A juvenile specimen of *Anshunsaurus huangguoshuensis* Liu, 1999 (Diapsida: Thalattosauria) from the Upper Triassic of China

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A b s t r a c t

A new specimen, an almost complete skeleton with a well-preserved skull, of the askeptosaurid thalattosaur *Anshunsaurus huangguoshuensis* is described from the Xiaowa Formation (Carnian) of Guanling County, Guizhou Province, southwestern China. It is the third described specimen and the first juvenile or subadult of this taxon, being only about half the size of the holotype. It therefore offers, for the first time, the possibility to record some ontogenetic changes in the skeleton of that species. These affect, among other features, proportions of the skull, lack of co-ossification of certain cranial and postcranial bones, and proportions of the appendicular skeleton. The new specimen also provides additional information on numerous details of the anatomy of this rare taxon that were hitherto unknown or insufficiently known.

K e y w o r d s : Diapsida. Thalattosauria, Guizhou, Triassic, anatomy, ontogeny.

1. Introduction

The Middle and Upper Triassic marine strata of Guizhou Province in southwestern China have recently produced an immense diversity of marine reptiles (Yin et al. 2000; Wang et al. 2001; Li 2006; Maisch & Hao 2008). Skeletons of sauropterygians, ichthyosaurs and many other forms are preserved in a hitherto unknown quality and quantity.

Of particular importance are the numerous finds of thalattosaurs in the Upper Triassic (Carnian) Xiaowa Formation. Thalattosaurs are a group of Triassic marine diapsids, the exact phylogenetic position of which is still unclear. Recent studies (Müller 2003, 2004) proposed them either as a sister group of Sauria or of the Ichthyosauria, another group of Mesozoic marine amniotes of controversial phylogenetic position.

Prior to the discoveries in southwestern China, thalattosaurs have been mainly known from the Middle Triassic Grenzbitumenzone of Monte San Giorgio and Besano (Switzerland and Northern Italy), where the genera *Askeptosaurus*, *Clarazia* and *Hescheleria* are documented by associated skeletons (Nopcsa 1925; Peyer 1936a, b; Kuhn-Schnyder 1952, 1960, 1971; Rieppel 1987; Müller 2002, 2005; Rieppel et al. 2006), as well as from California and British Columbia in Western North America, where the genera *Nectosaurus*, *Thalattosaurus*, *Agkistrognathus* and *Paralonectes* have been reported, largely based on incomplete or even fragmentary remains (Merriam 1904, 1905, 1908; Nicholls & Brinkman 1993; Nicholls 1999; Rieppel et al. 2006). Articulated material of the basal thalattosaur *Endennasaurus* is known from the Norian of Lombardy (Renesto 1992; Müller et al. 2005).

The thalattosaurs from the Xiaowa Formation are known from a high quantity of well-preserved, articulated skull and skeletal material. Liu et al. (2013) correctly pointed out that this thalattosaur fauna is the best preserved and most diverse in the world today.

The first thalattosaur to be described from Guizhou was the askeptosaurid (Rieppel et al. 2000) *Anshunsaurus huangguoshuensis*, initially misidentified as a pistosaurid sauropterygian by Liu (1999). In addition, the cranial morphology of *A. huangguoshuensis* and the postcranial skeleton were studied by Liu & Rieppel (2005). The second thalattosaur discovered was *Xinpusaurus suni* (Yin in Yin et al. 2000). It was also first not recognized as a thalattosaur, but described as a cymbospondylid ichthyosaur, a misinterpretation rectified by Liu & Rieppel (2001) and Liu (2001), who provided further details on the cranial and postcranial skeleton of *Xinpusaurus*. Two new species, *Xinpusaurus bamaolinenesis* and *X. kohi*, were introduced by Cheng (2003) and Jiang et al. (2004). According to recent claims (Liu & Rieppel 2005; Rieppel et al. 2006), *X. kohi* is clearly distinct from *X. suni,* but possibly conspecific with *X. bamaolinensis*, as a restudy of the original material has confirmed (Maisch 2014). Liu (2013) even suggested to synonymize all three species of *Xinpusaurus*, a conclusion not accepted by Maisch (2014).

The genera *Wayaosaurus* and *Sinasaurus*, also from the Xiaowa Formation, were introduced by Yin et al. 2000 and are probably also of thalattosaurian affinities (Sun et al. 2004), but as restudy of the original material is hampered, and the original descriptions are rather incomplete, a well-founded evaluation of these taxa is, at present, difficult.

A second species of *Anshunsaurus*, *A. wushaensis*, was described by Rieppel et al. (2006). A juvenile specimen

referable to the same taxon was announced by Liu (2007). A third species, A. *huangnihensis*, was described by Cheng et al. (2007, 2011). The short-snouted thalattosaur *Miodentosaurus brevis* was announced in 2007 by Cheng et al. and further described by Wu et al. (2009) and Zhao et al. (2010). A phylogenetic study of the species of *Anshunsaurus* (Cheng et al. 2011) recently demonstrated that they belong to the Askeptosauridae and form an evolutionary lineage.

Most recently, another new genus and species of thalattosaur, *Concavispina biseridens*, was announced by Zhao et al. (2013) and described in more detail by Liu et al. (2013).

The purpose of this paper is to provide a description of a well-preserved specimen (GMPKU 2000-028) of the askeptosaurid A. *huangguoshuensis* Liu, 1999. As this taxon is hitherto only known from two well-preserved skeletons, the holotype (IVPP V11835) and the referred specimen (IVPP V11834), and as thalattosaur skeletons of this quality are still among the rarest of all marine reptile fossils, such an account is certainly warranted. As the morphology of A. *huangguoshuensis* has been described in considerable detail by Rieppel et al. (2000) and Liu & Rieppel (2005), the following description will concentrate on features that have hitherto been not or little known, or which are at variance to the existing descriptions. The specimen is of considerable interest, as its skull length is only about half that of the holotype and referred specimen of Liu & Rieppel (2005), and therefore it presumably represents a juvenile or early adult instead of a fully-grown individual. Thus, it provides for the first time data on the ontogeny of this important basal thalattosaur taxon.

2. Systematic palaeontology

Thalattosauria Merriam, 1904

Family Askeptosauridae Kuhn-Schnyder, 1952

Genus *Anshunsaurus* Liu, 1999

T y p e   s p e c i e s : *Anshunsaurus huangguoshuensis* Liu, 1999 (Figs. 1–3, Pls. 1–2)

H o l o t y p e : IVPP V11835, a well-preserved skull and incomplete postcranium of an adult individual, largely exposed in dorsal view but with the skull prepared from both sides. Described by Liu (1999), Rieppel et al. (2000) and Liu & Rieppel (2005).

T y p e   l o c a l i t y : Xinpu, Guanling County, Anshun area, Guizhou Province, PR China.

T y p e   h o r i z o n : Xiaowa Formation, Carnian, Upper Triassic.
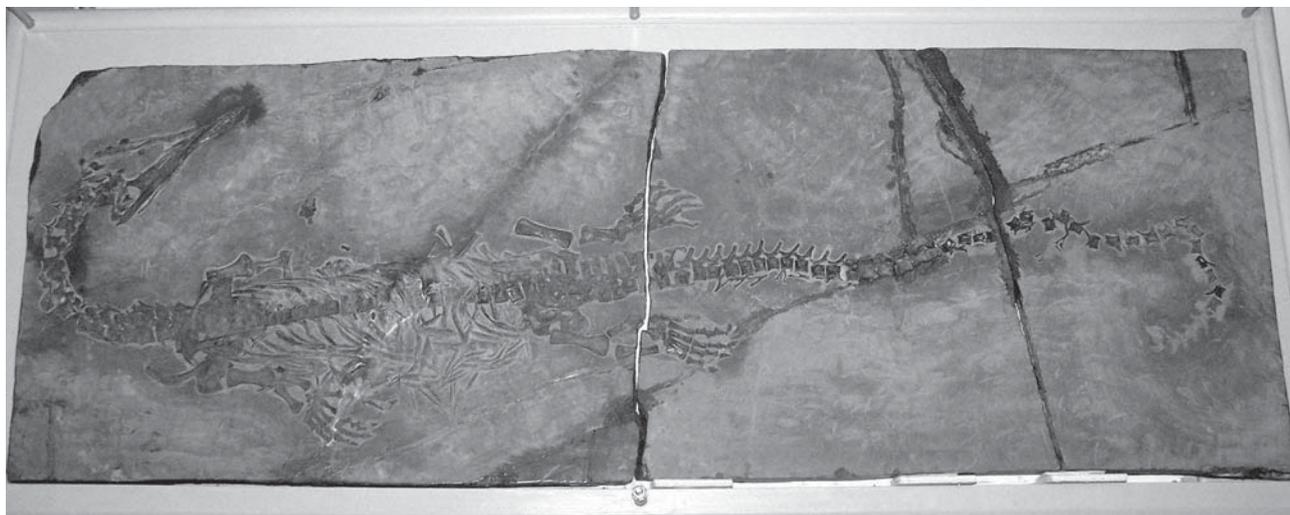
Fig. 1. Complete juvenile skeleton of *Anshunsaurus huangguoshuensis* Liu, 1999, GMPKU 2000-028, from the Upper Triassic (Carnian) Xiaowa Formation of Guanling County, Guizhou, People's Republic of China as displayed in the Geological Museum of Peking University, Beijing.

Referred specimens: IVPP V 11834, a virtually complete skeleton of an adult individual, largely exposed in ventral view, from the same locality and horizon as the type specimen, described by LIU & RIEPPEL 2005. GMPKU 2000-028, a virtually complete skeleton of a juvenile to subadult individual, largely exposed in ventral view but with the skull prepared from both sides, described in this study.

Diagnosis: (emended from LIU & RIEPPEL 2005 including features of the new specimen unrelated to its juvenile status): Maxilla forms anteroventral orbital margin, short anteriorly, lacrimal absent, postorbitofrontal present, posterolateral frontal processes extend posteriorly beyond anterior margin of infratemporal fenestra, approaching but not contacting supratemporal, squamosal with long ventral process reaching lower margin of cheek, jugal with elongate posterior process almost reaching quadrate, lateral exposure of angular as large as that of the surangular, deltopectoral humeral crest well developed, fibula expanded distally.

3. Description

The specimen, GMPKU 2000-028, is a well-preserved, articulated skeleton. It is largely exposed in ventral aspect (Figs. 1–3). The slab has been partially prepared from the other side to observe of the dorsal aspect of the skull, as well (Pl. 1, Figs. 1–3). The skeleton is largely complete. The dorsal surface of the skull is quite well-preserved (Pl. 1, Figs. 1–3). Both mandibular rami remain in articulation with the skull and with each other (Pl. 1, Figs. 4–5). Of the palate, only the left side was exposed (Pl. 1, Figs. 4–5). The neck is complete and articulated, except for some vertebral centra, which are somewhat detached from their corresponding neural arches, and the atlas, of which most parts could not be unequivocally identified (Figs. 1–3, Pl. 2, Figs. 1–3). The shoulder girdle shows some disarticulation. The right clavicle has detached from the interclavicle, and both scapulae and coracoids are somewhat dislocated as well (Figs. 1–3, Pl. 2, Figs. 2–3). The right forelimb is complete with minor disarticulation in the manus. The left forelimb, however, lacks most of the manus and the few remaining elements are disarticulated and displaced (Figs. 1–3, Pl. 2, Figs. 6–7).

The vertebrae of the trunk are all in good articulation, but the ribs and gastralia are largely displaced (Figs. 1–3, Pl. 2, Fig. 3). The pelvic girdle is complete but, again, shows considerable displacement of individual elements, which makes observation of some bones difficult or impossible (Figs. 1, 3). Both left and right hind limbs are, in contrast, well-preserved (Figs. 1–3, Pl. 2, Figs. 8–9). The caudal vertebral column is well-articulated anteriorly, with more considerable dislocation in its posterior preserved half (Figs, 1, 3, Pl. 2, Figs. 4–5). The terminal six vertebrae were originally artefacts, which were removed during re-preparation; the tip of the tail is thus missing and was certainly lost prior to burial, except for a single posterior caudal vertebra that lies close to the right manus.

3.1. Cranial skeleton (Figs. 1–2, Pl. 1)

The dorsal side of the skull is well preserved and largely articulated (Pl. 1, Fig. 1). Some areas could not be completely exposed due to the fragility of the specimen. Behind the skull, parts of the axis and third cervical vertebra are seen also in dorsal view. Two small elements situated directly behind the parietals may represent the atlantal neural arches. In ventral view, nothing of the atlas is visible (Pl. 1, Fig. 4). The skull generally confirms to the descriptions of RIEPPEL et al. (2000) and LIU & RIEPPEL (2005), nevertheless, it shows some noteworthy features.

The premaxilla forms the elongate, robust, parallel-sided rostrum. Nothing can be observed of the premaxillary dentition. Posteriorly, the premaxilla forms only a short part of the anteromedial margin of the teardrop-shaped external naris. The sutures with the maxilla are very clear on both sides of the skull, as both maxillae have rotated slightly laterally due to dorsoventral compression and lost immediate contact to the surrounding elements (Pl. 1, Figs. 1, 3). The maxilla extends only a short distance – equalling about one narial diameter – anterior to the external naris. It was therefore much shorter than it was assumed for the holotype specimen by LIU & RIEPPEL 2005, but is in accordance with the earlier description of RIEPPEL et al. (2000) which seems to be more correct in this point. The maxillary dentition is only exposed on the right side (Pl. 1, Fig. 3). Remains of six teeth with bluntly conical crowns can be identified. Between the fourth and fifth preserved tooth, there is a large gap, which could accommodate two additional teeth. The maxillary tooth count in the specimen was therefore probably eight or more, as it is quite conceivable that anterior to the first preserved tooth there was yet another one. Seven maxillary teeth were identified in the holotype by LIU & RIEPPEL (2005), but the exact number could not definitely be observed in their specimen. It is also conceivable that the number of maxillary teeth changed during ontogeny.

The postnarial process of the maxilla is much wider than indicated in LIU & RIEPPEL's (2005) figure, where it is but a narrow splint of bone and much more elongate than indicated by RIEPPEL et al. (2000). In the new specimen, it is a lanceolate, relatively wide bony flange, which extends dorsally along the anterior margin of the prefrontal (Pl. 1, Fig. 3). Due to its slight displacement, it remains uncertain whether the maxilla really took part in the formation of the anterior orbital border, as claimed by LIU & RIEPPEL (2005), but it does seem unlikely.

The prefrontal shows no sign of subdivision on the right side. On the left side, however, one gets the impression that a suture runs right above a marked depression on the lateral surface of the prefrontal. This suture is not evident on the left side of the skull, but preservation there is less good. The presumable suture can only be followed for

Fig. 2. *Anshunsaurus huangguoshuensis* Liu, 1999, GMPKU 2000-028, anterior half of trunk skeleton showing the forelimbs and shoulder girdle; scale bar equals 50 mm.

a very short distance, extending from the anterior orbital margin. More anteriorly, the prefrontal is covered by a thin bony flange, which overlaps it and is in turn overlapped by the postnarial process of the maxilla. This flange is most probably part of the nasal, but as the postnarial process of the maxilla covers its contact with the rest of the nasal this cannot be proven beyond doubt.

The nasal forms almost the entire medial and part of the posterior margin of the external naris (Pl. 1, Figs. 1, 3). The nasal extends far posteriorly, up to more than two fifths of the orbital length, as is clearly seen on both sides of the skull, as a narrow strip of bone accompanied by the prefrontal laterally and the frontal medially. Its posterior extension is thus larger than described for the holotype by Liu & Rieppel (2005). The prefrontal corresponds to their description, being much larger than depicted by Rieppel et al. (2000). As mentioned above, it shows a distinct depression on its lateral surface on both sides, situated at about half orbital height close to the suture with the

maxilla. On the left side, it appears as if a foramen was present in the bottom of this depression (Pl. 1, Fig. 3). Posteriorly, the prefrontal almost meets the postorbitofrontal on both sides. On the left side, it is separated from the postorbitofrontal by a distance of only about 1 mm. It is even conceivable, that some bone substance was lost prior to or during preparation and that the two bones originally contacted each other. The frontal corresponds to Liu & Rieppel's (2005) account. Its posterior suture with the parietal is hard to detect, and its anterior borders are clearest on the right side, where the anteromedial and distinctly more extensive anterolateral process can be clearly identified. The parietals are, as in the holotype, pierced by a remarkably large parietal foramen (Pl. 1, Fig. 2).

The postorbitofrontal, as seen particularly on the left side, extends posteriorly alongside the dorsal squamosal margin as indicated by Liu & Rieppel (2005). There is no evidence for a fenestra supratemporalis. The lateral process of the squamosal is aligned to, and partially covers,

the lateral surface of the quadrate, as envisioned by Liu & Rieppel 2005 (Pl. 1, Figs. 1–2). In the specimen, the posteriormost exposed tip of the jugal (which is, in fact, not completely exposed) ends only about 5 mm anterior to the squamosal. As the jugal has slightly rotated laterally, the distance may have been even smaller in an undistorted specimen. In fact, it is even conceivable that some kind of weak contact between the two elements was still present. Part of the margin of the suborbital fenestra, scleral plates and part of the dorsal surface of the pterygoid are exposed inside the right orbit (Pl. 1, Figs. 2–3). There is no clear evidence for the pterygoid-ectopterygoid suture, even though the entire posterior margin of the fenestra suborbitalis is preserved.

The ventral aspect of the cranial skeleton exposes both lower jaw rami, much of the left half of the palate and much of the basicranium (Pl. 1, Figs. 4–5). Of the palate, only part of the left and right vomers, most of the left pterygoid, as well as part of the ramus quadratus of the right pterygoid, are exposed. The pterygoid confirms to the description of Liu & Rieppel (2005), except that the sharp crest on the ventral surface for origin of the pterygoideus musculature could not be identified (Pl. 1, Fig. 5). The pterygoid seems to extend also for a short distance along the lateral margin of the suborbital fenestra, as a suture towards the ectopterygoid is, as on the dorsal palatal surface, not apparent. The pterygoid seems to contact the vomer anteriorly not medially but laterally, but this may be due to preservation and displacement of individual elements (Pl. 1, Fig. 5).

The parabasisphenoid complex is well-preserved and corresponds to Liu & Rieppel's (2005) description (Pl. 1, Fig. 5). The foramen for the cerebral branch of the carotid artery is well discernible on the right side. Grooves for the palatal branch of the nervus facialis and the carotid artery medial to the basipterygoid processes and subdivided by a sharp medial crest are clearly identifiable. The processus cultriformis remains unprepared. The suture with the basioccipital is clear. It extends transversely in a slightly undulating course anterior to the tubera basioccipitalia. The basioccipital is well visible in ventral and posterior view (Pl. 1, Fig. 5). The tubera basioccipitalia are prominent, extending ventrolaterally and somewhat anteriorly, being clearly separated from the tubera basisphenoidalia by the suture between the two elements and an accompanying groove. The occipital condyle is of somewhat transversely elliptical shape. Its posterior surface is moderately convex, most so in its centre where it forms a distinct hump. The exoccipitals are, in contrast to Liu & Rieppel's (2005) adult material, still unfused to the opisthotic and are somewhat displaced (Pl. 1, Fig. 5). The left exoccipital is seen in posterolateral view. The contact surface for the basioccipital is almost flat, that for the supraoccipital is strongly inclined posteroventrally. A small foramen nervi hypoglossi pierces the posterior surface of the columnar

central part of the bone. The right exoccipital remains in somewhat closer contact to the basioccipital but has been displaced somewhat laterally. Part of its contact surface to the basioccipital is exposed. Posteriorly, it is again pierced by at least one foramen nervi hypoglossi. A second foramen, separated from the first one by a small ridge may be present, as well. Anterolateral to the hypoglossal foramina, the exoccipital seems to form a small bony flange.

The opisthotics remain almost in situ (Pl.1, Fig. 5). They form long, elongate paroccipital processes. The paroccipital process is slender and rod-like. The ventral surface of the better preserved right paroccipital process is distinctly concave, its distal end is slightly thickened and rugose. The two processes enclose an angle of about 90 degrees. On the contact surface for the basioccipital, a deep groove is found on both sides, exposed due to slight lateral displacement of both elements. This groove may have served for transmission of the nervus glossopharyngicus. Part of the right prootic seems to be exposed anterior to the right opisthotic, but shows little detail except for a small foramen on its medial surface, probably for transmission of the nervus facialis.

The quadrates show the condylar region and part of their anterior and medial surfaces in ventral view. Due to some displacement of the lower jaw rami, both condyles are well visible (Pl. 1, Fig. 5). The right one is particularly well preserved, and although it remains almost in natural articulation with the lower jaw, much of its medial portion is exposed, so that not its entire condylar surface is in contact with the articular. The condyle is strongly widened transversely but rather short anteroposteriorly. It is longer laterally than medially and convex in both anteroposterior and mediolateral direction. Dorsal to the condyle, both quadrates are seen to develop considerable bony flanges above their medial margins that extend far anteriorly and dorsally, although they are not completely exposed. The presence of a large anterior quadrate flange, suggested by Liu & Rieppel (2005) can thus be confirmed (Pl. 1, Fig. 2).

The lower jaw confirms to Liu & Rieppel's (2005) description (Pl. 1, Figs. 4–5). Interestingly, the left articular has detached from the rest of the lower jaw and flipped over, so that it now exposes its deeply concave dorsal surface for reception of the quadrate condyle. This glenoid facet is expanded transversely and trough-like, with an almost straight anterior and a convex posterior margin. Part of the left articular, showing a small foramen chordae tympani and much of the glenoid, is visible in dorsal view.

3.2. Postcranial skeleton (Figs. 1–3, Pl. 2)

The axial skeleton of the new specimen is well preserved. The cervical region lacks the atlas, however. The axis is clearly identifiable by its anteroposteriorly expanded

Fig. 3. *Anshunsaurus huangguoshuensis* Liu, 1999, GMPKU 2000-028, posterior half of trunk skeleton showing most of the hind limbs and the pelvic girdle; scale bar equals 50 mm.

processus spinosus. It is evident that the specimen had 16 cervical vertebrae, not 15 as suggested by Liu & Rieppel (2005) whose material did not allow a definitive assessment. The 16th presacral vertebra clearly shows well-separated dia- and parapophyses, and a clearly double/headed rib is associated with it, so that, following the terminology of Müller (2002) it still belongs to the cervical region (Pl. 2, Figs. 2–3). The following 17th presacral vertebra does not show the costal facets, as they are covered by part of the dermal shoulder girdle. The 18th presacral has lost an individualised parapophysis and therefore, although the corresponding rib is too ill-preserved for observation, can be assumed to have borne an unicephalous rib which makes it, by definition, a dorsal vertebra (Pl. 2, Fig. 3). The minimal number of cervicals in *Anshunsaurus* is thus 16, the maximum number 17. In strong contrast to Liu & Rieppel (2005) clear parapophyses are developed on cervicals 14–16 (Pl. 2, Figs. 2–3). In the more anterior cervicals, the region where the parapophysis should be situated along the anterior margin of the cervical centrum is only slightly thickened (Pl. 2, Figs. 1–2). In cervicals 11–13, the condition may be described as intermediate, with a more conspicuous and anteroposteriorly elongate thickening that can be identified as a parapophysis, as well. In contrast to *Askeptosaurus* (Müller 2002), and as described by Liu & Rieppel (2005), the position of the parapophyses is, however, along the anteroventral margin of the centrum.

The number of presacral vertebrae is 40. The cervicals and the first 13 dorsals (if one counts the 17th presacral as the 1st dorsal) are completely exposed, then follow several that are partially covered by the adjacent ribs, but clearly identifiable. Then follow four further vertebrae that are again well-exposed in lateral view and the two sacrals, clearly identifiable by their extensive costal facets. Liu & Rieppel (2005) considered the number of presacrals in *Anshunsaurus* as at least 38, possibly 39. The new specimen confirms their suggestion and definitely shows the higher number.

In contrast to Liu & Rieppel's (2005) account, the neural arches and centra of the dorsal vertebrae are largely unfused in the specimen (Figs. 2–3). Although all neural arches remain in place (in contrast to some of the cervicals) the neurocentral suture can still be well identified in all accessible dorsal vertebrae. This is certainly a result of the smaller size and presumably earlier ontogenetic stage of the specimen, as compared to the holotype.

In the sacral vertebrae (Fig. 3), as well as in the first ten caudals (with possible exception of the ninth), the neurocentral sutures are also widely open and several neural arches, i.e. those of the 1st to 3rd and the 7th caudals, have clearly detached from their respective centra. In the following caudals, up to the posteriormost preserved elements, the neural arches seem to be considerably better attached to the centra (Pl. 2, Figs. 4–5). Open neurocentral sutures cannot be identified and there is no indication of dislocation. Caudal ribs or their rudiments can be identified up to the 11th vertebra, as described by LIU & RIEPPEL (2005). 45 caudal vertebrae are preserved more or less in articulation in the specimen. A single vertebra considerably smaller than the posteriormost one in the articulated series is located close to the left manus. It can be assumed that at least 50 caudals, as in IVPP V11834 (which also has an incomplete caudal vertebral column) were present in *Anshunsaurus*.

Several caudal ribs are preserved, but have all been so much dislocated from the respective centra that their correspondence with them is unclear or can at most be tentatively suggested. Two well-preserved caudal ribs are found adjacent to the neural spine of the second caudal. Another one lies half-covered below the centrum of the first caudal. Two more are clearly exposed between the neural spines of the 4th and 5th caudals. The first haemapophysis is preserved between caudals six and seven. Whether there were any further anteriorly is unlikely, given the generally good preservation of this region, but not impossible. In LIU & RIEPPEL's material (2005) the first haemapophysis was found behind the 4th caudal centrum.

The cervical ribs are all clearly double-headed (Pl. 2, Figs. 1–3). The few well-exposed rib-heads of the mid-dorsal region show a distinct sagittal constriction of the rib heads, which thus bear two facets, situated, however, on a single rib head. Sacral and caudal ribs are unicipital.

The interclavicle is well-preserved and exposed in ventral view (Figs. 1–2, Pl. 2, Figs. 2–3). As the right clavicle has detached, its articulatory surface with the interclavicle is exposed. The interclavice shows a distinct, small and pointed anterior sagittal process on its anterior margin, which is otherwise of semilunate shape. The posterior bar is very elongate and tapers smoothly posteriorly. The right clavicle is, as mentioned, dislocated from the interclavicle and shows its dorsal aspect, whereas the left clavicle remains in close articulation and natural position. Neither is it recurved anterolaterally but rather posterolaterally, nor is its posterior portion wider than the anterior portion in ventral view, as described for the material of LIU & RIEPPEL (2005). Instead, the clavicle is clearly inclined posterolaterally (Pl. 2, Fig. 3). Its posterior portion, which is free of the interclavicle articulation, is considerably narrower than the anterior, articular region in ventral view. The right clavicle, exposed in dorsal view,

shows a deep and wide groove, extending for about 4 cm from the medial margin, for reception of the interclavicle. Ventral to the lateral half of this groove, a bony shelf is developed that covered part of the interclavicle ventrally in the articulated state, as well seen on the left side of the specimen. The articulation of the bones thus correspond to the description of LIU & RIEPPEL (2005) and casts some additional doubts on the reconstruction of the *Askeptosaurus* shoulder girdle provided by KUHN-SCHNYDER (1952, 1960) and MÜLLER (2002).

Only part of the right scapula in medial view and most of the left scapula in lateral view are observable (Fig. 2). In strong contrast to LIU & RIEPPEL's (2005) specimens, the anterior margin of the scapula is deeply concave. However, since it is somewhat damaged as well, this might, at least in part, be enhanced by the overzealous original preparation. This is the more likely, because a part of the anterodorsal margin of the bone also fell victim to careless development of the specimen. Nevertheless, it appears equally unlikely that the anterior margin of the scapula was originally strongly convex. This discrepancy is probably best accounted for by ontogenetic changes in the outline of the scapula. The dorsal margin of the scapula is smoothly rounded and convex, the posterior margin is also concave, but less so than the anterior margin.

Both left and right coracoids are identifiable (Fig. 2). The right one is completely exposed in dorsal view. The left one is seen in ventral view but largely covered by the posterior process of the interclavicle. The coracoid corresponds in position and shape to IVPP V11834. Its medial margin is slightly convex, its lateral margin almost straight anterior to the elongated glenoid and articulatory region. The glenoid and articulation for the scapula are clearly subdivided by a deep groove. Furthermore, this groove extends along the dorsal surface of the bone towards the medial margin for half the width of the coracoid. It may indicate an initial subdivision of the coracoid in a pro- and metacoracoid ossification, a feature otherwise completey unknown in thalattosaurs. A more likely explanation would be that it is pathological. The coracoid foramen is clearly visible in the new specimen. It is situated about 6 mm medial to the lateral margin and 17 mm from the anterior margin. It is mediolaterally elongate and thus of elliptical shape, the long axis of the ellipse is inclined anterolaterally-posteromedially.

The pelvic girdle is mainly represented by the ilia (Fig. 3). The left ilium is dislocated, overlying the sacral centra. It is completely exposed in medial view. Of the right ilium, only the acetabular portion and the posterior margin of the shaft is seen in lateral aspect, the rest of the bone is covered by the right pubis. The ilium shows a deep notch on its ventral acetabular portion in medial view. This is antero- and posterodorsally accompanied by two strongly depressed pits, which are inclined towards the antero- and

posteroventral extremities of the bone. The may represent facets for the sacral ribs. The shaft of the ilium extends posterodorsally, but apparently at a lower angle than in the material described by LIU & RIEPPEL (2005). In further contrast, the posterodorsal end of the ilium, which is somewhat pointed in IVPP V11835 is completely straight and reinforced by a pronounced ridge in the new specimen. Another ridge, which meets the posterodorsal ridge at a right angle, extends towards the ventral margin along the medial surface for about 9 mm, shortly behind the anterior rim of the bone. The anterior margin of the iliac shaft, and, to a lesser extent, its posterior margin, are narrow sharpened blades. The lateral surface of the acetabular portion of the ilium is smooth.

The right ischium is almost completely exposed (Fig. 3). It has flipped over and now exposes its ventral instead of its dorsal view. Its shape corresponds to the material described by LIU & RIEPPEL (2005), except that the lateral and the acetabular margins almost meet at a right angle, whereas this angle is much lower in IVPP V11835. The medial margin is largely covered by the femur, but, as far as it is exposed, is strongly convex, as is the posterior margin which shows a distinct notch very close to the medial margin. Similar notches are also figured, but not described, in IVPP V 11835 by LIU & RIEPPEL (2005), although they are placed further laterally. They seem, as corroborated by the new specimen, genuine features instead of preservational or preparational artefacts, as one could assume from their figure only. At any rate, the posterior margin of the ischium can, in contrast to LIU & RIEPPEL (2005), certainly not be described as concave, but is clearly strongly convex, except for the aforementioned notch. Too little is exposed of the right pubis to allow for meaningful observations. The foramen obturatum is not observable.

The forelimbs are well-preserved (Figs. 1–2, Pl. 2, Figs. 6–7). Both humeri and all zeugopodials are exposed in ventral view. On the right side, these elements remain in natural articulation, whereas the left radius has been dislocated and rotated for 90 degrees. The right carpus remains articulated, as does the entire manus, except for a slight displacement of the phalanges of the fifth digit, which retain their connection to each other, however (Pl. 2, Fig. 7). Of the left manus only few disarticulated elements remain, which are, except for a single, posteriorly displaced phalanx, forming two heaps of bones separated for considerable distances from the rest of the forelimb. One of them is situated directly dorsal to the vertebral column and includes four metacarpals, the other one, situated further dorsally, includes only carpals and phalanges.

The humerus largely corresponds to the account of LIU & RIEPPEL (2005). The deltopectoral crest is well developed and can be followed for about half the length of the bone on both sides. The ent- and ectepicondyles are present but insignificant, there are no foramina or grooves associated with them. The ulnar and radial articulation surfaces are subequal in length and meet at a very low angle.

The radius apparently shows less development of its distal expansion than in the adult material described by LIU & RIEPPEL (2005) (Fig. 2, Pl. 2, Fig. 6). This remains somewhat uncertain, though, as in none of the two elements both heads are completely exposed. The distal end of the right radius is, however, only 20 % wider than the proximal end of the left radius. The ulna shows an almost straight proximal head, corresponding to IVPP V 11834, but in contrast to the holotype (LIU & RIEPPEL 2005). This feature found in a subadult individual confirms their suggestion that the difference between these two adult specimens can be explained by a different degree of ossification. The distal articulation surface is strongly convex, as in the adult material.

The right carpus is complete (Pl. 2, Fig. 7). LIU & RIEPPEL (2005) describe seven elements in the adult holotype. There, the intermedium and ulnare are present in the proximal series. One centrale is ossified. The distal carpal series consists of distal carpals 1–4 in the holotype (IVPP V 18835). In the referred specimen (IVPP V 18834) only five carpals are present in the right forelimb and six in the left forelimb (LIU & RIEPPEL 2005). From the figure LIU & RIEPPEL provide, it is clear that the right carpus of the referred specimen has been dislocated, which may account for the loss of two carpal elements. The left carpus, however, seems well articulated. It lacks the centrale, which is the smallest carpal element in *Anshunsaurus*, as confirmed by both the holotype and the new specimen. Two possibilities of interpretation are there, either the centrale got lost before fossilisation or during preparation, or it failed to ossify. The latter would be remarkable, as it is already well-ossified in the much smaller specimen described here.

The new specimen shows the complete set of carpal ossifications, as does the holotype specimen. There is a small ulnare, which is situated more or less in a row with the distal carpals and lies right in the middle between the ulna and metacarpal five. Then follows the intermedium, which is the largest carpal element, of kidney-shape with a strong proximal concavity. The centrale is situated between the intermedium and the distal carpals 2 and 3. It is the smallest carpal element. The distal carpals form a distally convex row. Distal carpals 1 and 2 are the smallest and of comparable size. Distal carpal three is larger, and distal carpal 4 is the largest of the series, being, among the carpal elements, second only to the intermedium.

The metacarpals are all preserved in articulation (Pl. 2, Fig. 7). Metacarpal 1 is the widest and shortest. Whereas in the material discussed by LIU & RIEPPEL (2005) all other metacarpals are subequal in length, both metacarpal 2 and metacarpal 5 are distinctly shorter than metacarpals 3–4 in the present specimen.

The phalanges are well- and completely preserved, except that a large crack runs through the proximal phalanges of digits 2 and 3, and the distal phalanx of digit 1 leaving only its tip identifiable, and that all phalanges of digit 5 have been disarticulated from the fifth metacarpal and displaced posteriorly for about 20 mm, however, retaining their articulation with each other. As there is no evidence of any other dislocated or isolated phalanges, one might assume that the fifth digit is complete. However, the most proximal phalanx preserved is much too small and narrow to have formed a functional articulation with metacarpal 5, and it must therefore be assumed that at least one phalanx is missing. Keeping this in mind, the phalangeal formula of the manus in the specimen is 2–3–4–4–4, the same that was suggested by LIU & RIEPPEL (2005), although they also had to cope with some uncertainty due to incomplete preservation. Taking the evidence from all three specimens into account, the phalangeal formula of 2–3–4–4–4 is, however, certain, as the fifth digit, the only one incomplete in the new specimen, is well and completely preserved in the material of LIU & RIEPPEL (2005).

Both hind limbs of the specimen are exposed in ventral view (Fig. 3, Pl. 2, Figs. 8–9). The right zeugopodium and tarsus show some disarticulation, whereas all elements of the left hind limb remain approximately in situ. The femoral head is, in contrast to LIU & RIEPPEL's (2005) adult material, not convexly rounded but almost completely straight (Fig. 3). Strong ridges reinforce the medial and proximal margins of the proximal region of the femur. Another strong ridge that runs along the lateroventral surface of the proximal part of the femur terminates in a pronounced bony knob that represents the trochanter internus. It has been squeezed in the right femur, but is well preserved in the left one. The posterior (medial) margin of the femur is not straight, as described by LIU & RIEPPEL (2005), but as concave as the anterior (lateral) edge. Tibia and fibula correspond well to LIU & RIEPPEL's (2005) account. Although the fibula is incomplete distally, it seems, however, unlikely that its distal expansion was as considerable as in the adult specimens, which may be related to the smaller size and presumable subadult age of the animal (Fig. 3).

The tarsus is best preserved in the right hind limb (Pl. 2, Fig. 8). The astragalus is not as large as in the specimens described by LIU & RIEPPEL (2005) and does not contact all distal tarsals. Instead, it only forms a very weak contact with distal tarsals 2–3. The calcaneum is of almost circular shape. It is proportionally considerably larger than in the adult specimens, but forms no direct contact with the astragalus. Distal tarsals 1–4 are well-ossified. The distal tarsal 1 is the smallest, distal tarsal 4 by far the largest. Distal tarsals 2 and 3 are both distinctly larger than distal tarsal 1, with distal tarsal 3 being clearly the more extensive of the two. This, again, contrasts with the situation in the adult specimens (LIU & RIEPPEL 2005), where the distal tarsals 1–3 are usually subequal in size, with distal tarsal 1 being, sometimes, slightly larger than the others. These differences are certainly ontogenetic. In the metatarsals (Pl. 2, Figs. 8–9), metatarsal 1 and 5 are clearly shorter than the others. But metatarsals 2-4 also increase considerably in size, whereas they are subequal in length in the adult material (LIU & RIEPPEL 2005), reminiscent of the condition seen in the metacarpals. Again this is likely to be an ontogenetic variation. Metatarsal 5 also is unusually slender distally, particularly on the right side (where this feature is probably slightly exaggerated), in further contrast to the adult specimens. A combination of the evidence available from both pes (Pl. 2, Figs. 8–9) demonstrates that the phalangeal formula is 2–3–4–5–4 exactly as in the material described by LIU & RIEPPEL (2005).

4. Discussion

The specimen described above clearly represents the smallest specimen of *Anshunsaurus huongguoshuensis* discovered so far. It is only about half the size of both the holotype and the referred specimen described by LIU & RIEPPEL (2005). Not surprisingly, it shows numerous differences, a lot of which can be accounted for by ontogenetic variation. If one compares the skulls of the new specimen, with a lower jaw length of 210 mm, to that of the holotype, with a mandibular length of 400 mm, some remarkably constant features are apparent. The snout length is obviously unaffected during the part of ontogeny represented by the two specimens; it is 60% of the lower jaw length in the new specimen and 59 % in the holotype. The orbit of the smaller specimen is, however, somewhat larger with about 20 % jaw length compared to about 16 % in the holotype. The length of the temporal fenestra, on the other hand, is almost constant again with 17 % jaw length in the holotype and 16 % in the new specimen. The width of the skull shows no remarkable change as well, being 24 % jaw length in the holotype and 22 % in the new specimen. The number of maxillary teeth seems to be somewhat higher in the smaller specimen (about 8-9 versus 7 in the holotype, but as noted above this remains uncertain). The anterior extension of the maxilla is definitely much smaller than in the type specimen, and, with regard to the great similarity that the two skulls otherwise display, is probably over-exaggerated due to a misinterpretation in the illustrations of the type specimen, where, according to LIU & RIEPPEL (2005) the premaxilla-maxilla suture cannot be clearly identified.

A remarkable feature of the small specimen is the retention of separately ossified opisthotics and exoccipitals, which in adult thalattosaurs are universally co-ossified into an otoccipital, as far as it is known. The absence

of a remarkable pterygoid crest on the ventral surface of the bone for muscle attachment may be another juvenile feature.

If one compares the relative sizes of skull and forelimb, further ontogenetic changes are apparent. In the holotype, the humerus has about 38 % lower jaw length; it is only 27 % in the small specimen. Humerus and radius combined have 60% jaw length in the holotype, it is only 45% in the small specimen. If one takes the same values for the hind limbs – femur vs jaw length and femur plus tibia vs jaw length- one gets values of 40 % and 65% for the holotype and only 32 % and 52 % for the small specimen. The limbs are thus proportionally much smaller in relation to the skull in the small specimen, at least the stylo- and zeugopodial parts. The manus and pes are, however, not affected. If one compares the length of the longest metacarpal (4 in both cases) to the jaw length, it is about 12 % in both specimens. For the metatarsals the value is 14 % in both individuals, thus indicating that the manus and pes are proportionally much larger in comparison to the rest of the limbs in the small individual.

Some changes in the proportions of the carpal, tarsal, metacarpal and metatarsal ossifications and the zeugopodials have already been recorded in the description. It is also remarkable that both distal and proximal ends of both femur and humerus are all more expanded in the small individual, indicating that both bones become more slender during ontogeny. In the axial skeleton, the lack of fusion of centra and neural arches up to the anterior caudal region is remarkable.

In this context it is interesting to compare the juvenile specimen of the closely related species *Anshunsaurus wushaensis* described by LIU (2007) which is even somewhat smaller than the specimen described here (see LIU 2007 and this study for measurements). It also shows little co-ossification of the neural arches and vertebral centra. As in the specimen described here, the carpal and tarsal elements are also already well ossified. LIU (2007) also noted interesting asymmetries in the ossification pattern of several bone elements in *A. wushaensis* that have not been recorded in the specimen described above. As the adult proportions of the two species differ considerably it is difficult to compare their ontogenies in detail otherwise with the limited material presently at hand.

Concerning the anatomy of *Anshunsaurus huangguoshuensis* in general, the new specimen has provided some valuable new information on the skull and particularly the postcranial skeleton of this rare species, which supplements the detailed descriptions of RIEPPEL et al. (2000) and LIU & RIEPPEL (2005). *Anshunsaurus huangguoshuensis* is certainly, apart from *Askeptosaurus italicus*, its sister-taxon, the best-studied and thus best-known thalattosaur. It is hoped that future studies, particularly on the plentiful material of *Xinpusaurus* from Guizhou, will add to the knowledge of derived forms of this still enigmatic group of marine reptiles.

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Appendix – Measurements of the specimen (in cm)

S k u l l

Tip of snout to anterior orbital margin	125
To anterior margin of fenestra temporalis	167
To posterior margin of parietal skull table	183.5
To posterior tip of supratemporal	207.5
To posterior margin of basioccipital	194.5
Width across posterior tips of supratemporal	47
Longitudinal orbital diameter	41
Longitudinal temporal diameter	34
Internarial bar	17
Lower jaw length	
(anterior tip of dentary to posterior tip of articular)	210

A x i a l   s k e l e t o n

Standard length as defined by MüLLER (2002)	68
Length of centrum 3	19.5
Height of centrum 3	11
Length of neural spine 3	9.5
Height of neural spine 3	2.5
Length of centrum 10	17
Height of centrum 10	15
Length of neural spine 10	11
Height of neural spine 10	4
Length of rib 4	15
Length of rib 12	35
Length of presacral 19	16.5
Height of presacral 19	14.5
Length of sacral 1	17
Length of sacral 2	16.5
Height of sacral 2	14.5
Sacral rib 1 length	27
Sacral rib 1 distal width	11
Sacral rib 1 proximal width	4.5
Sacral rib 2 length	25
Length of caudal 1	14.5
Height of caudal 1	15
Caudal 1 neural spine length (distal)	11
Caudal 1 neural spine height (anterior)	20
Caudal 10 length	15.5
Caudal 10 height	15.5
Caudal 10 neural spine length	5
Caudal 10 neural spine height	17
Caudal 25 length	15
Caudal 25 height	10.5
Caudal 25 neural spine length	3.5
Caudal 25 neural spine height	
(measured at right angle to long axis)	8
Caudal 44 length	15.5
Caudal 44 height	9.5
Caudal 44 neural spine length	2
Caudal 44 neural spine width	6.5

S h o u l d e r   a n d   p e l v i c   g i r d l e

Interclavicle length	110.5
Interclavicle width	ca. 50
Interclavicle stem length	90
Length of calvicle (sin)	ca. 85
Maximum width of clavicle (sin)	13
Length of coracoid (dextr)	46.5
Width of coracoid anterior to glenoid (dextr)	25
Width across glenoid (dextr)	30

Distal length of ilium (sin)	11
Height of ilium (sin)	44
Ilium shaft minimal width (sin)	13,
Ilium acetabular portion width (sin)	24.5
Length of ischium (dextr)	31

F o r e l i m b

Length of humerus (sin)	56.5
Proximal width of humerus (sin)	20
Distal width of humerus (sin)	30.5
Minimal width (sin)	11.5
Length of ulna (dextr)	36
Proximal width of ulna (sin)	14.5
Distal width of ulna (dextr)	15
Minimal width (sin)	6.5
Length of radius (dextr)	38.5
Proximal width of radius (sin)	14.5
Distal width of radius (dextr)	18.5
Minimal width (dextr)	6.5
Length of mc 1	19.5
Length of mc 2	22.5
Length of mc 3	24.5
Length of mc 4	24
Length of mc 5	22
Proximal width of mc 1	11
Proximal width of mc 2	7
Proximal width of mc 3	8.5
Proximal width of mc 4	8.5
Proximal width of mc 5	9
Distal width of mc 1	9
Distal width of mc 2	8.5
Distal width of mc 3	8
Distal width of mc 4	6.5
Distal width of mc 5 (all dextr)	8.5
Minimal width of mc 1	6
Minimal width of mc 2	3.5
Minimal width of mc 3	3.5
Minimal width of mc 4	3
Minimal width of mc 5	4.5
Largest diameter of Intermedium	9.5
Opf ulnare	6.5
Of centrale	4.5
Of dc 1	6
Of dc 2	5
Of dc 3	7
Of dc 4	8.5
Length of digit 1	31.5
Length of digit 2	43
Length of digit 3	50
Length of digit 4 (reconstructed)	46

H i n d   l i m b

Femur length (dextr)	66.5
Femur proximal width	18.5
Femur distal width	25.5
Femur minimal width	12
Tibia length (sin)	43.5
Tibia proximal width	15
Tibia distal width	13
Tibia minimal width	9.5
Fibula length (dextr)	43.5

Fibula proximal width	9.5	Mt 4	8
Fibula minimal width	8.5	Mt 5	9.5
Astragalus width (dextr)	16	Mt 1 distal width	9.5
Astragalus height	11.5	Mt 2	8.5
Calcaneum diameter	11.5	Mt 3	8.5
Dt 1 diameter	5.5	Mt 4	8
Dt 2 diameter	6.5	Mt 5	5
Dt 3 diameter	7.5	Mt 1 minimal width	5
Dt 4 diameter	10	Mt 2	4.5
Metetarsal 1 length	23.5	Mt 3	4.5
Mt 2 length	26.5	Mt 4	4
Mt 3 length	28.5	Mt 5	4
Mt 4 length	29.5	Digit 1 length (rec)	3.4
Mt 5 length	25	D 2	4.7
Mt 1 proximal width	12	D 3 (all dextr)	5.4
Mt 2 proximal width	7	D 4 (sin)	ca. 5.4
Mt 3	8	D 5 (sin)	ca. 4.8

Plate 1

Anshunsaurus huangguoshuensis Lɪᴜ, 1999, GMPKU 2000-028, cranial skeleton. Scale bars equal 20 mm.

Fig. 1. Skull in dorsal view.
Fig. 2. Posterolateral part of the skull in dextral view.
Fig. 3. Circumnarial region in dextral view.
Fig. 4. Anterior part of the skull and mandible in ventral view.
Fig. 5. Posterior part of the skull and mandible in ventral view.
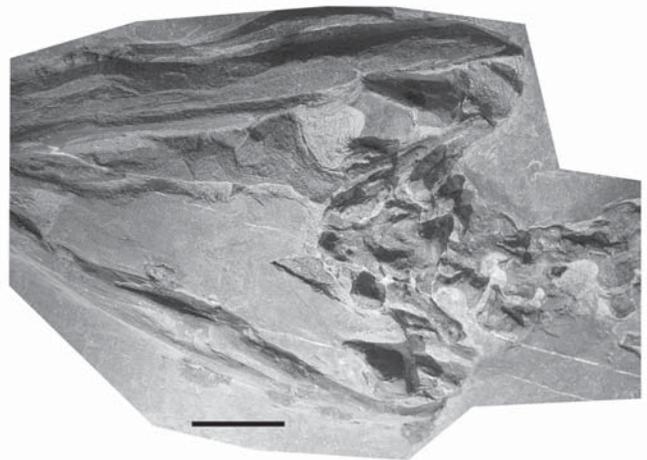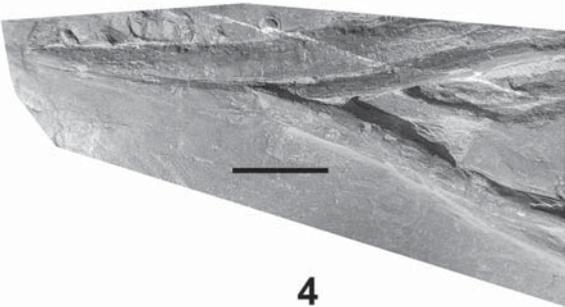
Plate 2

Anshunsaurus huangguoshuensis Lɪᴜ, 1999, GMPKU 2000-028, postcranial skeleton. Scale bars equal 20 mm.

Fig. 1. Anterior cervical vertebrae.
Fig. 2. Posterior cervical region in ventral view.
Fig. 3. Clavicular region in ventral view.
Fig. 4. Anterior caudal vertebrae.
Fig. 5. Posterior caudal vertebrae.
Fig. 6. Left anterior stylo- and zeugopodium.
Fig. 7. Right manus.
Fig. 8. Right pes.
Fig. 9. Left pes.