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EVIDENCES FOR A SEMI AQUATIC LIFE STYLE IN THE TRIASSIC DIAPSID REPTILE *TANYSTROPHEUS*

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Abstract. The paleoecology of the bizarre, long-necked tanystropheid diapsid *Tanystropheus* from the Middle and Late Triassic of Western and Eastern Tethys has been debated since the first discoveries. In the present work, osteological features related with gait and locomotion are reanalysed, and a reconstruction of the pattern of the musculature of the tail, pelvic girdle and hindlimb is proposed. The anatomical correlates, along with the inferred functional interpretation of the musculature support the hypothesis that 1) *Tanystropheus* was able to lift the body off the substrate when on land, 2) it lacked adaptations for continuous swimming, either tail-based or limb-based, 3) it was able to swim for by rowing with symmetrical strokes of the hind limbs. Rowing is a discontinuous swimming pattern that occurs in animals with a semi-aquatic life style which return frequently to emerged land, thus the proposed model is consistent with the hypothesis that *Tanystropheus* was a shoreline dweller rather than a fully aquatic animal.

INTRODUCTION

The Tanystropheidae are a clade of bizarre archosauromorph diapsids from the Middle and Late Triassic (see Pritchard et al. 2015 and references therein) that are characterized mainly by a long and rather stiff neck, made by eight (*Macrocnemus*) to thirteen (*Tanystropheus*) elongate cervical vertebrae, depending on the taxon. The elongate cervical vertebrae had low neural spines and long, rod-like ribs that run parallel to the ventral margin of the centra. Tanystropheids were firstly included in the Prolacertiformes, then in the Protorosauria, but these clades are now considered as paraphyletic in recent phylogenetic hypotheses (Pritchard et al. 2015; Ezcurra 2016). The clade Tanystropheidae comprise the genera *Macrocnemus, Tanystropheus, Amotosaurus, Langobardisaurus* and *Tanytrachelos* (Pritchard et al. 2015). *Macrocnemus* and *Langobardisaurus* are supposed to have been terrestrial animals, possibly facultative bipedal runners (Rieppel 1989; Renesto et al. 2002). Other genera, like the very small (about 20 cm long) *Tanytrachelos ahynis* (Olsen 1979) have been considered as aquatic, living in freshwater environments. The life style of *Tanystropheus,* the largest and most bizarre of all tanystropheids, remained uncertain since its discovery.

Tanystropheus is mostly known based on the Middle Triassic species *Tanystropheus longobardicus* of northern Italy, southern Switzerland and *Tanystropheus conspicuus* of Central Europe (Peyer 1931; Wild 1973; Nosotti 2007). *Tanystropheus meridensis* (Wild 1980a) is known from a single specimen consisting of a skull and partial neck, but it may be a small individual of *T. longobardicus* (Fraser & Rieppel 2006). Remains from the Middle East (Rieppel 2001) have been attributed to a different species, *T. haasi*. Also nearly complete skeletons from China (Li 2007; Rieppel et al. 2010) are virtually undistinguishable from *T. longobardicus,* according to their describers. Isolated *Tanystropheus* remains are also reported from the Middle Triassic of North America (Sues & Olsen 2015); some isolated cervical vertebrae from the Norian (Late Triassic) of Northern Italy have also been assigned to *Tanystropheus* (*T. fossai* Wild 1980 a, b; *Tanystropheus* sp. Dalla Vecchia 2000).

Even if the genus comprises species of different size, all shared the same body architecture (Fig. 1).

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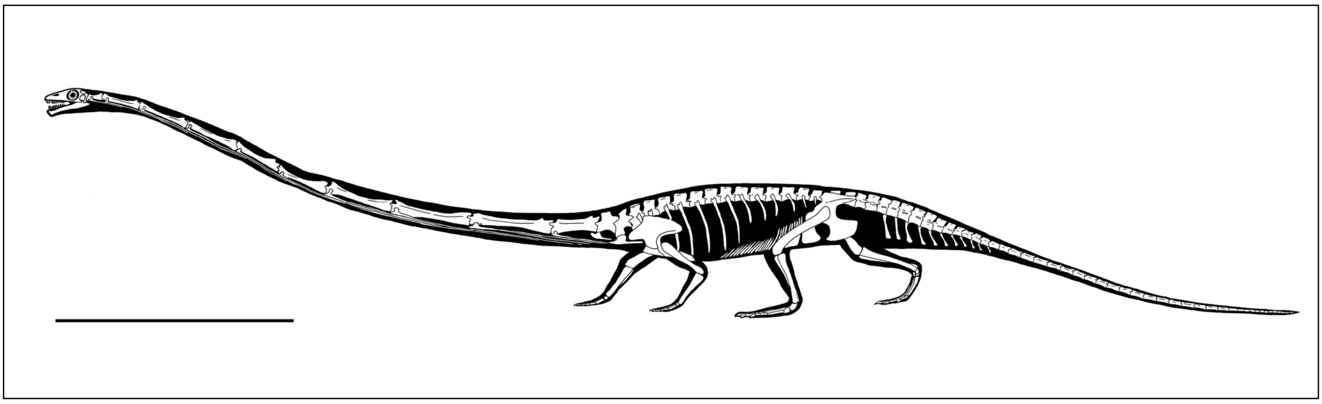


Fig. 1 - Reconstruction of the skeleton of a large specimen of *Tanystropheus longobardicus* in walking posture. Scale bar equals 1m.

PREVIOUS STUDIES

In *Tanystropheus,* the elongation of the neck, which consists of 13 cervical vertebrae (Rieppel et al 2015), is extreme, since it could equal the length of the rest of the body, tail included (Peyer 1931; Wild 1973; Cox 1975; Tschanz 1986, 1988; Bürgin et al. 1989; Li et al. 2004; Fraser & Rieppel 2006). This peculiar structure, along with the impressive overall size (the largest individuals of *T. longobardicus* reached up to five meters in length) rendered the animal rather weird in appearance and a palaeoecological and functional enigma. Excluding earlier intepretations as a flying reptile, based on isolated elements (Nopcsa 1923), the first reconstructions (e.g. Peyer 1931) depicted *Tanystropheus* as a terrestrial, lizard-like animal, with a sprawling gait and a somewhat laterally flexible neck kept close to the ground. Instead, Wild (1973) proposed that *Tanystropheus* could have raised the neck off the substrate to a great extent, in a giraffe-like fashion and that the individuals shifted habitat during ontogeny: the juveniles were terrestrial insectivores, while the adults were aquatic predators.

Subsequent studies (e. g. Tschanz 1986, 1988) concluded that T*anystropheus* lacked an adequate dorsal musculature to keep the neck raised off the substrate as proposed by Wild, and that the elongated cervical ribs significantly stiffened the neck, thus preventing lateral flexion and vertical bending. In addition, the ribs granted adequate support (by transmitting the weight to the shoulder and anterior limbs) only if the neck was held in horizontal position. According to Tschanz's reconstruction, the stiff, rod-like neck of *Tanystropheus* was a hindrance in a terrestrial environment and consequently a fully aquatic life-style was proposed. According to Tschanz (1986, 1988), Rieppel (1989), and Nosotti (2007), *Tanystropheus* lived in the sea and swam by lateral undulations of the trunk and tail.

A different interpetation was proposed by Renesto (2005), who suggested that *Tanystropheus* may have been a semi-aquatic reptile, that lived in a shoreline habitat. The hollow cervical centra, which housed the neural canal (Wild 1973), and the relative flexibility of the thin cervical ribs may have allowed the neck to be kept off the substrate to some extent when the animal walked on land (Fig. 1A). In addition, the presence of large muscles at the base of the tail may have shifted back the centre of mass, helping to balance the body even with the neck slightly raised. Renesto (2005) also pointed out that *Tanystropheus* lacked adaptations for continuous swimming, both in the limbs and in the tail.

Rieppel et al. (2010: 1086, fig. 3) discovered also that the thirteenth cervical vertebra of *Tanystropheus* (previously considered as the first dorsal) is modified and may have allowed some raising of the neck, as already suggested by Renesto (2005), based on the slanting posterior surface of the centrum of the twelfth cervical vertebra.

Recently, Beardmore and Furrer (2017) compared the skeletal taphonomy of *Tanystropheus* with that of terrestrial and aquatic genera from the same deposits and concluded that the "carcasses of *Tanystropheus* originated in terrestrial or at least marginal and near-shore, shallow marine settings" (Beardmore & Furrer 2017, p. 1).

AIM OF THE PRESENT WORK

The presence of hooklets from belemnoid cephalopods in the stomach region of one specimen (Wild 1974), was cited as a further evidence for life in an open marine environment. This latter assumption however does not take into account that there is a great variety of extant decapodiform cephalopods (e. g. suborder Myopsida) that live in shallow waters (Bartol et al 2001; Anderson 2000) or reach shallow waters to spawn (Arkhipkin et al. 2004; Hatfield et al. 1990). Thus, evidence of cephalopod remains in the stomach region of a single, or few, *Tanystropheus* specimen does not necessarily support an open-marine life style, but it may suggest that *Tanystropheus* may have lived at the shoreline and fed on aquatic animals in shallow waters. The neck of *Tanystropheus,* however is different from that of herons or other wading birds, lacking of the powerful ventral muscles for head projection present in those birds and it could not have been used to dart at preys from a S-shaped starting position. Thus, its hunting strategy and feeding mechanics must have been different.

In the present work, a re-analysis of the osteology of *Tanystropheus* has been carried out. The study focused mostly on the post-dorsal sections of the vertebral column, on the pelvis and hind limb; the pattern of hindlimb and caudal musculature has been reconstructed and a model for *Tanystropheus* locomotion is proposed, which is consistent both with feeding on aquatic prey and with an semi aquatic life-style in a littoral environment.

ANATOMICAL DESCRIPTION

Skeletal correlates

Several detailed descriptions of *Tanystropheus* have been published (Peyer 1931; Wild 1973; Renesto 2005; Nosotti 2007; Rieppel et al. 2010) thus only the osteological features relevant to the present study will be reported here. Reanalysis of *Tanystropheus* osteology has been based mainly on specimen MCSN 4451 of the Museo Cantonale di Storia Naturale di Lugano (Switzerland), already described by Renesto (2005), and specimen T2917 of the Palaeontologisches Institut und Museum Universität Zürich (Switzerland) on the basis of an extremely accurate resin cast.

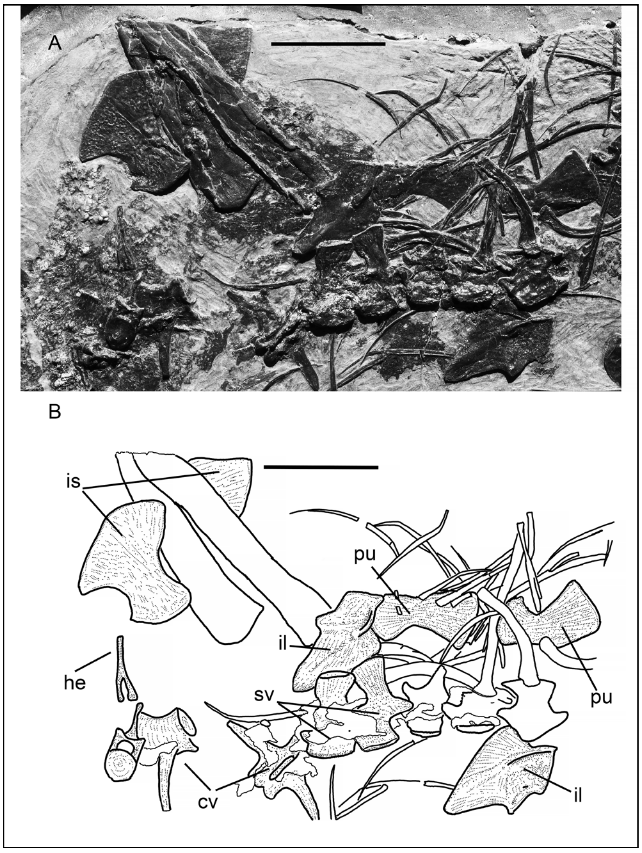


Fig. 2 - *Tanystropheus longobardicus*, specimen MCSN 4451 A) Sacral region and base of the tail; B) interpretative drawing. Abbreviations in (B) are: cv, caudal vertebrae he, haemal spine; il, ilium, is, ischium, pu, pubis, sv sacral vertebrae. Scale bar equals 30 mm.

Vertebral column. The centra of the dorsal vertebrae (Fig. 2) are hourglass shaped, laterally and ventrally constricted, and their anterior and posterior articular surfaces are vertically oriented. The articular facet for the tuberculum of the rib is rounded, and located on the lateral tip of a short, stout transverse process that projects laterally from the anterior part of the vertebra shortly behind the prezygapophysis. No trace of a neurocentral suture is present. The neural spines are rectangular in outline, and increase slightly in height towards the posterior region of the trunk. The pre- and postzygapophyses are distinct, and at least in the posterior-most dorsal vertebrae, their articular surface is more or less horizontally oriented. As in other tanystropheids, the dorsal margin of the neural spines is expanded at its top, forming a small "table".

There are two robust sacral vertebrae (Fig. 2); their centra are similar to those of the dorsal ones, being laterally and ventrally constricted. The pleurapophyses are fused with the vertebrae, and distinctly expanded laterally. The proximo-distal axis of the pleurapophyses of the second sacral vertebra are bent anteriorly so that they meet those of the first sacral vertebra, stiffening the sacral region. Neural

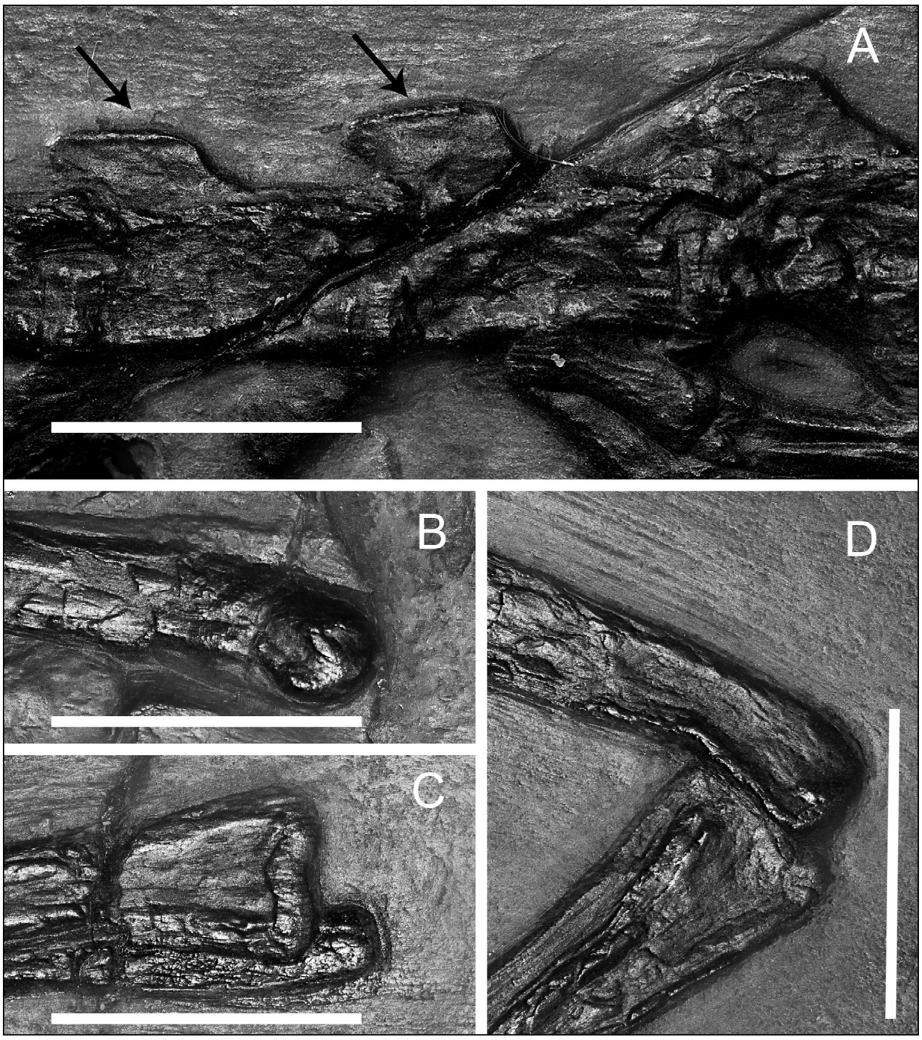


Fig. 3 - A) *Tanystropheus longobardicus* specimen T2197 (cast). (A) Mid caudal vertebrae, arrows point to expanded tips of the neural spines; B) distal articular area of the right femur; C) proximal articular area of the right tibia and fibula; D) left knee joint with bones in anatomical connection. Scale bars equal 10 mm.

spines are longer than high, subrectangular in lateral view and distinctly expanded at their dorsal tip.

The caudal vertebrae also have laterally and ventrally constricted centra (Figs 2-3). The pre- and postzygapophyses are connected by a distinct crest from which projects a laterally extending pleurapophysis. The first caudal vertebra has the same size and shape of the sacral vertebrae and bears two stout pleurapophyses that project laterally and slightly caudally, in the second caudal vertebra the pleurapophyses are longer than those borne by the first caudal vertebra, and their axis slants slightly forward. The pleurapophyses decrease gradually in size virtually disappearing after the eighth caudal vertebra. The size of the neural spines decreases rather quickly and they slant posteriorly so that at the level of the 10-11th caudal vertebra they are reduced to small projections between the postzygapophyses. Haemal spines are intercentral and Y shaped, their size also decreases along the caudal series so that at the level of the 11-12th caudal centra they reach half the length of the first ones. Pritchard et al (2015) report that "caudal spinous expansions" are visible at least in one *T. longobardicus* specimen (MCSN BES SC 1018, Nosotti 2007); similar expansions are visible also on the neural spines of the caudal vertebrae of specimen T2975 (Fig. 4), thus it is feasible that also the neural spines of the first caudal vertebrae of *Tanystropheus* had slightly expanded dorsal margins like the dorsal and sacral ones.

*Pelvic girdle***.** The ilium forms a well-expanded, posteriorly elongate dorsal blade and a thick ridge of bone hangs over the anterodorsal portion of the acetabular area. The pubis is a stout bone with convex anterior margin and concave posterior one, surrounding anteriorly the wide, oval thyroid fenestra. A small obturator foramen is present anteroventral to the acetabular facet. The ventral part of the pubis is slightly expanded but does not contact the anteroventral margin of the ischium, thus the thyroid fenestra is ventrally open. The ischium shows a thick acetabular area, then ventrally is present a constricted 'neck' area, followed by a thinner but expanded ventral plate with gently convex ventral (medial) and posterior margin.

Hind limb. The hind limb is much longer than the fore limb: the length of the whole hind limb is approximately 1.6 times that of the fore limb, and the length of the metatarsus and pes is about 2.3-2.5 times that of the metacarpus and manus (Peyer 1931; Wild 1974; Nosotti 2007). The femur is long and slender with a very slight sigmoid curvature (Renesto 2005; Rieppel et al. 2010) and only moderately expanded proximal end. The distal end of the femur displays two rounded condyles. The tibia and fibula have a straight shaft, are sub-equal in length and surround a very small spatium interosseum. The tibia has moderately expanded proximal and distal ends, while only the proximal end of fibula is slightly expanded. The knee joint is hinge-like and permitted a great degree of flexion and extension to the fore leg. The tarsus consists of four elements: a subrectangular astragalus, a rounded calcaneum and distal tarsal IV and a much smaller distal tarsal III. The astragalus and calcaneum meet along a straight line and their mutual mobility was precluded; the two elements can be reasonably considered as a single unit (Rieppel et al. 2010), the proximal surface of the astragalus forms, along with the dorsal surface of the calcaneum, a slightly concave continuous articular area that housed the distal head of the fibula.

The laterodistal borders of the astragalus and calcaneum meet the medial border of the rounded fourth distal tarsal, which contacts medially the tiny third distal tarsal and laterally the medial margin of the hooked fifth metatarsal. Nosotti (2007) stated that *Tanystropheus* had a primitive, mesotarsal joint, in which the flexion of the ankle occurred between proximal and distal tarsals. However, in *Tanystropheus* specimens with articulated tarsal bones (e.g. Nosotti 2007: 43 fig. 35; Renesto 2005, fig. 8B), the proximal surface of the astragalus forms with the dorsal surface of the calcaneum a slightly concave continuous articular surface for the distal head of the fibula, so that the tarsus of *Tanystropheus* is similar to that of *Macrocnemus* (Rieppel 1989), apart for the lesser degree of ossification, namely the lack of an ossified centrale, and presence of only one ossified distal tarsal. The fifth metatarsal lies lateral to the fourth distal tarsal and distally it meets the calcaneum forming a solid unit. It is thus probable that in *Tanystropheus* the flexion occurred between the crus and the proximal tarsal ossifications, allowing flexion and rotation of the foot relative to the tibia during locomotion, as proposed by Rieppel (1989) for *Macrocnemus*.

The first four metatarsals are much elongated, and closely juxtaposed. The length of the metatarsals increases significantly from the first to the third, while the fourth is slightly shorter than the third, unlike in *Macrocnemus* and *Langobardisaurus*. The fifth metatarsal is much shorter and hooked. The phalangeal formula is 2, 3, 4, 5, 4.

The first phalanx of each toe is much more elongate than the following ones and the first phalanx of the fifth toe is elongate and metatarsal-like. The long pes of *Tanystropheus* may have represented an effective rowing device if the feet were webbed.

INFERRED MYOLOGY

Tanystropheids are bracketed phylogenetically by lepidosaurs and crocodylians, and the reconstruction of the musculature of its tail, pelvic girdle and hind limb was based on knowledge about extant squamates and crocodylians (Gasc 1981; Romer 1923; Snyder 1954; Rewcastle 1983; Gatesy 1990; Otero et al 2010; Ritzman et al 2012). The overall morphology of the pelvic girdle and hind limbs is more similar to that of lizards than of crocodiles or other archosaurs, suggesting a sprawling gait and a muscle arrangement that may have been closer to that of lepidosaurs rather than archosaurs. Preservation of specimens and lack of distinct processes on some bones, however did not allow inferences about the exact position of origin and insertion of some muscles.

Caudal musculature. The squared neural spines of the first six to seven caudal neural spines of *Tanystropheus* suggest the presence of a well-developed spinalis caudalis muscle at the base of the tail (Fig. 3A); this muscle is considered a stabilizer of the proximal caudal portion of the vertebral column. The reduction in size of the neural spines of the following caudal vertebrae, indicates an attenuation of most axial muscles, such as the longissimus and the spinalis caudalis. Because the haemal spines also become much smaller starting in the middle portion of the tail and virtually disappear in the distal portion, it is feasible that also the ischiocaudalis muscle

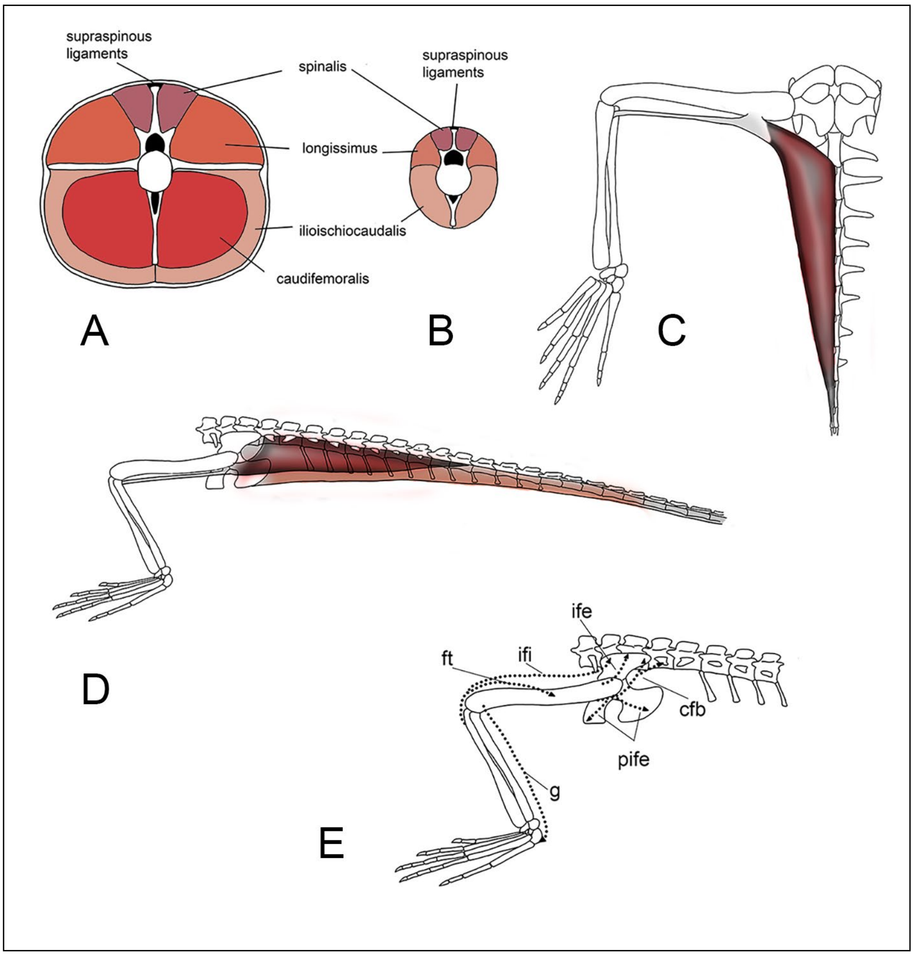


Fig. 4 - *Tanystropheus longobardicus* A) transversal section the base of the tail wth reconstruction of the pattern of the muscles; B) transversal section at mid tail; C) reconstruction of the development of the caudofemoralis longus in ventral view; D) reconstruction of the caudofemoralis longus (dark grey) and ilioischioocaudalis (light grey) in lateral view; E) path of the main leg muscles in *Tanystropheus*. Abbreviations in E: cfb, caudofemoralis brevis, ft, femorotibialis, g, gastrocnemius, ife, iliofemoralis, ifi, iliofibularis, pife, puboischiofemoralis.

significantly reduced its size distally (Fig. 3C), thus the tail section was quickly tapering posteriorly.

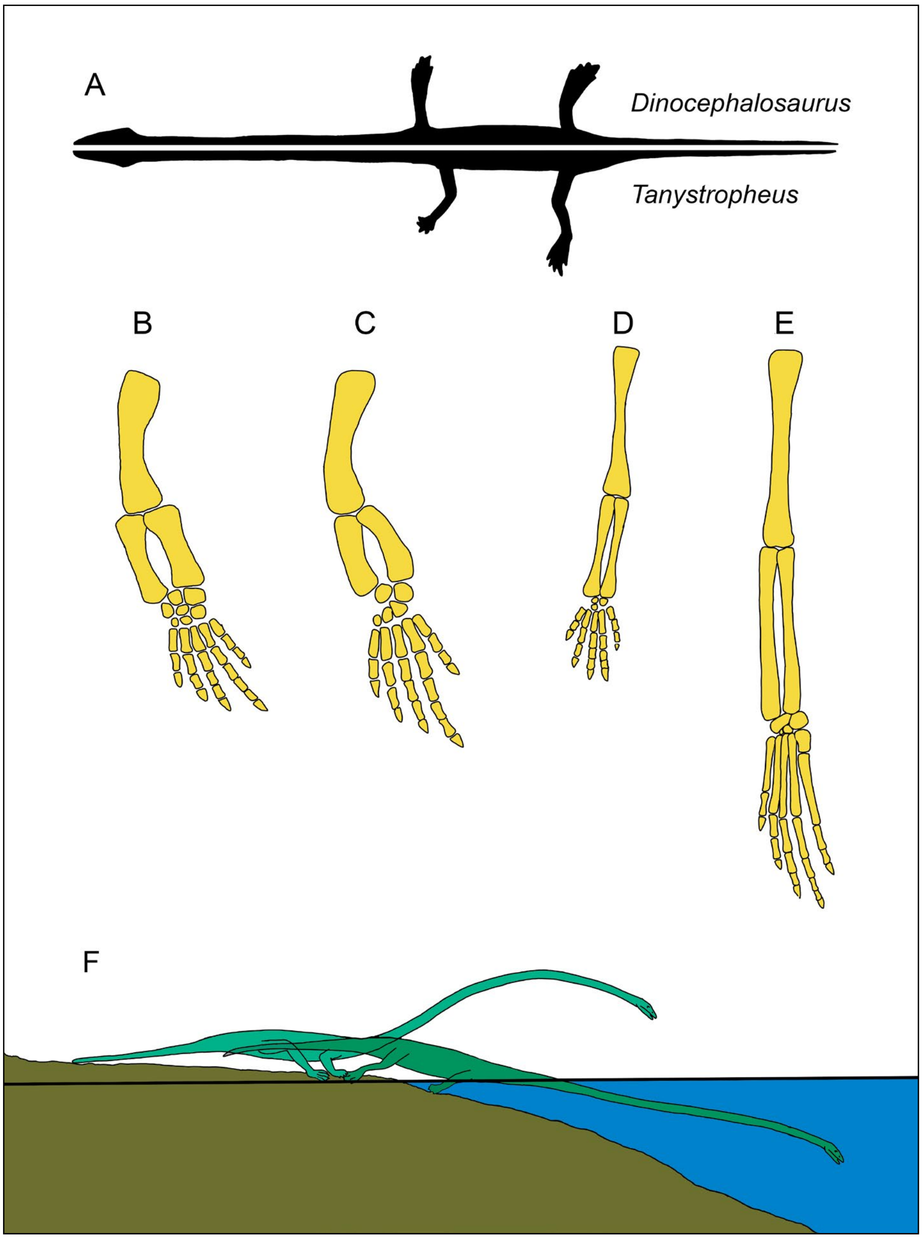
Hind limb musculature. The ventrally expanded puboischiadic plate and the wide pleurapophyses of the proximal caudal vertebrae of *Tanystropheus* suggest the presence of large muscles for limb movements (Fig. 4), especially femoral retraction, rotation (mainly the caudofemoralis longus) and abduction.

The wide surface of the ischium and ilium suggest that they housed robust iliofemoralis, puboischiofemoralis externus and internus muscles for abduction and rotation of the femur along with the M. ischiofemoralis pars posterior, which in lepidosaurs arises from the dorsal or inner surface of the pubo-ischiadic plate to end on the proximodorsal surface of the femoral shaft (Herrell et al. 2008), had to be large, acting as a strong femoral retractor.

The well-developed laterally projecting hemapophyses of the first eight- to twelve caudal vertebrae of *Tanystropheus* suggest the presence of a short but stout caudofemoralis longus muscle (Figs 3 B-C). This muscle in extant reptiles originates from the proximal lateral surface of the haemapophyses and part of the ventrolateral surface of the centra and ends with a stout tendon that divides in two parts: a short and robust section that inserts on the proximoventral portion of the femur about at the proximal one-fifth of the femur length (in archosaurs on a prominent fourth trochanter, which is absent in *Tanystropheus*), and a thin and long tendon that runs parallel to the femur ending at the posterior side of the knee joint, at the origin of the gastrocnemius muscle. The caudofemoralis longus is considered as the main retractor muscle of the hind limb (e.g. Gatesy 1990; Otero et al. 2010). In *Tanystropheus*, the caudofemoralis may have acted as it does in lepidosaurs, causing both powerful femur retraction and medial rotation, along with hip extension and flexion of the knee joint (Rewcastle 1983).

The wide lateral surface of the ischium offered a large area for the origin of a robust adductor femoris muscle, that inserts on the ventral surface of the femur, as well as abductors like the iliofemoralis (Anzai et al. 2014). The adductor femoris, other than acting as the main femoral adductor it also helps in femoral retraction. The length of the

Fig. 5 - A-E) Comparison between body outlines (A) and limb skeleton of *Dinocephalosaurus* and *Tanystropheus* B-C: *Dinocephalosaurus* fore and hind limb D-E *Tanystropheus* fore limb and hind limb; F) Sketch representing *Tanystropheus* diving quickly into water by symmetrical stroke of the hind limbs (grey) starting from resting position (white). A-E Redrawn from Renesto (2005) and not to scale.



femur, of the tibia and fibula offered wide areas for the insertion of well-developed flexor (e.g iliofibularis) and extensor muscles for the knee and of the pes. The wide fifth metatarsal probably housed the insertion of a well-developed gastrocnemius muscle (Brinkman 1980; Rieppel 1989). When the muscle contracts, it generates an upward force that acts across the joint and flexes the foot, the elongate and tightly articulated metatarsal may have offered good leverage for effective pushing against the substrate.

A small tubercle on the lateral border of the plantar surface of the fifth metatarsal of *Macrocnemus* may have housed the insertion of a well-developed peroneus longus (Rieppel 1989), which is another extensor of the pes. In *Tanystropheus* a small tubercle is also present in the same position (see Nosotti, 2007 p. 37 fig. 28), thus it is feasible that the muscle arrangement was the same.

FUNCTIONAL INTERPRETATION

Terrestrial locomotion. The elongate and slender limbs of *Tanystropheus* are more similar to those of non-marine tetrapods as already shown. The disparity in length between fore and hind limb (Fig. 1B-C), with proportionally shorter forelimbs suggests that the main propulsion during locomotion came mostly from the hind limb whose musculature was well developed and may have allowed effective protraction, retraction and rotation, along with a high degree of flexion/extension at the knee and at the

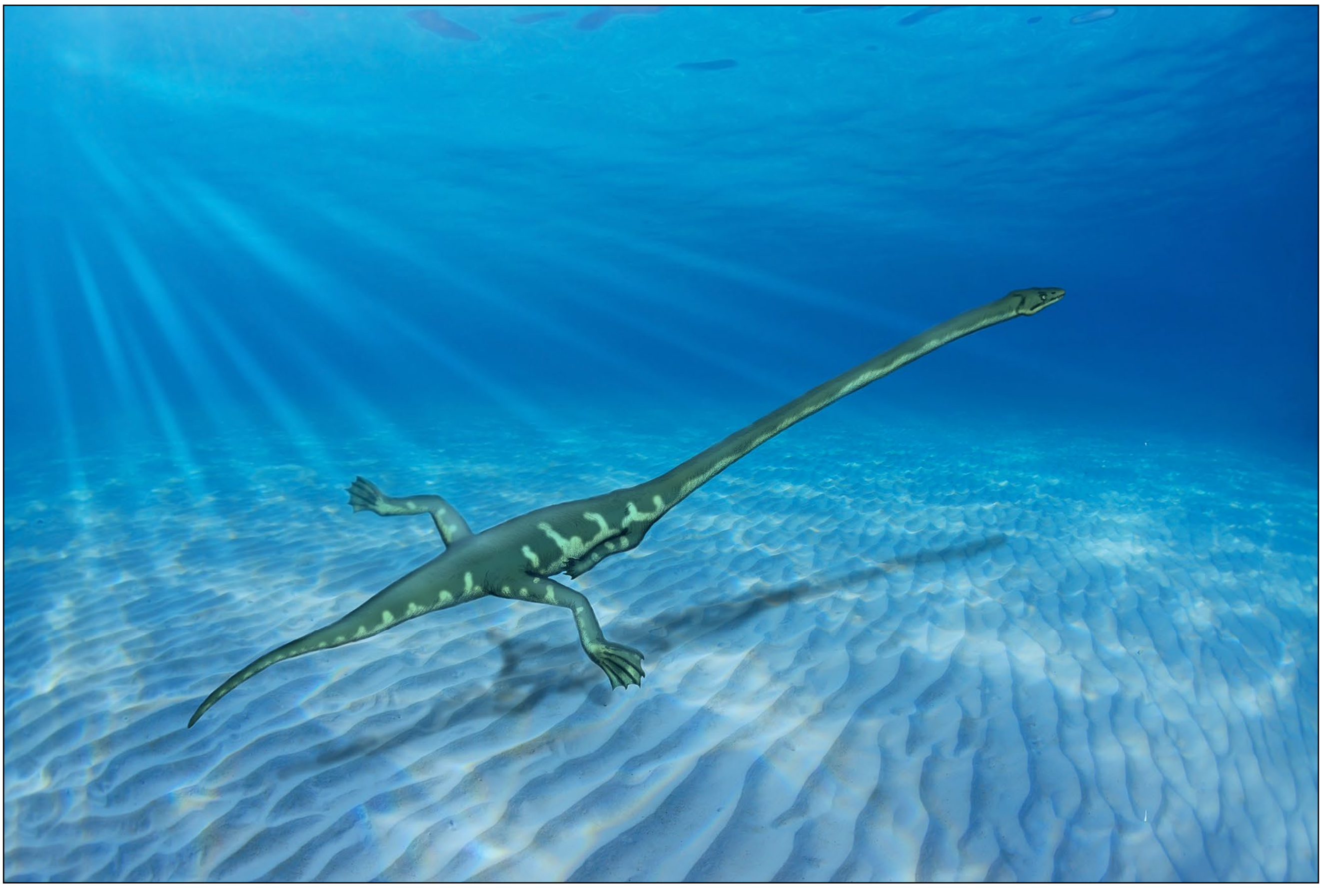


Fig. 6 - Reconstruction of *Tanystropheus* swimming in shallow sea.

ankle, either for walking or swimming.

The rounded articular end of the femur that extends onto the ventral surface of the bone indicates the possibility of substantial degree of flexion at the knee joint (Fig. 3B-D). The compactness and structure of the tarsus suggest that the contact between tibia and tarsus is increased, forming a solid complex during pes rotation and pedal plantarflexion, when maximal propulsive force is developed.

The presence of an expanded tip of the neural spines of the dorsal, sacral and first caudal vertebrae, may have housed a supraspinous ligament (Frey 1988; Tsuihiji 2004, 2005). The possible function of these ligaments may have been to brace together the neural spines to stiffen and strengthen the trunk (Frey 1988; Tsuihiji 2005; Molnar et al. 2014) to prevent falling into flexion caused by the extreme elongation of the neck (Pritchard et al. 2015) when walking on land. These stiffening structures avoided the sagging by the trunk between limbs (Frey 1988; Tsuihiji 2005) and, along with the presence of strong femoral adductors, may have allowed *Tanystropheus* to keep the belly off the substrate during walking (Fig. 1).

Locomotion in water. Renesto (2005) already suggested that the tail of *Tanystropheus* was not suited for propulsion in water and that the limbs of *Tanystropheus* are different from those of limb-propelled marine reptiles like those of the related genus *Dinocephalosaurus* (Li et al. 2004, Fig. 5), which had oar-shaped, sauropterygian-like limbs. The tail of *Tanystropheus* was thick and dorsoventrally flat at its base, becoming very narrow distally; this is the opposite of what occurs in reptiles that swim by caudal undulation or oscillation, like ichthyosaurs, crocodilians or thalattosaurs. In the latter, the tail remains dorsoventrally expanded for most of its length and most caudal vertebrae are robust with high neural spines and deep haemal spines (see Müller 2005 and reference therein). In addition, adult individuals of *Tanystropheus* (and of *Tanytrachelos*) of one sex had extensive extra ossifications at the base of the tail ("heterotopic bones" Wild 1974; Olsen 1979; Rieppel et al. 2010) that would be a serious hindrance to lateral movements of the proximal portion of the tail. Nosotti (2007) tried to address this contradiction by proposing that *Tanystropheus* could have had a fleshy tail fin (an assumption unsupported by any evidence). Nosotti (2007) suggested also that the retention of several anatomical traits from their terrestrial ancestors in the limbs was a consequence of *Tanystropheus* being a late invader of the sea, thus less specialized for marine life than its contemporaries (ichthyosaurs, sauropterygians, thalattosaurs). This statement would assume that *Tanystropheus* was not well adapted to the environment in which it should have lived; this assumption however is contradicted by the wide geographical diffusion and long persistence of the genus, which testifies that *Tanystropheus* was well-adapted for its environment. Rather than imperfect adaptation to life in open water, the retention of terrestrial features may simply indicate thet *Tanystropheus* could have moved also on land as well as in water.

The osteological and myological feaures described above may have allowed *Tanystropheus* to swim by symmetrical rowing: the development of the spinalis muscles and the expanded supraspinous ligaments may have stiffened the trunk and the base of the tail (Bels et al. 1992; Losos 1990; Garland & Losos 1994; Melville & Swain 2000) stabilizing the body, thus allowing rapid extension of both hind limbs for propulsion (Figs 5-6). The sacral vertebrae bore anteroposteriorly wide pleurapophyses that were in contact with each other distally (a character overlooked by Renesto 2005), made the sacrum a stout and rigid structure that may have supported rowing. In water, the long distal elements of the hind limbs, along with the presence of robust retractors and protractors, and the good degree of rotation allowed by the knee and ankle joints enabled *Tanystropheus* to protract the hind limbs forward to the fore limbs then exert a powerful retraction of both hind limbs simultaneously (a pattern of locomotion observed in jumping lizards: Losos 1990; Garland & Losos 1994; Melville & Swain 2000). The active stroke was performed mainly by a contraction of iliofemoralis and caudofemoralis muscles, while the recovery stroke was performed mainly by the tibialis anterior, and puboischiofemoralis internus and externus muscles.

Alternate rowing seems instead unsuitable for *Tanystropheus*, as already suggested by Renesto (2005): owing to the marked size difference between foreand hindlimbs and especially between manus and pes, the movement of the forelimb on one side could not balance effectively that of the hindlimb of the other side to avoid side waving.This would have been further increased by the elongate and laterally inflexible neck, thus compromising the efficiency of subaqueous locomotion (Braun & Reif 1985).

Evidence of a symmetrical subaqueous locomotion in a possible tanystropheid may be represented by some *Gwyneddichnium* trackways (Lockley 2006; Lucas et al. 2014), which are attributed to *Tanytrachelos* and possibly to other taxa of the same clade. Some trackways show a series of symmetrical pairs of left and right tracks of the pedes, in a symmetrical, saltatory kind of locomotion. The hands may have not touched the bottom (Lockley et al. 2006) or alternatively they left no tracks (Lucas et al. 2014). Interestingly, *Tanytrachelos* specimens exhibit spinous expansions in the dorsal, sacral, and caudal regions that may have housed ligaments that stiffened the whole body during swimming.

Gwyneddichnium tracks are known from Middle and Late Triassic of the USA and Europe (Lucas et al 2014). According to Lockley (2006), one *Gwyneddichnium* trackway shows a progressive acceleration of the animal.

Conclusions

In conclusion, *Tanystropheus* may have had lived in a shore line environment, where the elongate neck, may have been used to cach preys in shallow water by dashing at the prey propelled by hindlimbs, either starting from the shoreline from a resting position (Fig. 5) or, in water, eventually after slowly closing the distance. In water, the long neck would have allowed *Tanystropheus* to conceal its real size while slowly approaching to fish or squid schools by reducing the disturbance caused by body surrounding water, avoiding to be detected by the prey's lateral line. When close enough, *Tanystropheus* may have shifted to fast pursuit for the sudden propulsive final phase, with a series of rapid symmetrical strokes of the hind limbs (Fig. 6).

Swimming by symmetrical rowing is however a discontinuous kind of locomotion that occurs in animals with an amphibious life style and make frequent excursions on land (Braun & Reif 1985). Any kind of discontinuous propulsion does not represent an effective adaptation for vertebrates living permanently in open waters, especially if they attain a fairly large size (Braun & Reif 1985), the latter exploit some kind of axial or paraxial continuous propulsion, like caudal undulation/oscillation or subacqueous "flying". Thus the proposed model of *Tanystropheus* locomotion is consistent both with the overall body architecture of the animal, and with the retention of terrestrial features, since they are needed for locomotion on land, all pointing to a semi-aquatic (crocodile-like) life style in a shoreline and/or shallow-water environment.

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