Postcranial Anatomy of
Tanius Sinensis Wiman, 1929
(Dinosauria; Hadrosauroidea)

Postkraniala anatomin hos Tanius sinensis
Wiman, 1929 (Dinosauria; Hadrosauroidea)

Niclas H. Borinder
Postcranial Anatomy of
*Tanius Sinensis* Wiman, 1929
(Dinosauria; Hadrosauroidea)

Postkraniala anatomin hos *Tanius sinensis*
Wiman, 1929 (Dinosauria; Hadrosauroidea)

Niclas H. Borinder
Abstract

Postcranial Anatomy of Tanius Sinensis Wiman, 1929 (Dinosauria; Hadrosauroida)
Niclas H. Borinder

Tanius sinensis Wiman, 1929 was one of the first hadrosaurid or “duck-billed” taxa erected from China, indeed one of the very first non-avian dinosaur taxa to be erected based on material from the country. Since the original description by Wiman in 1929, the anatomy of T. sinensis has received relatively little attention in the literature since then. This is unfortunate given the importance of T. sinensis as a possible non-hadrosaurid hadrosauroid i.e. a member of Hadrosauroida outside the family of Hadrosauridae, living in the Late Cretaceous, at a time when most non-hadrosaurid hadrosaurids had become replaced by the members of Hadrosauridae. To gain a better understanding of the anatomy of T. sinensis and its phylogenetic relationships, the postcranial anatomy of it is redescribed. T. sinensis is found to have a mosaic of basal traits like strongly opisthocoelous cervical vertebrae, the proximal end of scapula being dorsoventrally wider than the distal end, the ratio between the proximodistal length of the metatarsal III and the mediolateral width of this element being greater than 4.5. Derived traits present in T. sinensis include curved dorsal surface of the scapula, arcuate fourth trochanter of the femur, cnemial crest of the tibia extending ventrally into the proximal half of the shaft, and the distal end of the fibula expanding into a club shape in lateral view. A potential autapomorphy is noted, being the caudal fusion of the medial and lateral condyles of the femur forming a completely enclosed “tunnel”. The body mass of the holotype of T. sinensis, is also estimated, and found to have been around 2950 kg. The phylogenetic analysis agrees with previous studies placing T. sinensis as a non-hadrosaurid hadrosauroid. Furthermore, in the phylogenetic analysis, T. sinensis is recovered as non-hadrosaurid hadrosauroid, forming a clade with Bactrosaurus johnsoni Gilmore, 1933, which shares the following unambiguous synapomorphies; the width of the orbital margin of the jugal being almost equally wide to that of the infratemporal margin of the bone; the ratio between the mediolateral width of the skull roof across the postorbitals and that across the quadrate cotyli of the paired squamosals being more than 1.20.

Keywords: Tanius, Jiangjiuding, postcranial, hadrosauroid, phylogeny

Degree Project E1 in Earth Science, IG025, 30 credits
Supervisor: Nicolás E. Campione
Department of Earth Sciences, Uppsala University, Villavägen 16, SE-752 36 Uppsala (www.geo.uu.se)

ISSN 1650-6553, Examensarbete vid Institutionen för geovetenskaper, No. 320, 2015

The whole document is available at www.diva-portal.org
Populärvetenskaplig sammanfattning

Postkraniala anatomin hos *Tanius sinensis* Wiman, 1929 (Dinosauria; Hadrosauroidea)
Niclas H. Borinder

Den här uppsatsen handlar om *Tanius sinensis* Wiman, 1929 som levde under Kritaperioden i Shandongprovinsen i nordöstra Kina. *Tanius sinensis* hörde till gruppen ”Anknäbbsdinosaurier” som utvecklades under början av Kritaperioden för mellan 130-100 miljoner år sedan. I slutet av Kritaperioden för ungefär 84 miljoner år sedan så blev de ”primitiva” ”anknäbbsdinosaurierna” bortträngda av de mer ”avancerade” ”anknäbbsdinosaurierna”. *Tanius sinensis* är viktig på så vis att den kan ha varit en ”primitiv” ”anknäbbsdinosaurie” som överlevde vid en tidpunkt när de flesta andra ”primitiva” ”anknäbbsdinosaurier” hade trängts undan. För att få en bättre bild av *T. sinensis* anatomiska kännetecken och en bättre bild av dess släktskapsförhållanden, så ombeskrivs anatomin hos den del av skeletten som inte omfattar kraniet. En släktskapsanalys görs också baserat på de kännetecken jag själv och tidigare forskare har observerat i skeletten. De anatomiska observationerna avslöjar en mosaik av ”primitiva” och mer ”avancerade” karaktärer, som tillsammans med släktskapsanalysen pekar på att *T. sinensis* var en sent överlevande ”primitiv” ”anknäbbsdinosaurie”.

Nyckelord: *Tanius*, Jiangjunding, postcranial, hadrosauroid, fylogeni

Examensarbete E1 i geovetenskap, 1GV025, 30 hp  
Handledare: Nicolàs E. Campione  
Institutionen för geovetenskaper, Uppsala universitet, Villavägen 16, 752 36 Uppsala (www.geo.uu.se)

ISSN 1650-6553, Examensarbete vid Institutionen för geovetenskaper, Nr 320, 2015

Hela publikationen finns tillgänglig på www.diva-portal.org
# Table of Contents

1. Introduction .................................................................................. 1

2. Aim ............................................................................................ 2

3. Background .................................................................................. 3
   3.1 Geological context .................................................................. 3
   3.2 Paleoenvironmental context ..................................................... 5
   3.3 Historical context .................................................................. 5

4. Methodology ................................................................................ 6
   4.1 Osteological comparisons ....................................................... 6

5. Results ........................................................................................ 7
   5.1 Systematic palaeontology ....................................................... 7
   5.2 Holotype ............................................................................... 7
   5.3 Locality and horizon ............................................................... 8
   5.4 Diagnosis ............................................................................. 8
   5.5 Description .......................................................................... 9
      5.5.1 Axial skeleton .................................................................. 9
      5.5.2 Appendicular skeleton ....................................................... 13
   5.6 Referred material PMUR235 and PMUR239 ......................... 18
   5.7 Locality and horizon ............................................................... 18
   5.8 Comments ........................................................................... 18
   5.9 Description .......................................................................... 18
   5.10 Referred material PMUR271 and PMUR27 ......................... 19
   5.11 Locality and horizon ............................................................. 19
   5.12 Comments ........................................................................... 19
   5.13 Description .......................................................................... 19
   5.14 Referred material small vertebra without registration number .. 20
   5.15 Locality and horizon ............................................................. 20
   5.16 Description ........................................................................... 20
   5.17 Referred material, two fragmentary vertebrae centra ............ 21
   5.18 Locality and horizon ............................................................. 21
   5.19 Description ........................................................................... 22
   5.20 Referred material, two pubic bones PMUR245, and one without number 22
   5.21 Locality and horizon ............................................................. 22
   5.22 Description ........................................................................... 22
   5.23 Comparisons between the two humeri .................................. 22

6. Phylogenetic systematics .............................................................. 23
   6.1 Methods and materials ........................................................... 23
   6.2 Results of phylogenetic tree .................................................... 24

7. Discussion .................................................................................... 27
   7.1 Postcranial character complex in *Tanius sinensis* .................. 27
   7.2 Paleobiological implications .................................................... 30
   7.3 The size of *Tanius sinensis* .................................................... 31

8. Conclusions ................................................................................. 32

9. Acknowledgements ..................................................................... 32

10. References .................................................................................. 34

11. Plates .......................................................................................... 43

Appendix 1 Axial skeleton measurements ........................................... 109

Appendix 2 Appendicular skeleton measurements .............................. 111
### 1. Introduction

Hadrosauroids, here defined as the as the least inclusive taxon containing *Equijubus normani* You et al 2003a and *Parasaurolophus walkeri* Parks, 1922, where a major group of ornithopods that first appears in the fossil record of the Early Cretaceous, with the earliest member *E. normani* (Norman 2004; Horner, Weishampel and Forster 2004) from China being found in deposits dated as Late Barremian-Albian, upper Lower Cretaceous (Tang et al. 2001). By the end of the Cretaceous they had spread to all continents except Africa and Australia, and especially in Laurasia, becoming one of the most diverse and abundant large-sized tetrapods of the Late Cretaceous (Horner, Weishampel and Forster 2004; Lund and Gates 2006). From the Santonian and onward, the hadrosauroids outside the family of Hadrosauridae became replaced by the members of the Hadrosauridae (Norman 2004; Prieto-Márquez 2010b; Campione et al. 2013; Xing et al. 2014b).

*Tanius sinensis* Wiman, 1929, is a hadrosaurid from the Jiangjunding Formation of the Upper Cretaceous Wangshi Group, Shandong Province, China (Hu et al. 2001; Poropat and Kear 2013). *Tanius sinensis* is not the only hadrosaurid known from the Wangshi Group; Young (1958) described and named *Tanius chingkankouensis* and the lambeosaurine *Tsintaosaurus spinorhinus*. The validity of *T. chingkankouensis* is generally not accepted, and, for example, it is regarded as “doubtful” by Buffetaut (1995) or treated as synonymous with *T. sinensis* (Horner, Weishampel and Forster 2004; Lund and Gates 2006). Other hadrosaurid taxa from the Wangshi Group include the giant hadrosaurine *Shantungosaurus giganteus* Hu, 1973. Both *Zhuchengosaurus maximus* Zhao et al., 2007 and *Huaxiaosaurus aigahtens* Zhao, Wang and Li, 2011, have recently been considered junior synonyms of *Shantungosaurus* (Xing et al. 2014a). Although the phylogenetic affinities of *S. giganteus* have varied (Horner, Weishampel and Forster 2004; Prieto-Márquez 2010a,b; Xing et al. 2014a,b) most recent analyses consider it as more closely related to *Edmontosaurus* than to other hadrosaurines (e.g., Xing et al. 2014a).

One more species of *Tanius* was erected besides the already mentioned *T. sinensis* and *T. chingkankouensis*, *T. laiyangensis* Zhen, 1976 from the Late Cretaceous of Laiyang county, Shandong province. Both *T. chingkankouensis*, and *T. laiyangensis* are based solely on postcranial material. Based on advanced traits in their ilia, such as a marked curvature of the dorsal edge and a very prominent supraacetabular processes, Buffetaut and Tong-Buffetau (1993) and Buffetaut (1995) judged them as being far too advanced to be referred to *Tanius*. *T. laiyangensis* was later synonymised with *Tsintaosaurus* (Horner et al. 2004). Wiman (1929) described *T. sinensis* as a member of Hadrosauridae, a view shared by Young (1958). However, von Huene (1956; cited by Prieto-Márquez 2010a) coined the family Prohadrosauridae where he placed *Tanius* with taxa like *Telmatosaurus*, Young (1958) sank Prohadrosauridae into a subfamily of Hadrosauridae; Prohadrosaurinae.
Horner, Weishampel and Forster (2004, after Weishampel and Horner 1990) placed *Tanius* as a basal member of Hadrosauridae outside the subfamilies Lambeosaurinae and Hadrosaurinae, based on several cranial characters but added that features like the tall neural spine and robust, and angular deltopectoral crest suggested affinities with lambeosaurines. Recent studies have regarded *Tanius* as a non-hadrosaurid hadrosauroid (Sues and Averianov 2009; Prieto-Marquez 2010a; Xing et al. 2014b), somewhat echoing of von Huene’s (as described by Young (1958) and Prieto-Marquez 2010a).

Given the historical importance of *T. sinensis* as one of the first named hadrosauroids from China, it has received relatively little attention in the literature since then. Furthermore the age of the Jiangjunding Formation places *T. sinensis* within the Late Cretaceous (Hu et al. 2001), a time when most non-hadrosaurid hadrosauroids are thought to have largely gone extinct (Norman 2004), at least in North America (Campione et al. 2013).

Since its original description by Wiman (1929), the post-cranial anatomy of *T. sinensis* has not been studied in detail. However, considering its historical, phylogenetical and temporal importance, this study aims to adjust that. Further work on its phylogenetical affinities would be useful to confirm or disprove the hypothesis that *T. sinensis* was a non-hadrosaurian hadrosauroid, which together with other non-hadrosaurian hadrosauroids survived at least in parts of Asia and Europe until the end of the Cretaceous.

2. Aim

The aim of this work is to describe the postcranial anatomy of *T. sinensis* within the modern comparative framework and give a clearer understanding of its phylogenetic affinities. In addition, this study presents a photographic atlas of each of the postcranial bones attributable to *T. sinensis*. The study was conducted in the following steps: Step 1, a physical examination of the postcranial remains attributed to *T. sinensis*, while comparing it to four other selected comparison taxa. Additional skeletal remains that may possibly be attributable to *T. sinensis* were examined too. Step 2, postcranial remains attributable to the holotype were measured. Step 3, photographs were taken, in order to create a visual reference of each bone. Step 4 anatomical descriptions were placed within a broader comparative context. Step 5, the body mass of the holotype, was calculated following the method developed by Campione and Evans (2012), and compared with estimates for other taxa recovered from the literature. Step 6 involved a phylogenetic analysis of *T. sinensis* based on observed characters and characters retrieved from the literature.
3. Background

3.1 Geological context

The labeling of the holotypic and referred material is inconsistent, making the determination of the provenance problematic (pers. obs.). However, the type locality is situated one li (∼500 m [Buffetaut 1995]) southwest of the village of Jiangjunding (Chiang Chün Ting alt. Chiang-Chün-Ting on the labels), which some labels state as being situated 16 li (∼8 km) southwest of the city of Laiyang. (See Fig. 1 for a map of the area). The remains where excavated in 1923 by H.C. T’an and Otto Zdansky in April and October 1923 (Wiman 1929). Referred material was found in the vicinity of the village Tianqiaotun (T’ien Ch’iao T’un on the labels), which some labels state as being one li northeast of Tianqiaotun, and another label states it as one li east of Tianqiaotun) and about three li (∼1.5 km) northwest of Jiangjunding (Buffetaut 1995). Neither explanation corresponds to the locality mentioned in Poropat and Kear (2013). It was also in this locality that the Pinacosaurus cf. grangeri material was found (Buffetaut 1995). Tianqiaotun in turn, is situated 15 li (∼7.5 km) southwest of the city of Laiyang (Buffetaut 1995). One of the bones in the collection, a dorsal rib, lists its locality as 5 li (∼2.5 km) southwest of Jiangjunding. However, this locality is not listed in the description by Wiman (1929), and might therefore be an error.

Figure 1. Map of China with an enlarged map of the Shandong Province, showing the type locality at the village of Jiangjunding as well as the village of Tianqiaotun. Scale bar = 100 km. Figure modified from Poropat and Kear (2013).
The exact age and, stratigraphic subdivision of the Wangshi group, as well as the correlations of the different parts with each other are controversial, and outside the scope of this work. For a review of different subdivisions of the Wangshi group see discussion in Buffetaut (1995) and Hu et al. (2001, table 1). To summarize, the Wangshi group can be divided (from oldest to youngest) into the; Linjiazhuang Formation, Xingezhuang Formation, Hongtuya Formation, Jiangjunding Formation (which yielded *T. sinensis*), Jingangkou Formation and the Changwangpu Formation (Xing et al. 2014a; He et al. *in press*). This stratigraphic framework is adopted in this work. However, the correlations of the different parts of the Wangshi group are as already stated, controversial. Young (1959) concluded that *T. sinensis* was found in the lower part of the Wangshi Group, a view followed by Buffetaut (1995). Hu et al. (2001) were more specific and concluded that *T. sinensis* was found in the lower to middle part of the Jiangjunding Formation.

The age of the Wangshi Group, and the Jiangjunding Formation, generally regarded as pertaining to Late Cretaceous (T’an 1923, cited in Buffetaut 1995; Horner, Weishampel and Forster 2004; Prieto-Márquez 2010a; Xing et al. 2014a), with the exception for the Linjiazhuang Formation regarded as Early Cretaceous (He et al. *in press*). Buffetaut (1995) correlated parts of the Wangshi group with the Campanian-aged Djadokhta Formation (Mongolia) based on the identification of remains attributed to *Pinacosaurus cf. grangeri*, which is otherwise known from the Djadokhta Formation and other coeval deposits in East Asia (Burns et al. 2011). The Djadokhta Formation has in turn been dated to 75-71 Ma, (Late Campanian) based on magnetostatigraphy (Dashzeveg et al. 2005). Hong and Miyata (1999) obtained an age estimate of 82.4-81.8 Ma for the Wangshi Group based on fission track zircon ages and the gastropod *Campeloma liui* Chow, 1953. In contrast, K-Ar dating from samples taken from layers identified as the Hongtuya Formation underlying the Jiangjunding Formation, have yielded ages of 76 Ma (Meng et al. 2006 cited by He et al. *in press*), while 40K-39K datings of deposits from the same formation have yielded ages of 73.5-72.9 Ma (Yan et al. 2003; Yan et al. 2005, cited in Xing et al. 2014a). Based on the biostratigraphic presence of the *Talicypridea-Cypridea-Quadracypris-Candona* assemblage of ostracods, the Wangshi group has been interpreted to be of Campanian-Maastrichtian age (Wang et al. 2012). According to the stratigraphic scheme used by Xing et al. (2014a), the Jiangjunding Formation likely pertains to the latest Campanian to early Maastrichtian, and this age estimate is adopted here. For context, the hadrosaurine *S. giganteus* is from the stratigraphically older Xingezhuang and Hongtuya formations (Xing et al. 2014a), and *T. spinorhinus* occurs in the younger Jingangkou Formation (Hu et al. 2001).

The Jiangjunding Formation (*sensu* Cheng Zhengwu et al. 1995 cited by Hu et al. 2001) is 991 m thick, consisting of brown-red, purple-grey muddy siltstones, sandstones, pebbly sandstones, and conglomerates (Hu et al. 2001). The upper and lower parts of the Jiangjunding Formation consist of pebbly sandstones and siltstones, while the middle part consists to a higher degree of conglomerates (Hu et al. 2001). It should be noted that the Wangshi Group as defined by Cheng Zhengwu et al. (1995; cited by Hu et al. 2001) does not recognize the Hongtuya Formation between the Xingezhuang
and the Jiangjunding Formations as used by later authors (e.g. Xing et al. 2014a; Hone et al. 2014; He et al. in press). The sedimentological characteristics given above for the Jiangjunding Formation may therefore apply to the Hongtuya Formation as well.

3.2 Paleoenviromental context

The paleoenvironment of the Wangshi group has been interpreted as being fluvial to lacustrine (Chen 1983; Ji et al. 2011; Liu et al. 2011). Regarding the paleoclimate, Zhao (1992; cited by Buffetaut 1995), used palynological evidence to infer a “tropical-subtropical hot and slightly dry climate”. A similar view based on sedimentary evidence was expressed by Liu et al. (2011), indicating that at least the top part of the Wangshi Group was hot and dry during the Late Cretaceous. A different approach was taken by Zhao et al. (2013) using $\delta^{18}$O values preserved in dinosaur egg-shells from the Jiangjunding- and the overlying Jingangkou Formation. Using this approach they concluded that the climate was warm and humid during the deposition of the Jiangjunding Formation, and that it dried out by the time the Jingangkou Formation was deposited.

The recognized fauna from the Jiangjunding Formation, besides *Tanius*, includes indeterminate coelurosaurian theropods (Poropat and Kear 2013), ankylosaurian remains identified as *Pinacosaurus* cf. grangeri (Buffetaut 1995), indeterminate sauropods (Wiman 1929), possibly *Micropachycephalosaurus hongtuyanensis* Dong, 1977 (its exact stratigraphic position is unclear) originally described by Dong (1977) as an pachycephalosaur but later established to be an indeterminate cerapodan (Butler and Zhao 2009), indeterminate non-archosaurian cheloniids (Wiman 1929), whose remains show similarities to the member of Nanhsiungchelyidae (Tong et al. 2012), and a prolific assemblage of dinosaur egg material (Zhao et al. 2013).

3.3 Historical context

Although this work concerns the anatomy and phylogenetic relationships of *T. sinensis*, it would be most unfortunate not to mention the role that *T. sinensis* played in the history of palaeontology. While *T. sinensis* was named and described by Wiman (1929), it was not the first hadrosauroid named from China. In 1925 *Trachodon amurense* was described from the Jiayin locality in the Heilongjiang Province by Riabinin (1925; cited in Godefroit et al. 2011), but later being transferred to its own genus *Mandschurosaurus* Riabinin, 1930. As opposed to *T. sinensis*, the taxonomy of *M. amurensis* remains dubious (Horner, Weishampel and Forster 2004; Prieto-Márquez 2010a; Godefroit et al. 2011 and ref. therein). The historical importance of *T. sinensis* lies in the fact that it is the earliest erected hadrosauroid genus from China that remains valid.
4. Methodology

4.1 Osteological comparisons

Direct observations of the postcranial remains referred to *T. sinensis* where made and compared to that of the following species who were chosen for comparison with that of *T. sinensis* because of their well-known and described postcranial skeleton: the non-hadrosaurid iguanodontian *Iguanodon bernissartensis* Boulenger, 1881 known from numerous localities and formations of the Valanginian-Albian, Early Cretaceous, of western Europe (Norman 2004): the non-hadrosaurid hadrosauroid *Eolambia caroljonesa* Kirkland, 1998, from the early Cenomanian, Late Cretaceous of the Cedar Mountain Formation, Utah western United States (McDonald et al. 2012); the non-hadrosaurid hadrosauroid *Bactrosaurus johnsoni* Gilmore, 1933, from the middle-late Campanian, Late Cretaceous Iren Dabasu Formation of the Inner Mongolia Autonomous Region, northern China (Godefroit et al. 1998); the hadrosaurine hadrosaurid *Edmontosaurus regalis* Lambe, 1917 from the Late Campanian Horseshoe Canyon and Wapiti formation of Alberta (Campione 2014).

Other material, which may be associated with *T. sinensis* but not part of the holotype was studied, including a small vertebra that was found in the collection and was compared with the following species: the non-hadrosaurid iguanodontians *Dryosaurus altus* Marsh, 1878 and *Dysalotosaurus lettowvorbecki* Virchow, 1919, (postcranial anatomy described by Galton 1981); *Cumnoria prestwichii*, Hulke, 1880, (postcranial anatomy described by Galton and Powell 1980); *Tenontosaurus tilletti*, Ostrom, 1970, (postcranial anatomy described by Forster 1990) and *Zalmoxes robustus* Nopcsa, 1902, (postcranial anatomy described by Weishampel et al. 2003). Regarding the definition of the different clades used in this work, the following are the most important: Iguanodontia is here defined as all taxa more closely related to the hadrosaur *Edmontosaurus* Lambe, 1917 than the hypsilophodontid *Thescelosaurus* Gilmore, 1913 (Norman 2004). The definition of Hadrosauroidia follows that of You et al. (2003) and Xing et al. (2014b) as the least inclusive taxon containing *E. normani* and *P. walker*. Hadrosauridae is defined as the monophyletic group consisting of *Saurolophus osborni* Brown, 1912, *P. walker* and all their descendants (Sereno 1998). Hadrosauridae are further divided into two major clades, Hadrosaurinae and Lambeosaurinae (Horner, Weishampel and Forster 2004).

The anatomical terminology in this report follows that of Campione (2014). The prefix "PMU" for the designations of referred material stands for Palaeontological collections, Museum of Evolution, Uppsala University.
5. Results

5.1 Systematic Palaeontology

Dinosauria Owen, 1842
Ornithischia Seeley, 1887
Ornithopoda Marsh, 1881
Iguanodontia Dollo, 1888
Hadrosauroida Cope, 1870
*Tanius sinensis* Wiman, 1929

5.2 Holotype

The holotype was apparently rather complete at the beginning of the excavation but crumbled during the course of excavation (Wiman 1929). Although the holotype has been given the collective number of PMU24720, the old registration numbers for each individual bone will be written out; it consist of a nearly complete but un-articulated series of cervical vertebrae consisting of the axis PMUR246, the 3rd cervical vertebra PMUR248, the 4th cervical vertebra PMUR249, the 5th cervical vertebra PMUR244, the 6th cervical vertebra PMUR250, the 7th cervical vertebra PMUR251, the 8th cervical vertebra PMUR247, the 9th cervical vertebra PMUR260, the 10th cervical vertebra PMUR252, isolated 6th cervical rib PMUR254, isolated 9th cervical rib PMUR255, isolated cervical rib of uncertain placement PMUR256, dorsal vertebra PMUR237, caudal vertebra PMUR243, isolated haemal spine PMUR257, right scapula PMUR241, right sternal plate PMUR258, left humerus PMUR236, a partial right ulna without a registration number, three radius fragments consisting of two distal ends and one proximal end, these fragments having no registration number, dorsal rib fragments without a registration number, left and right ilia PMUR242a and PMUR242b, right femur PMUR242c, the right fibula PMUR242e, the right tibia PMUR242d, left metatarsal III PMUR259, an ungual PMUR253. A complete dorsal rib PMUR238, is of uncertain provenance. The caudal portion of a cranium is known, which will be the focus of a separate study. See Fig. 2 for a photographic composite picture of the holotype, bar the cranium. Specimens including a right humerus PMUR235, complete radius PMUR239, metatarsal without registration number from the locality at the village of Tianqiaotun might also pertain to a very similar taxon. All specimens studied in this work are deposited in the palaeontological collections of the Museum of Evolution, Uppsala, Sweden.
5.3 Locality and Horizon

The type locality is situated one li (≈500 m [Buffetaut 1995]) southwest of the village of Jiangjunding (Chiang Chün Ting alt. Chiang-Chün-Ting on the labels), which some labels state as being situated 16 li (≈8 km) southwest of the city of Laiyang. The excavation locality belongs to the Jiangjunding Formation. The formation has been dated as latest Campanian-Early Maastrichtian, Late Cretaceous (Xing et al. 2014a). See Fig. 1 for a map of the area.

5.4 Diagnosis

*T. sinensis* can be diagnosed by the following possible autapomorphy: medial and lateral condyles in the distal region of the femur fused caudally, to form a completely enclosed “tunnel”: *T. sinensis* is also diagnosed by the unique combination of following traits: the ratio between the height and length of the neural spines of the middle dorsal vertebrae is 4.0 or greater; dorsal surface of the scapula being curved, rendering the dorsal surface a convex appearance in medial and lateral view; maximum dorsoventral width of the proximal end of the scapula being bigger than the dorsoventral width at the distal end (212 mm vs. 144 mm); recurved cranial end of the acromial process of the scapula being craniadorsally directed; presence of a postacetabular ridge; arcuate fourth trochanter in the femur; cnemial crest in the tibia that extends ventrally into the proximal half of the shaft; distal end of the fibula expanding into a club shape in lateral view; the ratio between the proximodistal length of the metatarsal III and the mediolateral width of this element being greater than 4.5.
5.5 Description

5.5.1 Axial skeleton

**Cervical vertebrae:** An unarticulated series of cervical vertebrae consisting of the axis to the 10th cervical vertebra and three isolated cervical ribs are known. The cervical vertebrae are strongly opisthocoelous as is common among hadrosauroids, except for the axis that is strongly diagenetically flattened mediolaterally. When preserved the neural spine is only a small ridge, except for in the 6th cervical vertebrae where it forms a small knob. The parapophysis of the cervical vertebrae does not migrate caudally like they do in *B. johnsoni* and *I. bernissartensis*, and in this respect *T. sinensis* is similar to *E. caroljonesa*. The prezygapophyses are located dorsally on the transverse processes similar to all the comparison species. When preserved the postzypophyses in all cervicals extends caudolaterally beyond the caudal articulation surface in dorsal view, and are roughly triangular in cross section. On some of the centra a horizontal keel runs, starting from the parapophysis, to the caudal end in lateral view being similar in this respect to *E. caroljonesa* and *B. johnsoni*, and this horizontal ridge is more pronounced in the more caudal cervical vertebrae, although this may be further pronounced due to dorsoventral crushing.

The axis (**Plate 1**), is severely diagenetically crushed mediolaterally. The caudal articulation surface is concave. The odontoid process is similar to *I. bernissartensis* in that the ventral side grow out from the centra in a roughly diagonal line, whereas in *B. johnsoni* the ventral side of the odontoid is not as straight ventrally from the centra. Furthermore the odontoid tip appears slightly more pointed than in *B. johnsoni* and more similar to *I. bernissartensis*, although this might at least partially be an artefact of the plaster reconstruction. Although partly obscured by plaster covering, when seen in lateral view the neural spine is concave in the middle, whereas in *B. johnsoni* it is arcuate in front but then goes down to a plateau that last until the caudal end, but in *I. bernissartensis* the neural spine is roughly convex. The neural spine is broken at the cranial end. The caudal surface of the neural spine is slightly concave in lateral view while in *I. bernissartensis* there appears to have been one slightly concave depression (Norman 1980: Fig. 24a), although this might be an artefact of the bad preservational state of the axis. The diapophysis is roughly at the same dorsoventral level as the prezygapophyses in lateral view, whereas in *B. johnsoni* the diapophysis is clearly at a lower level. The postzygapophysis goes upwards and backwards, but is not perfectly preserved, making comparisons with other taxa a bit difficult. Since no axis is known from *E. regalis*, comparisons with some other hadrosaurids are made. The axis has a wedge-like intercentrum, fused to the cranioventral articulation surface as a cranially projecting lip similar to that in hadrosaurine *Brachylophosaurus canadensis* Sternberg, 1953 (Cuthbertson and Holmes 2010). Although incomplete, the axis neural spine shows some similarities to the derived condition in Hadrosaurinae, where the offsett cranial process is separated from the postzygapophyseal region by a distinct embayment (morph B *sensu* Campione, Evans and
The plesiomorphic condition which is represented by *I. bernissartensis* and *B. johnsoni* as well as lambeosaurines, is for the neural to be convex dorsally, extending caudally beyond the diapophysis in lateral view and the cranialmost region of the postzygapophyseal buttress (Campione, Evans and Cuthbertson 2007). Although, the plaster reconstruction of the axis might give a false impression of the appearance in life, the appearance of the preserved part of the neural spine suggests the possibility that the derived condition was present.

The 3rd cervical vertebra (Plate 2) is diagenetically flattened mediolaterally. The transverse process is short. The parapophysis is rounded, not subrectangular as in *I. bernissartensis*.

The 4th cervical vertebra (Plate 3) is strongly diagenetically distorted, mediolaterally. While the horizontal keel is present on the centra, the parapophyses have eroded away. The left transverse process is missing. A partial right transverse process is present but ending shortly after the egg-shaped prezygapophyses. Both the postzygapophyses are broken.

The 5th cervical vertebra (Plate 4) is due to diagenetic reasons diagonally flattened in craniocaudal view. Otherwise, no particular distinguishing features are present in it.

The 6th cervical vertebra (Plate 5) is slightly dorsoventrally flattened from diagenetic reasons. The neural spine is present as a knob at roughly halfway between the cranial and caudal ends of the neural arch in dorsal view. The 7th cervical vertebra (Plate 6) is diagonally flattened from diagenetic reasons similar to the 5th cervical vertebra. Together with the 8th cervical vertebra (Plate 7), it otherwise lacks particular distinguishing features and are similar to the rest of the cervical vertebrae. The 9th cervical vertebra (Plate 8) is similar to the 8th cervical vertebra, although slightly smaller and dorsoventrally compressed because of diagenetic processes. No ventral groove is present in contrast to the 8th cervical vertebra. The 10th cervical vertebra (Plate 9) also lacks the ventral groove similar to the 9th cervical.

Isolated 6th cervical rib (Plate 10 E-F): The rib shaft is straight like in more posterior cervical ribs of *I. bernissartensis* and *E. caroljonesa*, but differing from the curved rib shaft in *B. johnsoni*. Similar to *E. caroljonesa*, the rib shaft forms a distinct process between the capitulum and tuberculum that extends cranially. The rib shaft is convex laterally and concave medially like *I. bernissartensis* and *B. johnsoni*. The capitulum is slightly more robust and longer than the tuberculum like in *E. caroljonesa*, and the caudal cervical ribs of *B. johnsoni*. The articulation surface of the capitulum and tuberculum is convex.

Isolated 9th cervical rib (Plate 10 A-B): Overall it is similar to the 6th cervical rib although slightly more robust, less medially concave, and with a broader rib shaft.

Isolated cervical rib of uncertain placement (Plate 10 C-D): It is similar to the 6th and 9th cervical ribs but smaller. The rib is medially concave, similar to cervical ribs of *I. bernissartensis*.

Although recognition of variation along the cervical series is hampered by the crushed and incomplete state of some of the vertebrae, some degree of change can be observed through the series. Cervical centra 3-8 are heart-shaped in caudal view, while cervical centra 9 and 10 have a flat dorsal
border of the caudal articulation surface. Change in the size of the vertebral foramen is not a reliable character in difference to *E. regalis*, because the height of the spinal canal in cranial aspect varies from 48 mm in the 8th cervical vertebra to 30 mm in cervical vertebrae 5 and 6. The width of the spinal canal in cranial aspect varies from 53 mm in the 10th cervical vertebra to 27 mm in the 4th cervical vertebra. Cervical centra become proportionally wider relative to height in caudal view through the series. A ventral groove is present in vertebrae from the cranial half of the cervical series similar to the cranial-most known cervical in *E. regalis*, but is lost from the cervical centra of the 9th and 10th cervical vertebrae. Transverse processes extend further out laterally in craniocaudal view through the series, although it should be noted that some transverse processes are incompletely preserved and/or distorted. The prezygapophyses widen mediolaterally with the transverse processes when preserved. In the 10th cervical vertebra the transverse processes are similar to the more caudal cervical vertebrae of *E. caroljonesa* and *E. regalis*. Finally, postzygapophyses become increasingly more robust caudally and curving more outwards in dorsal view through the series.

**Dorsal vertebrae:** Only one dorsal vertebra (Plate 11) is preserved. It is platycoelous with the cranial articulation surface being more concave than the caudal articulation surface. The transverse process is almost horizontally angled, and similar in this regard to dorsal vertebra 15 of *I. bernissartensis* and *E. regalis*, and the more caudal dorsal vertebrae of *E. caroljonesa*. The cranial articulation surface has a relatively flat dorsal border, while the dorsal border of the caudal articulation surface is heartshaped. The heart shape of the caudal articulation surface is common in hadrosauroids (*E. caroljonesa*) but to a lesser degree in *I. bernissartensis*. The prezygapophyses are angled forward and slightly upward. Like in the prezygapophyses of *E. regalis*, they are not associated with the transverse process as was the case in the cervical series. Furthermore the prezygapophyses are placed cranially at the base of neural spine. The neural spine is considerably longer than the neural spines of the comparison species being 4.06 times the length of the centra (440 mm vs. 109 mm, measured along its caudal aspect, with the length of the neural spine measured from the spinal canal), and mostly vertical like the more caudal dorsal vertebrae spines in *E. regalis* and *E. caroljonesa*, although it tips slightly forwards towards the top.

In craniocaudal view the neural spine expands into a club shape somewhat similar to *B. johnsoni*, but also seen in other long spined hadrosaurids (e.g. *Barsboldia sicinskii* Maryańska and Osmólska, 1981 [Prieto-Márquez 2011]). The top of the neural spine is rugose, suggesting cartilage covering. The postzygapophyses are horizontal in caudal view like in more caudal dorsal vertebrae of *E. regalis*. A deep embayment is present above and between the postzygapophyses, and below the transverse processes. The height of the neural spine of the dorsal vertebrae in hadrosaurids is known to increase caudally through the dorsal series (Horner, Weishampel and Forster 2004), and the centra of the dorsal vertebrae are known to become thinner caudally through the dorsal series (Godefroit et al. 1998; Campione 2014). The high neural spine and the craniocaudally thin centra of the specimen, therefore suggests a position in the middle of the dorsal series for it.
Caudal vertebrae: At least one caudal vertebra with the neural arch is present, and an isolated haemal spine. The complete caudal vertebra (Plate 12) is slightly platycoelous similar to the cranial to mid-caudal caudal vertebrae of *I. bernissartensis*, while in *E. regalis* they are amphiplatyan and in *E. caroljonesa* they are slightly amphicoelous. Specifically, the caudal articulation surface is more concave, than the cranial aspect. The centra is slightly taller than long, and like in *I. bernissartensis*, the centra are slightly taller than wide. Owing to its size and lack of transverse processes, this vertebra is likely from the middle to caudal portion of the caudal series, as interpreted from those elements preserved in *E. caroljonesa*, *E. regalis*, *B. johnsoni*, and *I. bernissartensis*. The right prezygapophysis is completely broken off, while the left one is present but partially broken. The prezygapophyses project cranially like in all four comparison taxa. The articulation surface of the prezygapophysis is flat and angled dorsomedially similar to *E. regalis*. A haemal arch articulation site is present caudoventrally. It was possibly once present under the cranial articulation surface too, but eroded off. The neural spine is angled caudally more similar in this regard to mid-caudal vertebrae of *E. caroljonesa* and the more caudal caudal vertebrae of *B. johnsoni* and *I. bernissartensis*, but not to the extent seen in the caudal-most preserved caudal vertebrae of *E. regalis*. However, the neural spine is broken off shortly after where the unpreserved postzygapophyses would have been situated. The ventral surface has a concave fossa in ventral view, and haemal spines would have articulated at the cranial and caudal ends.

The haemal spine (Plate 13) is v-shaped in craniocaudal view with two facets almost in contact with each other, and which together forms the haemal canal. It is similar to the cranial haemal spine of *E. caroljonesa*, mid-caudal to caudal haemal spines in *E. regalis* and *I. bernissartensis* in overall appearance.

The complete dorsal rib (Plate 14) consist of the capitulum, tuberculum and a gently curved shaft. The capitulum is craniocaudally flattened, dorsoventrally broad, and with a rugose articulation surface. The capitulum is similar in proportion to *B. johnsoni*. It is notably distinct from that of *I. bernissartensis* in that the latter is rounded. The tuberculum is mediolaterally flattened like in *E. regalis* but more tear-dropped in shape in medial view, and not elliptical as in *B. johnsoni*. It is also slightly similar in this respect to the shallow, depressed articular surface of the tuberculum in *I. bernissartensis*. The rib shaft is mediolaterally flattened. Comparisons with other taxa are hampered however by the protective plaster packaging of the fragile rib. Concerning the provenience of the specimen, it is labelled as being from five li southwest of Jiangjunding. Given that no other of the specimens are from this locality, it cannot be excluded that the distance given from Jiangjunding is an error and it is instead from the type locality one li southwest of Jiangjunding. Given its overall similarity in size, it is here attributed to the holotype. Numerous rib fragments similar in appearance and size are known from the type locality, which might or might not be attributable to *T. sinensis*. 
5.5.2 Appendicular skeleton

**Pectoral girdle:** From the pectoral girdle a complete right scapula and an incomplete right sternal plate is known. The right scapula (Plate 15) is long and gently curved backwards, similar to but not as extreme in *E. regalis*. The dorsal margin is not straight as in *B. johnsoni* but gently convex and the ventral margin is concave. The scapular blade is uniformly wide throughout its length in medial view, and the dorsal and ventral margins meet at roughly right angles like in *I. bernissartensis*, *E. regalis*, and *E. caroljonesa*, but not in *B. johnsoni*. At the proximal end of the scapula, the glenoid forms a depression in proximal view. The acromion process is prominent and rugose, extending slight forwards and sidewards. The deltoid ridge extends distally from the acromion process laterally merging progressively with the scapular blade similar to *E. regalis*, *E. caroljonesa* and *B. johnsoni*. The coracoid articulation surface of the scapula is incompletely preserved and so its shape is hard to discern.

The right sternal plate (Plate 16) has a long and slender shaft, widening mediolaterally into a blade at its proximal extent. The proximal blade like part of the sternal plate is lost. The shaft is round on the ventral side, but sports a ridge on the ventral side of the blade like in *E. regalis*. The dorsal side of the shaft is flat but becomes gently concave towards the blade. The distal end is elliptic in distal view. The forelimb of the holotype is known from the left humerus. A partial right ulna, might also belong to it, as well as three fragmentary radii, which may or may not be attributable to *T. sinensis*, but are consistent with a hadrosaurid identification.

**Humerus:** The left humerus (Plate 17) is very similar to the right humerus from the Tianqiaotun locality. It is somewhat bowed medially like in all comparison taxa, although it is not as marked as in *E. caroljonesa*, *B. johnsoni* and *I. bernissartensis*. In proximal view the proximal head is slightly lunate, and the humeral head is shorter and blunter than in *E. regalis* and *B. johnsoni*, but similar to *E. caroljonesa* and *I. bernissartensis*. Two ledges extend medially and laterally from the humeral head. The lateral ledge curves forward and downward, and merges with the deltopectoral crest. The medial ledge curves outward and downward and merges with the concave medial side of the shaft. The lateral and proximal margins of the humerus forms an obtuse angle similar to in *E. regalis* and *E. caroljonesa*, but a right angle in *I. bernissartensis*. The deltopectoral crest is well-developed (39.6% the total length of the humerus) compared to *I. bernissartensis* (XX %), similar to *E. caroljonesa* (42.9 %). No measurements of the deltopectoral crest for *B. johnsoni* where given by Godefroit et al. (1998). However, it is said to be less than 50 % the total length of the humerus in *B. johnsoni* by Prieto-Márquez and Norell (2010), but no measurements were given for it. The condition is uncertain for *I. bernissartensis* since Norman (1980) does not give any measurement for it. All, however, are in contrast to the typical hadrosaurid condition, typified by *E. regalis* at 55.3% the length of the humerus. Furthermore there is no strong constriction ventral to the deltopectoral crest as in *E. regalis*, but similar to the other comparison taxa. A small knob is present on the upper half of the caudal side of the shaft, possibly representing the attachment site for *m. latissimus dorsi*. The distal...
head is partially covered by matrix, but the medial and lateral condyles are visible and separated from each other by a shallow intercondylar groove.

**Ulna:** A possible right ulna (Plate 18) is partly preserved, from roughly the mid-point of the bone to just before the proximal head. It is consistent in overall appearance to the ulna in the comparison species. A distally tapering trough is present in cranial and caudal view that is similar in overall shape to the proximal halves of the ulnas in the comparison species. Judging from how the lateral flange is situated, it appears to be from the right side of the animal, being most similar to the right ulna of *E. regalis* and *E. caroljonesa*, but appearing laterally reversed compared to the left ulna of *B. johnsoni*. At the proximal end the shaft has an irregular T-shape in cross section, while the distal end of the shaft is elliptical in cross section.

**Radius:** The proximal end of a radius (Plate 19) without a registration number. It is diagenetically flattened, and having a small flange at the trochlear articulation surface that extends caudally. The shaft appears to have been cup shaped when view from the boken end. The trochlear articulation surface, although badly preserved, appears to have been concave and sloping laterally, but this may at least partly be the result of diagenetic distortion. Also, the distal ends of two radii (Plate 20), both without a registration number are known. They are long and straight, and flat in lateral and medial view. Furthermore, both have a tapering trough in cranial view, and expanding towards the distal end. The distal articulation surfaces are convex and rugose, and triangular in distal view. Where the shaft is broken off, both the distal fragments are oval in cross-section. In overall appearance the radii fragments are similar to the complete radius PMUR239 from the Tianqiaotun locality described together with the rest of the Tianqiaotun material.

**Pelvic girdle:** The pelvic girdle is known only from the left and right ilia. Wiman originally interpreted and described a bone as the distal booted end of a right “ischium”. However, this specimen has since been identified as the pubic boot of a theropod (Buffetaut and Tong-Buffetaut 1993) and will be described separately.

The left ilium (Plate 21 A-B), is sigmoid in lateral view similar to *B. johnsoni*, not straight as in *E. caroljonesa*. The preacetabular process projects cranially from the central plate and gradually tapers towards its cranial end. It is not dorsoventrally expanded near its cranial end as in *E. caroljonesa* or *I. bernissartensis*. As is common the preacetabular is ventrally deflected relative to central plate like in all comparison taxa except *E. caroljonesa* whose preacetabular process is more or less horizontal, but the degree of ventral deflection is less ventrally deflected than in *B. johnsoni* and in *I. bernissartensis* but similar to *E. regalis*. The preacetabular process is longer compared to total length of the ilium than in *E. caroljonesa* and more similar to *E. regalis*. The pubic peduncle is short and blunt, more so than in any of the comparison taxa with the peduncle preserved, so that its ventral extent does reach that of the ischial peduncle when the ilium is placed horizontally. The pubic peduncle is slightly thickened in cranial view, similar to *E. caroljonesa*. The acetabulum is shallowly concave in lateral view, unlike the deep acetabulum of *B. johnsoni*. It is also less concave than in *E. regalis* and more similar to *E.
caroljonesa and I. bernissartensis. The caudal and dorsal surfaces of the postacetabular process are not completely preserved. However, the dorsal and ventral surfaces are relatively straight, somewhat similar to the postacetabular process in I. bernissartensis and B. johnsoni. The postacetabular process might have tapered dramatically in the caudal end of the ilium, and it was longer than in B. johnsoni and E. caroljonesa, but more like I. bernissartensis and E. regalis. Overall, the postacetabular process is symmetric in lateral view, unlike the asymmetry seen in E. regalis. A brevis shelf is present on the ventral side of the postacetabulary process like in I. bernissartensis. Roughly at the level of the pubic peduncle, the supra-acetabular process forms with a rugose and everted rim similar to B. johnsoni and I. bernissartensis, but more everted than in E. caroljonesa and less than in E. regalis. The ventral surface becomes rugose at the base of the preacetabular process. A postacetabular ridge forms at the level of the folding of the medial ridge, giving the ilium a strongly concave profile in lateral view. In medial view a ridge runs from above the cranial half of the acetabulum, and then turns upwards, ending on the dorsal surface of the preacetabular process. This might serve as attachment site for the sacral vertebrae.

The right ilium (Plate 21 C-D) is similar to the left ilium, but much more fragmentary, and reconstructed with plaster which might give a false signal about its appearance. The hindlimb is known from a right femur, a right fibula, the right tibia, a left metatarsal III, and an ungual. The distance and direction on the label for the right tibia is unreadable.

**Femur:** The right femur (Plate 22) is long, straight and stout. The proximal and distal articulation surfaces are rugose. Unlike E. regalis, but similar to E. caroljonesa, B. johnsoni and possibly I. bernissartensis, the bone is bowed in caudally. The proximal end of the femur is somewhat compressed mediolaterally compared to the comparison taxa, although this might be a diagenetic artefact. The femoral head is medially expanded like all comparison taxa. The greater trochanter is broad and paddle like in lateral view, somewhat similar in this aspect to E. regalis, and B. johnsoni, and less similar to E. caroljonesa and I. bernissartensis. The greater trochanter extends down the length of the shaft about 1/5 of its length. The cranial trochanter is located cranially to the greater trochanter and smaller than the latter. Both have convex proximal surfaces in lateral view and taper down the shaft. The cranial trochanter is separated from the greater trochanter by a groove, which is plaster reconstructed in the specimen. A ridge starts distally on the greater trochanter and continues down the shaft towards the distal end. The fourth trochanter is partly reconstructed with plaster, however it extends from roughly the midline of the bone in medial and lateral view like all the comparison taxa. Furthermore, the fourth trochanter appears to have been more flattened caudally than in E. caroljonesa, E. regalis and B. johnsoni, but possibly similar to I. bernissartensis, although this is obscured by the plaster reconstruction. Attachment site for m. pubischiofemoralis internus is clearly visible on the medial surface of the fourth trochanter like in E. regalis. However, no muscle scar attributable to m. caudofemoralis longus is visible. The distal articulation surface is divided into the lateral and medial condyles, which are craniocaudally expanded like in all comparison taxa. The
lateral condyle has a pointed corner cranially unlike *E. regalis* and *E. caroljonesa*, the character state being unclear in *B. johnsoni* and *I. bernissartensis*. This might however be a diagenetic artifact. Both cranially and caudally, the lateral and medial condyles are separated by well-developed intercondylar grooves, like all comparison taxa. However, unlike all comparison taxa except *B. johnsoni*, the condyles have fused cranially to form a completely enclosed extensor tunnel. Unlike all comparison taxa however, the condyles also fuse caudally forming a fully enclosed flexor tunnel, which has not been seen in any hadrosaurid.

**Tibia:** The right tibia (Plate 23) is long, robust and straight. The proximal and distal articulation surfaces are rugose and their main axis is perpendicular to each other. The proximal articulation surface is markedly expanded craniocaudally in comparison to *E. regalis*, but similar to *E. caroljonesa*, *I. bernissartensis*, and similar to the condition in *B. johnsoni* in cranial view. The proximal articulation surface is flat in medial view like *I. bernissartensis*, not sloping as in *E. caroljonesa*. The proximal articulation surface consists of the cnemial crest, which is separated in lateral view by a wide depression from the condyles unlike *E. regalis*, *E. caroljonesa* and *B. johnsoni* where the depression is narrower. This may simply be a diagenetic artifact. The condition is not visible in *I. bernissartensis*, although Norman (1980) describes that a groove is separating the condyles. Similar to *E. regalis*, the cnemial crest extends down the shaft about 1/3 of its length. The inner condyle is slightly smaller than the outer condyle, similar to the condition in *E. caroljonesa* and *E. regalis*. Similar to all comparison taxa, a deep cleft separates the inner condyle from the outer condyle, although it appears to be relatively wide in the specimen compared to *E. regalis*, *E. caroljonesa* and *B. johnsoni*. The shaft is flattened in cross section unlike *E. regalis* where it is round, and *B. johnsoni* where it is ovoid, although this may be a diagenetic artifact. The distal articulation surface is divided into a lateral malleolus and medial malleolus like in all comparison taxa except *I. bernissartensis*. The medial malleolus expands mediolaterally at its distal end like *E. regalis* and *E. caroljonesa*. Similar to *E. regalis*, the lateral and medial malleoli are divided by a groove in cranial and caudal view.

**Fibula:** The right fibula (Plate 24) is long and slender like in *E. regalis*, *E. caroljonesa* and *I. bernissartensis*, except *B. johnsoni* for which only the proximal half of the fibula is known, although it was at least slender. The fibula is lunate in proximal view like all comparison taxa, with a rugose proximal surface similar to *E. regalis*. The distal head is tear-drop shaped similar to *E. regalis* and *E. caroljonesa*. Both proximal and distal heads are craniocaudally expanded into a club shape like in all comparison taxa, although the club shape is more pronounced than in the distal ends of the fibula in *E. regalis* and *E. caroljonesa* and more similar to *I. bernissartensis*. A trough in medial view extends from the proximal end similar to *E. regalis*, but only extending about 1/3 the length of the shaft compared to 1/2 of the shaft in *E. regalis*. The distal end is slightly twisted compared to the proximal end. Furthermore, the distal end of the shaft is flat in medial view. The bone tapers distally from the proximal head in medial view, to about the lower 1/4 of the shaft,
where it gradually expands to the distal head, which is rugose. In medial view the proximal half of the bone is concave, while the distal half of the bone is flattened.

**Metatarsal III: (Plate 25)** was originally interpreted by Wiman (1929) as a metatarsal IV (MT IV) without any justifications for this based on comparisons with metatarsals from other taxa. However, Wiman (1929, p.55) mentions that ‘the distal articular surface is so placed, that the toe IV is directed outwards and forwards’. What speaks against Wiman’s original interpretation of the bone as a MT IV is its long and straight profile in craniocaudal view. In all of the comparison taxa MT IV is curved in craniocaudal view. The bone is partially reconstructed with plaster, although the characteristics of the bone are still visible. The proximal end is strongly lunate in proximal view, and rugose. The proximal end extends medially, where it forms the border of a slightly concave flank which continues distally to the distal articulation surface, although it tapers towards the distal articulation surface. This is probably the articulation surface for MT II. In lateral view there are two troughs, one shallow, which continues distally into the depression on the lateral side of the distal articulation surface. This is probably the articulation surface for MT IV. The other trough tapers as it continues distally until shortly before the distal articulation surface, and this trough appears to be deeper than the trough visible in lateral view on *E. caroljonesa*. The two troughs are divided by a ridge starting on the shaft below the proximal articulation surface, which continues distally to the distal articulation surface. In craniocaudal view, the distal articulation surface is saddle shaped, and the depression on the medial side of it is not preserved. In distal view, the distal articulation surface is rugose and has an irregular shape. Compared to the other taxa, the bow shape of the proximal articulation surface is unlike the roughly triangular proximal articulation surfaces of MT III in *I. bernissartensis* and *B. johnsoni* and the irregular shape of the proximal articulation surface on MT III in *E. caroljonesa*. In craniocaudal view, the bone appears less robust than the MT III in the comparison taxa.

**Ungual:** The ungual (Plate 26) is strikingly similar in overall appearance to the ungual of *B. johnsoni* (Godefroit et al. 1998, Plate 14, Fig. 5A) which probably is an ungual III based on its symmetrical shape, it shows some similarities in overall shape to distal phalanx of digit III of *I. bernissartensis* and distal phalanx of digit II in *E. regalis*. However the distal phalanx of digit III is too short when viewed dorsally in *I. bernissartensis*, and the unguals of *I. bernissartensis* are too elongated. The ungual of *T. sinensis* is most similar to that identified as the ungual of digit III in *E. caroljonesa* and the ungual of *B. johnsoni* in that it is medilaterally broad and hoof like, although it is proportionally slightly longer in dorsal view than in *B. johnsoni*. It is convex dorsally and concave ventrally. The claw groove is well marked and rugose similar to *B. johnsoni* and *E. caroljonesa*, but partially lost to erosion. The articulation surface is concave, and roughly oval in proximal view. In overall proportions, however the ungual is most similar to an ungual of digit II (Zheng, Farke and Kim 2011). Godefroit et al. (1998) mentions that the unguals of digits II and IV are asymmetrical, being twisted away from digit III. The ungual is asymmetric too in dorsoventral view. The relative position of
the apex suggests it is from digit II of the right pes. Something which *T. sinensis* lacks is a plantar median ridge on the ventral surface of the ungual, which can be found in the Brachylophosaurine hadrosaurids *Maiasaura peeblesorum* Horner and Makela, 1979, and in *B. canadensis*, (Fiorillo 1993; Prieto-Márquez 2005).

5.6 Referred Material

Right humerus **PMUR235**, complete radius **PMUR239**, metatarsal without registration number.

5.7 Locality and Horizon

Referred material was found in the vicinity of the village Tianqiaotun (T’ien Ch’iao T’un on the labels), which some labels stats as being one *li* northeast of Tianqiaotun, and another label states it as one *li* east of Tianqiaotun) and about three *li* (~1.5 km) northwest of Jiangjunding (Buffetaut 1995). See fig. 1 for a map of the area. Hadrosauroidea Cope, 1870 (*sensu* You et al. 2003) Gen. et sp. indet. **Plates 27-29**

5.8 Comments

This material is here referred to as Hadrosauroidea gen. et sp. indet.

5.9 Description

The right humerus **PMUR235** (Plate 27), from the Tianqiaotun locality is bowed medially in cranial and caudal views like in all comparison taxa. The deltopectoral crest is short, and among the comparison taxa is most similar to *I. bernissartensis*. The deltopectoral crest is 40.1 % the length of the humerus. The humeral head is bulbous, slightly lunate in proximal view, and more prominently so than in *E. regalis* and not as round as in *E. caroljonesa*. The shape of it is not discernible in *B. johnsoni* and *I. bernissartensis*. Laterally to the humeral head, the proximal head consists of a rugose ledge that curves forward and downward and merges with the shaft. Medially, there is another rugose ledge curving outwards and downwards to the concave caudal side similar to all comparison taxa. The distal end of the humerus is dominated by the radial condyle; the ulnar condyle is not as well preserved. The two condyles are separated by an intercondylar groove similar to all comparison taxa. However, the distal articulation surface is not complete with the caudal portion of the ulnar condyle missing. The left and the right humeri are compared in the end of the systematic paleontology section.

A complete radius **PMUR239** (Plate 28), described by Wiman (1929) as being from the left side is preserved from this locality. It is long, straight and somewhat flattened in craniocaudal view. The trocheal end is gently expanded from slightly distally of the proximal end in lateral view. The
distal end expands from roughly the lower ¼ of the bone. In lateromedial view the radius is gently curved similar to *E. caroljonesa* and *B. johnsoni*. The trochlear end is leaf shaped in proximal view, and the distal end is roughly square shaped.

Metatarsal of uncertain position without registration number (Plate 29). The specimen appears to be mediolaterally flattened. The proximal and distal ends are hardly discernible, because of matrix covering. Both the proximal and distal ends seem to be expanded in medial and lateral view like MT II and IV of *E. regalis*, and MT II, III and IV of *E. caroljonesa*. At the distal articulation surface there is in medial view a tear drop-shaped depression similar to MT III and IV in *E. regalis* and *E. caroljonesa*. In cranial and caudal view, the bone is straight, except for a slightly diagonal pointed distal end, similar to MT II of *E. regalis*, but the specimen lacks the triangular distal half of the shaft in cranial and caudal view. Furthermore, in *E. regalis* MT II lacks the already mentioned tear drop-shaped depression. MT II, III and IV of *E. caroljonesa*, *I. bernissartensis* and *B. johnsoni* are much thicker. Furthermore metatarsals II and IV of *E. caroljonesa* is comparatively bowed in cranial and caudal view. In medial view, the specimen is concave. Based on the craniocaudal width of the specimen, it might be a metatarsal II (Zheng, Farke and Kim 2011).

?Hadrosauroidea Cope, 1870 (*sensu* You et al. 2003)
Gen. et sp. indet.
(Plates 30-31)

5.10 Referred material

Two fragmentary caudal centra, PMUR271 and PMUR272.

5. 11 Locality and horizon

No label with locality information is known for the centra.

5. 12 Comments

Because of their fragmentary nature, the two centra are only tentatively assigned to Hadrosauroidea gen. et. sp. indet.

5.13 Description

The two caudal centra PMUR271 (Plate 30) and PMUR272 (Plate 31) are slightly amphiplatyan, similar to *E. regalis* and *B. johnsoni*. Caudal articulation surface of PMUR272 are circular similar to *E. regalis* and the more cranial caudal vertebrae of *E. caroljonesa*. The caudal ventral margin of PMUR272 is flattened. PMUR271 is similar to PMUR272 but smaller and shorter. The ventral surfaces of both PMUR271 and PMUR272 are lacking the distinct fossa of
the holotype caudal vertebra. However, they cannot belong to the holotype of *T. sinensis*. The reasons for this is their small size in comparison to the more complete holotype caudal vertebra, with the centrum height in cranial aspect of PMUR271 and PMUR272 being 61 and 56 mm vs. 83 mm in the holotype caudal vertebra. The centrum lengths of PMUR271, PMUR272 and the holotype caudal vertebra are 53, 57 mm and 79 mm respectively. Prieto-Márquez and Norell (2010) noted that the usual condition in iguanodontians is for the centra of the cranial caudal vertebrae to be large and cranio-caudally compressed, becoming progressively longer, caudally in the caudal series. Assuming a similar pattern in *T. sinensis*, PMUR271 and PMUR272 would not follow this pattern, as it would suggest that they are more proximal than the holotype caudal vertebra despite being smaller.

**Ornithopoda Marsh, 1881**  
**Gen. et sp. indet.**  
(Plate 32)

5.14 Referred Material

A small vertebra.

5.15 Locality and Horizon

The small vertebra without a registration number (Plate 32) is from the type locality one li southwest of Jiangjunding.

5.16 Description

The vertebra is weakly amphicoelous and the centra is longer than high, and parallelogram-shaped like in cranial cervical vertebrae in *Tenontosaurus tilletti* and non-hadrosaurid ornithopods (Norman et al. 2004), the axis and 5th dorsal vertebra of *Cumnoria prestwichii* and the 3rd cervical vertebra of *Dysalotosaurus lettowvorbecki*. However the parallelogram shape is unlike any of the *Dryosaurus altus* vertebrae. The prezygapophysis is more curved outwards than in *T. tilletti*, *Zalmoaxes robustus*, *D. altus*, *D. lettowvorbecki*, and it makes a drawn out appearance in left lateral view. Although fragmentary, the transverse process projected in lateral view similar to 3rd and 4th cervical vertebrae in *C. tilletti*, and slightly similar to 9th or 10th dorsal vertebrae of *D. altus*, and 4th and 9th caudal of *C. prestwichii*. The embayment shaped ridge between the prezygapophyses and the neural spine is similar to the caudal vertebrae of *D. lettowvorbecki*, and more cranial cervical vertebrae and mid-caudal vertebrae of *T. tilletti*. The postzygapophyses are short and not extending like the cervical vertebrae in the comparison species, but more like in the dorsal vertebrae. Furthermore, the neural spine pointed vertically, most similar to dorsal vertebrae in *D. altus*, *D. lettowvorbecki*, *C. prestwichii*, although both dorsal and cranial- to mid-caudal vertebrae of *T. tilletti* and *Z. robustus* also had vertical neural spines. The small size, the parallelogram shape of the centra, and the drawn out
appearance of the prezygapophysis is highly unlike the vertebrae from *T. sinensis* and the hadrosaurid comparison taxa, and the vertebra therefore cannot have belonged to a hadrosaurid. However, these traits combined with the vertical neural spine and horizontal transverse processes suggest that the vertebra were a cranial dorsal vertebra, more likely of an ornithopod.

?Hadrosauridea Cope, 1870 (*sensu* You et al. 2003)
Gen. et sp. indet.
(Not illustrated)

5.17 Referred Material

Two fragmentary vertebrae centra, without a registration number.

5.18 Locality and Horizon

From one *li* northwest of Jiangjunding.

5.19. Description

Two more vertebrae (not illustrated) of uncertain affinities are also present in the collection. They are large but fragmentary centra, both being without registration number and not being from the same localities as the rest of the vertebrae. The first one of the two, have a concave articulation surface and a ventral groove as well as a slight horizontal keel. Only lumps remains of the pedicle. The second large centrum is probably a caudal vertebra, based on its overall similarities to the caudal vertebra of the holotype, although it is larger and more oval in craniocaudal view. Furthermore, when compared to caudal vertebra of the holotype, the ventral fossa between the ventral haemal articulation sites is more open at the cranial and caudal ends and also narrower in diameter. The cranial articulation surface is concave, while the caudal articulation surface is weakly concave. Only fragmentary lumps are left of the pedicle.

Theropoda Marsh, 1881
Gen. et sp. indet.
(Plate 33)

5.20 Referred material

Two theropod pubic bones, *PMUR245* and one without a registration number.

5.21 Locality and Horizon

These fragmentary elements of the pelvic girdle are from the type locality at the village of Jiangjunding.
5.22 Description

Theropod pubis **PMUR245** (Plate 33 C-D). Only its distal end is preserved, and the shaft curves continuously into a strongly booted process, that continue onto the opposite side of the shaft into a “spur” in lateral view, which then curves back onto the shaft. The bone is mediolaterally flattened. The “boot” is thickened in distal view and the distal surface is rugose, but most so in lateral and distal view, not in medial view. While the bone appears to have been continuously flattening similar to *B. johnsoni*, it also appears to lack the ridge visible in proximal view. While all comparison taxa have expanding distal ends to varying degree, none of them have the strongly expanded “boot”-like end, nor do they have the marked “spur” at the opposite end of the boot. This might suggest that the pubis does not come from an ornithischian at all.

Theropod pubis without registration number (Plate 33 A-B), only the distal end is preserved. It is similar in overall shape to **PMUR245**, but slightly bigger and more robust, and not as well preserved. Furthermore, the caudal surface is not as straight, but slightly more convex. Although broken off, the curvature of the shaft towards the distal end suggests the presence of a “spur” at the opposite end of the “boot”. And just like **PMUR245** it is flattened in lateral and medial view. It might have had a blade like process in the proximal part of the preserved of the shaft, although it largely consists of plaster reconstruction. This “process” is not found in any of the comparison taxa. Otherwise, the comparison comments between **PMUR245** and the comparison taxa apply to this specimen as well. The affinities of the two specimens will be discussed further in the discussion.

5.23 Comparisons between the two humeri

The holotype humerus **PMUR236** from Jiangjunding is overall similar to **PMUR235**. However, there are some slight differences, such as differences in the proportions of the deltopectoral crest; the holotype humerus is longer than **PMUR235**, 56.3 cm vs. ~52 cm. The deltopectoral crest of the holotype humerus **PMUR236** is also slightly longer than that of **PMUR235**, ~22.3 cm vs. ~21.3 cm. Translated into percentage of the length of the humerus, the deltopectoral crest of the holotype humerus **PMUR236** is 39.6% of the humerus length vs. 40.1 % in **PMUR235**. But as already pointed out, these differences should be taken with caution, given the fact that the distal articulation surface of **PMUR235** is not complete. Furthermore, the holotype humerus **PMUR236** is slightly less bowed in medial view than **PMUR235**, although it cannot be excluded that this is a diagenetic artefact. The humeral head in the holotype humerus is shorter and blunter in proximal view than in **PMUR235**, although this may be a diagenetic artefact. The intercondylar groove continues further up the shaft as a groove in caudal view in holotype humerus **PMUR236** than in **PMUR235**. The holotype humerus **PMUR236** is slightly more lunate in proximal view than **PMUR235**. Finally, the ledge medially of the humeral head is less expanded in proximal view than in **PMUR235**, and the attachment site for *m. latissimus dorsi* on the caudal side is more marked.
on the holotype humerus than in PMUR235. The distal end is partly covered by matrix, although
the ulnar condyle is slightly better preserved. The similarity of the humerus PMUR235 from the
Tianqiaotun locality to the holotype humerus PMUR236 from the type locality at Jiangjunding at
least suggests the presence of a very similar form, if not the presence of the same species at the two
localities.

6. Phylogenetic systematics

6.1 Materials and methods

Previous phylogenetic analysis starting with Weishampel and Horner 1990 (cited by Horner,
Weishampel and Forster 2004) placed Tanius as a basal member of Hadrosauridae outside the
subfamilies Lambeosaurinae and Hadrosaurinae. Later phylogenetic studies have tended to place T.
sinesis as a non-hadrosaurid hadrosauroid, although the exact position has varied. The phylogenetic
tree of Sues and Averianov (2009), for example placed it in a polytomy with Telmatosaurus
transsylvanicus Nopcsa, 1900 outside Hadrosauridae, but more derived than for example B. johnsoni.
The phylogenetic trees of Dalla Vecchia (2009) also placed it as more derived than B. johnsoni but
less derived than T. transsylvanicus. The phylogenetic analysis of Prieto-Márquez (2010a) and Xing et
al. (2014b) on the contrary retrieved T. sinensis as a non-hadrosaurid hadrosauroid less derived than
both B. johnsoni and T. transsylvanicus. For the phylogeny part, the observations made here regarding
the postcranial anatomy of T. sinensis were used to revise its scoring in the character matrix of Xing et
al. (2014b) using Mesquite 3.02 (Maddison and Maddison 2011). Specifically, the following
characters where amended; character 242 (the ratio between the height and the length of the
middleneural spines of the middle dorsal vertebrae) where changed from ? to 1 (1 constituting a ratio
of 4.0 or greater); the score for character 245 (ratio between the height of the neural spine and that
of the centrum of the tallest sacral vertebra) where changed from 1 to ?, based on the fact that no
sacral vertebrae are known from T. sinensis; the score for character 263 (morphological character
of the acromial process of the scapula) where changed from 0 to 1 (0 constitutes strongly recurved,
with the cranial end of the acromial process directed dorsally, while 1 constitutes slightly recurved,
with the anterior end of the acromial process directed craniodorsally); The score for character
270 (ratio between the width of the distal third of the deltopectoral crest and the width of the distal
constriction of the humerus) where changed from 0 to 1 (0 constitutes less than 1.65 and 1
constitutes 1.65 to 1.90); the score for character 333 (general profile of the caudal margin of femoral
fourth trochanter in lateral view) where changed from ? to 1 (1 constitutes arcuate and smooth); the
score for character 334 (morphological character of the cranial intercondylar groove in the distal
region of femur) where changed from ? to 1 (1 constitutes nearly or completely enclosed by the
lateral and medial condyles owing to the fusion of these two condyles); the score for character 335

23
(morphological character of the cnemial crest of the tibia) where changed from ? to 1 (1 constitutes presence of an expanded ventrally cnemial crest along the proximal half the tibial shaft); the score for character 341 (ratio between the proximodistal length of the metatarsal III and the mediolateral width of this element at midshaft) where changed from ? to 0 (0 constitutes being greater than 4.5); the score for character 345 (general shape of pedal unguals in dorsal view) where changed from ? to 1 (1 constitutes being hoof-shaped, with the presence of faint claw grooves or absence of claw grooves); the score for character 346 (plantar median ridge on the ventral surface of pedal ungual) where changed from ? to 0 (0 constitutes the ridge being absent).

The program PAUP (Swofford 2002) was used to run the phylogenetic analysis with the non-hadrosaurid Ouranosaurus nigeriensis Taquet, 1976, used as the outgroup. A heuristic search was used, (100 replicates) using the TBR branch swapping algorithm.

6.2 Results of phylogenetic tree

The phylogenetic analysis recovered 392 most parsimonious trees with 1109 steps, a consistency index of 0.5275, a retention index of 0.8530, and a rescaled consistency index of 0.4499. In the strict consensus tree, T. sinensis was recovered in a polytomy consisting of all hadrosaurids to the exclusion of Eolambia, Probactrosaurus gobiensis Rozhdestvensky, 1966, Xuwulong yueluni You, Li and Liu, 2011 and Equijubus, and containing a monophyletic Hadrosauridae. This clade (Fig. 3: node 1), is supported by the following unambiguous synapomorphies: the absence of the surangular accessory foramen on the anterolateral surface of the surangular (character 60); the position of the quadratojugal notch relative to the dorsoventral height of the quadrate, with the midpoint of the quadratojugal notch being located well below half the dorsoventral height of the quadrate (character130); presence of a strongly concave anteroventrally orbital margin that is often semicircular or lunate (character 180); the triangular ventral process of the postorbital being slender and gradually tapering ventrally (character 181). In the 50% majority consensus tree there is a clade (Fig. 3: node 2) that unites T. sinensis with some non-hadrosaurid hadrosauroids and hadrosaurids, to the exclusion of Levnesovia transoxiana Sues and Averianov, 2009, Protohadros byrdi Head, 1998 and the taxa already excluded from node 1. Node 2 is united by the following unambiguous synapomorphies: the number of dentary teeth per centimetre of the dental battery being 0.7 or more (character 2); the angle between the edentulous slope of dentary anterior portion and the level being 150° or greater (character 39); the position of the angular of the mandible being in such a way that the angular is not exposed in lateral view, with a medial position (character 67); the ratio between length of the lateral margin of the scapular articular surface of the coracoid and that of the lateral margin of the glenoid being less than 1.0 (character 252). In the 50% majority consensus tree T. sinensis is recovered as the sister taxon of B. johnsoni (Fig. 3: node 3), based on the following unambiguous synapomorphies: the width of the orbital margin of the jugal being almost equally wide
to that of the infratemporal margin of the bone (character 126); the ratio between the mediolateral width of the skull roof across the postorbitals and that across the quadrate cotyli of the paired squamosals being more than 1.20 (character 232). Finally, the remaining the non-hadrosaurid hadrosauroids, to the exclusion of *T. sinensis* and *B. johnsoni* are more closely related to hadrosaurids (Fig. 3: node 4) based on the ratio between maximum mediolateral width of the dentary symphysial region, and the minimum breadth of the dentary posterior to the dentary symphyseal region in dorsal view being up to 1.65 (character 43); the presence of a markedly inclined posterovertrally ectopterygoid shelf with an angle between 10° and 20° from the horizontal (character 112); the ratio between the dorsoventral height and anteroposterior length of the iliac central plate being less than 0.8 (character 290).
Figure 3. Phylogenetic tree for *T. sinensis*. The left tree is the 50% majority consensus tree, while the tree to the right is the strict consensus tree. The nodes discussed in the text are numbered as 1, 2, 3 and 4 respectively.
7. Discussion

7.1 Postcranial character complex in Tanius sinensis

*Tanius sinensis* boasts a mix of basal and derived characters within Hadrosauroidea. To start, opisthocoelous cervical vertebrae are a basal trait within hadrosaurs, appearing in non-hadrosaurid iguanodontians (Norman 2004), and maintained by non-hadrosaurid hadrosaurs and hadrosaurid hadrosaurs (Horner, Weishampel and Forster 2004; McDonald et al. 2012). A derived character present in the dorsal vertebra of *T. sinensis* includes the ratio between the height and length of the neural spine (≥4.0 or greater; character 242), present for example in lambeosaurines like *Olorotitan arharensis* Godefroit, Bolotsky and Alifanov, 2003: Godefroit, Bolotsky and Bolotsky (2012) and *Magnapaulia laticaudus* Prieto-Márquez, Chiappe and Joshi, 2012.

The rod like shaft of the sternal plate first appears in the non-hadrosaurid iguanodontian *Lurdusaurus arenatus* Taquet and Russell, 1999, (Norman 2004), and is maintained by the hadrosaurs (Horner, Weishampel and Forster 2004).

A derived character which *T. sinensis* shares (convergently) with the hadrosaurids is the curved dorsal margin of the scapula, rendering the dorsal surface a convex appearance in medial and lateral view. Such a character was considered synapomorphic for hadrosaurs by Prieto-Márquez (2010a) but may have occurred elsewhere in hadrosaur evolution as shown here. Among non-hadrosaurid hadrosaurs the dorsal surface of the scapula is relatively straight in medial and lateral view. The only other non-hadrosaurid hadrosaur to have this trait is *Zhanghenglong yangshengensis* Xing et al., 2014b, which holds a higher phylogenetic position relative *T. sinensis*. A basal trait found in the scapula of *T. sinensis* is the maximum dorsoventral width of the proximal end being bigger than the dorsoventral width at the distal end (212 mm vs. 144 mm) (Prieto-Márquez and Norell 2010). The derived condition, which is found in hadrosaurs is for the dorsoventral width of the distal end to be bigger than the width at the proximal end (Prieto-Márquez and Norell 2010). Regarding the character of the recurved cranial end of the acromial process of the scapula being craniodorsally directed, Prieto-Márquez (2010a) recovered this character state as an ambiguous synapomorphy for Lambeosaurinae, noting it as being convergent amongst other taxa, both non-hadrosaurid iguanodontians and non-hadrosaurid hadrosaurs; *I. bernissartensis*, *E. caroljonesa*, and *T. sinensis*. Judging by the illustrations of the scapula in the work by Norman (1980, Fig. 52) and McDonald et al. (2012, Fig. 27), this view is here supported.

Concerning the pelvic anatomy, the long and ventrally deflected preacetabular process in *T. sinensis* appears to be common among some non-hadrosaurid iguanodontians like *Iguanodon* Mantell, 1825 and all hadrosaurs (Norman 2004; Horner, Weishampel and Forster 2004). The positioning of the ventral apex of the supra-acetabular process caudodorsal to the ischial peduncle, as observed in the left ilium (Plate 21a) is a basal condition within Hadrosauroida, present in the non-hadrosaurid *I. bernissartensis* (Norman 1980; Prieto-Márquez and Norell 2010) and in all non-
hadrosaurid hadrosauroids (Prieto-Márquez and Norell 2010). The derived condition, interpreted as a synapomorphy for Hadrosauridae by Prieto-Márquez (2010a) is for the ventral apex of the supra-acetabular process to be placed craniodorsally of the postacetabular ridge of the ischial peduncle. However, when reorienting the ilium in such a way that the pubic peduncle is in a straight line to the ischial peduncle, the supra-acetabulary process get located in a straight line dorsally to the postacetabular ridge. This is problematic, and may represent a transitional state. The presence of a postacetabular ridge in itself is regarded as a derived trait, that occurs in T. sinensis, at least in one specimen of B. johnsoni, although not explicitly mentioned (Godefroit et al. 1998, Fig. 30a) and in Gilmoreosaurus mongoliensis Gilmore, 1933, but is largely confined to Hadrosauridae (Brett-Surman1975 cited by Godefroit, Zan and Jin 2001), while non-hadrosauroid iguanodontians and other non- hadrosaurid hadrosauroids lack this ridge (Godefroit, Zan and Jin 2001).

Parts of the material from the Jiangjunding locality might not belong to T. sinensis. Wiman (1929) referred what he interpreted as a distal end of an ischium PMUR245 (Plate 33 C-D) to T. sinensis on the basis that it was similar to distal end of the ischium in Hypacrosaurus alispinus Brown, 1913. Especially the strongly anteroposteriorly expanded distal end was problematic to Buffetaut and Tong-Buffetaut (1993) who found this condition to be too extreme in comparison to known hadrosaurids. Coupled with the fact that it is mediolaterally compressed made Buffetaut and Tong-Buffetaut (1993) to suggest instead that it might be the distal end of a theropod pubis, subsequently supported by Hu et al. (2001). Prieto-Márquez (2010a) on the contrary, apparently unaware of Buffetaut and Tong-Buffetaut’s (1993) assessment simply attributed the bone as an ischial fragment to T. sinensis. The theropod material from the type locality of T. sinensis at the village of Jiangjunding consists of vertebrae, described with close affinities to ornithomimids and tyrannosauroids (Poropat and Kear 2013), the anatomy of which is consitant with that of the pubes. Since this material is no longer considered to pertain to the holotype of T. sinensis, it will not be discussed any further.

The hindlimb elements of T. sinensis contain one particularly unusual trait, the fusion of the lateral and medial condyles of the femur booth cranially and caudally. This morphology was noted in the original description as ‘two holes between the condyles’ ‘Zwischen den beiden condyli liegen zwei löcher...’ by Wiman (1929, p. 55). While the cranial fusion of the lateral and medial condyles has been described from the non-hadrosaurid B. johnsoni (Godefroit et al. 1998) and it is present to varying degree in hadrosaurids, apparently having arisen independently numerous times (Godefroit et al. 1998; Horner, Weishampel and Forster 2004; Juárez Valieri et al. 2010), and it is known from hadrosaurine hadrosaurids like S. osborni (Brown 1913b) and in lambeosaurin hadrosaurids like Tsintaosaurus (although it appears to be variable in this species) (Young 1959) and O. arharensis (Godefroit, Bolotsky and Bolotsky 2012). It cannot be excluded that the cranial fusion of the lateral and medial condyles, at least in some species like Tsintaosaurus is simply down to individual variation. The caudal fusion of the lateral condyles however, has so far not been observed in any other
hadrosauroid, and may well be an autapomorphy for *T. sinensis*. The caudal fusion of medial and lateral condyles do not show any signs of being a taphonomical or preservational artefact, therefore suggesting that the fusion is genuine. The general profile of the posterior margin of the fourth trochanter in lateral view being arcuate and smooth, was regarded as a derived trait, although not synapomorphic for any clade according to the character matrix of Prieto-Márquez (2010a) and the updated character matrix of Xing et al. (2014b), although Horner, Weishampel and Forster (2004) stated that the overall shape of the fourth trochanter in hadrosaurids (*sensu* Horner, Weishampel and Forster 2004) is variable. The presence of the trait in *T. sinensis* suggests that it is homoplastic. The tibia has a cnemial crest that extends ventrally into the proximal half of the shaft, which is a derived trait within Hadrosauroidea that besides being present in *T. sinensis*, *B. johnsoni*, *G. mongoliensis* and *T. transsylenicus*, is mostly found in Hadrosauridae (Godefroit et al. 1998). The basal condition on the other hand is for the cnemial crest to be restricted to the proximal end (Godefroit et al. 2001).

The fibula is also derived, namely the distal end expands into a club shape in lateral view. This trait is shared with some lambeosaurs like *O. arharensis* (Godefroit, Bolotisky and Bolotisky 2012), *Charonosaurus jiayinensis* Godefroit, Zan and Jin, 2000, and *Parasaurolophus cyrtocristatus* Ostrom, 1961. This character state was regarded by Prieto-Márquez (2010a) as an ambiguous synapomorphy for Lambeosaurinae, although convergent in *T. sinensis*. The basal condition, found in most hadrosauroids, is for the distal end to be moderately expanded into a ball-shape (Brett-Surman and Wagner 2007).

A primitive trait present in metatarsal III is the ratio between its proximodistal length and the mediolateral width (greater than 4.5, Prieto-Márquez 2010a).

The blunt and hoof-like appearance of the pedal ungual is typical for non-hadrosaurid iguanodontians (Norman 2004), however they tend to become proportionally shorter and broader in dorsal view in Hadrosauroida (Horner, Weishampel and Forster 2004). Prieto-Márquez (2010a) identified the character of mediolaterally broad and proximodistally shortened pedal unguals, rounded shield or hoof-like shaped, with reduced claw grooves as a synapomorphy for Lambeosaurinae, convergent in *B. johnsoni*. However, the ungual of *T. sinensis* is broad and hoof-like, although proportionally longer than broad in dorsal view. As pointed out by McDonald et al. (2012) this condition is found in several non-hadrosaurid hadrosauroids. Accordingly the ungual of *T. sinensis* is derived compared to non-hadrosaurid iguanodontians, but not within Hadrosauroida.

The characters above, including several of which have been considered hadrosaurid synapomorphies, suggests that *T. sinensis* may be phylogenetically closer to hadrosaurids than previously hypothesized by other authors in previous years (Sues and Averianov 2009; Prieto-Márquez 2010a; Xing et al. 2014b). Its problematic phylogenetic placement is evident from the large polytomy that occurs on the hadrosaurid stem. Regarding the result of the phylogenetic analysis, only two of the characters mentioned in the result section as being unambiguous synapomorphies for various clades, concern the postcranial skeleton: 1) the ratio between length of the lateral margin of the
scapular articular surface of the coracoid and that of the lateral margin of the glenoid being less than 1.0 (character 252, corresponding to node 2; not preserved in Tanius), and 2) the ratio between the dorsoventral height and anteroposterior length of the iliac central plate being less than 0.8 (character 290, corresponding to node 4). The rest of the unambiguous synapomorphies for the nodes 1, 2, 3, 4 are cranial characters. This can either be interpreted as evidence to the phylogenetic importance of the hadrosauroid cranium, or an overall lack of understanding regarding postcranial variation in these forms. Such a lack underscores the importance of the study undertaken here. It is worth mentioning the non-hadrosaurid hadrosauroid taxa in the tree which are based solely on cranial material: *L. transoxiana*, which was retrieved between node 1 and node 2; *Jintasaurus meniscus* You and Li 2009, which together with *Shuangmiaosaurus gilmorei* You et al. 2003b, is recovered in the polytomy at the base of node 4. To this list should also be added *Penelopognathus weishampeli* Godefroit, Li and Shang 2005. *P. weishampeli* is not included in the phylogenetic analysis, because it is absent from the dataset on which the analysis is based on, namely that of Xing et al. 2014b, but it was described as a non-hadrosaurid hadrosauroid. On the contrary some taxa in the phylogeny are known only from postcranial material, namely *Nanyangosaurus zhuji* Xu et al. 2000, which is recovered higher up in the tree than the previously mentioned taxa, in a polytomy with *Z. yangshengensis* just outside Hadrosauridae. Postcranial and cranial material respectively from these taxa would undoubtedly give a more nuanced view of their phylogenetic affinities. In this context, *T. sinensis* is important in being known from both cranial and postcranial material. Another problematic aspect is that of character 252 (corresponding to node 2) which concerns the coracoid, which is unknown from *T. sinensis*, and therefore will not be discussed any further. Character 290 (corresponding to node 4), concerning the ratio between the dorsoventral height and craniocaudal length of the iliac central plate, with the derived condition being a ratio of less than 0.8. This character is also derived in *T. sinensis*, and the condition is therefore considered homoplastic. Given the tree and a DELTRAN character optimization criterion, the derived condition may be considered autapomorphic for *T. sinensis*. However, given the 50% majority topology, the evolution of this character under an ACCTRAN criterion would indicate a reversal to the primitive condition in *B. johnsoni*. Node 3, the sister relationship between *T. sinensis* and *B. johnsoni*, has not been retrieved in previous phylogenetic analyses including both taxa (Sues and Averianov 2009; Prieto-Márquez and Norell 2010; Xing et al. 2014b), except for the strict consensus tree of Dalla Vecchia (2009) where *T. sinensis* formed a polytomy with *B. johnsoni* and *G. mongoliensis*.

**7.2 Paleobiological implications**

The Late Cretaceous age, interpreted for the deposits of the Wangshi Group (Hu et al. 2001), suggest that *T. sinensis* was one of the few late surviving non-hadrosaurid hadrosauroids. Non-hadrosaurid hadrosauroids from the Campanian and onwards include *G. mongoliensis* and *B. johnsoni* both from the middle-late Campanian of the Upper Cretaceous Iren Dabasu Formation of China (Godefroit et al. 1998; Prieto-Márquez and Norell 2010; Xing et al. 2012); *Plesiohadros*
*djadokhtaensis* Tsogbaatar et al., 2014 from the Campanian of the Upper Cretaceous Djadokhta Formation of Mongolia; *Tethyshadros insularis* Dalla Vecchia, 2009 from the late Campanian-early Maastrichtian of the Upper Cretaceous Liburnian Formation of Italy; *T. transsylvanicus* from the Maastrichtian-aged Sânpetru Formation of Upper Cretaceous in Hăţeg and southwestern Transylvania of Romania (Codrea et al. 2010; Csiki-Zava et al. 2015). The non-hadrosaurid hadrosauroids within the latest Cretaceous of Asia and Europe temporally overlapping and sympatric with hadrosaurids is in stark contrast to the North-American megaherbivorous community where as of the Campanian, non-hadrosaurids went extinct (Evans et al. 2011; Campione et al. 2013). It is worth noting that *Glishades ericksoni* Prieto-Márquez, 2010c was originally described as a non-hadrosaurian from the late Campanian Two Medicine Formation of western USA. However, the remains of *G. ericksoni* was later deemed to represent an indeterminate juvenile hadrosaurid by Campione et al. (2013), suggesting that non-hadrosaurid hadrosauroids had become extinct in western North America by a least the Late Campanian (Campione et al. 2013). The fact that *T. sinensis* was found in layers overlying the Xingezhuang- and Hongtuya formations, where the hadrosaurid *S. giganteus* is found and under the Jingangkou Formation were *T. spinorhinus* found indicates that, unlike North America, Asian dinosaur communities include a possible sympatric relationship between hadrosaurids and non-hadrosaurid hadrosauroids. The recovered relationship, if standing further scrutiny, in the phylogenetic analysis between *T. sinensis* and *B. johnsoni*, may suggest that this sympatry was not just random taxa that persisted, but possibly a lineage that survived.

### 7.3 The size of *Tanius sinensis*

The body mass of the type specimen from the Jiangjunding locality was estimated using the following equation from Campione and Evans (2012):

\[
\log_{10}BM = 2.749 \times \log_{10}C_{H+F} - 1.104
\]

where \( \log_{10}C_{H+F} \) stands for the logarithm of the combined minimum circumference of the humerus and femur. Whith this equation the body mass is calculated to be 2950 kg. To put this result into perspective, body mass estimates of some other non-hadrosauroid iguanodontian and hadrosaurid taxa can be mentioned: The result of the body mass calculation for *T. sinensis* is far less than the estimate for *E. regalis* at 7936 kg ± 1991 kg (Campione 2014), but within the range of most hadrosaurids including *Prosaurolophus maximus* Brown, 1916 being 2900 kg, 3100 kg for the species of *Lambeosaurus*, Parks, 1923, and 3200 kg for the species of *Corythosaurus* Brown, 1914 (Brown et al. 2013). Benson et al. (2014) calculated the body mass for a whole range of non-avian dinosaurs using the equations of Campione and Evans (2012). They estimated the body mass of *I. bernissartensis* to 15000 kg, 1797 kg for *B. johnsoni*, and 1300 kg for *G. mongoliensis*. The estimated body mass for the largest hadrosauroid, *S. giganteus* (Hone et al. 2014) was 17000 kg. The body mass of *T. sinensis* might therefore have been relatively large as a non-hadrosaurid hadrosauroid.
8. Conclusions

The postcranial anatomy of *T. sinensis* was re-studied and compared to that of the non-hadrosaurid iguanodontian *I. bernissartensis*, the non-hadrosaurid hadrosaurs *E. caroljonesa* and *B. johnsoni* and the hadrosaurid *E. regalis*. As already noted the anatomy shows several symplesiomorphies like, strongly opisthocoelous cervical vertebrae, the maximum dorsoventral width of the proximal end of the scapula being bigger than the dorsoventral width at the distal end, and the ratio between the proximodistal length of the metatarsal III and the mediolateral width of this element being greater than 4.5. However, the postcranial skeleton of *T. sinensis* also exhibits several apomorphies like the convex dorsal margin of the scapula, an arcuate fourth trochanter in the femur, a clubshaped distal end of the fibula, and a cnemial crest of the tibia that extends ventrally along the proximal half of the shaft. A possible autapomorphy is noted in the distal region of the femur, being the fusion of the medial and lateral condyles caudally, to form a completely enclosed “tunnel”. The body mass of the holotype of *T. sinensis* is calculated to be have been approximately 2950 kg, which represents one of the heaviest estimates for a non-hadrosaurid hadrosaurid. The phylogenetic analysis confirms previous studies in retrieving *T. sinensis* as a non-hadrosaurid hadrosaurid, but unlike previous studies we recover a large polytomy at the hadrosauroid base, of which *Tanius* is a part. However, in approximately 70% of the trees *T. sinensis* forms a clade with *B. johnsoni*, which share the following unambiguous synapomorphies; the width of the orbital margin of the jugal being almost equally wide to that of the infratemporal margin of the bone and the ratio between the mediolateral width of the skull roof across the postorbitals and that across the quadrate cotyli of the paired squamosals being more than 1.20. The fact that *T. sinensis* may have been one of the last non-hadrosaurid hadrosaurs in Asia that might have been sympatric with hadrosaurs, as well as being one of the oldest valid non-avian dinosaur taxa from Asia underscores the importance of this material.

9. Acknowledgements

Supervisor Nicolás E. Campione is thanked for support and for providing necessary literature as well as help with running the phylogenetic analyses and for very valuable help with fig. 35 and 36, Benjamin Kear is thanked for providing literature, and for advice regarding the phylogenetic analyses. Jan Ove R. Ebbestad is thanked for generous practical assistance and for providing litterature. Stephen F. Poropat is thanked for providing useful literature. Hai Xing is thanked for kindly providing his updated character matrix. Penélope Cruzado Caballero is thanked for providing useful comparative photographs and literature. My friends Frank Guldstrand and Lisa Samrock are thanked for very valuable assistance with image handling software, and for help with modifying figure 1. My family is thanked for unconditional support and especially my brother Daniel is thanked for assistance with malfunctioning computer software and formatting. Giannis Kesidis, is thanked for very valuable
comments regarding the language of the manuscript. Michael Streng is thanked for help with the printing of references. Furthermore Pär Eriksson of the Museum of Evolution, Uppsala is thanked for the repair of damaged specimens. Finally, my friend and mentor Illiam Jackson is thanked for all his support and friendship during my years as a student at Uppsala.
10. References


Gilmore, CW, 1913, ‘A new dinosaur from the Lance Formation of Wyoming’, *Smithsonian Miscellaneous Collections*, vol. 61, no. 5, pp. 1-5.


Norman, DB, 1980,’On the Ornithischian Iguanodon bernissartensis from the Lower Cretaceous of Bernissart (Belgium’), Mémoires de l’Institut Royal des Sciences Naturelles de Belgique, no. 178, pp. 1-103.


Riabinin, AN, 1930, ‘Mandschurosaurus amurensis nov. gen. nov. sp. a hadrosaurian dinosaur from the Upper Cretaceous, Amur River’, Société de Paléontologique de Russie, vol. 59, no. 2, pp.1-55.


Xing, H, Wang, D, Han, F, Sullivan, C, Ma, Q, He, Y, Hone, D, WE, Yan, R, Du, F, & Xu, X, 2014b, ‘A new basal Hadrosauroid Dinosaur (Dinosauria: Ornithopoda) with transitional features from the Late Cretaceous of Henan Province, China’, *PLoS ONE*, vol. 9, no. 6, pp. 697-705, doi: 10.1371/journal.pone.0098821


11. Plates

Note: Caption refers to plate on opposite page
Plate 1 The Axis. A = caudal view; B = cranial view; C = lateral view; D = dorsal view; E = ventral view. Abbreviations: ic = intercentrum; ns = neural spine; poz = postzygapophysis; prz = prezygapophysis; odpr = odontoid process; vf = vertebral foramen.
Plate 2 The 3rd cervical vertebra. A = cranial view; B = caudal view; C = dorsal view; D = ventral view; E = left lateral view; F = right lateral view. Abbreviations: d = diapophysis; ns = neural spine; par = parapophysis; poz = postzygapophysis; prz = prezygapophysis; tp = transverse process; vf = vertebral foramen.
Plate 3 The 4th cervical vertebra. A = cranial view; B = caudal view; C = dorsal view; D = ventral view; E = left lateral view; F = right lateral view. Abbreviations: ns = neural spine; par = parapophysis; poz = postzygapophysis; prz = prezygapophysis; tp = transverse process; vf = vertebral foramen.
Plate 4 The 5th cervical vertebra, A = cranial view; B = caudal view; C = dorsal view; D = ventral view; E = left lateral view; F = right lateral view. Abbreviations: ns = neural spine; par = parapophysis; poz = postzygapophysis; prz = prezygapophysis; tp = transverse process; vf = vertebral foramen.
Plate 5 The 6th cervical vertebra, A = cranial view; B = caudal view; C = dorsal view; D = ventral view; E = left lateral view; F = right lateral view. Abbreviations: ns = neural spine; par = parapophysis; poz = postzygapophysis; prz = prezygapophysis; tp = transverse process; vf = vertebral foramen.
Plate 6 The 7th cervical vertebra, A = cranial view; B = caudal view; C = dorsal view; D = ventral view; E = left lateral view; F = right lateral view. Abbreviations: ns = neural spine; par = parapophysis; poz = postzygapophysis; prz = prezygapophysis; tp = transverse process; vf = vertebral foramen.
Plate 7 The 8th cervical vertebra, A = cranial view; B = caudal view; C = dorsal view; D = ventral view; E = left lateral view; F = right lateral view. Abbreviations: ns = neural spine; par = parapophysis; poz = postzygapophysis; prz = prezygapophysis; tp = transverse process; vf = vertebral foramen.
Plate 8 The 9th cervical vertebra, A = cranial view; B = caudal view; C = dorsal view; D = ventral view; E = left lateral view; F = right lateral view. Abbreviations: ns = neural spine; par = parapophysis; poz = postzygapophysis; prz = prezygapophysis; tp = transverse process; vf = vertebral foramen.
Plate 9 The 10th cervical vertebra, A = cranial view; B = caudal view; C = dorsal view; D = ventral view; E = left lateral view; F = right lateral view. Abbreviations: ns = neural spine; par = parapophysis; poz = postzygapophysis; prz = prezygapophysis; tp = transverse process; vf = vertebral foramen.
**Plate 10** Isolated cervical ribs. A-B PMUR255 in A = lateral view; B = medial view. C-D PMUR256 in C = lateral view; D = medial view. E-F PMUR 254 in E = lateral view; F = medial view. Abbreviations: cap = capitulum; tub = tuberculum.
Plate 11 Isolated dorsal vertebra, A = cranial view; B = caudal view; C = dorsal view; D = ventral view; E = left lateral view; F = right lateral view. Abbreviations: ns = neural spine; poz = postzygapophysis; prz = prezygapophysis; tp = transverse process; vf = vertebral foramen.
Plate 12 Isolated caudal vertebra, A = left lateral view; B = right lateral view; C = cranial view; D = caudal view; E = dorsal view; F = ventral view. Abbreviations: ha = haemal arch articulation site; ns = neural spine; prz = prezygapophysis; vf = vertebral foramen.
Plate 13 Isolated haemal spine, A = cranial view; B = caudal view; C = left lateral view; D = right lateral view.
Plate 14 Complete dorsal rib. Abbreviations: cap = capitulum; tub = tuberculum.
Plate 15 Right scapula, A = lateral view; B = proximal view; C = medial view. Abbreviations: ap = acromion process; coa = coracoids articulation; gl = glenoid.
Plate 16 Right sternal plate, A = ventral view; B = dorsal view; C = lateral view; D = medial view; E = distal view.
Plate 17 Left humerus, A = medial view; B = lateral view; C = cranial view; D = caudal view; E = proximal view. Abbreviations: dp = deltopectoral crest; hh = humeral head.
Plate 18 Right ulna. A = caudal view; B = cranial view; C = lateral view; D = medial view; E = proximal view; F = distal view.
Plate 19 Proximal radius fragment in A = medial view; B = lateral view; C = caudal view; D = cranial view; E = distal view; F = proximal view.
Plate 20 Distal radii fragments A-F = medial view; B-G = lateral view; C-H = cranial view; D-I proximal view; E- J = distal view.
Plate 21 Left (A-B) and (C-D) right ilia. A, C = lateral view; B, D = medial view. Abbreviations: ac = acetabulum; brs = brevis shelf; isp = ischial peduncle; it = attachment site for the *m. iliotibialis*; par = postacetabular ridge; pifi = attachment site for the *m. pubischiofemoralis internus*; poap = postacetabular process; pp = pubic peduncle; prap = preacetabular process.
Plate 22 Right femur, A = lateral view; B = medial view; C = caudal view; D = cranial view; E = distal view; F = cranial view. Potential autapomorphy in circle with arrow. Abbreviations: 4tr = fourth trochanter; ct = cranial trochanter; gt = greater trochanter; lc = lateral condyle; mc = medial condyle; pifi = attachment site for the *m. pubischiofemoralis internus.*
Plate 23 Right tibia. A = cranial view; B = caudal view; C = lateral view; D = medial view; E = distal view; F = proximal view. Abbreviations: cc = cnemial crest; ic = inner condyle; lm = lateral malleolus; mm = medial malleolus.
Plate 24 Right fibula. A = lateral view; B = medial view; C = cranial view; D = caudal view; E = distal view; F = proximal view.
**Plate 25** Metatarsal III. A = medial view; B = lateral view; C = cranial view; D = caudal view; E = proximal view; F = distal view.
Plate 26 Ungual. A = dorsal view; B = ventral view; C = left lateral view; D = right lateral view; E = proximal view.
Plate 27 Right humerus. A = medial view; B = lateral view; C = cranial view; D = caudal view; E = proximal view; F = distal view. Abbreviations: dp = deltopectoral crest; hh = humeral head.
Plate 28 Complete radius. A = cranial view; B = distal view; C = proximal view; D = caudal view; E = lateral view; F = medial view.
Plate 29 Metatarsal II. A = medial view; B = lateral view; C = distal view; D = cranial view; E = caudal view; F = proximal view.
Plate 30 Caudal centra. A = cranial view; B = caudal view; C = dorsal view; D = ventral view; E = lateral view (lateraly reversed).
Plate 31 Caudal centra. A = cranial view; B = caudal view; C = dorsal view; D = ventral view; E = lateral view.
**Plate 32** Isolated cervical or dorsal vertebra. A = right lateral view; B = left lateral view; C = dorsal view; D = ventral view; E = cranial; F = caudal view. Abbreviations: ns = neural spine; poz = postzygapophysis; prz = prezygapophysis; tp = transverse process.
Plate 33 Theropod pubis without registration number and PMUR245. A, C = lateral view; B, D = medial view.
# Appendix A: Axial skeleton measurements

<table>
<thead>
<tr>
<th></th>
<th>Total Height</th>
<th>Post-zygapophysis length from neural spine</th>
<th>Pedicle cranio-caudal length</th>
<th>Pre and Post-zygapophysis length</th>
<th>Centrum length</th>
<th>Width between post-zygapophyses</th>
<th>Spine height</th>
<th>Centrum height along the cranial aspect</th>
<th>Centrum height along caudal aspect</th>
<th>Centrum width along cranial aspect</th>
<th>Centrum width along caudal aspect</th>
<th>Spinal canal height at cranial opening</th>
<th>Spinal canal width at cranial opening</th>
</tr>
</thead>
<tbody>
<tr>
<td>Axis</td>
<td>218 mm</td>
<td>40 mm</td>
<td>71 mm</td>
<td>142 mm</td>
<td>77 mm</td>
<td>39 mm</td>
<td>65 mm</td>
<td>94 mm</td>
<td>80 mm</td>
<td>-</td>
<td>60 mm</td>
<td>46 mm</td>
<td>34 mm</td>
</tr>
<tr>
<td>Cervical 3</td>
<td>168 mm</td>
<td>101 mm</td>
<td>64 mm</td>
<td>132 mm</td>
<td>91 mm</td>
<td>-</td>
<td>-</td>
<td>77 mm</td>
<td>86 mm</td>
<td>128 mm</td>
<td>71 mm</td>
<td>43 mm</td>
<td>35 mm</td>
</tr>
<tr>
<td>Cervical 4</td>
<td>154 mm</td>
<td>-</td>
<td>50 mm</td>
<td>-</td>
<td>95 mm</td>
<td>11 mm</td>
<td>89 mm</td>
<td>84 mm</td>
<td>88 mm</td>
<td>85 mm</td>
<td>46 mm</td>
<td>27 mm</td>
<td></td>
</tr>
<tr>
<td>Cervical 5</td>
<td>-</td>
<td>103 mm</td>
<td>60 mm</td>
<td>129 mm</td>
<td>118 mm</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>30 mm</td>
<td>35 mm</td>
</tr>
<tr>
<td>Cervical 6</td>
<td>83 mm</td>
<td>90 mm</td>
<td>64 mm</td>
<td>139 mm</td>
<td>109 mm</td>
<td>75 mm (right post-zygapophysis broken of just before the tip)</td>
<td>5 mm</td>
<td>35 mm</td>
<td>54 mm</td>
<td>127 mm</td>
<td>94 mm</td>
<td>30 mm</td>
<td>36 mm</td>
</tr>
<tr>
<td>Cervical 7</td>
<td>161 mm</td>
<td>105 mm</td>
<td>49 mm</td>
<td>107 mm</td>
<td>60 mm</td>
<td>120 mm</td>
<td>11 mm</td>
<td>11 mm (but diagonally flattened)</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>48 mm</td>
<td>41 mm</td>
</tr>
<tr>
<td>Cervical 8</td>
<td>169 mm</td>
<td>101 mm</td>
<td>42 mm</td>
<td>94 mm</td>
<td>41 mm</td>
<td>136 mm</td>
<td>94 mm</td>
<td>89 mm</td>
<td>125 mm</td>
<td>104 mm</td>
<td>47 mm</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cervical 9</td>
<td>122 mm</td>
<td>127 mm</td>
<td>48 mm</td>
<td>119 mm</td>
<td>65 mm</td>
<td>142 mm</td>
<td>6 mm</td>
<td>45 mm</td>
<td>63 mm</td>
<td>132 mm</td>
<td>122 mm</td>
<td>36 mm</td>
<td></td>
</tr>
<tr>
<td>Cervical 10</td>
<td>168 mm</td>
<td>110 mm</td>
<td>37 mm</td>
<td>99 mm</td>
<td>44 mm</td>
<td>163 mm</td>
<td>3 mm</td>
<td>84 mm</td>
<td>79 mm</td>
<td>136 mm</td>
<td>142 mm</td>
<td>36 mm</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th>Total height</th>
<th>Pedicle cranio-caudal length</th>
<th>Pre and postzygapophyseal length</th>
<th>Centrum length</th>
<th>Spine cranio-caudal width at base</th>
<th>Spine cranio-caudal width distally</th>
<th>Spine height from spinal canal</th>
<th>Spine height from post-zygapophysis</th>
<th>Centrum height along cranial aspect</th>
<th>Centrum height along caudal aspect</th>
<th>Centrum width along cranial aspect</th>
<th>Centrum width along caudal aspect</th>
<th>Spinal canal height at cranial opening</th>
<th>Spinal canal width at cranial opening</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dorsal vertebra</td>
<td>559 mm</td>
<td>34 mm</td>
<td>119 mm</td>
<td>57 mm</td>
<td>45 mm</td>
<td>45 mm</td>
<td>440 mm</td>
<td>375 mm</td>
<td>109 mm</td>
<td>102 mm</td>
<td>103 mm</td>
<td>102 mm</td>
<td>35 mm</td>
<td>30 mm</td>
</tr>
<tr>
<td></td>
<td>Total height</td>
<td>Pedicle cranio-caudal length</td>
<td>Pre and postzygapophyseal length</td>
<td>Centrum length</td>
<td>Spine cranio-caudal width at base</td>
<td>Spine cranio-caudal width distally</td>
<td>Spine height from postzygapophyses</td>
<td>Spine height from spinal canal</td>
<td>Centrum height along cranial aspect</td>
<td>Centrum height along caudal aspect</td>
<td>Centrum width at cranial aspect</td>
<td>Centrum width at caudal aspect</td>
<td></td>
<td></td>
</tr>
<tr>
<td>----------------</td>
<td>--------------</td>
<td>-------------------------------</td>
<td>----------------------------------</td>
<td>----------------</td>
<td>-----------------------------------</td>
<td>------------------------------------</td>
<td>-----------------------------------</td>
<td>----------------------------------</td>
<td>----------------------------------</td>
<td>----------------------------------</td>
<td>-------------------------------</td>
<td>-------------------------------</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Caudal vertabra R243</strong></td>
<td>145 mm</td>
<td>42 mm</td>
<td>98 mm</td>
<td>79 mm</td>
<td>20 mm</td>
<td>21 mm</td>
<td>48 mm</td>
<td>Broken right after postzygapophyses</td>
<td>83 mm</td>
<td>84 mm</td>
<td>70 mm</td>
<td>71 mm</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Caudal centra R271</strong></td>
<td>85 mm</td>
<td>46 mm</td>
<td>-</td>
<td>53 mm</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>61 mm</td>
<td>58 mm</td>
<td>59 mm</td>
<td>63 mm</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Caudal centra R272</strong></td>
<td>76 mm</td>
<td>56 mm</td>
<td>-</td>
<td>57 mm</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>56 mm</td>
<td>58 mm</td>
<td>64 mm</td>
<td>68 mm</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
## Appendix B: Appendicular skeleton measurements

<table>
<thead>
<tr>
<th></th>
<th>Length</th>
<th>Width at constriction</th>
<th>Width at distal end</th>
<th>Width at coracoid</th>
<th>Glenoid length</th>
</tr>
</thead>
<tbody>
<tr>
<td>Scapula (right)</td>
<td>787 mm</td>
<td>127 mm</td>
<td>144 mm</td>
<td>119 mm</td>
<td>106 mm</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th>Distal head width</th>
<th>Minimum shaft width</th>
<th>Cranial blade length</th>
<th>Cranial blade maximum width</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sternal plate</td>
<td>55mm (broadest side in distal view)</td>
<td>40 mm (in dorsoventral view)</td>
<td>138 mm (in dorsal view)</td>
<td>too incomplete to measure</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th>Length</th>
<th>Minimum shaft circumference</th>
<th>Deltopectoral crest length</th>
<th>Deltopectoral crest width</th>
<th>Proximal head width</th>
<th>Mediolateral width of condyle</th>
<th>Distal head width</th>
<th>Minimum shaft width craniocaudally</th>
</tr>
</thead>
<tbody>
<tr>
<td>Humerus R235</td>
<td>520 mm</td>
<td>214 mm</td>
<td>213 mm</td>
<td>157 mm</td>
<td>180 mm</td>
<td>33 mm</td>
<td>87 mm</td>
<td>28 mm (measured in proximal half of the shaft in caudal view)</td>
</tr>
<tr>
<td>Humerus R236</td>
<td>563 mm</td>
<td>206 mm</td>
<td>223 mm</td>
<td>142 mm</td>
<td>172 mm</td>
<td>21 mm</td>
<td>115 mm</td>
<td>45 mm (measured in proximal half of the shaft in caudal view)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th>Length</th>
<th>Prearticular length</th>
<th>Minimum circumference</th>
<th>Minimum shaft width mediolaterally</th>
<th>Minimum shaft width craniocaudally</th>
<th>Mid-shaft width mediolaterally</th>
<th>Mid-shaft width craniocaudally</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ulna</td>
<td>Shaft to incomplete to take measurements</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th>Length</th>
<th>Minimum circumference</th>
<th>Minimum shaft width mediolaterally</th>
<th>Minimum shaft width craniocaudally</th>
<th>Medial condyle length</th>
<th>Lateral condyle length</th>
<th>Fourth trochanter to distal head length</th>
<th>Fourth trochanter to proximal head length</th>
</tr>
</thead>
<tbody>
<tr>
<td>Femur (right)</td>
<td>1003 mm</td>
<td>346 mm</td>
<td>120 mm</td>
<td>75 mm (diagnostically flattened)</td>
<td>204 mm (from &quot;tip of toe&quot; to &quot;heel&quot;)/140 mm (from &quot;foot sole&quot; to the side above it)</td>
<td>261 mm (from &quot;toe tip&quot; to &quot;heel&quot;)/136 mm (from foot sole to saide above it)</td>
<td>330 mm</td>
<td>340 mm</td>
</tr>
<tr>
<td></td>
<td>Length</td>
<td>Minimum circumference</td>
<td>Proximal head width</td>
<td>Distal head width</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>----------------</td>
<td>---------</td>
<td>-----------------------</td>
<td>------------------------------------------</td>
<td>----------------------------------------</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Tibia (right)</strong></td>
<td>915 mm</td>
<td>292 mm</td>
<td>303 mm (in caudal view)/62 mm (in lateral view)</td>
<td>201 mm (in caudal view)/130 mm (in lateral view)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Fibula</strong></td>
<td>901 mm</td>
<td>134 mm</td>
<td>165 mm (in lateral-medial view)/46 mm (in cranio-caudal view)</td>
<td>110 mm (in caudal view)/60 mm (in cranio-caudal view)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th>Metatarsal III minimum width</th>
<th>Metatarsal III distal width</th>
<th>Metatarsal III proximodistal length</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Pes</strong></td>
<td>62 mm</td>
<td>75 mm</td>
<td>362 mm</td>
</tr>
</tbody>
</table>