A Morphological and Morphometric Redescription of *Tanytrachelos ahynis*

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Introduction

First described in 1979 by P. E. Olsen, *Tanytrachelos ahynis* was a small, aquatic protorosaur that lived in a Triassic lake along what is now known as the Virginia-North Carolina border.

Specimen Locality

All specimens in this study of *Tanytrachelos ahynis* were found in the second, third, and sixteenth cycles of the Solite Quarry B in Cascade, Virginia (Figure 1). The quarry is located in a Triassic rift basin near the border between Virginia and North Carolina, and exposes roughly thirty lacustrine cycles of the Cow Branch Formation.

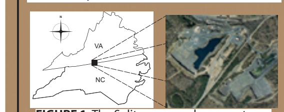

FIGURE 1. The Solite quarry, where most specimens of *Tanytrachelos* have been found.

An array of other vertebrate, invertebrate, and plant fossils have also been found here, including the gliding reptile *Mecistotrachelos apeoros* (known only from this locality), a variety of fish, one type of phytosaur, and over 2,000 insect specimens. The quality of the specimens and their high quantity diagnose the Solite quarry as a konservat and konzentrat laggerstatte.

Previous Research on *Tanytrachelos*

In 1979, P.E. Olsen wrote the first description of *Tanytrachelos ahynis* based on over 100 specimens. This publication described the ribs and vertebrae, compared the lengths of the forelimb to the hindlimb, and described the family Tanystrophidae to which it belongs.

The next publication on *Tanytrachelos*, written by Casey et al. in 2007, used quantitative morphometrics to examine the frequency of specimen completeness, degree of articulation in specimens, and frequency of soft tissue preservation as a way to describe the taphonomy of *Tanytrachelos* and the depositional environment of the Solite quarry.

Study Purpose and Impact

This study can ultimately impact how we view the phylogenetic structure of Archosauromorpha by fulfilling two purposes:

1. To provide a new, detailed redescription of *Tanytrachelos* that is based on 200 more specimens than was the first description and that utilizes CT scans and extensive morphometrics.

2. To provide data that were previously missing for *Tanytrachelos* in past cladistic analyses of Protorosauria in order to test the hypothesized monophyly (Rieppel et al. 2003) of this group. If this group were found to be paraphyletic, the dispersion of protorosaurs within Archosauromorpha would then require the phylogeny of the latter group to be reexamined.

Procedures

Specimens Studied

314 hand specimens and two CT scans of *Tanytrachelos* were examined. Of these, 307 belong to the Virginia Museum of Natural History (Martinsville, VA) and the remaining seven belong to the Yale Peabody Museum (New Haven, CT).

Gathering Quantitative Data: Length and Angle Measurements of Individual Elements

A total of 68 types of length measurements of individual elements were taken from digital photographs in Adobe Photoshop CS4. Additionally, the angles of the paired heterotopic bones were measured with respect to the vertebral column (four total measurements).

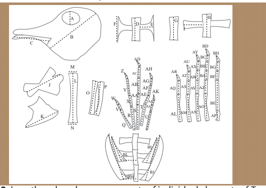

FIGURE 2. Length and angle measurements of individual elements of *Tanytrachelos*. Illustrations are not to scale. A, orbit diameter; B, skull diameter; C, dentary length; D, length of cervical centra; E, width of cervical ribs; F, length of cervical ribs; G, length of centra of dorsals and caudals 7 through 31; H, length of centra of sacrals and caudals 1 through 6; I, length of sacral and caudal transverse processes; J, ischium length; K, ilium length; L, length of femur and humerus; M, proximal width of femur and humerus; N, distal width of femur and humerus; O, length of the fibula and radius; P, length of the tibia and ulna; Q through T, length of metacarpals I through V; V through AK, length of manus phalanges; AL through AP, length of metatarsals I through V; AQ through BH, pes phalanges length; BI and BH, heterotopic bone length; BL and BM, angles of heterotopic bones with respect to the vertebral column.

Derived Variables

An additional 5 morphometric variables were derived from the length measurements:

- Skull lateral area: SA=3.14(diameter/2)^2
- Orbit Lateral Area: OA=3.14(diameter/2)^2
- Percentage of skull area occupied by orbit: %=100(OA/SA)
- Humerus and femur aspect ratio:

$$\frac{\text{distal width} + \text{proximal width})/2}{\text{length of bone}}$$

Nonparametric test for Presence of Heterotopic Bones vs. Body Size

In order to look for a correlation between the presence or absence of heterotopic bones and body size, a nonparametric Wilcoxon two-tailed test was run in the program SAS, using femur lengths as approximations to overall body sizes. Eight specimens belonged to the group without heterotopic bones, and five belonged to the group with heterotopic bones.

Abbreviations

A	astragalus	LDC	lateral distal carpal
AT	axis/atlas	LH	lateral heterotopic
C	caudal vertebra	MDC	medial distal carpal
CA	calcaneum	MH	medial heterotopic
CE	cervical vertebra	MT	metatarsal
CO	coracoid	N	nasal
D	dorsal vertebra	O	orbit
DC	distal carpal	P	pubis
DE	dentary	PM	premaxilla
DT	distal tarsal	PO	postorbital
F	femur	Q	quadrate
FI	fibula	R	radius
FR	frontal	RE	radiale
H	humerus	S	sacral vertebra
IL	ilium	SC	scapula
IS	ischium	SQ	squamosal
L	lacrimal	T	tibia
M	maxilla	U	ulna
MC	metacarpal	UE	ulnare

Results

Skull

FIGURE 3. The skull of *Tanytrachelos* is seen in only seven specimens, including VMNH982. All of the skulls are so poorly preserved that the exact labels of individual elements are uncertain. The dentition is pleurodont and homodont, with the most posterior tooth resting on the maxilla. The orbits occupy 11%-13% of the skulls' lateral surfaces.

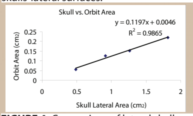

FIGURE 4. Comparison of lateral skull area to the area of the orbit, based on morphometric measurements from specimens YPM7496A, 7622, VMNH982, and VMNH3651.

Cervical Vertebrae

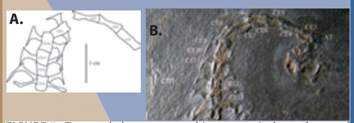

FIGURE 5. *Tanytrachelos* possesses thirteen cervical vertebrae, starting with the axis, which has no centrum and is fused to the atlas. The remaining 11 cervicals each have a pair of long, low cervical ribs. The length of the neck comprises roughly 25% of the vertebral length of the animal. **A.** Partial cervicals of a yet unnumbered specimen. **B.** Cervicals of VMNH3651.

Dorsal Vertebrae

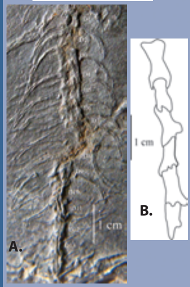

FIGURE 6. The thirteen procoelous dorsal vertebrae that follow the cervical vertebrae span 21% of the animal's vertebral length. Dorsal vertebrae 11 through 13 have short transverse processes. **A.** Dorsal vertebrae of VMNH3651. **B.** Partial dorsal vertebrae of lot 30.251.

Sacral Vertebrae

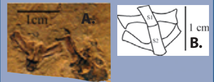

FIGURE 7. Two sacral vertebrae support the hip structure. In articulated specimens, the first sacral vertebra has transverse processes perpendicular to the centrum, and the second sacral vertebra has transverse processes that are anteriorly angled to meet those of the first sacral vertebra. **A.** Disarticulated sacral vertebrae of lot 30.245. **B.** Articulated sacral vertebrae of a yet unnumbered specimen.

Caudal Vertebrae

FIGURE 8. *Tanytrachelos* has at minimum 31 caudal vertebrae, the first six of which possess tranverse processes. The tail occupies roughly half of the entire body length. **A.** The entire tail of lot 30.267. **B.** A caudal vertebra in anterior view and a caudal vertebra in dorsal view of lot 30.325 #23. **C.** The second sacral and first four caudal vertebrae of YPM7621.

Dorsal Ribs

FIGURE 9. Each dorsal vertebra has a pair of unfused, holocephalous dorsal ribs except for dorsal vertebrae 11 through 13. **A.** Articulated dorsal rib sequence of a yet unnumbered specimen. **B.** An isolated dorsal rib of FN17A4.

Gastralia

FIGURE 10. Thin gastralia, shown here in lot 30.267, occupy the torso between the fourth dorsal and first sacral vertebrae.

Heterotopic Bones

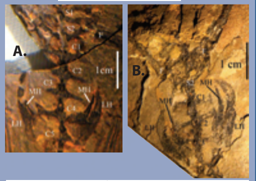

FIGURE 11. Pairs of curved heterotopic bones are found in some specimens on either side of caudal vertebrae 4 and 5. The angle between the tail and these bones ranges from 95 to 129 degrees. This variation, as well as the selective disarticulation found in specimen 04-23, indicate that these bones were not fused to the vertebral column. **A.** A yet unnumbered specimen, articulated. **B.** Specimen 04-23 is partially disarticulated from an anteriorly directed postmortem force. While the heads of the femurs remain in place, the heterotopic bones are pushed up to caudal vertebrae 2 and 3.

Smallest Found Juvenile

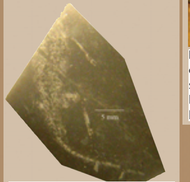

FIGURE 12. The smallest juvenile specimen of *Tanytrachelos* found to date lacks the neck and skull, and is approximated between 3 and 4 cm in total length. Unlike larger specimens, the outer soft tissue imprints mask the details of individual bones. There is a 5 mm long sac-like structure directly behind the pelvis that follows the proximal caudal vertebrae. This structure is interpreted as the location of the heterotopic bones due to its location and length. The length of the sac spans 23.4% of the 21.4 mm tail, a ratio that in larger specimens ends at the posterior end of the seventh caudal vertebra. This is congruent with lengths of heterotopic bones in larger specimens, which span approximately seven caudal vertebrae.

Pectoral Girdle

FIGURE 13. The pectoral girdle consists of unfused fan-shaped scapulae and coracoids, shown here in a disarticulated unnumbered specimen.

Pelvic Girdle

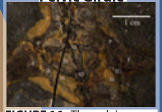

FIGURE 16. The pelvis, shown in this unnumbered specimen, shows no discernable obturator foramen.

Anterior Limb

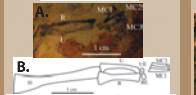

FIGURE 14. A. Right forelimb of an unnumbered specimen. **B.** Right forelimb of lot 30.267.

Posterior Limb

FIGURE 17. The hindlimb, shown in this unnumbered specimen, is longer than the forelimb.

Manus

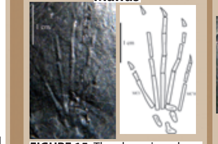

FIGURE 15. The above is a photograph and illustration of the right manus of lot 30.315. The manus has the phalangeal formula 2-3-4-4-3, and has a radiale, an ulnare, and two distal carpals.

Pes

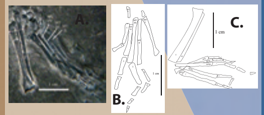

FIGURE 18. The pes has the phalangeal formula 2-3-4-5-4 and has a calcaneum, astragalus, and distal tarsals 3 and 4 in the tarsus. The fifth metatarsal is much shorter than the other four and has a slight proximal hook. **A.** YPM7621 left pes. **B.** VMNH2827 right pes. **C.** YPM7540 right pes.

Type Specimen

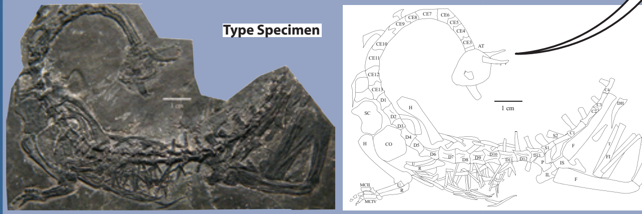

FIGURE 19. Photograph and labeled Illustration of the type specimen of *Tanytrachelos* (YPM7496A).

Abstract

Tanytrachelos ahynis is a small (approximately 21 cm long) aquatic protorosaur recorded from the Newark Supergroup. Most specimens are known from exposures of the Cow Branch Formation at the Solite Quarry on the Virginia-North Carolina border. Originally described on the basis of roughly 100 specimens, an additional 200 specimens have since been collected. The new material provides added insights into *Tanytrachelos*. Although the vast majority of specimens are impossible to mechanically or chemically prepare from the sediment matrix, Computed Tomography has allowed anatomical details otherwise obscured by sediment to be revealed. The use of quantitative morphometrics has also provided a more quantitative description. The in-depth study resulting from these resources allows for the suite characters missing for *Tanytrachelos* in previous cladistic analyses of Protorosauria and Archosauromorpha to be added so that future reanalyses may take place. Three hundred and fourteen specimens and two CT scans of *Tanytrachelos* where studied to create a new qualitative description of its morphology. Additionally, 68 length measurements and four angle measurements of individual elements (from which five variables were derived) were taken from these specimens for a quantitative description. The vertebral column of *Tanytrachelos* is comprised of thirteen cervicals, thirteen dorsals, two sacrals, and at least thirty-one caudals. The few preserved skulls show rows of homodont, pleurodont teeth and an orbit that consistently occupies 11%-13% of the lateral area of the skull. The carpus contains an ulnare, radiale, and two distal carpals, and the tarsus contains a calcaneum, astragalus, and distal tarsals 3 and 4. The fifth metatarsal is significantly short, with a hooked shape at its proximal end. Pairs of curved, unfused heterotopic bones are found in some specimens between caudal vertebra 4 and 5. Traces of soft tissue are seen in a select few specimens, including a remarkable juvenile specimen (measuring approximately 3-4 centimeters in length), which displays a nearly complete body outline.

Conclusions

Possible Function of Paired Heterotopic Bones

Although the nonparametric test showed no correlation between the presence of heterotopic bones and the size of the body as proxied by femur length (z=1.2, p=0.23), the distribution of heterotopic bones among several yet not all specimens is highly indicative of sexual dimorphism, as this distribution has been shown not to be a result of taphonomic signals (Casey et al. 2007). Although extant xantusiids and gekkonoids have cloacal bones, these bones differ in shape, number, and orientation to the degree that they are not thought to be homologous to the heterotopic bones of *Tanytrachelos* (Kluge 1982). As seen in Figure 11, these pairs of bones are not attached to the caudal vertebrae, and the juvenile specimen in Figure 12 shows that they are strictly internal structures. This renders hemipenes or claspers as unlikely functions of the heterotopic bones, as such structures would be partly external. Instead, these bones more likely may have provided support for the egg clutch in the female, which then leads to the question of *Tanytrachelos* oviparity versus ovoviviparity (the latter being sometimes employed by aquatic reptiles), a question that cannot be answered with the currently available specimens.

Diagnostic Qualities of *Tanytrachelos*

Tanytrachelos is a very small (21 cm long) member of Tanystrophidae with 25% of the length of the vertebral column occupied by the cervical vertebrae, 21% occupied by the dorsal vertebrae, 4% occupied by the sacral vertebrae, and 50% occupied by the caudal vertebrae. It was probably insectivorous due to its homodont dentition. Furthermore, *Tanytrachelos* has consistently large orbits compared to the size of its skull (11-13% occupancy). This characteristic, coupled with the presence of heterotopic bones in the 4 cm long juvenile shown in Figure 12, may indicate that *Tanytrachelos* was neotenic. The hindlimbs and pedes are significantly larger than the forelimbs and manus. Transverse processes on the vertebrae of *Tanytrachelos* range from the eleventh dorsal vertebra to the sixth caudal vertebra.

Tanytrachelos Compared to Its Sister Taxon *Tanystropheus*

Similarities

- -13 cervical vertebrae (Rieppel et al. 2010)
- -13 dorsal vertebrae
- -Dorsal vertebrae 11-13 have short, straight robust transverse processes
- -Fan-shaped scapulae
- -Same phalangeal formulae on manus and on pes
- -Carpus comprised of radiale, ulnare, and 2 distal carpals
- -Tarsus comprised of astragalus, calcaneum, and distal tarsals 3 and 4
- -Extremely short, slightly hooked metatarsal V
- -Post-pubic heterotopic bones in some specimens

Differences

Tanytrachelos	*Tanystropheus*
Average length: 21 cm	Average total length is 6 m
Homodont teeth	Heterodont Teeth (Nosotti 2007)
Procoelous dorsal vertebrae	Amphicoelous dorsal vertebrae (Wild 1973)
All dorsal ribs holocephalous	First three dorsal ribs dichocephalous, rest holocephalous (Nosotti 2007)
At least 31 caudal vertebrae	At least 41 caudal vertebrae (Nosotti 2007)
All metacarpals roughly the same length	Metacarpals I and V shorter than II-IV (Nosotti 2007)

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