A NEW SPECIMEN OF *TANYSTROPHEUS* (REPTILIA PROTOROSAURIA) FROM THE MIDDLE TRIASSIC OF SWITZERLAND AND THE ECOLOGY OF THE GENUS

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Abstract. A new specimen of the protorosaurian diapsid reptile *Tanystropheus* is described. The specimen was collected at the Valle Serrata locality (Switzerland) and is of Ladinian (Middle Triassic) age. Its study elucidates some issues regarding the anatomy of *Tanystropheus* to be addressed, and allows to suggest hypotheses about its mode of life. In particular, the specimen is the first one in which the skin and other soft tissues can be described. In particular, wide patches of black phosphatic material, filled with small carbonate spherules are preserved, as it occurs in corpses lying in stagnant water due to decomposition of consistent amount of proteins. This suggests that a huge mass of flesh was present in the caudal part of the body, shifting posteriorly the center of mass of the animal and helping in balancing the weight of the neck even if raised off horizontal plane and out of water. In addition, no evidence of caudal autotomy is present in *Tanystropheus* and the structure of the tail and of the limbs are consistent with a shoreline habitat rather than with a fully aquatic mode of life.

Riassunto. Viene descritto un nuovo esemplare del rettile protorosauro *Tanystropheus*, proveniente dalla località di Val Serrata (Canton Ticino, Svizzera) risalente al Ladinico Inferiore (Triassico Medio). Si tratta del primo esemplare nel quale vengono descritte le squame e altre parti organiche. Lo studio dell'esemplare contribuisce a risolvere alcune controversie sull'anatomia ed il modo di vita di questo rettile. Di particolare importanza sono le chiazze di materiale fosfatico che si riscontrano alla base della coda, le quali contengono numerose sferule di carbonato di calcio. Questo fenomeno si verifica durante la decomposizione di una cospicua quantità di materiale proteico. Si ipotizza quindi la presenza di una notevole massa muscolare alla base della coda, che avrebbe spostato in direzione caudale il centro di massa dell'animale, contribuendo fra l'altro a controbilanciare il peso del collo anche mantenendo quest'ultimo in posizione sollevata fuori dal mezzo liquido. Inoltre, si è potuto appurare che in *Tanystropheus* non esiste alcun indizio di autotomia caudale e che la morfologia della coda e degli arti non sono congruenti con uno stile di vita completamente o prevalentemente acquatico, suggerendo piuttosto che questo rettile vivesse lungo le rive, con la possibilità di frequenti escursioni sulla terraferma.

Introduction and geological setting

The Protorosauria Huxley, 1881 (Prolacertiformes Camp, 1945) constitutes the clade of Triassic diapsid reptiles that comprises the genera *Protorosaurus, Boreopricea, Cosesaurus, Prolacerta, Macrocnemus, Tanystropheus, Tanytrachelos, Langobardisaurus, Jesairosaurus* plus a few other less well known genera (see Rieppel et a. 2003 for a survey). Both the relationships of protorosaurian reptiles to other diapsids and the interrelationships within the clade have been subject to several reviews in recent years (Jalil 1997; Benton & Allen 1997; Dilkes 1998; Peters 2000; Rieppel et al.

Fig. 1 - Index map of the Monte S. Giorgio area, the arrow point indicates the locality in which the fossil was collected.

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2003): at present, there is a broad consensus nesting them within the Archosauromorpha, close to the most basal archosaurs.

The presence of a long neck, formed via elongation of individual cervical vertebrae rather than by an increase in their number, characterizes the Protorosauria, but in the genus *Tanystropheus* v. Meyer, 1852 this elongation is so extreme as to render this taxon the most bizarre from the Middle Triassic. In fact, in *Tanystropheus* the length of the neck could equal that of the rest of the body including the tail, rendering the animal rather impressive (some specimens reached five meters in length), and also a biomechanical and palaeoecological enigma.

Recently, a new *Tanystropheus* specimen with preserved soft tissue (Pl. 1) has been collected from a locality in Val Serrata, Canton Ticino, Switzerland (Fig. 1), which lies within the famous fossiliferous area of Monte San Giorgio (Switzerland and Italy). Its study, along with data from other *Tanystropheus* specimens and from the recently discovered protorosaurian *Dinocephalosaurus* (Li et al. 2004), allows a review of the hypotheses concerning the posture and mode of life of this strange diapsid, as well as the proposal of a new interpretation about its palaeoecology.

The specimen was collected from an isolated slab which had fallen from the side of the slope. According to Dr. Heinz Furrer (pers. comm. 2005) the stone came from the levels of the Lower Meride Limestone corresponding to the Cava Inferiore beds, very probably beds 29-30, (Sander 1989), which are of Early Ladinian age (Furrer 1995). The level roughly corresponds to the horizon in the Cava Inferiore named as "scherzi" by Sander (1989). This is the first finding of a specimen of *Tanystropheus* in the Cava Inferiore levels.

Systematic Palaeontology

Reptilia

    Diapsida Osborn, 1903

        Protorosauria Huxley, 1871

            Tanystropheidae Gervais, 1858

                Tanystropheus von Meyer, 1852

        Type species: *Tanystropheus conspicuus,* Meyer, 1852

Tanystropheus cf **T. longobardicus** Bassani, 1886

Pl. 1-2; Figs 2-3, 5-7, 9

Material. Specimen MCSN 4451, (Museo Cantonale di Scienze Naturali di Lugano, Switzerland). The specimen is incomplete, lacking the head, the first eight cervical vertebrae and most bones of both hind limbs. The very long and low cervical vertebrae, the extremely elongate and thin cervical ribs running parallel to the body axis, and the pattern of the carpus and of the tarsus indicate that it belongs to the protorosaurian genus *Tanystropheus*, all other preserved elements are also consistent with this identification.

Horizon and locality. Lower Cava Inferiore beds, Meride Limestone (Early Ladinian), Val Serrata, Monte San Giorgio, Switzerland.

Description

Vertebral column.

Cervical vertebrae. Only cervical vertebrae nine to twelve (Fig. 2-3) are completely preserved, along with the caudal half of eight cervical vertebra. All cervical vertebrae are exposed on their left side and their shape is that typical for *Tanystropheus*, with extremely elongate and weakly amphicoelous centra (the length of the ninth cervical vertebra reaches nearly ten times its height at mid section of its body) with slightly expanded ends. The vertebral arches and spines are greatly reduced, especially in the middle of each vertebra, where the vertebral spines resemble small keels which are somewhat higher at their cranial and caudal ends. The postzygapophyses overlap the prezygapophyses dorsally and the articular facets are subvertical, suggesting that lateral mobility was restricted. On either side of the vertebral body, close to the cranioventral margin, two distinct suboval articular areas for the heads of the cervical ribs can be detected. The 12th cervical vertebra is much shorter than the preceding ones and it bears a higher, squared vertebral spine. Interestingly, the caudal articular surface of the body is craniocaudally inclined so that the body has a rhomboid shape in lateral view.

Dorsal vertebrae. Most dorsal vertebrae are disarticulated. The first dorsal vertebra is still articulated with the last cervical, caudal to this, at least five disarticulated vertebrae are visible (Pl. 2B), exposed in either left or right lateral views as isolated elements scattered amongst ribs and gastralia, thus their correct numbering is difficult, whilst the last three dorsals are in anatomical connection with each other and with the sacral vertebrae. Since the usual number of dorsal vertebrae in *Tanystropheus* is 13 (Wild 1973) it is feasible that some of the cranialmost dorsal vertebrae are covered by the disarticulated elements of the pectoral girdle. Each dorsal vertebra (Fig. 4) exhibits an hourglass-shaped body, with a distinctly concave ventral margin, postzygapophyses which are stouter than prezygapophyses and subrectangular vertebral spines; these latter are approximately two-times longer than tall, and their morphology is thus quite different from that described in Wild (1973), where the dorsal vertebrae were reconstructed with higher than long vertebral spines. Two distinct processes for the articulation of ribs are present (Fig. 4A): a stubby transverse process lies in the middle of the vertebra where the vertebral vertebral arch meets the body, while another process is borne by the body; these two processes are connected by a bony ridge. Along the vertebral series, the processes gradually be-

come confluent (Fig. 4B) until a single articular area for the rib is present, which is borne by a short transverse process at the base of the vertebral arch (Fig. 4C). The last two dorsal vertebrae (Fig. 5) are shorter than the preceding ones, bear larger zygapophyses and short but craniocaudally expanded transverse processes onto which is firmly sutured a short "lumbar" rib.

Sacral vertebrae. The two sacral vertebrae (Fig. 5) are exposed in dorsolateral view. The vertebral arches and spines are damaged and partially obscured by patches of black material and an array of small, spherical concretions. The main feature of the sacral vertebrae is represented by the stout transverse processes. The first pair are subtriangular in shape with expanded distal ends, whilst those borne by the second sacral vertebra are distinctly more expanded in their craniodistal portion so that their proximodistal axis is bent cranially.

Caudal vertebrae. Twelve intact caudal vertebrae are completely preserved along with fragments of two others. The first caudal vertebra is still articulated with the last sacral (Fig. 5), while the second (Pl. 2G) through fourth lie as scattered isolated elements close to the base of the tail. Caudal vertebrae 5-10 are articulated and exposed in right oblique ventrolateral view (Fig. 6). The 10th caudal vertebra is only partially preserved because the margin of the stone slab runs close to its cranial margin. On a separate but contiguous slab, four other vertebrae are preserved, plus a fragment of a fifth.

The first caudal vertebra is exposed on its dorsal side and the vertebral arch and spine are crushed over the body. Two stout transverse processes project laterally and somewhat caudally from each side of the body, the second caudal vertebra is disarticulated and somewhat flattened so that the slightly concave caudal surface is visible, its transverse processes are longer than those borne by the first caudal vertebra and their axis slants slightly forward. The third caudal vertebra is again exposed in ventrolateral view, overlapping the right transverse process. The caudal margin is partially obscured by the vertebral arch of the fourth caudal vertebra; this latter is exposed in either cranial or caudal view, showing the subrectangular outline of the vertebral canal and the concave articular surface of the body. An isolated elongate element might be the haemal spine, but its identification is difficult due to the presence of concretions and a layer of organic matter. Caudal vertebrae 5-10 are exposed in right lateral view, the centra are somewhat narrower than those borne by the preceding vertebrae and the vertebral spines are low; the transverse processes gradually decrease in length until the eighth, then they virtually disappear. The following preserved section of the tail is apparently connected to the preceding one (Fig. 6), but the vertebrae are exposed on their left sides and there is neither a trace of the missing part of the 10th caudal vertebra nor a clue of where the rotation occurred. Perhaps during preparation of the specimen, the two slabs were juxtaposed in tight contact but it might be possible that at least as fragment of the caudal portion of the 10th caudal vertebra was lost. The bodies of the vertebrae lying on the second slab are slightly longer and narrower than those of the preceding vertebrae; their vertebral spines are twice longer than high with suboval dorsal margins. Y-shaped haemal spines are present; the first two-to-three are disarticulated, but the following ones are preserved in intercentral articulation. The sizes of the haemal spines decreases along the series, so that the third preserved vertebral spine is 11mm deep, the ninth is 6 mm in depth and the 11-12th are only 5mm deep. Close examination reveals that none of the preserved caudal vertebrae present a fracture plane or any other evidence of caudal autotomy.

Ribs and gastralia. The cervical ribs show the shape typical for *Tanystropheus*: they are extremely thin and elongate; their shafts being more than two times longer than the longest cervical vertebrae. These ribs run parallel to the cervical vertebrae forming two tight bundles. The proximal end of each cervical rib bears a pointed cranial process, followed by two distinct articular facets divided by a narrow groove (Pl. 2A).

Most dorsal ribs are disarticulated and intermeshed with gastralia, and with the long broken shafts of the cervical ribs. The first three dorsal ribs are robust and dicephalous with an elongate capitulum and a short and stout tuberculum (Fig. 3). The following dorsal ribs are holocephalous, much narrower and gracile than the preceding ones. Caudal to the 10-11th dorsal vertebrae, the ribs again become robust and decrease in length. The last three dorsal ribs are much shorter than the preceding ones, forming a distinct lumbar region.

A large number of thin gastralia are preserved; they consists of a central and two lateral elements forming a stretched U-shaped structure, with the medial element nearly horizontal and the two lateral ones which are bent dorsally close to their distal ends.

Two disarticulated elements of ambiguous identification are preserved near the right side of the sacral vertebrae: they are elongate bifurcated structures with pointed ends (Pl. 2C), their structure recalls that of gastralia but they are much larger. Such elements have never been before described in *Tanystropheus* despite the fact they are present also in specimens *d,i* (Wild 1973, pl. 5, 9) and *w* (Wild 1980, pl. 5), where they lie again close to the pelvic girdle. The morphology of these elements is completely different from that of the eterotopic bones (*sensu* Olsen 1979 and Evans 1988) lying at the base of the tail of some large specimens and considered by Wild (Wild 1973, pp. 122-123 fig. 79) as baculae (but Olsen 1979 suggested that the same bones in *Tanytrachelos* may have supported an egg

Fig. 2   - *Tanystropheus* cf *longobardicus*. Specimen MCSN 4451, cervical vertebrae 8-11 other abbreviations are: ra) radius; ul) ulna; rhu) right
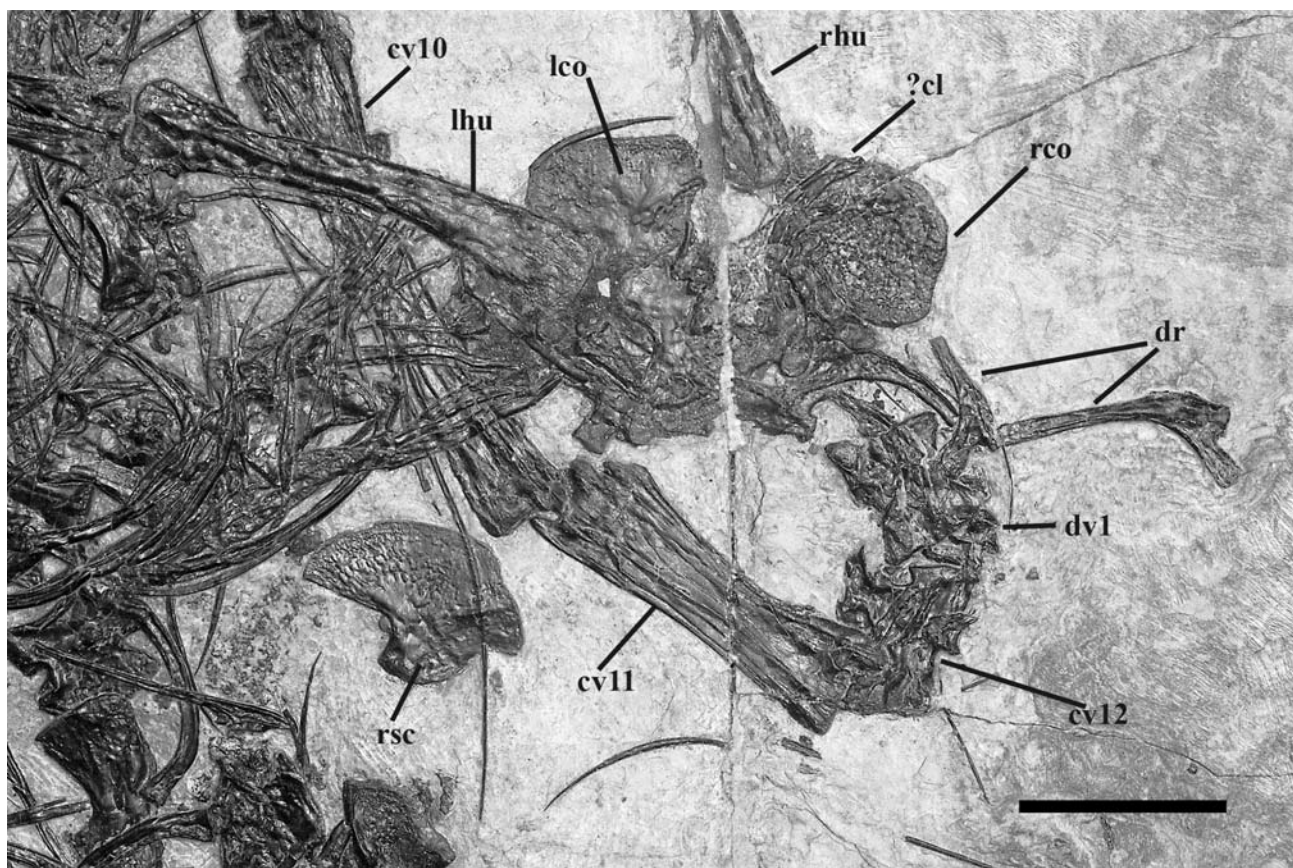   humerus. Scale bar equals 2 cm.

Fig. 3   - *Tanystropheus* cf *longobardicus*. Specimen MCSN 4451, the base of the neck, pectoral girdle and forelimbs. Abbreviations are: cv 10-12) cervical vertebrae 10-12; ?cl) clavicle; dv1) dorsal vertebra 1; dr) dorsal ribs; lco) left coracoid; lhu) left humerus; rco) right coracoid; rhu) right humerus; rsc) right scapula. Scale bar equals 2 cm.

pouch). These latter bones are thicker and exhibit pointed cranial extremities and blunt caudal ends with no bifurcation, and there are two elements on each side of the tail (Wild 1973), in addition they are reported only for some of the large specimens, whilst the bifurcate elements are more gracile, proportionally longer and apparently there is only one element on each side. The bifurcate elements are of difficult interpetation: they may represent a functional equivalent of the eterotopic bones present in the larger specimens, or even an earlier ontogenetic stage, but both hypotheses are highly speculative.

Pectoral girdle. The pectoral girdle (Fig. 3) lies at the junction of three slabs, thus some elements are, in part, broken and others are disarticulated or overlapped by vertebrae and ribs. In addition, the two halves of the pectoral girdle have shifted with respect to one another. The right coracoid is well exposed, it is sub-oval in shape, its craniodorsal margin bears an embayment just in front of the glenoid, as in other *Tanystropheus* specimens. A small coracoid foramen is visible slightly cranioventral to the shallow glenoid.

A scapula, very probably the right one, is separated from the rest of the skeleton, and it can be ob-
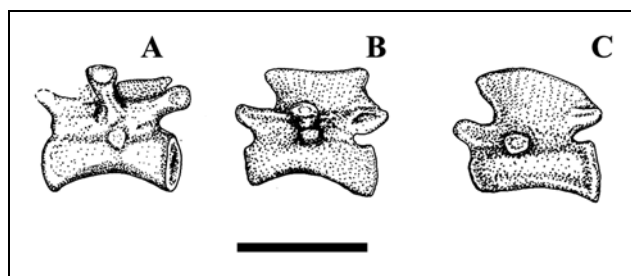

Fig. 4   - *Tanystropheus* cf *longobardicus*. Specimen MCSN 4451, drawing of isolated mid dorsal vertebrae to show how the processes for rib articulation change craniocaudally (A, more cranial; C, more caudal). Scale bar equals 1 cm.

served in detail: the bone is exposed in medial view so that the glenoid fossa cannot be described. Its overall shape matches the description by Wild (1973): a thin craniocaudally expanded scapular blade forms a very thin cranial flange. Around the glenoid fossa, the bone becomes thicker and more robust. The cranioventral margin of the scapula exhibits a concavity that mirrors the embayed craniodorsal portion of the coracoid, thus surrounding an open area cranial to the glenoid.

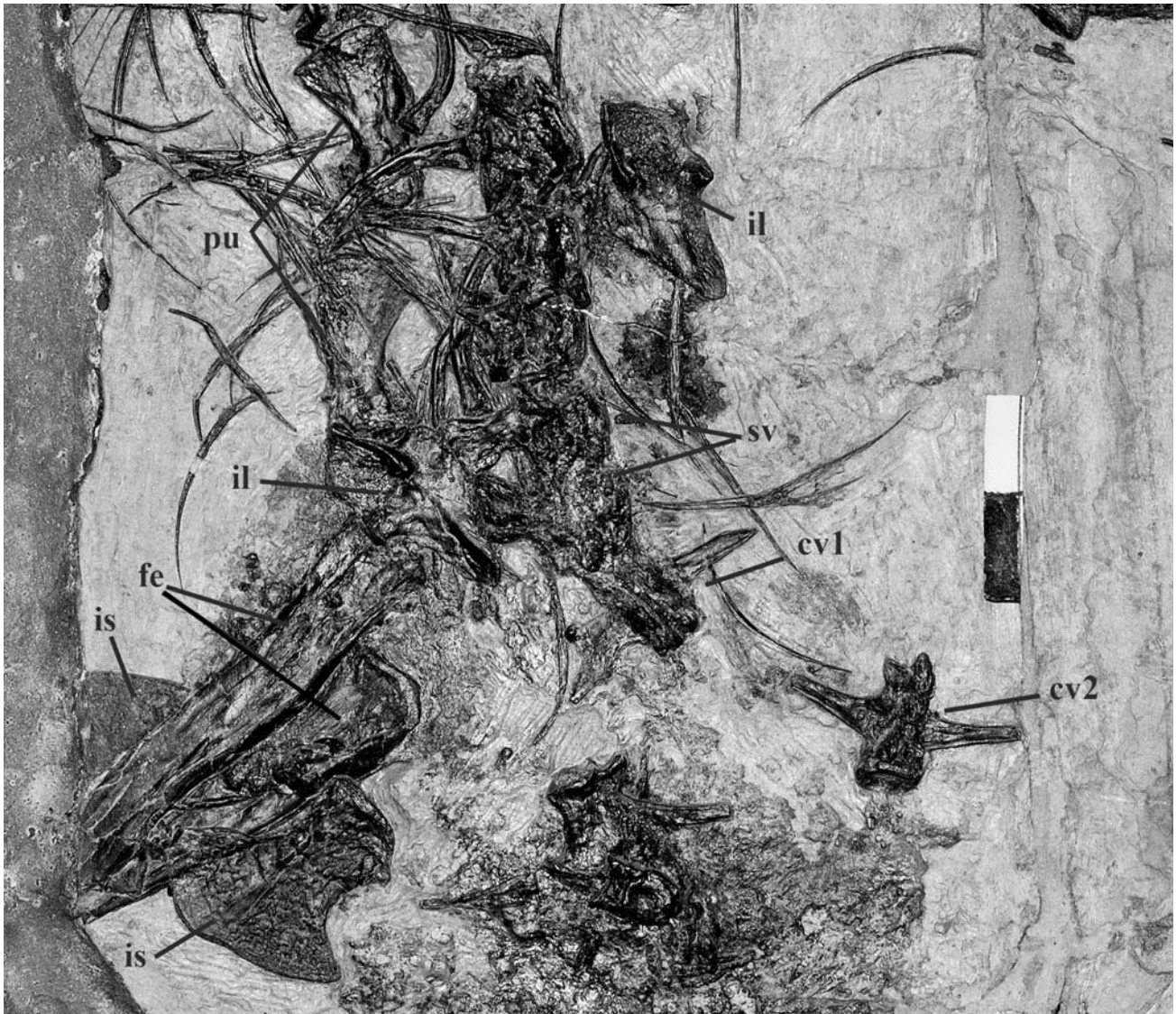A poorly preserved clavicle can be detected above the medial surface of the right coracoid. It is a

Fig. 5   - *Tanystropheus* cf *longobardicus*. Specimen MCSN 4451, the caudal dorsal, sacral and proximal caudal regions. Abbreviations are: cv1-2) caudal vertebra 1-2; fe) femur; il) ilium; is) ischium; pu) pubis; sv) sacral vertebrae. Notice the large black areas of preserved soft tissue. Scale bar equals 2 cm.
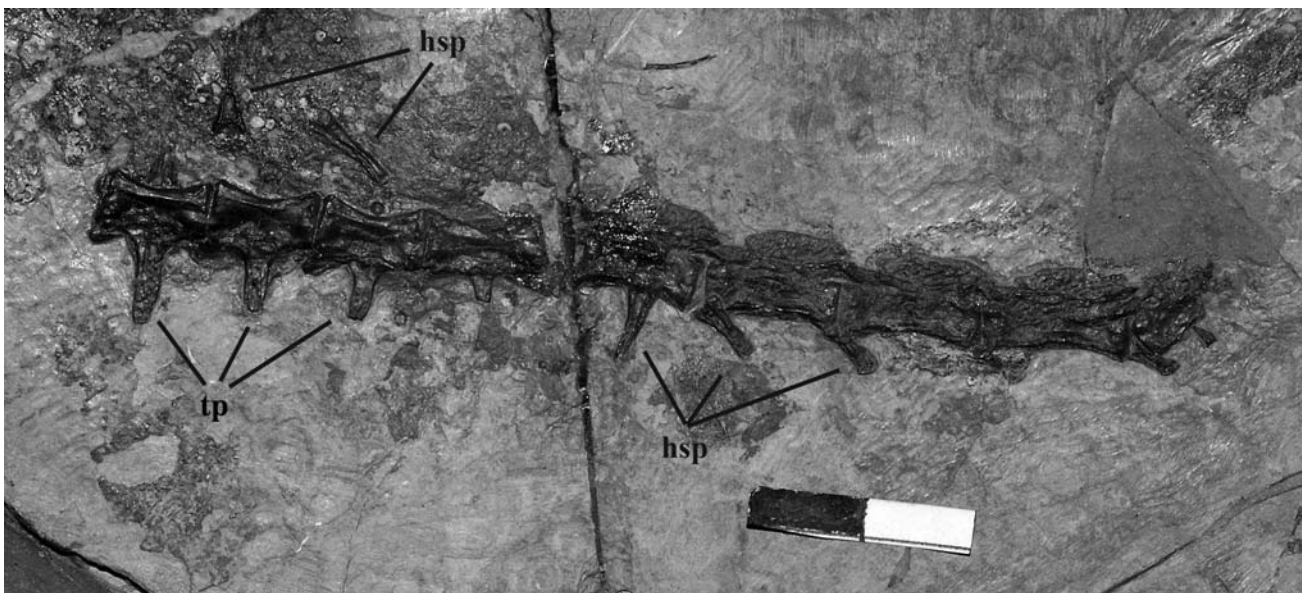

Fig 6   - *Tanystropheus* cf *longobardicus*. Specimen MCSN 4451, central section of the caudal vertebral column. Abbreviations are tp) transverse processes; hsp) haemal spines. Notice the black areas of preserved soft tissue. Scale bar equals 2 cm.

flat, crescent-shaped structure, with a thicker proximal end.

Pelvic girdle. All the bones of the pelvic girdle (Fig. 5) are disarticulated and most have also shifted far from their original positions. The ilium (Pl. 2F) forms a well expanded, caudally elongate, dorsal blade. A thick ridge of bone hangs over the craniodorsal portion of the acetabular area. The pubis (Pl. 2E) is a stout bone with convex cranial margin and concave caudal one, that formed the cranial border of a wide, oval thyroid fenestra. The ischium (Pl. 2D) is very thick in the acetabular area, then ventrally forms a thinner but wide, fan-shaped, ischiadic plate. As noted by Rieppel (1989) the pelvic girdle of *Tanystropheus* looks small compared to the length of the hind limbs.

Forelimb. The left humerus is complete (Fig. 3), while only the heads of the right one are preserved, along with a small part of the proximal portion of its shaft. The proximal articular surface is slightly convex. On the distal head, two distinct convex articular surfaces are present for the radius and ulna. Neither medial nor lateral epicondylar foramina are present. The radius and ulna show straight shafts and moderately expanded heads with flat articular surfaces. The right radius and ulna (Fig. 7) are crossed together, and the carpus lies above the ninth cervical vertebra so that carpals and metacarpals are somewhat displaced; the left hand has shifted dorsally with respect to the left forelimb. Only two rounded almost equally sized bones are visible in the right carpus, along with a subrectangular bone that is, very probably, a displaced phalange. The rounded elements could be interpreted as the ulnare and either a radiale or distal carpal 3. The first metacarpal is short and stubby, approximately half the length of the second. The third metacarpal is slightly longer than both II and IV and the fifth metacarpal is much smaller than the others. Phalanges are short and the last ones have the shape of a small claw.

Hindlimb. The preserved elements of the hindlimbs consist of the proximal portions of both femora (Fig. 5) plus the tarsus of one pes and the left metatarsals and phalanges of the other (Fig. 8 and Pl. 2H-I). Due to displacement of these elements, it is impossible to state which is right or left. The femoral heads are only slightly convex; the preserved portions of the femoral shafts show no trace of sigmoidal curvature. They have been diagenetically flattened, crushed, and split along the axis such that each shaft has collapsed into what appears to be a medial hollow.

The tarsus is made up of three tightly packed bones: a subrectangular astragalus, a rounded calcaneum and a distal tarsal IV. On one of the preserved pedes, tarsals are preserved in articulation with the proximal "hook" of metatarsal V and the proximal heads of metatarsals I-IV. The proximal surface of the astragalus, along with the dorsal surface of the calcaneum, forms a slightly concave articular area which probably housed the distal head of the fibula, a pattern recalling the crurotarsal articulation described in *Macrocnemus* (but without contribution of an ossified centrale). The distolateral borders of the astragalus and calcaneum meet the medial border of the rounded fourth distal tarsal, that contacts laterally the squared medial margin of the hook of the fifth metatarsal. The first four metatarsals are closely appressed and the proximal head of each metatarsal laterally overlaps slightly the head of the following one. The length of the metatarsals increases significantly from the first to the third, whilst the fourth is slightly shorter than the third, unlike in *Macrocnemus* and *Langobardisaurus*. Combining information from the preserved phalanges and the impressions of others, the phalangeal formula can be in part reconstructed as follows: 1+, 2+, 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 exceptionally elongate and metatarsal-like, as in other *Tanystropheus* specimens.

Soft parts. The lumbar, sacral and, especially, the proximal caudal sections of the vertebral column, are surrounded by wide patches of black material (Pl. 1, Fig. 5, 9); smaller patches are also present in the dorsal and mid caudal region. In most cases it is impossible to identify the structure of or within these patches. A notable exception is an area close to the lumbar section of the vertebral column, near the dorsally displaced right ilium, where an arrangement of subrectangular, non-overlapping scales can be detected (Fig. 9A), suggesting that in these areas at least the black matter is indeed fossilized skin, similar to that reported in two specimens of *Macrocnemus* (Renesto & Avanzini 2002). This is the first report of preserved skin in *Tanystropheus*. Traces of scales may also be present in other areas but their preservation is poor and they can barely be distinguished. At the base of the tail the black material is much thicker than in other areas and cover a wider area. No scales are visible, though a large number of small spherules is present (Fig. 9B) which, in cross-section, show an onion-like structure. Both the spherules and the massive patches of black matter are not preserved elsewhere in the fossil. Chemical investigation by using nitric acid and ammonium molibdate revealed that the spherules consist of tiny calcium carbonate crystals, whilst the surrounding matter is rich in phosphate. The spherules may be interpreted as the result of precipitation of calcium carbonate which can be deposited rapidly within a corpse if the surrounding aqueous environment is alkaline enough and supersaturated with
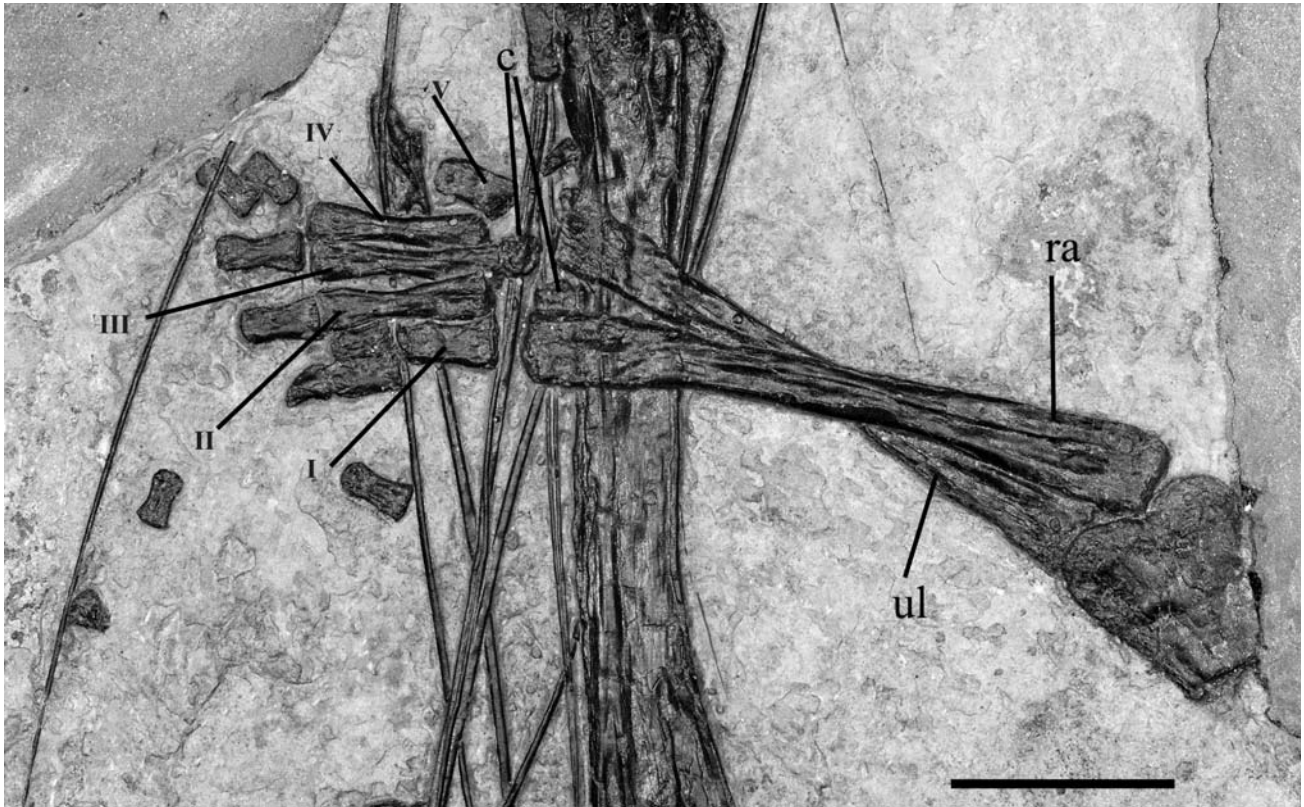
Fig. 7 - *Tanystropheus* cf *longobardicus*. Specimen MCSN 4451, left forelimb; abbreviations are: c) carpal elements, I-V) metacarpals, ra) radius, ul) ulna. Scale bar equals 1cm.
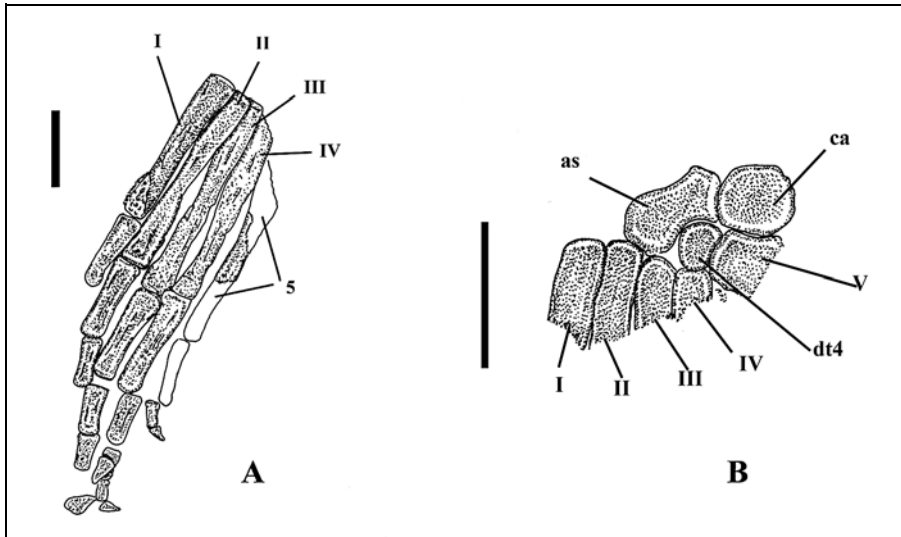

Fig. 8 - *Tanystropheus* cf *longobardicus*. Specimen MCSN 4451, interpretative drawing of isolated metatarsus and phalanges (A) and isolated tarsus (B), Abbreviations are as) astragalus; ca) calcaneum; dt4) distal tarsal 4; I-V) metatarsals. Scale bars equal 1 cm.

carbonate (Allison 1990; Maisey 1991). Usually decay processes occur in acidic conditions, but, according to Hecht (1933), the liberation of ammonia and ammines from the decay of proteins in a stagnant bottom environment can raise the pH to a level where precipitation of carbonates can occur. The concentration of carbon dioxide decreases and this, in warm conditions and at high pH levels, in turn, allows the formation of phosphates (Ames 1959).

The area in which the black matter is preserved in MCSN 445 is the same as in two *Macrocnemus* specimens (Renesto & Avanzini 2002), i.e. the base of the tail. According to anatomical analyses, Rieppel (1989) suggested that a huge mass of muscles was present there in *Macrocnemus*, and the same may apply to *Tanystropheus*. The decay of this substantial mass of muscles may have been responsible for creating the microenvironmental conditions favoring the precipitation of carbonate and formation of the phosphates (Maisey 1991). In other parts of the body, the lack of such huge musculature did not allow the process to occur.
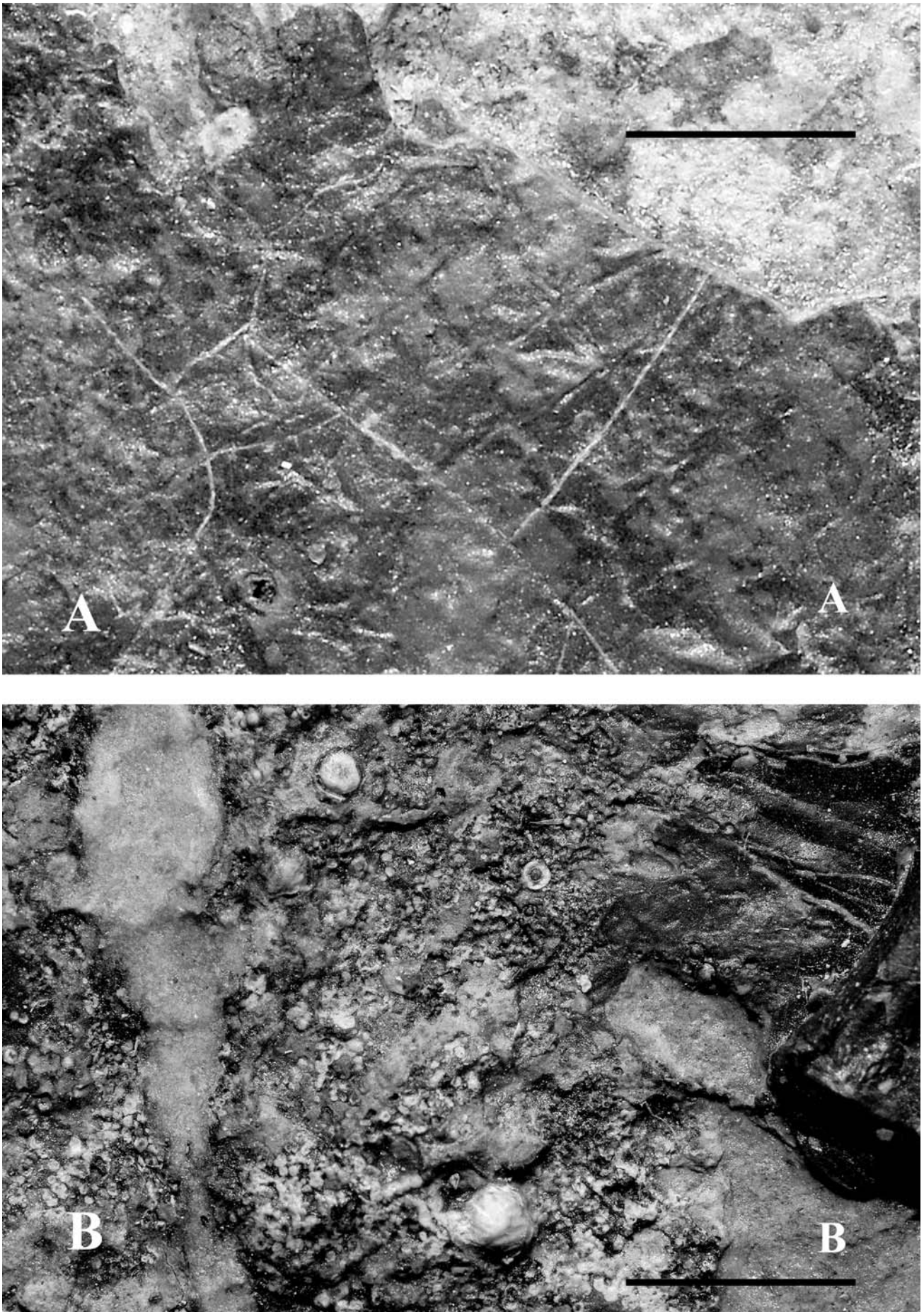
Fig. 9 - *Tanystropheus* cf *longobardicus*. Specimen MCSN 4451: A) preserved portion of skin with square scales; B) preserved soft tissue with spherules. Scale bar equals 2.5 mm.

Specimen	MCSN 4451
Length of cervical vertebra 9	51
Length of cervical vertebra 10	52
Length of cervical vertebra 11	32
Length of cervical vertebra 12	15
Length of dorsal vertebra 5	12
Length of dorsal vertebra X	9
Length of caudal vertebra 2	12
Length of the humerus	45 (left)
Length of the radius	30 (right)
Length of the ulna	29 (right)
Length of metacarpal 1	5 (right)
Length of metacarpal 3	10 (right)
Length of metacarpal 5	3.5 (right)
Length of metatarsal 1	22
Length of metatarsal 2	26
Length of metatarsal 3	28
Proximodistal width between tranverse processes of caudal vertebra 2	10
Pubis height	18

Tab. 1   - Measurements (in mm) taken on specimen MCSN 4451.

The muscular mass at the base of the tail, probably consisted largely of retractor muscles for the femur (the *M. caudifemoralis* complex, mainly the *M. caudifemoralis brevis* which originates only from the proximal portion of the tail) and presumably added considerable weight to the caudal part of the body.

Systematic Discussion

From the previous description, specimen MCSN 4451 can without doubt be ascribed to the genus *Tanystropheus* (as described by Peyer 1931, Wild 1973, Evans 1988, Jalil 1997, Benton & Allen 1997, Rieppel et al. 2003). The specific assignment, however, is more difficult, mainly due to the uncertainty about the validity of the different *Tanystropheus* species. According to Wild (1973, 1987, 1980) the genus *Tanystropheus* should comprise at least *T. antiquus* from the upper Bundsandstein and lower Muschelkalk of Germany, *T. longobardicus* from the Grenzbitumenzone (Anisian) of Switzerland and Italy, *T. conspicuus* from the Upper Muschelkalk (Anisian) of Germany, *T. meridensis* from the Meride Limestone (Ladinian) of Switzerland and *T. fossai* from the Argillite di Riva di Solto (Norian) of Italy. If Wild assumptions were correct, the genus *Tanystropheus* should span for most of the Triassic.

However, Evans (1988) noticed how *T. antiquus* does not match the generic diagnosis for *Tanystropheus*, and also Wild, in 1987, stated that *T. antiquus* "is no longer considered to belong to this genus" and stated that "a redescription of this species is in preparation" (Wild 1987, p. 37). *T. fossai* Wild, 1980 consists of a few isolated cervical vertebrae which may indeed have belonged to a protorosaur but, again they are proportion-

ally shorter (pers. obs.) and lack unequivocal characters for assigment to *Tanystropheus*. Furthermore, *T. longobardicus* and *T. conspicuus* may well be synonous (Wild 1987; Fraser et al. 2004). Thus the valid species could be only *T. longobardicus* and *T. meridensis*. The latter, however, was erected on the basis of one very incomplete, and possibly juvenile, specimen consisting of a skull and the first seven cervical vertebrae, nearly in anatomical connection. According to Wild (1980) *T. meridensis* differs from *T. longobardicus* in the pattern of the bones forming the snout region, the presence of a sclerotic ring, and for the proportionally narrower cervical vertebrae with supplementary foramina. According to Wild (1980, 1987) the characters of the cervical vertebrae that distinguish *T. meridensis* from *T. longobardicus* could also represent a further step along an evolutionary trend toward an increasing elongation and narrowing of the neck. Recently, Fraser et al. (2004) even questioned the validity of *T. meridensis*; despite to the different stratigraphic age, suggesting that the differences in skull morphology and proportions of the cervical vertebrae seem to fall within the normal range of variability recorded for the specimens collected in the Grenzbitumenzone. Fraser & Nosotti (2004) suggested instead that two separate taxa may indeed have coexisted in the Grenzbitumenzone, which can be distinguished by the shape of the caudal process of the premaxilla and for the different development of cusps in the cheek teeth of the small individuals. According to these authors, the largest specimens of both *T. conspicuus* and *T. longobardicus*, along with smaller individuals with very weakly tricuspidate teeth should belong to the same taxon, whilst small individuals with strongly tricuspidate teeth might form an other (and thus *T. meridensis* would belong to the latter group). In this context, MCSN 4451 might have added useful data, because it was collected from an outcrop of the Lower Meride Limestone which is coeval with the Cascina Inferiore levels (Sander 1989; Rohel et al. 2001), thus stratigraphically positioned between the Grenzbitumenzone which yielded the specimens of *T. longobardicus* and the Upper Meride Limestone beds which yielded the holotype of *T. meridensis*. However, the absence of skull and cranialmost cervical vertebrae in MCSN 4451 renders impossible direct comparison between the two specimens in order to confirm the hypotheses of Fraser & Nosotti (2004). The only peculiarity which can be noted in MCSN 4451 is that the 10th cervical vertebra is slightly longer than the 9th (Tabs. 1-2), a feature shared only by specimen *w* from the Grenzbitumenzone, (Tab. 2, Wild, 1980 p. 12; Tschanz, 1986 tab. 11), whilst in other published specimens ascribed to *T. longobardicus* or *conspicuus*, the longest cervical vertebra is the 9th (see Wild 1973, tab. 3, p. 53 and fig. 29, p. 54). Unfortunately the incompleteness

of the cervical series in the holotype of *T. meridensis* and the lack of a skull in MCSN 4451 does not allow assessment of the eventual taxonomic significance of this character in the light of Fraser & Nosotti (2004) assumption. Thus at our present state of knowledge, mainly due to the uncertain status of *T. meridensis,* it is preferred here to consider MCSN 4451 as *Tanystropheus* cf. *longobardicus.*

Mode of Life of *Tanystropheus*

The life habits of *Tanystropheus* have been debated since the first discoveries of the animal. The odd morphology of this reptile renders it ambiguous any attempt to interpret its ecology. In particular, the exaggeratedly long, yet scarcely flexible, neck seems unsuitable in any environment. The discovery of soft parts in MCSN 4451, adds some knowledge to the morphology of *Tanystropheus* as does the recently described marine protorosaur *Dinocephalosaurus* (Li et al. 2004), which has an overall morphology quite *Tanystropheus*-like. Together they are useful elements of comparison for an analysis whose goal is to determine what possible palaeoecological niche *Tanystropheus* occupied that is consistent with its bizarre anatomy.

Previous studies. Based on fragmentary specimens comprised of slender and elongate, but disarticulated bones, the first describers (e.g. Bassani 1886; Nopcsa 1923), hypothesized that *Tanystropheus* was a flying reptile. Subsequently, Peyer (1931) considered *Tanystropheus* as a long-necked terrestrial reptile with a lizard-like gait, clumsy and slow locomotion, and a rather mobile neck held horizontally (Fig. 10A). In Peyer's (1931) view, *Tanystropheus* may have hunted fishes or other aquatic animals from the shoreline, with the neck hanging over or plunging into the water. Wild (1973) suggested that *Tanystropheus* changed its life style during ontogeny: juveniles with tricuspid cheek teeth and relatively smaller size could have been terrestrial insect hunters, while the larger adult specimens with conical, possibly procumbent, teeth were fully aquatic and fed upon fishes and cephalopods (this latter assumption has some support in the form of stomach contents found in some specimens). According to the conclusions of Wild (1973), *Tanystropheus,* when on land, was capable of great cervical dorsiflexion and thus it was been able to raise the neck considerably (Fig. 10B), assuming a monoclinal, loosely S-shaped configuration. Kummer (1975), however, argued that keeping the neck off the ground as in Wild's (1973) reconstruction, would have caused a weight imbalance, making the animal tumble onto its head; he therefore proposed that *Tanystropheus,* when on land, had to assume a more curved, "question mark" or "swan-like" position of the neck (Fig. 10C), in order to shift the center of gravity caudally to gain static
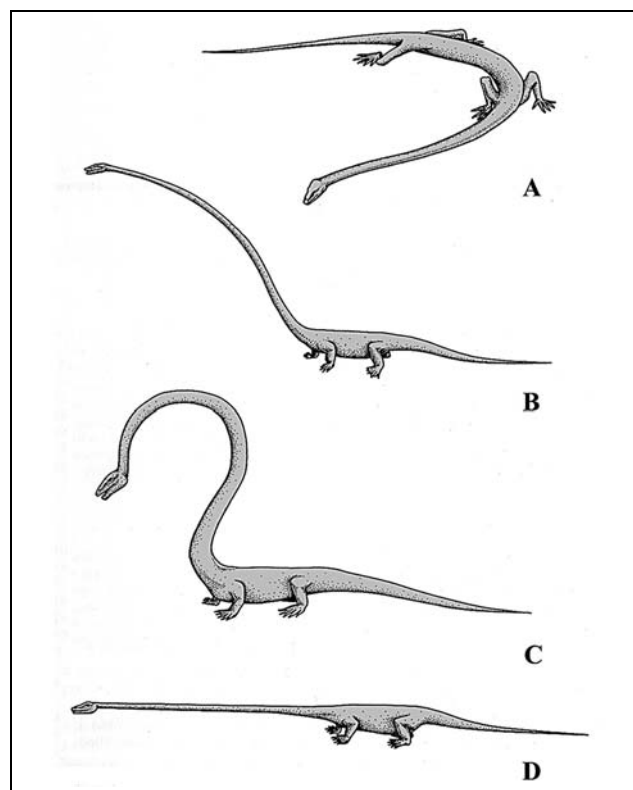

Fig 10 - Different reconstructions of the neck posture in *Tanystropheus*: A) Peyer (1931), B) Wild (1973), C) Kummer (1975), D) Tschanz (1986), modified from Tschanz (1989).

equilibrium. More recently, Tschanz (1986, 1988) compared the morphology of the cervical and cranial dorsal vertebrae of *Tanystropheus* with those of some extant squamates (with particular reference to the genera *Varanus* and *Iguana*) and concluded that several features did not permit *Tanystropheus* to raise the neck above shoulder level, mainly the absence of tall and stout vertebral spines in the cranial dorsal region that could offer sufficient insertion space for powerful epaxial musculature (other than intervertebral muscles). According to Tschanz (1986, 1988), *Tanystropheus* could only have held the neck horizontally just off the ground. In this position, the extremely elongate shafts of the cervical ribs, bundled together, formed two stiff ventral braces whose function was to transmit part of the craniocervical weight to the shoulder girdle. This would also have reduced the shearing stresses between each vertebra. According to Tschanz (1986, 1998) the stiffness of the rods formed by the bundled rib shafts, however, would have precluded the possibility of bending the neck and, as a consequence, the neck had to be held horizontally (Fig. 10D). Such a nearly inflexible and elongate neck would have represented a serious hindrance to any kind of terrestrial locomotion, and the unbalanced posture would have continually caused the animal to tilt head-down. As a consequence, Tschanz (1986, 1988) discarded the hypothesis that even juvenile individuals

might have been terrestrial and suggested a fully aquatic life habit for *Tanystropheus*. In water, buoyancy would support the long neck. Other authors (Carroll 1985; Rieppel 1989; Taylor 1989), agreed with Tschanz on the hypothesis of a fully aquatic *Tanystropheus*, though none of these authors outlined what kind of aquatic locomotion would have been suitable for this reptile. Carroll (1985), in his survey of aquatic diapsids, did not categorize the swimming method of *Tanystropheus*, Rieppel (1989) proposed that *Tanystropheus* swum mainly propelled by undulation of the tail, whilst Taylor (1989), following Wild's (1973) erroneous assumptions about the capacity for caudal autotomy in *Tanystropheus*, suggested that this reptile paddled with the hind limbs.

Comparative analysis. The recently discovered Chinese protorosaur *Dinocephalosaurus* (Li et al. 2004) reconstructed as a fully aquatic animal, consitutes an excellent basis for morphological comparison to test the likeliness of hypoteses purporting aquatic adaptations in *Tanystropheus*. *Dinocephalosaurus* has an overall morphology which is quite *Tanystropheus*-like (Fig. 11E), but its limbs exhibit a completely different architecture (Fig. 11A-B) that is definitely consistent with fully aquatic life habits. In *Dinocephalosaurus*, the fore- and hindlimbs are of equal size and show similar, very sauropterygian-like, morphologies: the humerus and the femur are thick, robust, and distally enlarged, the radius and ulna are stubby as well and surround a large spatium interosseum, the carpal and especially the tarsal bones are rounded and loosely articulated to each other, and finally the digits and the toes give a flipper-like outline to the limbs. These characters enforce the perception of *Dinocephalosaurus* as an effective, limb-propelled, swimmer with little, if any, doubt. The morphology of the limbs of *Tanystropheus*, however, is completely different (Fig. 11 C-D) and testifies to the absence of any evident adaptation for swimming in open water. In *Tanystropheus* the limb bones are slender and hollow as in other purported terrestrial protorosaurs, like *Macrocnemus* (Rieppel 1989) and *Langobardisaurus* (Renesto 1994; Renesto et al. 2002). The forelimb, especially the manus, is much smaller than the hindlimb and, along with the minimal degree of ossification of the carpus, suggests that it gave little contribution to any kind of locomotion this reptile may have adopted. As a consequence, the main source for locomotion in *Tany-*

stropheus had to be the long hindlimbs, the architecture of which, however, is completely different from those of *Dinocephalosaurus* and, more generally, of any appendage-propelled aquatic vertebrate (sensu Braun & Reif 1982, 1985). In *Tanystropheus* the pelvic girdle is small; the hindlimb bones are hollow and relatively gracile, the femur is very long and slender, and not enlarged distally; the tibia and fibula are similarly long and narrow as well, and form a nearly non existent spatium interosseum, and the knee joint is a well developed trochlea and highly mobile. The tarsus is also compact as in terrestrial reptiles and the pattern of the tarsus and crus is similar again to that of the presumably terrestrial taxa *Macrocnemus* or *Langobardisaurus* (Rieppel 1989; Renesto et al. 2002; Renesto & Avanzini 2003). In articulated specimens, the long metatarsal are not that spread out as reconstructed in Wild (1973, fig. 78) reconstruction, but are always preserved associated, with the proximal ends superimposed, again as in the terrestrial *Macrocnemus* and *Langobardisaurus*.

The limb architecture of *Tanystropheus* rules out the possiblity of subaqueous flight, and also paddling or rowing seems equally unsuitable for this reptile: most paddlers and rowers adopt an alternate locomotion so that the movement of the forelimb on one side balances that of the hindlimb of the other side to avoid side waving of the entire body during each power stroke (Braun & Reif 1985). The marked size difference between its fore- and hindlimbs means that such waving would be an issue for a swimming *Tanystropheus*. Furthermore, the elongate and laterally inflexible neck may have increased this waving, further compromising the efficiency of subaqueous locomotion. Ducks and other aquatic birds paddle with the hindlimbs only, but they float on the water surface and the limbs are oriented parasagittally, a posture that can be excluded for *Tanystropheus*. A frog-like, symmetrical swimming style, by contemporaneous power strokes of both hindlimbs can also be excluded; because it requires the development of an even stouter sacrum and pelvic girdle than in alternate rowers. Moreover, it is a discontinuous kind of locomotion, and ineffective for fully aquatic vertebrates, especially if they attain a fairly large size (Braun & Reif 1985).

There is also morphological evidence against the reconstruction of *Tanystropheus* as a lateral sculling, tail-propelled, swimmer: its tail is *dorsoventrally* flattened and widest proximally, and has long, stiffening

Specimen	MCSN 4451	*a* (Wild 1973)	*e* (Tschanz 1986)
Length of cervical vertebra (CV) 9	51	51	57
Length of cervical vertebra 10	**52**	45	54
Length of cervical vertebra 11	32	27	34
Length of cervical vertebra 12	15	12	14

Tab. 2 - Comparison between the length (in mm) of caudal cervical vertebrae in MCSN 4451 and in other specimens of *Tanystropheus longobardicus* of comparable size.

transverse processes that would have hindered lateral undulation. More posteriorly, the caudal vertebrae bear low vertebral spines and short haemal spines, bestowing the tail with a narrow and cylindrical shape. Tetrapods which swim via lateral undulation of the tail have, in contrast, long, strong and laterally flattened tails constructed by robust, high vertebral spines and equally stout and deep haemapophyses (Carroll 1985; Braun & Reif 1985) that increase the area producing thrust against water. Also, in some of the larger specimens of *Tanystropheus*, the proximal portion of the tail was further widened and stiffened by the presence of paired craniocaudally elongated eterotopic bones (considered elements supporting paired hemipenes by Wild 1973), and it is possible that the bifurcate elements (Pl. 2C) which are preserved close to the sacral-proximal caudal region, may have produced the same effect of widening and stiffening the base of the tail.

In conclusion, the evidence from the morphology of both the limbs the tail indicates that *Tanystropheus* lacked any adaptation for efficient swimming, strongly arguing against a fully, or prevalent, life in open water for this reptile.

The posture of the neck. Dinocephalosaurus shares with *Tanystropheus* a high neck to body ratio, but neck elongation in the former was attained by the addition of vertebrae rather than by elongation of existing vertebrae: the neck of *Dinocephalosaurus* consists of 25 cervical vertebrae instead of 12. This may have imparted on the Chinese taxon greater flexibility and indicates different feeding mechanics (Li et al. 2004; Peters et al. 2005). The neck of *Tanystropheus*, if stretched horizontally, was undoubtedly an impediment for even a partially terrestrial life but would also have proven an obstacle in water. Some features suggest, however, that *Tanystropheus* was capable to held the neck in an inclined, rather than horizontal posture and that the neck was more flexible and mobile than suggested by Tschanz (1986), The forward-slanting outline of the caudal surface of the last cervical body may indicate that when articulated with the first dorsal vertebra, it produced an inclined, rather that horizontal, angulation at the base of the neck. This apparently does not represent an artifact of preservation of specimen MCSN 4451 because the same slanting caudal surface is also visible in the last cervical vertebra of specimen *a* of Wild (1973) (pers. obs.), it may thus be hypothesized that the neck articulated with the trunk forming an angle and the neck maintained a linear configuration cranial to this point. Osteology notwithstanding, however, this reconstruction of the neck of *Tanystropheus* requires two issues
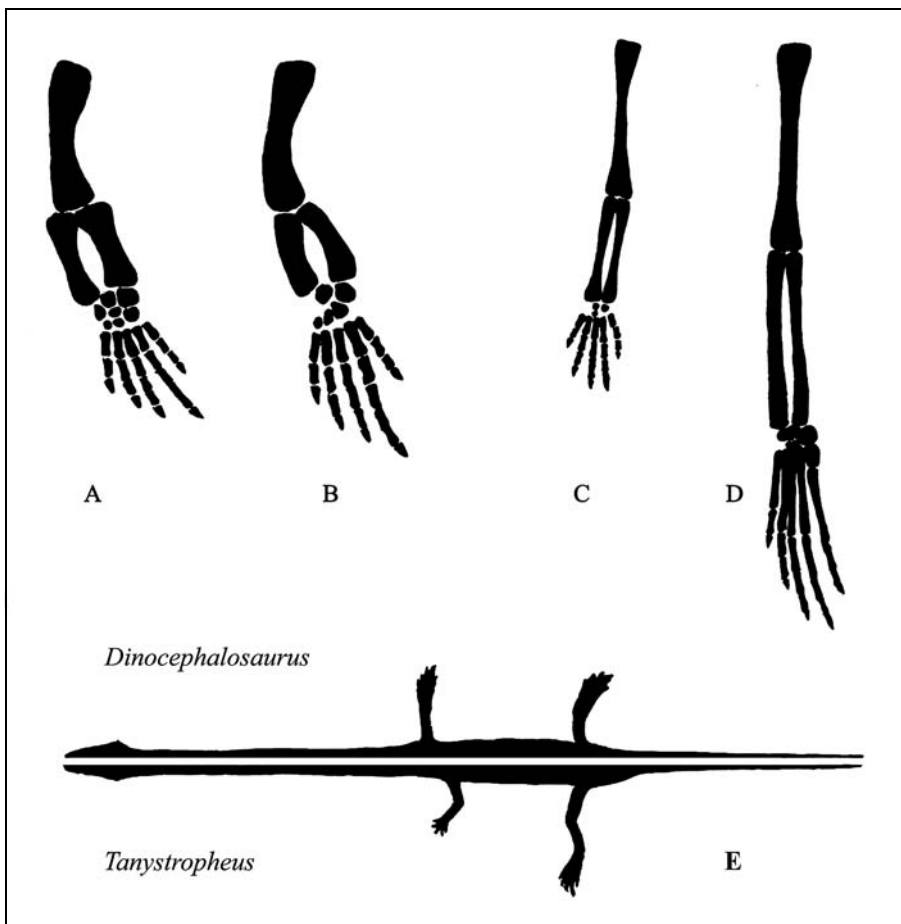

Fig 11 - A-B) sketched reconstructions of the fore-limb (A), and of the hind-limb (B) of *Dinocephalosaurus*; C-D) sketched reconstructions of (C) the fore- and (D) hindlimbs of *Tanystropheus*; E) comparison between the body outlines of the two taxa in dorsal view. Drawings not to scale.
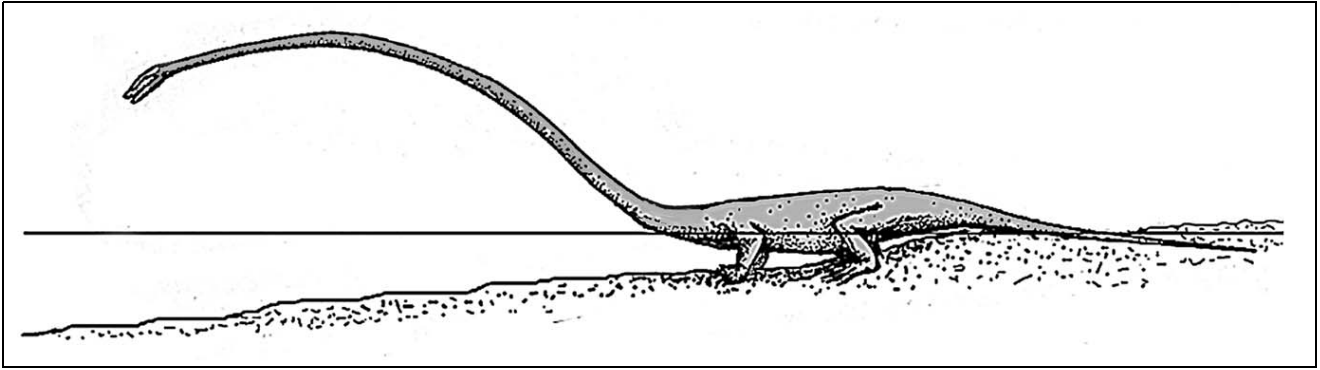
Fig. 12   - Reconstruction of *Tanystropheus* in its environment as proposed here.

be addressed. First, whether *Tanystropheus* had the myological capability to retain the neck in position and, second, whether or not the distribution of mass within the body would, by assuming this posture, make *Tanystropheus* tilt forward due to a weight imbalance.

All articulated specimens of *Tanystropheus* are preserved with the neck deeply bent dorsally, often just over to the trunk or even curled into a "ring", while the equally long necked sauropterygians are always preserved with a nearly straight, loose neck posture (e.g. Sander 1989). The dorsal curling of the neck is usually due to post mortem contraction of strong dorsal muscles or ligaments. According to Tschanz, (1986, 1988), however, the reduced neural spines allowed only minimal attachment areas for epaxial muscles, so that only the short intervertebral muscles had extensive insertional areas. As a consequence, Tschanz (1986, 1988) concluded that the epaxial musculature was too weak to lift the neck beyond the horizontal position. In the neck of *Tanystropheus,* however, the vertebral bodies are hollow, with the vertebral canal running *inside* them (Wild 1973, p. 72-73 fig 43-44, p.81 fig 51) and this feature rendered the neck much lighter than if it had fully ossified vertebral bodies. It has to be noted also that this peculiar morphology of the cervical vertebrae is strikingly similar to that of azdarchid and ctenochasmatoid pterosaurs (Dong 1982; Howse 1986; Unwin & Jungchan 1996). Both in *Tanystropheus* and in these pterosaurs, the middle cervical vertebrae are extremely elongate (length > 5 width), the neural spine is vestigial or reduced and the neural canal is confluent with the vertebral body. In addition, the orientation of the articular facets of the zygapophyses is also similar in *Tanystropheus* and in azdarchid pterosaurs, allowing mainly dorsiflexion of the neck. It is thus possible that *Tanystropheus* neck was light enough and that the musculature was sufficient to keep the neck raised, as if *Tanystropheus* developed independently a muscle/ligament system similar to that of the long necked pterosaurs which had undoubtedly the capability to keep the neck raised above the horizontal plane.

In the long necked pterosaurs, the danger of lateral torsion of the vertebral column was minimized by the development of exapophyses (Wellnhofer 1991) which formed extra articular processes at the ventral ends of the vertebral body, and prevented vertebral torsion as well as lateral movements of the neck. The bundled shafts of the cervical ribs of *Tanystropheus* other than a support bracing the neck, may have played a similar role, protecting the neck from dangerous torsions and greatly reducing the possibility of lateral movements.

Concerning the problems of balance out of water and the risk of tilting forward, it is worthwhile to note that not only the neck, but the whole cranial portion of the body was much lighter than the caudal one: the cranial limbs were much smaller. Along with the reduction of weight in the cranial portion of the body, there was an increase of weight caudally: the soft parts preserved in MCSN 4451, along with the development of the transverse processes of the proximal caudal vertebrae, suggest the presence of huge muscle mass at the base of the tail which would have added considerable weight to that area, thus shifting the centre of mass posteriorly. This may have rendered *Tanystropheus* balanced enough to keep the neck raised off the ground without tilting forwards even out of water. The rods formed by the bundled shafts of the cervical ribs may have played the same role of passive support for the neck also dorsiflexed in a diagonal angle with the rest
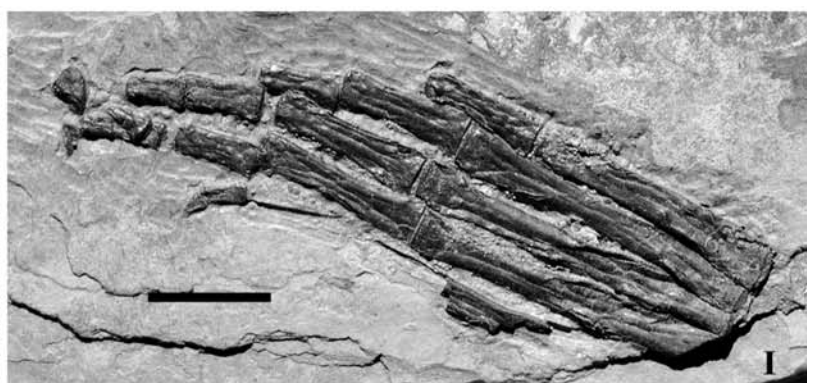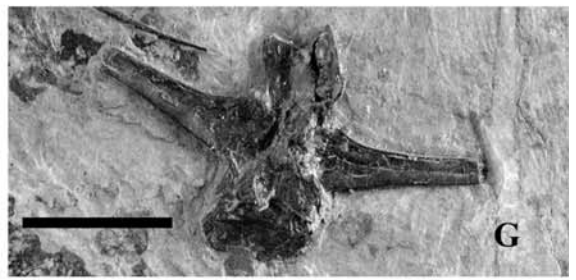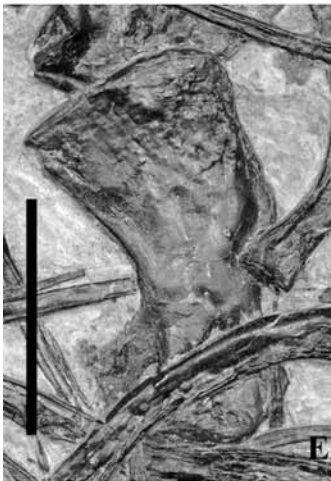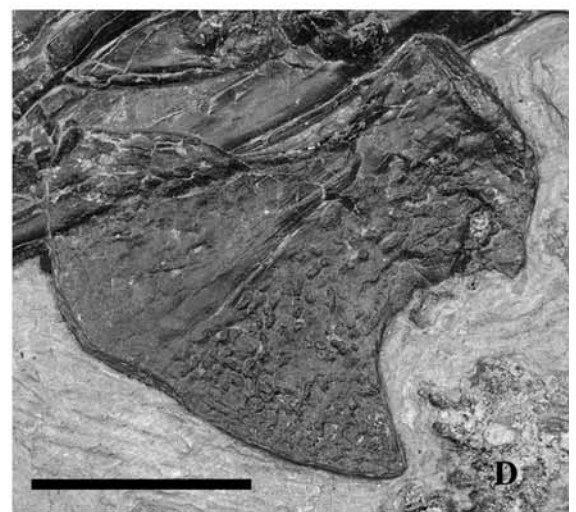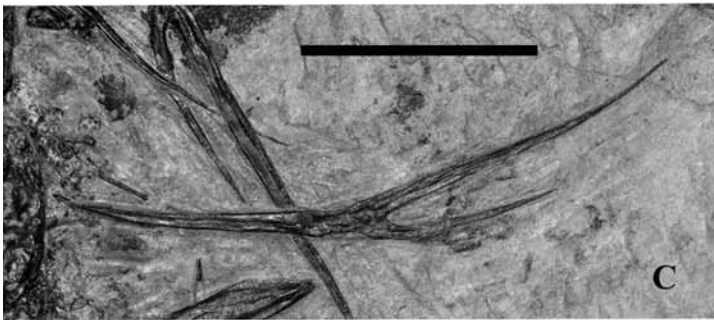
PLATE 1

Tanystropheus sp. Specimen MCSN 4451, as preserved, scale bar equals 5 cm.

PLATE 2

Tanystropheus sp. Specimen MCSN 4451; A) head of cervical rib, B) disarticulated thoracic vertebrae, C) bifurcate element, D) left ischium, E)?left pubis F) right ilium, G) second caudal vertebra, H) tarsus, I) metatarsus. Scale bars equal 0.5 cm (A) and 1 cm (B-I).
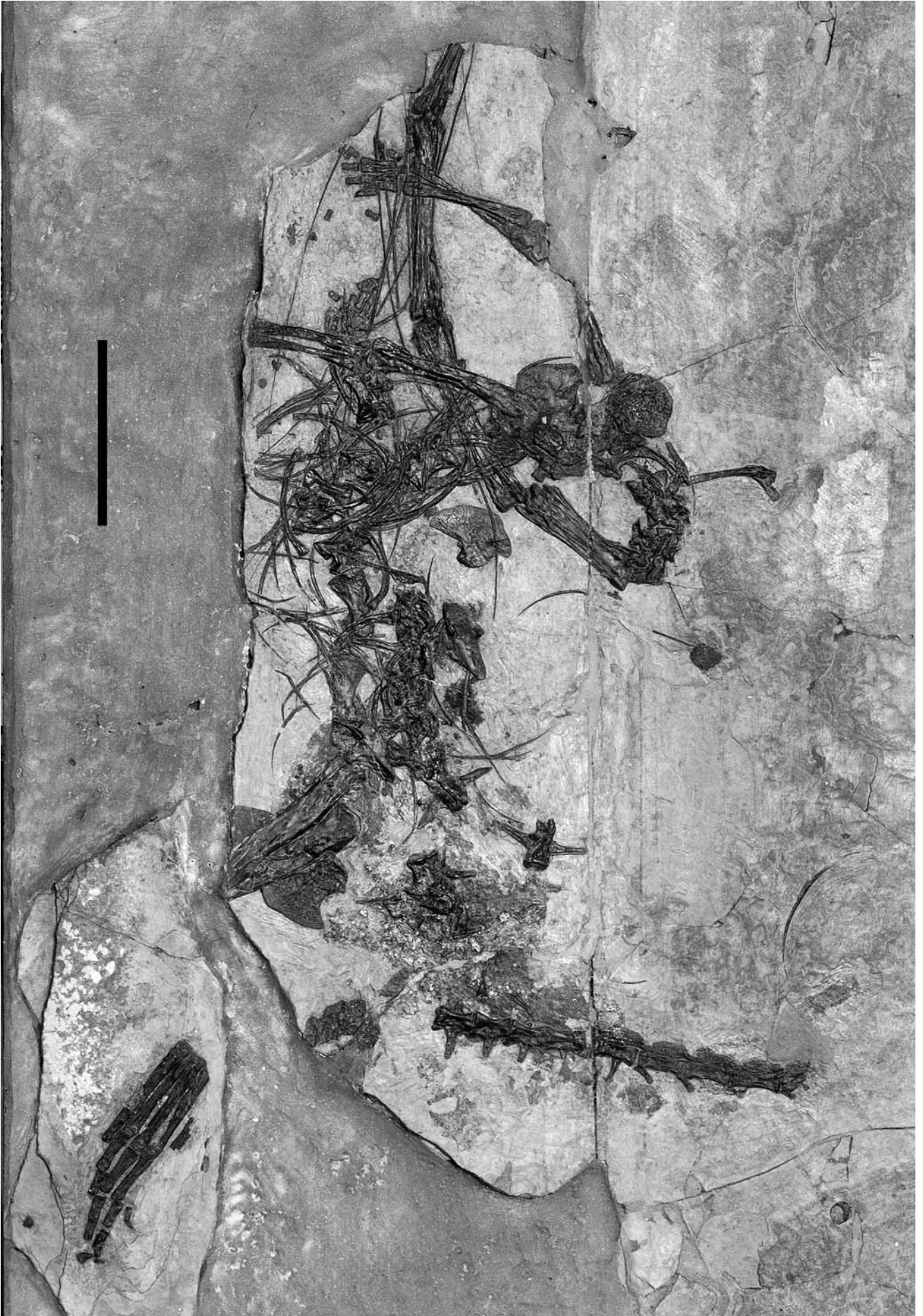
of the body. These rods surely reduced at some extent the possibility of dorsoventral flexion of the neck, but did not render it stiff, in fact, thin bony rods, especially in humid conditions, as when inside the body, are quite flexible allowing a certain degree of flexion to the structure, thus permitting to the ventral musculature (*longus colli, rectus captis anterior*) to bend the neck along the sagittal plane.

Taphonomical evidence. Within the Grenzbitumenzone, the finds of *Tanystropheus* are restricted to the middle levels, which according to Roehl et al (2001) corresponded to an intraplatform basin where large fishes and ichthyosaurs were abundant and which was slightly deeper and more open than the more restricted and shallow carbonate platforms of the upper and lower levels. This scenario, at first, seems to speak for a fully aquatic *Tanystropheus*, but just the opposite may be true. In fact, the middle levels of the Grenzbitumenzone are the only ones which have yielded remains of terrestrial reptiles; like the protorosaur *Macrocnemus* (which, with 19 collected specimens, is even more abundant than *Tanystropheus*, despite its alleged terrestrial habitat) and the rauisuchid *Ticinosuchus* (2 specimens). It is perhaps feasible that the more open water conditions, allowed the ingress of large fishes and ichthyosaurs, which outcompeted other less specialized predators; in the middle levels of the Grenzbitumenzone sauropterygians are in fact missing, while they are more common in the upper levels, where ichthyosaurs are virtually absent, whilst only semi-aquatic and terrestrial taxa did not suffer from competition. Surely, *Tanystropheus*, being even less adapted to swimming than nothosaurs, if aquatic, would have suffered even more than sauropterygians from competition. It thus seems more feasible that *Tanystropheus* lived closer to or even on, the emerged land. Also "*T. meridensis*" and

MCSN 4451 have been collected in a marine, yet coastal, environment that reflects more open water environment than the upper and lower levels of the Grenzbitumenzone. It is thus feasible that also these specimens were transported from their original life habitat to the bottom of the basins after death.

In conclusion, both morphological and taphonomic data concur to suggest that *Tanystropheus* was not a primarily aquatic reptile. More probably, *Tanystropheus* did not swim but lived along the shoreline, as already suggested for other protorosaurs like *Langobardisaurus* (Renesto & Dalla Vecchia 2000; Renesto et al. 2002) and *Macrocnemus* (Renesto & Avanzini 2002; Avanzini & Renesto 2002). *Tanystropheus* could have lived just out of the water as in Peyer's (1931) original hypothesis, (Fig. 12), slowly moving along, patrolling the shoreline in search for food with its long neck kept just raised above the water surface, to avoid scoring by potential prey. The survey range allowed by the long neck might have been even greater if the animal was able to turn the cranial part of the body on each side, by action of the long caudal limbs making a fulcrum on the pelvic area while the weight of the massive caudal region, acted as a counterbalance. When prey was spotted, the reptile could have caught it by suddenly bending and straightening the neck.

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