

## Reassessment of the Middle Triassic rauisuchian archosaurs *Ticinosuchus ferox* and *Stagonosuchus nyassicus*

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**Abstract** The Middle Triassic (Anisian) rauisuchian archosaurs *Ticinosuchus ferox* and *Stagonosuchus nyassicus* are two of the earliest representatives of this group and therefore of special importance for our understanding of the evolution and early diversification of Rauisuchia. Both taxa are well preserved and, in the case of the holotype of *Ticinosuchus ferox*, nearly complete and articulated. However, the original descriptions and recent revisions of the material do not sufficiently cover all aspects of their osteology. We identify new skull elements previously unknown for *Ticinosuchus ferox* and present new reconstructions of the pectoral and pelvic girdle elements. Vertebral laminae and fossae are described for the first time in both *Ticinosuchus ferox* and *Stagonosuchus nyassicus*. Newly recognised character states of *Stagonosuchus nyassicus* include the presence of additional infraprezygapophyseal and infrapostzygapophyseal laminae in the cervical vertebrae, a hyposphene-hypantrum articulation in the dorsal vertebrae and a fibula with a posteromedial

depression. Furthermore, we provide a revised and emended diagnosis for both taxa, including several autapomorphies for *Stagonosuchus nyassicus* (e.g. a boss-like protuberance on the postacetabular process of the iliac blade and a marked short dorsolateral crest on the proximal ischium). We review the taxonomic status of a further specimen of *Ticinosuchus ferox*, as well as material related to *Stagonosuchus nyassicus* from the Manda Beds of Tanzania. Additionally, we discuss the distribution and possible function of rauisuchian characters, such as accessory neural spines in the caudal vertebrae, in these and other rauisuchian taxa.

**Keywords** Archosauria · Rauisuchia · Pseudosuchia · Grenzbitumenzone · Manda Beds

**Kurzfassung** Aufgrund ihres stratigraphischen Alters sind die beiden Rauisuchier *Ticinosuchus ferox* und *Stagonosuchus nyassicus* aus der Mittleren Trias (Anisium) für das Verständnis der Evolution und frühen Diversifikation der Rauisuchier von besonderer Bedeutung. Obwohl beide Taxa gut erhalten sind, und der Holotyp von *Ticinosuchus ferox* fast vollständig und artikuliert ist, weisen sowohl die Erstbeschreibungen, als auch neuere Bearbeitungen, Lücken auf. Wir beschreiben bisher unbekannte Schädelelemente von *Ticinosuchus ferox* und präsentieren neue Rekonstruktionen des Schulter- und Beckengürtels. Erstmals beschreiben wir detailliert die Lamina und Fossa der Hals- und Rückenwirbel beider Taxa, sowie neu identifizierte Merkmalen von *Stagonosuchus nyassicus*. Dazu zählen: Zusätzliche infraprezygapophyseale und infrapostzygapophyseale Lamina in den Halswirbeln, Hyposphen-Hypantrum-Gelenkungen in den Rückenwirbeln und eine charakteristische posteromediale Vertiefung in der Fibula. Desweiteren präsentieren wir eine erweiterte und

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revidierte Diagnose für beide Taxa, sowie einige Autapomorphien für *Stagonosuchus nyassicus* (z.B. eine buckelartige Wölbung am postacetabularen Fortsatz des Iliums und ein dorsolateral verlaufender Grat am proximalen Abschnitt des Ischiums). Außerdem geben wir einen Überblick über ein weiteres Exemplar von *Ticinosuchus ferox* sowie über weiteres Material von *Stagonosuchus nyassicus* aus den Manda Beds aus Tansania und dessen taxonomische Zuordnung. Zusätzlich diskutieren wir die Verteilung und mögliche Funktion spezieller Merkmale, wie z.B. ein akzessorischer Dornfortsätze der Schwanzwirbel, bei Rausuchiern.

**Schlüsselwörter** Archosauria · Rausuchia · Pseudosuchia · Grenzbitumenzone · Manda Beds

## Introduction

Rausuchian archosaurs have been an enigmatic group among Triassic vertebrates since the discovery and description of the first specimen in 1861 (von Meyer 1861). Their exact placement in Archosauria has posed considerable difficulties due to the lack of unambiguous characters or conflicting character states, and even though it seems to be confirmed now that they form a distinct group within Pseudosuchia (Benton 2004; Nesbitt 2007; Brusatte et al. 2010), their phylogeny is still strongly debated. Current research and phylogenetic analyses have provided evidence both for (Nesbitt 2007; Lautenschlager 2008; Desojo and Rauhut 2009; Brusatte et al. 2010) and against (Nesbitt 2005; Gower and Nesbitt 2006; Weinbaum and Hungerbühler 2007) the monophyly of Rausuchia. We here follow Brusatte et al. (2010) in using their definition of Rausuchia. We further adopt the terms Rausuchoidea and Popsauroidea, as suggested by Brusatte et al. (2010), to distinguish between the large, quadrupedal taxa (such as *Rausuchus*, *Ticinosuchus*, *Stagonosuchus* or *Saurosuchus*) and the more gracile, bipedal or sail-backed taxa (e.g. *Poposaurus*, *Arizonasaurus* or *Effigia*).

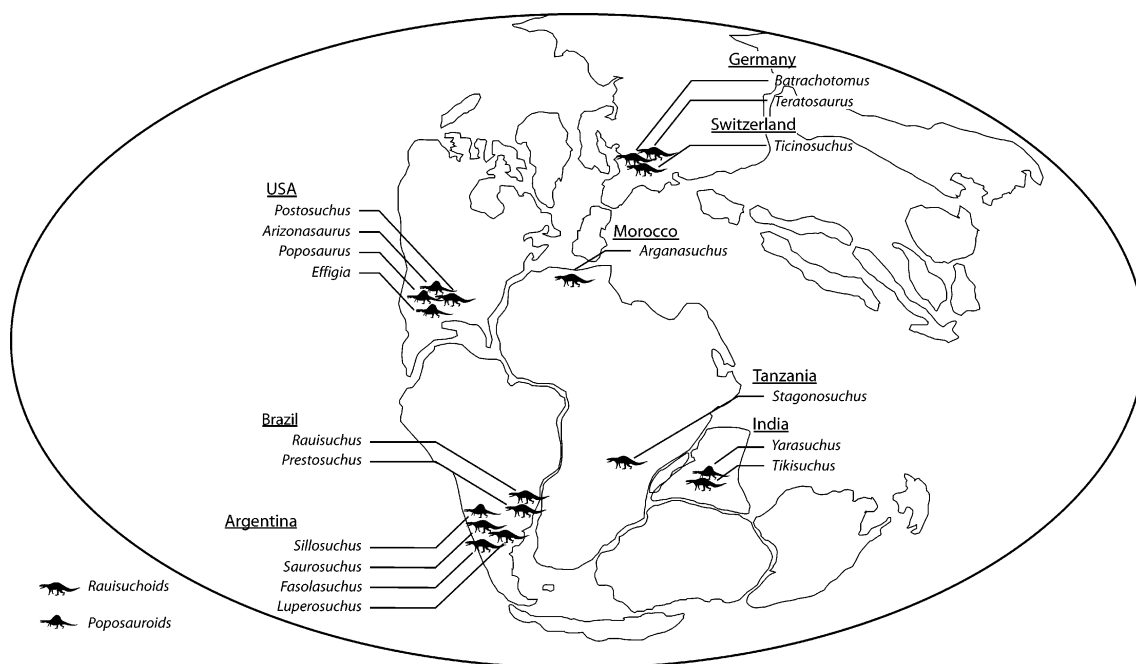
The study of rausuchian archosaurs has always suffered from the sparse fossil record and the fragmentary nature of the specimens. Moreover, several taxa have been shown to be chimeras, composed of different taxa and therefore misleading, such as *Postosuchus* (Long and Murry 1995) or *Yarasuchus* (Sen 2005), which comprises skeletal elements of a rausuchian archosaur and a prolacertiform (JBD, personal observations).

In the last 20 years rausuchian archosaurs have therefore been in the focus of extensive research, mainly because of the discovery of new taxa and specimens (Gower 1999; Sulej 2005; Nesbitt 2005, 2007; Gower and Schoch 2009; Desojo and Arcucci 2009; Trotteyn et al.

2011), but also because of the revision of known and historical material (Alcober 2000; Weinbaum and Hungerbühler 2007; Lautenschlager 2008). The latter is an especially important factor for the understanding of Rausuchia and their evolution—however, many taxa collected during the first half of the last century (and before the application of numerical phylogenetic analyses) remain scientifically neglected. These suffered in particular from the lack of a binding nomenclature and an exact methodology, such as the missing designation of type specimens (von Huene 1938, 1942). *Ticinosuchus ferox*, although providing an articulated and nearly complete specimen, was described in German by Krebs in 1965 and is not included in most of the published phylogenetic analyses (Parrish 1993; Nesbitt 2007; Weinbaum and Hungerbühler 2007). Another poorly known rausuchian is *Stagonosuchus nyassicus* from Tanzania. Although it has recently been redescribed by Gebauer (2004), it is rarely considered in works on rausuchian systematics and phylogeny.

Even though rausuchian archosaurs had a nearly global distribution (Fig. 1), they were restricted to a comparably short period of time from the Middle to the Late Triassic. The first unequivocal rausuchians appeared in the Anisian and were already highly diversified (see Nesbitt 2007; Lautenschlager 2008). However, Gower and Sennikov (2000) reported several taxa from the Olenekian of Russia with ambiguous affinities. A clarification of the taxonomic status of this material could shift the origin of Rausuchia well into the Early Triassic. *Ticinosuchus ferox* and *Stagonosuchus nyassicus* are two of the few taxa known from Anisian strata and therefore of special interest in terms of rausuchian origins and evolution. Despite both taxa being among the first representatives of this lineage, they show a considerably different morphology. Whereas *Ticinosuchus ferox* was a small (2.5 m) and gracile animal, *Stagonosuchus nyassicus* represented a larger (4–6 m) and stoutly built morphotype. This might have important ramifications for the palaeobiology of these species.

The aim of the present contribution is to describe and introduce new characters and osteological features of these two important rausuchian taxa from the Middle Triassic, to correct the existing descriptions (von Huene 1938; Krebs 1965; Gebauer 2004), and to provide an emended and revised diagnosis. It expands the discussion of character states and makes comparisons possible, which were not available to the original authors. Furthermore, the presented description of the material of *Ticinosuchus ferox* and *Stagonosuchus nyassicus* complements the works of Lautenschlager (2009), Brusatte et al. (2010), and Desojo and Rauhut (2009, submitted), in which phylogenetic characters were scored for these taxa based upon novel and previously unpublished observations.



**Fig. 1** Palaeogeographic map showing the distribution of selected Rausuchia during the Middle and Upper Triassic (modified after Scotese 2002)

Institutional abbreviations: BES—Museo Civico di Storia Naturale, Milan, Italy; BP—Bernard Price Institute for Palaeontological Research, Johannesburg, South Africa; BSPG—Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; GPIT—Institut für Geowissenschaften, Universität Tübingen, Germany; MNHN—Muséum National d’Histoire Naturelle, Paris, France; MSM—Mesa Southwest Museum, Mesa, AZ, USA; NHM—The Natural History Museum, London, United Kingdom; PIMUZ/PIZ—Paläontologisches Institut und Museum der Universität Zürich, Switzerland; SAM—South African Museum, Cape Town, South Africa; SMNS—Staatliches Museum für Naturkunde, Stuttgart, Germany; UFRGS-PV—Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil; UMMP—University of Michigan Museum of Paleontology, Ann Arbor, MI, USA; ZPAL—Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

### Revised osteology of *Ticinosuchus ferox*

#### Systematic Palaeontology

**Archosauria** Cope, 1869 *sensu* Gauthier and Padian, 1985

**Pseudosuchia** Zittel, 1887–1890 *sensu* Gauthier and Padian, 1985

**Rausuchia** von Huene, 1942 *sensu* Brusatte et al. 2010  
***Ticinosuchus*** Krebs, 1965

**Type species:** *Ticinosuchus ferox* Krebs, 1965

**Revised diagnosis:** Same as for the only known species (by monotypy).

***Ticinosuchus ferox*** Krebs, 1965

**Holotype:** PIZ T 2817, articulated skeleton.

**Paratype:** PIZ T 2471, six articulated caudal vertebrae and osteoderms.

**Referred specimens:** BES 189, fragmentary right dentary, right humerus, left and right ulna, left and right radius, right clavicle, one cervical vertebra, one dorsal vertebra, four osteoderms, isolated tooth.

**Type horizon:** Mittlere Grenzbitumenzone, late Anisian (*polymorphus*-Zone), Middle Triassic.

**Revised diagnosis:** *Ticinosuchus ferox* differs from all other raiusuchian archosaurs by the combination of the following characters: antorbital fenestra tapers sharply anteriorly; maxilla with pronounced rostral ramus; maxilla with dorsoventrally expanded ascending process and fused medial interdental plates; centra of cervical vertebrae elongated and approximately twice as long as high; two

sacral vertebrae; ventral margin of coracoid continuous (not interrupted by a notch or edge); pubis without distal expansion; postacetabular process of ilium with horizontal medial ridge; dorsal margin of ilium blade notably rounded and convex; ischia joined by a pronounced ventral crest, arrowhead-shaped and symmetrical anterior to mid-caudal osteoderms with a sharp and pronounced midline keel.

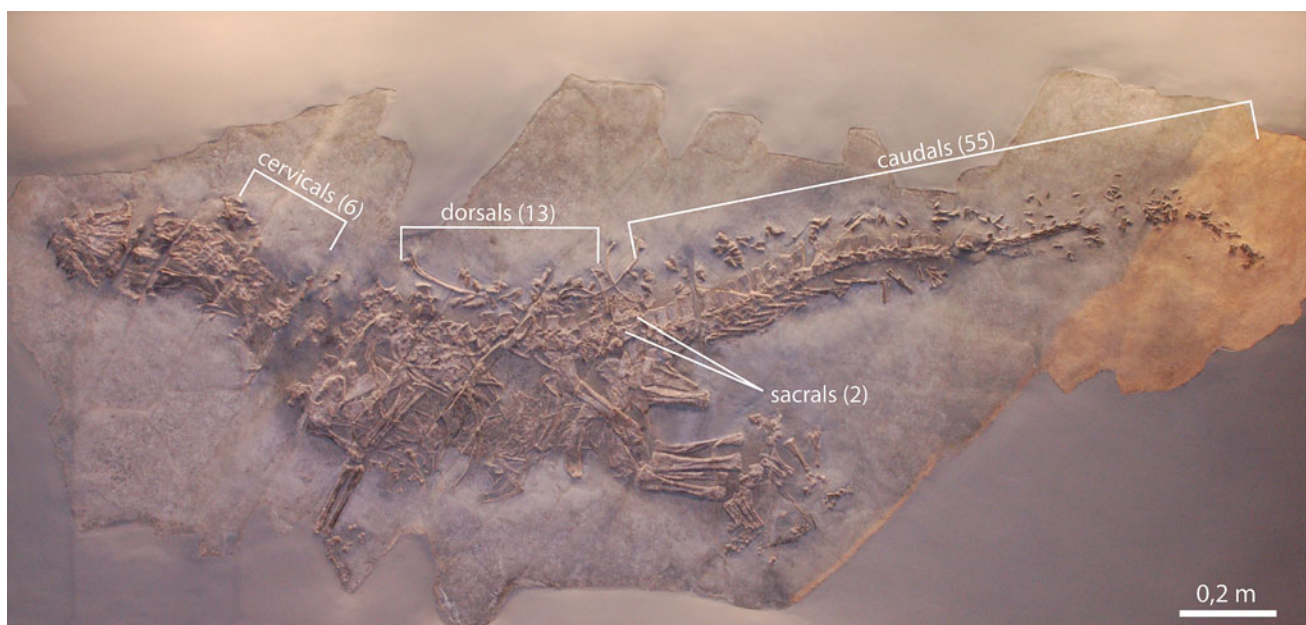
**Remarks:** In his emended diagnosis of the type material, Krebs (1976) considered the relative lengths of the radius (105% the length of the humerus) and the tibia (76% the length of the femur) as diagnostic characters. However, we regard length estimations of this material, especially of long bones, because of its compaction and the related artificial increase of the dimensions, to be problematic. Corresponding elements of the left and right side were found to have different dimensions in our examination, and a reliable ratio as stated above cannot be established. Therefore we do not consider these characters as diagnostic.

*Ticinosuchus ferox* is represented by the nearly complete and articulated holotype (PIZ T 2817) (Fig. 2), as well as a paratype (PIZ T 2471) consisting of six articulated caudal vertebrae with an attached single row of osteoderms. The specimens were found in 1933 and 1943, respectively, in the bituminous shales of the “Grenzbitumenzone” of Monte San Giorgio in southern Switzerland. It is one of the most diverse Triassic fossil Lagerstätten, well known for its abundant vertebrate fauna, including different groups of fishes, ichthyosaurs, sauropterygians and placodonts

(Kuhn-Schnyder 1964). With the exception of a single prolacertiform reptile (*Macrocnemus bassanii*), *Ticinosuchus ferox* represents the only terrestrial faunal element of the “Grenzbitumenzone”.

The “Grenzbitumenzone” consists of an alternating series of shales and dolomites, and has an average thickness of 16 m. Its sediments were deposited during the Anisian/Ladinian transition in a restricted marine intra-platform basin under oxygen-depleted conditions (Röhl et al. 2001). Rieber (1973) distinguished three separate biostratigraphic subdivisions—the lower (Untere), middle (Mittlere) and upper (Obere) “Grenzbitumenzone”. The holotype of *Ticinosuchus ferox* comes from the middle “Grenzbitumenzone”, which is of upper Anisian age (*polymorphus*-Zone after *Ticinites polymorphus*) (Rieber 1973; Stockar 2010). The paratype cannot be accurately placed stratigraphically, because it was found among fallen debris. Due to the high diagenetic pressure the specimens have been heavily compacted and in parts distorted. They are otherwise well preserved and articulated, indicating only minor transportation and the prevention of scavenging by the anoxic benthic conditions.

A further specimen (BES 189) of *Ticinosuchus ferox* was found in Besano, Northern Italy, in 1975 during an excavation conducted by the Museo Civico di Storia Naturale in Milan (Pinna and Arduini 1978). This specimen is disarticulated and consists, among various unidentifiable or strongly fragmented elements, of an incomplete right mandibular ramus, a right humerus, ulna and radius (of both sides), and four osteoderms. All elements correspond



**Fig. 2** Holotype of *Ticinosuchus ferox* (PIZ T 2817) (numbers in brackets indicate the number of preserved vertebral elements)



well in size, dimension and shape with the holotype. The preserved osteoderms can be regarded as diagnostic for *Ticinosuchus ferox* in showing the characteristic arrow-head-shaped morphology and a sharp midline keel.

Although the holotype material has been extensively described by Krebs in 1965, our study revealed new information and interpretations, which will be described and discussed in the following sections. Descriptions of elements by Krebs (1965), which are still valid, will not be treated in closer detail.

#### Skull bones

The holotype of *Ticinosuchus ferox* is for the most part still articulated and nearly complete, but the skull has been heavily crushed and dispersed. The cranium and postcranium have postdiagenetically been dislocated by a fault of approximately 30 cm. The respective part of the slab is riddled by fractures, which makes an identification of the single bones difficult. Among the cranial elements Krebs only tentatively distinguished the left maxilla and the left dentary, as well as several isolated teeth with confidence, pointing out the lack of comparative material of other pseudosuchians (Krebs 1965, p. 10) at the time of description.

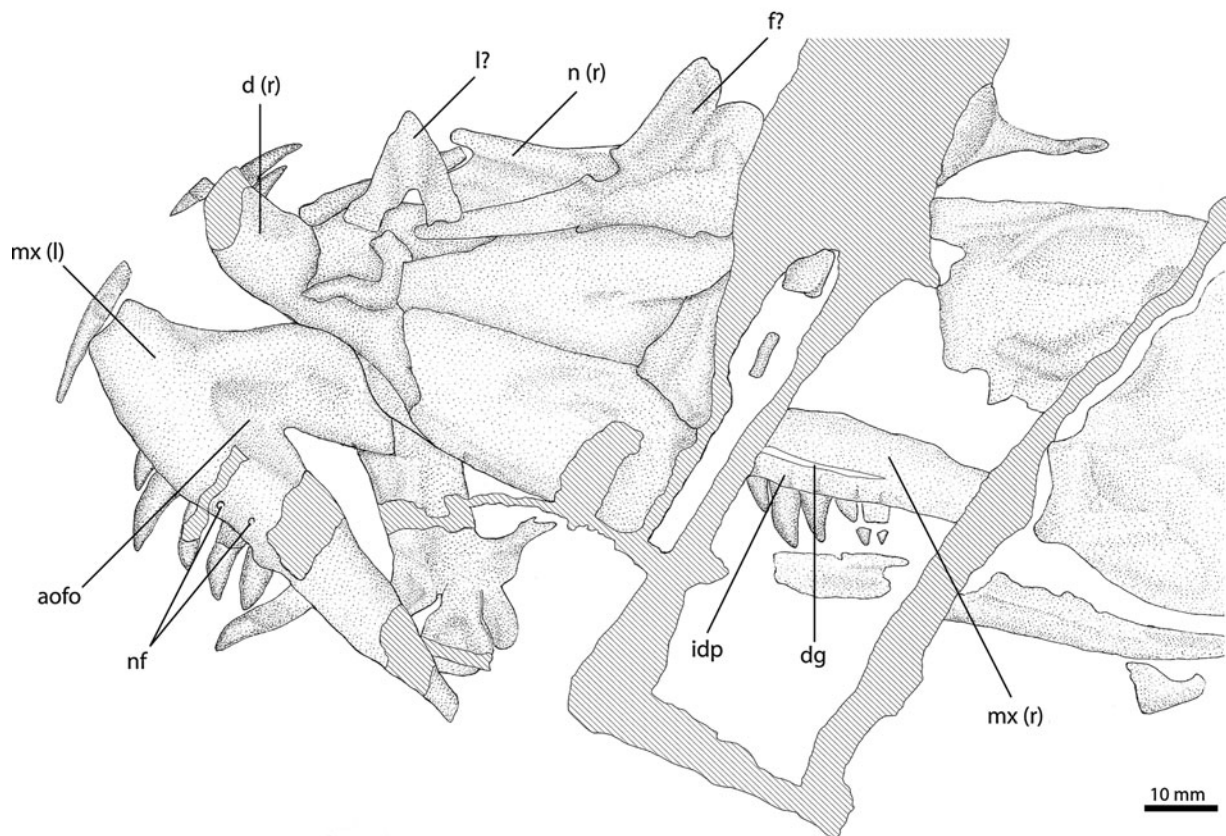
The left maxilla lies in the lower left corner of the skull remains (Fig. 3). It is one of the few cranial elements, which is readily identifiable and appears to be comparably large. The triradiate maxilla consists of a main body with an anterior and posterior portion, and a dorsally ascending process. The main body of the maxilla is elongated, dorsoventrally narrow and tapers posteriorly. The anterior margin of the maxilla is incomplete and gives no evidence of the presence or absence of a small fenestra between premaxilla and maxilla (subnarial fenestra *sensu* Parrish 1993). Anterior to the six teeth preserved in situ, three further alveoli are visible in the form of concave indentations on the ventral margin of the maxilla. The full extent of its anterior margin cannot be determined, but a further alveolus seems improbable. A single tooth to the left of the maxilla is larger than the anterior portion of the maxilla and thus unlikely to represent another tooth position anteriorly. This tooth most probably derived from one of the more posteriorly situated alveoli. In the posterior part of the maxilla no further alveoli are visible. Ventrally, the maxilla is considerably recurved, more so than in the tentative reconstruction suggested by Krebs (1965).

Compared to its smooth posterior surface, the anterior part of the maxillary main body ventral to the ascending process is uneven and pitted in lateral view. These structures indicate the presence of several moderately sized nutrient foramina. Two completely preserved foramina are visible dorsal to the fourth preserved tooth. These foramina

were presumably arranged in a row, tracing the ventral margin of the maxilla, as for example seen in *Postosuchus kirkpatricki* (Chatterjee 1985; Long and Murry 1995) or *Batrachotomus kupferzellensis* (SMNS 52970).

The ascending process of the maxilla was depicted as very narrow and tapering. It is actually more expanded both anteriorly and posteriorly and hence comparably broad. The part Krebs (1965) described as the ascending process is only a small portion of it. The actual ascending process has a prominently developed convex lateral part. Only this part was considered by Krebs (1965). However, the actual margin of the ascending process lies posterior and medial (deeper within the slab) to the convex part. The margin is recessed and thin lateromedially, and forms an antorbital fossa. The antorbital fenestra of *Ticinosuchus ferox* is therefore much smaller at its anterior margin and forms an acute angle with the main body of the maxilla, which gives the fenestra a teardrop-shaped outline, and resembles that of *Saurosuchus galilei* (Alcober 2000) and *Prestosuchus chiniquensis* (Barberena 1978). At the anterior margin, the ascending process of the maxilla of *Ticinosuchus ferox* is discontinuous with the margin of the main body and forms a concave step. Dorsally, the ascending process does not taper as described by Krebs (1965), but is developed as a broad and flattened process. A similar morphology is present in *Batrachotomus kupferzellensis* (SMNS 52970), in which the ascending process bears a thickened and rounded ridge anterior and lateral to the antorbital fossa. Because of the high compaction in *Ticinosuchus ferox*, only the prominent part of the ascending process remains clearly visible, whereas the rest of the process and the part containing the antorbital fossa were much more crushed and came to rest below (posteromedial to) it. The ascending process is shifted posteriorly and set off from the anterior margin of the maxilla. As with the main body of the element, the posterior process is very slender and tapers to a point. This condition resembles the maxilla of *Arganasuchus dutuitti* (MNHN ALM 1, Jalil and Peyer 2007), which additionally possesses an elongated anterior process or rostral ramus (after Brusatte et al. 2009), giving the maxilla a Y-shaped outline. Although its full anterior extent cannot be defined, a rostral ramus is also present in *Ticinosuchus ferox*.

There are indications that a correlation exists between a dorsally broadened and laterally flattened ascending process and the presence of an enlarged antorbital fossa. *Postosuchus kirkpatricki* (Chatterjee 1985; Long and Murry 1995; Weinbaum 2002), *Polonosuchus silesiacus* (Sulej 2005; Brusatte et al. 2009) and *Teratosaurus suevicus* (Benton 1986; Brusatte et al. 2009) possess a broad ascending process with a moderately developed protuberance, which separates the main process from the anterior border of an antorbital fenestra.



**Fig. 3** *Ticinosuchus ferox* Krebs, 1965 (PIZ T 2817), photograph and interpretative drawing of skull elements. *Hatched areas* indicate fractures. Abbreviations: (*l/r*) left/right element, *aofo* antorbital fossa,

*d* dentary, *dg* dental groove, *f* frontal, *idp* interdental plates, *l* lacrimal; *mx* maxilla, *n* nasal, *nf* nutrient foramina

A closer examination of *Ticinosuchus ferox* shows that the right maxilla, a right nasal and a possible frontal and lacrimal (Fig. 3) are also present in addition to the elements identified by Krebs (1965). The right maxilla lies to the right of the left dentary, separated from the remaining skull elements by two large vertical fractures. It is seen from the medial view. Anteriorly, it is broken posterior to the ascending process, which is not preserved, so that only the posteromedial side of the main body is visible. As in its right counterpart, the main body of the left maxilla is elongated and becomes dorsoventrally narrower in posterior direction. The posteriormost part is missing because of another large fracture in the slab. Five teeth, which correspond well with those of the left maxilla in shape and size, are preserved. By comparison to the left maxilla, they presumably represent the fifth to the ninth teeth, and no further tooth positions are visible posteriorly. Therefore each maxilla most likely contained only nine teeth in total. Although the maxillary tooth number varies both intraspecifically (Gower 1999) and interspecifically, most rauisuchians possess between 10 and 13 maxillary teeth (Chatterjee 1985; Alcober 2000; Nesbitt 2005; Jalil and Peyer 2007; Brusatte et al. 2009; Desojo and Arcucci 2009). Apart from *Tikisuchus romeri* (Chatterjee and Majumdar 1987), for which also nine maxillary teeth have been reported, *Ticinosuchus ferox* shows therefore the lowest maxillary tooth count.

At the ventral margin, the right maxilla possesses a row of interdental plates, which appear to be fused. Whereas the single interdental plates are still clearly distinguishable in *Teratosaurus suevicus* (Brusatte et al. 2009), where the plates are also fused, they seem to form a uniform lamina in *Ticinosuchus ferox*. Although absent in most other crurotarsans, fused interdental plates are not uncommon in rauisuchian archosaurs, such as *Postosuchus kirkpatricki* (Chatterjee 1985), and *Prestosuchus chiniquensis* (BSPG AS XXV 1, 28). The interdental plates are separated from the main body of the maxilla by a dental groove, although its size is exaggerated by the compaction of the element and a resulting break along the dental groove. Furthermore, the presence of replacement foramina dorsal to the interdental plates is indicated, but this break hampers an accurate identification.

The right nasal (Fig. 3) is exposed in lateral view and lies above to the rest of the skull remains. It has been shifted, so that it is now visible from dorsolateral view, with the descending process pointing upwards. The anteriormost part is covered by the putative lacrimal, whereas the posterior part came to lie below the putative frontal. The descending process, which would articulate with the maxillary ascending process and probably with the posterior process of the premaxilla, is short and projects anteroventrally, forming an angle of approximately 30 degrees

to the long axis of the nasal. The lateral surface of the descending process is well developed and rounded in contrast to the main body of the nasal, which is transversely flattened. In posterodorsal direction, the descending process grades into a thin ridge. An equally developed ridge runs horizontally on the main body parallel to the long axis of the nasal. Both ridges form an elongated external narial fossa between them, which tapers sharply posterodorsally at the junction of both ridges. Posteriorly, the ridge of the descending process separates the external narial fossa from the nasal contribution of the antorbital fossa. A similar, but more prominently developed, narial fossa and lateral ridges are developed in the nasals of *Batrachotomus kupferzellensis* (Gower 1999) and *Postosuchus kirkpatricki* (Chatterjee 1985).

A putative frontal (Fig. 3) is located above the nasal and the dentary. It has a wedge-shaped outline and is seen in dorsal aspect. Anteriorly, it is very slender and widens towards the posterior end, where a wing-like structure projects laterally. The medial margin of the frontal is nearly straight, whereas the lateral margin is concave. At approximately half its length the lateral margin is interrupted by a prominent notch, which is interpreted as the articulation socket for the prefrontal. A similar articulation between these elements has been described and illustrated for *Batrachotomus kupferzellensis* (Gower 1999) and *Saurosuchus galilei* (Alcober 2000). Posterior to this socket, the lateral border of the frontal is rounded and more prominently developed than anteriorly, forming the dorsal border of the orbit. The wing-like process has been flattened by compaction and was probably directed more laterally, overlapping the orbital rim and forming a dorsally bulged “brow”, as seen in *Saurosuchus galilei* (Alcober 2000). The dorsal surface exhibits two depressions, separated by a weak ridge, which runs mediolaterally and splits up to border the prefrontal socket. The first depression is elongated and oval, and situated anteriorly near the medial margin. The second is shallower and follows the projection of the wing-like process. A comparable dorsal surface topography is seen in the frontal of *Batrachotomus kupferzellensis* (Gower 1999). Posteromedially, the bone is prominently bulged. Whether this is part of the frontal or remains of the dorsally arched parietal cannot be determined with absolute certainty, as possible sutures have been obliterated by the compaction of the element.

A putative lacrimal (Fig. 3) lies left of the frontal and the nasal. It is a V-shaped element with two short processes rising from a stout base. In its present position both processes point ventrally. Between them, the lacrimal is rounded, forming the posterodorsal border of the antorbital fenestra. The base of the lacrimal is triangular and tapers to a point. Along its longitudinal axis it appears to be vaulted and is thus interpreted as being visible in lateral aspect.



Due to the preservation of this putative element, no further details can be described.

### Cervical vertebrae

The centra of the cervical vertebrae of *Ticinosuchus ferox* are on average of uniform dimensions and nearly twice as long as high (length:height = 1.8–1.9:1), which makes them a characteristic feature and gave the animal a comparatively long neck. Krebs considered the dimensions of the cervicals in his description and his differential diagnosis of *Ticinosuchus ferox*, in being different from *Rauisuchus*, *Prestosuchus*, and *Stagonosuchus* (Krebs 1965, p. 132). However, he did not differentiate between the two species of *Prestosuchus*: *P. chiniquensis* and *P. loricatus*. The cervical vertebrae are short and high in *Prestosuchus chiniquensis*, whereas they are actually considerably longer in “*Prestosuchus*” *loricatus*<sup>1</sup> (BSPG AS XXV 13). A single cervical vertebra, tentatively referred to *Saurosuchus galilei* by Sill (1974), is also very elongated (length:height = 3.7:1), but the discovery and recent description of new material, including one complete and several fragmentary cervical vertebrae of *Saurosuchus galilei*, showed that the respective vertebra described by Sill (1974) did not belong to *Saurosuchus galilei*, but might possibly belong to another pseudosuchian (Trotteyn et al. 2011). The cervicals of *Saurosuchus galilei*, however, are short and nearly isometric (op. cit.).

The length of the (anterior) cervical vertebrae has been considered as phylogenetically informative (Nesbitt 2003; Weinbaum and Hungerbühler 2007; Brusatte et al. 2010) in raiusuchian archosaurs, as taxa referred to as Poposaurioidea (including *Poposaurus*, *Arizonasaurus* and *Sillosuchus*) possesses cervicals with a length:height ratio greater than 2:1. However, *Ticinosuchus ferox*, which represents a more gracile and slender morphotype than other Raiusuchioidea, also possesses elongated cervical vertebrae.

### Dorsal vertebrae

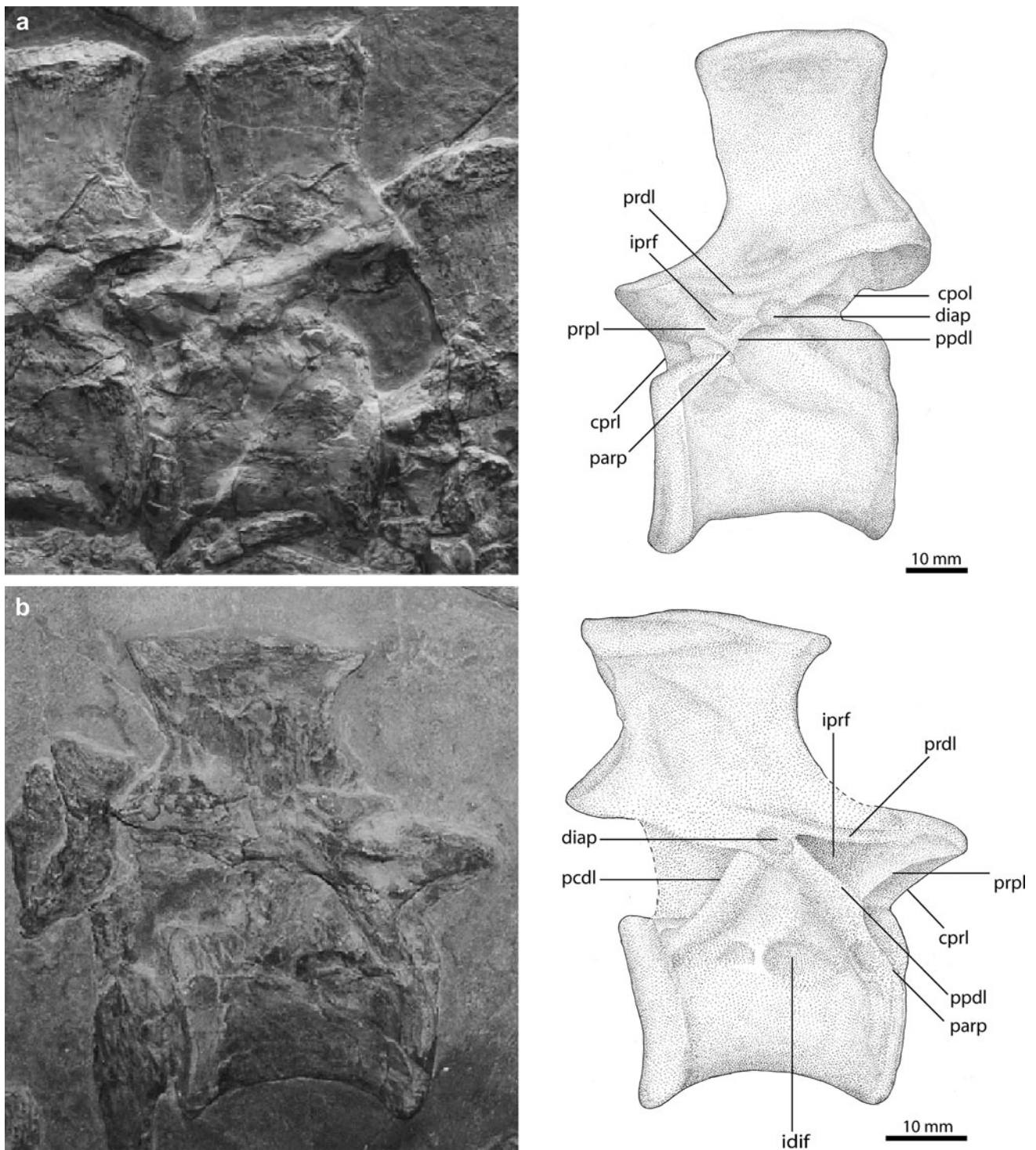
Thirteen definite dorsal vertebrae are preserved from the presacral series, several of them still articulated. Because of a broad fracture in the slab, the transition from the cervical to the dorsal vertebrae cannot be observed and a definite sequence of the anterior dorsals cannot be defined. For this reason Krebs designated the dorsals as “d1” to “d13”, starting at the last dorsal and numbering them

consecutively in ascending order in cranial direction (Krebs 1965, Fig. 7). Even though vertebrae are normally numbered from anterior to posterior, we follow the designation of Krebs (1965) here for ease of comparison and to avoid confusion. They are only visible from the left side, with the exception of two dorsals visible from the right side (d10, d12) and one embedded perpendicular to its longitudinal axis (d11). A further dorsal vertebra is poorly preserved and of unknown orientation (d13). The extensive compaction notwithstanding, various vertebral laminae are identifiable in several of the dorsal vertebrae and have not been described before. As a result of the preservation of the specimen, the vertebral laminae are not equally visible in all vertebrae. Therefore two dorsals have been chosen to exemplarily describe the various laminae (Fig. 4a, b): an anterior dorsal, visible in right lateral view, identified as the 12th vertebra (d12, Fig. 4b), which can be attributed to the pectoral to mid-dorsal series, and a posterior dorsal vertebra (d3, Fig. 4a) in left lateral aspect. The nomenclature of the vertebral laminae follows the classification established by Wilson (1999).

A posterior centrodiapophyseal lamina (pcdl) connects the diapophysis with the posterior rim of the centrum. It plainly forms a thin, vertical ridge at the posteroventral part of the centrum (d3, d12). A prominent prezygodiapophyseal lamina (prdl) is indicated in the 3rd (d3) and clearly visible in the 12th vertebra (d12), starting laterally at the upper half of the prezygapophysis and forming a horizontal lamella. Posteriorly, it is attached to the remains of the diapophysis and the transverse process, respectively, which has been reduced to a small bump by compaction. The paradiapophyseal lamina (ppdl) is strongly developed in both exemplary vertebrae (d3, d12) and connects the diapophysis with the parapophysis. In the 12th vertebra the parapophysis is no longer clearly visible and indicated by a slightly different topology to the anterior central rim. Because of the anatomical position of this dorsal, the diapophysis and the parapophysis are still separated, and the paradiapophyseal lamina is long and slightly recurved anteriorly. In the posterior dorsals, including d3, both the parapophysis and the diapophysis are conspicuous and positioned close together. As a result the paradiapophyseal lamina is comparably short. A centroprezygapophyseal lamina (cprl) is only weakly visible at the anterior margin of the 12th vertebra (d12) due to its lateral orientation, but obvious in the 3rd dorsal (d3). It joins the top of the anterior rim of the centrum with the upper half of the prezygapophysis. In vertebra d12 a prominent prezygoparapophyseal lamina (prpl) runs along the lateral side of the prezygapophysis and crosses the prezygapophysis centrally. At its posterior end this lamina merges with the paradiapophyseal lamina. Together, the prezygodiapophyseal, the paradiapophyseal, and the prezygoparapophyseal

<sup>1</sup> The cervical vertebrae of “*Prestosuchus*” *loricatus* are represented by an incomplete example, consisting of a neural spine and attached pre- and postzygapophyses. The actual centrum is missing. However, the size, arrangement and distance between the prezygapophyses and the postzygapophyses imply an elongated and low centrum. These and other anatomical differences necessitate the assignment to a different genus (JBD, personal observation, also see Desojo and Rauhut 2009).





**Fig. 4** *Ticinosuchus ferox* Krebs, 1965 (PIZ T 2817). **a** Photograph and interpretative drawing of dorsal vertebra “d3” in left lateral view. **b** Photograph and interpretative drawing of dorsal vertebra “d12” in right lateral view. Abbreviations: *cpol* centropostzygapophyseal lamina, *cprl* centroprezygapophyseal lamina, *diap* diapophysis, *idif*

infradiapophyseal fossa, *iprf* infraprezygapophyseal fossa, *parp* parapophysis, *pcdl* posterior centrodiapophyseal lamina, *ppdl* paradiapophyseal lamina, *prdl* prezygodiapophyseal lamina, *prpl* prezygoparapophyseal lamina

laminae form a deep, triangular infraprezygapophyseal fossa (*iprf*) between them. A circular infradiapophyseal fossa (*idif*) can be recognised laterally at the dorsal margin

of the vertebral centrum, located between the paradiapophyseal lamina and the posterior centrodiapophyseal lamina. Both fossae are most conspicuous in vertebra d12, but

also present in d3. The presence of an infrapostzygapophyseal fossa cannot be observed, though this might be concealed by the compaction of the specimen. Additionally, the posteriormost dorsals (d3 to d5) also possess centropostzygapophyseal laminae (cpol) that connect the posterior central rim vertically with the ventral margin of the postzygapophyses.

With the exception of the centropostzygapophyseal laminae, all described laminae can be observed in the anterior (d12) as well as the posterior (d3) examples, so that their presence can most likely also be inferred for the intervening dorsal vertebrae. The presence of similar vertebral laminae and fossae has been reported for various rauisuchians [e.g. *Arizonasaurus babbitti* (MSM 4590, P3307, Nesbitt 2005), *Rauisuchus tiradentes* (BSPG AS XXV 77, 112, Lautenschlager 2008) and *Hypselorhachis mirabilis* (NHM R16586, Butler et al. 2009)] and basal archosauriforms (e.g. *Erythrosuchus africanus*, NHM R 3592, 8667, Gower 2001, 2003). However, the distribution of both the single laminae and fossae in the various vertebrae, but also their presence among the various taxa varies considerably and should be considered in a separate investigation.

#### Pectoral girdle

The preserved elements of the pectoral girdle consist of the right scapula and coracoid and a fragmentary left coracoid (Fig. 5). As these elements are situated in a region where the slab is badly fractured, they are only incompletely preserved and had in part to be reconstructed by Krebs (1965). Accordingly, the right scapula was depicted as a broad and nearly rectangular element with flaring anterior and posterior expansions at both ends and a particular large coracoid. A comparison with the actual specimen, though, shows no indication for the anterior expansion of the distal part of the scapular blade. Its anterior margin is not as extensively broken as described by Krebs (1965), and the outline is clearly visible. Although a small part of the anterodorsal edge of the scapular blade is covered by two ribs, the extension of the scapula can be reconstructed by tracing the anterior and dorsal margins. With this method, it can be concluded that the anterior-posterior expansion, especially dorsally, has to be some 25% smaller than suggested by Krebs (1965). Therefore the scapular blade is not as strongly waisted as originally illustrated, but is more rectangular and with subparallel anterior and posterior margins. Only the area where the scapular blade grades into the glenoid part shows a notable curvature. Anteriorly, the scapular appears to be thin, whereas it is more rounded and bulged along its posterior edge. The ventral part of the scapula was reconstructed by Krebs (1965) with a similarly exaggerated anterior extent, although the respective region

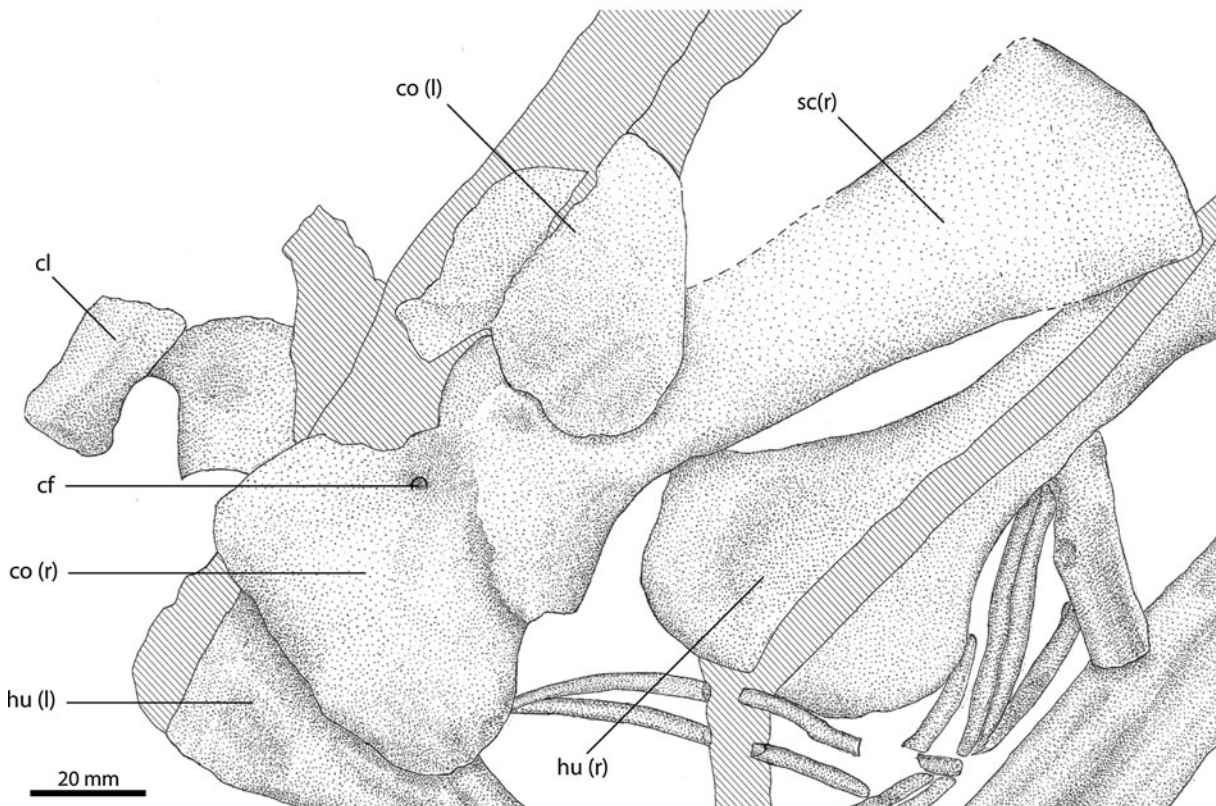
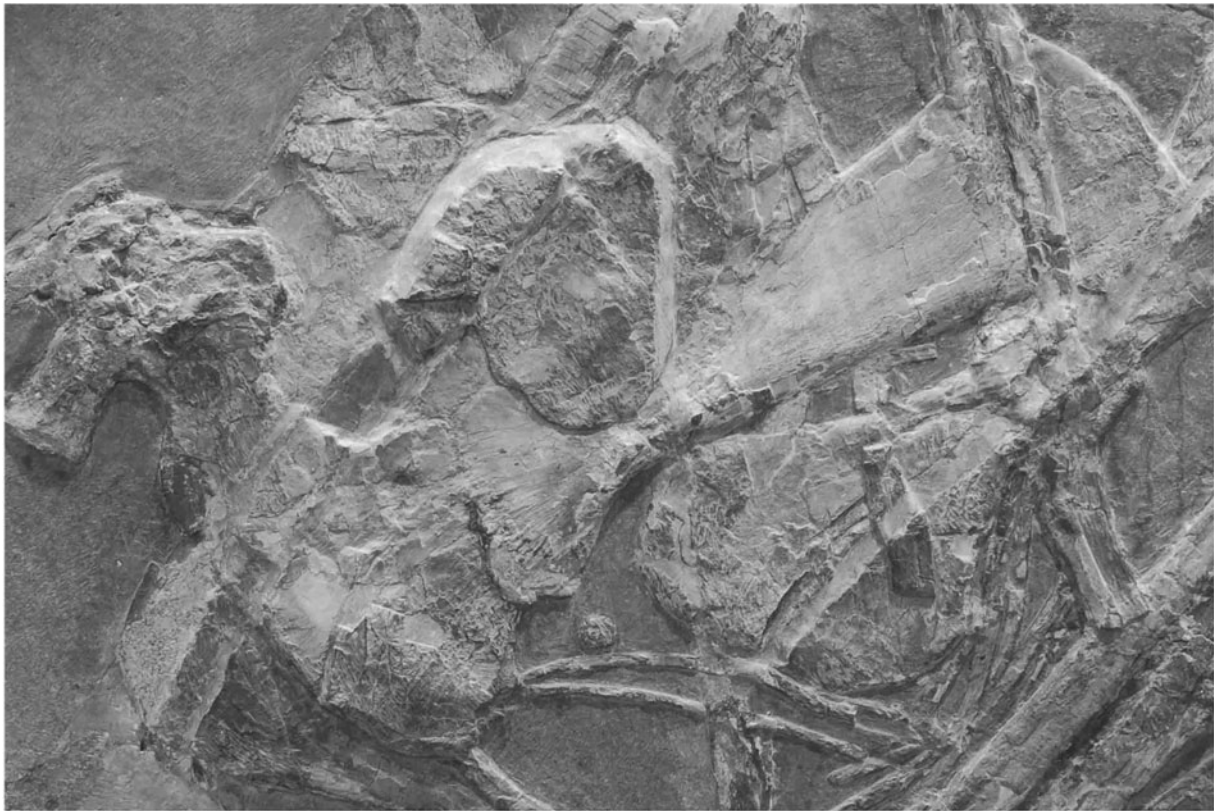
is covered by the remains of the left coracoid and borders a major fracture in the slab. Therefore, the preserved element only suggests a slight expansion, which corresponds to the dorsal part.

Due to the fracture mentioned above, the true contact between the scapula and the coracoid is not visible. The size and position of the anterior notch between both elements are similarly arbitrary in the reconstruction of Krebs (1965). Posteriorly, the scapula has been displaced in an anteroventral direction and lies upon the coracoid. A similar movement is indicated by the displacement of the skull and pelvic girdle elements. Therefore only the anterior part of scapula/coracoid suture is natural, whereas the posterior part and the glenoid cavity are covered by the protruding scapular rim. Remains of the glenoid surface in the right and left coracoid, though, suggest a larger, notch-like cavity than originally depicted, meeting at an angle of approximately 105 degrees, which is in stark contrast to the assumption of 75 degrees by Krebs (1965).

Both coracoids (Fig. 5) are broken, and their complete outline is unknown. Krebs (1965) reconstructed this element as a large anterior-posteriorly elongated, oval bone. Again its reconstructed size seems exaggerated when compared to the specimen. The right coracoid, which is still attached to the scapula, only shows the posterior half, whereas the anterior margin of the left coracoid has been set off by the fracture. Several unidentifiable bony remains, lying on the other side of this fracture and bordering the left coracoid, have been attributed as its anterior part by Krebs (1965). However, both coracoids actually show a more circular and anteroposteriorly less expanded morphology. In contrast to the smooth surface of the scapular blade, the coracoids possess a rough and uneven surface structure. A small coracoid foramen (Fig. 5) is visible in the right coracoid close to its anterior margin and the scapular suture. The respective region is obliterated by a fracture in the left coracoid. The posterior and ventral margins are continuous and do not show any notches or indentations. An obvious postglenoid process, as seen in *Postosuchus* (Weinbaum 2002; Peyer et al. 2008) and *Batrachotomus kupferzellensis* (Gower and Schoch 2009), is not developed in the coracoids of *Ticinosuchus ferox*.

As shown above, the scapula and coracoid of *Ticinosuchus ferox* were actually only moderately expanded and less waisted. Respectively, the coracoids are only moderate-sized. This corresponds well with the body size of this species, which represents one of the smallest known rauisuchian archosaurs. Specimens with a comparable body size, as for example *Rauisuchus tiradentes* (Lautenschlager 2008), show an equally slender scapula, which contrasts the large and expanded scapulae of large species, such as *Prestosuchus chiniquensis* (von Huene 1942) and *Saurosuchus galilei* (Trotteyn et al. 2011).





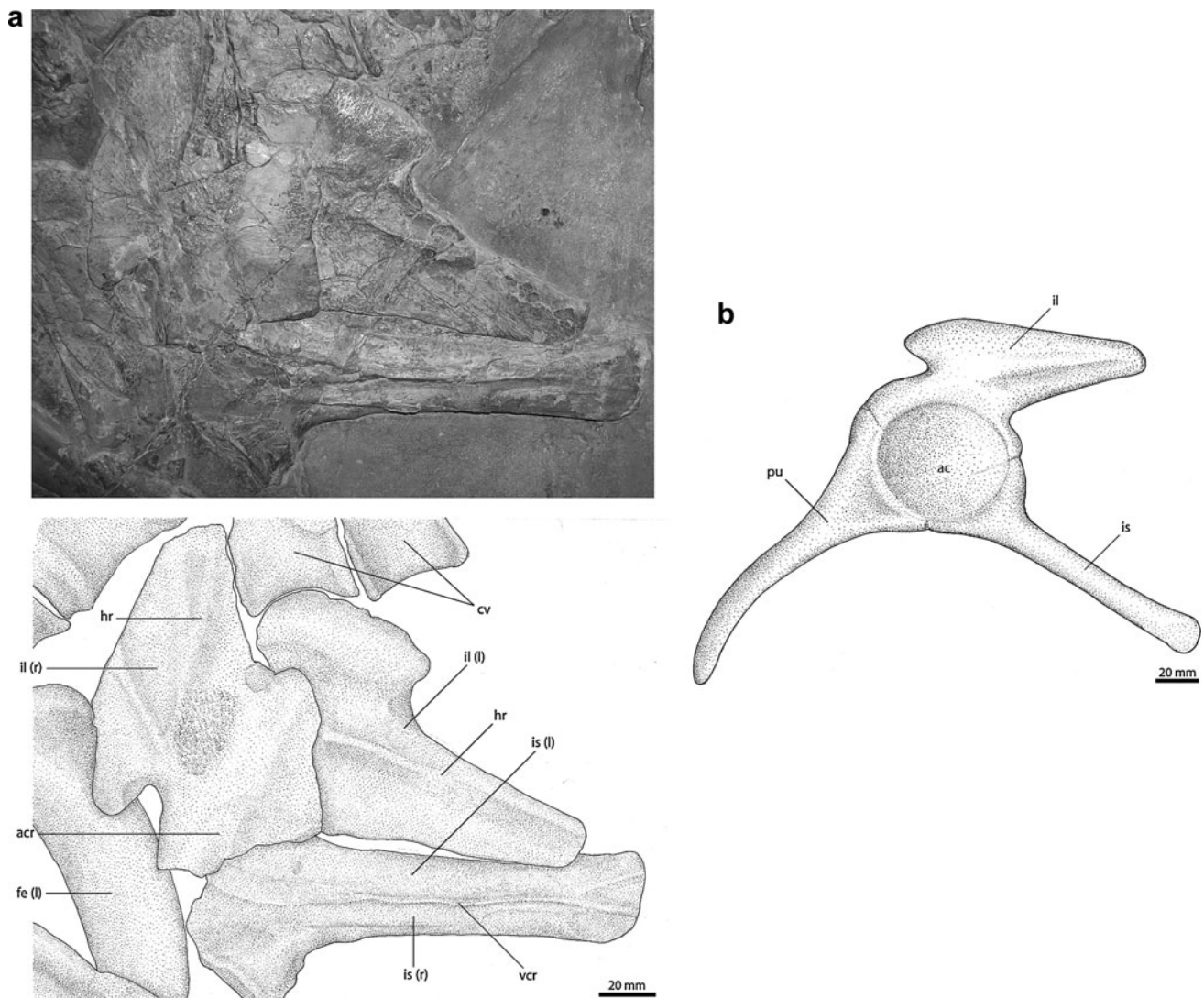
**Fig. 5** *Ticinosuchus ferox* Krebs, 1965 (PIZ T 2817), photograph and interpretative drawing of pectoral girdle elements. Hatched areas indicate fractures. Abbreviations: (*l/r*) left/right element, *cf* coracoid foramen, *cl* clavicle, *co* coracoid, *hu* humerus, *sc* scapula

A small fragmentary element located to the left of the right coracoid was tentatively identified as a possible clavicle by Krebs (1965). We confirm his designation here. It represents the enlarged distal part of the clavicle in lateral view, although the preservation does not allow identifying it as a left or right one. The distalmost part shows a prominent rim and was probably more club- or drop-shaped before the compaction, as seen in the clavicles of *Prestosuchus chiniquensis* (BSPG AS XXV 12) and *Batrachotomus kupferzellensis* (Gower and Schoch 2009). The lateral surface bears a weak ridge parallel to the long axis of the element. A further specimen from Besano (BES 189) referred to *Ticinosuchus ferox* also exhibits a fragmentary proximal part of the clavicle. Its state of preservation does not allow any further observations than that it is slightly

curved, probably to attach to the scapula. Although Krebs (1965) reconstructed a complete clavicle and interclavicle attached to the scapula and coracoid, no interclavicles are known from *Ticinosuchus ferox*. Both clavicles and interclavicles are rarely preserved in rauisuchian archosaurs, and we therefore refrain from the reconstruction of either for *Ticinosuchus ferox*.

#### Pelvic girdle

The pelvic elements (Fig. 6a) are disarticulated and were loosely embedded below to the sacral part of the vertebral column. Both ilia are preserved and were identified as visible from the medial side by Krebs (1965), although no reason for this assumption was presented. The presence of



**Fig. 6** *Ticinosuchus ferox* Krebs, 1965 (PIZ T 2817). **a** Photograph and interpretative drawing of pelvic girdle elements, **b** reconstruction of the pelvis in left lateral view. Abbreviations: (*l/r*) left/right

element, *ac* acetabulum, *acr* acetabular rim, *cv* caudal vertebrae, *fe* femur, *hr* horizontal ridge, *il* ilium, *is* ischium, *pu* pubis, *vcr* ventral crest



a roughened area between the iliac blade and the main body, presumed to be the attachment area for the sacral ribs (Krebs 1965), provides tentative support for his hypothesis. Gower and Schoch (2009) noted that this attachment area does not seem to expand so far onto the anterior extension of the iliac blade in *Ticinosuchus ferox* as in *Batrachotomus kupferzellensis* or poposauroids. It remains unclear, however, whether the respective structures are natural or formed by diagenesis. If these were in fact articulation points for the sacral ribs, the number and differentiation cannot be distinguished. Krebs (1965) suggested two sacral vertebrae to be present, as their length approximately matches the dimensions of the respective facets on the ilia, although the size and extent of the sacral ribs can exceed the vertebra centrum length (e.g. in *Batrachotomus kupferzellensis*, Gower and Schoch 2009). Two sacral vertebrae are preserved in *Ticinosuchus ferox*, and the mostly complete vertebral column gives no indication of a further sacral vertebra.

As both ilia are covered by each other or other elements, their full outline is not fully visible. A comparison with the reconstruction made by Krebs (1965) shows that the dorsal margin of the iliac blade is more expanded dorsally and convex, even taking into account a considerable compaction of the element. The preacetabular process is short and rounded, and does not extend beyond the pubic process. The postacetabular process is elongated and dorsoventrally enlarged, although this is exaggerated by the compaction to some parts. A weak horizontal ridge is recognisable in each ilium, which runs nearly centrally along the postacetabular process and suggests a dorsomedial edge. Such an edge, which divides the postacetabular process in a dorsomedially flattened and a ventrally directed part, is present in an ilium referred to *Raiusuchus tiradentes* (compare von Huene 1942; Lautenschlager 2008) and the ilia of *Batrachotomus kupferzellensis* (Gower and Schoch 2009). Although flattened by compaction, the dorsomedial region of the postacetabular process appears to bear an elongated depression along its length. The dimensions and position of the acetabulum are only weakly marked on both ilia by a bulge or swelling on the main body. They are directed outwards and do not form a depression in the slab, which indicates that the acetabula are traced from the lateral side and that both ilia do seem to represent the medial side. However, a new reconstruction (Fig. 6b) of the ilia indicates that the contribution of the ilium to the acetabulum is smaller than originally reconstructed by Krebs (1965).

Krebs (1965) claimed that only the right ischium had been preserved, though he commented on the absence of the left counterpart as unexpected considering the moderately disarticulated nature of the specimen (Krebs 1965: p. 84). The present reexamination indicates that the left ischium is also present and attached to the right one—

though not completely covered by it, as Krebs (1965) surmised. Both elements are fused along the medial margin and form a conspicuous ventral crest. The crest connects the ischia from the distal end up to approximately 7 cm from the proximal end. A similar crest is known from *Prestosuchus chiniquensis* (von Huene 1942) and *Postosuchus kirkpatricki* (Long and Murry 1995). In a later diagnosis of *Ticinosuchus ferox*, Krebs (1976) erroneously described this crest to be on the lateral side of the right ischium and considered it to be a diagnostic feature. The proximal part with the main body is only visible on the right ischium, as the left one came to rest below the ilia. The acetabular portion of the ischium is poorly and only fragmentarily preserved. Only the acetabular rim is clearly visible. Although the full extent is unknown, the ischium seems only to make a small contribution to the acetabulum. Distally, the main body grades into the iliac shaft in a smooth rounded margin, but does not form an angular spur as illustrated by Krebs (1965). The right ischium also seems to bear a thin longitudinal ridge on the upper half of the shaft, which merges with the obturator blade proximally. The respective part on the left ischium is not visible, so it remains questionable whether this is an actual morphological feature or the result of diagenesis. In general, the ischia are rod-like and more slender than originally described because of the erroneous identification of both elements by Krebs (1965). The distal end is not expanded and rounded. Because the contribution of the ilium to the acetabulum is less than in the original reconstruction, the respective part on the pubis seems to be bigger. The actual acetabular area is not preserved in both pubes, so its dimensions were also conjectural in the description of Krebs (1965).

#### Metatarsus

The metatarsus of *Ticinosuchus ferox* is represented by metatarsals I-IV of the right foot in semi-articulation and metatarsals I-V of the left foot, which are no longer in natural articulation, but retain their relative anatomical position, with the exception of metatarsal V. The latter lies below metatarsal I and is very conspicuous in being an unusually thin and delicate element compared to the other metatarsals. Krebs (1965) reconstructed the pes accordingly with a long, thin metatarsal V, which is strongly splayed from the rest of the pes. In his description, the author stated that neither its orientation nor its origin from the left or right side can be determined. Nevertheless, he positively assigned it as a left metatarsal V. A detailed examination of the putative metatarsal V, however, shows no characters that would confirm its designation as a metatarsal V or a metatarsal at all. A proximal and a distal articular surface is not visible in the respective element, and it does not show the more

wedge-shaped and robust morphology, with an expanded proximal end, seen in *Batrachotomus kupferzellensis* (Gower and Schoch 2009), *Postosuchus alisonae* (Peyer et al. 2008), *Prestosuchus chiniquensis* (BSPG AS XXV 11e) and *Saurosuchus galilei* (Sill 1974). Furthermore, the questionable element is more gently curved and lacks the distinctive hooked outline of the preserved metatarsals V in the aforementioned taxa. The right metatarsal V is not preserved and, given the close association of the remaining metatarsals of both sides, the position of the doubtful left element is unusual in lying below the left metatarsal I.

Instead of a metatarsal, this element rather represents a rib fragment. Complete and fragmentary ribs are dispersed among the complete skeletal remains and found intermixed with other elements (Fig. 2). The rounded surface and the curvature correspond to a completely preserved thoracic rib and support this designation. The metatarsal V is therefore unknown in *Ticinosuchus ferox*. Several phalanges are preserved with the respective metatarsal bones and were identified by Krebs (1965). Mainly, due to their size, this author designated some of the smaller elements as phalanges of the fifth pedal digit, although a reliable designation is very speculative. With the exception of the fifth pedal digit, for which no reliable information exists, the reconstruction of the pes, as suggested by Krebs (1965), appears to be solid and validated.

### Revised osteology of *Stagonosuchus nyassicus*

#### Systematic Palaeontology

**Archosauria** Cope, 1869 *sensu* Gauthier and Padian, 1985

**Pseudosuchia** Zittel, 1887–1890 *sensu* Gauthier and Padian, 1985

**Rauisuchia** von Huene 1942 *sensu* Brusatte et al. 2010  
***Stagonosuchus*** von Huene, 1938

**Type species:** *Stagonosuchus nyassicus* von Huene, 1938

**Revised diagnosis:** Same as for the only known species (by monotypy).

***Stagonosuchus nyassicus*** von Huene, 1938

**Lectotype:** GPIT/RE/3831/1-21, right articular, atlantal centrum and neural spine, axial centrum, four cervical vertebrae, nine dorsal vertebrae, two sacral vertebrae, three caudal vertebrae, proximal part of left scapula, left coracoids, left fibula, right ilium, right pubis.

**Paralectotype:** GPIT/RE/3832/1-15, right postfrontal, one sacral vertebra, six caudal vertebrae, accessory neural

spine of caudal vertebra, right humerus, left ilium, proximal part of left pubis, articulated ischia, proximal part of right tibia, proximal part of left tibia.

**Type horizon:** “Upper Bonebed”, Lifua Member of the Manda Beds, late Anisian, Middle Triassic.

**Revised diagnosis:** *Stagonosuchus nyassicus* can be distinguished from all other rauisuchian archosaurs by the combination of the following characters (\* indicates autapomorphies): centra of presacral vertebrae higher than long (length:height = 0.75–1:1); additional infraprezygapophyseal and infrapostzygapophyseal laminae in the eighth cervical vertebra\*; last cervical and dorsal vertebrae with hyposphene-hypantrum articulations; neural spines of sacral vertebrae unfused, but interlocking and inclined in posterior direction; distal expansion of humerus approximately 65% of proximal expansion; ilium without a well-defined vertical ridge or swelling above the supracetabular rim; a boss-like protuberance on the postacetabular process of the iliac blade\*; a marked short dorsolateral crest on the proximal ischium\*; rounded protuberances at the midline of the ventral ischia contact\*, ischium with posteriorly expanded distal end; elongate (lunate) depression on the posteromedial surface of the distal part of the fibula.

**Remarks:** In 1930, Stockley collected a large amount of fossil material in the course of a geological survey in the Ruhuhu Coalfields in Tanzania (Stockley 1932; Houghton 1932). The collection included material of various therapsids, archosauromorphs and archosaurs, originating from three different localities, which relate to the different stratigraphic levels K6 (=Upper Permian Usili-Formation), K7 (=Lower Triassic Kingori Sandstone), and K8 (=Middle Triassic Lifua Member, each after Catuneanu et al. 2005) of the Songea Group. Among this material Houghton (1932) described a new species of rhynchosaur, *Stenaulorhynchus stockleyi*, based on the proximal part of a right humerus designated as holotype. Several femoral fragments, three dorsal vertebrae, an incomplete isolated vertebra and a fragmentary left maxilla were also referred to this species, although Houghton (1932) remarked on their archosaurian affinities and placed them as paratype. A distal half of a left humerus was assigned to the species *Stenaulorhynchus major* in reference to its larger size. Von Huene (1939) noted that the distal element is nearly indistinguishable in size and shape from the humerus of *Stagonosuchus nyassicus*, which originated from the same locality and level, and attributed the fragmentary left humerus also to *Stagonosuchus nyassicus*.

Although we base this identification on Houghton’s (1932) description and illustrations only, several anatomical details indicate that the maxilla and the vertebrae do not belong to a rhynchosaur (*Stenaulorhynchus stockleyi*),

but an archosaur. The maxilla (as illustrated by Haughton 1932) consists of remains of the main body with an ascending process. The anterior and posterior parts are missing. The maxilla bears four alveoli, which still hold remains of flattened and serrated teeth, characteristic for carnivorous archosaurs. The ascending process is robust and projects posterodorsally and forms an antorbital fossa with a sharply angled antorbital fenestra, in which the maxilla is very similar to that of *Ticinosuchus ferox* (see above), *Batrachotomus kupferzellensis* (Gower 1999) and *Arganasuchus dutuiti* (Jalil and Peyer 2007). Medially, a fragmentary part of the right maxilla is closely attached, indicating a long and narrow snout.

Of the dorsal vertebrae, only one was illustrated by Haughton (1932). It is amphicoelous and possesses a spool-shaped centrum. The parapophysis and the diapophysis are depicted as separated but close together and located above the neural canal. Vertebral laminae and fossae are not recognisable in the illustration or described.

At present none of this material mentioned above can be confidently referred to *Stagonosuchus nyassicus*, although the similar size of the single elements and the type material, the stratigraphic origin and the proximity of the single localities of the different material might speak for it.

Boonstra (1953) described a single right humerus (SAM 11754) collected by Stockley from the “Upper Bone Bed” of the Njalila locality. Based on a close resemblance to the material described by von Huene (corresponds to the paralectotype, GPIT/RE/3832/10), he assigned the humerus to the same genus, *Stagonosuchus*. Because of specific differences in size and proportions, he further attributed it to a new species, *Stagonosuchus tanganyikaensis*. Krebs (1976) regarded *Stagonosuchus tanganyikaensis* as a synonym of *Stagonosuchus nyassicus*. Compared to the preserved humerus of the paralectotype, we cannot confirm the assignment of the element described by Boonstra (1953) to either a different species or the genus *Stagonosuchus* at all. According to the description and illustrations of Boonstra (1953), the respective humerus is approximately 60% smaller than GPIT/RE/3832/10, and the humerus shaft is shorter and more expanded in SAM 11754. In contrast to the condition in GPIT/RE/3832/10, where the distal width is approximately 65% of the proximal width, the proximal and distal expansions are nearly equal to SAM 11754. In this, the latter rather resembles the humeri of rhynchosaurs (Benton and Kirkpatrick 1989; Hunt and Lucas 1991; Long and Murry 1995). The deltapectoral crest is flexed medially, and the radial and ulnar condyles are widely separated. Both conditions are not seen in GPIT/RE/3832/10. Based on these differences, we do not refer SAM 11754 to *Stagonosuchus*.

*Stagonosuchus nyassicus* is represented by two incomplete specimens, consisting mainly of postcranial material.

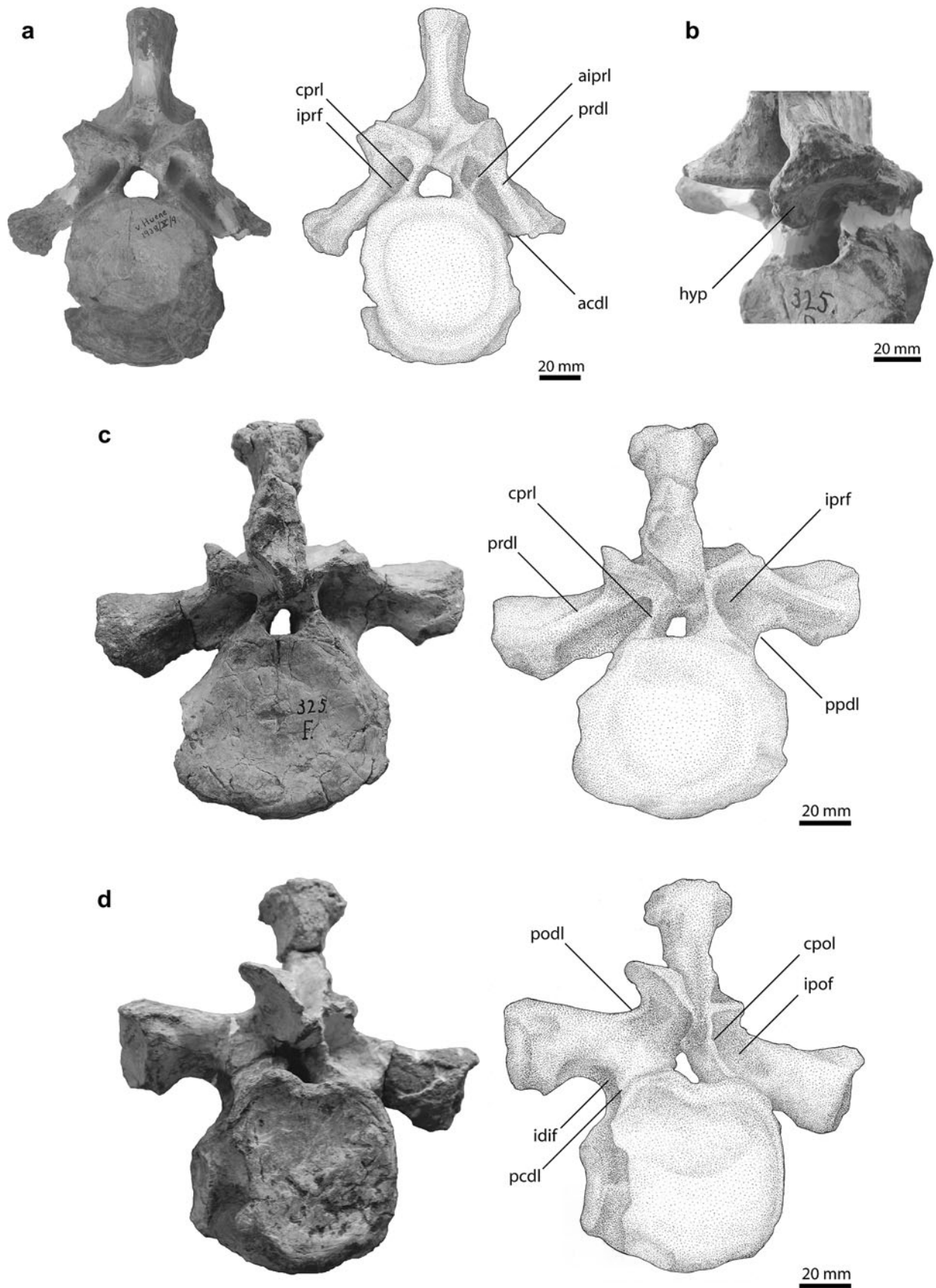
Both specimens were collected by Nowack between 1934 and 1936 on a German expedition in Tanzania and later described by von Huene (1938), who considered it to be a stagonolepidid. Von Huene referred this species to the family Stagonolepididae, to which he also assigned, among other groups of pseudosuchians, the subfamily Rauisuchinae, consisting of *Prestosuchus* and *Rauisuchus* (von Huene 1936). Not until 1956 did he place *Stagonosuchus nyassicus* to the family Rauisuchidae (von Huene 1956). A recent revision by Gebauer (2004) identified some new postcranial elements and determined a new lectotype for the bigger specimen (GPIT/RE/3831) and a paralectotype for the smaller specimen (GPIT/RE/3832), because von Huene had not defined a holotype. The material originated from the northwestern slope of the Lihandje Mountains/Njalila from the uppermost levels (K8) of the “Upper Bonebed” of the Manda Beds (von Huene 1938, p. 1). According to Catuneanu et al. (2005), this corresponds to the Middle to Upper Anisian section of the Lifua Member.

Despite the recent work on the specimens, several new undescribed characters were identified by our reexamination, making the introduction of these and some osteological revisions necessary.

#### Cervical vertebrae

von Huene (1938) and Gebauer (2004) described the cervical and dorsal vertebrae of *Stagonosuchus nyassicus*, which are only known from the lectotype (GPIT/RE/3831). Six cervical vertebrae (including atlas and axis) are preserved. In contrast to the dorsal vertebrae, the cervicals do not show unambiguous vertebral laminae, with the exception of a posterior cervical (GPIT/RE/3831-8), which von Huene (1938) considered to be the eighth cervical. The anterior cervical vertebrae are only poorly and fragmentarily preserved.

On the left lateral side, the posterior cervical (GPIT/RE/3831-8) (Fig. 7a) bears the remains of a lamina connecting the diapophysis to the dorsolateral margin of the centrum. A corresponding lamina is missing on the right side. As the vertebra shows clear signs of preparation and reconstruction, it is not absolutely clear whether this represents a fragmentary anterior centrodiapophyseal lamina (acd1) or an artificial structure. Posteriorly, a posterior centrodiapophyseal lamina (pcdl) is visible as a weakly developed, small ridge between the diapophysis and the upper half of the lateral margin of the posterior centrum. A prominent prezygodiapophyseal lamina (prdl) runs from the head of the diapophysis to the prezygapophysis on either side. Towards the prezygapophysis the prezygodiapophyseal lamina is gently curved dorsally. The postzygodiapophyseal lamina (pod1) is equally strongly developed, but curves





◀ **Fig. 7** *Stagonosuchus nyassicus* von Huene, 1938. **a** Posterior cervical vertebra (GPIT/RE/3831-8) in anterior view. **b** Detail of a posterior dorsal vertebra (GPIT/RE/3831-14) in posterior view. **c** Anterior dorsal vertebra (GPIT/RE/3831-9) in anterior and **d** posterior view. Abbreviations: *acdl* anterior centrodiapophyseal lamina, *aiprl* additional infraprezygapophyseal lamina, *cpol* centropostzygapophyseal lamina, *cpri* centroprezygapophyseal lamina, *hyp* hyposphene, *idif* infradiapophyseal fossa, *ipof* infrapostzygapophyseal fossa, *iprf* infraprezygapophyseal fossa, *pcdl* posterior centrodiapophyseal lamina, *podl* postzygodiapophyseal lamina, *ppdl* paradiapophyseal lamina, *prdl* prezygodiapophyseal lamina

posteriorly towards the postzygapophysis. Anteriorly, the dorsal margin of the centrum and the base of the prezygapophyses are joined by two distinct centroprezygapophyseal laminae (*cpri*), which converge dorsally at an angle of approximately 70 degrees. Posteriorly, two prominent centropostzygapophyseal laminae (*cpol*) attach to the upper margin of the centrum and below the postzygapophyses.

Several distinctive depressions or fossae (*sensu* Wedel 2007) are enclosed by the aforementioned laminae. The centroprezygapophyseal and the prezygodiapophyseal laminae form the margins of a deeply excavated and elongated infraprezygapophyseal fossa (*iprf*). It is separated by an additional (infraprezygapophyseal) lamina (*aiprl*), which runs perpendicular to the longitudinal axis of the fossa and divides it into a smaller, but deeper proximal and an elongated distal subfossa. On the left side this additional lamina is more prominent, whereas it is only moderately developed on the right side. The centropostzygapophyseal, the posterior centrodiapophyseal and the postzygodiapophyseal laminae enclose a large infrapostzygapophyseal fossa (*ipof*). An additional (infrapostzygapophyseal) lamina (*aipol*) similarly divides the fossa into two equally developed subfossae. A similar accessory lamina subdividing the infrapostzygapophyseal fossa was reported by Butler et al. (2009) for *Hypselorhachis* for a dorsal vertebra. An additional infraprezygapophyseal lamina is so far only described for *Stagonosuchus nyassicus*. The anterior cervical vertebrae do not show either lamina, but they are only fragmentarily preserved, whereas the sixth and seventh cervical are not preserved.

#### Dorsal vertebrae

Six anterior dorsal vertebrae are preserved and show a variety of vertebral laminae and fossae, which are missing in the existing descriptions (von Huene 1938; Gebauer 2004). The laminae are present in all of the dorsal vertebrae. Therefore, the anteriormost of the dorsals (GPIT/RE/3831-9) will be used as an example, as it is well preserved and shows the most details (Fig. 7b, c, d).

A posterior centrodiapophyseal lamina (*pcdl*) is moderately developed between the proximal part of the

prominent diapophysis and the upper posterolateral rim of the centrum. Anteriorly, the lamina merges with the diapophysis and is only faintly visible. Towards the centrum it increases in size and forms a sturdy lamella. On the anterior surface of the diapophysis a pronounced prezygodiapophyseal lamina (*prdl*) joins the prezygapophyses. It extends anteromedially, which results in a triangular outline in dorsal aspect. A postzygodiapophyseal lamina (*podl*) is only weakly developed in the form of a small longitudinal elevation between the diapophysis and the postzygapophysis. The diapophysis and the parapophysis are connected by a paradiapophyseal lamina (*ppdl*). It is thin and sheet-like, and extends up to half the length of the diapophysis and the parapophysis, respectively. The centroprezygapophyseal and centropostzygapophyseal laminae (*cpri*, *cpol*) are prominently developed. The centroprezygapophyseal laminae attach centrally to the ventrolateral surface of the prezygapophyses, whereas the centropostzygapophyseal laminae converge at the ventral fusion of the postzygapophyses.

A deep infraprezygapophyseal fossa (*iprf*) is located anteriorly between the prezygodiapophyseal, the paradiapophyseal and the centroprezygapophyseal laminae. On the lateral side, the dorsal part of the centrum beneath the attachment point of the diapophysis is excavated by an infradiapophyseal fossa (*idif*). It is bordered by the posterior centrodiapophyseal and the paradiapophyseal laminae. Posteriorly, the posterior centrodiapophyseal, the postzygodiapophyseal and the centropostzygapophyseal laminae enclose an infrapostzygapophyseal fossa (*ipof*). An additional fossa is located on the lateral surface of the centrum.

Contrary to the diagnosis of Gebauer (2004), two posterior dorsal vertebrae (GPIT/RE/3831-13, 14) show well-defined remains of a hyposphene below the postzygapophyses (Fig. 7b). A fragmentary hypantrum is visible on the anteriormost dorsal (GPIT/RE/3831-10). These accessory vertebral articulation structures are very common among raiisuchoids (see also below), such as *Fasolasuchus* (Bonaparte 1981), *Saurosuchus* (Trotteyn et al. 2011), *Prestosuchus chiniquensis* (UFRGS PV 0156T) and *Batrachotomus* (Gower and Schoch 2009).

#### Sacral vertebrae

In addition to a single, fragmentary sacral vertebra of the paralectotype of *Stagonosuchus nyassicus*, both sacral vertebrae of the lectotype are preserved in natural articulation. The centra are isometric and spool-shaped with strongly pronounced central rims. Both centra are closely articulated but not co-ossified, and a suture is visible between them. The neural spines are short and, although they are in close contact, not fused. They are inclined

posteriorly and seem to interlock dorsally, which probably gave them some stability. Additionally, the anterior and posterior margins of the neural spines bear a slight, vertical groove. These might have served as attachment points for ligaments, providing additional stability of the sacrum, as neither the centra nor the neural spines were coalesced.

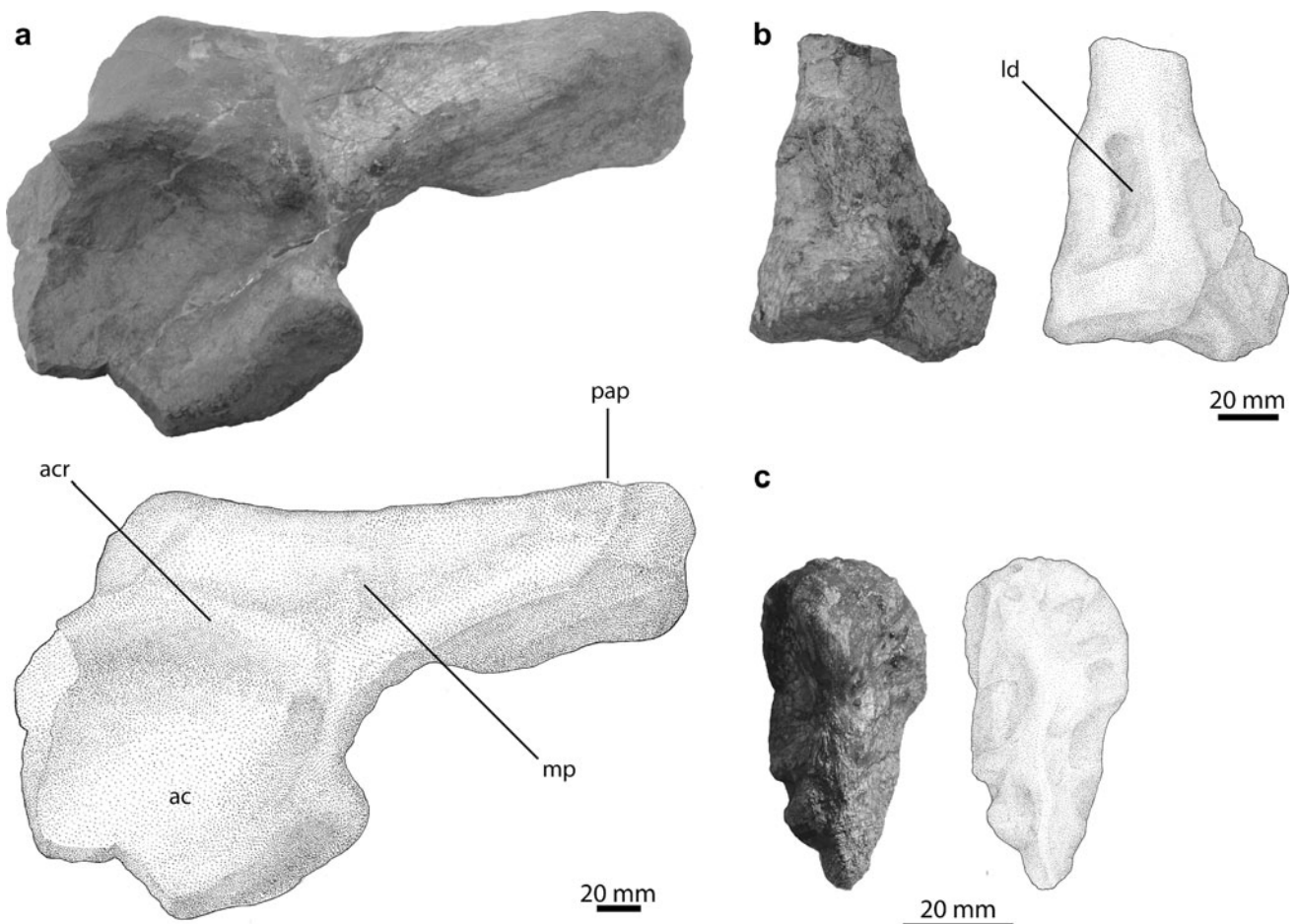
The sacral rib of the first vertebra emanates from the rim of the neural arch at the level of the zygapophyses and broadens laterally, giving it a flattened, club-like shape. The second sacral rib is more slender near its contact with the centrum and angled posteriorly. Laterally, it expands to a wing-like, flat element. In contrast to the nearly horizontal anterior counterpart, it inclines anteroventrally, and its posterior part is expanded medially. The size of their articulation surfaces fits well with the preserved right ilium. The transverse process of the first caudal is short and did not contribute to the pelvis.

With two sacral vertebrae *Stagonosuchus nyassicus* still retains a plesiomorphic condition for Archosauria (Gauthier 1986; Benton 1999) and several rauisuchian taxa,

such as *Ticinosuchus ferox* (see above), *Postosuchus kirkpatricki* (Long and Murry 1995), and *Prestosuchus chiniquensis* (von Huene 1942). Three sacral vertebrae have been reported for *Batrachotomus kupferzellensis* and *Teratosaurus suevicus* by Gower and Schoch (2009), whereas poposauroids possess three or more sacrals, which are also co-ossified or fused (Alcober and Parrish 1997; Nesbitt 2007; Weinbaum and Hungerbühler 2007).

#### Pelvic girdle

The pelvis and in particular the ilium of *Stagonosuchus nyassicus* have been discussed by Gower (2000) and subsequently by Gebauer (2004) in her revision, including a brief comparison to *Ticinosuchus ferox*, *Batrachotomus kupferzellensis* and *Postosuchus kirkpatricki*. The right ilium of the larger specimen (GPIT/RE/3831-20) and the left ilium of the smaller specimen (GPIT/RE/3832-11) (Fig. 8a) are preserved, and both are characteristic in the absence of a vertical ridge or swelling above the



**Fig. 8** *Stagonosuchus nyassicus* von Huene, 1938. **a** Left ilium (GPIT/RE/3832-11) in lateral view. **b** Left fibula (GPIT/RE/3831-19) in posteromedial view. **c** Rausuchoidea indet., caudal osteoderm

(GPIT/RE/7287). Abbreviations: *ac* acetabulum, *acr* acetabular rim, *ld* lunate depression, *mp* medial protuberance, *pap* postacetabular process

supracetabular rim, although Gower (2000) mentioned a “weakly defined ridge” on the smaller ilium. A similar faint ridge is visible also on the right ilium, but because this is only weakly expressed, its presence remains a subject of interpretation. However, a more diagnostic feature can be found on the postacetabular process of the iliac blade in form of a conspicuous boss-like protuberance (Fig. 8a). It is located centrally on the proximal half of the postacetabular process and projects laterally. Three small ridges radiate from it, bounding shallow depressions between them. As this structure is present on the ilia of both the lectotype and the paralectotype, it is unlikely to be a diagenetic effect. Long and Murry (1995) illustrated a similar protuberance on an ilium of *Postosuchus kirkpatricki* (UMMP 7266), although it is unclear if this is a preservational artefact or ontogenetically variable, as it is not visible in other ilia of this species.

The ischia of *Stagonosuchus nyassicus* are only known from the smaller specimen (GPIT/RE/3832-13). They are fused along the medioventral margin and form a crest similar to that in *Ticinosuchus ferox* and *Prestosuchus chiniquensis* (see above), although it is limited to the proximal part of the shaft below the obturator blade. Distally, the single ischia split up, and they are only connected medially in *Stagonosuchus nyassicus*. Both ischia bear an additional short ridge or crest on the lateral surface. It extends from below the acetabular rim and occupies the upper half of the shaft. This ridge is strongly developed and possesses a rounded margin. Anteriorly and posteriorly, it is bordered by a deep groove. A hunched protuberance is visible anterior to the ridge just below the extension of the obturator blade. These ventrolateral protuberances as well as the longitudinal ridge are equally expressed on both ischia. Nesbitt (2005) reported a comparable ridge on the ischium of *Arizonasaurus babbitti*, and it is also present, though more faintly, in *Prestosuchus chiniquensis* and possibly in *Ticinosuchus ferox* (see above).

#### Fibula

A 9-cm-long fragment of a long bone (Fig. 8b), belonging to the smaller specimen (GPIT/RE/3831-19), was originally identified by von Huene (1938) as either the right distal or the left proximal part of a radius. It consists of an expanded epiphyseal part with a lunate cross section and a short, circular diapophyseal part of approximately 3 cm, where it is broken. At one side the epiphysis is concave. In his original description von Huene (1938) was non-committal regarding the orientation of this element. He considered the expansion of the diaphysis to be indicative of a distal radius, although it is not considerably expanded. Moreover, broad and circular (proximal and distal) shafts are also present in other long bones in archosaurs,

including ulna, tibia and fibula. On the other hand, von Huene (1938) favoured a proximal position so that the concave side would articulate with the head of the ulna. Gebauer (2004) followed this assumption in her revision of the material. Again the mere presence of an articulation surface alone is not representative for the proximal part of the radius, as a similar contact occurs between fibula and tibia.

A comparison with *Prestosuchus chiniquensis* (BSPG AS XXV 11b) and *Rauisuchus tiradentes* (BSPG AS XXV 90) suggests that this element is actually the distal end of the left fibula. Although this part is often reduced in size in archosaurs, several raiisuchoids possess a similarly expanded fibula with a concave medial side, including *Postosuchus* (Weinbaum 2002; Peyer et al. 2008), *Fasolasuchus tenax* (Bonaparte 1981), *Arganasuchus dutuiti* (Jalil and Peyer 2007), as well as *Prestosuchus chiniquensis* (BSPG AS XXV 11b) and *Rauisuchus tiradentes* (BSPG AS XXV 90, Lautenschlager 2008). The medial concavity would hence articulate with the fibular facet of the astragalus and possibly the tibia. Of the bigger specimen of *Stagonosuchus nyassicus* only the proximal parts of both tibiae are preserved, and the tarsal complex is unknown.

The most conspicuous feature of the fibula of *Stagonosuchus nyassicus* is the presence of a deep depression on the posteromedial side. It is approximately 4 cm long and 1 cm broad, and covers the epiphyseal part up to the shaft. A similar depression can be found in the fibula of *Rauisuchus tiradentes* (Lautenschlager 2008), identified as a lunate depression, and *Prestosuchus chiniquensis* (BSPG AS XXV 11b). Although the fibula of *Rauisuchus tiradentes* is considerably altered by diagenesis and amalgamated with the tibia and the astragalus, the depression along the anterior side is clearly visible. In addition to the major part of the hind limb the fibula is well preserved in *Prestosuchus chiniquensis*, which indicates a similar morphology for *Stagonosuchus nyassicus*. On the lateral side the fibula of *Stagonosuchus nyassicus* bears a further small depression with a circular outline.

#### Caudal osteoderm

Among the material of *Stagonosuchus nyassicus*, we found a single osteoderm (Fig. 8c), which has not been described or illustrated before. von Huene (1938) mentioned numerous poorly preserved elements, which he did not consider in his description, but the osteoderm holds no reference or collection number. Only the probable location number “282” has been written on the element, indicating its origin from the “Upper Bonebed” in Njalila. Nowack (1937) divided the “Upper Bonebed” into three sections with a thickness of approximately 25 m each. If the respective



number is indeed the location number, the osteoderm would come from the stratigraphically slightly older middle section of the “Upper Bonebed” than the type material of *Stagonosuchus nyassicus* from the upper section.

The osteoderm has a length of 5 cm and a maximal width of 2.6 cm. Posteriorly, it tapers to a point, which gives the whole element a symmetrical, leaf-shaped morphology. Along the longitudinal axis, it is strongly arched. The dorsal surface is rough, but without obvious sculpturing. A ridge runs longitudinally from the posterior end, where it is prominently developed, to the anterior end, where the ridge becomes less obvious and merges with the pointed tip of the osteoderm. There are no signs of articulation facets on the lateral margins, which indicate that the osteoderm originated from a single median row of osteoderms and was not part of a paramedian series. Whereas a paramedian row of osteoderms is found along or attached to the cervical and dorsal vertebrae in raiisuchian archosaurs (Peyer et al. 2008; Gower and Schoch 2009; Trotteyn et al. 2011), single median rows of symmetrical osteoderms originated from the tail section (Peyer et al. 2008). Symmetrical and pointed osteoderms, similar to the one in question, are present in *Ticinosuchus ferox* from the posterior part of the tail dorsally and ventrally, *Prestosuchus chiniquensis* (UFRGS-PV0629T), and *Raiisuchus tiradentes* (Lautenschlager 2008).

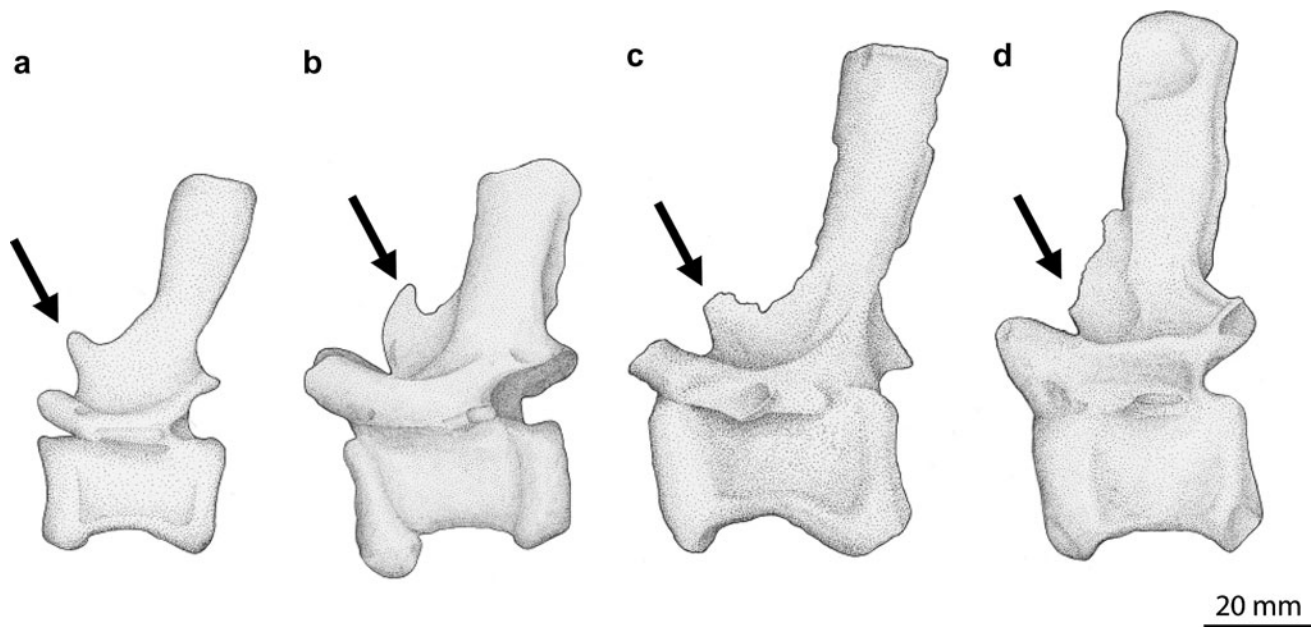
As no osteoderms are known from *Stagonosuchus nyassicus*, no unequivocal assignment of the single element can be made. Its size would roughly correlate with the

caudal vertebrae of the paralectotype, and the kind of preservation is similar to the type material, and the presence of spine tables in the dorsal vertebrae implies the presence of osteoderms in *Stagonosuchus nyassicus*. Other archosauromorph taxa known from the Lifua Member, including ‘*Teleocrater*’, ‘*Mandasuchus*’ (Charig 1956) and *Parringtonia* (von Huene 1939) are considerably smaller, and an attribution to the respective material is most unlikely. The probable differences in location and therefore stratigraphic age, on the other hand, rule out the possibility that the osteoderm was part of the paralectotype of *Stagonosuchus nyassicus*. Therefore we only assign this osteoderm to an indetermined raiisuchoid taxon (*Raiisuchoida* indet., new collection number GPIT/RE/7287).

### Discussion of special characters in *Ticinosuchus ferox*, *Stagonosuchus nyassicus* and further raiisuchian archosaurs

#### Accessory neural spines in caudal vertebrae

A closer examination of caudal vertebrae in raiisuchian archosaurs shows that an additional neural spine is present in several taxa. The most prominent and best preserved are found in *Raiisuchus tiradentes* (Fig. 9b) (Lautenschlager 2008) and *Ticinosuchus ferox* (Fig. 9a), where the distribution of this feature along the caudal vertebral column can be observed as an example. The accessory neural spine is



**Fig. 9** Accessory neural spines in the caudal vertebrae of different raiisuchoid taxa **a** *Ticinosuchus ferox* (PIZ T 2817). **b** *Raiisuchus tiradentes* (BSPG AS XXV 81). **c** *Polonosuchus silesiacus* (ZPAL Ab

III 563). **d** *Batrachotomus kupferzellensis* (SMNS 80339). All in left lateral view. Arrows indicate accessory neural spines



generally found in the mid-caudal vertebrae. It starts at the sixth caudal in *Ticinosuchus ferox* and can be traced up to the 35th to 40th vertebrae. Within this range, the accessory neural spine varies in its morphology and position. It is developed as a simple protrusion or step at the lower anterior margin of the main neural spine in the anterior caudals, whereas it forms a more discrete and pointed element in the mid-caudals. It is completely separated from the main neural spine in the posterior caudal vertebrae. With the disappearance of the main neural spine, the accessory neural spine is also lost in the posterior caudals. Although *Ticinosuchus ferox* is the only known rauisuchian archosaur with a nearly complete and articulated vertebral column, the comparison of known taxa with accessory neural spines further suggests not only different states due to their anatomical position, but also considerable interspecific variations in the morphology of this feature. For instance, *Rauisuchus tiradentes* shows a large hook-like accessory neural spine, making up a large part of the anterior margin of the main neural spine (BSPG AS XXV 81, Lautenschlager 2008), in contrast to the smaller and rounded morphology in *Ticinosuchus ferox*. Though only a single caudal of *Rauisuchus tiradentes* is completely preserved with such an accessory neural spine, two further fragmentary caudal vertebrae (BSPG AS XXV 79, 82) show remains of it. These vertebrae can tentatively be referred to the mid-caudal section approximately between the 15 and 25th caudal.

Further examples of caudal vertebrae with an accessory neural spine are only known from fragmentary vertebrae and pieces. Thus, the caudal vertebrae of *Polonosuchus silesiacus* (ZPAL Ab III 563, Sulej 2005) show only remnants of where an actual accessory neural spine had to be attached (Fig. 9c). The preserved vertebral section consists of nine articulated caudals from the anterior part of the tail. The anterior elements still possess a comparably high and narrow main neural spine with an obvious broken edge at its lower anterior margin, where the accessory neural spine was located. The three posterior caudal elements show a beginning reduction in size and a posterior shift of the main neural spine. The remains of the accessory neural spines are more distinctly separated from it, so that these vertebrae may already belong to the mid-caudal series (approximately the 20–30th). The indicated pattern of arrangement is therefore similar to that described for *Ticinosuchus ferox*, though the actual morphology and outline are lost in *Polonosuchus silesiacus*. In anterior view the basal fragment of the accessory neural spine is broadened between the prezygapophyses and seems to bear a longitudinal depression.

A comparable morphology has been illustrated by Krebs (1965) for an isolated fragment of a neural spine, referred to *Stagonosuchus nyassicus* by von Huene (1938). Gebauer

(2004) attributed it to a mid-caudal to posterior vertebrae, though its position and allocation are tentative. The remaining caudal vertebrae of *Stagonosuchus nyassicus* belong to the anterior tail section in both preserved specimens and bear no accessory neural spine.

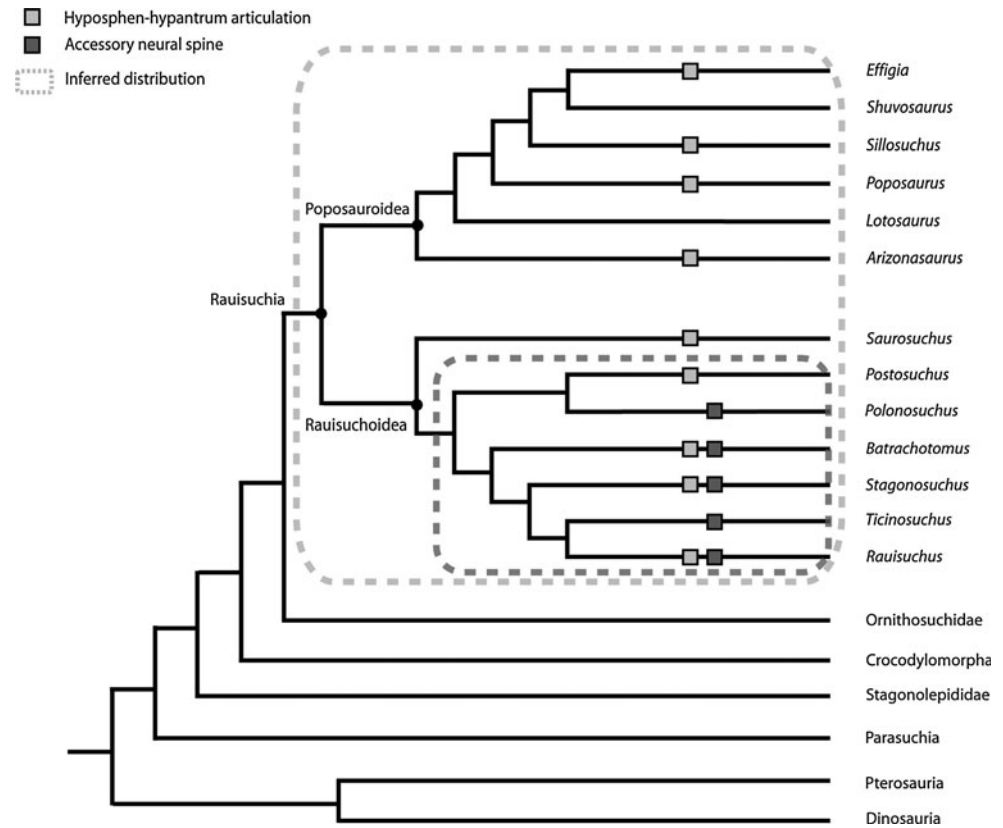
In *Batrachotomus kupferzellensis* most caudal vertebrae are incompletely preserved, lacking the main neural spine. Only one example from the mid-caudal series shows a broken edge along the lower third of the neural spine (SMNS 80339, Gower and Schoch 2009, Fig. 1K), which indicates the presence of an accessory neural spine (Fig. 9d). Its morphology compares well with the short, step-like spines of the anterior caudal vertebrae in *Ticinosuchus ferox*.

A single posterior caudal vertebrae belonging to the hypodigm of “*Prestosuchus*” *loricatus* (BSPG AS XXV 16) bears a horizontal fracture surface anterior to the main neural spine, where an accessory neural spine was probably attached to. They are connected by a low and thin lamella. The position and morphology are consistent with that of the caudal vertebrae of *Ticinosuchus ferox*.

As shown above, accessory neural spines are limited to approximately 30 vertebrae within the whole vertebral column and suffer from incomplete preservation, as they are easily broken and lost postmortem. Therefore this feature has so far only been observed in comparably few rauisuchian specimens or not been noticed. Although accessory neural spines are also known from a wider range of archosaurs, such as ornithosuchids (Krebs 1976), sphenosuchids (Crush 1984) or Thalattosuchia (*Geosaurus*, *Metriorhynchus*, (Krebs, 1965)), their distribution within the Rauisuchia seems to be limited to the Rauisuchoidea. Posauroidea do not show this feature (as far as respective caudal elements are preserved), which could mean that it might be indicative as a rauisuchoid synapomorphy. A simplified phylogeny of Rauisuchia based on phylogenetic analyses from Lautenschlager (2008, 2009) maps the distribution of this character (Fig. 10).

The function of such an accessory neural spine has been discussed by Krebs, who proposed an additional attachment point for the interspinal ligaments (Krebs 1965, p. 49). In fossil and extant crocodylomorphs the ligament connection between the single caudal vertebrae is achieved mainly by two types of ligaments: The *ligamentum suprspinale* connects the dorsal margins of the neural spines, whereas the *ligamentum elasticum interlaminare* extends between the posterior margin and the anterior margin of the neural spines of subsequent caudals (Frey 1988; Schwarz-Wings et al. 2009). As the distance between the main neural spines increases towards the posterior tail section, such an accessory neural spine would provide the possibility for a stable connection between the single caudal vertebrae in rauisuchoids. The presence of postspinal laminae in the

**Fig. 10** Simplified phylogeny of Rausuchia and distribution of discussed characters. Based on Lautenschlager (2008, 2009)



caudal vertebrae of *Rausuchus tiradentes* (Lautenschlager 2008) would further serve as an enlarged attachment point for the *ligamentum elasticum interlaminae*, and hence form a firm ligament connection, at least in the anterior tail section. The postspinal laminae might also have the same function as the laminae spinosae in the vertebrae of *Alligator mississippiensis* and indicate the presence of thin cartilaginous plates to additionally strengthen the vertebral connection (Frey 1988). In *Rausuchus tiradentes* (Lautenschlager 2008), *Batrachotomus kupferzellensis* (Gower and Schoch 2009) and *Polonosuchus silesiacus* (ZPAL Ab III 563, Sulej 2005), the dorsal margins of the neural spines are broadened laterally, indicating the presence of a larger *ligamentum supraspinale* (Schwarz-Wings et al. 2009). This shows that the tail base and the anterior part of the tail, where such accessory structures are present, was probably firmly stabilised against dorsoventral and rostroterminal shear (Schwarz-Wings et al. 2009). Krebs (1965) explained this arrangement with the need to keep the body balanced during fast locomotion and as a possible means of defence. The latter assumption seems rather arbitrary, whereas the long tail, which equals the body in length in *Ticinosuchus ferox* and *Batrachotomus kupferzellensis*, could act as a taut and rigid counterbalance. In combination with the development of an erect gait in Rausuchia, a bracing of the tail might have been an important prerequisite. Schwarz-Wings (2009) showed that

the lack of such a stabilisation would restrict high-walk and gallop in crocodylomorphs. The fact that accessory neural spines are missing in the presumed bipedal poposauroids would indicate, though, that their tail had to be more flexible and movable for bipedal locomotion.

#### Hyposphene-hypantrum articulation in dorsal vertebrae

Accessory hyposphene-hypantrum articulation in trunk vertebrae has originally been described in saurischian dinosaurs (Sauropodomorpha and several members of Theropoda) (Gauthier 1986), providing additional stability for the vertebral column. With the exception of Rausuchia, this type of articulation between the single vertebrae is nearly unknown in all other extant and extinct groups of Pseudosuchia (Apesteguía 2005). Within Rausuchia this feature seems to be equally distributed between the quadrupedal rausuchoids [e.g. *Batrachotomus* (Gower and Schoch 2009); *Stagonosuchus* (see above); *Saurosuchus* (Trotteyn et al. 2011); *Postosuchus* (Peyer et al. 2008)], the bipedal poposauroids [*Effigia*, *Sillosuchus* (Nesbitt 2007); *Puposaurus* (Weinbaum and Hungerbühler 2007)], as well as the peculiar sail-backed forms [*Arizonasaurus* (Weinbaum and Hungerbühler 2007); *Hypselorhachis* (Butler et al. 2009)], although without a clear pattern of distribution (Fig. 10). This is complicated by the incomplete fossil material of most specimens.

Within Archosauria, only Rausuchia in the crurotarsan branch and Dinosauria in the avemetatarsalian branch show this feature (Apesteguía 2005). As closer relationships between both groups can be ruled out, this might be an effect of convergence. Rausuchians and dinosaurs have most likely occupied the same ecological niches and independently evolved an erect gait by modification of the pelvis/femur configuration (Benton 2004). The erect posture has been discussed as critical for the successful evolution and diversification of these groups, allowing for fast locomotion and increased agility (Benton 1984). In several crurotarsan groups, an extensive set of dorsal osteoderms provided additional stabilization of the axial skeleton (Frey 1988; Schwarz-Wings et al. 2009; Buchwitz and Voigt 2010). In raiisuchoids, however, the osteoderms are limited to a paramedian or single row, whereas they are completely absent in poposauroids. The development of additional hyposphene-hypantrum articulations in the dorsal vertebrae—similar to the bracing of the tail (see above)—are therefore linked to the requirements of a firm and rigid connection of the dorsal vertebral column (Wilson and Carrano 1999). Thus, such a supporting system could have been adapted to compensate for the increased strain forces resulting from a different mode of locomotion. To date, no investigations exist regarding the functional significance among erect gait, bidepalism and the presence of hyposphene-hypantrum articulations, but the facts that theropod dinosaurs (Coria et al. 2002) show both features and, with some minor exceptions, do not possess osteoderms (Gilmore 1920) indicate a possible connection.

## Conclusions

The reassessment of *Ticinosuchus ferox* and *Stagonosuchus nyassicus* shows that both taxa possess a suite of characters that have not been recognised before. The presence of vertebral laminae and fossae might prove to be of (phylogenetic) importance, as more of these structures become known in raiisuchian archosaurs.

The revised osteology, especially in the pectoral and pelvic girdle of *Ticinosuchus ferox*, corrects several inaccurate details of the anatomy, which have been persistently used for morphological comparisons in the past (e.g. Benton and Clark 1988; Parrish 1993; Gebauer 2004; Peyer et al. 2008). The size of the coracoids and the expansion of the scapula in *Ticinosuchus ferox* are considerably smaller than originally described. Both ischia have been shown to be present and fused along the anteroventral margin, allowing for a more accurate reconstruction of the pelvis.

The presence of additional infraprezygapophyseal and infrapostzygapophyseal laminae in the eighth cervical vertebra of *Stagonosuchus nyassicus* is, among other

characters, an autapomorphy for this taxon and included in a revised diagnosis. The correctly identified fibula indicates a character state uniting *Stagonosuchus nyassicus*, *Raiisuchus tiradentes* and *Prestosuchus chiniquensis*, although this has to be tested in a phylogenetic analysis, results of which will be reported elsewhere (Desojo and Rauhut, submitted). The identification of a caudal osteoderm of an indetermined raiisuchoid would either suggest the presence of osteoderms in *Stagonosuchus nyassicus* or the presence of another large raiisuchoid taxa in the Lifua Member.

The new anatomical details of the presented taxa show that raiisuchian archosaurs had a high diversity during the Middle Triassic, including different morphotypes, which probably resulted from ecological differences. Currently we can distinguish two morphotypes within Rausuchoidea: small and slender forms with long necks, such as *Ticinosuchus ferox*, and larger, stoutly built taxa with short necks like *Stagonosuchus nyassicus*. The Poposauroidea on the other hand were generally a group of smaller, gracile animals, which show equally high degrees of specialisation, such as the development of elongated dorsal neural spines (e.g. *Arizonasaurus*) or herbivorous diet (e.g. *Lotosaurus*). This high level of diversification indicates that the origin of Rausuchia occurred during the Early Triassic or even sooner. Furthermore, special osteological characters, such as accessory neural spines in the caudal vertebrae or a hyposphene-hypantrum articulation, suggest that the achievement of erect gait and/or bipedalism necessitated a specialisation not only of the hind limb and pelvis, but also of the vertebral column.

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