trochanter is displaced further posteriorly than in other *Tanystropheus* femora due to compression. The proximal head is somewhat broken, whereas the distal head is complete. It is indistinguishable from the femora of the large morphotype of *T. longobardicus* (e.g., PIMUZ T 2817) and those from the Upper Muschelkalk (SMNS 54623) and therefore we corroborate its identification as *Tanystropheus* sp. (Eichenberger, 1986).

The isolated *Tanystropheus* remains from the late Anisian deposits of the Aupa Valley, Friuli, Italy, represent comprehensive material consisting of a single caudal vertebra (MFSN 25761) and possible dorsal rib (MFSN 25762) (Dalla Vecchia, 2000), and 30 specimens comprising cervical, dorsal, sacral, and caudal vertebrae, as well as teeth, a clavicle, and ilium described in Dalla Vecchia (2005). This material was identified as *T. cf. T. lon-*

*gobardicus* but was considered as possibly representing a different species based on the reduction of the neural spine on the posterior end of the cervical vertebrae and the long transverse processes of the dorsal vertebrae (Dalla Vecchia, 2005). Although representing extensive material, the absence of articulated specimens and cranial material precludes its precise taxonomic affinity, and therefore we consider it as *Tanystropheus* sp.

MTSN 3652, the partial isolated cervical vertebra from the late Ladinian of the Mendola Pass, Trentino, Italy, allows only for observation in lateral and ventral view and thus a very limited comparison is possible with the cervical vertebrae from the Upper Muschelkalk of Bindlacher Berg and Makhtesh Ramon, since no observations of important features such as those on the postzygapophyseal trough or the neural canal can be made. Therefore, we concur with the identification of this specimen to *Tanystropheus* sp. (Dalla Vecchia and Avanzini, 2002). Similarly in MFSN 25760, the posterior half of a cervical vertebra from the Fusea site of Friuli, Italy (late Ladinian to early Carnian), the same limitations in observation apply and this specimen is therefore also referred to *Tanystropheus* sp. (Dalla Vecchia, 2000).

YPM VPPU 022000, the virtually complete cervical vertebra from the Early to Middle Triassic Nova Scotia was identified as cf. *Tanystropheus* sp. by Sues and Olsen (2015). It is distinctly larger than *Sclerostropheus fossai* and apparently lacks wing-like laminae on its centrum and possesses a low neural spine. The relative length of the vertebra in comparison to the minimum height of its centrum (approximately 13) exceeds that known for *T. antiquus* (<3 sensu Fraser and Rieppel, 2006). Its size and overall morphology is in agreement with that observed for *T. conspicuus*, *T. haasi*, and the large morphotype of *T. longobardicus*, and therefore the specimen is identified here as *Tanystropheus* sp.

The articulated small-sized specimen preserving the posterior five cervical vertebrae, the trunk, forelimbs and girdles, and part of the hind limbs and girdles from the Falang Formation of Chajiang, Guizhou Province, China, IVPP V 14472, was considered morphologically indistinguishable from specimens referred to *Tanystropheus longobardicus*, but not identified on the species level (Li, 2007). Although its overall size is in correspondence with that of the small morphotype of *T. longobardicus*, no skull material is preserved that allows for the identification of characters associated with the small morphotype of *T. longobar-*



**FIGURE 9.** The isolated right femur, PIMUZ A/III 771, from the S-charl Formation of Piz Ravigliel, referred to *Tanystropheus* sp. in (A) lateral; (B) medial; (C) anterior or dorsal; (D) posterior or ventral; (E) proximal; and (F) distal view.

*dicus*, such as the presence of tricuspid marginal teeth. Therefore, we corroborate its identification as *Tanystropheus* sp.

Apart from the material assigned to *Tanystropheus haasi*, two additional morphotypes of *Tanystropheus* from Makhtesh Ramon in Israel were recognized in (Rieppel, 2001), and it was suggested that multiple species of *Tanystropheus* might have coexisted there through habitat partitioning as hypothesized for the genera *Nothosaurus* and *Saurichthys* (Rieppel et al., 1997). Specimens referred to these two morphotypes were identified as *Tanystropheus* sp. They were recognized based on overall size and small morphological differences such as the postzygapophyses being oriented more ventrally rather than ventrolaterally, and the depth of the excavation of the horizontal groove also described for *T. haasi*. As shown in Supplementary Table 2 such variation also occurs in the cervical vertebrae from the Upper Muschelkalk of Bindlach, Germany. We consider this variation to be attributable to variation that occurs throughout the cervical column depending on the position of each cervical, as well as taphonomic alteration and intraspecific variation. However, the very large size of one of the two morphotypes, which is apparently distinctly larger than that of any other known *Tanystropheus* material, might be an indication that the two represent separate species. However, since this morphotype is represented by very limited material, we maintain its identification, as well as that of the smaller morphotype, as *Tanystropheus* sp. as proposed by Rieppel (2001). The *Tanystropheus* specimens described from the Jilh Formation of Saudia Arabia were not figured, and their identification therefore could not be assessed and we therefore tentatively maintain its identification as *Tanystropheus* sp. (Vickers-Rich et al., 1999).

The isolated cervical vertebrae from the Anisian of Romania were initially referred to *Tanystropheus biharicus* (Jurcsák, 1975, 1976, 1978, 1982) and subsequently reassigned to *T. cf. longobardicus* (Wild, 1980a). We find that the morphology, length to height ratio, and overall size of the vertebrae fit that seen for the large morphotype of *T. longobardicus*, *T. conspicuus*, and *T. haasi*, and refer this material to *Tanystropheus* sp.

## SYSTEMATIC PALAEOLOGY

DIAPSIDA Osborn 1903

ARCHOSAURMORPHA von Huene, 1946

TANYSTROPHEIDAE Gervais, 1859

Genus TANYSTROPHEUS von Meyer, 1852

**Diagnosis.** Long-necked tanystropheid archosauromorphs distinguished from other genera by the following combination of characters (autapomorphy among non-archosauriform archosauromorphs marked with an asterisk): 1) the absence of shagreen-like teeth on the vomers and palatines; 2) mid-cervical vertebrae with a vertebral centrum length more than 2.5 times their minimum height; 3) a low neural spine of the cervical vertebrae; 4) very long and extremely thin cervical ribs, being approximately three times the length of their corresponding vertebra in the mid-cervical region, bearing short anterior free ending processes; 5) ribs of second sacral vertebrae not bifurcated; 6) curved anterior margin of scapular blade, which is consequently directed posteriorly; 7) the absence of hyperphalangy; 8) only two ossified distal carpals\*; and 9) a thyroid fenestra present between the pubis and ischium.

**Type species.** *Tanystropheus conspicuus* (nomen dubium)

**Included species.** *Tanystropheus longobardicus*, *Tanystropheus haasi* (nomen dubium), and *Tanystropheus antiquus*.

**Remarks.** *Tanystropheus conspicuus* is considered to be represented by insufficient material to distinguish it convincingly from other *Tanystropheus* taxa, and we therefore consider it a nomen dubium. Nevertheless it remains the type species as the first named species of the genus, and it is diagnostic on the genus level based on the characteristic cervical vertebrae of the type material that are unique to the genus *Tanystropheus*.

*Tanystropheus antiquus* von Huene, 1905, currently only encompasses the material described in Huene (1907-1908) since the analysis of more recent material assigned to the species (e.g., Wild, 1973; Fraser and Rieppel, 2006; Sennikov, 2011) did not take most of this material into consideration as it was presumed to have been lost, which is not the case (Skawiński et al., 2017). This original material is currently under study, and, therefore, we refrain from assessing this taxon in detail and consider all material later assigned to this taxon preliminarily to *Tanystropheus* cf. *T. antiquus*.

Like *Tanystropheus conspicuus*, *T. haasi* is considered a nomen dubium as the limited material assigned to the species is insufficient to confidently distinguish the species from other species within the genus. *Sclerostropheus fossai* was previously attributed to *Tanystropheus* but is herein considered sufficiently distinct from other known *Tanystropheus* species to merit assignment to a separate genus.

<i>Tanystropheus conspicuus</i> (von Meyer, 1855) Figures 5-6			
1846	<i>Smilodon laevis</i> (partim) Plieninger, p. 153, 247; plate 3, figure 4	1932	<i>Tanystropheus conspicuus</i> von Huene p. 6-8 ( <i>Thecodontosaurus latespinatus</i> and <i>Zanclodon laevis</i> considered to be likely attributable to this species herein)
1855	<i>Tanystropheus conspicuus</i> von Meyer, plate 30, figure 1-6, plate 46, figures 1-4	1935	<i>Macroscelosaurus conspicuus</i> Kuhn, p. 118-119
1890	<i>Tanystropheus conspicuus</i> Zittel, p. 567, 733; figure 514	1938	<i>Tanystropheus conspicuus</i> Schmidt, p. 75-76, figure 1188a
1896	<i>Tanystropheus conspicuus</i> Fraas, p. 14-15	?1952	<i>Tanystropheus conspicuus</i> Rühle von Lilienstern, p. 27
1902	<i>Chelyzoon blezingeri</i> von Huene, p. 51-52; plate 7, figure 1 (also mentioned in Kuhn, 1971, but appears very different from <i>Tanystropheus</i> )	1953	<i>Tanystropheus conspicuus</i> Adam, throughout text; figure 1
1902	<i>Chelyzoon latum</i> von Huene, p. 50-51; plate 7, figure 2 (also mentioned in Kuhn, 1971, but appears very different from <i>Tanystropheus</i> )	1955	<i>Tanystropheus conspicuus</i> Peyer, p. 489
1902	<i>Procerosaurus cruralis</i> von Huene, p. 64-65; plate 9, figure 1	1955	<i>Tanystropheus conspicuus</i> Peyer and Kuhn-Schnyder, p. 578; figure 1
1902	<i>Pectenosaurus strunzi</i> von Huene, p. 65; plate 6, figure 5 (synonymous with <i>Tanystropheus</i> sensu Kuhn, 1971, p. 11)	1970	<i>Thecodontosaurus latespinatus</i> Colbert, p. 31-33
1905	<i>Thecodontosaurus latespinatus</i> von Huene, p. 349	1971	<i>Tanystropheus conspicuus</i> Kuhn, p. 11; figures 21, 21a, 41b
1905	<i>Tanystropheus conspicuus</i> von Huene, p. 349	1971	<i>Thecodontosaurus latespinatus</i> Kuhn, p. 11; figure 21
1907-1908	<i>Thecodontosaurus latespinatus</i> von Huene, p. 218-223, 263, 265, 270, 307, 310-312; text-figures 237-243; plate 91, figures 1-8, plate 92, figures 1-7	1973	<i>Tanystropheus conspicuus</i> Wild, p. 52-60, 67-94; figures 39-62; p. 105-106; figure 67; p. 114-115; figures 73, 97; p. 148-150
1907-1908	<i>Tanystropheus conspicuus</i> von Huene, p. 4, 223, 226-230, 231, 237-239, 264-265, 270, 305, 307, 312, 319, 321; text-figures 250-251, 351; plate 95, figures 1-4; plate 96, figures 1-10	1975	<i>Tanystropheus conspicuus</i> Wild, p. 153; figure 1
1915	<i>Tanystropheus conspicuus</i> Broili, text; plate 2-3	1976	<i>Tanystropheus conspicuus</i> Wild, p. 20; figure 3
1924	<i>Tanystropheus conspicuus</i> Edinger, figures 1-4	1980a	<i>Tanystropheus conspicuus</i> Wild, p. 7, 10, 12-13, 25
1928	<i>Thecodontosaurus latespinatus</i> Corroy, p. 126; text-figure 12; plate 4, figure 11	1980b	<i>Tanystropheus conspicuus</i> Wild, p. 201, 204-205
1928	<i>Tanystropheus conspicuus</i> Schmidt, p. 424-425; figure 1188	1986	<i>Tanystropheus conspicuus</i> Benton, p. 296-297
1928	<i>Thecodontosaurus latespinatus</i> Schmidt, p. 434; figure 1213	1986	<i>Tanystropheus conspicuus</i> Tschanz, p. 6, 59, 66-68, 84
1931	<i>Tanystropheus conspicuus</i> Peyer, p. 11; text-figures 1-2; p. 21, 75-76, 92, 95-98; text-figures 24-25	1987	<i>Tanystropheus conspicuus</i> Wild, throughout text
1931	<i>Tanystropheus conspicuus</i> von Huene, 1931, throughout text and figures 1-6 ( <i>Thecodontosaurus latespinatus</i> and <i>Zanclodon laevis</i> considered to be likely attributable to this species herein)	1988	<i>Tanystropheus conspicuus</i> Tschanz, p. 997-998, 1002
		1988	<i>Tanystropheus conspicuus</i> (synonymized with <i>T. longobardicus</i> ) Evans, p. 227
		1997	<i>Tanystropheus conspicuus</i> Benton and Allen, p. 945, 947
		2000	<i>Tanystropheus conspicuus</i> Dalla Vecchia, p. 136, 138-139
		2001	<i>Tanystropheus conspicuus</i> Rieppel, throughout text
		2005	<i>Tanystropheus conspicuus</i> Dalla Vecchia, p. 40-42
		2005	<i>Tanystropheus conspicuus</i> Renesto, p. 386
		2007	<i>Tanystropheus conspicuus</i> Nosotti, throughout text

2012	<i>Tanystrophaeus conspicuus</i> Diedrich, p. 23; figure 14	?1907-1908	<i>Thecodontosaurus primus</i> von Huene, p. 217-218, 263, 265, 307-308, 311; plate 92, figures 8-9
2015	<i>Tanystropheus conspicuus</i> Pritchard, Turner, Nesbitt, Irmis, and Smith, p. 4, 9, 15	1915	<i>Tanystropheus antiquus</i> Broili, p. 52-53, 58, 61
2015	<i>Tanystropheus conspicuus</i> Nesbitt, Flynn, Pritchard, Parrish, Ranivharimanana, Wyss, p. 23, 26-27, 62, 64	?1928	<i>Tanystrophaeus</i> cf. <i>antiquus</i> Corroy, p. 126-127; text-figure 13 (not <i>Tanystropheus</i> sensu (Peyer 1931) p. 13)
2016	<i>Tanystropheus longobardicus</i> Ezcurra, throughout text; figures 14a-b, 31b, 33b, 35, 43a-b	1928	<i>Tanystrophaeus antiquus</i> Schmidt, p. 424; figure 1187
2017	<i>Tanystropheus conspicuus</i> Skawiński, Ziegler, Czepiński, Szermański, Tałanda, Surmik, and Niedźwiedzki, p. 4, 14-15; figure 50-p	?1928	<i>Thecodontosaurus primus</i> Schmidt, p. 434; figure 1212
2018	<i>Tanystropheus conspicuus</i> Renesto and Saller, p. 23	1931	<i>Tanystropheus antiquus</i> Peyer, p. 93-94, 104-106; text-figure 28
		1931	<i>Tanystropheus antiquus</i> von Huene, throughout text; figures 7-17
		1935	<i>Macroscelosaurus antiquus</i> Kuhn, p. 119
		1938	<i>Tanystropheus antiquus</i> Schmidt, p. 74-75, figure 1187
		1944	<i>Tanystropheus latespinatus</i> von Huene, p. 127
		1971	<i>Tanystropheus antiquus</i> Kuhn, p. 11; figures 21, 21a, 41a
		1971	" <i>Thecodontosaurus primus</i> " Kuhn, p. 11, 17; figure 21
		1973	<i>Tanystropheus antiquus</i> Wild, p. 142-143, 151-152
		1975	<i>Tanystropheus antiquus</i> Wild, p. 153
		1980a	<i>Tanystropheus antiquus</i> (partim) Wild, p. 5, 17-18, 25
		1980b	<i>Tanystropheus antiquus</i> (partim) Wild, throughout text; plate 2
		1986	<i>Tanystropheus antiquus</i> (partim) Tschanz, p. 84-85, 97
		1986	<i>Tanystropheus antiquus</i> Benton, p. 296-297
		1987	" <i>Tanystropheus</i> " <i>antiquus</i> (partim) Wild, throughout text
		1988	<i>Tanystropheus antiquus</i> (partim) Tschanz, p. 1001-1002, 1008, 1010
		1988	<i>Tanystropheus antiquus</i> Evans, p. 227
		1994	" <i>Tanystropheus</i> " <i>antiquus</i> (partim) Renesto, p. 298
		1997	<i>Tanystropheus antiquus</i> (partim) Benton and Allen, p. 945, 947
1905	<i>Tanystrophaeus antiquus</i> (nomen nudum) von Huene, p. 349	2001	<i>Tanystropheus antiquus</i> (partim) Rieppel, p. 273, 276
?1905	<i>Thecodontosaurus primus</i> (nomen nudum) von Huene, p. 349	2005	<i>Tanystropheus antiquus</i> (partim) Dalla Vecchia, p. 41, 43
1907-1908	<i>Tanystrophaeus antiquus</i> von Huene, p. 223-226; text-figures 246-249; p. 264-265, 305, 311; plate 93, figures 1-6, plate 94, figures 2-5	2005	<i>Tanystropheus antiquus</i> (partim) Renesto, p. 386
1907-1908	<i>Tanystrophaeus primus</i> von Huene, p. 221	2005	" <i>Tanystropheus</i> " <i>antiquus</i> Sennikov, p. 201, 208

**Referred specimens.** See Supplementary Table 1  
**Localities and occurrence.** The Upper Muschelkalk (late Anisian to early Ladinian) of Central Europe; exact localities are listed in Supplementary Table 1. The type locality is the Upper Muschelkalk of Bindlacher Berg, near Bayreuth, Germany.

**Previous diagnosis.** The diagnosis for *Tanystropheus conspicuus* was provided in Wild (1973, p. 149; translated from German): "Up to six(?) meters long species, that can be distinguished from *T. longobardicus* by the wider attachment sites of the cervical ribs and the split anterior end of the neural spine for the attachment of the dorsal ligament. Although these minor differences in the construction of the cervical vertebrae of *T. conspicuus* are insufficient for a species definition, it is maintained as a separate species until later finds can offer clarification."

**Remarks.** *Tanystropheus conspicuus*, represented by isolated vertebrae, femora, and a humerus, can currently not be distinguished from the large morphotype of *T. longobardicus*. However, the material of *T. conspicuus* is currently too limited to allow for a detailed comparison, and therefore the two species cannot be synonymized and we consider *T. conspicuus* to be a nomen dubium.

*Tanystropheus antiquus* (von Huene 1907-1908)

1905	<i>Tanystrophaeus antiquus</i> (nomen nudum) von Huene, p. 349
?1905	<i>Thecodontosaurus primus</i> (nomen nudum) von Huene, p. 349
1907-1908	<i>Tanystrophaeus antiquus</i> von Huene, p. 223-226; text-figures 246-249; p. 264-265, 305, 311; plate 93, figures 1-6, plate 94, figures 2-5
1907-1908	<i>Tanystrophaeus primus</i> von Huene, p. 221

- 2006 *Tanystropheus antiquus* Fraser and Rieppel, p. 866, 869-870
- 2007 *Tanystropheus antiquus* Nosotti, p. 5
- 2011 *Protanystropheus antiquus* Sennikov, p.98-99, figures 6-7
- 2015 *Protanystropheus antiquus* Pritchard, Turner, Nesbitt, Irmis, and Smith, p. 12, 15
- 2016 *Protanystropheus antiquus* and *Protanystropheus* sp. Surmik, Boczarowski, Balin, Dulski, Szade, Kremer, and Pawlicki, p. 3-6, figure 2
- 2016 *Protanystropheus antiquus* Ezcurra, p. 24
- 2017 *Protanystropheus antiquus* Jaquier, Fraser, Furrer, and Scheyer, p. 26
- 2017 *Tanystropheus antiquus* Skawiński, Ziegler, Czepiński, Szermański, Tałanda, Surmik, and Niedźwiedzki, p. 2, 4-5, 9-13; figure 5h-m
- ?2017 *'Thecodontosaurus' primus* Skawiński, Ziegler, Czepiński, Szermański, Tałanda, Surmik, and Niedźwiedzki, p. 2, 4-6, 9-12; figure 5a-c
- 2019 *Protanystropheus* Ullmann, Pandya, and Neller-moe, p. 2
- 2019 *Tanystropheus antiquus* Spiekman, Winkelhorst, Bleeker, Dorst, De Haan, and Voeten, throughout text

**Syntype.** SMNS 16687, SMNS 10110, MGUWr 3872s, MGUWr 3888s, MGUWr 3895s, MGUWr 3902s and some uncatalogued MGUWr specimens, all consisting of isolated cervical vertebrae. These specimens were all part of the original material used in the description of the species in Huene (1907-1908) (see also Skawiński et al., 2017). Out of these specimens no lectotype is currently assigned as the material is under revision (Szczygielski, personal commun., 2019).

**Localities and occurrence.** Lower part of the Gogolin Formation (lowermost Muschelkalk, lower Anisian or possibly uppermost Olenekian) of Gogolin and Krapkowice, Upper Silesia, Poland (Skawiński et al., 2017).

**Previous diagnoses.** The most recent diagnosis was provided in Sennikov (2011, p. 98) for *Protanystropheus antiquus*: "Large massive tanystropheid. Neck consisting of nine vertebrae. Cervical vertebrae elongated, their centra 2493 mm long. Length to anterior height ratio of cervical vertebral centra 3.7–6.5. Axis of cervical vertebral centra positioned at 2°–5° to horizontal. Articular surfaces of cervical vertebral centra relatively high, slightly higher than wide. Neural spines of cervical vertebrae low, elongated, in shape of flat crest, most projecting at midlength. Postzygapophyses elon-

gated, terminating in pointed projections projecting posterior to their articular surfaces. Femur sigmoidal."

The most recent diagnosis referring to *Tanystropheus antiquus* was provided in Fraser and Rieppel (2006, p. 869): "Protosaurus from the Lower Muschelkalk that has neck vertebrae with central length less than three times the minimum height [...]".

*Tanystropheus antiquus* was diagnosed in Wild (1973, p. 152) as follows (translated from German): "Cervical vertebrae distinctly shortened and bearing a less reduced neural spine in comparison to *T. conspicuus* and *T. longobardicus*; the zygapophyses always overlapping. The postzygapophyses comparatively more elongated than in *T. conspicuus*."

**Remarks.** Previous systematic palaeontology sections did not consider all the material used in the original description by Huene (1907-1908) (the species name was coined in Huene, 1905), since they thought this material was lost (Wild, 1973; Fraser and Rieppel, 2006; with SMNS 10110 being assigned as the lectotype, and Sennikov, 2011; with SMNS 16687 being assigned as the lectotype for "*Protanystropheus*" *antiquus*). However, these specimens that were presumed lost are still in existence, and thus any systematic diagnosis of the taxon should include these (Skawiński et al., 2017). Therefore, assignment of other specimens from the Lower Muschelkalk of Europe similar in morphology to that described by Huene (1907-1908) can only confidently be assigned to the species following a redescription of the original material. Because of this, this section only refers to the original material described by Huene (1907-1908). Since no emended diagnosis based on observations of the original material was provided in Skawiński et al., (2017) and revision of this material is currently ongoing, we refrain from providing a diagnosis for *Tanystropheus antiquus*. Nevertheless, *T. antiquus* can likely be preliminarily distinguished from other *Tanystropheus* species based on the cervical vertebrae having a central length less than three times their minimum height (sensu Fraser and Rieppel, 2006). Material that can likely be assigned to *T. antiquus* originates from the Lower Muschelkalk of Rüdersdorf near Berlin, Jena, and possibly Bonnhof (all Germany) (Wild, 1980a, 1980b), and the Lower Muschelkalk of Winterswijk, the Netherlands (Wild and Oosterink, 1984; Spiekman et al., 2019), as well as a single cervical vertebra from Dietersweiler near Freudenstadt, Germany (SMNS 56836; Supplementary Table 1).

The assignment of the specimens previously identified as “*Thecodontosaurus primus*” to *T. antiquus* is uncertain and this material is in need of revision (Skawiński et al., 2017).

*Tanystropheus* cf. *T. antiquus*

**Referred specimens.** See Supplementary Table 1  
**Localities and occurrence.** See Supplementary Table 1

**Remarks.** The specimens previously identified as *Tanystropheus antiquus* in Fraser and Rieppel (2006) or *Protanystropheus antiquus* (Sennikov, 2011) that do not originate from the Gogolin Formation are preliminarily referred to *T. cf. T. antiquus* here in expectation of a revision of the type material of *T. antiquus* (see also Skawiński et al., 2017; Spiekman et al., 2019), since these specimens have not been compared to the majority of the material used in the original description in Huene (1905, 1907-1908).

*Tanystropheus longobardicus* (Bassani 1886)  
Figure 2, 4

Taxa first described before 1973 that are referred to *Tanystropheus longobardicus* were also listed in the synonymy list of *T. longobardicus* of Wild (1973, p. 150-151). Here, an updated synonymy list is provided for both morphotypes of *T. longobardicus* separately:

**Small morphotype**

1886	<i>Tribelesodon longobardicus</i> Bassani, p. 25-29	1955	<i>Tanystropheus longobardicus</i> (partim) Peyer and Kuhn-Schnyder, p. 591-604; figures 17, 19, 24-25; plate 2-3
1890	<i>Tribelesodon</i> Zittel, p. 799	1956	<i>Tanystropheus longobardicus</i> (partim) von Huene, p. 648-650; figure 657
1922	<i>Tribelesodon longobardicus</i> von Arthaber, p. 6-7; figure 3	1959	<i>Tanystropheus longobardicus</i> (partim) Kuhn-Schnyder, throughout text; figures 6-9, 14-15
1923	<i>Tribelesodon longobardicus</i> Nopsca, throughout text; text-figures 1-4, 6	1967	<i>Tanystropheus longobardicus</i> (partim) Kuhn-Schnyder, plate 1
1925	<i>Tribelesodon longobardicus</i> Wiman, p. 3	1969	<i>Tribelesodon longobardicus</i> Kuhn, p. 71; figures 21-22
1926	<i>Tribelesodon longobardicus</i> Wiman, throughout text	1971	<i>Tanystropheus longobardicus</i> (partim) Kuhn, p. 11; figure 21
1930	<i>Tanystropheus longobardicus</i> (partim) Peyer, throughout text	1973	<i>Tanystropheus longobardicus</i> (partim) throughout text; text-figures 2-4, 7a, 8, 10a, 11c, 15-16, 20, 24, 26-27, 30, 71a, 81; plate 3, 5-6, 8, 17-18
1931	<i>Tanystropheus longobardicus</i> (partim) Peyer, throughout text; text-figures 3-23, 26; plate 1-4, 6-10, 11, figures 1-2, plate 13-14	1975	<i>Tanystropheus longobardicus</i> (partim) Wild, throughout text; figures 2-3, 6a
1934	<i>Tanystropheus longobardicus</i> (partim) Peyer, p. 259-260	1975	<i>Tanystropheus longobardicus</i> (partim) Cox, p. 655
1935	<i>Macroscelosaurus longobardicus</i> (partim) Kuhn, p. 119-120	1976	<i>Tanystropheus longobardicus</i> (partim) Wild, throughout text; figures 1-2, 6a
1937	<i>Tanystropheus longobardicus</i> (partim) Peyer, p. 97-105	1980a	<i>Tanystropheus meridensis</i> Wild, p. 5-12; text-figures 1-4, 5a; plate 1-3
1939	<i>Tanystropheus longobardicus</i> (partim) Peyer, throughout text	1980a	<i>Tanystropheus longobardicus</i> (partim) Wild, throughout text; figure 5b; plate 4-5, 6b
		1980b	<i>Tanystropheus longobardicus</i> (partim) Wild, throughout text
		1984	<i>Tanystropheus longobardicus</i> (partim) Wild and Oosterink, p. 146
		1985	<i>Tanystropheus longobardicus</i> (partim) Benton, p. 119, 122
		1986	<i>Tanystropheus meridensis</i> Tschanz, p. 97
		1986	<i>Tanystropheus longobardicus</i> (partim) Tschanz, throughout text; plate 1
		1987	<i>Tanystropheus longobardicus</i> (partim) Wild, throughout text
		1987	<i>Tanystropheus meridensis</i> Wild, throughout text
		1988	<i>Tanystropheus longobardicus</i> (partim) Tschanz, throughout text
		1988	<i>Tanystropheus longobardicus</i> (partim; synonymized with <i>T. conspicuus</i> ) Evans, p. 227
		1989	<i>Tanystropheus longobardicus</i> (partim) Taylor, throughout text
		1994	<i>Tanystropheus longobardicus</i> (partim) Renesto, p. 296, 298, 300
		1997	<i>Tanystropheus longobardicus</i> (partim) Benton and Allen, p. 945, 947, 950-951
		1997	<i>Tanystropheus meridensis</i> Benton and Allen, p. 945, 950

- 2000 *Tanystropheus longobardicus* (partim) Dalla Vecchia, p. 137
- 2001 *Tanystropheus longobardicus* (partim) Rieppel, throughout text
- 2001 *Tanystropheus meridensis* Rieppel, p. 276
- 2002 *Tanystropheus meridensis* Dalla Vecchia, p. 228
- 2003 *Tanystropheus longobardicus* (partim) Rieppel, Fraser, and Nosotti, p. 272, 276, 278, 285
- 2003 *Tanystropheus meridensis* Rieppel, Fraser, and Nosotti, throughout text
- 2004 *Tanystropheus longobardicus* (partim) Fraser, Nosotti, and Rieppel, throughout text
- 2004 *Tanystropheus meridensis* Fraser, Nosotti, and Rieppel, throughout text
- 2005 *Tanystropheus longobardicus* (partim) Dalla Vecchia, p. 31, 40-43
- 2005 *Tanystropheus meridensis* Dalla Vecchia, p. 41-43
- 2005 *Tanystropheus longobardicus* (partim) Renesto, p. 386
- 2005 *Tanystropheus meridensis* Renesto, p. 386-387
- 2006 *Tanystropheus longobardicus* (partim) Fraser and Rieppel, p. 866, 870
- 2006 *Tanystropheus meridensis* Fraser and Rieppel, p. 866
- 2007 *Tanystropheus longobardicus* (partim) Nosotti, throughout text; figures 1-29, 36-38, 40-41, 43-45, 48-53, 56, 58-60, 62, 64-65; plate 1-4
- 2007 *Tanystropheus meridensis* Nosotti, throughout text; figure 39
- 2008 *Tanystropheus longobardicus* (partim) Rieppel, Li, and Fraser, p. 95, 99
- 2010 *Tanystropheus longobardicus* (partim) Rieppel, Jiang, Fraser, Hao, Motani, Y-L Sun, and Z-Y Sun, throughout text
- 2010 *Tanystropheus meridensis* Rieppel, Jiang, Fraser, Hao, Motani, Y-L Sun, and Z-Y Sun, p. 1088
- 2010 *Tanystropheus longobardicus* (partim) Stockar, p. 104
- 2010 *Tanystropheus meridensis* Stockar, p. 104
- 2015 *Tanystropheus longobardicus* (partim) Pritchard, Turner, Nesbitt, Irmis, and Smith, throughout text; figures 14f, 15a
- 2015 *Tanystropheus longobardicus* (partim) Nesbitt, Flynn, Pritchard, Parrish, Ranivharimanana, Wyss, throughout text; figure 49d
- 2016 *Tanystropheus longobardicus* (partim) Ezcurra, throughout text
- 2017 *Tanystropheus longobardicus* (partim) Beardmore and Furrer, throughout text; figure 2
- 2017 *Tanystropheus longobardicus* (partim) Jaquier, Fraser, Furrer, and Scheyer, p. 26
- 2018 *Tanystropheus longobardicus* (partim) Renesto and Dalla Vecchia, p. 296-297
- 2018 *Tanystropheus longobardicus* (partim) Renesto and Saller, throughout text
- 2018 *Tanystropheus meridensis* Renesto and Saller, p. 23
- Large morphotype**
- 1930 *Tanystropheus longobardicus* (partim) Peyer, throughout text
- 1931 *Tanystropheus longobardicus* (partim) Peyer, p. 65-71, plate 11 figure 3, plate 12
- 1934 *Tanystropheus longobardicus* (partim) Peyer, p. 259-260
- 1935 *Macroscelosaurus longobardicus* (partim) Kuhn, p. 119-120
- 1937 *Tanystropheus longobardicus* (partim) Peyer, p. 97-105
- 1939 *Tanystropheus longobardicus* (partim) Peyer, throughout text
- 1955 *Tanystropheus longobardicus* (partim) Peyer and Kuhn-Schnyder, p. 591-604; figures 18, 22-23
- 1956 *Tanystropheus longobardicus* (partim) von Huene, p. 648-650; figure 657
- 1959 *Tanystropheus longobardicus* (partim) Kuhn-Schnyder, throughout text
- 1967 *Tanystropheus longobardicus* (partim) Kuhn-Schnyder, text-figure 3
- 1971 *Tanystropheus longobardicus* (partim) Kuhn, p. 11; figure 21
- 1973 *Tanystropheus longobardicus* (partim) Wild, plates, throughout text; text-figures 1, 5-6, 7b, 9, 10b, 14, 17-19, 21, 23f, 31, 35, 64, 66c, 68, 74, 101; plate 4, 9, 13-16
- 1975 *Tanystropheus longobardicus* (partim) Wild, throughout text; figure 6b
- 1975 *Tanystropheus longobardicus* (partim) Cox, p. 655
- 1976 *Tanystropheus longobardicus* (partim) Wild, throughout text; figures 4, 6b
- 1980a *Tanystropheus longobardicus* (partim) Wild, throughout text
- 1980b *Tanystropheus longobardicus* (partim) Wild, throughout text
- 1984 *Tanystropheus longobardicus* (partim) Wild and Oosterink, p. 146
- 1985 *Tanystropheus longobardicus* (partim) Benton, p. 119, 122

- 1986 *Tanystropheus longobardicus* (partim) Tschanz, throughout text, plate 2
- 1987 *Tanystropheus longobardicus* (partim) Wild, throughout text
- 1988 *Tanystropheus longobardicus* (partim) Tschanz, throughout text
- 1988 *Tanystropheus longobardicus* (partim; synonymized with *T. conspicuus*) Evans, p. 227
- 1989 *Tanystropheus longobardicus* (partim) Taylor, throughout text
- 1994 *Tanystropheus longobardicus* (partim) Renesto, p. 298
- 1997 *Tanystropheus longobardicus* (partim) Benton and Allen, p. 945, 947, 950-951
- 2000 *Tanystropheus longobardicus* (partim) Dalla Vecchia, p. 137-138
- 2002 *Tanystropheus longobardicus* Dalla Vecchia, p. 228
- 2003 *Tanystropheus longobardicus* (partim) Rieppel, Fraser, and Nosotti, throughout text
- 2004 *Tanystropheus longobardicus* (partim) Fraser, Nosotti, and Rieppel, throughout text
- 2005 *Tanystropheus longobardicus* (partim) Dalla Vecchia, p. 31, 40-43
- 2005 *Tanystropheus longobardicus* (partim) Renesto, p. 386
- 2006 *Tanystropheus longobardicus* (partim) Fraser and Rieppel, p. 866, 870
- 2007 *Tanystropheus longobardicus* (partim) Nosotti, throughout text; figures 42, 47, 55
- 2008 *Tanystropheus longobardicus* (partim) Rieppel, Li, and Fraser, p. 95, 99
- 2010 *Tanystropheus longobardicus* (partim) Rieppel, Jiang, Fraser, Hao, Motani, Y-L Sun, and Z-Y Sun, throughout text; figure 2
- 2010 *Tanystropheus longobardicus* (partim) Stockar, p. 104
- 2015 *Tanystropheus longobardicus* (partim) Pritchard, Turner, Nesbitt, Irmas, and Smith, throughout text
- 2015 *Tanystropheus longobardicus* (partim) Nesbitt, Flynn, Pritchard, Parrish, Ranivharimanana, Wyss, throughout text
- 2016 *Tanystropheus longobardicus* (partim) Ezcurra, throughout text; figures 15c, 30
- 2017 *Tanystropheus longobardicus* (partim) Beardmore and Furrer, throughout text; figure 1
- 2017 *Tanystropheus longobardicus* (partim) Jaquier, Fraser, Furrer, and Scheyer, p. 26
- 2018 *Tanystropheus longobardicus* (partim) Renesto and Dalla Vecchia, p. 296-297
- 2018 *Tanystropheus longobardicus* (partim) Renesto and Saller, throughout text

**Neotype.** PIMUZ T 2791 (small morphotype), a strongly compressed and almost completely articulated specimen missing the posterior part of the tail.

**Referred specimens.** Small morphotype: PIMUZ T 2779, PIMUZ T 2781, PIMUZ T 2795, PIMUZ T 2485, PIMUZ T 2482, PIMUZ T 2484, PIMUZ T 3901, PIMUZ T 1277, MSNM BES SC 265, MSNM BES SC 1018.

Large morphotype: PIMUZ T 2787, PIMUZ T 2793, PIMUZ T 2790, PIMUZ T 2818, PIMUZ T 2819, PIMUZ T 183, SNSB-BSPG 1953 XV 2, MSNM V 3663.

**Localities and occurrence.** The Besano Formation (Anisian-Ladinian boundary, Middle Triassic) and Meride Limestone (Cassina beds, Ladinian, Middle Triassic) of Monte San Giorgio, the border of Switzerland (canton Ticino) and Italy (Lombardy) (Stockar, 2010).

**Previous diagnosis.** The most recent diagnosis of *Tanystropheus longobardicus* was provided in Ezcurra (2016, p. 25). Based on the set of characters treated therein, *T. longobardicus* was distinguished based on the following 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 too[t]h 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.”

Another important diagnosis was provided in Wild (1973, p. 148), in which *Tanystropheus longobardicus* was diagnosed based on the following combination of characters (translated from German): “Up to five or possibly six metres long lacertilian with a relatively small and lightly built skull with two temporal openings. Elongate nares positioned close to the midline of the skull. Relatively large orbits. Lacertilian-like palate with infraorbital fenestrae and interpterygoid, posteromedial, and posterolateral openings. Presence of a posttemporal fenestra. A streptostylic quadrate, movable(?) basiptyergoid joint, and metakinetic skull. Triradiate jugal. Squamosal similarly shaped as in modern lacertilians. Quadratojugal and most likely postpari-

etal absent. Small rod-shaped supratemporal present. Maxilla with 12 to 14 teeth, which in juveniles are tricuspid in the posterior part of the jaw. Pre-maxilla with five or six monocuspid teeth. Vomer with 12 monocuspid teeth, palatine and pterygoid only in the juvenile stage with shagreen-like teeth, of which four to six are present on the former. Lower jaw with a ventral flange anteriorly and 17 to 20(?) teeth. Twelve cervical vertebrae, of which nine are extremely elongated. The ninth cervical is generally the longest. Atlas with paired pro-atlases and a separate atlas intercentrum. Eleven dorsal, two lumbar, two sacral, and approximately 46 caudal vertebrae. In the caudal vertebrae, the 13<sup>th</sup>(?) or 14<sup>th</sup> provides the possibility of autotomy. Cervical ribs, already occurring at the atlas and axis, are more than double the length of their associated vertebrae, particularly those of the mid-cervical region, and are pseudo-holocephalous. Anterior dorsal ribs dichoccephalous, middle and posterior dorsal ribs holocephalous. The capitulum is reduced in the posterior dorsal ribs. Gastral ribs each consisting of four elements, of which the two medial elements are angled at their tip. Forked chevrons positioned intervertebrally and occurring from the first(?) until approximately the 25<sup>th</sup> caudal vertebra. Pectoral girdle with a broad scapula and a broad coracoid pierced by a coracoid foramen, rhombic and long-stalked interclavicle, and a clasp-shaped clavicle. Short and strong humerus with an entepicondylar groove. Radius stronger and more curved than ulna. Four carpal elements present. Manual phalangeal formula of 2-3-4-4-3. Terminal phalanges formed by claws. Pelvic girdle consisting of a small ilium and wide ischium and pubis. Pubis bearing an obturator foramen. Femur typical lacertilian, sigmoidal. Tibia stronger and more curved than fibula. Astragalus weakly L-shaped and calcaneum disc-shaped with a foramen in between the two elements. Two distal tarsals present. Hooked fifth metatarsal. Foot adapted to swimming with age. Pedal phalangeal formula: 2-3-4-5-4. First phalanx of digit five elongated. Terminal phalanges forming powerful claws.”

**Emended diagnosis.** Large-sized tanystropeid distinguished by the following combination of characters (autapomorphies among non-archosauriform archosauromorphs marked with an asterisk): 1) presence of tricuspid teeth on the maxilla and dentary (small specimens only); 2) fang-like anterior marginal dentition; 3) mid cervical vertebrae with a maximum length to height ratio larger than 15\*; 4) presence of 13 cervical vertebrae\*; 5) presence of heterotopic bones in approximately 50% of

the known specimens preserving an articulated pelvic region.

**Remarks.** Based on the findings in this study, the two morphotypes of *Tanystropeus longobardicus* that have previously been acknowledged (e.g., Wild, 1973; Fraser et al., 2004; Nosotti, 2007), can be clearly distinguished from each other based on traits summarized in Table 2. Although it is unclear whether the two represent different species or distinct ontogenetic stages of the same species, a synonymy list and specimen list is provided for both morphotypes. We are providing these separate lists as we find it important to distinguish between the two morphotypes in future comparative studies, for instance for use in phylogenetic analyses, due to the cranial discrepancy between the two.

*Tanystropeus cf. T. longobardicus*

**Referred specimens.** Small morphotype: MCSN 4451, PIMUZ T 2780, PIMUZ T 2789, PIMUZ T 2481, MSNM V 3730.

Large morphotype: PIMUZ T 2817, PIMUZ T 2483, PIMUZ T 2480, PIMUZ T 1270, PIMUZ T 1307, PIMUZ T 2794, PIMUZ T 2788, GMPKU-P-1527, MSNM BES 351.

**Localities and occurrence.** Small morphotype: The Besano Formation and the Cava Inferiore beds of the Meride Limestone of Monte San Giorgio on the border of Switzerland and Italy (Wild, 1973; Renesto, 2005; Stockar, 2010).

Large morphotype: The Besano Formation of Monte San Giorgio, the border of Switzerland and Italy (Wild 1973; Stockar 2010), and the upper part of the Zhuganpo Member of Falang Formation of Heshangsi of Nimaigu Village, Wusha District, Xingyi City, Guizhou Province, southwestern China.

**Remarks.** Various articulated specimens of *Tanystropeus* have been found that are indistinguishable from *T. longobardicus* but that do not preserve cranial material. Thus, these specimens cannot be assigned to either morphotype. However, for this list we distinguish between these specimens based on their size. If both morphotypes represent two different species, it can of course not be excluded that smaller specimens represent juvenile forms of the large morphotype.

*Tanystropeus haasi* (Rieppel 2001) Figure 7

- |      |  |
|------|--|
| 1955 | <i>Tanystropeus</i> sp. Peyer, p. 488-490; figure 3        |
| 1956 | <i>Tanystropeus/Tanystropheus</i> sp. Brotzen, p. 199, 208 |
| 1973 | <i>Tanystropeus</i> sp. Wild, p. 152                       |

- 2001 *Tanystropheus haasi* Rieppel, throughout text; figures 1-2, 4a  
 2005 *Tanystropheus haasi* Dalla Vecchia, p. 41-43  
 2018 *Tanystropheus haasi* Renesto and Saller, p. 23

**Referred specimens.** See Supplementary Table 1  
**Localities and occurrence.** Makhtesh Ramon (Anisian to Ladinian), Negev Desert, Israel

**Previous diagnosis.** The diagnosis for *Tanystropheus haasi* was provided in Rieppel (2001): “A species of the genus *Tanystropheus* which is diagnosed by a deep groove separating the centrum from the neural arch at the posterior end of the vertebrae of the middle cervical region (cv 6 through 8); margins of the postzygapophyseal articular facets distinctly thickened; posterior margin of the postzygapophyseal trough forming a straight transverse line in its middle portion, located above the dorsal margin of the posterior articular surface; neural spine forming a long (one third of the length of the postzygapophyseal process), pointed posterior process which projects into the postzygapophyseal trough.”

**Remarks.** *Tanystropheus haasi* is represented by fragmentary isolated cervical vertebrae. Detailed comparison with other isolated cervical vertebrae from Bindlacher Berg assigned to *T. conspicuus* reveals that most of the characters considered diagnostic for *T. haasi* (Rieppel, 2001) fall within the range of variation seen within the *T. conspicuus* material. This highlights that the morphology of the cervical vertebrae is highly variable depending on their relative position in the vertebral column and intraspecific variation and isolated cervical vertebrae are therefore problematic for species assignment within the genus *Tanystropheus*. Although the referred material of *T. haasi* possibly differs from the Bindlacher Berg specimens assigned to *T. conspicuus* in bearing a particularly deepened horizontal groove dorsal to the posterior end of the centrum and the presence of a distinctly expanded posterior end of the neural spine, we do not deem these minor differences from other *Tanystropheus* taxa sufficient for an assignment to a separate species. Therefore we consider *T. haasi* a nomen dubium since the referred material is not diagnostic.

*Tanystropheus* sp.

**Referred specimens.** See Supplementary Table 1  
**Localities and occurrence.** See Supplementary Table 1

**Remarks.** These specimens identified as *Tanystropheus* sp. include fragmented and isolated speci-

mens that do not possess diagnostic features for assignment to any of the known species of the genus.

*Sclerostropheus* gen. nov. Figure 8

zoobank.org/55B551F2-87D1-4A8C-92E8-5D751A7DF804

- 1980 *Tanystropheus fossai* Wild, p. 14-15, figure 11, plate 6e  
 1987 *Tanystropheus fossai* Wild, p. 39, 42  
 1994 *Tanystropheus fossai* Renesto, p. 296  
 1997 *Tanystropheus fossai* Benton and Allen, p. 945, 947  
 2000 *Tanystropheus fossai* Dalla Vecchia, p. 139-140  
 2001 *Tanystropheus fossai* Rieppel, p. 273, 276  
 2002 *Tanystropheus fossai* Dalla Vecchia, p. 228  
 2005 *Tanystropheus fossai* Dalla Vecchia, p. 41-43  
 2005 *Tanystropheus fossai* Renesto, p. 386  
 2007 *Tanystropheus fossai* Nosotti, p. 5  
 2015 *Tanystropheus fossai* Pritchard, Turner, Nesbitt, Irmis, and Smith, p. 15-16  
 2018 *Tanystropheus fossai* Renesto and Dalla Vecchia, p. 297  
 2018 *Tanystropheus fossai* Renesto and Saller, p. 23

**Etymology.** *Sclerostropheus* is a combination of the Ancient Greek words *skleros*, meaning ‘hard’ or ‘hardened’, and *stropheus* meaning ‘joint’. The name refers to the ossified tendons present in the cervical column of *Sclerostropheus* and the stiffened cervical column that is typical of tanystropheids due to their strongly elongated vertebrae and ribs.

**Diagnosis.** Long-necked tanystropheid differentiated from other tanystropheids by the following combination of characters (autapomorphies among non-archosauriform archosauromorphs marked with an asterisk): 1) complete absence of a neural spine in mid-cervical vertebrae\*; 2) the presence of two distinct lamina running along each lateral side of the mid-cervical vertebral centra that are most pronounced at the ends of the centrum\*; and 3) the presence of an elongate anterior free-ending process of the anterior to mid-cervical ribs, protruding far anteriorly beyond the anterior extent of its corresponding vertebra.

**Remarks.** In addition to the traits indicated in the diagnosis, MCSNB 4035 also bears bifurcating cervical ribs. However, this likely represents a pathological malformation and it is therefore not included in the diagnosis. *Sclerostropheus fossai* is currently poorly known from a single specimen consti-

tuting a few mid-cervical vertebrae and associated ribs. Nevertheless, considering the known taxonomic diversity of Tanystropheidae, we deem the taxon to be morphologically distinct from other taxa attributed to the genus *Tanystropheus* and therefore reassign it to a new, separate genus. Together with *Langobardisaurus pandolfii* and *Tanytrachelos ahynis*, *S. fossai* currently represents the third known Late Triassic tanystropheid taxon (Olsen, 1979; Renesto, 1994; Renesto and Dalla Vecchia, 2000, 2007).

**Type species.** *Sclerostropheus fossai* (Wild 1980) gen. nov.

**Holotype.** MCSNB 4035, four articulated cervical vertebrae and associated cervical ribs.

**Locality and occurrence.** N-slope of Canto Alto near the village of Poscante in Val Brembana, Bergamo, part of the Argillite di Riva di Solto (late Norian, Late Triassic; Rigo et al., 2009; Tackett and Tintori, 2019).

**Diagnosis.** Same as for the genus.

Tanystropheidae indet.

**Referred specimens.** GIM L53 Vert. II and BSPG As I 779

**Localities and occurrence.** See Supplementary Table 1

**Remarks.** These specimens are considered insufficient for assignment on the genus level but bear characteristics that link them to the tanystropheid clade.

## DISCUSSION

### Relation to Other Tanystropheid Taxa

In recent years the known diversity of tanystropheids has increased substantially with the discovery of new species assigned to new genera; e.g., *Amotosaurus rotfeldensis*, *Langobardisaurus pandolfii*, and *Augustaburiania vatagini*, *Dinocephalosaurus orientalis*, and *Fuyuansaurus acutirostris* (Renesto, 1994; Li, 2003; Fraser and Rieppel, 2006; Sennikov, 2011; Fraser et al., 2013); and new species of previously established genera; e.g., *Macrocnemus obristi* and *Macrocnemus fuyuanensis* (Li et al., 2007; Jiang et al., 2011; Fraser and Furrer, 2013; Jaquier et al., 2017); as well as isolated remains that can very likely be attributed to the clade; e.g., the Hayden Quarry tanystropheid material (Pritchard et al., 2015) and the isolated cervical vertebrae from the Sanga do Cabral Formation (De Oliveira et al., 2018), indicating that strongly elongated cervical vertebrae occurred in a more diverse set of early archosauromorphs than previously appreciated. Therefore, the assignment

of *Tanystropheus antiquus* to the genus *Tanystropheus* should be reconsidered taking specifically into consideration the cervical morphology of other tanystropheid taxa not assigned to the genus *Tanystropheus*. For instance, the relative elongation of cervical vertebrae attributed to *Augustaburiania vatagini* is much larger (ratio centrum length/minimum height: 8.79, based on PIN, no. 1043/1392 from Sennikov (2011, figure 3h) than that of *T. antiquus* (less than three sensu Fraser and Rieppel, 2006). *Au. vatagini* is also similar to *Tanystropheus* spp. in the shape and size of the postzygapophyses and the presence of a low neural spine, but differs in having a distinctly curved ventral margin of the centrum. However, our results indicate that morphological characters of isolated cervical vertebrae should be considered carefully before being applied to distinguish taxa, as their morphology varies strongly within a single taxon due to variation throughout the cervical column and intraspecific variation. Much variation occurs in the degree of curvature of the ventral margin of the centrum in the cervical vertebrae attributed to *Au. vatagini*, which should therefore be evaluated critically in order to verify the assignment of the material to a taxon separate from the known *Tanystropheus* species (Sennikov, 2011). *Am. rotfeldensis*, which has cervical vertebrae with a relative elongation close to that seen in *T. antiquus*, is known from more comprehensive and articulated material and can be distinguished from *Tanystropheus* species based on various characters, including the total number of cervical vertebrae (which, due to the isolated nature of the material, cannot be confidently established for *T. antiquus* nor *Au. vatagini*), the tarsal morphology, and the palatal dentition (Fraser and Rieppel, 2006). Therefore, its assignment to a separate genus is justified. Unfortunately, detailed comparison of the cervical vertebrae of *Am. rotfeldensis* to those assigned to *T. antiquus* is problematic, since the known *Am. rotfeldensis* vertebrae are all strongly flattened, and their poor preservation severely hampers the observation of many characters.

### Biogeographical Implications

Our findings show that currently two species of *Tanystropheus* can be distinguished: *T. longobardicus* and *T. antiquus*, with the former being divided into two distinct morphotypes and with “*T. conspicuus*” and “*T. haasi*” considered as nomina dubia. Furthermore *T. antiquus* and its taxonomic affinities are currently under revision (Skawiński et al., 2017). Therefore, the taxonomic diversity of the

genus is reduced compared to the six different *Tanystropheus* species previously acknowledged. However, the two distinct morphotypes of *T. longobardicus* and the presence of different morphotypes of *Tanystropheus* at Makhtesh Ramon in Israel provide a good indication that the genus was more speciose, but they can currently not be assigned to a valid species.

The genus *Tanystropheus* is largely known from the Triassic Tethys coastal regions, with numerous occurrences in the western Tethys region (much of Europe, Saudi Arabia, and Israel), as well as the Germanic basin connecting to the Tethys on its northwestern margin (e.g., Hagdorn and Rieppel, 1999; Feist-Burkhardt et al., 2008), and two known occurrences in the eastern Tethys (southern China) (Figure 1). The possible exception is the only known North American specimen attributed to the genus, YPM VPPU 022000 (Sues and Olsen, 2015). The specimen appears morphologically very similar to the large morphotype of *T. longobardicus*, as well as to the material attributed to “*T. conspicuus*” and “*T. haasi*”, and originates from the Wolfville Formation of Carrs Brook, Nova Scotia, Canada, which is part of the Fundy basin (Sues and Olsen, 2015). This basin was, at least during certain periods in the Triassic, connected to the Germanic basin and Tethys Ocean (Leleu and Hartley, 2010). Therefore, it is reasonable to assume that *Tanystropheus* spp. had a Tethys-wide occurrence, including extensions into connected shallow marine basins in the northern hemisphere. YPM VPPU 022000 is also of interest as it represents the only known occurrence of the genus in non-marine sediments, since the Economy Member of the Wolfville Formation comprises fluvial sandstones with occasional aeolian dune deposits (Leleu and Hartley, 2010; Sues and Olsen, 2015). This indicates that, at least in the Fundy Basin, the genus also occurred in fresh water lake or river environments. In this regard it is important to consider that, in contrast to the viviparous *Dinocephalosaurus orientalis* (Liu et al., 2017), it is possible that *Tanystropheus* spp. had to venture on land for oviposition.

The reassignment of *Sclerostropheus fossai* from the late Norian of northern Italy to a new genus drastically reduces the temporal distribution of the genus *Tanystropheus*, which is now mainly known from the Anisian and Ladinian (Middle Triassic), with some specimens also occurring in the earliest Carnian (*T. cf. T. longobardicus* and *Tanystropheus* sp. from the Falang Formation, and *Tanystropheus* sp. from layer E of the Fusea site of

northern Italy and possibly the Wolfville Formation), and possibly in the latest Olenekian (*T. antiquus*).

## CONCLUSIONS

We reviewed and revised in detail the material attributed to the genus *Tanystropheus*, with a focus on the material from Monte San Giorgio and the specimens previously referred to *T. conspicuus*, *T. haasi*, and *T. fossai*. Based on a large disparity in cranial morphology, we find that *T. longobardicus* can be distinguished into a small and a large morphotype. These morphotypes could represent two different species rather than different ontogenetic stages of the same species as was previously suggested (e.g., Wild, 1973). However, the lack of an overlapping size range between the two morphotypes precludes an unambiguous conclusion based on our morphological comparison and further research including histological sectioning and microtomographic scans are required to establish with certainty whether the two morphotypes represent separate species. PIMUZ T 3901, previously the holotype and only known specimen of *T. meridensis*, is indistinguishable from the small morphotype of *T. longobardicus*, and, therefore, *T. meridensis* is established as a junior synonym of *T. longobardicus*. Furthermore, we found that the morphology of cervical vertebrae of *Tanystropheus* spp. exhibits much intraspecific variation, which is in part related to the position of the vertebra in the cervical column. A detailed comparison of cervical vertebrae assigned to *T. conspicuus*, *T. haasi*, and the large morphotype of *T. longobardicus* reveals that insufficient characters separate these specimens morphologically to merit assignment to a separate species. Because the material assigned to *T. conspicuus* and *T. haasi* is (largely) represented by (partial) cervical vertebrae, we consider these two species to represent nomina dubia. MCSNB 4035, the only known specimen previously assigned to *T. fossai*, is considered to differ distinctly from other *Tanystropheus* species and is therefore reassigned to a new genus: *Sclerostropheus*.

The known diversity of the genus *Tanystropheus* is reduced from six to two species. Nevertheless, the genus was likely more speciose based on fragmentary material that cannot be diagnosed confidently currently, as well as the presence of two morphotypes of *T. longobardicus* that might represent separate species rather than an ontogenetic series of a single species.

These findings result in new biogeographical considerations, with the genus largely being restricted temporally between the latest Olenekian or earliest Anisian and the earliest Carnian (latest Early Triassic to earliest Late Triassic), and extending spatially between the eastern and western Tethys, as well as the Germanic and Fundy basins (Figure 1). Furthermore, our study highlights the difficulty of differentiating closely related tetrapod species based on isolated material. This is particularly the case for vertebrae, as these elements are shown to exhibit much intraspecific variation, in part related to the relative position of each element in the vertebral column.

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## APPENDICES

**SUPPLEMENTARY TABLE 1.** Overview of all the known *Tanystropheus* specimens, including their original and revised taxonomic assignment, occurrence, age, specimen information, and references (available at <https://palaeo-electronica.org/content/2019/2870-revision-of-tanystropheus>).

**SUPPLEMENTARY TABLE 2.** Overview of the morphological variation present in the cervical vertebrae of *Tanystropheus conspicuus* from the Upper Muschelkalk of Bindlach, Germany (available at <https://palaeo-electronica.org/content/2019/2870-revision-of-tanystropheus>).