The Axial and Posterior Appendicular Morphology of the First Theropod Skeleton (Saurischia, Dinosauria) of Switzerland (Late Triassic; Frick, Canton Aargau)

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1. Summary

In 2006 a dinosaur was discovered in the Quarry Gruhalde in Frick (Canton Aargau) from sediments near to the Triassic-Jurassic boundary. This fossil represents the first theropod skeleton of Switzerland. A morphological comparison of this specimen with other Late Triassic and Early Jurassic theropod material indicates the Swiss theropod is a member of the Family Coelophysidae consisting of the American *Coelophysis bauri* and *Syntarsus kayentakatae,* and the African *C. rhodesiensis*. The presence of open sutures in the dorsal, sacral, and caudal vertebrae, the scapulocoracoid, and between all the elements of the pelvic girdle supports the inference that the Frick theropod is of juvenile to subadult age. In addition, the very anterior arrangement of the first chevron and the narrow space between the proximal parts of the ischia suggest a male specimen. Subsequently, a phylogenetic analysis has been performed in order to clarify the position of the newly discovered theropod within the Family Coelophysidae and to neglect any closer relationship to *Liliensternus liliensterni* which is geographically and chronologically similarly distributed. The results put the Swiss theropod closest to the only remaining species of *Syntarsus*: *S. kayentakatae*. Therefore, the new material is considered to represent the first coelophysid dinosaur of Switzerland.

1. Zusammenfassung

Im Jahr 2006 wurde in der Tongrube Gruhalde, die sich in der Aargauer Gemeinde Frick befindet, das erste Schweizer Theropoden-Skelett entdeckt. Das Material stammt aus Sedimenten nahe der Trias/Jura-Grenze. Der morphologische Vergleich des axialen sowie des Appendikular-Skelettes mit anderen Theropoden-Funden aus der Späten Trias und dem Frühen Jura zeigt, dass der neue Fund zur Familie Coelophysidae gehört. Die Familie Coelophysidae umfasst die Taxa *Coelophysis bauri* und *Syntarsus kayentakatae* aus Amerika sowie die Art *C. rhodesiensis* aus Afrika. Noch offene Suturen an den Dorsal-, Sacral- und Caudalwirbeln, und die noch nicht verschmolzenen Beckenelemente, legen die Vermutung nahe, dass es sich bei dem Fricker Theropoden um ein juveniles bzw. subadultes Individuum handelt. Die ausgesprochen anteriore Anordnung des ersten Hämalbogens und der enge Abstand zwischen den proximalen Bereichen der beiden Ischia deuten auf ein männliches Exemplar hin. Das Ergebnis der phylogenetischen Analyse stellt den Schweizer Theropoden ebenfalls in die Familie Coelophysidae und schliesst eine nähere Verwandtschaft mit *Liliensternus liliensterni* aus, der eine ähnliche geographische und chronologische Verbreitung hat. Damit handelt es sich bei dem neuen Theropoden um den ersten Schweizer Nachweis eines Coelophysiden. Seine Schwesterart ist *Syntarsus kayentakatae* aus Amerika.

2. Institutional and anatomical Abbreviations

AMNH	American Museum of Natural History, New York, America
AMNH 2705	*Coelophysis bauri*, discovered in 1881 in Ghost Ranch Quarry by David Baldwin; first described by Cope in 1887 as belonging to *Tanystrophaeus longicollis*. Huene identified it in 1915 as a fragment of *Coelophysis bauri*.
AMNH 2708	*Coelophysis bauri*, discovered in 1881 in Ghost Ranch Quarry by David Baldwin; first described by Cope in 1887 as belonging to *Tanystrophaeus longicollis*. Huene identified it in 1915 as a fragment of *Coelophysis bauri*.
AMNH 7223	*Coelophysis bauri* (adult: robust morphotype), first described by Colbert 1989.
AMNH 7224	*Coelophysis bauri* (adult: gracile morphotype), first described by Colbert 1989.
AMNH …	Other fragmentary *Coelophysis bauri* specimens stored in the American Museum of Natural History, New York; described by Colbert 1989.
YPM	Yale Peabody Museum, New Haven
YPM 41197	*Coelophysis bauri*, excavated by the American Museum of Natural History, America; described by Colbert 1989.
TM	Tyrell Museum of Palaeontology, Drumheller, Alberta, America
TM 84-63-33	*Coelophysis bauri*, excavated by the Carnegie Museum, described by Colbert 1989.
MNA	Museum of Northern Arizona, Flagstaff, Arizona, America
MNA V2623	Holotype of *Syntarsus kayentakatae* (adult), first described by Timothy Rowe (1989).
TMM	Texas Memorial Museum, Austin, Texas, America
TMM 43688-1	*Syntarsus kayentakatae*; synonym of the field number TR 97/12 (subadult) in the master thesis of Ron Tykoski (1998) and my work; TR = field numbers of specimens collected under direction of Timothy Rowe.
QG	Queen Victoria Museum, Salisbury, Rhodesia, Africa
QG1	Holotype of *Coelophysis rhodesiensis* (adult), first described by Raath (1969).
QG445	*Coelophysis rhodesiensis* specimen, described by Raath (1977) *.
QG691	
QG696	

* *"Note: since this work was carried out, all natural science collections of the National Museums and Monuments of Zimbabwe have been centralised at the Natural History Museum of Zimbabwe, in Bulawayo. The Coelophysis bauri material retains its original registration numbers, although the registration prefix now differs. Enquiries should be directed to the Curator of Palaeontology, Natural History Museum of Zimbabwe, P O Box 240, Bulawayo, Zimbabwe" (Raath 1977).*

PVL	Fundación 'Miguel Lillo', San Miguel de Tucumán, Argentina, America
PVL 2566	Holotype of *Herrerasaurus ischigualastensis* (adult); first described by Reig 1963
UCMP	University of California Museum of Paleontology, America
UCMP 37302	Type specimen of *Dilophosaurus wetherilli*; first described by Welles 1984
UCMP 32101	Holotype of *Segisaurus halli*; first described by Camp 1936
MB. R.	Museum of Natural History Berlin, Germany
MB. R. 2175	Number merges a small and a large *Liliensternus liliensterni*; first described by Huene 1934a
CM	Carnegie Museum, Pittsburgh, Pennsilvania, America
CM…	Holotype of *Lophostropheus airelensis* without collection number; first described by Larsonneur and Lapparent 1966
SMNS	Museum of Natural History Stuttgart, Germany
SMNS 12591	Holotype of *Procompsognathus triassicus*; first described by Fraas 19

aaf	anterior articulation facet
ab	anterior blade
ac	acetabulum
ach	anterior chonos
af	acetabular fossa
al	anterior lamina
ap	anterior process
ash	anterior shoulder
at	antitrochanter
bf	brevis fossa
c	caudal vertebra
caf	cranial articulation facet
cat	component of antitrochanter
cauf	caudal fossa
cav	cavity
cp	cap
cr	caudal rim
craf	cranial fossa
crb	cervical rib
crf	cervical rib fragment
ct	capitulum
d	dorsal vertebra
di	diapophysis
dk	distal knob
dr	dorsal rib
e	emargination
f	fossa
g	gastralia
gp	gap
h	haemapophysis
ia	ischiadic apron
id	interdigitation
if	iliac facet
is	ischiadic shaft
isc	ischia
isf	ischial facet
isp	ischial peduncle
ldr	left dorsal rib

lf	longitudinal fossa
li	left ilium
lis	left ischium
lp	left pubis
lsr	left sacral rib
ltp	left transverse process
mr	median rim
na	neural arch
nc	neural canal
ncs	neurocentral suture
ns	neural spine
ofor	obturator foramen
p	pubis
pa	parapophysis
paf	posterior articulation facet
pap	pubic apron
pb	posterior blade
pf	pubic facet
pfen	pubic fenestrum
pl	posterior lamina
poz	postzygapophysis
pp	pubic peduncle
ppl	pubic plate
prz	prezygapophysis
ps	pubic shaft
psh	posterior shoulder
rdr	right dorsal rib
ri	right ilium
ris	right ischium
rp	right pubis
rsr	right sacral rib
rtp	right transverseprocess
s	sacral vertebra
sc	supraacetabular crest
sp	spine table
sr	sacral rib
sra	sacral rib & sacral transverse process attachment
stc	stomach content
tb	tuberculum
tp	transverse process
v	ventral
vg	ventral groove
vk	ventral keel
vr	ventral ridge

3. Introduction

The Keller AG in Frick (Canton Aargau, Switzerland) has several mine localities with limy, sandy, clayey and marly sediments. The famous quarry Gruhalde also in Frick is one such mine, which is the most productive dinosaur site of the whole country since decades. There, the most impressive horizon is built up with the Arieten- and the Angulaten-Limestones (see fig. 1) showing a thickness of approximately 3.5 m and bearing inter alia a diverse ammonite fauna of the Lias (MÜLLER, HUBER, ISLER, and KLEBOTH 1984; SANDER 1990; MEYER & FURRER 1995; SANDER 1999). Beneath these beds, there is the 'Insekten-Mergel' which is of Early Hettangian age (MÜLLER, HUBER, ISLER & KLEBOTH 1984; RIEBER 1985; SANDER 1990; MEYER & FURRER 1995) and represents the first horizon clearly recognizable as belonging to the Early Jurassic. The 'Insekten-Mergel' is underlain by a marly horizon called 'Obere Bunte Mergel', which is at times used for fabricating bricks. The first dinosaur remains were found at this horizon of the Rhaetian stage (Late Triassic) in 1961. In 1973, one of these findings was identified as a toe fragment of *Plateosaurus* (RIEBER 1985). Then, in 1976 the first excavations were accomplished by the preparator Urs OBERLI (RIEBER 1985).

Field activities have continued until today amongst others with the aid of financial support from the Fricker council. As a result of this engagement, the quarry Gruhalde has yielded several of the best preserved *Plateosaurus* skeletons during the last fifty years (classic dinosaur layer, approximately 10 m beneath the Triassic-Jurassic boundary). Beside these herbivorous dinosaurs, other vertebrate fossils have been recovered often as a result of elutriating the marl: these include teeth of the shark *Lissodus sp.* and the teleostian *Lepidotes sp.,* toothplates of the lungfish *Ceratodus sp.*, and teeth of mammal-like reptiles. Additionally several isolated small teeth of theropod dinosaurs have been collected during this period (RIEBER 1985; SANDER 1990).

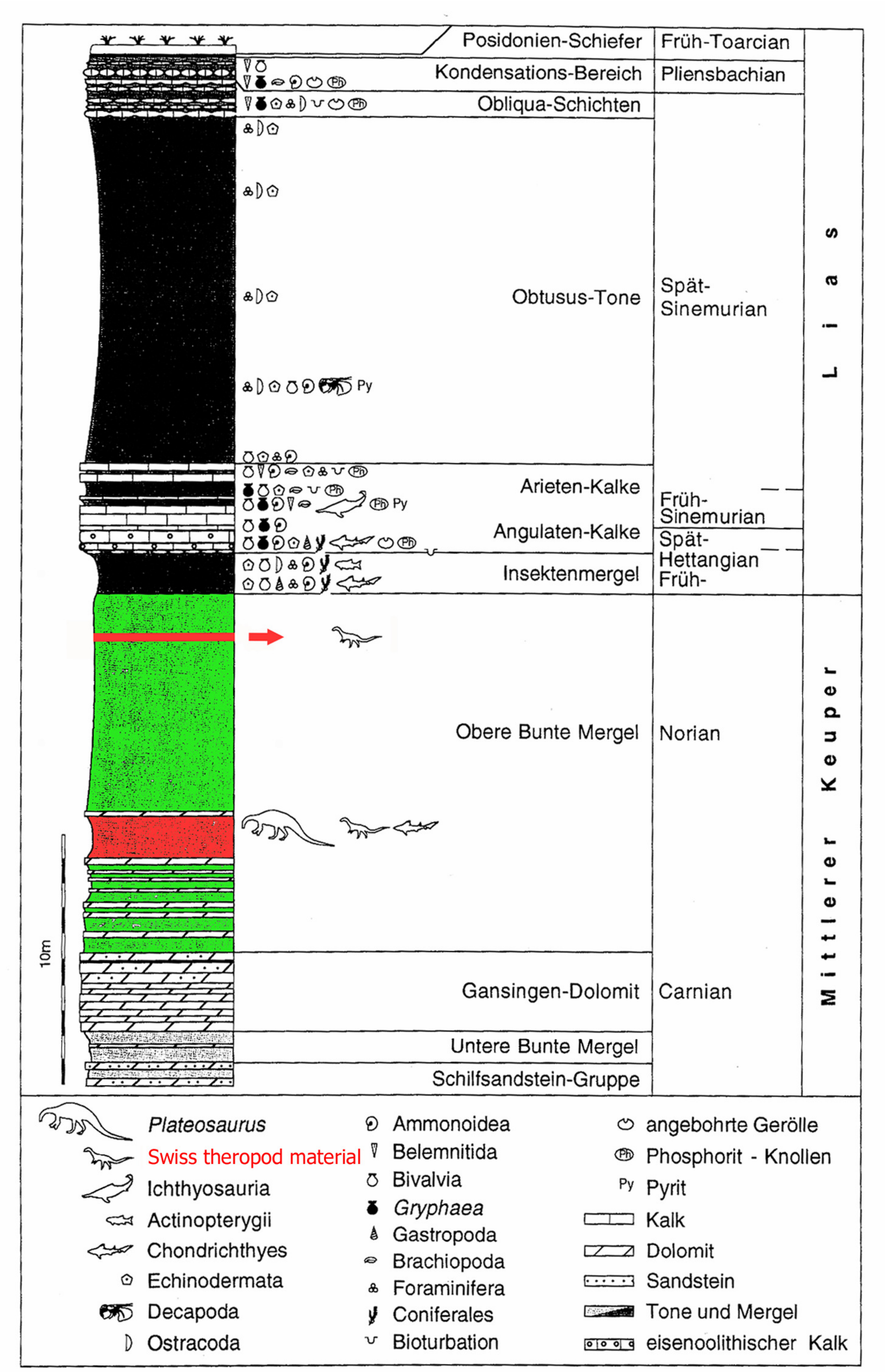


Figure 1: after MEYER & FURRER (1995): modified stratigraphic profile of the quarry Gruhalde located in Frick (AG)

More theropod material was discovered in April 2006 by Michael Fischer, an amateur and fossil collector from Basel. This discovery was a sensation for palaeontologists, as well as for the media (‘Neue Fricktaler Zeitung’; ‘Aargauer Zeitung’; ‘Schweizer Fernsehen’), because it represents the first carnivorous dinosaur skeleton ever found in Switzerland.

The preparators Ben Papst and Esther Premru worked on the excavation underneath the Triassic-Jurassic boundary supported by the 'Saurierkommission' of the Fricker council, and retrieved parts of a postcranial skeleton. The remains were discovered in a higher fossil horizon than the classic plateosaur findings also belonging to the 'Obere Bunte Mergel'. These beds, the new dinosaur layer, are almost eight meters above the initial sites of discovery (ca. two meters underneath the 'Insekten-Mergel'). In the range of the Triassic-Jurassic boundary, there is a stratigraphic gap (hiatus) spanning approximately 5 million years (MEYER & FURRER 1995; FURRER pers. communication). Thus, the age of the Swiss theropod material cannot be determined exactly, being assessed as Rhaetian or less probably as Early Hettangian (see «6. Systematic Palaeontology»).

4. Material and Methods

Descriptions and drawings are made of the preserved bones of the axial and posterior appendicular skeleton of the Swiss theropod (see also «Portrait of the Swiss theropod», fig. 41, in appendix). The material is compared to other theropod specimens of the Late Triassic and the Early Jurassic. These investigations will provide sufficient information regarding the systematic position of the Swiss theropod material.

4.1. Specimen

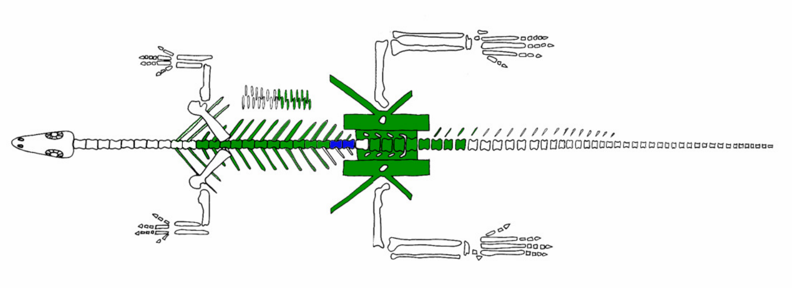
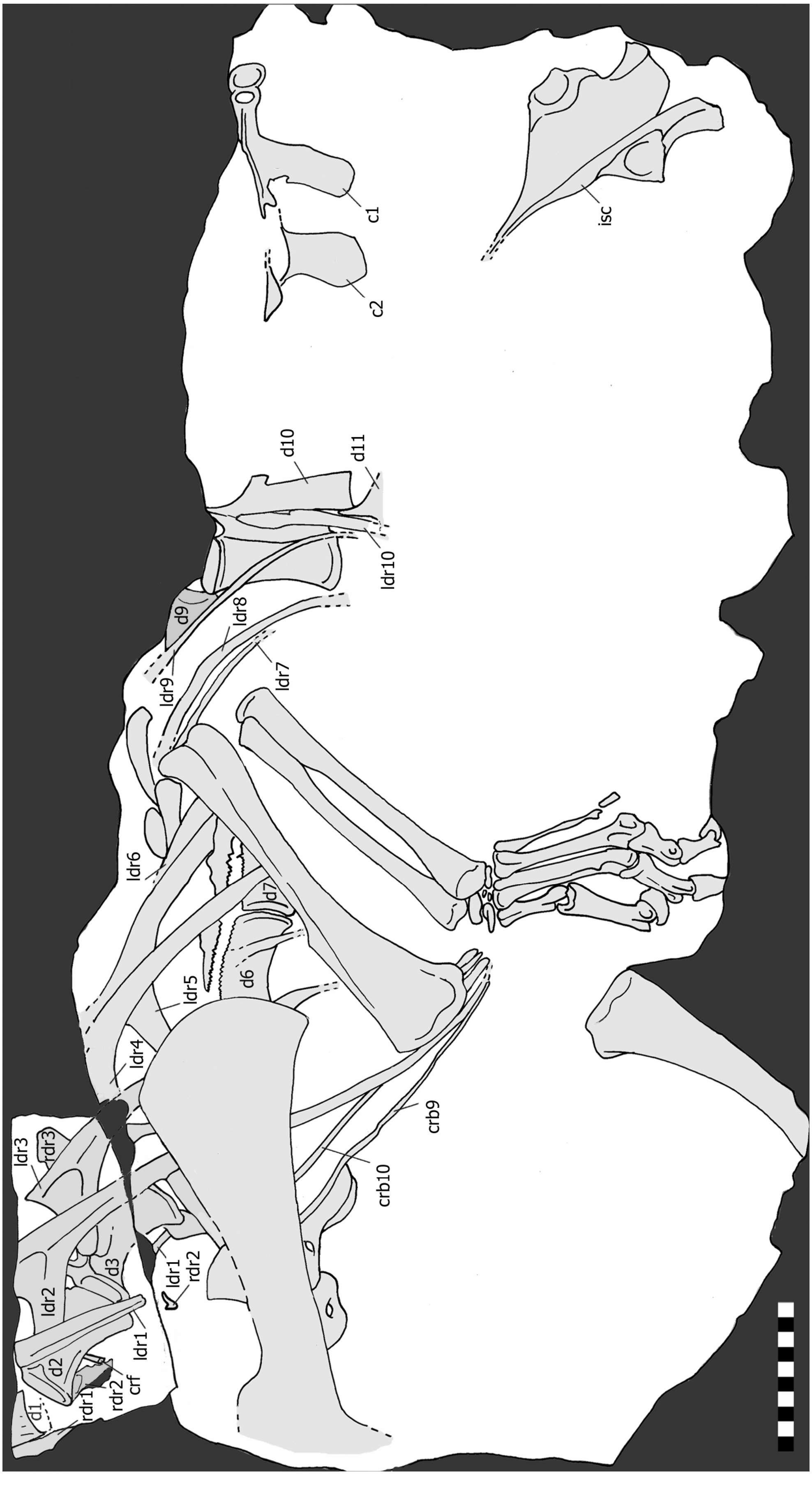


Figure 2: modified from Raath 1977; shows all the available skeletal elements which are important for this study. The green marked bones are visible to the naked eye, whereas the blue ones can only be seen in the CT.

The Swiss theropod material (fig. 2-6) consists of two almost complete arms with their pectoral girdles, the ilia, ischia and pubes, 13 dorsal, four sacral and four proximal caudal vertebrae with their chevrons. Additionally, there are two cervical and several dorsal rib fragments, gastralia and the stomach content. The arms, the pectoral girdle, and the stomach content are the master thesis subject of Lui Unterrassner.

The skeletal elements are often disarticulated and strongly displaced from their natural position. They are arranged in four slabs subsequently named as A, B, C, and D, whereas only three are representative for this work (A, B, D). The largest slab A embeds partly the left and the right arm, both scapulae and coracoids, 11 dorsal vertebrae associated with dorsal rib portions (left dorsal rib 1 to 10; right dorsal rib 1 to 2 and 4 to 13), fragments of two cervical ribs (number 9 and 10), four caudal vertebrae with their haemapophyses, both ischia and pubes, gastralia as well as the stomach content. Slab B contains the three most anterior located dorsal vertebrae (number 1 to 3) sharing the last one with slab A. Dorsal rib portions are also situated on slab B (number 1 to 3 of the left, number 1 and 2 of the right side), fitting perfectly well to slab A, leaving only space for a few millimetres between them. Slab D displays both ilia and four sacral vertebrae.

The preserved dorsal ribs are consistent with the general dorsal vertebrae number of examined theropod dinosaurs. Concerning the number of the sacral and caudal vertebrae, the same formula as in the genera *Coelophysis* and *Syntarsus* is assumed. Therefore, ten cervical, 13 dorsal, five sacral and about 40 caudal vertebrae may have built up the vertebral column of the theropod under study.


c1
c2
isc
d10
d11
ldr10
d9
ldr8
ldr7
ldr9
ldr6
d7
d6
ldr5
ldr4
crb9
crb10
ldr3
rdr3
d3
ldr1
rdr2
ldr2
ldr1
d2
crf
rdr2
rdr1
d1

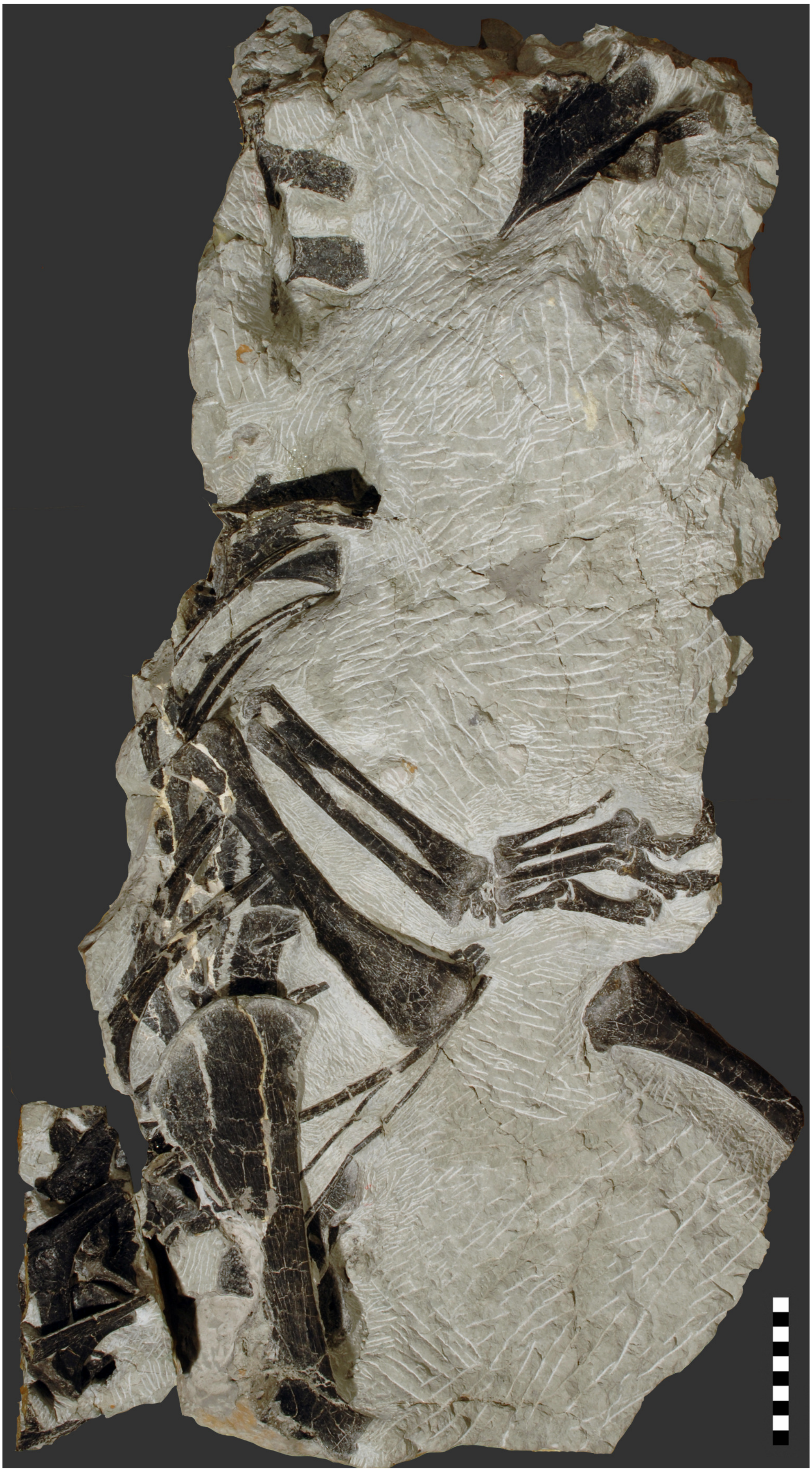


Figure 3: upper side of slab A and B showing amongst other things the ischia, caudal vertebra 1 and the neural arch of caudal 2, several elements of dorsal vertebra 1 to 11 with their corresponding ribs (scale bar 50 mm).

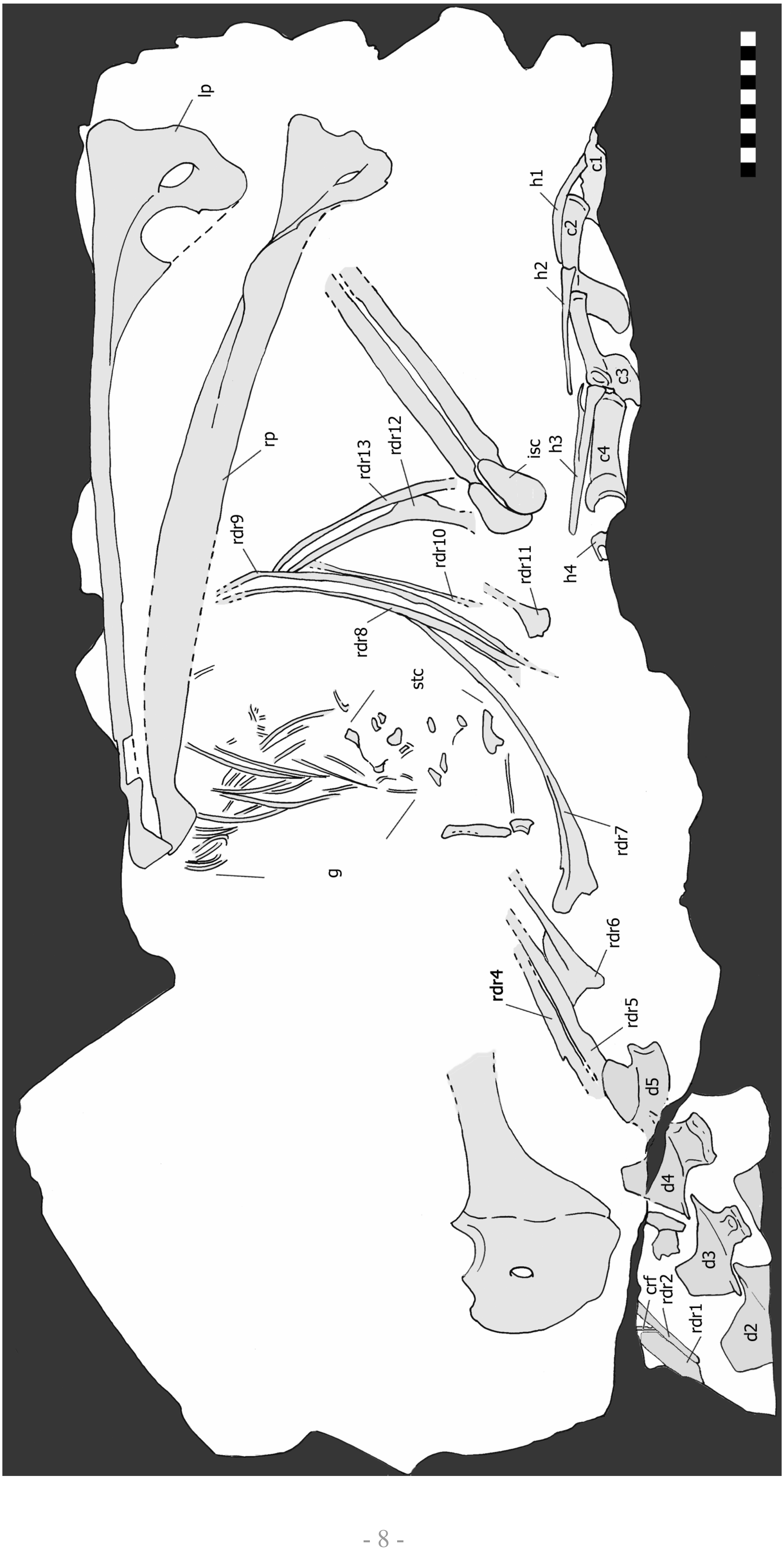

lp
rp
h1
c1
c2
h2
c3
isc
h3
c4
h4
rdr13
rdr12
rdr9
rdr10
rdr11
rdr8
stc
rdr7
g
rdr6
rdr4
rdr5
d5
d4
d3
crf
rdr2
rdr1
d2

Figure 4: lower side of slab A and B with both the ischia and pubes, four caudal vertebra and their appropriate chevrons, the neural arches of dorsal vertebra 2 to 5, several dorsal ribs, and gastralia (scale bar 50 mm).

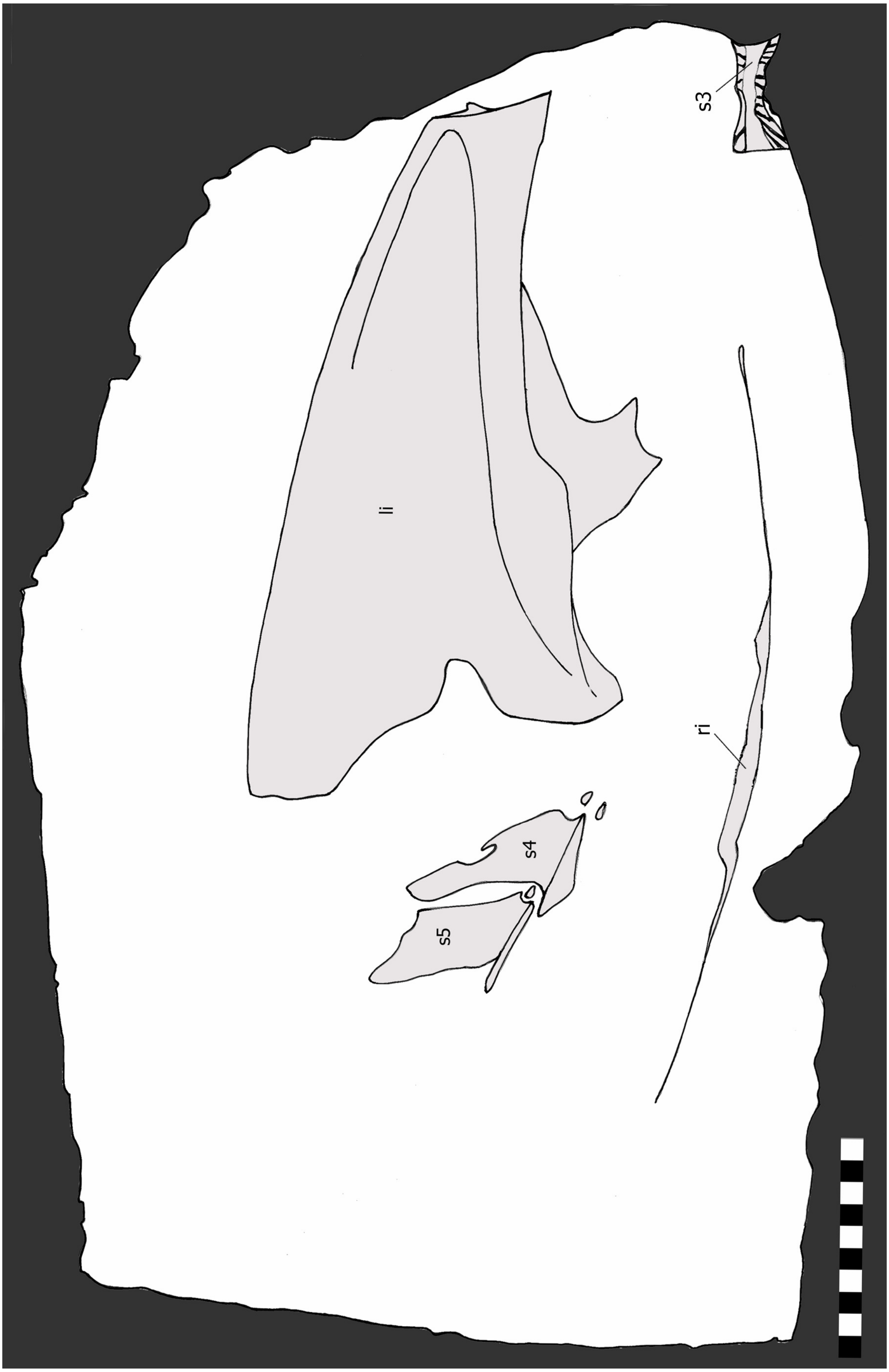

s3
li
ri
s4
s5

Figure 5: upper side of slab D showing the right and left ilium as well as the neural arches of sacral vertebra 4 and 5 (scale bar 50 mm).


s2
s5
s2
s3
s4
s1
ri
s3

Figure 6: lower side of slab D displaying the right ilium, the centra of sacral vertebra 2 to 5, as well as portions of the neural arches of sacral 1 to 4 scale bar 50 mm).

The preparation of slab A has been performed in two steps: (1) most of the bones were excavated to maximum extant, (2) a separate piece of matrix was assembled to slab A containing parts of the left scapula and dorsal ribs.

The bones of the new theropod are small, very thin walled, and fragile. Overall, the material is well preserved. Areas consisting of thin bones as seen in the ilium as well as in the pubis, and regions of the neural arches of the vertebrae display weathering, though this affects only small regions of the skeleton. One ilium could even be restored completely. Many parts of the axial and posterior appendicular skeleton were still covered by the sediment in the field and thus remained unaffected by atmospheric conditions. Furthermore, only the pelvis, the right and left scapula, the left coracoid, the sacral vertebrae, and two dorsal vertebrae are found completely disarticulated. Additionally, few bones of the pelvis show extensive fine surface disadvantages and several have gaps due to stress cracking during diagenesis.

Sedimentary transportation, indicated by the presence of limy nodules, undulation of layers and the scattered embedding of the skeletal elements, is evident in the horizon where the Swiss theropod material has been recovered.

4.2. Procedure

Most of the drawings of bones are based on tracings from photographs (dpi 300; 2:1 of natural size). For this purpose, transparent paper and rapidographs of 0.5 mm and 0.35 mm coat thickness are used (STAEDTLER marsmatic 700). Parts of the original contour of the elements are drawn with the thicker pen, while the incomplete margins of the bones are traced with the thinner one. This technique provides the basic outline or silhouette of each element, and its correct proportions. The relief, cracks and other details are then added by shading using the pen of 0.35 mm thickness, to reflect light coming from a 'North-West' direction onto the bony surface. The drawings are then minimized to 70% of their double-original size. The resulting size with a ratio of 1 to 1.4 fits best for showing every bone in detail.

The photographs as well as the minimized drawings are adjusted with ADOBE® PHOTOSHOP® CS2 for better contrast, colours, and for adjusting the sizes.

In addition to the conventional method of photographing and drawing, modern technology has been adopted: the studied bones were scanned with x-ray in the hospital of the University of Zurich, Switzerland, as well as x-ray and neutron tomography in the Neutron Transmission Radiography Station (NEUTRA) at the Paul Scherrer Institute (PSI) in Villigen/Switzerland. In the PSI, the samples were positioned on a table which rotated horizontally in a circular path of 180 degrees while 301 transmission projections were taken (fig. 7). The electrons and the neutrons were converted into light by a scintillator screen which was imaged with a 1024 x 1024 pixel CCD camera, cooled down to -45 degrees in order to reduce the dark current. The field of view was constantly maintained at 279 x 279 mm. The resulting image stack of 301 transmission projections was then reconstructed into a 3-D-model with the program OCTOPUS 8.1 (http://www.octopus.ch/updates_service/fr1set_peritrend.html). The next step was to visualise the single bones without their matrix which was performed using the program VGSTUDIO MAX (http://www.volumegraphics.com/products/vgstudiomax/) based on the difference of grey values resulting from the different attenuation coefficients of the single elements (see «11.4.1. Attenuation coefficient of every element» table 7 & 8, in appendix). Volitional pictures of the bones were exported into the program ImageJ® for improving their quality.

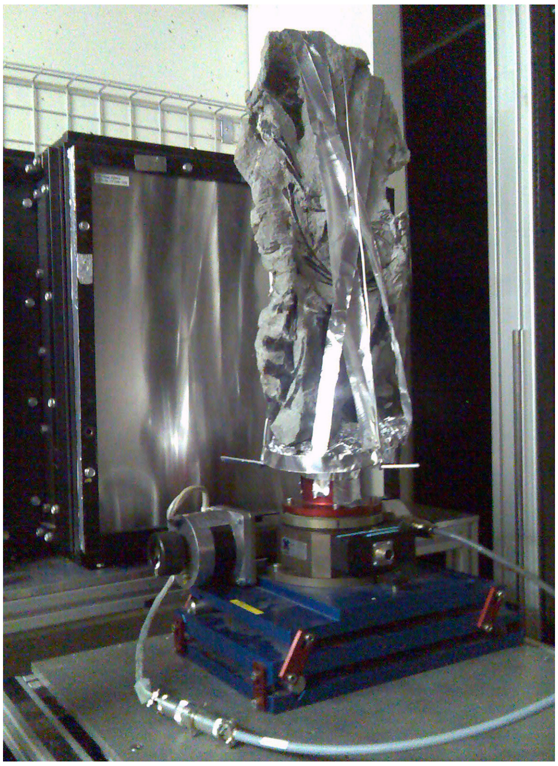


Fig. 7: slab A is positioned on the rotating table in front of the scintillator screen at the Paul Scherrer Institute in Villigen, Switzerland.

The cladistic approach for clarifying the systematic position of the Swiss theropod material is deconstructed of Late Triassic and Early Jurassic Theropoda. Several palaeontologists have published phylogenetic analyses of the Theropoda (e.g. GAUTHIER 1986; ROWE & GAUTHIER 1990; HOLTZ 1994; SERENO 1999; TYKOSKI 1998, 2005; RAUHUT 2003; EZCURRA & CUNY 2007). This data is the basis for the actual analysis. Several characters are used from GAUTHIER (1986), TYKOSKI (1998) and RAUHUT (2003), whilst the majority of characters follow those of EZCURRA & CUNY (2007) (see «11.1.1. Character description» and «11.1.2. Data Matrix», in appendix).

The antecedent literature research confirms the Swiss theropod to belong to the Coelophysoidae (see chapter «9.5. Excursus D: Geographical and chronological distribution» for definition) and more precisely to the Coelophysidae (see «9.5. Excursus D: geographical and chronological distribution» for definition) (SERENO 1998; PADIAN et al. 1999; EZCURRA & CUNY 2007). Thus members of the former group are analysed with particular attention to Coelophysidae including *Coelophysis* and *Syntarsus* (HOLTZ 1994) for ascertaining the phylogenetic position of the Swiss theropod material. Therefore, nine taxa for the ingroup are chosen, representing putative Coelophysoids: *Coelophysis bauri*, *C. rhodesiensis, Dilophosaurus wetherilli*, *Liliensternus liliens*terni, *Lophostrophaeus airelensis*, *Procompsognathus triassicus*, *Segisaurus halli*, *Syntarsus kayentakatae*, and the Swiss theropod material. *Herrerasaurus ischigualastensis* is used as successive outgroup. The primary matrix includes 258 characters («11.1.1. character description», in appendix) mostly based on the paper of EZCURRA & CUNY (2007) reanalysed the relationship of *Lophostropheus airelensis*. After a first analysis 177 characters were stated as being constant or uninformative. Thus they were dropped from the analysis, proceeding with 81 valid characters (7 of these 81 characters are ordered). No character is weighted because to the fact that the impact factor cannot be determined in the other not available fossils. Alignment gaps are coded as 3rd character state. The next step was to analyse the data with the program PAUP 4.0. BETA (SWOFFORD 2002). PAUP 4.0. BETA (SWOFFORD 2002) is employed to conduct maximum parsimony searches using heuristic and branch-and-bound search methods with tree bisection-reconnection (TBR) branch-swapping on all most parsimonious trees (MPT's.)

5. Excursus A: history of the genera *Coelophysis* COPE, 1889 and *Syntarsus* RAATH, 1969

The genus name *Coelophysis* COPE, 1889 is based upon a few skeletal remains of theropod dinosaurs, which were found in the Chinle Formation of the Whitaker or Ghost Ranch quarry in Rio Arriba Country, north-western New Mexico, by David Baldwin in 1881 (COPE 1887 a, b, COLBERT 1989, 1995; HUNT & LUCAS 1991). Before COPE (1889) finally erected the new genus *Coelophysis*, he described some of these specimens as two new species of the already known genus *Coelurus* COPE, 1887: *C. longicollis* COPE, 1887; based on one cervical, one dorsal, and one caudal vertebra, as well as on one femur; and *C. bauri* COPE, 1887 founded on one cervical vertebra, one sacrum, and the distal end of a femur (COPE 1887a; PADIAN 1986). In a second paper which he published in the same year (COPE 1887b), the two species were moved into the genus *Tanystropheus* MEYER, 1855 as *T. longicollis* (COPE, 1887) and *T. bauri* (COPE, 1887), and moreover, he named a third species as *T. willistoni* COPE, 1887 based on one partial acetabular border and one single dorsal centrum (COLBERT 1989, 1995; PADIAN 1986). In 1889, COPE published a brief article in which he rejected the genus *Tanystropheus* for the assignment of the Ghost Ranch material and therefore, he established the new genus *Coelophysis* COPE, 1889 for the three species which were then named *C. longicollis* (COPE, 1887), *C. bauri* (COPE, 1887), and *C. willistoni* (COPE, 1887). However, COPE did not formally designate any one of these three species as a type for the genus (COPE 1889; COLBERT 1989, 1995; HUNT & LUCAS 1991), and furthermore, no holotypes were determined so far (HUNT & LUCAS 1991).

In 1906 and 1915, FRIEDRICH VON HUENE illustrated many specimens of COPE's *Coelophysis* remains and tried to clarify the taxonomic state of additional material COPE had not referred (PADIAN 1986; HUNT & LUCAS 1991). HUENE (1906, 1915) still did not provide any specimen numbers and also designated no type species formally. At the same time, he reassigned a lot of COPE's already referred material from one *Coelophysis* species to another, and thus, he confused the uncertain taxonomy once again (PADIAN 1986; COLBERT 1989, 1995; HUNT & LUCAS 1991). The reassignments were mainly based on size differences, which COLBERT (1964) interpreted later as different ontogenetic stages in the *Coelophysis* species. Finally in 1930, HAY designated *C. bauri* as the type species of the genus *Coelophysis*, although COPE mentioned this one after *C. longicollis* in his publications in 1887 (1887a, b), what has been accepted by later scientists.

More than 15 years later, in 1947, George Whitaker discovered several new theropod skeletons at the Ghost Ranch quarry, and until now, the locality has yielded dozens of individuals of small dinosaurs of this kind (COLBERT 1989, 1995). The high numbered and well preserved specimens were assigned to *Coelophysis* COPE, 1889 by COLBERT (1947), and later to *C. bauri* (COPE, 1887) by the same author (COLBERT 1964).

In 1984, WELLES apparently designated a lectotype for *Coelophysis bauri* (COPE, 1887) based on AMNH 2708 which had been reassigned from *C. longicollis* to *C. bauri* by HUENE in 1915, represented by a fragmentary right ilium found in 1881. According to Article 74 of the International Code of Zoological Nomenclature, AMNH 2708 cannot be a lectotype of *C. bauri* as it was not one of the original syntypes of this taxon (HUNT & LUCAS 1991). Indeed AMNH 2708 could even not be classified as a syntype of *C. longicollis* because COPE did not mention it in the original description of this species in 1887 (1887a), and only noted it in a succeeding article in the same year (COPE 1887b). WELLES (1984) also determined a lectotype for *C. longicollis* (COPE, 1887) based on COPE's AMNH 2705, removed this species from the genus *Coelophysis* and erected the new genus *Longosaurus* WELLES, 1984 for it. Therefore, the lectotype of *C. longicollis* changed into the holotype of *L. longicollis* (COPE, 1887) (1887a). However, the genus *Longosaurus* WELLES, 1984 is a younger synonym of *Coelophysis* COPE, 1889, and additionally, AMNH 2705 has the same issues as the previously mentioned AMNH 2708 being an ineligible lectotype for *C. longicollis* (HUNT & LUCAS 1991): it has not been noted in the original publication (COPE 1887a). Last but not least, the material numbered AMNH 2726 has been designated as a lectotype for the third species *Coelophysis willistoni* (COPE, 1889) by LUCAS & HUNT (1991). However, since this taxon is not diagnostic beyond its primitive theropod status, it is considered a nomen dubium (LUCAS & HUNT 1991).

PADIAN (1986) and COLBERT (1989) provided useful reviews of the taxonomic states of COPE's *Coelophysis* material. COLBERT analysed several specimens of the Ghost Ranch quarry and referred them all to *Coelophysis bauri.* He designated an own lectotype (AMNH 2722) for this species, neglecting the one selected by WELLES in 1984. COLBERT's choice is considered as valid after HUNT & LUCAS (1991). However, AMNH 2722 is indistinguishable from *Syntarsus rhodesiensis* RAATH, 1969 (RAATH, 1969), and therefore, *Coelophysis bauri* was considered as a nomen dubium by LUCAS & HUNT (1991). Thus, the latter authors erected a new genus and species named as *Rioarribasaurus colberti* LUCAS & HUNT, 1991 for the *Coelophysis* material from the Ghost Ranch quarry with the holotype AMNH 7224. Until today, the heated debates over the appropriate name for the dinosaur material of the Ghost Ranch quarry have been going on. As a consequence, all coelophysid remains from that locality are considered as *Coelophysis bauri*, but they are still not diagnosed by unique apomorphies and thus are only a metataxon possessing characters shared with Coelophysidae (TYKOSKI & ROWE 2004).

In the last decade, several palaeontologists have recognized the morphological similarities *Coelophysis bauri* (COPE, 1887) and *Syntarsus rhodesiensis* RAATH, 1969 share (RAATH 1969, 1977; PAUL 1988, 1993; COLBERT 1989; ROWE 1989; TYKOSKI 1998; DOWNS 2000; BRISTOWE & RAATH 2004). During this time span, the genus *Syntarsus* RAATH, 1969 has been thought to be at least closely related to the genus *Coelophysis* COPE, 1889 or even to be a younger synonym of the latter. In 2004, it became clear that *S. rhodesiensis* is actually a species of the genus *Coelophysis* by the work of ANTHEA BRISTOWE and MICHAEL A. RAATH. BRISTOWE & RAATH (2004) reconstructed a juvenile specimen of '*Syntarsus' rhodesiensis* collected from the Forest Sandstone Formation of Zimbabwe, showing cranial characters that hitherto were used for distinguishing and justifying the separation of *Coelophysis bauri* (COPE, 1887) and *Syntarsus rhodesiensis* RAATH, 1969 at genus level. The results of the reconstruction of the cranium of the new juvenile theropod individual confirms the very close relationship of both taxa and shows that the differences are artificial and based on incorrectly assembled, disarticulated cranial bones. Therefore, *Syntarsus rhodesiensis* RAATH, 1969 must be assigned to *Coelophysis* COPE, 1889 as *C. rhodesiensis* (RAATH, 1969). After this analysis, there are still cranial features that differentiate *Coelophysis rhodesiensis* from *C. bauri*. However, these elements are no longer sufficient to justify a separation at the genus level, but are adequate to assess species level relationships.

In conclusion, from 2005 onwards the species *rhodesiensis* has been accepted as a member of the genus *Coelophysis* by several authors (e.g. GAY 2005; EZCURRA & CUNY 2007). The single *Syntarsus* species left is *S. kayentakatae*'s whose phylogenetic position still remains unsolved (TYKOSKI 1998, 2005; BRISTOWE & RAATH 2004). RON TYKOSKI (pers. communication) is going to publish results from his current study that will likely assign another genus name to, *Syntarsus kayentakatae*.

6. Systematic Palaeontology

DINOSAURIA OWEN, 1842
SAURISCHIA SEELEY, 1887
STHEROPODA MARSH, 1881
NEOTHEROPODA BAKKER, 1986, sensu SERENO 1998
COELOPHYSOIDEA NOPCSA 1928, sensu HOLTZ, 1994

Family COELOPHYSIDAE PAUL, 1988

Locality

Quarry Gruhalde of the brickyard Keller AG, Frick, Canton Aargau, Switzerland

Horizon

'Obere Bunte Mergel', Late Keuper (?Rhaetian) or ?Early Jurassic.

The material of the Swiss theropod is found approximately two meters beneath the 'Insekten-Mergel'. The stratigraphy of the 'Insekten-Mergel' horizon is well-known and accredited to the Early Jurassic (Early Hettangian). Underneath these beds, there are sediments assigned to the Late Triassic. These are called 'Obere Bunte Mergel' representing the Norian of the Late Keuper and probably also bearing the Rhaetian in its uppermost part (LABHART 1983; MÜLLER, HUBER, ISLER & KLEBOTH 1984; HSÜ & BRIEGEL 1991; BEUTLER, HAUSCHKE & NITSCH 1999; BEUTLER & SZULC 1999). The 'Obere Bunte Mergel' are twelve meters thick, of light-grey colour and were laid down during a period of a continental climate in the Upper Keuper. The geological hiatus between the Triassic and Jurassic deposits prevents accurate age estimations of the boundary. At the end of the Triassic, the Tethys returned, and flooded areas of North Switzerland during the Lower Lias (GYGI & RIEBER 1988). Thus, the Rhaetian was affected by flooding, and as a consequence of either low sedimentation rates or erosive mechanics there was an absence of sediment accumulation (MÜLLER, HUBER, ISLER & KLEBOTH 1984; SANDER 1990). The geological hiatus reflects a period of approximately five million years as already mentioned (MEYER & FURRER 1995; FURRER, pers. communication).

7. Excursus B: pleurocoels

Several definitions of pneumatic structures are documented in vertebrae of pterosaurs, prosauropods, sauropods, and theropods. WELLES (1984: 103) gave a definition of the term pleurocoel in his study about *Dilophosaurus wetherilli*: the 'pleurocoels are cavities lying on the lateral sides of the centrum'. Other authors equate this term with pneumatic fossa or foramen (e.g. ROWE & GAUTHIER 1990; TYKOSKI 1998; RAUHUT 2003; TYKOSKI & ROWE 2004). There is great uncertainty in defining the term 'pleurocoel' and sometimes no such pneumatic morphology is recognized by the writer due to the lack of clear definition (e.g. COLBERT 1989, 1995). There is also misunderstanding in the linguistic derivation: the greek word pleurocoel is composed of 'pleuro' which means lateral, and 'coel' standing for hollow (BRITT 1993). Thus it is incorrect to apply this term to pneumatic fossa or foramina that are not located on the lateral side of the neural arch or centrum.

In this study, the term pleurocoel is strictly avoided (except for the phylogenetic analysis: «11.1.1. character description», in appendix). In contrast, fossa or foramen are used whether the bone is pneumatic or not. After BRITT (1993) fossil bones are pneumatic if they exhibit internal chambers, or bear fossae with crenulated texture, smooth or crenulated tracks or have thin outer walls, and large foramina. The inference that a blind fossa is pneumatic based on texture alone is uncertain and WEDEL (2005) states that any blind fossae of early saurischians are, at best, equivocal evidence of pneumaticity. In the Swiss theropod material we have such blind fossae in the anterior dorsals (longitudinal fossa as well as cranial and caudal fossa on centrum), in the sacrals (fossa on centrum) and also in the anterior caudals (longitudinal fossa on centrum and fossa on neural arch = infra-diapophyseal fossa, sensu CARRANO, HUTCHINSON & SAMPSON 2005). It was not possible to observe the inside of these bones with the CT Scans: the resulting pictures simply did not provide adequate resolution to determine camerate or camellate chamber states (BRITT 1990; 1993; 1995). Additionally, it cannot be said if these cavities were combined with the existence of internal air sac filled chambers for maintaining pneumatisation, or if these cavities contained muscles or adipose tissue (RAATH 1977; BRITT 1993, 1995; WEDEL 2005; O'CONNOR & CLAESSENS 2005). Thus, it is the best to refer to these structures as fossae (cavities), or foramina (diverticula piercing into an air sac filled chamber inside the centrum or neural arch) without any indication of the pneumatic conditions.

The presence of two laminae or strutting is another morphological feature probably connected with the existence of such fossae or foramina (JANENSCH 1947; BRITT 1990; 1993, 1995). The laminae are located underneath the transverse process on the neural arch, reaching from the diapophysis to the centro-neural suture and forming a triangle fossa between them. BRITT (1995) states that the neural arches of camerate vertebrae consist only of simple laminae which intersect to form deep, external fossae and all but the bases of the apophyses are apneumatic. The known sections of the examined theropods are all camerate (simple) in their internal structure. The achievement of these strutting or laminae varies between cervicals, dorsals, sacrals, and caudals of an individual, and between individuals (BRITT 1995). CARRANO, HUTCHINSON & SAMPSON (2005: 636) note 'a small pocket is present in the infra-diapophyseal fossa [between the laminae] presumably indicating some sort of soft tissue association (e.g., respiratory, circulatory) in the caudals of *Segisaurus halli*'.

8. Morphological analysis

8.1. Axial skeleton

The vertebrae of the dorsal and sacral regions are each described along with their corresponding ribs. The cervical and caudal series do not apply to this rule: no vertebrae are preserved of the former region, whereas in the latter ribs are not developed. The haemapophyses are addressed with their belonging vertebrae.

8.1.1. Cervical region

Remains of cervical ribs

fig.8-9

From this part of the vertebral column most notably two long segments of filiform cervical ribs can be seen belonging to the left ninth and the left tenth cervical vertebra, respectively (slab A, upper side). Furthermore, two other small, scattered fragments of a cervical rib are preserved on slab B (upper and lower side).

The ninth cervical rib is sub-surfaced distally by the left rib of the second dorsal vertebra and proximally by the left scapula displaying only 85 mm of its middle part. The tenth cervical rib shows even less of its length. (45 mm) due to the same condition: it is obscured distally by the identical dorsal rib, and its proximal termination is equally hidden by the left scapula. Both rib segments are antero-posteriorly compressed resulting in a medio-lateral width of 2.5 mm.

The first small fragment of an unidentified cervical rib, which can be found in tangency with the second dorsal vertebral centrum on the upper side of slab B, is not compressed at all, and displays a rounded transverse section (2 mm in diameter) typical for cervical ribs. The second just as small fragment lies on the lower side of slab B between the right ribs of the first and the second dorsal vertebrae. Both small fragments belong to the same cervical rib.

8.1.2. Dorsal region

The dorsal series is represented by dorsal vertebra 1 to 13 which are located on the slabs A and B. Anterior to the pectoral girdle of the material under study, four dorsal vertebrae are situated in line more or less in articulation either with their neural arches or centra. They represent the most anterior vertebrae of the whole dorsal series: the dorsals 1, 2, 3 and the neural arch of dorsal 4. The succeeding dorsal vertebrae 5, 6, 7, 8 and 9 are also nearly articulated and form a perfect straight, second line, which stands at a dorsally open angle of 120 degrees to the first line, consisting of the vertebrae 1 to 4. The centrum of dorsal vertebra 4 and dorsal vertebrae 10 to 13 are not in line, neither with the dorsals 1 to 3 and the neural arch of dorsal 4, nor with the dorsals 5 to 9. The centrum of dorsal vertebra 4 is located at the beginning of the second line lying at a slight angle, similarly the adjacent dorsal vertebrae 10 to 13 are situated at the end of the same line, also angled towards the centrum, building a third line on their own. As a rule the neural arches are shifted dorsally or antero-dorsally displaying their neuro-central sutures. The dorsal vertebrae 10 to 13 are the only dorsals of the complete series whose centra and neural arches still are articulated.

The beginning of the dorsal vertebral series is well recognizable with the changing in morphology of the ribs; although none of the cervical and dorsal ribs are preserved completely, one particular difference is clearly between the two: the changing in thickness. The compressed cervical ribs are 2.5 mm in width medio-laterally measured at their widest portion at mid-shaft, whereas the dorsal ribs add up to 5 millimetres at the analogous point. Additionally, the dorsal ribs bear a median rim on their anterior sides differentiating them from the flattened surfaced cervical ribs, which originally were rounded in profile. Since the total lengths of the cervical and dorsal ribs cannot be considered in any case, this feature is not meaningful here for differentiating the cervicals from the dorsals. Segments of

23 dorsal ribs are available. Only three fragments articulate more or less to their belonging vertebrae (dorsals 2, 3, 10) showing the migration of the capitulum and parapophysis from the lateral sides of the centrum onto the antero-distal and later onto the distal margin of the transverse processes. The other rib segments, which are not articulated, are either shifted dorsally or ventrally to their position in vivo. The proximal branching of the ribs into capitulum and tuberculum gains up to a maximum of 45 mm in width in antero-posterior direction, measured between the caudal margin of the rib and the cranial end of the capitulum. Only the antero-distal parts of the branchings are visible in some cases, leading to the instance that merely the capitula can be seen, whereas the tubercula are often broken off. All preserved parts of the dorsal ribs are more or less flattened and additionally compressed antero-posteriorly.

The thirteen dorsal vertebrae all show different states of preparation: they are either laterally completely free of matrix like dorsal number 2, 3 and 10, are re-embedded into the matrix by the preparator for technical reasons (compare chapter 4 «material and methods») like dorsals 4, 7 and 8, or are still predominantly or completely hidden by matrix (dorsals 5, 6, 11 to 13) or are badly preserved like dorsals 1 and 9. The overall length of the dorsal centra is rather inconstant: they become antero-posterior longer towards the pelvic girdle (contra COLBERT 1989) varying from 31 mm (second vertebra) to 42 mm (tenth dorsal vertebra). All anterior and posterior intervertebral contacts of the centra stand perpendicular to their longitudinal axis and are amphicoelous to somewhat platycoelous.

The dorsal vertebrae exhibit characteristic transverse processes, which have been regarded as an apomorphy of Ceratosauria (GAUTHIER 1986; ROWE 1989; ROWE & GAUTHIER 1990; TYKOSKI & ROWE

2004) and now are considered to be widely spread among Neotheropoda (CARRANO et al. 2005; EZCURRA & CUNY 2007). The transverse processes are typically backswept and triangular in shape, when viewed from dorsal position. Each posterior margin of the horizontally orientated dorsal transverse processes is either 90 degrees angled to the median plane of the belonging centrum (posterior dorsals), or it is directed about 45 degrees oblique cranio-laterally in the anterior dorsals. The dorsal transverse processes are only visible from dorsal position, thus they always show their upper sides.

The neural spines vary more or less in shape due to the cartilaginous nature of their dorsal ends.

First dorsal vertebra and ribs

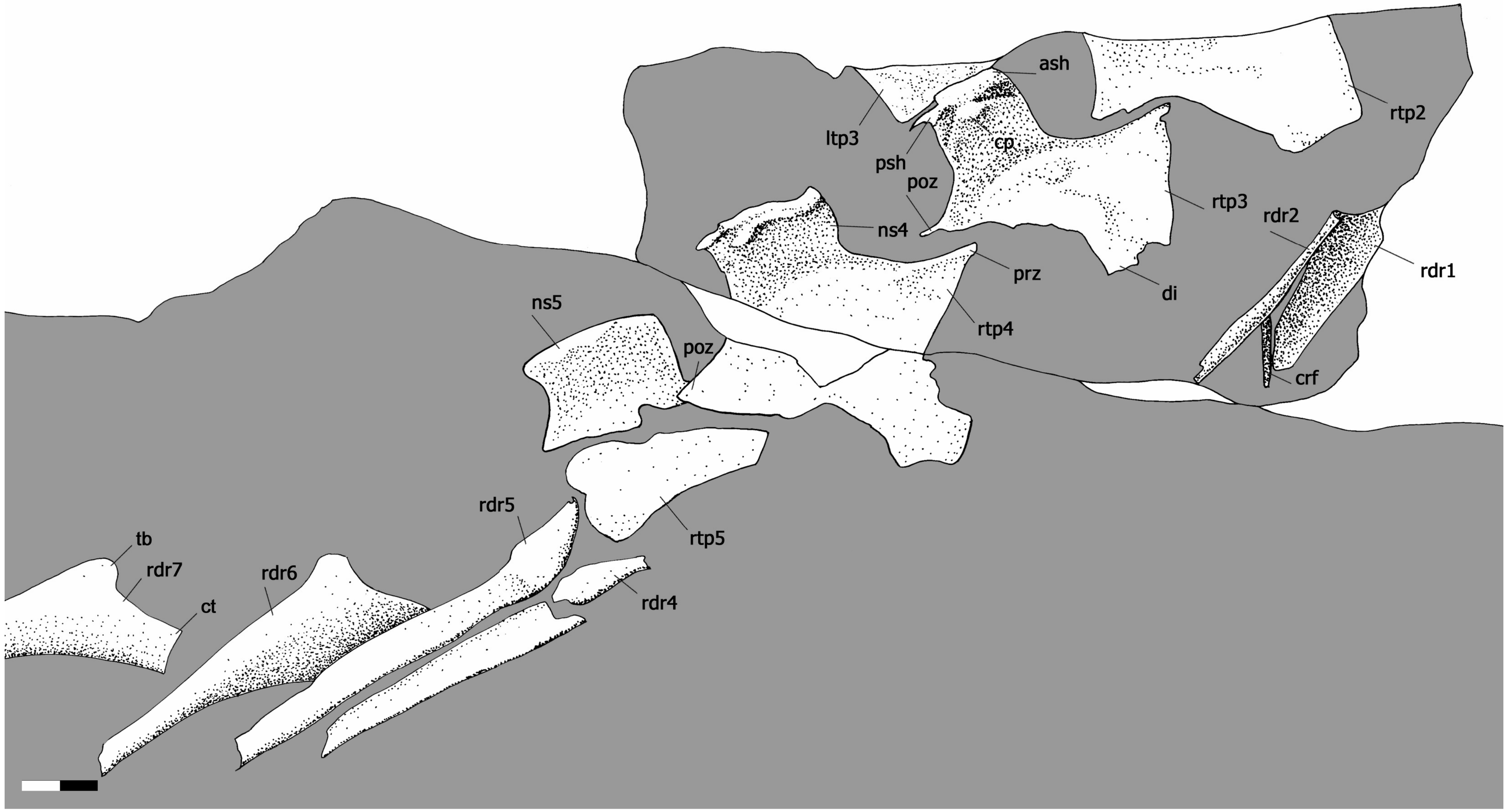
fig.8-10

The first dorsal vertebra is only preserved with a small posterior portion of its centrum measuring 6 mm along the ventral border and adding up to 15 mm along its distal height. The centrum is situated 12 mm cranial to the anterior articular face of dorsal 2. There is a dorsal rib directing with its proximal end to the assumed place of its articulation with both the centrum and the transverse process of dorsal 1. The rib portion preserved is very fragmentary measuring only 44 mm along its cranial border. However, the fact that it is directed to the first dorsal and that it shows a medial groove along its whole available length supports the assumption that this element can be identified as the left rib of dorsal number 1. The first right dorsal rib fragment is located underneath, but still on the right side of the preserved portion of dorsal vertebra 1 and dorsal 2. It measures 56 mm along its anterior margin and approximately 10 mm in medio-lateral width.

Second dorsal vertebra and ribs

fig.8-10

Dorsal number 2 displays the left side of the centrum as can be seen in dorsals 3, 4 and 10: the centrum has a spool-like habitus, being expanded at its faces and very constricted at its mid portion. The spool-like form is not developed to the extant seen in the sacral vertebrae. The centrum of dorsal 2 measures 31 mm along its ventral border. The cranial and caudal articular faces add up to 20 mm in height being both amphicoelous, whereas the widths cannot be measured due to the embedding in the sediment. The centrum is still fused to the neural arch.



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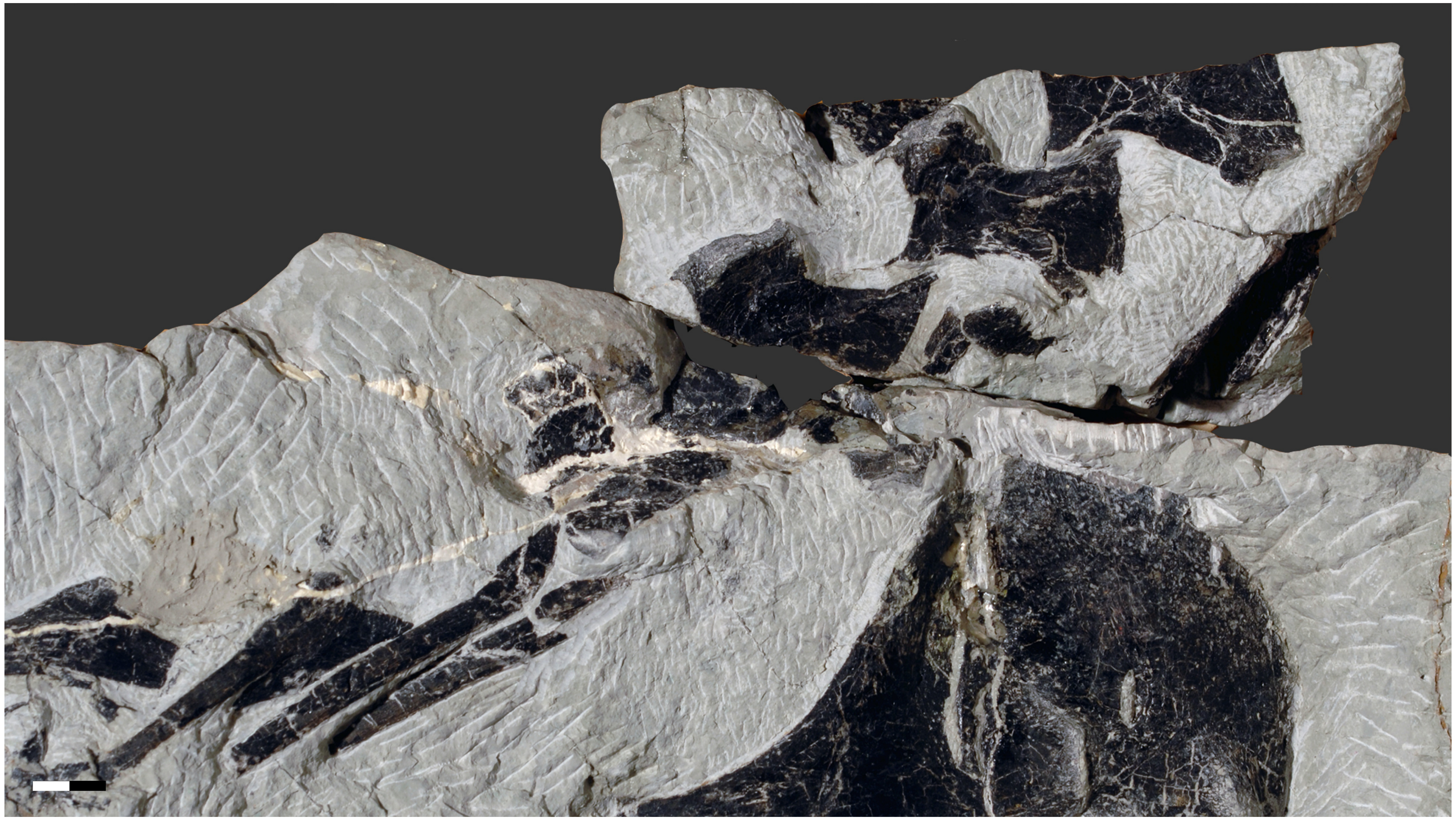
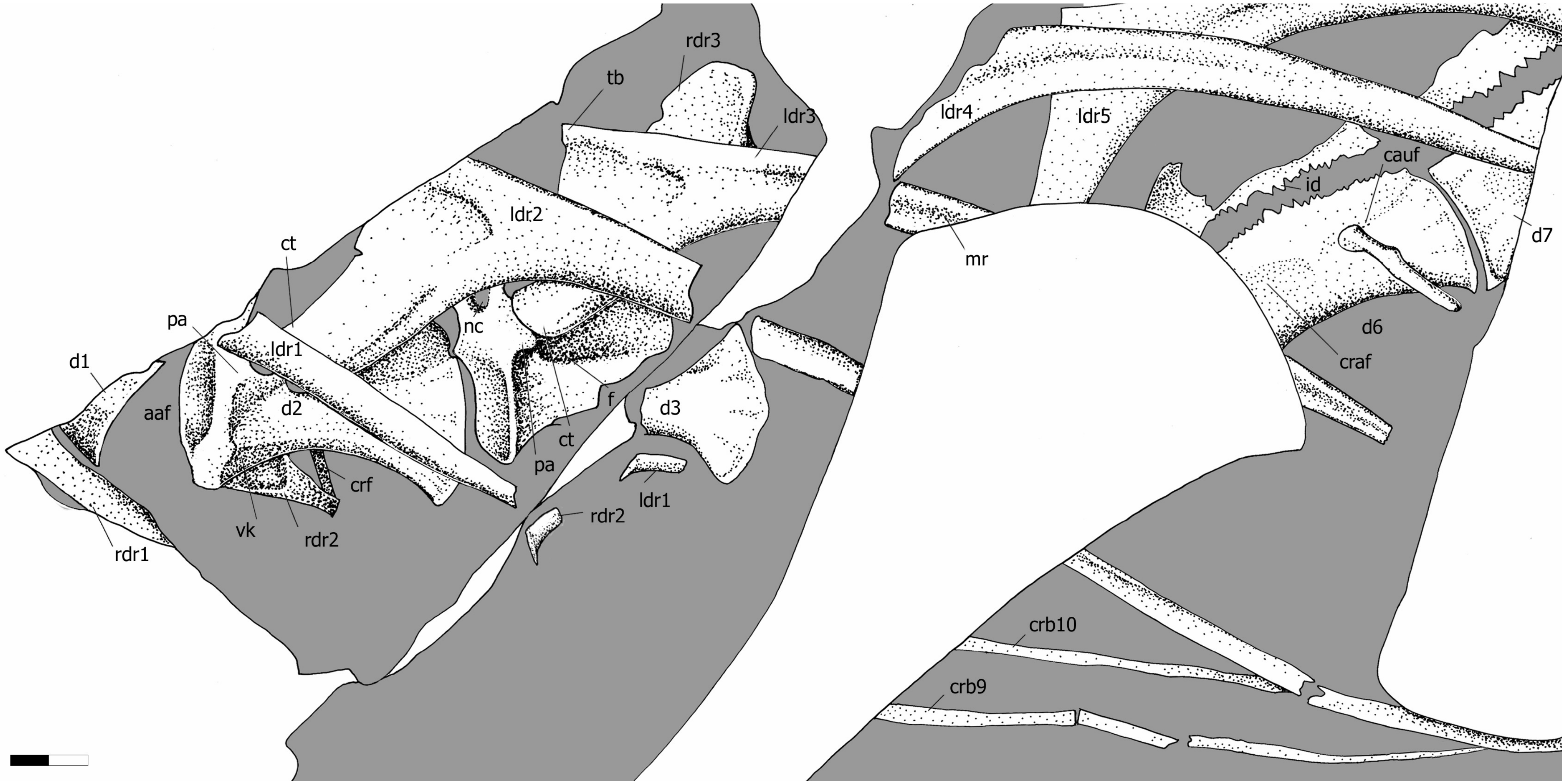


Figure 8: right dorso-lateral view on the neural arches of dorsal vertebra 2 to 5, with a cervical rib portion and fragments of dorsal rib 2, 4-7 (scale bar 10 mm).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mr
d6
craf
crb10
crb9

Figure 9: left lateral view on the partial centrum of dorsal 1 and 7, and on the more or less complete centra of dorsal 2, 3 and 6. Additionally, cervical rib fragments as well as several dorsal rib portions can be seen on this upper side of slab A and B (scale bar 10 mm).

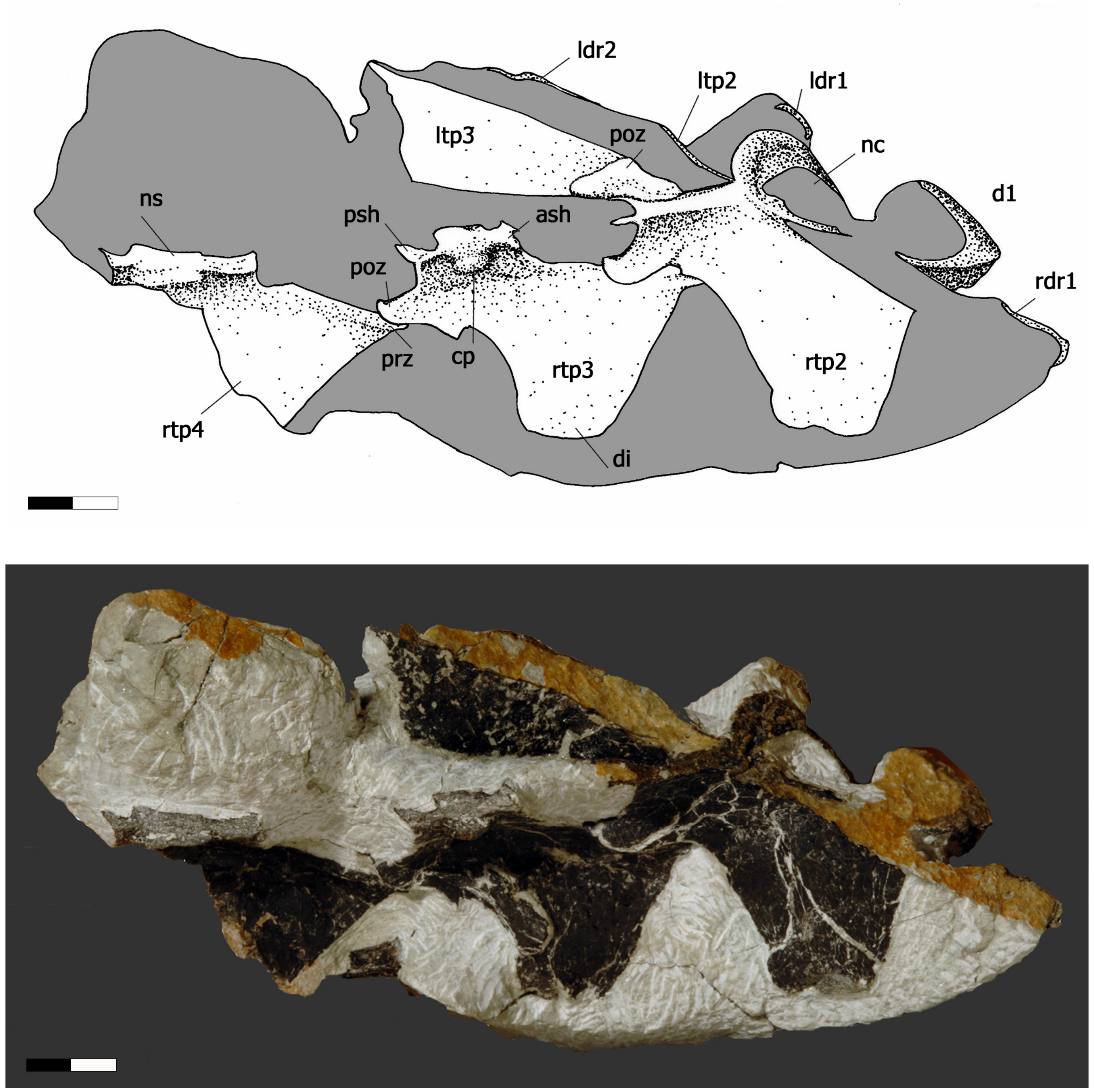


Figure 10: upper view on the neural arches of dorsal vertebra 2 to 4. Here, the first neural arch (dorsal 2) as well as the posterior portion of the centrum of dorsal 1 are obliquely sectioned (scale bar 10 mm).

The original horizontal position of the transverse processes of the dorsal vertebra 2 is nonexistent anymore. They are deformed to the same extant as described in dorsal 3 below. The transverse processes of dorsal 2 are not as complete as in dorsal 3 being obliquely eroded from the mid-anterior margin of the right to the proximo-posterior rim of the left transverse process. However, not only parts of the processi transversi are missing, also the cranial portion of the neural spine is lacking. In addition, few millimetres of the anterior part of the neural canal are absent as well. The dimensions

of the neural canal cannot be measured due to the nature of preservation, namely because of its inclined erosion. As the left transverse process only exhibits its cross section, only the grade of displacement to the dorsal direction, regarding to the horizontal plane can be observed. The portions visible of the right transverse process are similar to the corresponding areas of dorsal 3: the cranial border of the right transverse process of dorsal 2 is slightly backswept, whereas its caudal margin is bent forward. These two rims distally enclose the dorso-ventrally thin diapophysis, which is parallel positioned to the antero-posterior proceeding neural arch and measures a total length of 10 mm.

The right and left postzygapophyses are preserved; the right process exhibits an articulation area of 10 mm in antero-posterior length and 4 mm in medio-lateral width. It is still in contact with the appropriate prezygapophysis of dorsal number 3. Considering the vertebra from dorsal view, the shape of both postzygapophyses can be seen, looking like an oval caudally directing outgrowth. The left postzygapophysis is also still articulated to its counterpart of dorsal number 3 However, its dimensions cannot be measured because its anterior margin is eroded as well as the more cranially located whole left transverse process which is either eroded or compressed to the ventral direction.

As an extraordinary morphological feature dorsal 2 exhibits a cranio-caudally orientated, longitudinal fossa, which is located just underneath the neuro-central suture. Its presence is hardly indicated because it is still filled with matrix and in addition covered with the left rib of the first dorsal vertebra. Thus only the measuring of the length of this structure is possible (20 mm).

The parapohysis is found on the lateral side of the dorsal centrum at its anterior margin. It is dorso-ventrally extended and confluent with the cranial intervertebral contact, bearing a dorsally located ascending process. This appendage is 3 mm in height and its top measures 5 mm in antero-posterior length. The parapophysis proceeds downwards from the ascending process along 10 mm; at the end of this distance the parapophysis bulges caudally. From this point backwards a longitudinal groove runs along the centrum. This groove builds the dorsal flange of the ventral keel, which is developed on the lower side of the centrum. Although the centrum is slightly pinched medio-laterally, the keel is clearly visible being very sharp at the cranial one third of the centrum length and becoming more caudally shallow.

Both dorsal ribs 2 are incompletely preserved and only available as fragments. The capitulum of the left dorsal rib is nearly located to the ascending process of the parapophysis; it is swifted back and upwards but still almost remains in contact with the parapophysis. The dorso-ventral length at the tip of the capitulum measures 7 mm, whereas that of the tuberculum cannot be measured due to erosion. The available part of the left rib, which is separated into at least 3 parts located either on slab A or on slab B, adds up to 170 mm along its lower anterior margin (rib shaft without branching). The branching of the right rib is located underneath the right lateral side of the centrum of dorsal 2. The right capitulum is very well preserved, but its dimensions cannot be measured because it runs across slab B. For the first time also the tuberculum can be seen: it adds up to 9 mm along the antero-posterior length at its articular facet. The available anterior margin of the right rib fragment on slab B measures 30 mm, but it surely continues into slab A, since an additional fragment belonging to the right rib of dorsal 2 was found.

Third dorsal vertebra and ribs

fig.8-10

The third dorsal vertebra, as dorsal 1 and 2, does neither lay in line with the fourth, nor with the subsequent fifth, sixth, seventh, eighth and ninth vertebrae. The medio-laterally compressed centrum of the third vertebra is situated near above and in front of the centrum of the fifth dorsal vertebra. Its longitudinal axis lies at an angle of 130 degrees to its successors. The third dorsal vertebra has been covered with matrix being all-over hidden in slab A and B. Slab B, which also contains the spinal processes of dorsal number three to five, was initially uncovered in the second step of preparation. Now, the third centrum is broken in two parts revealing its whole left side. Nevertheless, its ventral border can be estimated of 33 mm in length. The height of both the anterior and posterior articular faces can be measured adding up to 19 mm and 24 mm. The neural arch is almost completely available only lacking the antero-lateral portions of the left transverse process. The right transverse process is backswept with a broad base and a small distal end. Its cranial border runs proximo-distally distinctly to posterior, measuring 14 mm in length. The caudal margin of the right transverse process proceeds proximo-distally to anterior, adding up to 19 mm in length. The distal margin is oriented parallel to the neural spine and measures 9 mm.

The neural arch is disarticulated from its centrum as also seen in dorsal 2, 4, 5, 6, 7, and 9; its neuro-central suture remains hidden in the matrix. The compression during diagenesis results in a non physiological position of the transverse processes: both the left and right one are still lying in-plane to each other; however the whole plane is bent 60 degrees to its original horizontal orientation, with the right transverse process being more ventrally than the left one. The dorsal spine is not deformed at all.

At the left lateral side of the centrum, there is a deep longitudinal fossa as seen in dorsal 2. The anterior, ventral and posterior borders of the fossa runs a semi-circle, starting 4 mm distal of the cranial face, measuring 19 mm in length and 6 mm in height. Its depth adds up to approximately 5 mm at the lowest point at mid-length and at mid-height. The dorsal and posterior rims are not as sharp as the other margins. The transition between the dorsal margin and the neuro-central suture is fluent. Cranial to the fossa there is the ascending process of the parapophysis is visible, which flanks the dorso-lateral margin of the anterior articular face. The upper rim of the ascending process declines suddenly 4 mm distal to the anterior articular face into the posterior margin, which proceeds both proximally into the antero-ventral border of the fossa and distally into the lateral border of the anterior articular face. In contrast to the conditions in dorsal 2, the parapophysis of dorsal 3 does not extend ventrally underneath its ascending process, which is still loosely in contact with the capitulum of the adjacent left rib along its posterior margin. The articulation facet of the tuberculum of the left rib and the diapophysis of the left transverse process cannot be observed. However, the latter can be seen on the right transverse process where it corresponds with the distal margin measuring 9 mm in length. According to this, the diapophysis is dorso-ventral narrow and antero-posterior long as already mentioned in dorsal 2. The area of the diapophysis is rather spongy indicating the preliminary presence of cartilage. There is an important difference to dorsal 10: in dorsal 3, and dorsal 2 the migration of the capitulum onto the transverse processes has not yet taken place; the parapophysis is still located on the lateral side of the centrum in dorsal 2 and 3.

The anterior and posterior margins of the neural spine are neither bent forward nor bent backwards: they are perpendicular to the horizontal longitudinal plane of the centrum. The neural spine begins mounting 10 mm posterior to the cranial border of the prezygapophysis. Then, the anterior rim of the neural spine strongly rises up to a height of 15 mm. The succeeding dorsal margin proceeds horizontally along 12 mm backwards, where the posterior border descends along 11 mm downwards reaching the base of the postzygapophysis. The horizontal aligned distal end of the neural spine is composed of three different areas as already described by WELLES (1984: 109) for *Dilophosaurus wetherilli*: the anterior shoulder, a cap, and the posterior shoulder. The anterior and posterior shoulders mark the horizontal top of the neural spine, whereas the caps are located approximately 2 mm underneath this border at mid-neural spine length, one cap on each side, standing at an angle of 45 degrees upwards.

The right and left prezygapophysis of the dorsal vertebra 3 still articulate to the corresponding postzygapophyses of the second dorsal vertebra. Both articulations take place over an antero-posterior length of 10 mm. In contrast, the articulation area of the right postzygapophysis cannot be determined; it seems rather abraded, but still is tangent with the prezygapophysis of dorsal 4. The left postzygapophysis of dorsal 3 is hidden by the matrix.

The preserved remains of the left dorsal rib 3 are, as mentioned above, in slight contact with the parapophysis and measure 117 mm in length along their caudal borders. At least two fragments of this skeletal element can be observed, which are either located on slab A or B. The most cranial portion of the tuberculum and the most caudal part of the rib shaft are not available. The capitulum of the left dorsal rib 3 can be measured along its dorso-ventral height adding up to 9 mm, whereas the tuberculum is weathered along its end. The presence of the right rib is assumed: there is a dorsal rib fragment, measuring roughly 12 x 10 mm, which protrudes from underneath the posterior rim of the left dorsal rib 3. This rib fragment looks like the portion of a branching into the capitulum and tuberculum. It shows its medial side and is dislocated approximately at right angles to its natural position.

Fourth dorsal vertebra and ribs

fig.8-10, 13

The centrum of the fourth dorsal vertebra has been visible during the first and second step of preparation, whereas its neural arch has been exposed during the third step. The centrum of the fourth vertebra is now completely re-covered after the second step of preparation. Therefore, the following description of the latter is based on the observations made during preparation step 1 and 2.

Preservation of the centrum is fragmentary. The only available articular face of the centrum is the posterior one measuring 22 mm in height. The anterior incomplete lower margin of the centrum is 10 mm long in lateral view. The centrum ventrally inclined at an angle of 60 degrees to the alignment of the centra of its five successors (dorsal 5 to 9). During the third step of preparation the neural arch was discovered: portions of the open neuro-central suture, an abraded right transverse process, the right prezygapophysis, and the whole neural spine. The transverse process, backswept as seen in dorsal 3, is only conserved with 19 mm of its cranial border. The prezygapophysis measures 9 mm and is situated close to the postzygapophysis of dorsal 5. The neural spine mounts caudal to the confluent dorsal margin of the prezygapophysis. The anterior border of the neural spine first increases gradually, then steeply to a height of 12 mm. The upper rim of the neural spine is rather horizontal oriented measuring 17 mm in length. The posterior border descends in a right angle from the caudal end of the upper rim, also showing a smooth transition to the postzygapophysis. The top of the neural spine is spongy and thickened to both lateral sides with indications for an anterior and posterior shoulder, as well as for caps. The latter are not as small and knob-like as seen in dorsal 3. They are rather flat, anteriorly and posteriorly expanded structures, which are located on both sides of the neural spine just underneath its dorsal margin.

The belonging left dorsal rib fragment, situated on the upper side of slab A, measures 86 mm in length along its anterior margin. Whereas the capitulum and tuberculum are missing, the beginning of the proximal branching of the rib as well as its mid-shaft are visible. The available part of the rib is swifted up- and forewards as all the other preserved fragments of the left dorsal ribs. The fragment of the left dorsal rib 4 also shows a median groove proceeding longitudinally on its shaft. A portion of the right dorsal rib 4 can be found on the lower side of slab A and measures 44 mm in length along its anterior margin.

Fifth dorsal vertebra and ribs

fig.8-9, 11A&B, 12-13

The centrum of the dorsal vertebra 5 is now hidden again in the matrix after the second step of preparation. It is only present with its posterior 12 mm, measured from its most caudo-ventral tip, and a very small anterior portion bearing the cranial articular face. Additionally, the centrum is anteriorly eroded, leaving only an impression of its absent part. As a result of this condition, the original length of the ventral border can be measured adding up to 36 mm. The still in vivo placed cranial articular face seems to be dislocated from the corporal conserved posterior part of the centrum due to the same kind of preservation.

The right transverse process and portions of the neural spine are present as well. Theses parts of the neural arch are slightly separated from the centrum. The right transverse process measures 24 mm at its greatest medio-lateral width and stands perpendicular to the median plane of the centrum. The basis of the right transverse process extends over the whole length of the latter, and does not overlap the posterior end of the centrum with its most postero-distal tip as seen in all dorsal vertebrae of the Swiss theropod material. The caudal border of the still horizontally aligned transverse process is slightly tilted forward at 10 degrees to the transversal axis of the centrum.

The sometimes diffuse outline of the neural spine with a maximal height of 17 mm resembles the shape of the dorsal fin of dolphins. Its anterior margin is backswept in the same way as it can be recognized in at least the mid up to posterior dorsal transverse processes. Also the concave nature of the distal rim of the neural spine is similar to the corresponding borders of the mid up to caudal dorsal transverse processes. In addition, the most dorsal tip of the neural spine is positioned anterior to the posterior end of the centrum, and does not overhang the latter caudally as seen in dorsal 2, 3, 4.

The fifth dorsal vertebra displays two prominent laminae confined underneath the anchorage of the transverse process on the right lateral side of the neural arch. These laminae arrange a triangle with their converging upper tips. The anterior lamina measures circa 15 mm, whereas the posterior one adds up to 30 mm in length. The laminae can now only be observed from pictures, because they were also re-covered with matrix during the second step of preparation. However, there is a shallow, three-cornered fossa with a length of 22 mm at its base, defined by the two above mentioned prominent laminae.

The left rib shaft is preserved with a fragment, measuring 55 mm along its anterior margin and showing the obligate median rim. The proximal branching is available as well as most of the capitulum exhibiting a length of at least 17 mm. A portion of the right rib also can be seen showing a length of 55 mm, measured along its anterior margin.

Sixth dorsal vertebra and ribs

fig.8-9, 11A&B, 12-13

The dorsal vertebra six reveals its left lateral side as the second, third, seventh, and tenth does. It is covered proximally by the distal margin of the left scapula. The centrum is separated from its neural arch displaying the centro-neural suture. Along this suture, closely spaced serrations proceed from the most available anterior dorsal margin of the centrum, to its posterior dorsal tip. The ventral border of the disarticulated neural arch exhibits the counterparts to the serrations along the centrum interdigitating to the latter. The number of visible serrations adds up to about 9 on both sides of the neural suture. However the counted total is incomplete as the most anterior portion of the centrum is still covered by the left scapula, and the serrations are eroded along the posterior half of the suture. Nevertheless, one speciality is certainly recognizable: there is a deeper notch on the ventral border of the neural arch at mid-length, and a counterpart, a larger 'tooth', is located directly underneath the former on the dorsal margin of the centrum.

The covered proximal end disguises the real centrum length and shortens it to 28 mm measured along that part of the ventral margin, which is free of matrix. The total dorsal length of the centrum was visible during the second step of preparation measuring 36 mm. In contrast, the anterior articular face was eroded and could not be restored. The left lateral side of the posterior face was not covered by matrix and exhibited a height of 18 mm.

There seems to be two shallow blind pockets (fossae) located at the mid-height of the centrum. The cranial cavity, which displays an oval outline, flanks the anterior articular face and measures 4 mm in height and 7 mm in length. The caudal fossa proceeds as a narrow, longitudinal band with a constant height of 1 mm from nearly the dorso-distal tip of the cranial one over a length of 18 mm. The ventral border of the posterior cavity soars distally until reaching the upper margin of the corresponding articular face, resembling the gradient of an exponential curve. The anterior fossa is separated from the more posterior cavity by 1 mm. Both fossae are very shallow, due to medio-lateral compression during fossilization.

The size of the right transverse process of dorsal vertebra 6 is the same as seen in the fifth vertebra and regarding the form only the anterior margin differs being slightly concave and not straight as that of dorsal 5. The shape of its neural spine looks like the strongly curved blade of an axe, which is directed dorsally with its cutting edge: its anterior border measures 12 mm, whereas its posterior rim adds up to 13 mm. Both rims are concave, protruding forward respectively backward with its upper parts. So, the anterior margin of the neural spine is not back-turned as those of the fifth, seventh and tenth dorsal vertebrae, and, in addition, it is also not straight as seen in dorsal 3 and 4. The dorsal margin is sharply convex and reaches its highest point half way, where it is situated 17 mm above the assumed mid-length of the centrum's dorsal border. The antero-posterior expansion of the neural spine amounts to 18 mm along its base and 24 mm at its broadest position directly underneath the

Figure 11A: left lateral view on the vertebra 5 and 6 as well as on the neural arch of dorsal 7 (scale bar 1 cm).
11B: provides the reader with a closer look on dorsal number 5 and 6, with special interests on the interdigitations and laminae, under the same conditions as seen in fig. A (scale bar 10 mm).

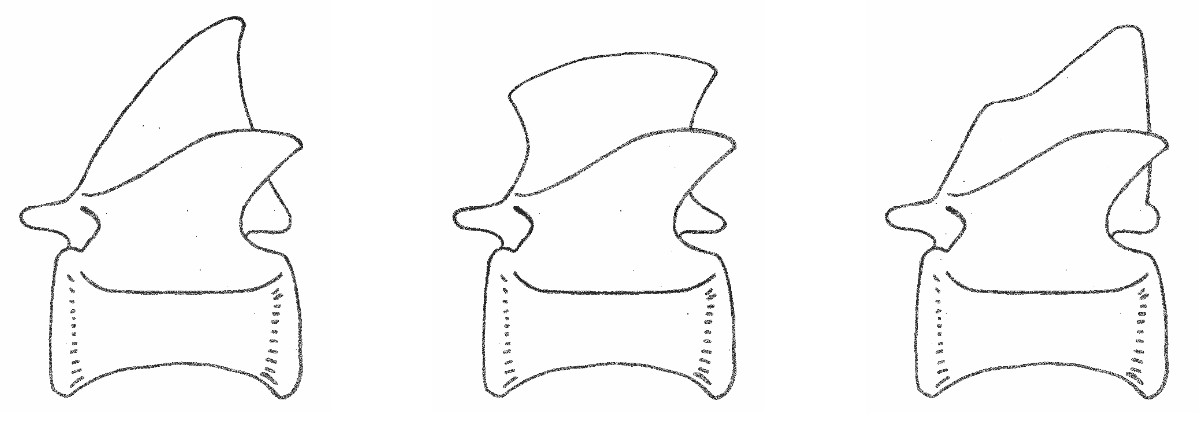


Figure 12: variations of the neural spine forms seen in dorsal 5 (left), 6 (middle) and 7 (right) (modified after COLBERT 1989).

curved dorsal border. Only the 18 mm short base of the neural spine does not span over the total longitudinal axis of the centrum; it begins 7 mm caudal the anterior face of the centrum and ends 5 mm cranial the posterior face of the centrum.

A preserved fragment of the left dorsal rib 6 is either covered proximally by the left rib of the fifth vertebra or distally by the left humerus. This condition results in only showing 29 mm of its length measured along its posterior margin. The fragmented right rib shows portions of shaft and proximal branching with the tuberculum and parts of the capitulum. The anterior margin of the right rib fragment measures 46 mm, whereas the articulation facet of the tuberculum adds up to 6 mm in dorso-ventral width.

Seventh dorsal vertebra and ribs

fig.8-9, 11A, 12-13

As in the sixth dorsal vertebra, the centrum and the neural arch are separated in dorsal 7. Here, only the anterior face and the dorso-anterior half of the centrum length can be recognized. The other parts are not accessible, covered with the left humerus, and the ribs of dorsal vertebrae 4 to 6. The anterior face of the centrum measures 19 mm in height, whereas the centrum itself adds up to 35 mm along its antero-posterior axis. Just as in dorsal 6, there is the presence of at least one cranial fossa (blind pocket) indicated on the antero-lateral side of the centrum.

There is one striking large notch in the sutural contact of the neural arch, above the mid-length of the centrum as seen in dorsal 6. This notch corresponds adversely with its counterpart, an equally large ‘tooth’ of the neural suture of the centrum, which perfectly fits in the former. Once again the complete number of serrations cannot be counted due to the above mentioned coverage of the centrum and neural arch, leaving only eight of them free of the matrix.

The habitus of the right transverse process of dorsal 7 is the same, its size is similar to those of the fifth and sixth vertebra. The proximal basis of the former only differs from those of the latter in being a few millimetres longer in its antero-posterior extension according to the likewise slightly increased centrum length. Both the dorsal border of the centrum and the insertion area of the transverse process onto the neural arch measure 34 mm in antero-posterior length.

The neural spine of dorsal 7 bend backwards with its highest tip, lying exactly above the posterior end of the centrum. The outline of the spine is characterized by an extraordinary shape: the posterior rim measures 20 mm in height and represents a single straight line in silhouette. The postero-dorsal tip of the hind margin descends into the dorsal border, which begins with a rounded edge. The continuing course of the dorsal rim then declines at 60 degrees to the anterior caudal margin. This declination takes place over the posterior third of the longitudinal length of the neural spine basis.

Thereafter, the dorsal border becomes concave for the next one third, before displaying convex curvature over the anterior third.

There are remains of both dorsal ribs 7 conserved. The portion of the left dorsal rib is 65 mm in length measured along its posterior margin, showing the median rim and ventral parts of the proximal branching. The fragmented right rib exhibits its proximal part, which is 112 mm in length, measured along the posterior margin. The most distal portion of the fragment is covered by the right rib of dorsal vertebra 8, whereas the most proximal part with the capitulum and the tuberculum is fully visible. The articulation facet of the capitulum measures 6 mm in dorso-ventral width, whereas the tuberculum adds up to 4 mm under the same condition.

Eighth dorsal vertebra and ribs

fig.13

Three elements of the dorsal vertebra 8 remain: the right and left transverse processes, as well as the basis of the neural arch. The latter measures 36 mm along its ventral antero-posterior length. It is assumed that the antero-posterior length of the centrum, which still lies completely embedded in the matrix, corresponds more or less to the length of the neural arch basis. The right transverse process does not appear different to the processi transversi of dorsal 5 to 7 and 10. The left part of dorsal vertebra 8 is pressed 80 degrees ventrally from its original horizontal position.

The visible part of the left rib fragment at hand measures 76 mm along its posterior margin. The available portion of the right rib has a caudal length of 85 mm. Both ribs only are preserved by their anterior and mid-shafts.

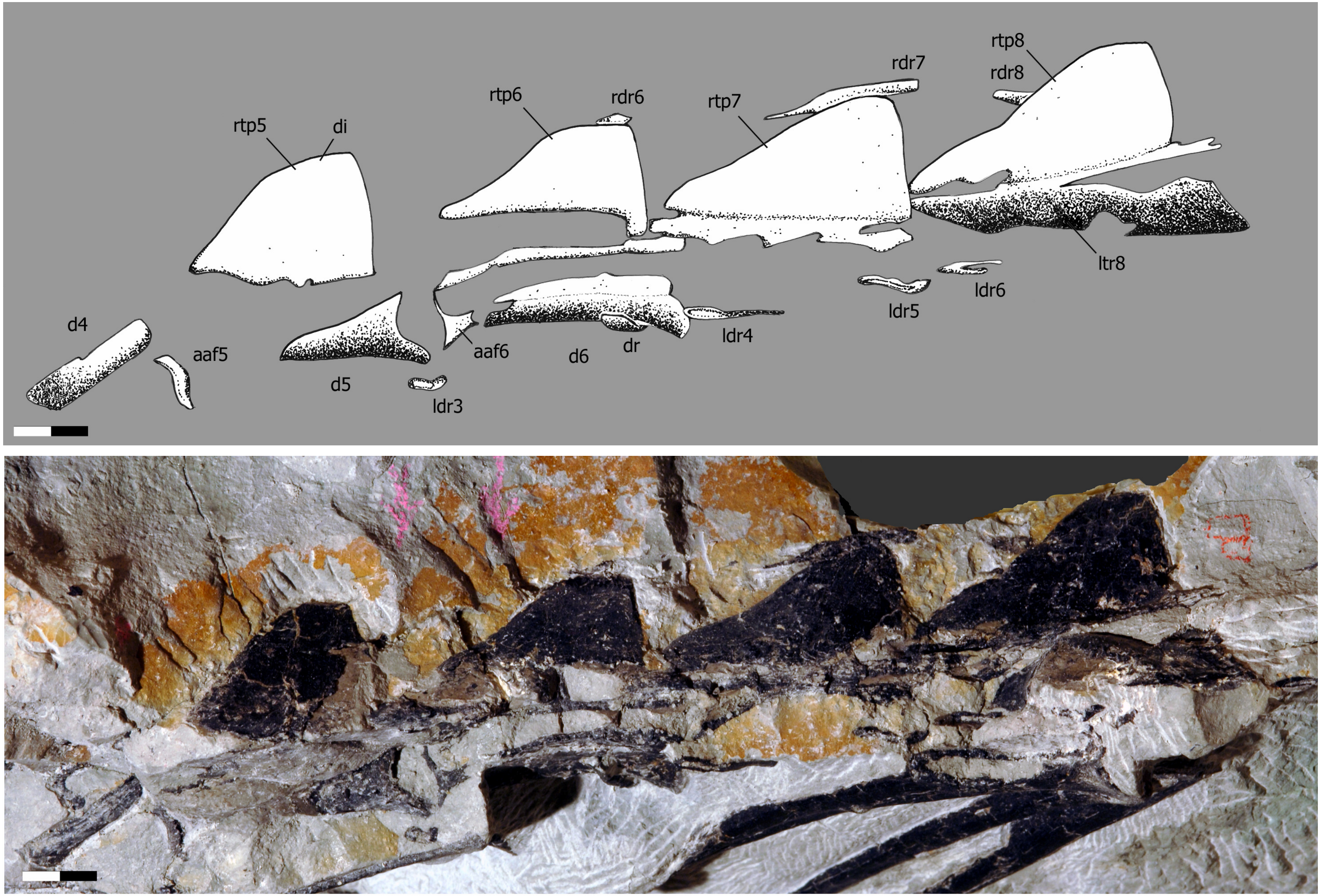


Figure 13: upper view on the right transverse processes and partially the centra of dorsal number 5 to 8. There are also several right and left dorsal ribs as well as the centrum in front of this dorsal series (scale bar 10 mm).

Ninth dorsal vertebra and ribs

This dorsal vertebra is, along with the first dorsal, one of the worst preserved vertebra of the whole dorsal series. Its centrum is longitudinally sectioned and badly crushed along its mid to distal portions. The damaged centrum is visible from the left lateral side as well as from dorsal where only the sliced lateral walls of the centrum can be seen. Additionally, portions of the left and right rib are available as well, measuring 68 mm and 105 mm along their anterior margins. Both remains belong to shafts of the ribs. Whereas only the right fragment displays a median longitudinal groove indicating its affiliation to a more proximal position, this feature is already lacking in the left fragment identifying it as a more distal portion of the shaft.

Tenth dorsal vertebra and ribs

fig. 14-15, 16A

The tenth dorsal vertebra lies distal to the ninth dorsal. This element is situated perpendicular to the longitudinal axes of the centra of its adjacent predecessors. The tenth dorsal vertebra reveals inter alia the whole lateral left side of the centrum with its fully visible platycoelous to somewhat amphicoelous anterior articular face. When viewed from a lateral position, the spool-like centrum is relatively long, measuring 42 mm along its ventral antero-posterior margin, and low in height. The centrum of dorsal 10 even exceeds with its length that of the sixth and thus, is the longest of at least the visible vertebrae of the dorsal series The anterior face is 22 mm high along its sagital plane, whereas the left lateral margin of the posterior face only adds up to 19 mm. Thus, the centrum of this quite caudally positioned dorsal vertebra is approximately twice as long as high. The articular area of the anterior face measures 15 mm along its largest medio-lateral width.

It is assumed in dorsal 10 that the capitulum has already migrated from the centrum onto the neural arch. The parapophysis is now lying just anterior below the base of the left transverse process at the point where the latter is attached to the neural arch, although, the capitulum heads underneath the transverse process into the matrix, this is most likely a result of diagenesis. The tuberculum is not well preserved either, but its position can clearly be spotted on the distal margin of the transverse process. In between of the assumed location of the parapophysis and the anterior portion of the transverse process lies a cavity, the anterior chonos (after WELLES 1984: 111). This recess, which points to lateral and frontal, cannot be prepared properly because of the delicate nature of its surroundings.. Nevertheless, the access of the anterior chonos is almost free of matrix: the exposed antero-posterior length adds up to 11 mm, whereas its cranial height measures 9 mm. Since there is an anterior chonos, the presence of appropriate medial and posterior recesses is also expected, although, the two latter cannot be detected. The medial chonos may be covered by the arborisation of the proximal end of the left rib, whereas the posterior chonos may still be hidden by the sediment.

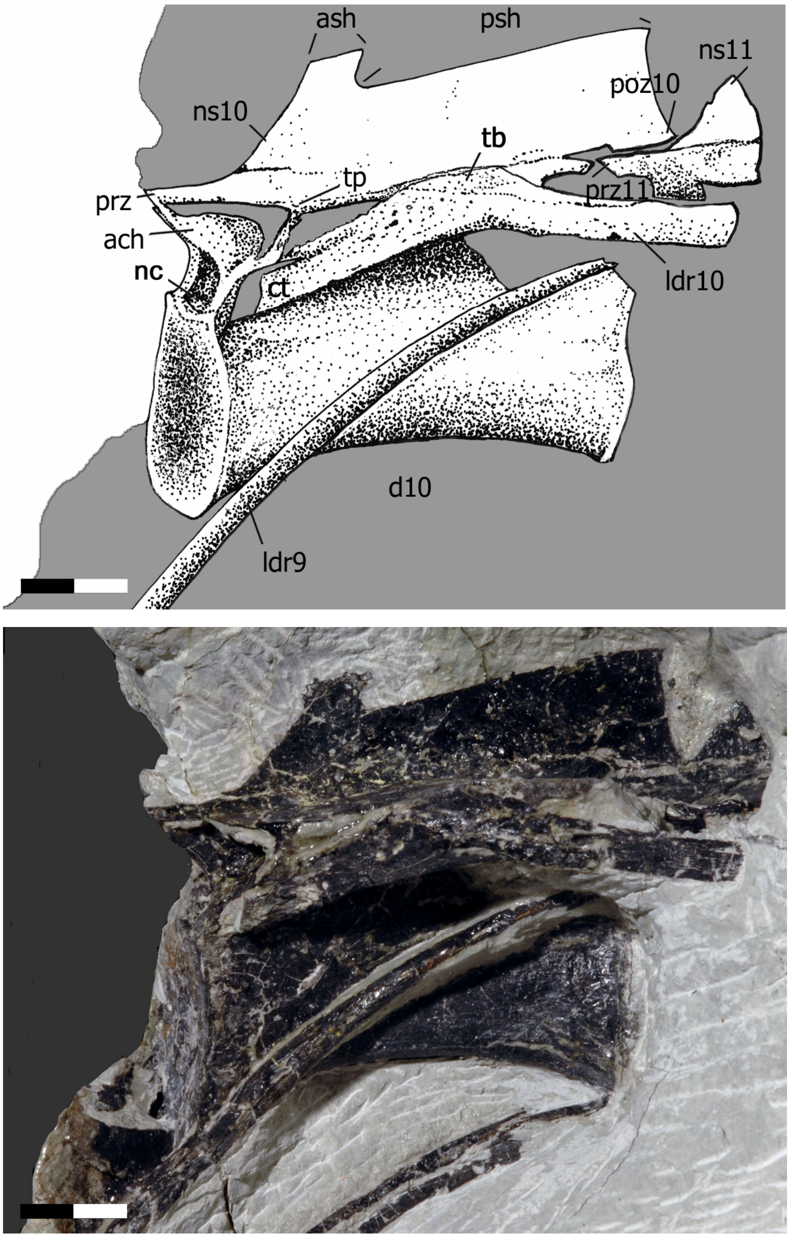


Figure 14: the left lateral side of dorsal vertebra 10 as well as portions of the neural arch of dorsal 11, and left dorsal rib fragments 9 and 10 (scale bar 10 mm).

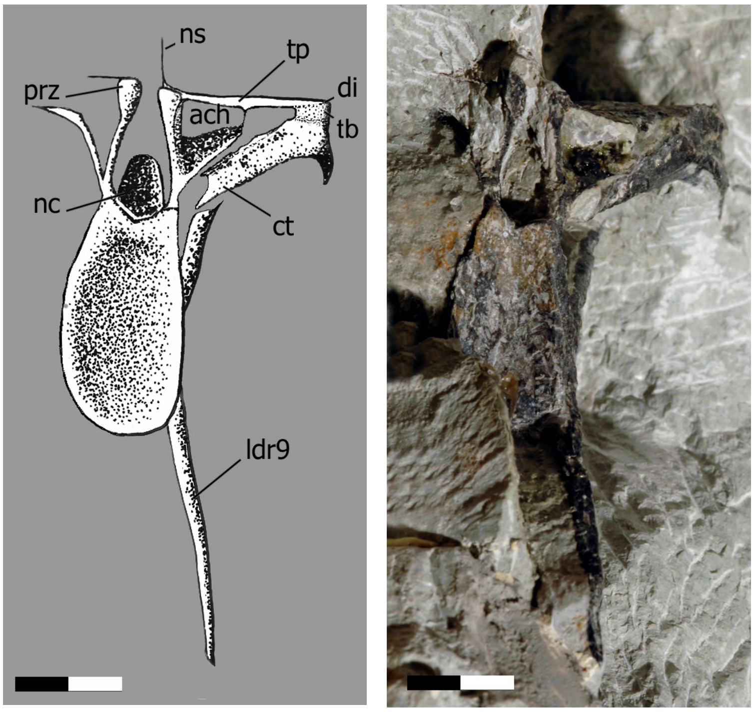


Figure 15: displays the tenth dorsal vertebra from frontal position (scale bar 10 mm).

In the tenth dorsal vertebra only the left transverse process can be seen, due to the right lateral imbedding of the centrum. The anterior margin of this still in physiological horizontal position lying process is back swept as those of its predecessors. In addition to dorsal 2 to 7, the tenth also shows its neural spine in lateral view. However, here it is still visible after the third step of preparation as in dorsal two to four. The measurements of the outline of the left transverse process corresponds to 9 mm (anterior margin), 30 mm (distal border), and 20 mm (posterior rim). The anterior margin is inclined at an angle of 50 degrees in the horizontal plane to posterior direction, the distal border only bends about 20 degrees under the same condition, whereas the posterior rim runs along a distal rounded edge measuring 5 mm in medio-lateral width before proceeding into a concave line which directs towards the caudo-ventral tip of the neural spine.

The neural spine arises 8 mm posterior to the anterior tip of the prezygapophysis, and is highest at its most dorso-posterior tip with a height of 28 mm above the upper margin of the hind end of the centrum. The neural spine is divided into a short anterior (6 mm in length) and long posterior shoulder (33 mm in length) (after Welles 1984: 109) whose dorsal margins each gradually mount at an angle of 23 degrees to the horizontal plane when heading to caudal. The apex of the first shoulder is situated 18 mm behind the cranial border of the prezygapophysis, whereas the second .marks the highest dorsal point of the neural spine. The straight anterior rim of the neural spine increases gradually at an angle of 45 degrees after the caudal border of the prezygapophysis until reaching the upper margin of the first shoulder. The posterior border is slightly concave measuring 11 mm. The caudo-ventral tip of the neural spine runs forward into the articulation facet of the postzygapophyses.

The neural canal including contained matrix, is slightly crushed medio-laterally being now 5 mm in width, and 10 mm in height.

The articular surfaces of the prezygapophyses show straight dorsally strongly aligned horizontally. When viewing these processes from above, they are 3 mm separated from each other. The left postzygapophysis still lies in perfect articulation with its counterpart of the successive vertebra. The distance between the postzygapophyses cannot be seen. The articulation facets of the zygapophyses are at exactly the same level as the basis of the neural spine. While the prezygapophyses do only slightly extend over the anterior articular face of the centrum by 2 mm, the postzygapophses overlap its posterior face three times the length of the former.

The fragmented right rib is only available with 50 mm of its distal shaft lying on the lower side of slab A.

Eleventh dorsal vertebra and ribs

fig.16A&B

The eleventh dorsal vertebra still is mainly hidden in the clay. Only the Computer Tomography pictures indicate its centrum length measuring 42 mm along the ventral margin. Its neural arch surely is located dorsally to the centrum, but whether it is articulated to the latter or being slightly separated to it can not be said. The elements visible to the naked eye consist of the left prezygapophysis as well as the most anterior portions of the neural spine and the left transverse process. As already mentioned above, the left prezygapophysis is still articulating with the left postzygapophysis of the tenth dorsal vertebra. Both articular areas measure 7 mm. The anterior margin of the neural spine 11 rises the same way as seen in dorsal 10 at an angle of 45 degrees. However, in the eleventh dorsal vertebra only the cranial 9 mm of this border are visible. The rest is hidden in the sediment. The transverse process exhibits 21 mm of its anterior border vanishing into the matrix as well.

The right dorsal rib 11 exhibits its most proximal portion: the fragment belongs to the area distal to the branching and comprises a size of 18 mm x 15 mm x 11 mm. This preserved portion lies next to the right rib of the ninth dorsal vertebra.

Twelfth and thirteenth dorsal vertebra and ribs

fig.16A&B

Dorsal vertebrae 12 and 13 are completely hidden in the matrix and only visible on Computer Tomography pictures. The pictures only reveal their approximate ventral centrum lengths measuring 41 mm and 38 mm, due to the non successive segmentation (see «9.1. Computertomography»). However, their neural arches are not only present, but seem to articulate to the centra.

A

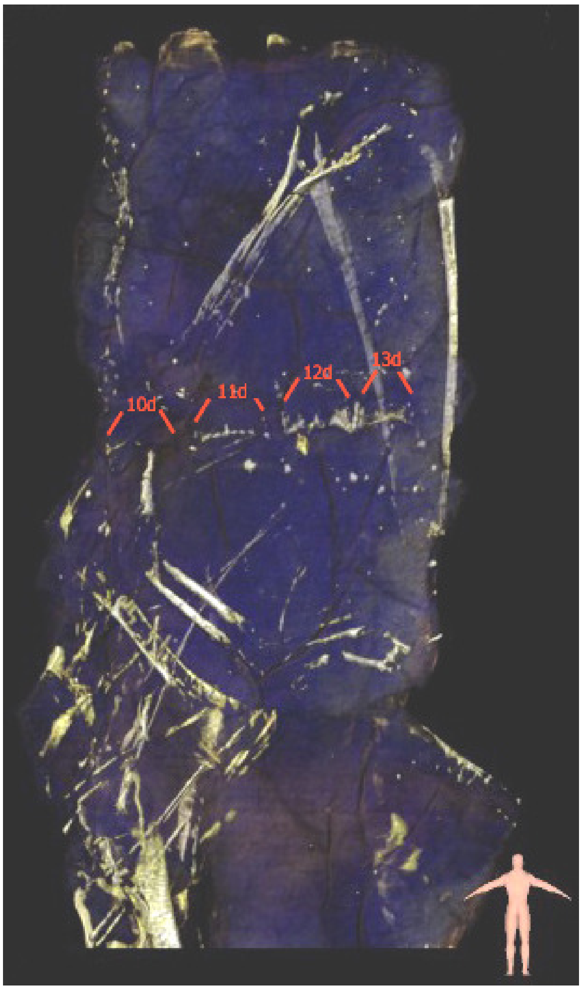
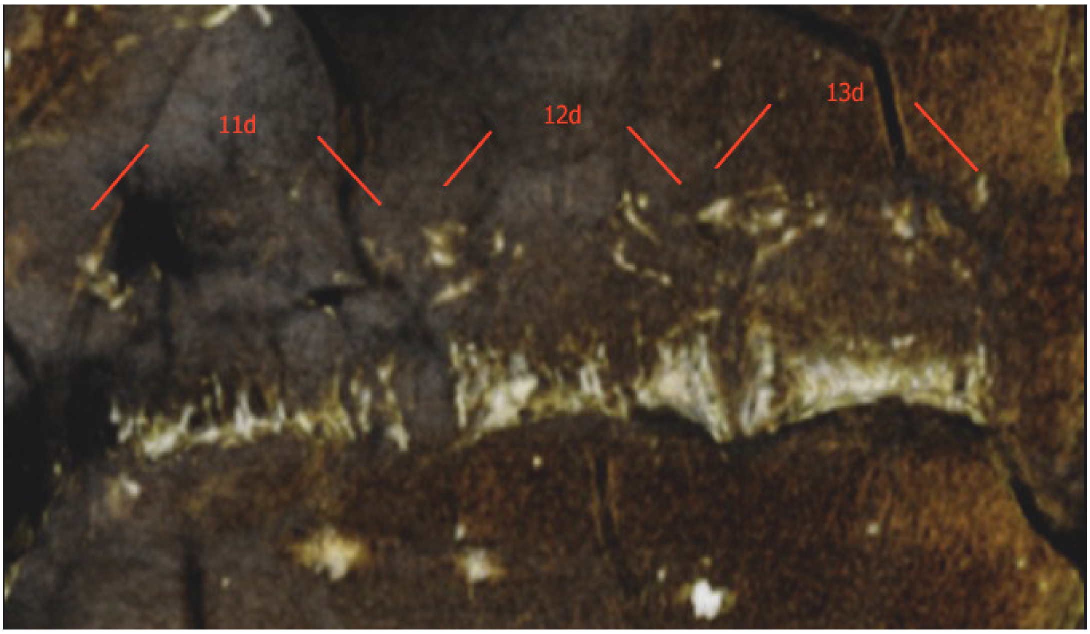


Figure 16A: shows one of the resulting pictures of the X-ray Computer Tomography performed at the Hospitality of the University of Zurich. The red numbers stand for the corresponding dorsal vertebra 10 to 13.

Figure 16B: The three still hidden in the matrix dorsal vertebrae in more detail (dorsal 11-13).

B



There are two right rib fragments, which are located posterior to the right rib sequence of dorsal vertebrae 8 to 11 on the lower side of slab A. These two remains belong to the dorsal ribs 12 and 13.

The fragmented rib of dorsal 12 measures 61 mm along its anterior rim showing the proximal branching and most parts of the capitulum, whereas the portion of the dorsal rib 13 exhibits 69 mm along its posterior shaft margin.

8.1.3. Gastral ribs

The gastral or abdominal ribs of the Swiss theropod material are not very informative because they are still predominantly embedded in the matrix and, where visible, they are often partially abraded at their ends. In theropods the number of gastral ribs ranges from approximately 8 to 21 metameric rows depending on size of each species. Each row consists of four bones: two lateral and two medial rods. The gastral ribs located cranial- and caudalmost are coalesced. However, these ribs are not different in outline from the rest of the abdominal ribs, which are all characteristically boomerang-shaped forming a basket ranging from the posterior edge of the sternum (pectoral girdle) to the distal end of the pubes (pelvic girdle). Gastral ribs of theropods normally show ventral cranio-distal grooves and have articular facets located either medio-dorsally or medio-ventrally (CLAESSENS 2004). However, none of these morphological features are recognizable in any gastral rib fragment of the material under study.

In the Swiss theropod material a great quantity of gastralia is preserved: there is an amount of at least 19 abdominal rib fragments directly lying near the distal portions of both pubes. These gastral rib remains are located in two groups of nine and ten ribs crossing each other. Thus, although the abdominal ribs are now totally disarticulated, the former ventral basket is still apparent. The area on slab A (lower side) containing all ribs amounts to 95 mm in length and 55 mm in width.

The length of each gastral rib preserved cannot be estimated due to the imbrication of these skeletal elements with matrix and their partial weathered ends. In contrast, the antero-posterior width can be measured, ranging from 0.4 mm to 2 mm. The narrower ones still lie directly anterior to the distal ends of both pubes as in vivo, ranging up their size proportionally, ranging in size proportionally regarding widths and lengths in a cranial direction. All of the preserved abdominal ribs are metameric and have only been slightly disordered in the rows themselves. Although the medial and lateral ribs are disarticulated, they still lie close to each other. No further preparation can be guaranteed, because the available gastralial ribs are extremely thin.

8.1.4. Sacral region

In the Swiss theropod material four sacral centra and five neural arches are available on slab D. Two sacral centra, which are still nearly associated to their neural arches, are named as sacral 4 (sacral 2, sensu WELLES 1984; equal to sacral 2 of basic construction of Reptilia) and sacral 5 (caudosacral 1, sensu WELLES 1984), whereas two centra that are isolated from their neural arches are called sacral 2 (dorsosacral 2, sensu WELLES 1984) and sacral 3 (sacral 1 sensu WELLES 1984; equal to sacral 1 of basic construction of Reptilia). The centrum of sacral 1 (dorsosacral 1, sensu WELLES 1984) is not preserved. Only a fragmentary portion of the neural arch of sacral vertebra 1 is present. The upper side of slab D bears the sacral centrum 3 and the neural arches 4 and 5, whereas the lower side displays the centra 3 to 5 and neural arches 1 to 3.

The preserved vertebrae of the sacral series, which exhibit more or less the same length, are slightly shorter than those of the dorsal series that expand their lengths posteriorly. In fact, the sacrals are the shortest of all considered vertebrae of the Swiss theropod material. A further difference between the other centra of the vertebral column and those of the sacrals is the morphology of the anterior and posterior articular faces. The latter are vigorously expanded in all directions being fully platycoelous. Only the faces of the third sacral seem to be slightly amphicoelous probably resulting from diagenesis. All sacral centra become narrow immediately caudal to the anterior or cranial to the posterior faces producing a much more extreme spool-shaped form as seen in the dorsal vertebrae.

The horizontally aligned sacral ribs 2 (modified transverse process, sensu WELLES 1984), 3 and 4 (true sacral ribs, sensu WELLES 1984; equal to sacral ribs 1 and 2 of basic construction of Reptilia) as well as 5 (modified transverse process, sensu WELLES 1984) are preserved. In contrast to the transverse processes of the dorsal vertebrae, which become distally narrower, the lateral appendages of the sacrals are intensely expanded distally to antero-posterior tending to affiliate each other. Since the sacral ribs are still separated from each other, the fourth rib exhibits additional cavities on its distal and posterior border. Some sacral ribs display proximal weak developed, short transverse ridges.

Four neural spines of sacral vertebrae (2 to 5) are available. The uppermost parts of the processi spinosi 2 and 3 thicken distally. Although, these neural spines are rather abraded and shortened in height due to dorso-ventral compression, it is assumed that spine tables were originally developed. As already seen in the sacral ribs, the neural spines were also not fused to each other during life time.

First sacral vertebra

The first sacral vertebra is only present by a small, not closer determinable portion of its neural arch. This fragment is located at a right angle to, and 12 mm away from the neural arch of the third sacral vertebra and measures 34 x 23 mm at its largest diameters.

Second sacral vertebra and ribs

fig.17A&B, 19A&B

Although the second sacral centrum only exhibits its flattened ventral, a lateral, and a frontal side, it is the best visible of its kind available. The fully exposed platycoelous articular face measures 24 mm in width and 17 mm in height, whereas the hidden one adds up to 25 mm along the ventral margin. The articular faces lie at a distance of 30 mm away from each other measured along the lower rim of the centrum. The latter is constricted to a width of 12 mm at its mid-length. The still well preserved ventral expansion of the anterior and posterior articular faces confirms the fact that the influences of the diagenetic processes on the morphology of the centrum were slight and that, therefore, the resulting dorso-ventral compression was negligible. Thus, the flattened ventral side of sacral centrum 2 as well as the transverse-rectangular shape of its fully exposed articular face mirror the original habitus. When viewing the bone from lateral position, a distinct, oval fossa is visible. This concavity is located at mid-centrum height and length, measuring 10 mm vertically and 17 mm horizontally.

The neural arch of sacral 2 is situated approximately 43 mm away from its associated centrum. In addition, it is still coupled with the neural arch of sacral 3.The neural arch 2 lies half embedded in the matrix showing its neural spine and its right sacral rib. The slightly forwardly bent anterior margin of the neural spine measures 12 mm in length. The top of the spine is impressed and abraded from above thus showing the inner of the original spine table. The imprinting results in a width of 6 mm at the beginning and 4 mm at the ending of the dorsal margin of the spine. The un-weathered left upper border of the spine table is convex.

The right prezygapophysis measures 7 mm in length along its medial border, whereas its lateral rim is confluent with the anterior margin of the right sacral rib. The posterior border of the right sacral rib is inclined to the anterior at an angle of 45 degree to the neural spine. The sacral rib 2 is not very well preserved and thus only the length of its base and posterior border can be established measuring 21 mm and 25 mm, respectively. The latter is in turn confluent with the right postzygapophysis, which is hard to recognize as this region is extremely tenuous, having been barely compressed during diagenesis.

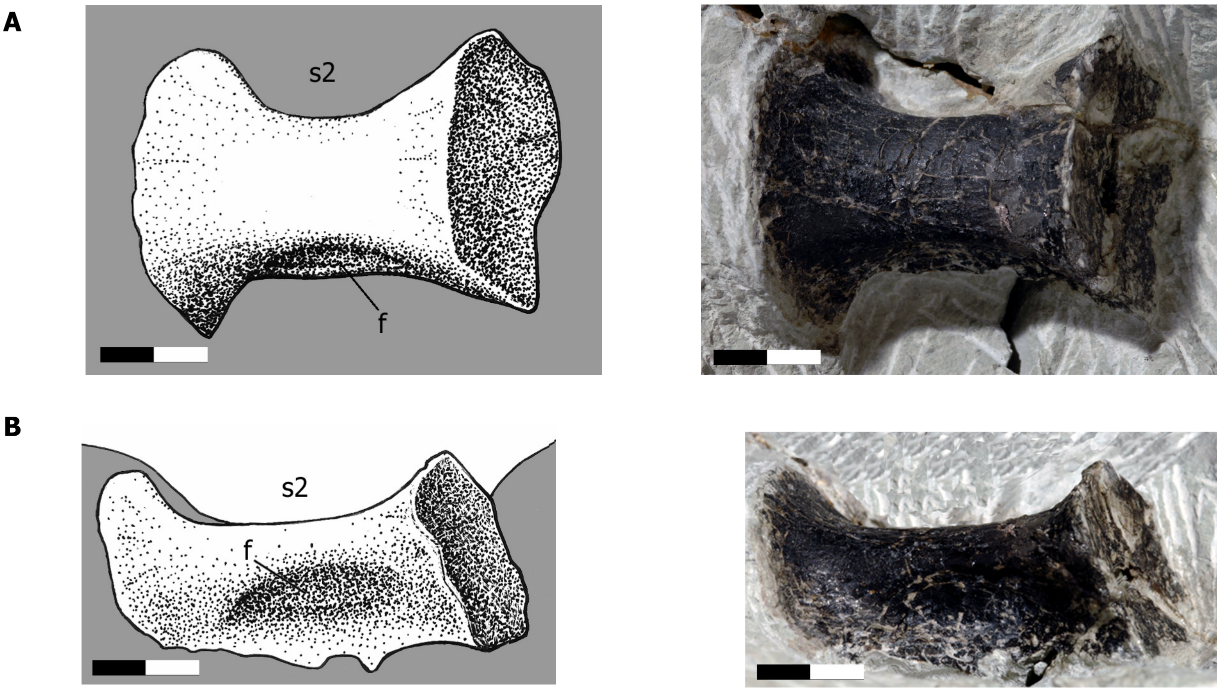


Figure 17A: displays the full ventral and one partial lateral side of the centrum of sacral vertebra 2 (scale bar 10 mm).

17B: here, the large oval fossa can be seen on the matrix free lateral side (scale bar 10 mm).

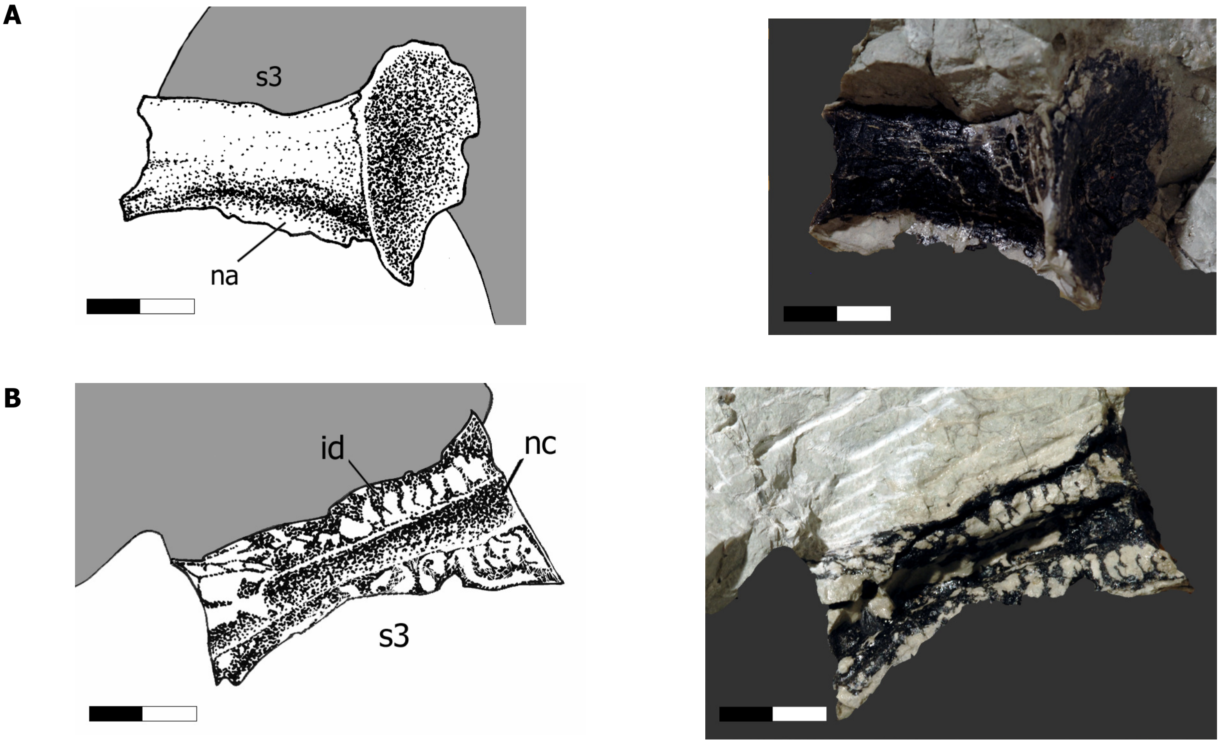


Figure 18A: the lateral side of sacral centrum 3 showing one of its amphicoelous articular faces (scale bar 10 mm).

18B: upper view on interdigitations and the neural canal of sacral 3 (scale bar 10 mm).

Third sacral vertebra and ribs

fig.18A&B, 19A&B

The centrum of sacral 3 is embedded with one lateral and partially ventral side. The length of the centrum measures 30 mm along its dorsal margin, whereas its height at mid-section adds up to 10 mm. Both articular faces are free of matrix and are more or less fully conserved. The expanded areas of the amphicoelous articular faces display an oval outline being wider than tall. The articular face directing to the fourth sacral vertebra adds up to 19 mm in height and 21 mm in width, whereas the other one is 15 mm in height and 24 mm in width. When viewing the centrum from dorsal position, there are serrations visible belonging to the neuro-central suture, which connected the former with the neural arch. These interdigitations count up to at least 14 on the well preserved half of the sutural area. Therefore, it is assumed that in this vertebra the total number of serrations is at least 28.

The left and the right sacral rib are not completely preserved. The left sacral rib only displays approximately its caudal half. The available portion of the posterior margin measures 26 mm in length and is bent to caudal at an angle of 60 degrees to the sagittal plane of the vertebra. The distal rim of the left sacral rib is parallel to its base measuring 23 mm in length. The preserved part of the right sacral rib extends 6 mm along its posterior margin, adds up to 26 mm along its preserved distal rim located parallel to the neural spine basis, and measures 17 mm in length along its anterior border. The right front rim is inclined at an angle of 60 degrees in an anterior direction, being exactly the opposite to the left hind border. The right sacral rib is distallo-posteriorly incompletely ossified due to the early ontogenetic stage of the specimen under study. The resulting rectangular recess measures 10 mm along its anterior length and 8 mm medially. The right postzygapophysis, which can surely be recognized at the proximo-posterior margin of the sacral rib looks like a narrow and high isosceles triangle when viewed dorsally: its 8 mm long legs represented by the lateral and medial rim, whereas the posterior width adding up to 2.5 mm, reflects the triangle base.

Though the neural arch of the third sacral vertebra is disarticulated from its centrum, it is still articulated to the neural arch of the second sacral vertebra. The neural spine of the third sacral vertebra measures 17 mm at largest height along its caudal border, whereas its base adds up to 31 mm in length. The distally convex spine table is partly eroded and dorso-ventrally compressed. The anterior width of the spine table measures 7 mm.

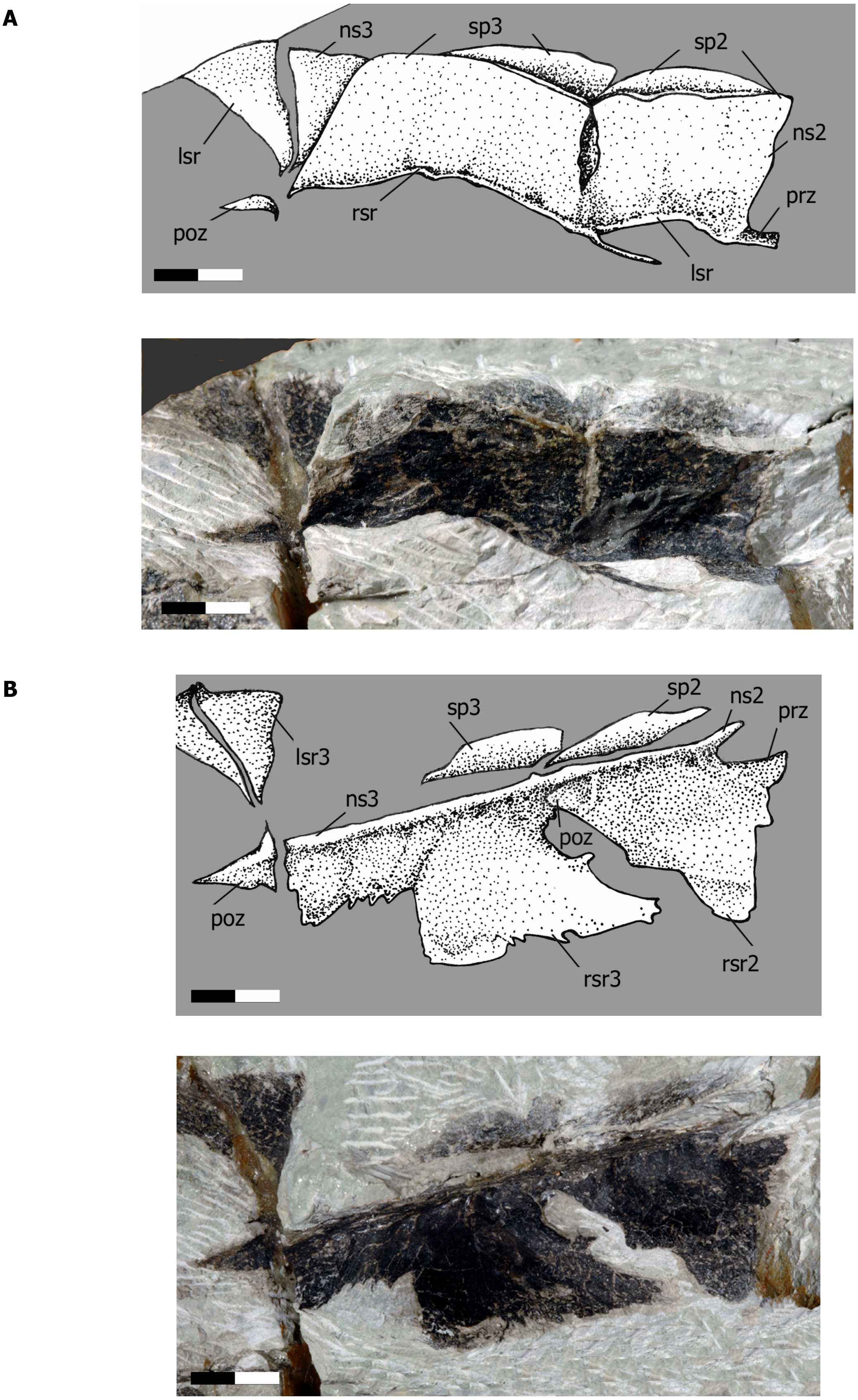


Figure 19A: right lateral view on the neural arches 2 and 3 with the compressed and partly eroded spine tables (scale bar 10 mm).

19B: the sacral ribs, which were not ossified to full extant, spine tables, pre- and postzygapophyses of sacral vertebra 2 and 3 (scale bar 10 mm).

Fourth sacral and ribs

fig.20-22

The fourth sacral vertebra is situated next to the fifth. The sacral centrum 4, which lies on its right lateral side, measures 31 mm in length along its ventral margin. The height of the mid-section of the centrum that adds up to 20 mm is medio-laterally highly deformed as well as the anterior and posterior articular faces, which are only present by their left lateral borders including partially their dorsal and ventral ones. The height of the posterior articular face is 25 mm and the width along its ventral rim adds up to 27 mm, whereas the anterior one is medio-laterally flattened to a great extant, leaving it unknown where the lateral side of the centrum ends and the ventral margin begins. By reason that both articular faces cannot be seen in frontal view, it is unknown if they are amphicoelous or platycoelous. When viewing the centrum from lateral position, there seems to be no oval fossa present at its mid-height and -length. The absence of this groove could either be a result of diagenetic processes or biological fact.

The neural arch is separated from its centrum by a distally convergent crevice ranging from 2 to 6 mm in height. The lower margin of the neural arch, which is also the upper part of the neuro-central suture, possesses serrations, whereas its facing side on the centrum is too eroded to make an assumption regarding its morphology. There are approximately 20 visible interdigitations of the upper border of the neuro-central suture bearing one outstandingly large tooth at mid-length as seen in dorsal vertebrae 6 and 7. The contact of the neural arch to the centrum measures 29 mm in length.

The left sacral rib, the processus spinosus and both prezygapophyses of the fourth sacral vertebra are preserved. The other portions of the neural arch are still in the matrix, or are missing. Sacral 4 can be recognized by a round cavity at the distal border of its left sacral rib, with an antero-posterior width of 9 mm and a depth of 8 mm. None of the other sacrals of the Swiss theropod material, whose corresponding regions are conserved, show anything comparable. This cavity of the sacral rib, which originally may have been filled with cartilage, is located 20 mm away from the basis of the neural arch. The anterior margin of the cavity is located 16 mm caudal to the cranio-distal edge of the sacral rib, whereas the latter is 15 mm away from the neural spine. The 15 mm also match the length of the concave anterior rim of the left sacral rib. The concave posterior border of the latter adds up to 32 mm, whereas its caudal portion of the distal margin measures 14 mm, until reaching the posterior rim of the cavity. The anterior border of the left sacral rib is perpendicular to the base of the neural spine, whereas its posterior counterpart runs obliquely in a caudal direction. The distal margin, which encloses the cavity, is inclined at an angle of 45 degrees to posterior with regard to the sagittal plane of its centrum. Since the caudal rim of the left sacral rib is concave, a gap is found between the former and the cranial margin of the subsequent sacral vertebra.

The neural spine of the fourth sacral vertebra is distally abraded as seen in the same structure of the fifth sacral vertebra. The cranial rim of neural spine 4 starts 9 mm behind the front end of the right prezygapophysis, and lifts dorso-posteriorly up along 21 mm. The succeeding dorsal margin of the preserved part of this process adds up to 16 mm in length being slightly tilted to ventral, whereas its 17 mm long caudal border stands vertically on the basis of the neural arch. The above mentioned prezygapophyses, whose articular areas are not well preserved, measure approximately 7 mm along their medial antero-posteriorly proceeding rims.

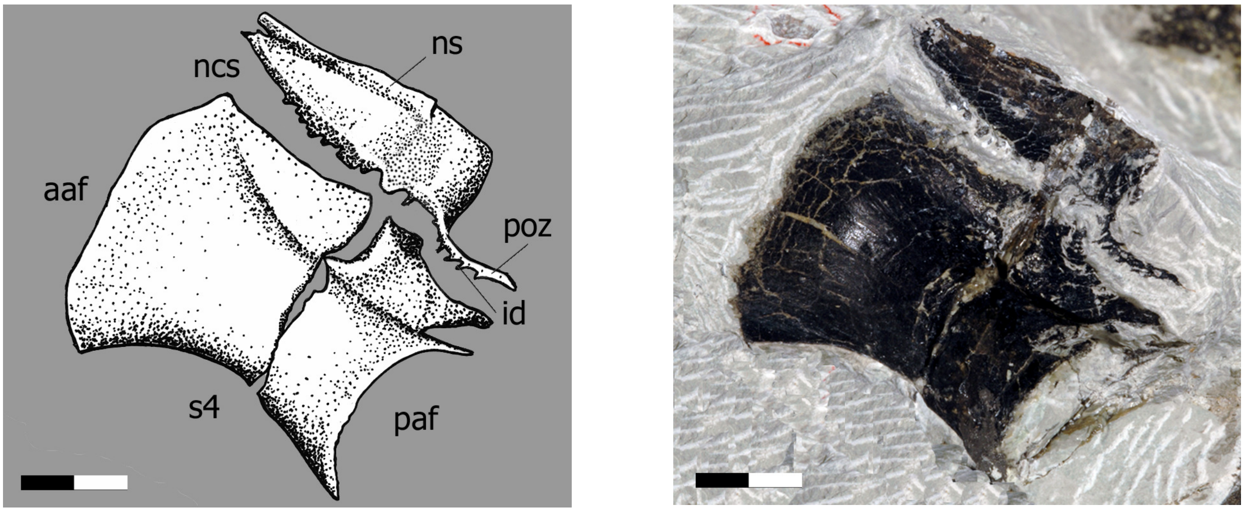


Figure 20: left lateral view of sacral vertebra 4; the centrum and neural arch are still closely situated showing interdigitations along their neuro-central suture borders (scale bar 10 mm).

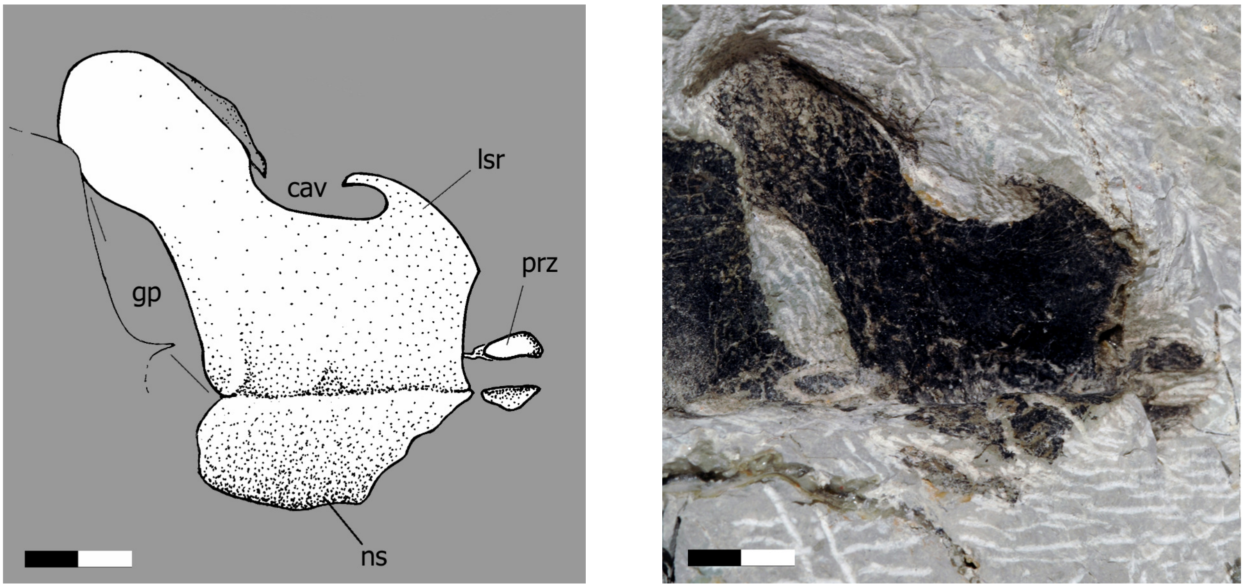


Figure 21: the dorsal position of sacral vertebra 4; here, the neural spine, the left sacral rib as well as both prezygapophyses are visible (scale bar 10 mm).

Fifth sacral vertebra and ribs

fig.22, 23A, B&C

The fifth sacral centrum lies on its dorsal side, hiding its right lateral and anterior aspects by the sediment. While the neural arches of the fourth and fifth sacral vertebrae are articulated to each other, their centra are situated at most 20 mm apart. The vertebral body of sacral 5 is cleaved from its right cranio-dorsal tip to the right caudo-ventral edge, not affecting the ventral length of the centrum which adds up to 31 mm. In addition to this disruption of the centrum, a medio-lateral compression during diagenesis took place. The centrum is pinched to a width of 11 mm at its mid-length, where it shows a height of 14 mm. The anterior and posterior articular faces of the centrum are compressed as well. The still fully hidden anterior articular face exhibits its left lateral and ventral margins being 23 mm and 7 mm in length, whereas the visible platycoelous posterior one displays its oval outline measuring 24 mm and 17 mm in sagittal and frontal planes, respectively.

The neural arch displays its left sacral rib, its neural spine and its left prezygapophysis. When viewing the preserved sacral rib from dorsal position, it resembles the shape of the one of the subsequent first caudal vertebra showing a backswept anterior margin, which lies nearly parallel to the posterior border. The anterior and posterior margins are bent at an angle of 80 degrees to caudal measured longitudinally to the centrum. The cranial rim of sacral rib 5 is shorter than its caudal one measuring 24 mm and 33 mm in length. The left sacral rib slightly expands its antero-posterior width from its base of 21 mm to its distal border of 24 mm. The neural spine can only be seen vaguely due its overall highly eroded surface. Its anterior margin, bent 45 degrees to caudal, adds up to 17 mm in length, whereas the dorsal border of the available part of the processus spinosus is horizontal measuring 15 mm in length. Its 10 mm long posterior rim runs along the anterior counterpart at an angle of approximately 45 degrees from distal to proximal into the posterior basis of the neural arch.

The left prezygapophysis of the fifth sacral vertebra is heavily eroded, only allowing an exact measurement of its distal margin, which is 9 mm long.

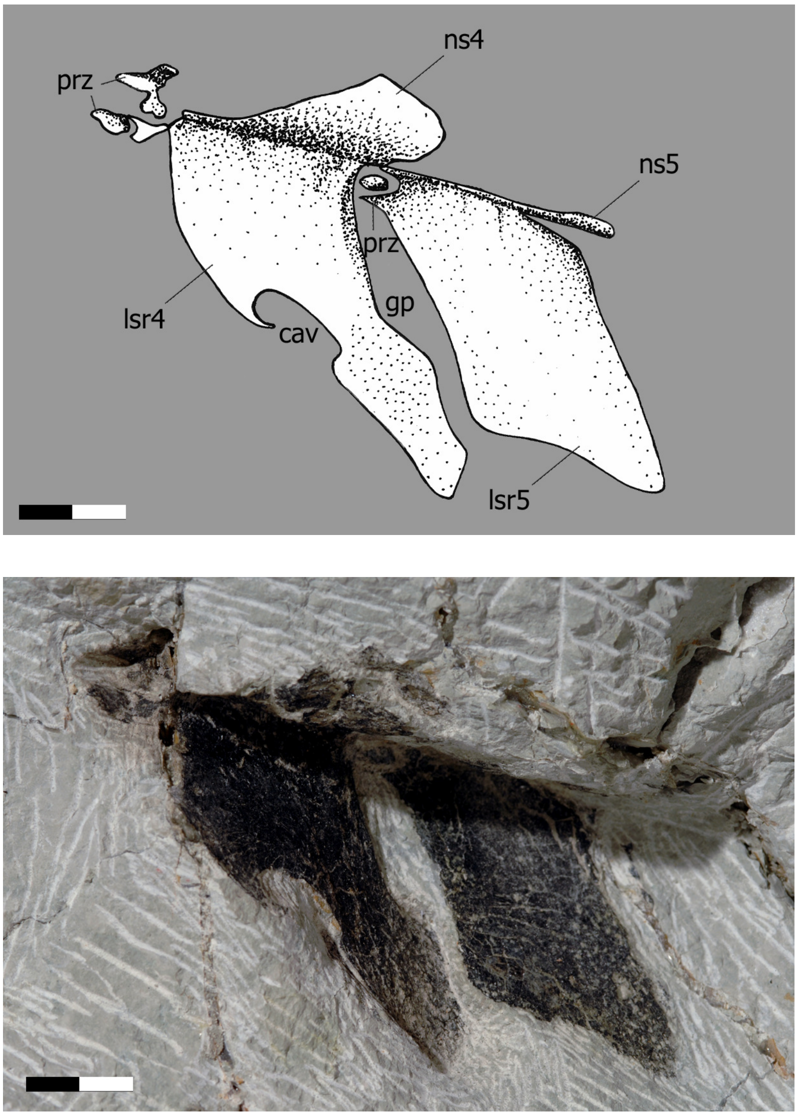


Figure 22: dorsal view on the neural spines and left sacral ribs of sacral vertebra 4 and 5 (scale bar 10 mm).

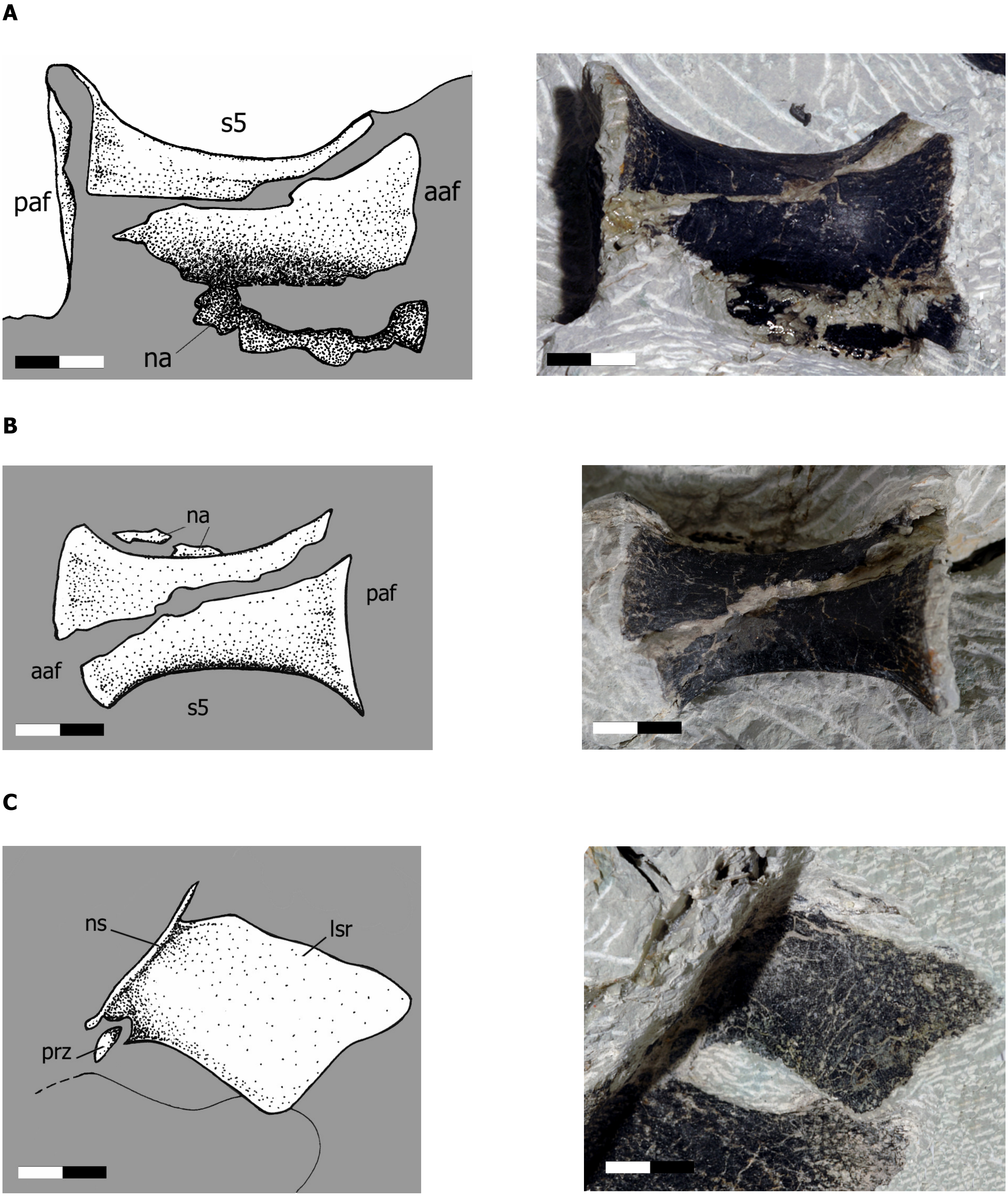


Figure 23A: partial neural arch and left lateral centrum side of sacral vertebra 5 (scale bar 10 mm).

23B: ventral view on centrum of sacral 5 (scale bar 10 mm).

23C: the neural spine and left sacral rib seen from dorsal position of sacral vertebra 5 (scale bar 10 mm).

8.1.5. Caudal region

Four caudal vertebrae are preserved in the Swiss theropod material, the vertebrae lie in a line on slab A and are still nearly articulated: the first, second, third and fourth caudal vertebra are available in left lateral view. Caudal 4 is the single vertebra of this series showing its right lateral and entire ventral side, whereas caudal 1 to 3 only exhibits this aspect partially. The dorsal view can be seen in caudal vertebra 1 and 2. The fourth caudal is the worst vertebra available of this series displaying a laterally damaged centrum resulting in an antero-posteriorly elongated defect.

The centra of the caudal vertebrae are medio-laterally narrow all over their lengths when viewed from dorsal position, whereas when considering the lateral sides their heights are constant and very low, being only ventrally expanded at their faces. These constant heights are associated with an accession of the centrum lengths, these range from 28 mm to 33mm when heading caudally. All articular faces of the centra are amphicoelous.

Each visible lateral side of the caudal centra exhibits one shallow longitudinal fossa with a deep median channel proceeding antero-posteriorly along the centrum below its centro-neural suture. The channel as such measures 0.5 mm in height, whereas the whole depression including the channel adds up to 4 mm in height. In addition to these depressions, the distallo-ventral portions of every caudal vertebra show an emargination, which is laterally flanked by small antero-posterior ridges for attaching the y-shaped chevrons to the centrum. The emargination migrates into a narrow but sharply defined ventral groove measuring 2 mm in medio-lateral width and proceeding along the entire antero-posterior centrum length where it thins out distally to a width of 1 mm.

The proximal bases of the transverse processes can be seen in the first (left and right), second (left and right), third (left), and fourth caudal vertebra (left). Compared to the attachment areas of the transverse processes onto the neural arches of the dorsal vertebrae, the caudal transverse processes are fixated much more posteriorly on the neural arches. The transverse processes of the caudal vertebrae gradually decrease their medio-lateral width to posterior with the increase of the antero-posterior length of their corresponding centra to the same direction. The transverse processes of the first three caudal vertebrae are approximately 45 degrees bent to dorsal regarding to the horizontal plane. Additionally, the processes of caudal 2 and 3 are standing at a right angle to the sagittal section of their corresponding centra. Each transverse process of the caudal vertebrae is enforced with two struttings (anterior and posterior lamina) located both underneath it, on the lateral sides of the neural arch. In the sequence of the transverse processes of caudal 1 and 2 a distinctive changing in shape occurs when viewing from dorsal position: whereas the right transverse process of the first caudal vertebra is constant in antero-posterior expansion all over its length, the appropriate processes of caudal 2 and 3 broaden antero-posteriorly at their distal ends.

The either damaged or still mostly covered neural spines of the preserved caudal vertebrae are low. These structures were probably slightly higher during life time, but diagenetic processes have shortened them resulting in a loss of several millimetres in height. The articular facets of the pre- and post zygapophyses are visible either to the dorsal or ventral respectively, being placed on sockets disposed from the neural arches.

The Swiss theropod material shows four well developed and cranially forked chevrons (haemapophyses) almost perfectly preserved measuring at least three to almost four times the height of the articular faces of their corresponding centra. Each chevron bears two articular facets at its proximal basis for attaching to the emarginations and lateral ridges of the postero-ventral part of the caudal sides of the centra. Additionally, there is a distinct process anterior to the proximal articulation facets of each haemapophysis, which does not articulate with the caudal vertebrae (RAUHUT 2003). Three of these four chevrons (1 to 3) are preserved completely and only the fourth is broken and its proximal part is missing. The first chevron is shorter in length than its successors; in contrast, it is cranio-caudally wider at its most distal portion than the other. This series of four chevrons shows that they become longer and all over their length antero-posteriorly smaller when heading caudally. The distinctive changing in shape of the chevrons is gender specific and occurs between chevron 1 and chevron 2.

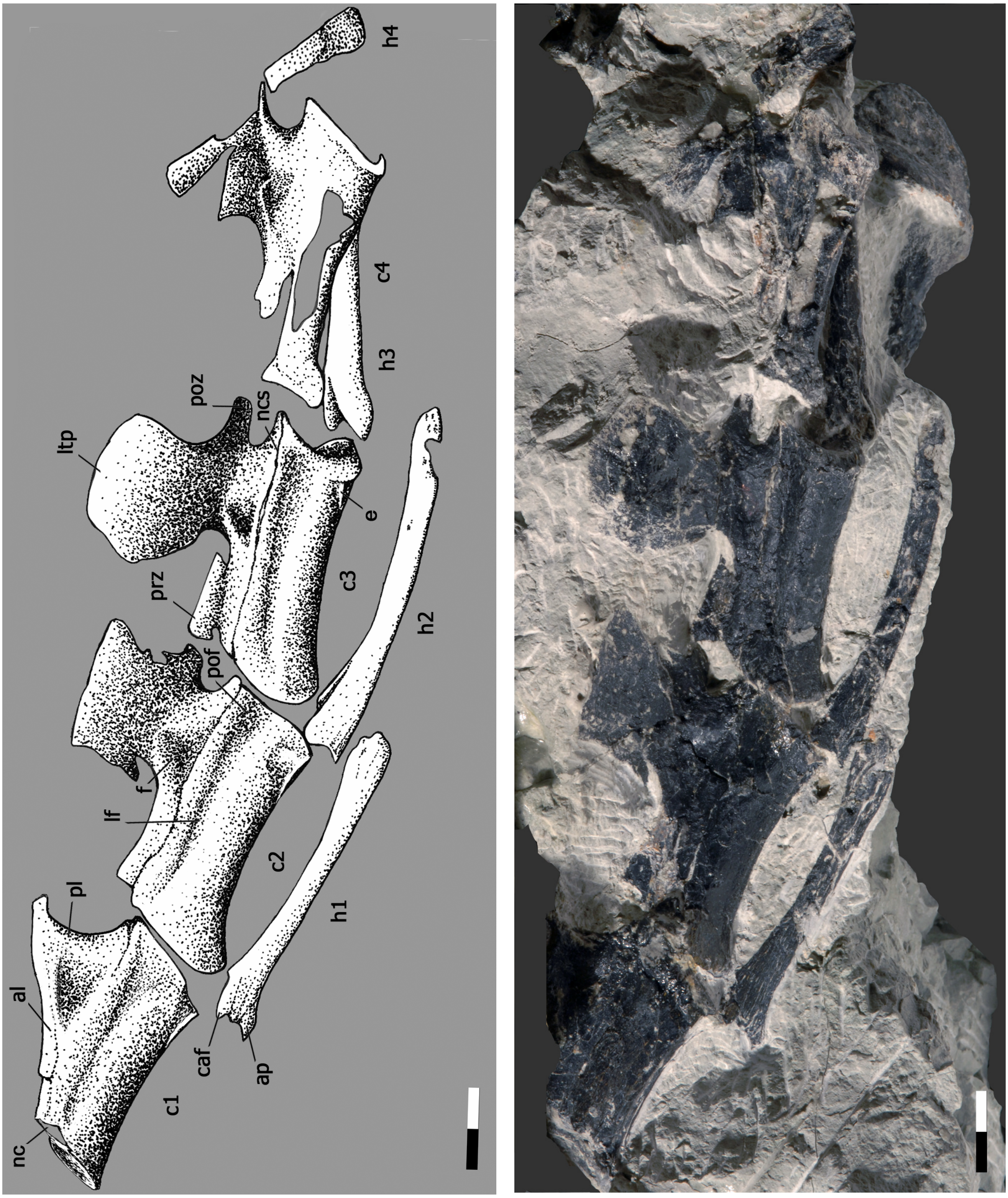


Figure 24: caudal series consisting of vertebra 1 to 4 and their chevrons all seen from left lateral position (scale bar 10 mm).

First caudal vertebra and chevron

fig.24-25

The first caudal vertebra is the shortest in length of all the caudals available. Its centrum only measures 28 mm along its ventral margin. The fully exposed anterior articular face adds up to 11 mm in width and 10 mm in height, whereas the posterior articular face only displays its left lateral margin, measuring 15 mm in height, The longitudinal fossa on the centrum proceeds along the whole antero-posterior length of the latter, with its dorsal border at approximately 2 mm underneath the neuro-central suture. The groove runs linearly during the first anterior 12 mm with a constant height of 2 mm, before it broadening ventrally Although the upper margin stays roughly straight, the lower rim descends ventrally. This changing of the lower border of the longitudinal fossa seen in the first caudal vertebra also takes place in at least the two caudal vertebrae that directly follow. The caudally broadened groove terminates less than 2 mm anterior to the hind end of the centrum.

The remains of the transverse processes of caudal vertebra 1 can either be seen from their ventral or dorsal side. The whole right transverse process, which is bent upward at an angle of 45 degrees to the horizontal plane, is present from dorsal, while only the proximal base of the left process is available and visible from ventral. In contrast to the transverse processes of its three successors, the antero-posterior width of the entirely preserved right transverse process of caudal 1 does not become broader distally when considered from dorsal position. Its width measures 11 mm constantly. Thus, the anterior and posterior margins of this transverse process lie parallel to each other, being additionally, slightly swift backwards at an angle of 20 degrees to the transverse plane of the corresponding centrum. The right transverse process of the first caudal vertebra bears 34 mm in length along its anterior margin and 24 mm measured along its posterior rim.

There is a triangle-shaped cavity located on the neural arch underneath the anchorage of the left transverse process, directly above the neural suture, which defines its ventral base, as seen in both caudals 2 and 3, and only partially in caudal 4. The outline of this fossa measures 8 mm along its antero-dorsal margin. The length of its postero-dorsal rim is 6 mm, whereas its basis adds up to 7 mm. The measurements create a triangle-shaped cavity with a long base and long leg, and one shorter leg producing a lying acute-angled triangle. The struttings, which frame the anterior and posterior margins of the fossa, are directly pending with their dorsal converging tips to the anchorage of the transverse process. These fore lamina measure 9 mm in length, whereas the hind one adds up to 7 mm.

The heavily damaged neural spine of caudal vertebra 1 is seen from its right lateral side. Its cranial margin starts 10 mm behind the anterior articular face of the centrum, bending posteriorly at an angle of 45 degrees and measuring 31 mm in length. The uppermost part of the front rim of the spine overlaps the tip of the right postzygapophysis of the neural arch posteriorly by 6 mm, before running acute-angled into the posterior border, which measures 13 mm and descends at a more or

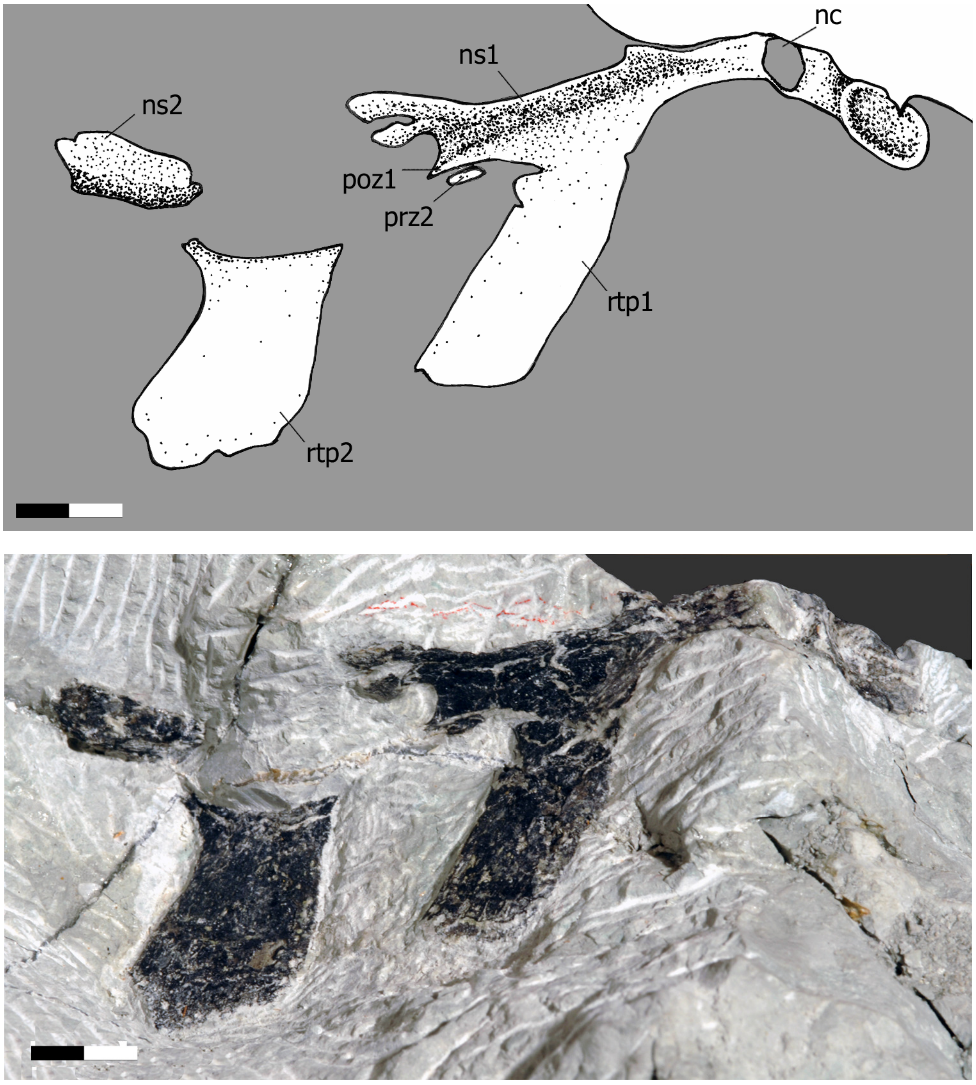


Figure 25: caudal vertebra 1 and 2 seen from right dorso-lateral position showing their different transverse processes' shapes (scale bar 10 mm).

less right angle to the horizontal plane of the centrum. The base of the neural spine measures 25 mm antero-posteriorly.

The base of the neural spine recoils 5 mm from its posterior rim to anterior, where it proceeds into the upper margin of the right postzygapophysis. The antero-posterior articulation length of the right postzygapophysis measures 5 mm, whereas its width adds up to approximately 2 mm.

The height and the width of any neural canal can only be measured in the first caudal vertebra, because it is the single one of this series showing the full aspect of the anterior side of its centrum and neural arch. The neural canal measures 7 mm in each direction.

The chevron of the first caudal vertebra measures 42 mm in length. Its cranio-caudal width ranges from 13 mm along its forked proximal tip, to 4 mm at mid-length, and ends up with 8 mm distally.

Second caudal vertebra and chevron

fig.24-25

The length of the second caudal vertebra adds up to 31 mm along the ventral border. Both articular faces are entirely covered with clay resulting in only having their left lateral and portions of the ventral margins. The height of the anterior articular face measures 14 mm, whereas the posterior one exhibits a height of 15 mm. The 4 mm dorso-ventrally expanded longitudinal fossa on the centrum, which proceeds antero-posteriorly 1 mm underneath the neuro-central suture, is somewhat eroded anteriorly. The borders of the remaining part of the groove run horizontally until reaching a distance of 16 mm proximal to the hind end of the centrum, where they furcate confining a recess. The dorsal margin slightly rises to the upper posterior tip of the centrum, whereas the ventral rim scales down, and ends 7 mm below its dorsal counterpart. The recess measures 16 mm in length at its dorsal and ventral borders and exhibits a caudal height of 5 mm.

Both transverse processes can be viewed from different aspects: the right process can only be seen from dorsal position, whereas the left one merely reveals its ventral side being weathered at its distal margin. Between the first and second caudal vertebra, a changing in the shape of the transverse processes happens: the left and right transverse process of caudal 2 becomes posteriorly broader both at their bases (17 mm, 17 mm) and distal margins (19 mm, 20 mm). Additionally, their anterior rims stand at a right angle to the longitudinal axis of the belonging vertebrae, whereas their posterior borders are slightly back-turned at an angle of 20 degrees to the same axis.

As in caudal vertebra 1, the neural spine of caudal 2 can hardly be recognized, due to dorsal abrasion along its anterior margin and because of the partial embedding into the matrix. Only areas of the spine caudal to the posterior margin of the transverse process are available, measuring 14 mm along its dorsal border, 10 mm at its basis, and 12 mm in posterior height. Neither the accurate position of the neural spine according to the basis of the neural arch, nor its height can be determined. Therefore, it cannot be said if there is a posterior degradation of neural spine height in the caudal series.

Both the complete right pre- and the left postzygapophysis can be seen, whereas the left prezygapophysis is only partly visible. The proximal portion of the right prezygapophysis and the distal rim of the left postzygapophysis are rather eroded and do not display their elongation at full range.

The two laminae, which can be seen on the left side of the neural arch underneath the transverse process, flank as hitherto the neuro-central suture ventrally. Both reinforcements of the neural arch measure 1 mm in thickness and 8 mm in length. The antero-ventral tip of the cranial strutting is located 14 mm posterior to the fore end of the centrum, whereas the postero-ventral tip of the caudal one is situated 7 mm anterior to the hind end of the centrum. The cavity which lies between these two laminae conforms to an isosceles triangle with a slightly longer base of 9 mm.

The chevron of the second caudal vertebra is 48 mm in length, whereas its antero-posterior widths add up to 8 mm at its forked proximal end, 4 mm at its mid-length, and 4 mm at its distal end.

Third caudal vertebra and chevron

fig.24, 26

The centrum length of the third caudal vertebra adds up to 31 mm along its ventral border. Again, neither the anterior nor the posterior articular face can be seen from frontal. Both display their left lateral margins, whereas the caudal one additionally exhibits its ventral rim. The lateral border of the anterior face measures 11 mm, and its posterior counterpart adds up to 12 mm in height. The centrum is not firmly fused, but closely attached to the neural arch.

The antero-posteriorly proceeding longitudinal fossa on the centrum begins here also at centrum mid-height just behind the fore end of the latter. The groove merely soars to a distance of 10 mm away from its initial, then staying horizontally for the next 5 mm, before its borders more separate continuously. As already seen in the other caudals, the upper rim of this fossa proceeds linearly to the dorso-posterior edge of its centrum, while the lower margin of this groove declines until lying 6 mm underneath its upper rim, both enclosing a recess.

Only the left transverse process can be viewed from ventral aspect, whereas its right counterpart remains fully hidden in the sediment. The left transverse process measures 24 mm at both its proximal and distal margins which are equal in length to the complete right one of the second caudal vertebra.

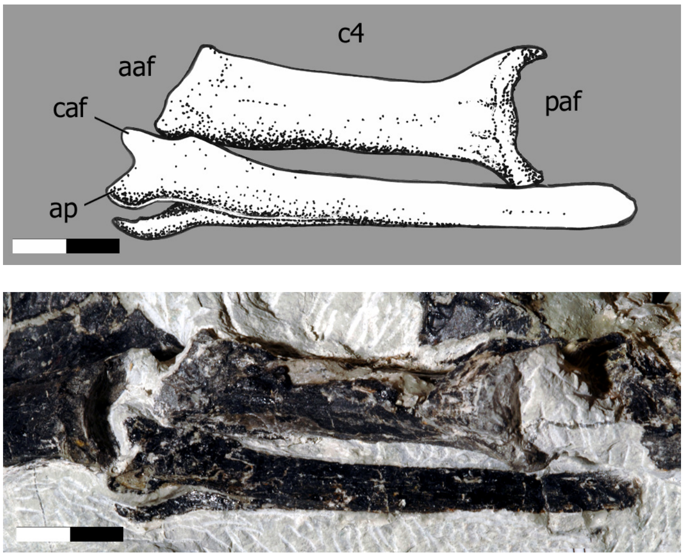


Figure 26: displays the centrum of the fourth caudal with the haemapophysis of its predecessor perfectly showing the anterior process (scale bar 10 mm).

The proximal cranio-caudal width of the transverse process of caudal 3 measures 14 mm, and therefore is 3 mm shorter than its corresponding distal border of 17 mm,

Underneath the base of the left transverse process and above the neuro-central suture two fragile struttings can be seen, adding up to 3 mm in length. The triangle-shaped cavity they surround is much smaller than those seen in its two predecessors: the height only measures 2 mm above mid-basis length, whereas the entire basis adds up to 6 mm. Additionally, the location of this cavity has changed compared to that of caudal 1 and 2: the slightly deepened area has moved more anteriorly along the neural arch, and is now located 17 mm posterior to the beginning of the left prezygapophysis. The distance between the caudo-ventral edge of the fossa and the distal tip of the left postzygapophysis measures 8 mm.

The left pre- and postzygapophyses are displayed almost at extant: the articular areas of the zygapophyses are placed on disposed sockets as seen in the second caudal vertebra. The upper end of the socket of the prezygapophysis is slightly elongated to posterior and even more to anterior, whereas the dorsal rim of the postzygapophysis proceeds seamlessly into the proximo-posterior margin of the transverse process. The articular facet of the prezygapophysis measures 12 mm in length, the corresponding articular facet of the postzygapophysis adds up to at least 7 mm since an unknown caudal part still is hidden by the matrix.

The third chevron is slightly longer (49 mm) compared to the second chevron. Its antero-posterior width adds up to 8 mm at its proximal portion, 4 mm at mid-length, and 2 mm distally.

Fourth caudal vertebra and chevron

fig.24, 26

The fourth caudal vertebra shows its centrum in left lateral and ventral view, and its badly preserved, weathered neural arch. The whole left side of the centrum is collaterally compressed resulting in a crack of 24 mm in antero-posterior length and a fluctuant height of 2 to 4 mm. Despite the badly sustainment, the ventral groove is recognizable as in all caudal predecessors running from the lower posterior emargination of the centrum with its lateral ridges, for the attachment of the haemapophysis, all over the 33 mm entire ventral length of the vertebral body. The anterior and posterior faces of the centrum are only available by their left lateral margins. The former adds up to 13 mm in height, whereas the latter is 12 mm under the same condition.

A small proximal portion of the left transverse process, and therefore its insertion onto the neural arch is visible at its full antero-posterior width measuring 12 mm. The other preserved parts of the left transverse process consist of two fragmented, more distally located pieces of only few millimetres.

The left postzygapophysis is rudimentary heavily abraded at its posterior tip. Thus, no articular facet length can be measured.

The haemapophysis of caudal vertebra 4 is notably dislocated to its natural position, which stands in contrast to those of its predecessors: chevron 4 lies at an angle of 60 degrees, measured from the longitudinal axis of its belonging centrum, pointing downwards with its proximal tip, which is located 12 mm caudal to the posterior articular centrum face. In addition to its dislocation, it is also damaged distally being only 14 mm in length. The antero-posterior widths range from 4 to 9 mm.

8.2. Appendicular Skeleton

8.2.1. Pelvis

All bones of the pelvis are more or less completely preserved and partially covered by the matrix. However, the grade of preservation and preparation does not matter, because all the bones are available twice. Thus, a good description can be made by complementing every element to its counterpart. The pelvis is diagenetically compressed like the other remains of the Swiss theropod.

Both ischia and pubes are almost perfectly conserved: only delicate bone portions of the pubo-ischiadic plate and other small proximal parts of the pubes along their acetabular as well as their iliac and ischiadic facets are missing. In contrast, in both ilia several portions are not complete or lacking. The anterior blade of the left ilium is weathered along its cranial margin, whereas the most caudal tip of the posterior blade is broken off. The right ilium is completely preserved with only a large crack posterior to the pubic peduncle proceeding from ventral to dorsal.

The ilium, ischium and pubis enclose an open acetabulum, whose shape is expected to be round to oval, only interrupted in its circular outline by a caudo-lateral located wedge-like spike, the antitrochanter. The latter is built of two portions (components of antitrochanter, respectively pseudoantitrochanter sensu RAATH 1977) which are either part of the iliac facet of the ischium or of the ischiadic peduncle of the ilium. The function of the antitrochanter is to constrict rotational movements of the femur. In addition, it strengthens the ilium-ischium contact due to the enlargement of the participating articular surfaces.

8.2.1.1. Ilium

fig.27-29

Both ilia are preserved on slab D. The left ilium displays its lateral and partially its ventral side, whereas the right ilium shows its ventral and partially its medial side: the ilium is of dolicho-iliac type (i.e. long and low in shape; sensu COLBERT 1964) typically implying a cranial and caudal extension of the bone. The anterior blade is higher but shorter than the posterior one, which is longer and lower. These expanded areas are dorsally arranged around an open acetabulum while overlapping both the pubic and ischiadic peduncles. Both peduncles are of similar length but differ in their diameter. The iliac margin of the acetabulum is not continuous bearing the upper part of the antitrochanter (iliac component of this process, sensu RAATH 1977) which extends into its circular outline. When viewed from laterally the acetabulum is covered dorsally by an extensive lip, the supraacetabular crest, preventing dorsal movements of the femur. The supraacetabular crest proceeds into a swelled band (caudal rim) upon the external side of the posterior blade flanking its lower border. It continues as a less prominent flaring along the dorsal margin of the posterior blade, before soon vanishing completely. Another swelling affects the ventro-lateral rim of the brevis fossa (= postero-ventral arch), which is a medial shelf originating posterior from the caudo-ventral margin of the supraacetabular crest and functions inter alia for the attachment of the sacral ribs or sacral transverse processes, respectively.

The complete dorsal border of the right ilium measures 180 mm, whereas the conserved part of the corresponding rim of the left cranially and caudally abraded counterpart is 156 mm long. The ilia are differently embedded in the sediment lying perpendicular to each other regarding their longitudinal axes. Due to this condition, the diagenetic mechanisms caused a dorso-ventral shortening of the height in the right ilium and a medio-lateral reduction of the thickness in the left one. Therefore, the description of this bone, which should reflect its original habitus, is based on a mixture of the less affected parts of both ilia. The reconstructed element is, as already mentioned, 180 mm in length, whereas its height measured above the distal end of the pubic peduncle is 85 mm (compared to 68 mm tectonically reduced height of the right ilium), resulting in a length-height ratio of almost 2 to 1.

The height of the vertically aligned cranial rim of the anterior blade of the ilium measures 29 mm. This border runs straight and is slightly inclined with its upper part overhanging 2 mm to the front.

The dorsal margin of the ilium decreases constantly from anterior to posterior at an angle of approximately 45 degrees to the horizontal plane. The ventral rim is much more complicated bearing the pubic and ischiadic peduncles, the supraacetabular crest and the caudal rim (supra acetabular buttress, sensu COLBERT 1989). Additionally, it accommodates the dorsal border of the acetabulum and the brevis fossa.

The ventral margin of the anterior blade begins with a straight horizontal rim measuring 20 mm in length lying cranially to the pubic peduncle. The adjacent dorsal border of the pubic peduncle is

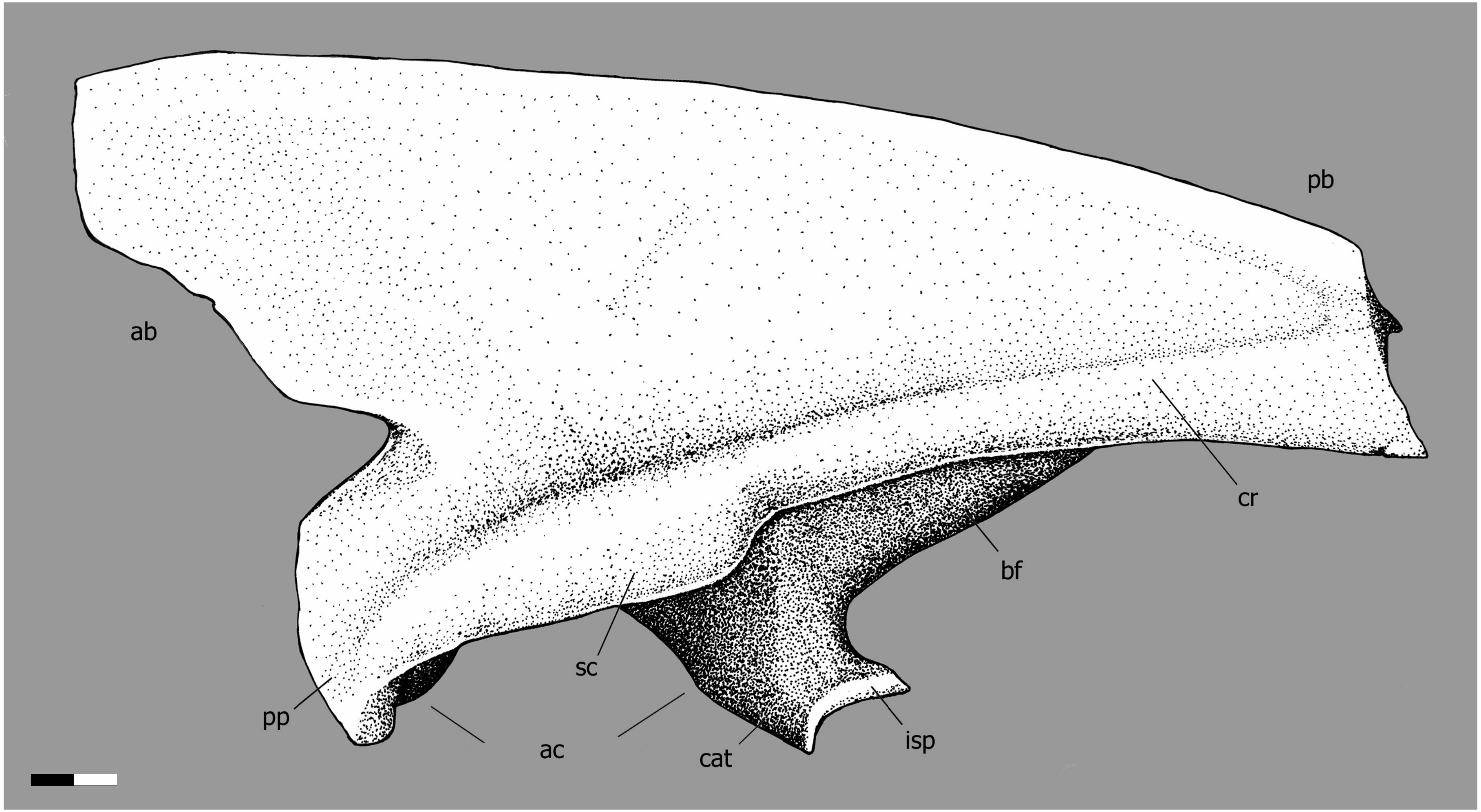

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Figure 27: shows the left ilium from lateral view (scale bar 10 mm).

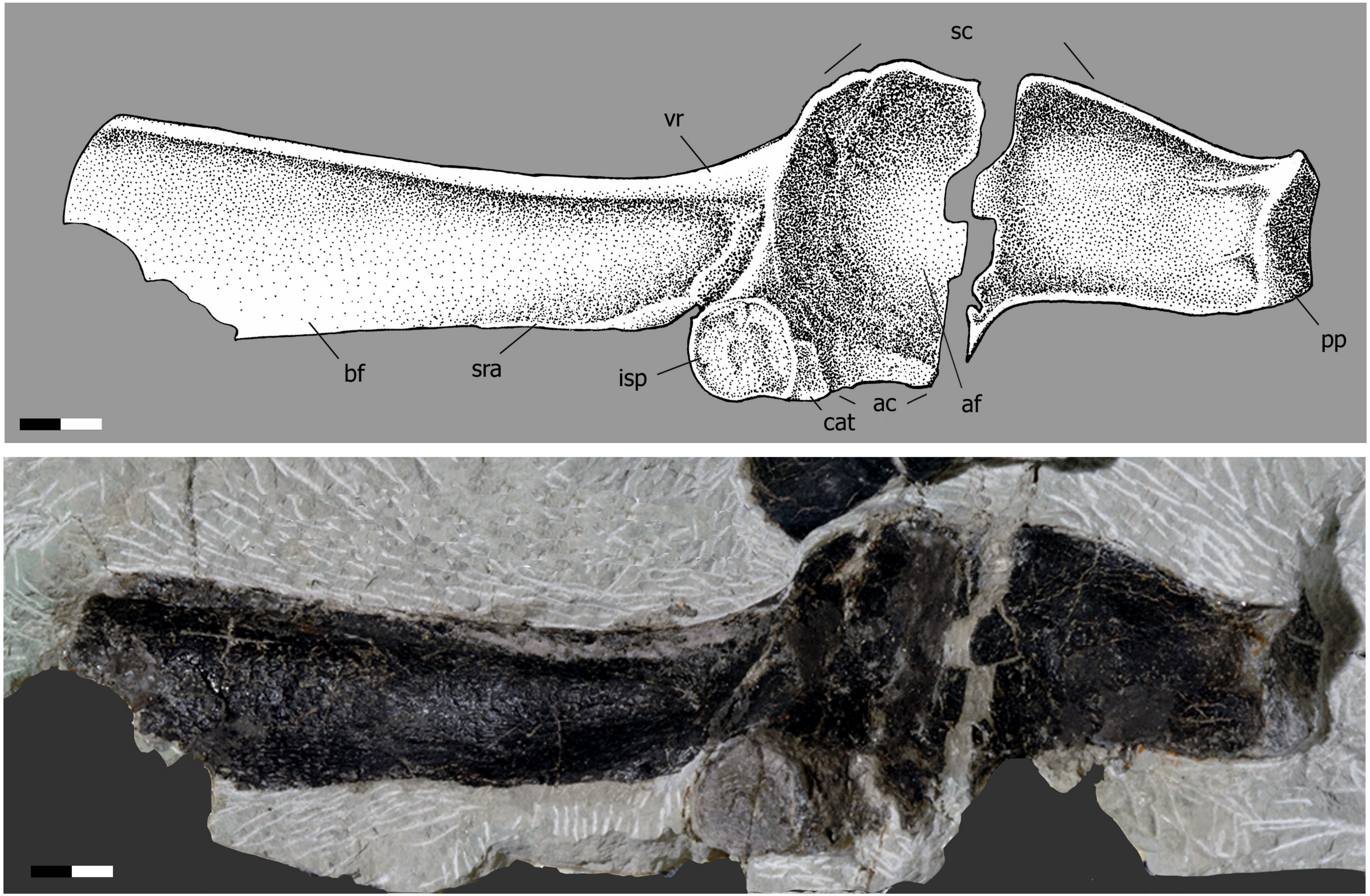

Figure 28: the right ilium from ventral position (scale bar 10 mm). Here, the acetabular fossa (af) and the lateral expansion of the supraacetabular crest are fully visible.

19 mm long and approximately 45 degrees bending cranially with regard to the ventral margin of the anterior blade. The anterior rim of the pubic peduncle, which flanks its articulation facet, measures 28 mm in length. When viewing from ventral position it becomes clear that the articulation facet of the peduncle is two-part: a medial egg-shaped concave portion measuring 15 mm x 12 mm and a latero-ventral spike attached to the former. Thus, the overall shape of the articulation area for the pubis resembles a triangle. The medio-ventral margin of the pubic peduncle proceeds into the border of the acetabulum. The latero-ventral rim of this process continues into the border of the supraacetabular crest.

The concave dorsal margin of the acetabulum measures 44 mm in length and proceeds into the anterior rim of the ischiadic peduncle that is 16 mm long bearing the flattened area of the iliac component of the antitrochanter. The postero-ventrally directed ischiadic peduncle of the ilium exhibits a round, concave articulation facet, which measures 14 mm in diameter and is maximally 6 mm deep at its centre. The posterior margin of the ischiadic peduncle, which adds up to 12 mm in length, passes into the medial border of the brevis fossa. When viewing from ventral position, the brevis fossa, which is inserted by M. caudofemoralis brevis (COLBERT 1989, 1995), is at first convex but soon becomes straight. The thickened lateral border of the brevis fossa (ventral rim) measures 86 mm in length and is 3 mm broad standing sub-parallel to its medial margin. The width of the brevis fossa is 18 mm anterior and 28 mm posterior. The ventral rim is anteriorly in contact with the supraacetabular crest. This extensive lip, bordered anteriorly by the latero-ventral margin of the pubic peduncle, extends laterally to the upper border of the acetabular fossa with 10 mm forming a strong and thick dorsal roof. The latter is oblique, inclining 30 degrees to the longitudinal axis of the ilium pointing downwards with its cranial tip. The supraacetabular crest first gains width posteriorly, before becoming suddenly smaller, proceeding into the caudal rim, a slightly swelled band for the insertion of M. iliofibularis (CARRANO & HUTCHINSON 2002; EZCURRA & CUNY 2007; contra M. iliofemoralis externus of ROMER 1923, 1956; GATESY 1990; ROWE & GAUTHIER 1990), which ends at the posterior extremity of the bone. The caudal rim continues over the whole ventral margin of the posterior blade measuring 12 mm at its beginning and 18 mm at its end in height. Here, it descends into a much more slightly swelled band running parallel to the dorsal iliac border. This thickening measures about 8 mm at the most posterior iliac tip, and vanishes more and more within a distance of 45 mm to anterior.

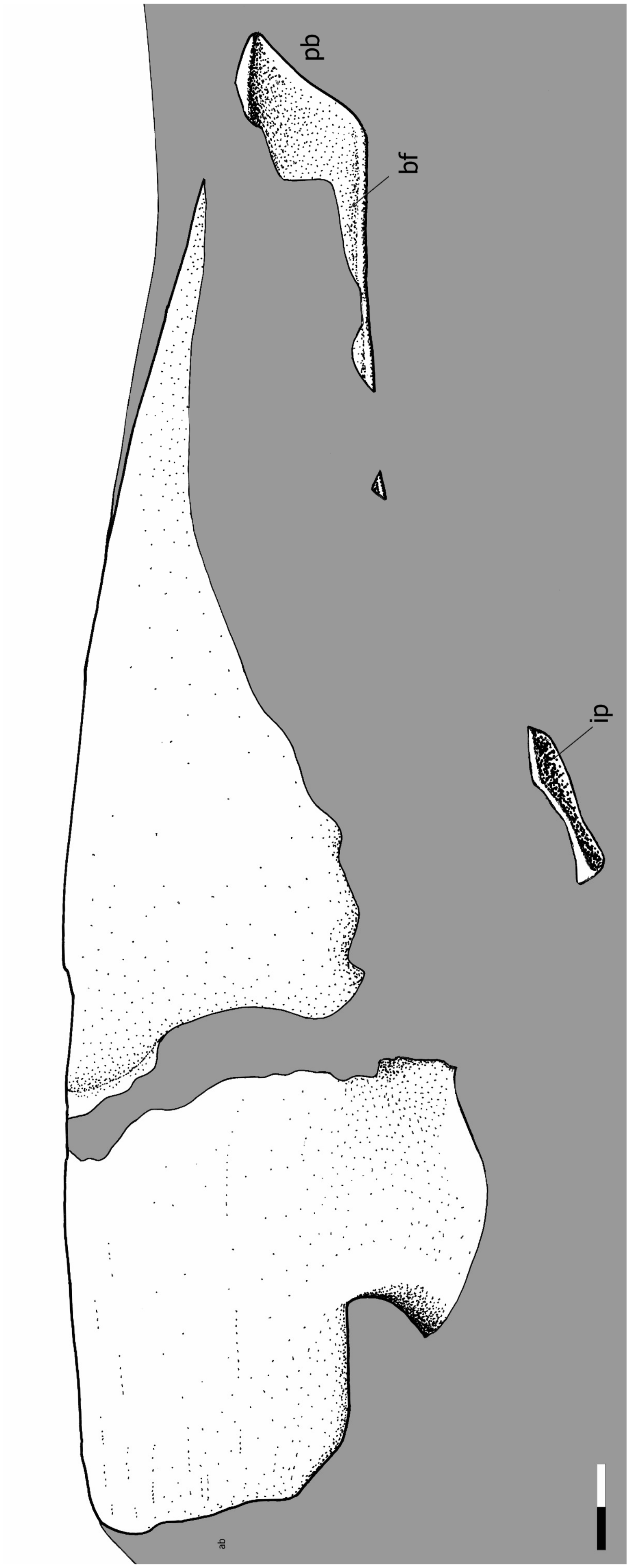
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Figure 29: displays the medial view of the right ilium, which still is partly covered with matrix (scale bar 10 mm).

8.2.1.2. Pubis

fig.30-31

The pubes participate in the antero-ventral margin of the acetabulum. Each pubis is a remarkably long, mainly rod-shaped bone, measuring 256 mm in overall length and, therefore, exceeds the appropriate dimension of the dorsal iliac border by more than one-third. Proximally, the element broadens into a conspicuous but delicate, thin pubic plate that is orientated nearly vertically. This basal enlargement is very incomplete in both pubes. The preserved maximal heights of the pubic plates are 60 mm (left) and 50 mm (right). The pubic shaft, a slender process, is distally attached to the pubic plate. The pubic shaft originates at the upper cranial rim of the pubic plate and ends antero-ventrally with a knob-like embossment (pubic boot). Medio-dorsally a thin walled bony sheet (pubic apron), which is chiefly directed horizontally, is developed along the pubic shaft most likely conjoining the pubic counterparts. The left pubis can be seen completely from a lateral view, whereas the right pubis exhibits the plate from a medial view with a shaft that is more visible from ventro-medially.

When viewed in a lateral or medial position, the pubic plate possesses two imperfect articulation facets along the dorso-caudal margin. The first facet (iliac facet) stands cranio-dorsally and connects to the ilium, whereas the second (ischiadic facet) is located more postero-dorsally. The ischiadic facet normally forms part of the pubo-ischiadic plate which connects the pubis and ischium, but here has been destroyed during diagenesis. Thus, particularly the latter, long articulation facet forming the pubic plate is often poorly preserved due to the highly fragile nature of this thin, laminar structure. Between these two articulation facets, a perfect half circled rim of the acetabulum can be identified.

The pubic plate is perforated twice: by a small, almost medially situated obturator foramen, and a larger second opening, the pubic fenestrum, which can be observed antero-ventrally of the former. Unfortunately, only the obturator foramen has been achieved entirely being oblique-oval with the major axis straightened from antero-dorsal to postero-ventral. The size of the left foramen is 13 x 7 mm, compared with 14 x 5 mm for the right foramen. In contrast only the anterior borders of the fenestra pubica were preserved, measuring approximately 48 mm in length (left element). The preserved part of the margin indicates a quite large, more or less rounded opening with a diameter of approximately 22 mm.

In lateral or medial position, the pubic shaft is almost straight, with a slight gentle downward curvature. The dorsal margin of the shaft is predominantly convex, only the antero-dorsal rim of the pubic plate is slightly concave. The ventral border of the shaft is correspondingly concave, and runs parallel to the dorsal rim. The shaft of the left pubis, which is observed laterally, has a mid-height of 7 mm. The measuring of the right pubic shaft, which is visible slightly from ventro-medial, is not possible due to fluent continuation into the pubic apron. However, both structures measure 24 mm in width at the same point. At the proximal basis of the shaft a smooth lateral groove is developed (measuring 22 mm x 2 mm) that proceeds longitudinally to the main axis of the shaft.

The pubic apron, originates medio-dorsally at the shaft, measuring approximately 20 mm in width at this point. This antero-posterior long but medio-lateral small, thin structure starts at the pubic plate and runs to the distal tip of the shaft and becomes narrower. Both pubes exhibit a pubic apron which has been originally medially affiliated with its respective counterpart, best observable (from beneath) in the right pubis. Here, this structure is almost aligned in one level with the longitudinal antero-posterior axis of the pubic shaft due to forces acting on the bone during sedimentary compaction. The left apron is still largely hidden in the matrix. In the right pubis it becomes obvious that the rim of the apron proximally passes straight over into the antero-ventral border of the basal plate. If the sutural connection between the pubic aprons extended at all their length or if they only conjoined over a confined distance in the life time of this dinosaur cannot be answered with certainty. Nevertheless, it seems that the pubic aprons were sutured along their entire length and that no median distal opening above the pubic boot was developed.

The pubic boot is relatively small and only posteriorly expanded. An anterior extension, found in later theropods, is not developed. When observed from a lateral or medial position the left pubic boot is three-cornered with the acute angle of the triangle pointing backwards, whereas the outline of the right pubic boot is semi-circular in shape. The cranio-caudal length of the left pubic boot is 12 mm; in comparison the right structure measures 10 mm. Here, it is assumed that the left pubic boot reflects the pristine form, whereas the shape of the right is likely the result of poor preservation. From ventral each pubic boot forms a small triangle with a robust anterior and a pointed posterior end. The pubic boots also form a triangle when viewed from the same position and when rearranged in life-position.

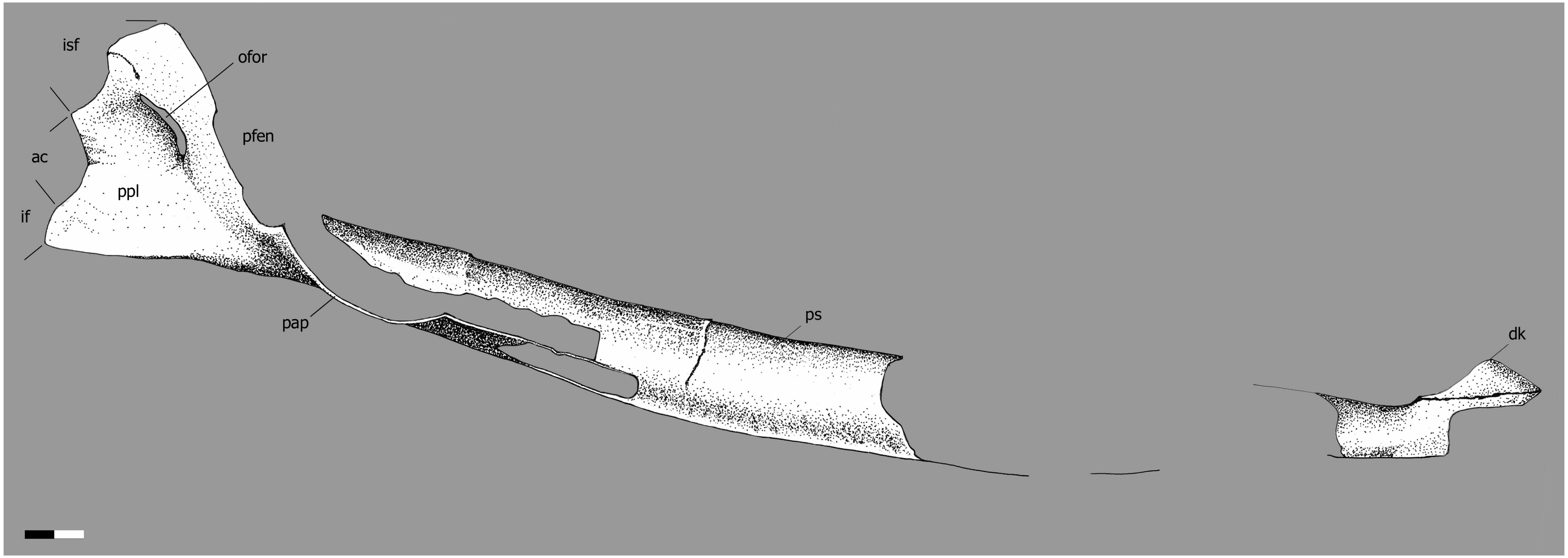
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Figure 30: right pubis from medial view (scale bar 10 mm).

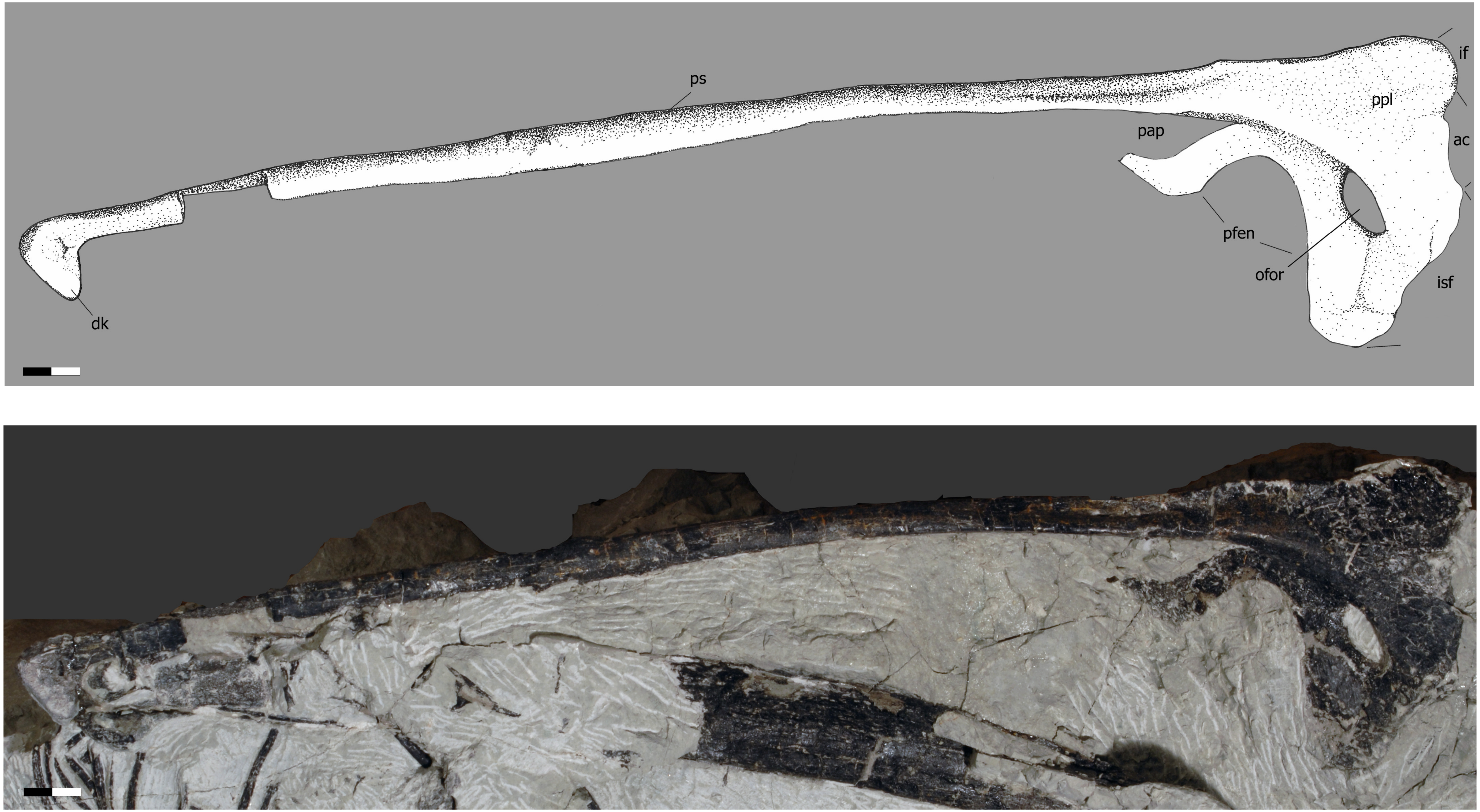

Figure 31: left pubis from lateral view (scale bar 10 mm).

8.2.1.3. Ischium

fig.32-34

The ischium is, like the pubis, a remarkably long, rod-like bone which is composed of a proximal solid basal plate and a relatively long distal process (ischiadic shaft) with a boot-like swelling at its caudal end, the so-called distal knob. The basal plate bears two articulation facets, one contact for the pubis and one for the ilium. The ischium forms the postero-ventral rim of the acetabulum. Here, the border of the acetabulum is confined anteriorly by the pubic facet, and posteriorly by the iliac facet, which possesses the ischiadic part of the antitrochanter (component of antitrochanter), In contrast to the slightly bent pubic shaft, the corresponding structure of the ischium is straight, measuring 8 mm in medio-lateral width at mid-length. In contrast to the pubis, the overall length of the ischium adds up to approximately 150 mm measured along its ventral margin, and, therefore, is about one third shorter than that of the former (ratio 1.4 to 1). The exact length of the bone cannot be measured due to the fact that the ends of the ischium are located on different sides of slab A: the plate is exposed on the upper, whereas the process with the distal knob is situated on the lower side.

The ischia are conjoined along the whole lengths of the medial shafts. It should be noted that these are the only elements of the pelvis, which are still articulated. The visible medial height of basal plate measures 33 mm directly posterior of the iliac facet, and 28 mm along the pubic facet. The strong iliac facet is situated at the caudo-dorsal border of the basal plate, pointing upwards and being medio-laterally thick. Its articulation area measures 31 mm along its rather straight medial border and 43 mm tracing its lateral semi-circular outline. The whole artication area consists of three areas: an anteriorly and posteriorly located triangle-shaped embossments measuring 12 mm and 7 mm in antero-posterior length, which frame a perfectly round, concave fossa with a cross section of 10 mm. The anterior heightening corresponds to the ischiadic component of antitrochanter. The more medio-laterally slender and dorso-ventrally long pubic facet of the ischium occupies the whole, 17 mm long cranial margin of the basal plate. The length of the upper adjacent medial rim of the open acetabulum adds up to 29 mm along its circular outline. The ischium is plesiomorphic in exhibiting an obturator process which is not separated from the basal plate. Therefore, this structure is confluent with the pubic facet. Another feature is located on the latero-distal shaft portions of both ischia: the otherwise straight shaft abruptly thickens into a swelling.

The dimensions of the distal knob are significantly larger than those seen in the pubic boot. When viewed from the lateral position, the distal knob looks like a caudally directed foot-like enlargement with an anterior extension of 3.5 mm and a posterior one of 14 mm. From caudo-ventral aspect, the distal knob is characterized by a moderate expansion that exhibits a sub-triangular outline, whose 28 mm long basis is orientated dorso-posteriorly to ventro-anteriorly. The lower leg of this ‘triangle’ adds up to 25 mm, whereas the dorsal one is 12 mm. Under the same condition, both knobs together exhibit a ball-like shape.

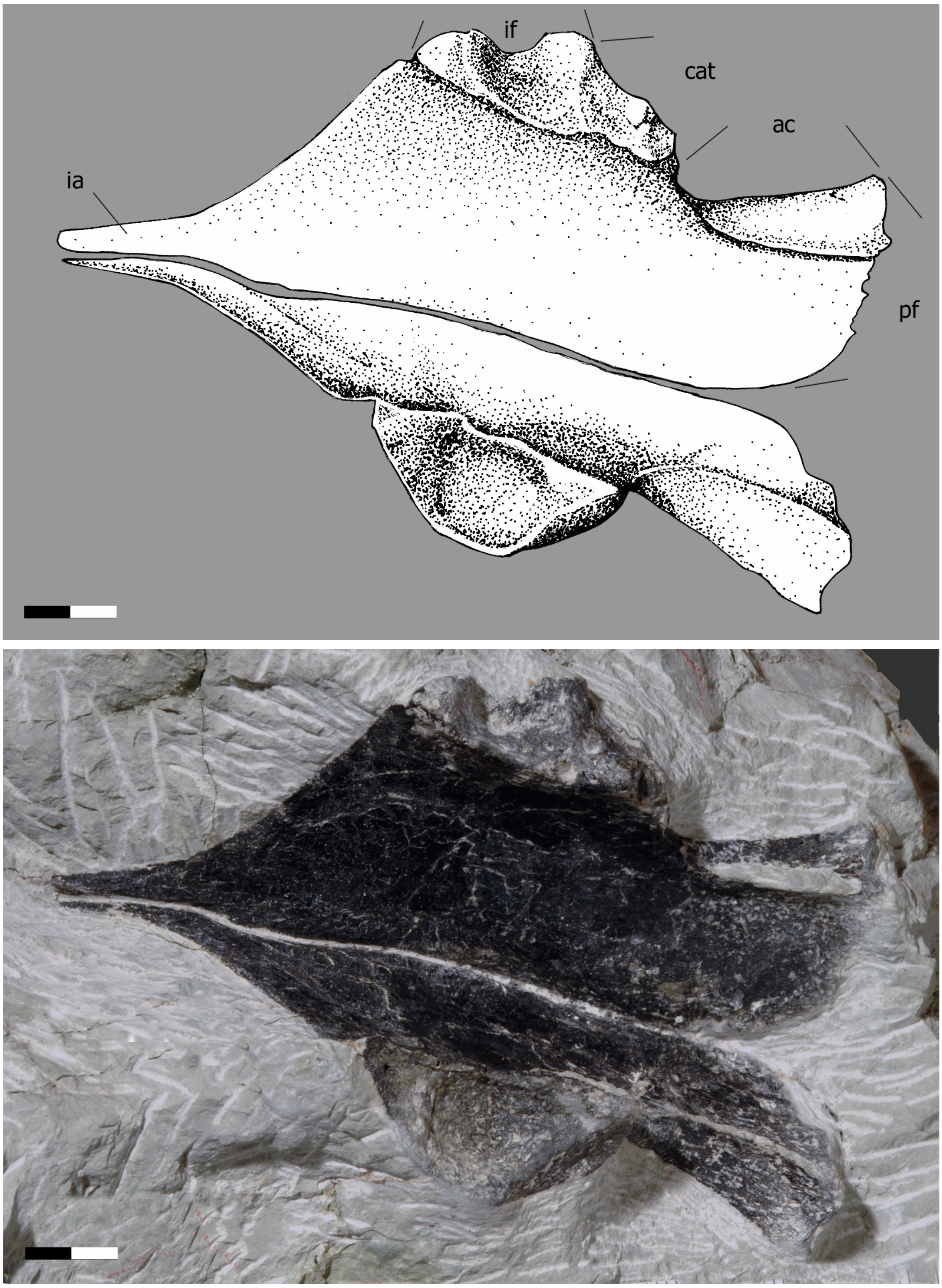

Figure 32: the articulated ischia from dorsal view almost perfectly preserved showing their iliac and pubic facets (if and pf) (scale bar 10 mm).

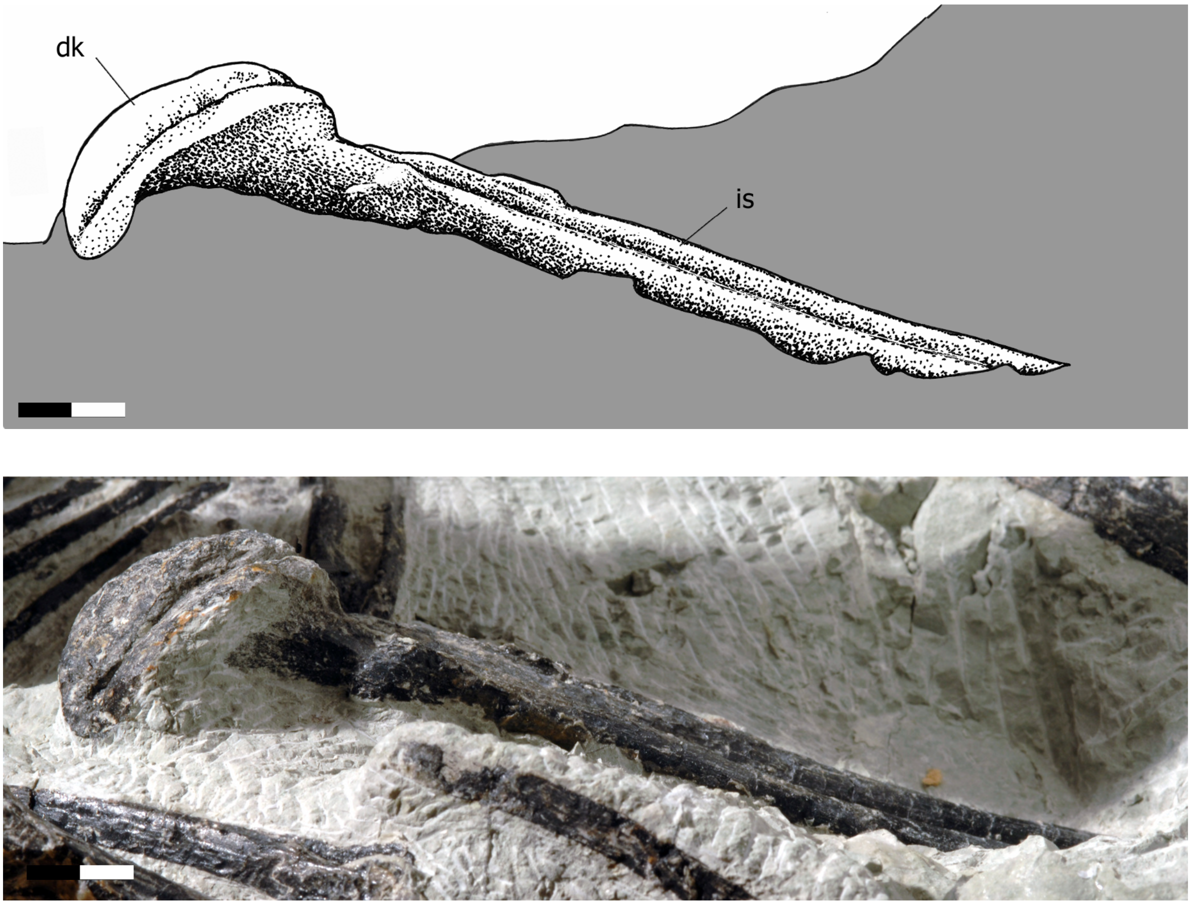

Figure 33: both the ischia from left lateral position (scale bar 10 mm).

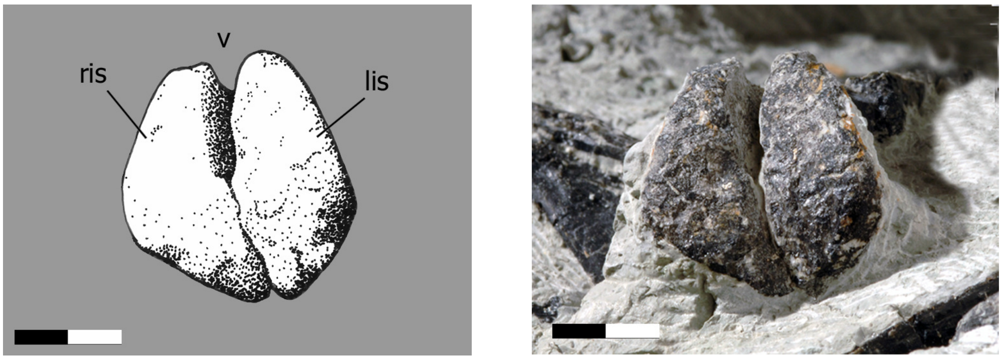

Figure 34: the distal knob shown from ventral view displaying its subrectangular outline (scale bar 10 mm).

9. Results

9.1. Computertomography

Investigations at the Paul Scherrer Institute and at the Hospital of the University of Zurich

Aims of the Radiology and Computer Tomography Scans

The Paul Scherrer Institute in Villigen, Switzerland, performs several hundred CT-Scans (neutrons and x-ray) per year, providing their users often successfully with a closer look in many scientific fields such as archaeology, engineering, forestry and palaeontology (e.g. SCHWARZ et al. 2005).

For information about different methods and investigations at the PSI, please contact:
Dr. Eberhard H. LEHMANN
Email: eberhard.lehmann@psi.ch
Supervisor of NEUTRA and ICON
Paul Scherrer Institute in Villigen, Switzerland

The team of the Institute for Diagnostic Radiology of the Hospital of the University of Zurich, Switzerland, supports other scientific institutions in scanning and visualising their material under study.

For information contact:
PD Dr. Hatem ALKADHI and Dr. Thomas FRAUENFELDER
Email: hatem.alkadhi@usz.ch or thomas.frauenfelder@usz.ch
Institute for Diagnostic Radiology
Hospital of the University of Zurich, Switzerland

The neutron and x-ray CT were accomplished to answer the following questions:

1) Are there still bones inside the sediment, which could not be prepared due to the brittleness of each block?
2) Is visualisation and subsequent segmentation possible? Can the pelvis be 3-dimensionally reconstructed? Can every bone be considered in 3-D? Can the compression of each bone be calculated?
3) Are the bones hollow and are there cavities in the vertebrae? Are there foraminae/diverticulae leading from a fossa into the centrum, visible in the dorsal, sacral, and caudal vertebrae (e.g. BERMAN & ROTHSCHILD 2005; SCHWARZ et al. 2005)?

The studies of the CT-scans performed at the Hospital of University of Zurich provided us with the answer to the first question. However, only the still hidden bones of slab A are partially visible on the pictures (see «8.1.2. Dorsal region»), all other slabs did not conform to the desired conditions as already seen at the PSI. The reasons for the very limited results of the CT-scans at the PSI are explained as the following:

The recovery and preparation of the bones were exceedingly difficult because of the brittleness of the material. Thus, a lot of acrylic varnish and resin were necessary for making the bones permanently maintainable.

There was only a minimal difference between the attenuation coefficients of the different elements in the fossilized bones and their surrounding marly matrix. Additionally, the acrylic varnish and resin used for conservation and preparation skills dispersed the ray (neutron or x-ray) to a greater extent. Another disturbing factor was the thickness of the horizontal and vertical axis of the blocks; even in areas of only 30 mm density, the bones virtually disappear in a diffuse grey area. The neutrons and electrons have not been able to penetrate the whole thickness of each block from all directions and thus only the bones on the surface can be seen at least to a depth of 2 mm. Finally, there is another factor for the decreasing picture quality: the thicker a sample, the greater possibility for a neutron or electron ray to disperse in different directions. This side effect has taken place in the neutron and electron pictures, resulting in diffuse clouds surrounding the blocks (especially in the neutron pictures).

As a result of these four factors, the partially embedded bones could not be visualised (i.e. virtually imaging without the surrounding matrix).

The visualisation can only work with single bones without any matrix, or with a matrix composed of more different elements delivering a great variety in grey values (see appendix 11.4.1., table 7-8).

In the follwing abstracts, regarding the investigations at the PSI (Neutron CT and X-ray CT), only the elemental cause for the diffuse pictures are discussed. Be aware that there are three other reasons for the resulting pictures.

9.1.1. Neutron CT

The acrylic varnish caused an additional dispersing effect on the already diffuse neutron CT pictures. The organic components of the varnish were one reason for the deterioration (acrylic varnish consists of acrylic resin and solvent, which both are based on H-elements). Hydrogen is a strong staining marker in the neutron CT because of its high attenuation coefficient (see «11.4.1. Attenuation coefficient of every element» table 8, in appendix), reacting/bonding heavily with the neutrons of the ray (Neutron Imaging and Activation Group (NIAG): Neutron Imaging an der Spallations-Neutronenquelle SINQ, Brochure of the Paul Scherrer Institute, Villigen 2006).

This effect is called absorption and causes in this case white areas on the resulting CCD pictures. In addition, not only the superficial bones are covered and soaked with the acrylic varnish, but the surrounding matrix as well. This effect caused from the essential application makes the visualization impossible; even the known bones are hardly recognizable in the CCD pictures.

The acrylic varnish infiltrated the marl to a depth of 20 mm. The stone and the bones which are lying beyond this area are not infected by the varnish. Here, a different, but additional problem is encountered: the bones can hardly be differentiated from the matrix because of similarity in their atomic components; thus, the bones and the marly sediment within the block contain nearly no organic elements and there is almost no difference between the inorganic materials at all (Mn, Fe, Si, Ca, Al, O; see «11.4.1. Attenuation coefficient of every element» table 8, in appendix).

9.1.2. X-ray CT

The x-rays react with the electrons of every atom. The higher the amount of electrons in the target atoms is the greater is the interaction. This effect results in darkened areas in the CCD pictures (Neutron Imaging and Activation Group (NIAG): Neutron Imaging an der Spallations-Neutronenquelle SINQ, Brochure of the Paul Scherrer Institute, Villigen 2006).

Although the bones consist of manganese and iron, containing high amounts of electrons in their atomic shells, the pictures are not better than those applied with the neutron method. The attenuation coefficients of the electrons of the bones do not show great difference in the greyscales compared to the attenuation coefficients of the electrons of the marly sediment consisting of silica, calcium, aluminium and oxygen. It is a matter of fact that the electrons available here, result in similar grey levels. Thus, it was not possible to answer the question with the PSI-equipment, if there are still undiscovered bones within each block. Thus, the x-ray CT of the PSI led to no other results than the method experiencing neutron CT. The only difference between these two methods is that the appliance did not affect the x-ray CT because the components do not cause any absorption with the electrons. The x-ray pictures are similar (i.e. diffuse) to the neutron pictures within the inner part of the blocks.

The x-ray CT-scans performed with the equipment of the hospital of the University of Zurich led to higher resolution resulting in better visualisation in at least slab A (the presence of dorsal vertebra 12 and 13 have been detected). All other examinations were as disappointing as the investigations at the PSI.

9.2. Phylogenetic Analysis Using Parsimony (PAUP)

The phylogenetic analysis was conducted with ten taxa (ingroup: *Coelophysis bauri, C. rhodesiensis, Dilophosaurus wetherilli, Liliensternus liliensterni, Lophostropheus airelensis, Procompsognathus triassicus, Segisaurus halli*, *Syntarsus kayentakatae*, and the Swiss theropod material; outgroup: *Herrerasaurus ischigualastensis*) and only the informative character data (81 characters) revealing significant resolution were used. Heuristic search methods resulted in only one most parsimonious tree (MPT). The full-heuristic search method produced a tree of 136 steps with CI = 0.7059 and RI = 0.6429 (time used 0.05 sec). The branch-and-bound search method retained five trees due to *Procompsognathus triassicus* and *Segisaurus halli* acting as 'wild cards' (hopping within Coelophysidae). This constraint results from the high amount of missing data these two dinosaur show in the matrix, coded as question marks (*Procompsognathus triassicus* 91.1% and *Segisaurus halli* 77.8%; see «11.1.3. Missing data per all informative characters», in appendix). However, the phylogenetic position of *Segisaurus halli* and *Procompsognathus triassicus* is still quite unknown regarding their relationship to the Coelophysidae which is beside the hopping another good reason for removing these taxa from the analysis. In succession, 'strict consensus' and 'Adams' were conducted. 'Strict consensus' resulted in two trees looking almost the same (steps 136, CI = 0.7059, RI = 0.6429; time used 0.00 sec), whereas 'Adams' led to better resolution within the Coelophysidae as well as *Procompsognathus triassicus* and *Segisaurus halli* producing one tree.

The resulting trees of the full heuristic and the branch-and-bound searches were then tested using a 'Jackknife' approach with 50 percent deletion for confirming the reliability of every single node producing generally high values. The 'Jackknife' of the branch-and-bound search additionally supported the decision to remove *Procompsognathus triassicus* and *Segisaurus halli* from the analysis. This procedure resulted in a tree of no resolution between the Coelophysoidea.

The whole analysis was then repeated with only seven ingroup taxa (*Coelophysis bauri, C. rhodesiensis, Dilophosaurus wetherilli, Liliensternus liliensterni, Lophostropheus airelensis*, *Syntarsus kayentakatae*, and the Swiss theropod material) and still one outgoup taxon (*Herrerasaurus ischigualastensis*) resulting in one parsimonious tree showing no difference between full heuristic and branch-and-bound search methods, except for slight variations in the Jackknife amounts (steps 129; CI = 0.7442; RI = 0.6667; full heuristic: time used 0.05 sec, branch-and-bound: time used 0.02 sec; see fig. 35 & 36).

The clades Neotheropoda, Coelophysoidea and Coelophysidae were finally recovered in this single tree (SERENO 1999; TYKOSKI 1998; EZCURRA and CUNY 2007; fig. 37).

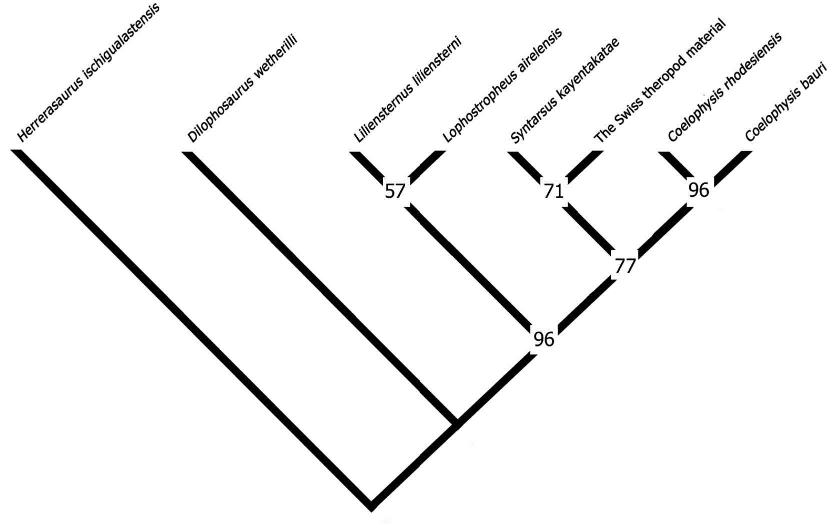

Figure 35: phylogenetic results: branch-and-bound search method of 1 MTP excluding *Procompsognathus triassicus* and *Segisaurus halli*.

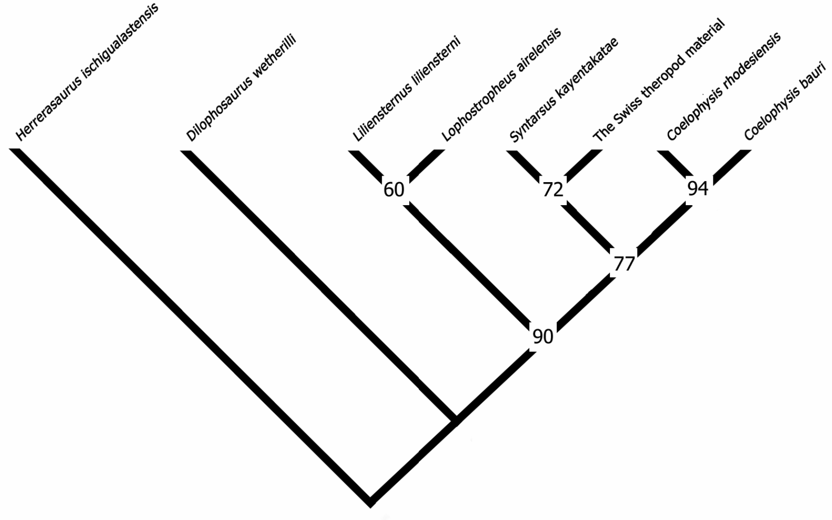

Figure 36: phylogenetic results: full heuristic search method of 1 MTP excluding *Procompsognathus triassicus* and *Segisaurus halli*.

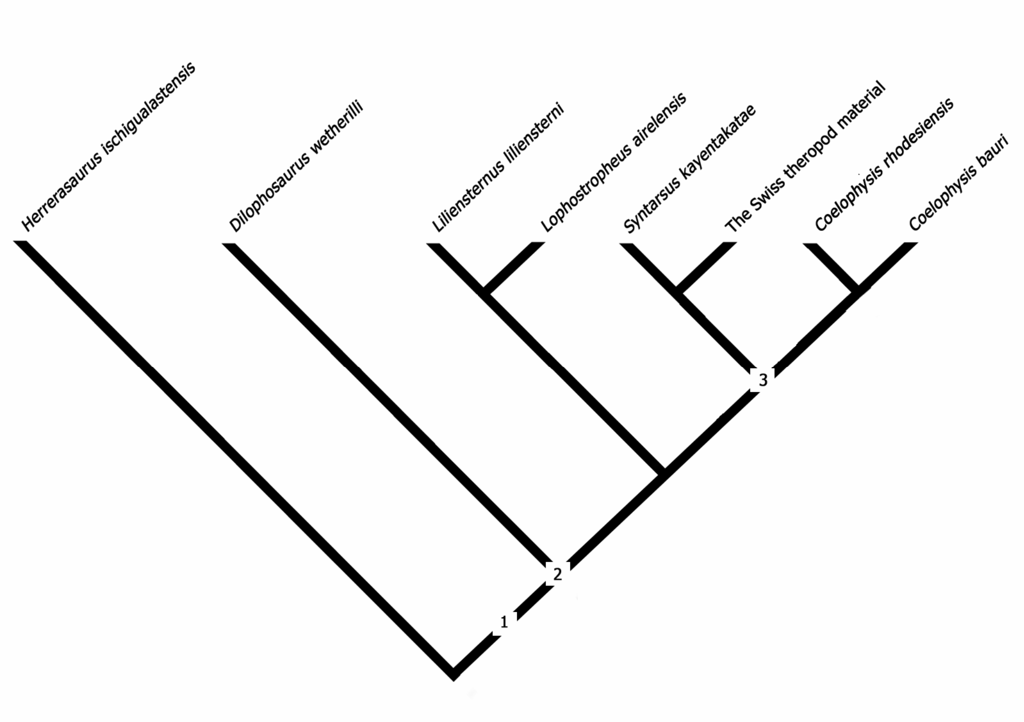

Figure 37: the phylogenetic analysis performed with the programm PAUP 4.0. BETA (SWOFFORD 2002) resulted in this tree. *Procompsognathus triassicus* and *Segisaurus halli* have been excluded due to their uncertain relationship within the Neotheropoda (1), Coelophysoidea (2), and Coelophysidae (3).

9.3. Excursus C: sexual dimorphism within Coelophysidae

The examination of a single immature specimen is always a problem: the ontogeny of an individual can, in addition to other factors, change morphological states.

The morphology of each skeleton is always influenced by '1. individual, 2. sexual (i.e. dimorphism), 3. ontogenetic, 4. geographical and chronological, [and] 5. intra-specific population' variations. Additionally, it may also have been affected by '6. post-mortem deformations, and 7. pathological changes. […] Any variant organism cannot necessarily be regarded as belonging to a different taxon. Equally, specimens that differ slightly do not necessarily pertain to a single biological species' (MOLNAR 1990: 72, 77).

COLBERT (1990) and RAATH (1990) both appear to have found sexual dimorphism in *Coelophysis bauri* and *C. rhodesiensis* regarding variation in fusion of the ankle and pelvic region (affiliation of sacral ribs and transverse processes to ilia as well as neural spines among each other). DOWNS (2000) considered these varieties rather as differences in the ontogenetic stages of juvenile to subadult and adult individuals. However, COLBERT (1990) and RAATH (1990) suggested further indications of sexual dimorphism including proportional changes in various parts of the skeletons of the two taxa. Specimens of *Coelophysis bauri* vary in the size of the skull and the orbit, the length of the neck, forelimb and hind limb, and the number of teeth (COLBERT 1990; MOLNAR 1995; LOCKLEY 2005; LOCKLEY & KUKIHARA 2005; FASTOVSKI & WEISHAMPEL 2005). The variation in *Coelophysis rhodesiensis* which is based on sexual dimorphism affects different parts of the skeleton including '… robustness of the humerus, extent of development of the olecranon process on the ulna, breadth of the metacarpus, flaring of the ilium, and configuration and size of muscle trochanters on the femur. […] Although the sample available for study is small, it seems that smaller specimens (juveniles) have narrow dolicho-iliac pelves with relatively unflared ilia, whereas some larger specimens have broadly flared brachy-iliac pelves as represented by the holotype [QG1]. [However], whether these variants represent a pelvic expression of dimorphism, or are merely part of a continuous range of variation related to growth, or are attributable instead to distortion resulting from compression, cannot be established with certainty' (RAATH 1990: 96). Both *C. bauri* and *C. rhodesiensis* are reported in a huge amount of fossils: the former is estimated to 500 by PAUL (1988) and over 1'000 fossils by GAY (2005), and thus, it is possible to recognise several of the above mentioned seven morphology-influencing factors which are not taxon-specific. However, COLBERT (1989; 1990; 1995) has not reported the variations in the flaring of the ilium. This is mainly accredited to the fact that many fossils of the Ghost Ranch are medio-laterally compressed, and thus, COLBERT simply neglected this morphological feature (DOWNS 2000; TYKOSKI, pers. communication).

Although there are only three individuals known from *Syntarsus kayentakatae*, ROWE (1989) also found sexual dimorphism in the skeleton of specimen TR97/12 based on distinguished hypertrophied muscle attachments. However, he does not give any further details.

The Swiss theropod material is as compressed as the majority of *Coelophysis bauri* specimens found in the Ghost Ranch Quarry: it shows rather dorso-ventrally narrow ilia with a little lateral flaring of the supraacetabular crest. However, it seems that true sexual dimorphism is found in the chevrons of the caudal series, which until now have not been considered in specimens of *C. bauri* and *C. rhodesiensis* when discussing this topic. The first chevron shows almost the same dorso-ventral length as the successors, it is slightly expanded among its distal portions, and positioned in front of the second caudal vertebra as seen in gracile morphotypes (males) of *Tyrannosaurus rex* (LARSON 1992, 1995, 1998; see «11.5. Sexual Dimorphism in Tyrannosaurus rex», in appendix). The angle between the longitudinal caudal centra axes and the corresponding axis of the ischiadic shafts as well as the proximal medio-lateral distance between the latter (the greater the better for the passage of eggs) provide additional information to determine the sex (ROMER 1956; CARPENTER 1990; LARSON 1995). In the Swiss theropod material, both morphological features (angle and distance) are not very useful for sex determination at this time, because it is found isolated and the sexual dimorphisms of other Coelophysidae or Coelophysoidea has not been studied yet.

9.4. Morphological Comparison

The comparison between the single examined theropods is mainly composed to point out the similarities and differences between *Coelophysis bauri*, *C. rhodesiensis*, *Syntarsus kayentakatae*, and the Swiss theropod material. *Dilophosaurus wetherilli*, *Herrerasaurus ischigualastensis*, *Lophostropheus airelensis*, *Liliensternus liliensterni*, and *Procompsognathus triassicus* are mentioned for complement, because they are also included in the phylogenetic analysis. The data matrix and matrix description in the appendix display all the character information needed; characters marked with a question mark are regularly not mentioned in the comparison.

The appendix also includes a table of measurement of all the examined theropods, only the data of *Procompsognathus triassicus* and *Segisaurus halli* are missing, because no measurement data could have been obtained.

9.4.1. Axial Skeleton

9.4.1.1. Cervical Region

The cervical region is only preserved by four distal rib fragments belonging to the ninth and tenth left cervical rib. Beside the fact that these portions are round and only measure 2 mm in diameter, nothing more can be surely stated. The Swiss theropod material is assumed to have cervical ribs which '… extend caudally at least three centra behind their vertebra of origin …' as found in *Coelophysis bauri*, *C. rhodesiensis* and *Syntarsus kayentakatae* (HOLTZ, 1994; EZCURRA & CUNY, 2007: 84).

9.4.1.2. Dorsal Region

All of the examined theropods are assumed to possess 13 dorsal vertebrae (HUENE 1934a; CAMP 1936; COLBERT 1947, 1964, 1989, 1995; REIG 1963; LARSONNEUR & LAPPARENT 1966; ROMER 1974; GALTON 1977; WELLES 1984; ROWE 1989; ROWE & GAUTHIER 1990; CUNY & GALTON 1993; TYKOSKI 1998; TYKOSKI & ROWE 2004; CARRANO, HUTCHINSON & SAMPSON 2005; EZCURRA & CUNY 2007). The only exception is *Herrerasaurus ischigualastensis* exhibiting 15 dorsals as a very basal theropod (NOVAS 1993). Beside the difference in number of the dorsal vertebrae, there are several morphological variations regarding the dorsal series between *Herrerasaurus* and the Coelophysoidea and of course within the latter:

First of all, the overall centrum length of the dorsal series is very constant in *Coelophysis bauri*, *Herrerasaurus ischigualastensis* and *Liliensternus liliensterni* (HUENE 1921, 1934a; COLBERT 1989, 1995; ROWE 1989; ROWE & GAUTHIER 1990; SERENO & NOVAS 1993; NOVAS 1993; TYKOSKI 1998; TYKOSKI & ROWE 2004). In *Coelophysis rhodesiensis* (QG1), the dorsal centra lengths are slightly increasing from anterior to posterior (RAATH 1969, 1977), but are still rather constant compared to the Swiss theropod material whose vertebrae increase with an absolute difference of 11 mm between the length of the second and tenth dorsal vertebra centrum. *Dilophosaurus wetherilli* (UCMP 37302) exhibits relative dorsal vertebrae lengths which are very similar to that of the Swiss theropod material; the vertebrae also increase their antero-posterior dimensions along the dorsal series and the smallest differs from the largest with 20 mm in length resulting in an analogical relative relation as in the former (WELLES 1984). *Syntarsus kayentakatae* (MNA V2623) only presents one dorsal vertebrae (dorsal 1) which is badly crushed and does not allow measurement. The dorsal centra lengths of the Swiss theropod material are similar in total average length (35.86 cm), though increasing and not constant, with those of *Coelophysis bauri* (35.45 cm; AMNH 7224). *C. rhodesiensis* (QG1) is about one seventh smaller to the two former under the same condition.

Another morphological feature allowing differentiation among the examined theropods are the lateral dorsal centrum shapes: the anterior, mid-dorsal and posterior dorsal centrum lengths of *Coelophysis bauri* and *C. rhodesiensis* are significantly elongated exhibiting centrum lengths which are more than two times the height of the associated articular faces, and resultantly resemble 'spools' (COLBERT 1989, 1995; RAATH 1969, 1977; ROWE 1989; TYKOSKI 1998; EZCURRA & CUNY 2007). This statement fits the description of the mid and caudal dorsals in the Swiss theropod material at any rate. Dorsal 2 is the only anterior dorsal vertebra whose faces and height can be measured resulting in a ratio of 1.74. This ratio of the centrum can either be biological fact or altered by its medio-lateral compression during diagenesis. The posterior dorsal lengths are also preserved in *Lophostropheus airelensis* and *Procompsognathus triassicus.* The caudal centrum lengths of the former are '… relatively short, equal or more than 1.33 times the height of the cranial articular surface …' (EZCURRA & CUNY 2007: 84), whereas the latter exhibits ones as elongated as for example in *Coelophysis bauri* (FRAAS 1913; OSTROM 1981; SERENO & WILD 1992; CHATTERJEE 1993). The vertebrae along the dorsal series of *Dilophosaurus wetherilli* and *Herrerasaurus ischigualastensis* are not elongated at all: the centrum lengths are subequal to the height of the articular faces (REIG 1963; WELLES 1970, 1984; ROWE & GAUTHIER 1990; NOVAS 1993; SERENO & NOVAS 1993; TYKOSKI & ROWE 2004; EZCURRA & CUNY 2007). The cranial and mid-dorsal centrum lengths of *Liliensternus liliensterni* are also subequal to the height of their articular faces, but become slightly elongated when going backwards towards the dorsal series (HUENE 1934a; EZCURRA & CUNY 2007).

In all the examined theropods, the articular faces of the dorsal vertebrae are perpendicular to the median axis of their centra to accentuate the stableness and strength of the back (COLBERT 1989, 1995). They are amphicoelous in *Coelophysis bauri*, *Dilophosaurus wetherilli*, *Herrerasaurus ischigualastensis*, *Lophostropheus airelensis*, *Liliensternus liliensterni*, *Segisaurus halli*, and *Syntarsus kayentakatae* (HUENE 1934a; CAMP 1936; COLBERT 1947, 1964, 1989, 1995; REIG 1963; LARSONNEUR & LAPPARENT 1966; GALTON 1977; WELLES 1984; ROWE 1989; ROWE & GAUTHIER 1990; NOVAS 1993; SERENO & NOVAS 1993; CUNY & GALTON 1993; GLUT 1997, 2003; TYKOSKI 1998; RAUHUT & HUNGERBÜHLER 2000; TYKOSKI & ROWE 2004; CARRANO, HUTCHINSON & SAMPSON 2005; EZCURRA & CUNY 2007). In *Coelophysis* *rhodesiensis* and the Swiss theropod material the dorsal faces are platycoelous to somewhat amphicoelous (RAATH 1969, 1977).

There is a well recognizable ventral keel in the anterior dorsals of *Coelophysis bauri, C. rhodesiensis, Dilophosaurus wetherilli, Herrerasaurus ischigualastensis, Liliensternus liliensterni,* and the Swiss theropod material (HUENE 1934a; COLBERT 1947, 1964, 1989, 1995; RAATH 1969, 1977; WELLES 1984; ROWE 1989; ROWE & GAUTHIER 1990; NOVAS 1993; RAUHUT 2003). The only dinosaur, whose keel clearly is illustrated, is *D. wetherilli* (WELLES 1984: 15, fig. 11): this theropod exhibits a ventral keel similar to the one seen in the Swiss theropod material being sharply bordered behind the parapophysis, then vanishing along the caudal two thirds of the centrum. Although it is assumed here that the achievement of the ventral keel of *D. wetherilli* and the Swiss theropod material is well developed rather than very poorly developed as stated by RAUHUT (2003) in his phylogenetic analysis for the Coelophysidae and *D. wetherilli*, it was impossible to compare the exact habitus of the mentioned keels to the ones of the other theropod dinosaurs due to the lack in description. In *Lophostropheus airelensis, Procompsognathus triassicus, Segisaurus halli*, and *Syntarsus kayentakatae* there exists either no anterior dorsals or the grade of preservation does not allow any statement (CAMP 1936; LARSONNEUR & LAPPARENT 1966; Rowe 1989; CUNY & GALTON 1993; TYKOSKI 1998; CARRANO, HUTCHINSON & SAMPSON 2005; EZCURRA & CUNY 2007).

Lateral fossae are available in the anterior dorsal centra (pectorals) of *Coelophysis bauri, Lophostropheus airelensis,* and *Procompsognathus triassicus* (FRAAS 1913; SERENO & WILD 1992; LARSONNEUR & LAPPARENT 1966; HOLTZ 1994; DOWNS 2000; RAUHUT 2003; EZCURRA & CUNY 2007), but their presence can vary intraspecies as the former or within one single individual as in the two latter (RAUHUT 2003). The Swiss theropod material exhibits a shallow to deep fossa on the lateral centrum sides of dorsal 2, 3, 5, 6, and 7. The impression of the depth of these fossae is altered by the medio-lateral compression during fossilization. It is important to state, that no successor of the seventh dorsal shows any fossa at the lateral centrum sides. Thus, the Swiss theropod material only displays fossae in its pectorals as almost all examined theropods. There is no exception with *Coelophysis rhodesiensis*, *Dilophosaurus wetherilli, Syntarsus kayentakatae,* and *Liliensternus liliensterni* which also always display fossae in the anterior dorsals, but never in their posterior dorsal vertebrae (HUENE 1934a; RAATH 1977; WELLES 1984; ROWE 1989; ROWE & GAUTHIER 1990; TYKOSKI 1998; RAUHUT 2003; TYKOSKI & ROWE 2004; TYKOSKI 2005). In contrast, *Herrerasaurus ischigualastensis* has not evolved any fossa or foramina on the lateral sides of the centra along its dorsal series (NOVAS 1993; RAUHUT 2003).

The upper form of the dorsal transverse processes of *Coelophysis bauri*, *C. rhodesiensis*, *Procompsognathus triassicus*, *Segisaurus halli* and the Swiss theropod material all conform to the morphology of the Ceratosauria (sensu GAUTHIER 1986; ROWE & GAUTHIER 1990; TYKOSKI & ROWE 2004; and others) being considered as an autapomorphy of this group: the cranial margins of the dorsal transverse processes are back-swept giving an outline which resembles triangle or at least subtriangle-shaped wings when viewed from above. *Dilophosaurus wetherilli*, *Herrerasaurus ischigualastensis*, and *Liliensternus liliensternus* rather have a subrectangular outlook becoming manifested in their dorsal transverse processes when viewed from the same position. Among the examined theropods, some variation is displayed in the alignment of the transverse processes: the ones of *Coelophysis bauri*, *Herrerasaurus ischigualastensis, Syntarsus kayentakatae* and the Swiss theropod material directly project horizontally to the longitudinal axis of the vertebra centrum. In contrast, the transverse processes of *Coelophysis rhodesiensis* are bent dorsally at an angle of about 25 degree measured from the horizontal (RAATH 1969), whereas the transverse processes of *Segisaurus halli* are bent ventrally (CARRANO, HUTCHINSON & SAMPSON 2005). At this point, one should note that the illustrations of the dorsal vertebrae of *Coelophysis bauri* in COLBERT (1989, 1995) seem to show other shapes of their transverse processes when viewed from dorsal position compared to *C. rhodesiensis*, *S. kayentakatae*, and the Swiss theropod material. In fact, there is no difference between the transverse process outline within the Coelophysidae. The shape of the dorsal transverse processes of *C. bauri* illustrated by COLBERT (1989) were later verified by DOWNS (2000) resulting in absolutely similar habiti as seen in *C. rhodesiensis*, *Syntarsus kayentakatae* as well as now in the Swiss theropod material.

There is another difference in shape of the dorsal transverse processes to mention: the posterior margin of the dorsal transverse processes is angled 90 degrees to the longitudinal section of the centrum or it is bending forward (about 45 degrees) in the Swiss theropod material. This feature is only illustrated and not mentioned in the studies of RAATH (1969, 1977) for *Coelophysis rhodesiensis*, and COLBERT (1989, 1995) and DOWNS (2000) for *C. bauri* showing either the two states seen in the Swiss theropod material or also dorsals with circa 10 degrees backwardly bent transverse processes, overlapping the posterior centrum faces with their caudal margins. In *C. rhodesiensis* the backward slant seems to be more extreme when going distal along the dorsal series; the posterior margin of the process tilts backwards with its postero-distal tip overhanging the caudal portion of the centrum (RAATH 1977). WELLES (1984) and NOVAS (1993) also did not describe the angle of this posterior margin of the dorsal transverse processes in *Dilophosaurus wetherilli* and *Herrerasaurus ischigualastensis*; it seems they are as forwardly swept as it is seen in the anterior dorsals of the Swiss theropod material; but this is only assumed from pictures from lateral position.

In addition to the achievement of the caudal margin of the transverse processes, the anchorage of the latter to the centrum also differs among the examined theropods. In the Swiss theropod material, each transverse process of the dorsal vertebrae does extend over the entire antero-posterior length of the centrum. In contrast, *Dilophosaurus wetherilli* and *Herrerasaurus ischigualastensis* do not exhibit transverse processes extending over the whole centrum lengths. However, this feature is only illustrated in drawings in the two latter (WELLES 1984; NOVAS 1993). COLBERT illustrates this same condition in the twelfth presacral vertebra of *Coelophysis bauri*, but also does not mention the appendages' manner (COLBERT 1989, 1995; TYKOSKI 1998).

Seven more or less complete neural spines are preserved in the Swiss theropod material, exhibited in dorsal number 2, 3, 4, 5, 6, 7, and 10. Almost all of these dorsals differ in their lateral appearance. The neural spine of the third dorsal has an anterior and posterior shoulder with a cap in the middle of the two latter, the neural spine of the fifth dorsal vertebra looks like a shark's fin, the one of the sixth resembles the shaft of an axe, the seventh has the shape of a 'couch' in lateral view with its backrest pointing posterior and the tenth shows a strange knob (i.e. anterior shoulder) in its antero-dorsal part, whereas the dorsal margin is very straight (i.e. posterior shoulder), before dropping at an angle of 90 degrees to its postero-ventral tip confluent with the postero-dorsal end of the centrum. Such forms of the neural spines are neither documented in *Coelophysis bauri*, nor in *C. rhodesiensis*, and *Syntarsus kayentakatae* (RAATH 1977; COLBERT 1989, 1995; ROWE 1989; TYKOSKI 1998). Accordingly, ROMER (1956) stated that there are no conspicuous neural spines developed in saurischians. In *Dilophosaurus wetherilli* (UCMP 37302), there is also an anterior and posterior shoulder plus a cap in some dorsal vertebrae (WELLES 1984), whereas in *Herrerasaurus ischigualastensis* no change in the lateral shape of the neural spines can be observed along the dorsals series (NOVAS 1993). However, the variety in neural spines of the Swiss theropod material is considered to be a result of its juvenile to subadult ontogenetic stage: at least the dorsal borders of vertebrae 3 and 4 are spongy and thus in conclusion cartilaginous tissue had been lying onto all neural spines resulting now in their above mentioned variety of forms.

The height of the most upper ends of the neural spines displayed in the Swiss theropod material constantly increases heading caudally along the dorsal series: the highest tip of the third neural spine measures 14 mm, decreases to 12 mm in the fourth, rises to 17 mm in the fifth and sixth, and to 20 in the seventh and finally, grows to 28 mm in the tenth dorsal vertebra. In addition to the overall increasing in height from anterior to posterior, the bases of the neural spines rises as well from measuring only approximately one half neural arch length (dorsal 3 and 4) to extending all over the latter (dorsal 10). RAATH states 1977 in his PhD thesis that the height of the neural spines of *Coelophysis rhodesiensis* does not change along the dorsal series, only the basis lengths of the neural spines do get larger from dorsal 3 backwards with the increasing centrum lengths. In contrast, the heights and the lengths of *Dilophosaurus wetherilli* and *Liliensternus liliensterni* stay the same along the dorsal series (HUENE 1934a; WELLES 1984; ROWE & GAUTHIER 1990; TYKOSKI & ROWE 2004). Additionally, *Herrerasaurus ischigualastensis* even decreases the height of its neural spines heading caudally (NOVAS 1993). The dorsals of *Syntarsus kayentakatae* are too incomplete for making any assumption about this alteration (ROWE 1989; TYKOSKI 1998). Although, COLBERT (1989, 1995) has got many specimens of *Coelophysis bauri* available, he neglects such observations in his studies completely.

Dislocated neural arches and open neural sutures can be seen in the third, fourth, sixth, seventh, and eighth dorsal vertebrae of the Swiss theropod material, supporting with their presence the assumption of having a juvenile to subadult individual. The slight separation between the neural arches and the centra is never visible in full aspect. There is always a part covered with clay along the antero-posterior neural suture length and thus the true number of serrations remains undetected in each case. However, the assumed number of serrations of every neural suture adds up to 20 in the Swiss theropod material, and thus, the serration count is the same as it is reported in *Coelophysis rhodesiensis* (Raath 1977). At mid-length of the neuro-central sutures of the Swiss theropod material, there is one interdigitating large tooth being clearly visible in dorsal 6 and 7. Raath (1977: 44) describes this tooth in his work as well: 'Several juvenile specimens in the collection have disassociated centra and neural arches. The centro-neural suture visible in these disassociated specimens is intricate. On each side the suture consists of closely spaced serrations, which interdigitate with their counterparts borne on the gently bowed up walls of the neural canal. The number of serrations per side varies between 15 and 20. At mid centrum length, a deeper notch on each side of the neural canal interdigitates with a correspondingly large 'tooth' in the middle of the neural arch'.

Many advanced saurischians (Romer 1956), respectively all saurischians (Fastovsky & Weishampel 2005) show hyposphene-hypanthrum articulations on at least the posterior trunk vertebrae. 'The hyposphene-hypanthrum articulation involves a 'positive' structure, the hyposphene, on the posterior side of the vertebra below the postzygapophyses, and a 'negative' structure, the hypanthrum, between the prezygapophyses of the next vertebra where the hyposphene fits' (Apesteguia 2005). None of these articulations are visible in the dorsal vertebrae of the Swiss theropod material. Although dorsal 2, 3, and 10 lie in lateral view, their neural arches are either slightly dislocated or not prepared accurately enough due to the paper thin bone structure preventing a perfect preparation. Colbert did not document hyposphene-hypanthrum articulation in the dorsals of *Coelophysis bauri*, whereas Raath has mentioned it for *C. rhodesiensis* (Raath 1977; Colbert 1989, 1995; Rauhut 2003). These articulations are also present in *Herrerasaurus ischigualastensis*, *Dilophosaurus wetherilli*, *Lophostropheus airelensis*, and *Liliensternus liliensterni* (Huene 1934a; Lapparent & Larsonneur 1966; Welles 1984; Rowe & Gauthier 1990; Novas 1993; Cuny & Galton 1993; Rauhut & Hungerbühler 2000; Rauhut 2003; Tykoski & Rowe 2004; Ezcurra & Cuny 2007). Hyposphene-hypanthrum articulations have not been mentioned in the dorsals of inter alia *Syntarsus kayentakatae* probably due to imperfect preservation (Rowe 1989; Tykoski 1998).

Strutting or laminae on the neural arches underneath the transverse processes are present in *Coelophysis rhodesiensis*, *Dilophosaurus wetherilli*, *Herrerasaurus ischigualastensis*, *Lophostropheus airelensis*, *Liliensternus liliensterni*, and *Syntarsus kayentakatae* (Huene 1934; Larsonneur & Lapparent 1966; Raath 1969, 1977; Colbert 1969, 1989, 1995; Welles 1984; Rowe 1989; Rowe & Gauthier 1990; Sereno & Novas 1993; Cuny & Galton 1993; Rauhut & Hungerbühler 1998; Tykoski 1998; Tykoski & Rowe 2004; Ezcurra & Cuny 2007). In the Swiss theropod material they exist at least on the neural arch of dorsal 5. All other dorsals do not display this important area accurately enough, except for dorsal number 10 which certainly does not exhibit any of these laminae. Although previous authors did not mention anything like a lamina in *Coelophysis bauri* and *Segisaurus halli* (Camp 1936; Colbert

1969, 1989, 1995; ROWE & GAUTHIER 1990; EZCURRA & CUNY 2007), TYKOSKI (2005) states its presence in both taxa.

The dorsal ribs are preserved numerously but not to full extant: almost all portions of the branching into the capitulum and tuberculum, as well as their most distal regions are not preserved. Additionally none of the ribs articulate exactly to the diapophysis or to the parapophysis of the centrum. There is no 'web of bones' visible at the articulation area where the capitulum and tuberculum should have been attached to the centrum and the transverse process as it is stated in *Coelophysis bauri*, *C. rhodesiensis*, and *Syntarsus kayentakatae* (COLBERT 1947, 1964, 1989, 1995; RAATH 1969, 1977; ROWE 1989; TYKOSKI 1998). RAATH (1969) stated that the parapophysis migrates from the wall of the neural arch underneath the transverse process onto the latter, where it moves distally when going backwards in the dorsal series. There is no changing in the position of the diapophysis being always situated on the distal margin of the transverse process as recognizable in dorsal vertebrae 2, 3, and 10 in the Swiss theropod material, which is the normal condition for dorsals in Saurischia (ROMER 1956; ROWE & GAUTHIER 1990; TYKOSKI & ROWE 2004). There are clear marks emphasizing the presence of a parapophysis in dorsal 2 and 3 consisting at least of an ascending process dorso-laterally located to the anterior articular face. In contrast, the marks are quite doubtful in dorsal 10 making it unclear whether the parapophysis has already migrated onto the transverse process as well. TYKOSKI (2005: 159) mentioned in his phylogenetic analysis that *Coelophysis bauri, C. rhodesiensis*, and *Syntarsus kayentakatae* display '… parapophyses on or close to the dorsal centrum …'. He did not state any indication for the presence of an ascending process. Thus, this morphological feature could represent a difference between the Swiss theropod and the Family Coelophysidae. Of course, the migration of the parapophysis takes place in all the examined theropods as well, although the important areas for recognizing the migration is not preserved in *Lophostropheus airelensis, Procompsognathus triassicus, Segisaurus halli,* and *Syntarsus kayentakatae* (HUENE 1934a; COLBERT 1947, 1964, 1989, 1995; WELLES 1984; ROWE 1989; ROWE & GAUTHIER 1990; RAUHUT & HUNGERBÜHLER 2000; TYKOSKI 1998; TYKOSKI & ROWE 2004).

In the Swiss theropod material, the anterior dorsal region is well recognizable from the posterior one by the changing of the width of the proximal parts of the rib shafts: the anterior dorsal ribs show their enormous medio-lateral widths at the bases of the branching into the capitulum and tumberculum (e.g. 30 mm in dorsal rib 3), whereas the successive ribs, probably posterior to dorsal 6, only exhibit approximately 14 mm under the same condition (as seen in dorsal 7). This transition is also described by RAATH (1977) for *Coelophysis rhodesiensis*: '… there is little doubt that the ribs were raked back in the living animal, giving a slender thorax and trunk. It seems likely that the large cervico-dorsal transitional ribs may have served as strong attachment points for some of the superficial muscles of the trunk, probably the serratus muscles in particular'. In conclusion, there is a difference in the medio-lateral widths at the bases of the proximal branching of the anterior dorsal ribs and that of the posterior dorsal ribs in *C. rhodesiensis* as well as in the Swiss theropod material.

9.4.1.3. Sacral Region

The vertebrates have increased their number of sacral vertebrae constantly, started from one in amphibian ancestors, across two in *Herrerasaurus ischigualastensis* (NOVAS 1993), and moving to five in Coelophysoids (e.g. PAUL 1988; COLBERT 1989; ROWE & GAUTHIER 1990; TYKOSKI & ROWE 2004). This increase has been accomplished by incorporating vertebrae into the sacrum either from the dorsal or from the caudal series thereby expanding and strengthening the sacral building (ROMER 1956, 1983; COLBERT 1989; TYKOSKI & ROWE 2004; CARRANO & SAMPSON 2004). The Swiss theropod is assumed to have had 5 sacral vertebrae (as discussed below) subsequently named as sacral 1 to 5. Sacral 1 and 2 were originally dorsal vertebrae, but later they have been included into the sacrum becoming dorsosacrals. As original dorsals and not true sacrals, they do not bear sacral ribs. Instead, they display modified transverse processes contacting the ilia by forming a sheet-like roof with the sacral ribs (ROMER 1956; RAATH 1977; WELLES 1984; TYKOSKI, pers. communication). Sacral vertebrae 3 and 4 are the so-called true sacrals. These vertebrae bear sacral ribs, which contact the ilia as well. The area on which these ribs are attached to the centra is dorso-ventrally and antero-posteriorly quiet enlarged compared to that of sacrals 1 and 2. Therefore, the fossae are either covered in sacral 3 and 4 with these appendages or simply do not exist. Sacral vertebra 5 is as number 1 and 2 not a true sacral; having originally been part of the caudal series. Thus, sacral 5 also bears, instead of sacral ribs, modified transverse processes (TYKOSKI, pers. communication), but here they are similar to caudal transverse processes in shape when viewed from dorsal position: they are backswept with their anterior and posterior margins lying parallel to each other.

The order of the sacral vertebrae is hard to reconstruct in the Swiss theropod material because only two neural arches are articulated to their centra. The original sequence cannot clearly be determined by neither the measurement of the widths and heights of the articular faces nor of the centra lengths. Only the last two sacral vertebrae are definitively placed on position 4 and 5, whereas the rest can only be assumed. The identification of the second and third neural arch is based on the lateral expansion of their transverse processes (number 2) and sacral ribs (number 3), respectively, which fit the appropriate parts of the corresponding neural arches in the description of *Coelophysis bauri* (AMNH 7223; COLBERT 1989, 1995). Sacral 2 is the only one of this series which exhibits a fossa on its lateral centrum side as seen in number 2 of *Syntarsus kayentakatae* (TYKOSKI, pers. communication).

The number of sacrals can vary during the ontogeny of *Coelophysis bauri, C. rhodesiensis, Dilophosaurus wetherilli* and *Liliensternus liliensterni* in showing only a sacral series composed of four instead of five vertebrae in juvenile stage, as stated by COLBERT (1989, 1990), RAATH (1977, 1990) and WELLES (1984). Since the Swiss theropod material only has four sacral centra preserved, it either means this number is a result of individual ontogenetic stage, or due to incomplete conservation. However, there is a diffuse portion of neural arch present also on slab D being identified as a remain of sacral 1 and therefore, the latter assumption is confirmed. Nevertheless, the fact that the dorsal centra often are disarticulated from their neural arches, and considering the incomplete fusion of the pelvic and sacral elements, supports the former assumption of having a juvenile to subadult individual. Thus in conclusion, although the Swiss theropod material is of early ontogenetic stage, it is assumed to have five sacral vertebrae. This number of sacral vertebrae would have perfectly fit into the iliac lengths. The total length of the four vertebrae under discussion measure 122 mm. Thus, the 180 mm long ilium length could accommodate a further centrum of approximately 30 mm in length, resulting in a sacral series of 152 mm (five centra) leaving enough free distance in the anterior and posterior portion of the ilium for the posterior half of the most hind dorsal vertebra centrum and the anterior half of the most fore caudal centrum as it is seen for example in most specimens of *Coelophysis bauri* and *C. rhodesiensis,* as well as in the individual of *Dilophosaurus wetherilli* (RAATH 1969, 1977; WELLES 1984; COLBERT 1989, 1995).

In the Swiss theropod material all vertebrae of the sacral series are slightly smaller in length than the constant dorsal centra: sacral 2 measures 30 mm in length along its ventral side, sacral 3 measures 30 mm under the same condition, sacral 4 adds up to 31 mm in length, and sacral 5 measures 31 mm. Thus, the lengths of the sacral centra stay constant heading caudally. TYKOSKI (1998) also stated the measurements of the sacral centra longitudinal lengths of *Syntarsus kayentakatae* in his master thesis: all of the sacrals are approximately one-sixth shorter than those of the Swiss theropod material (see «11.2. measurements» table 3, in appendix): although its series consists of five sacrals its overall length only adds up to 124 mm. However, the lengths rather decrease than stay constant. The only individual of *Syntarsus kayentakatae* with preserved sacral vertebrae is TR97/12, being stated as a subadult specimen with separated ilia to the sacral series but already firmly fused sacral centra to each other (ROWE 1989; TYKOSKI 1998). In this aspect, TR97/12 is even more ontogenetically developed as the Swiss theropod material, which additionally exhibits separated dorsal and sacral centra as well as unfused transverse processes and ribs (see «9.4.2.3. ischium»). COLBERT (1989, 1995) and RAATH (1969, 1977) do not specify the data of single sacral centra lengths. Both only mention the lengths of the whole sacral series: *Coelophysis bauri*'s sacrum lengths range from 89 mm (AMNH 7252) to 148 mm (AMNH 7224) (COLBERT 1989, 1995), whereas only one sacrum length is reported of *Coelophysis rhodesiensis* measuring 123 mm (QG1) (RAATH 1969, 1977). QG1 is the holotype of *C. rhodesiensis* and displays firmly fused sacrals, pelvic elements, and neural arches in the rest of the vertebrae indicative of adulthood (RAATH 1969, 1977), whereas the sacral data lengths of COLBERT's *Coelophysis bauri* include juveniles as AMNH 7252, probably subadults as AMNH 7249, and adults as AMNH 7224 (COLBERT 1989, 1990, 1995).

The extraordinary habitus of the articular faces differentiates the sacral vertebrae of the Coelophysidae from those of all other examined theropods: the sacral articular faces are extremely expanded regarding the mid-areas of the centra in *Coelophysis bauri*, *C. rhodesiensis*, *Syntarsus kayentakatae*, and the Swiss theropod material (RAATH 1969, 1977; COLBERT 1989, 1995; ROWE 1989; ROWE & GAUTHIER 1990; TYKOSKI 1998; TYKOSKI & ROWE 2004). TYKOSKI (1998) even describes the cranial and caudal shape of the articular faces of *Syntarsus kayentakatae* being as wide as tall and thus, perfectly fits the description of those of the Swiss theropod material.

An important morphological feature is the constitution of the ventral side of the sacral centra. In the Swiss theropod material, the ventral side of sacral 2 is strongly flattened, whereas the ventral portions of the other sacrals are too badly compressed to make any definitive statement. The ventral side of *Coelophysis rhodesiensis* is flattened as it is the condition in the Swiss theropod material for at least sacral 2 (Raath 1969, 1977), whereas all sacral ventral sides of *Coelophysis bauri*, *Dilophosaurus wetherilli, Herrerasaurus ischigualastensis, Lophostropheus airelensis,* and *Liliensternus liliensterni* are rounded or keeled (after Rauhut 2003; Huene 1934a; Larsonneur & Lapparent 1966; Welles 1984; Rowe & Gauthier 1990; Novas 1993; Cuny & Galton 1993; Ezcurra & Cuny 2007). The sacral vertebrae of *Segisaurus halli* and *Procompsognathus* are either not preserved or not described from this aspect (Fraas 1913; Camp 1936; Ostrom 1981; Rowe 1989; Rowe & Gauthier 1990; Chatterjee 1993; Rauhut 2003; Tykoski & Rowe 2004; Carrano, Hutchinson & Sampson 2005). Tykoski (1998) does not mention the ventral sides of *Syntarsus kayentakatae*. In a subsequent study, he states that '… the ventral margins of the sacral series are relatively straight' (Tykoski 2005: 173). Additionally, he says that this morphological state is also applied to *Coelophysis bauri, C. rhodesiensis, Dilophosaurus wetherilli, Herrerasaurus ischigualastensis, Liliensternus liliensterni* and *Lophostropheus airelensis*, denying the observations previous authors made (Huene 1934a; Larsonneur & Lapparent 1966; Welles 1984; Rauhut 2003). Another possible difference between the Family Coelophysidae and all other examined theropods is the sacral width of the centrum. Tykoski (2005: 173) mentions that all the theropods examined in this study (unknown in *Segisaurus halli* and *Procompsognathus triassicus*) show sacral mid centrum diameters that are '… approximately similar to those of the posterior dorsals and anterior caudals'. In the Swiss theropod material the sacral mid-centrum widths (sacral 3: 12 mm) are twice as thick as the ones of the posterior dorsals, and the anterior caudals (caudal 1: 6.5 mm). Both ratios are only assumptions as the elements remain embedded in the sediment and as they are somewhat compressed.

'Sacral pleurocoels are absent in basal dinosauriforms, ornithischians, basal sauropodomorphs, and many theropods' after Rauhut (2003: 85). The phylogenetic analysis indicates that there are at least three out of ten theropods displaying fossae on the lateral sides of their sacral vertebrae (see «1.2. matrix» table 1, in appendix). Rowe (1989) and Tykoski (1998) state the presence of no fossa or foramina in the sacral vertebrae of *Syntarsus kayentakatae*. Further, Tykoski (pers. communication) confirms the presence of a fossa at the lateral sides of sacral 2 in the TR97/12 specimen as mentioned above. Additionally, the sacral 3 and 4 exhibit no fossa. Their lateral sides are taken up by true sacral ribs covering the possible presence of these cavities in *Syntarsus kayentakatae* (Tykoski, pers. communication). The Swiss theropod material also shows a fossa at the lateral side of sacral 2, whereas all of the other preserved sacral vertebrae do not display any cavities in the same area. This observation could either be a result of high compression during diagenesis, or biological fact as seen in *Syntarsus kayentakatae*. RAATH (1969, 1977) neglects the presence of sacral fossae in *Coelophysis rhodesiensis* and COLBERT (1989; 1995) mentions no such structure in the sacral vertebrae of *Coelophysis bauri. Dilophosaurus wetherilli* does show a fossa in sacral 1: 'in lateral view there is a short, deep, longitudinal groove, concave dorsally, just above the spool' (WELLES 1984: 121). The rest of the examined theropods do not exhibit fossae in their sacrals as in *Herrerasaurus ischiagualastensis*, *Lophostropheus airelensis*, *Liliensternus liliensterni* (HUENE 1934a; LARSONNEUR & LAPPARENT 1966; ROWE 1989; ROWE & GAUTHIER 1990; SERENO & NOVAS 1993; CUNY & GALTON 1993; RAUHUT & HUNGERBÜHLER 2000; TYKOSKI 1998; TYKOSKI & ROWE 2004; EZCURRA & CUNY 2007). Otherwise, the authors are simply unaware of these morphological features or did not mention their presence due to the lack of preservation as in *Procompsognathus triassicus* and *Segisaurus halli* (FRAAS 1913; CAMP 1936; OSTROM 1981; ROWE & GAUTHIER 1990; SERENO & WILD 1992; CHATTERJEE 1993; TYKOSKI & ROWE 2004).

Coelophysis bauri and *C. rhodesiensis* are known to build a dorsal sheet with their sacral ribs or modified transverse processes for contacting the ilia (RAATH 1969, 1977; COLBERT 1989, 1995; ROWE & GAUTHIER 1990; RAUHUT 2003, EZCURRA & CUNY 2007). The achievement of the sacral ribs and sacral transverse processes in *Dilophosaurus wetherilli, Liliensternus liliensterni, Lophostropheus airelensis, Procompsognathus triassicus, Segisaurus halli, Syntarsus kayentakatae* and the Swiss theropod material is yet unsure either as a consequence of poor preservation or that the examination of material is of juvenile to subadult ontogenetic stage (FRAAS 1913; HUENE 1934a; CAMP 1936; LARSONNEUR & LAPPARENT 1966; OSTROM 1981; WELLES 1984; ROWE 1989; ROWE & GAUTHIER 1990; SERENO & WILD 1992; CUNY & GALTON 1993; CHATTERJEE 1993; TYKOSKI 1998; RAUHUT 2003; TYKOSKI & ROWE 2004; EZCURRA & CUNY 2007). Although the sheet forming construction is not yet known in *Syntarsus kayentakatae* because there are no neural arches preserved, the species certainly has extensively fused sacral centra with obliterated sutures as found in specimens of *Coelophysis bauri*, and *C. rhodesiensis* (RAATH 1969, 1977; COLBERT 1989, 1995; ROWE 1989; TYKOSKI 1998; EZCURRA & CUNY 2007). *Herrerasaurus ischigualastensis* and *Dilophosaurus wetherilli* exhibit sacral centra, sacral ribs and modified transverse processes as well as ilia which remain separate throughout ontogeny (ROWE & GAUTHIER 1990; WELLES 1984; NOVAS 1993; RAUHUT 2003; TYKOSKI & ROWE 2004). The original assumption, that the latter is an adult individual, is more and more doubted (TYKOSKI 1998, 2005).

The dorsal view of the sacrum of *Coelophysis bauri* looks different from that of *C. rhodesiensis*: while the former shows fused sacral ribs to the inner wall of the ilia with medial cavities at the transitions of the single sacral ribs and transverse processes (COLBERT 1989, 1995), the latter has got a sacral roof extending unbroken from the second sacral backwards (RAATH 1969, 1977). In addition, *Coelophysis rhodesiensis* displays small cavities between sacral centra 3 and 4, and 4 and 5 at the ventral side of the sacral sheet (RAATH 1977; TYKOSKI 1998: 124, intertransverse fontenalles). The Swiss theropod material resembles *Coelophysis bauri* and *C. rhodesiensis* with regard to the morphology of sacral 4: there are two cavities, one at the posterior rim as seen in *Coelophysis bauri* (COLBERT 1995) and one at the distal margin as in *Coelophysis rhodesiensis* (RAATH 1969, 1977).

However, the location is different compared to *Coelophysis rhodesienis.* In addition, *C. bauri* shows variation in the achievement of these vacuities: some individuals of various specimens do not have them (COLBERT 1995). However, COLBERT does not mention specimen numbers and their ontogenetic stages. Therefore, the Swiss theropod material can have these vacuities even in adult specimens, or their presence may reflect the juvenile to subadult age of the material. The vacuities may have been filled with cartilage, which first ossify in late ontogeny. In addition to the variation in the presence of cavities, COLBERT (1995) also found variation in the grade of ossification of the dorsal roof: He noted the occurrence of variable fusion in the sacrum of the American genus *Coelophysis* (in one specimen the sacral vertebrae are fused whereas in another there is no fusion). COLBERT considers that this, taken in conjunction with other characteristics, may represent a sexual difference in *Coelophysis bauri* (COLBERT, pers. communication, in RAATH 1969). RAATH (1977, 1990: 49) also discovered this kind of variation in *Coelophysis rhodesiensis* which he similarly accredited to sexual dimorphism: 'the centra of *Syntarsus* [*Coelophysis*] *rhodesiensis* fuse together on maturity and there is a corresponding but variable tendency for the transverse processes and neural spines to coalesce into continuous sheets of bone running the length of the sacrum' (see «9.3. Excursus C: sexual dimorphism» for more detail).

The neural spines of the sacral vertebrae can be seen in sacral 2 to 5. All the sacral neural spines are either vertically compressed or dorsally abraded. Therefore, these measurements have to be considered as a minimum: the neural spine of sacral 2 adds up to 14 mm in height, the one of sacral 3 is 15 mm, sacral 4 shows 21 mm, whereas the height of sacral 5 measures 17 mm. Nevertheless, typical theropod sacra exhibit straight or nearly straight horizontal dorsal neural spine margins (TYKOSKI 1998). In *Coelophysis bauri*, *C. rhodesiensis*, *Herrerasaurus ischigualastensis*, *Liliensternus liliensterni* and *Syntarsus kayentakatae* the height of the neural spines increases only slightly or not at all when going distally along the sacral series (HUENE 1934a; RAATH 1969, 1977; COLBERT 1989, 1995; ROWE 1989; NOVAS 1993; TYKOSKI 1998). 'The [neural spines of the] sacrum of *Syntarsus kayentakatae* arche[s] gently dorsally with the apex centred on the third sacral vertebra', stated by TYKOSKI (1998: 71). Here, in the Swiss theropod material it is not the third sacral with the highest neural spine apex but the fourth, and additionally, the increasing is not as slight as exhibited, for example, by *Syntarsus kayentakatae*. In contrast, there is a difference of 34 percent in minimal and maximal height of the neural spines in the Swiss theropod material. *Dilophosaurus wetherilli* exhibits a similar arching of 23 percent. Although the arching is less than in the Swiss theropod material, WELLES (1984) and TYKOSKI (1998: 166) describe the sequence of the sacral spine of *Dilophosaurus wetherilli* as '… strongly arched dorsally'. However, in the Swiss theropod material, one may note that the grade of development of the arching is affected by the abrasion and compression caused by diagenesis.

The upper margins of the neural spines of *Coelophysis rhodesiensis* are topped by a swollen longitudinal rim along the length of the roof composed of the sacral ribs and modified transverse processes (RAATH 1977). In the Swiss theropod material, these so-called spine tables are more or less available, as well as in the two sacrals of *Herrerasaurus ischigualastensis* (NOVAS 1993). In the former, these structures are rather destroyed due to dorso-ventral compression and abrasion of the neural spines during diagenesis.

9.4.1.4. Caudal Region

The anterior four of approximately 40 original caudal vertebrae are preserved in the Swiss theropod material. In *Coelophysis bauri*, *Dilophosaurus wetherilli*, and *Herrerasaurus ischigualastensis* less than 41 caudal vertebrae are reported (WELLES 1984; COLBERT 1989, 1995; ROWE & GAUTHIER 1990; NOVAS 1993; RAUHUT 2003; TYKOSKI & ROWE 2004), whereas *Coelophysis rhodesiensis* exhibits at least 41 caudals (RAATH 1977; RAUHUT 2003). Although this vertebral region is the best and most complete preserved part of *Liliensternus liliensterni*, the two available individuals of this species differ in their caudal vertebrae number resulting in a bivariate character state of less than 41 caudals or at least 41 caudals (ROWE & GAUTHIER 1990; RAUHUT 2003; TYKOSKI & ROWE 2004).

The caudal centra of the Swiss theropod material measure sequentially 28 mm, 31 mm, 31 mm, 33 mm in length; this data almost exactly corresponds with the sizes of adult *Coelophysis bauri* (AMNH 7223 and 7224; COLBERT 1989), whereas it is slightly larger than measurements of caudal centra lengths of *C. rhodesiensis* (QG445) (RAATH 1977). TYKOSKI (1998) does not refer to caudal size, or caudal features of *Syntarsus kayentakatae* due to its incomplete preservation. *Dilophosaurus wetherilli* (UCMP 37302) exhibits anterior caudal centrum lengths which are almost the same as the pendants of *Lophostropheus airelensis* (CM without collection number) being about twice as big as the Swiss theropod material (LARSONNEUR & LAPPARENT 1966; WELLES 1984). Additionally, the anterior caudal centrum lengths of *Liliensternus liliensterni* (MB. R. 2175 small) and *Herrerasaurus ischigualastensis* (PVL 2566) are similar (HUENE 1934a; REIG 1963; NOVAS 1993).

As the centra increase their lengths in the Swiss theropod material when heading backwards in the caudal series, this elongation is associated with the decline of their dorso-ventral height; both the first and second centra measure 13 mm, the third 12 mm and the fourth 10 mm in height along their anterior faces. The data of the dorso-ventral length of the posterior faces show a decrease in height as well; the first and second caudal vertical diameters are 16 mm, whereas the third and fourth caudal vertebrae measure 12 mm. It is notable that the caudal centra generally diminish faster in diameter than in length, so that frequently a substantial part of the caudal centra is relatively long and slender (ROMER 1956). TYKOSKI & ROWE (2004) also noted this phenomenon. However, there is a slight change in *Dilophosaurus wetherilli* and *Herrerasaurus ischigualastensis*. They decrease their antero-posterior caudal centra lengths along the series (WELLES 1984; NOVAS 1993), whereas *Coelophysis bauri*, *C. rhodesiensis,* the Swiss theropod material, and *Syntarsus kayentakatae* have increasing centra lengths (RAATH 1969, 1977; COLBERT 1989, 1995; ROWE 1989; TYKOSKI 1998). In contrast, *Liliensternus liliensterni* is the only examined theropod with constant caudal lengths (HUENE 1934a) (see «11.2. measurements» table 4, in appendix for the absolute centrum lengths of each examined theropod).

Saurischian dinosaurs typically exhibit amphicoelous to platycoelous centra along their axial series (ROMER 1956). Here in the caudals of the Swiss theropod material, the former is realized as in *Coelophysis bauri, C. rhodesiensis*, *Dilophosaurus wetherilli, Herrerasaurus ischigualastensis, Lophostropheus airelensis*, *Liliensternus liliensterni*, *Segisaurus halli,* and *Syntarsus kayentakatae* (GILMORE 1920; HUENE 1934; CAMP 1936; REIG 1963; LARSONNEUR & LAPPARENT 1966; RAATH 1969, 1977; WELLES 1984; COLBERT 1989, 1995; ROWE 1989; NOVAS 1993; TYKOSKI 1998; CARRANO, HUTCHINSON & SAMPSON 2005; EZCURRA & CUNY 2007). Whilst all vertebral centra of *Coelophysis bauri* are amphicoelous, the mid caudals are reported as slightly procoelous in *C. rhodesiensis* (RAATH 1977; COLBERT 1989, 1995). Nevertheless, it is not possible to examine the mid-caudals in the Swiss theropod material.

The centra available for the Swiss theropod material are medio-laterally and dorso-ventrally narrow. The lateral and dorsal shape of these caudals differentiate from the pendants of *Syntarsus kayentakatae, Coelophysis rhodesiensis,* and *C. bauri* showing cranial centra which are medio-laterally narrow as well, but dorso-ventrally deeper (TYKOSKI 1998). Generally, GAUTHIER (1986) and RAUHUT (2003) define the habitus of the anterior caudals as oval or subrectangular and box-like. The former characterisation (oval) fits with all examined theropods, except the Swiss theropod material that displays a box-like, rather than oval, shape. COLBERT (1989) states, that the first 10 to 12 caudals of *Coelophysis bauri* are comparable in length to the presacral vertebrae. Additionally, ROMER (1956) writes that the proximal caudals are nearly as robust as the dorsals in general and only gradually diminishing distally in size. The length and the shape of the cranial caudals of *C. bauri* resemble the associated dorsal vertebrae in *C. rhodesiensis* and *Syntarsus kayentakatae* (RAATH 1969, 1977; ROWE 1989; TYKOSKI 1998). In contrast, the anterior caudals of the Swiss theropod material are indeed similar to the lengths of the posterior dorsals, but display a different medio-lateral and dorso-ventral shape as already discussed. However, the caudals of the Swiss theropod material surely represent proximal caudals; the position is indicated by several morphological features:

(1) the position of the chevrons: usually, there are no chevrons (haemapophyses) in the first few caudals, they often begin at the 3rd to 7th caudal vertebrae (ROMER 1956). Thus, in conclusion, the preserved vertebrae could have been somewhere in the series of the 3rd to 12th caudal. The first haemapophysis preserved in the Swiss theropod material is articulated on the ventro-proximal portion of the second caudal vertebra. Thus, although ROMER (1956) states, the haemapophyses usually begin at the third to seventh caudal vertebrae, he does not exclude the possibility of haemapophyses start at more proximal caudals as shown in some male individuals as mentioned below (RAATH 1977, 1990; COLBERT 1990; LARSON & FREY 1992; LARSON 1995).

(2) sexual dimorphism: LARSON (1995) writes in his paper about sexual dimorphism discovered by Philip CURRIE from the Royal Tyrrell Museum in Drumheller, Alberta, in 1993. CURRIE had been studying species of *Sauronithoides* and other troodontids from China for several years and found out that this group of theropods may be divided into robust and gracile morphotypes as stated for *Tyrannosaurus*, and of course for *Coelophysis bauri* and *C. rhodesiensis*, as well (COLBERT 1990; RAATH 1990; see «9.3.

Excursus C: sexual dimorphism within Coelophysidae»). He stated that in the gracile form, the first chevron is positioned on the front of the first caudal vertebra (i.e. on the rear of the last sacral vertebra), and is approximately the same size and shape as the second. The first haemapophysis on the robust form is positioned on the rear of the first caudal vertebra, and is more wedge-shaped and shorter than the second. In other words, the gracile morphotype has an extra chevron to the robust one! LARSON (1995) found the same phenomenon in specimens of *Tyrannosaurus rex*; only the chevrons were one position more distally adjusted starting at the rear of the first caudal in gracile morphotypes, and not at the rear of the sacral 5 as in *Saurornithoides* (see «11.5. female and male of *Tyrannosaurus rex*» figure 40, in appendix). Here, in the Swiss theropod material the first chevron also begins in front of the second caudal vertebra, thus at the rear of the first caudal (as stated by COLBERT (1995) observed in *Coelophysis bauri*: the chevrons of this dinosaur usually begin at the junction between the first two caudal vertebrae). The length of the first chevron is one sixth shorter (42 mm) than that of the second chevron (48 mm). In addition, the lateral outline of the former differs from the latter in being only slightly expanded at its distal portion, whereas the second and third chevron resemble a rod. This changing in morphology involves an alteration of muscles: the more surfaced area on the postero-ventral part of the first chevron presumably functioned as a place of attachment for the 'penis-retractor muscle' as seen in male crocodiles (LARSON & FREY 1992; LARSON 1995). The female crocodiles only exhibit first caudal haemapophyses half the length of their immediate successors. Another possible alternative for determining the sex of a dinosaur when using the caudal series is the lack of the first chevron enables a female a greater passage for laying eggs (ROMER 1956; COLBERT 1989, 1995; CARPENTER 1990). However, both statements support the assumption the Swiss theropod material represents a gracile male individual (compare «9.3. Excursus C: sexual dimorphism within Coelophysidae»).

(3) The first eight or ten chevrons are three times the length of the appropriate neural spines in *Coelophysis bauri* and *Coelophysis rhodesiensis* (RAATH 169, 1977; COLBERT 1989, 1995). This is also true for the first three chevrons of the Swiss theropod material. Consequently, the tail evidently was deep. 'This may be contrasted with other theropod dinosaurs in which there is more of a balance between the neural spines above and the chevrons below' (COLBERT 1989: 87). Thus the caudal muscles were well developed, mainly in the ventral part of the tail. RAATH (1969: 6) noted: 'the tail is thick proximally, because of long caudal ribs, high neural spines and long chevrons, and tapers to a 'whiplash' distally …', in his study about *Coelophysis rhodesiensis*. This statement contradicts only in the aspects of the high neural spines, which are documented as very low in *Coelophysis bauri* and the Swiss theropod material (COLBERT 1989, 1995). Unfortunately, the haemapohyses are seldom illustrated for the other examined theropods. Additionally, no data has been given regarding these chevrons.

(4) sacral 5 of the sacral series shows exactly the same shape of transverse processes when viewed from dorsal position as those of the most anterior caudal vertebra which is evidence for having the first four proximal caudals available in the Swiss theropod material. There is also a certain changing in muscle insertion area at the transition of caudal 1 to caudal 2.

(5) The pre- and postzygapophyses bear a further hint for adjusting the correct order of the caudals of the Swiss theropod material. The pre- and postzygapophyses are already elongated in the anterior caudal vertebrae in *Coelophysis bauri*, and *C. rhodesiensis* (Rauhut 2003). Raath (1969: 6) noted that 'all of the caudal vertebrae, but more especially the more distal ones, have characteristically elongated pre- and postzygapophyses, the elongation affecting particularly the prezygapophyses'. The prezygapophyses exhibit extreme elongation in the posterior half of the theropod tail (Gauthier 1986; Gregory 2005; Langer & Benton 2006). They even overlap the adjacent caudal vertebra by approximately a quarter and build a rigid structure, preventing dorsoventral movement for balancing while running and leaping (Gay 2001; Langer & Benton 2006). Neither the prezygapophyses nor the postzygapophyses of the Swiss theropod material are elongated and only of approximate dorsal length and do not overlap the articular faces cranially or caudally. The same condition is found in the caudals of *Dilophosaurus wetherilli, Herrerasaurus ischigualastensis*, *Lophostropheus airelensis*, and *Segisaurus halli* (Camp 1936; Larsonneur & Lapparent 1966; Welles 1984; Cuny & Galton 1993; Novas 1993; Carrano, Hutchinson & Sampson 2005; Ezcurra & Cuny 2007). In *Liliensternus liliensterni* only the prezygapophyses are elongated as Huene (1934a) stated. Rowe & Tykoski were not able to recognize any zygapophyses in the caudals of *Syntarsus kayentakatae* (1989; 1998).

Several other morphological features do not give any statements about the possible position of the caudal vertebrae, but do vary within the examined theropod dinosaurs. While the extreme elongation of the prezygapophyses starts at the mid region of the tail in *Coelophysis bauri* and *C. rhodesiensis*, the hyposphene-hypanthrum articulations vanish after reaching the same transition in *Syntarsus kayentakatae* and *C. rhodesiensis* (Raath 1977; Tykoski 1998). Colbert does not mention any of these articulations in his studies about *Coelophysis bauri* (1989, 1995) and similarly none of them can be recognized in the Swiss theropod material. Nevertheless, the presence of the hyposphene-hypantrum articulations may be assumed as these are documented Saurischian synapomorphies (Langer 2004; Tykoski & Rowe 2004).

On the ventral side of every caudal centra there is a sharp groove in the Swiss theropod material. Rowe & Gauthier (1990) considered this feature as an autapomorphy of the Ceratosauria, but it is found to be more widely distributed within theropods and not only since the Coelophysoidea are regarded as sister group of the Ceratosauria (Rauhut 2003; Ezcurra & Cuny 2007). Thus, the examined theropods which all represent Coelophysoidea exhibit these ventral grooves in their anterior caudal vertebrae (Huene 1934a; Larsonneur & Lapparent 1966; Raath 1969, 1977; Welles 1984; Colbert 1989, 1995; Rowe 1989; Tykoski 1998; Glut 1997, 2003; Ezcurra & Cuny 2007). The only exception is of course *Herrerasaurus ischigualastensis* which is not a member of Coelphysoidea (Novas 1993). Raath (1977: 45) even gives an explanation for the use of these ventral grooves: 'the caudal centra are longitudinally grooved ventrally to guide the caudal blood vessels along the lower surface of the tail series'.

In *Coelophysis bauri*, *C. rhodesiensis, Lophostropheus airelensis, Liliensternus liliensterni, Procompsognathus triassicus, Segisaurus halli, Syntarsus kayentakatae* an absence of lateral fossae in the neural arches or the caudal centra has not been documented (FRAAS 1913; HUENE (1934a); CAMP 1936; LAPPARENT & LARSONNEUR 1966; RAATH 1969, 1977; OSTROM 1981; COLBERT 1989, 1995; ROWE 1989; ROWE & GAUTHIER 1990; SERENO & WILD 1992; Chatterjee 1993; CUNY & GALTON 1993; TYKOSKI 1998; TYKOSKI & ROWE 2004; EZKURRA & CUNY 2007). *Herrerasaurus ischigualastenis* is the single theropod dinosaur of the examined taxa whose absence of lateral fossae in the caudal centra is confirmed by NOVAS 1993 and SERENO & NOVAS 1993. In contrast, *Dilophosaurus wetherilli* (caudal 3, WELLES 1984: fig. 21) and the Swiss theropod material (all four caudals preserved) clearly show fossae on the lateral sides of their centra (WELLES 1954, 1984; ROWE & GAUTHIER 1990; TYKOSKI & ROWE 2004). WELLES (1984: 124) observed: 'in caudal 3 there is a shallow horizontal groove (i.e. longitudinal fossa in the Swiss theropod material) in lateral view just above the spool, the groove deepest posteriorly'. This is the same condition as noted in the four anterior caudal vertebrae of the Swiss theropod material.

In addition to the above mentioned changes in the caudal centra lengths and heights, there is a reduction in the neural spines (RAATH 1969, 1977; COLBERT 1989, 1995; TYKOSKI & ROWE 2004). Neural spines are usually well developed proximal of the caudal series in Saurischia; in many cases they tend to slant posteriorly, whereas their declination becomes greater when heading distally (ROMER 1956). Although the preserved caudal vertebrae of the Swiss theropod material are the most anterior ones (see above points 1. to 4.), they exhibit rather unimpressive neural spines which can be partially seen in caudal vertebra 1 and 2. In the former, the preserved height of the neural spine measures 13 mm along the posterior margin, whereas the height of the latter adds up to 12 mm under the same condition. The neural spines gradually decrease the just measured rims of the height associated with the increase of the centra lengths as seen in *Coelophysis bauri*, *C. rhodesiensis,* and *Syntarsus kayentakatae* (RAATH 1969, 1977; COLBERT 1989, 1995; ROWE 1989; TYKOSKI 1998). In *Coelophysis bauri*, the neural spines virtually disappear from the 15th or 16th to the 20th caudal vertebra (COLBERT 1989).

The dorsal view of the available transverse processes of the Swiss theropod material show transition points of different muscle insertion as already mentioned. The transverse processes of the first caudal vertebra resemble the one of sacral 5 when viewing from dorsal position. They are backswept, the proximal and distal margins are of same length and positioned parallel to each other, whereas the width does not change during its whole transverse process length. This affinity is not remarkable, because of the fact, that sacral 5 was originally a caudal vertebra, which has been incorporated to the sacrum with its transverse process articulating with the pelvis (ROMER 1956; LANGER & BENTON 2006). In addition, the Swiss theropod material displays another change in the dorsal shape of the transverse processes at the transition of the first to the second caudal vertebra: the following transverse processes (number 2 to 4) are distinct from the first in being perpendicular to the longitudinal axis of their belonging centra and broader along their distal margin than along their proximal base. HUENE (1934a) and CARRANO, HUTCHINSON & SAMPSON (2005) also describe the distal expansion in at least the first four caudal vertebrae of *Liliensternus liliensterni* and *Segisaurus halli*. While HUENE does not mention a right angled alignment, the transverse processes of *Segisaurus halli* are as backswept as seen in *Coelophysis bauri*, *C. rhodesiensis, Dilophosaurus wetherilli*, and *Herrerasaurus ischiagualastensis* (RAATH 1969, 1977; COLBERT 1989, 1995; WELLES 1984; NOVAS 1993; CARRANO, HUTCHINSON & SAMPSON 2005). The transverse processes of the Swiss theropod material are bent upward at an angle of 45 degrees as seen in *Liliensternus liliensterni* and *Segisaurus halli* (HUENE 1934a; CAMP 1936; SENTER & HUTCHINSON 2001; CARRANO, HUTCHINSON & SAMPSON 2005). In contrast, the transverse processes of *Coelophysis bauri* '… have large, broad, and horizontally oriented transverse processes …' (COLBERT 1989: 86). While the proximal caudals have backswept and horizontally positioned transverse processes in *Coelophysis rhodesiensis*, 'the mid caudal vertebrae are characterised by sharply up tilted transverse processes which protrude laterally, are not backswept, and which are broader distally than proximally' (RAATH 1977: 45). The description of the mid caudal vertebrae of *Coelophysis rhodesiensis* perfectly fits the description of the proximal caudals of the Swiss theropod material. However, all other morphological aspects (see above points 1. to 4.) deny a relocation of the caudals to a more distal position. There are no transverse processes preserved in *Syntarsus kayentakatae* (ROWE 1989; TYKOSKI 1998). The caudal transverse processes of *Dilophosaurus wetherilli* and *Herrerasaurus ischigualastensis* are horizontally aligned (WELLES 1984; NOVAS 1993).

The laminae, which are located on the lateral sides of the neural arches underneath each caudal transverse process in the Swiss theropod material, are not found in the preserved caudal vertebrae of *Coelophysis rhodesiensis* and *Dilophosaurus wetherilli* (RAATH 1969, 1977; WELLES 1954, 1984; ROWE & GAUTHIER 1990; TYKOSKI & ROWE 2004). The presence of laminae is questionable in *Coelophysis bauri*, *Herrerasaurus ischigualastensis, Liliensternus liliensterni*, *Procompsognathus triassicus*, *Syntarsus kayentakatae*, because their presence is neither mentioned in texts nor in illustrations (FRAAS 1913; HUENE 1934a; OSTROM 1981; COLBERT 1989, 1995; ROWE 1989; ROWE & GAUTHIER 1990; SERENO & WILD 1992; NOVAS 1993; CHATTERJEE 1993; TYKOSKI 1998; TYKOSKI & ROWE 2004). In contrast, there are laminae underneath the basis of the transverse processes in *Lophostropheus airelensis*, *Segisaurus halli*, and the Swiss theropod material (CAMP 1936; LARSONNEUR & LAPPARENT 1966; ROWE & GAUTHIER 1990; CUNY & GALTON 1993; EZCURRA & CUNY 2007; TYKOSKI & ROWE 2004).

The Swiss theropod material displays a tubercular process which lies antero-proximally on each four chevrons. This process is absent in *Coelophysis bauri* and unknown in *Herrerasaurus ischigualastensis, Liliensternus liliensterni, Lophostropheus airelensis, Procompsognathus triassicus, Segisaurus halli,* and *Syntarsus kayentakatae* (TYKOSKI 2005). While *Coelophysis rhodesiensis* and *Dilophosaurus wetherilli* exhibit small tubercules in the antero-proximal region of their chevrons (TYKOSKI 2005), the Swiss theropod material shows one large and forwardly projecting tubercule.

9.4.2. Appendicular Skeleton

9.4.2.1. Ilium

The ilia are disarticulated and separated from the rest of the pelvic bones and sacrals supporting the assumption that the Swiss theropod material represents a juvenile to subadult individual with not yet ossified junctions. *Coelophysis bauri*, *C. rhodesiensis*, and *Segisaurus halli* exhibit pelvic girdles fused together by late ontogeny, known from adult specimens (CAMP 1936; RAATH 1969, 1977; COLBERT 1989, 1995; ROWE 1989; TYKOSKI 1998; CARRANO, HUTCHINSON & SAMPSON 2005), whereas *Herrerasaurus ischigualastensis* is the only adult of the examined theropods with separate elements throughout ontogeny (REIG 1963; ROWE & GAUTHIER 1990; NOVAS 1993; TYKOSKI & ROWE 2004). The Swiss theropod material, *Dilophosaurus wetherilli*, *Lophostropheus airelensis*, *Liliensternus liliensterni*, *Procompsognathus triassicus*, and *Syntarsus kayentakatae* are preserved as too fragmentary (FRAAS 1913; LARSONNEUR & LAPPARENT 1966; OSTROM 1981; WELLES 1984; SERENO & WILD 1992; CUNY & GALTON 1993; EZCURRA & CUNY 2007) and some of them are even doubted to fit an adult model such as *Dilophosaurus wetherilli* and *Liliensternus liliensterni* (TYKOSKI 1998; 2005). *Syntarsus kayentakatae* (TR 97/12) exhibits fragmentary pelvic elements with an uncertain original fusion grade; only the sacrals are fused obliterating all sutures (TYKOSKI 1998). The smallest specimens of *Coelophysis rhodesiensis* also exhibit unfused pelvic elements (e.g. GQ691) (RAATH 1977, 1990; ROWE 1989; ROWE & GAUTHIER 1990; TYKOSKI 1998). Interestingly, COLBERT (1989, 1995) stated in his studies the pelvic girdle of *Coelophysis bauri* does not display fused elements in adults. Later, DOWNS (2000) prepared and examined himself several *Coelophysis bauri* individuals of the Ghost Ranch and observed the presence of fused pelvic girdles partially in subadults and most notably in adults.

The incorporation of sacral 2 into the iliac region has been associated with a cranial expansion of the preacetabular part of the ilium (anterior blade) in Dinosauria (GAUTHIER 1986; HUTCHINSON 2001). *Coelophysis bauri*, *C. rhodesiensis, Syntarsus kayentakatae*, and the Swiss theropod material have included inter alia an another dorsal (sacral 1), and one caudal vertebra (sacral 5) into the sacrum as the ilium became more and more dolicho-iliac (RAATH 1969, 1977; ROWE 1989; COLBERT 1989, 1995; TYKOSKI 1998; GAUTHIER 1986; HUTCHINSON 2001; sensu COLBERT 1964). In all the known ilia of the examined theropods the anterior blade and the posterior blade of this bone are expanded cranially and caudally, with the postacetabular process (posterior blade) being significantly longer than the preacetabular part (HUENE 1934a; COLBERT 1947, 1964, 1989, 1995; WELLES 1984; ROWE & GAUTHIER 1990; NOVAS 1993; RAUHUT & HUNGERBÜHLER 2000; TYKOSKI & ROWE 2004). COLBERT (1989: 99, 1995) wrote: 'the ilium of *Coelophysis bauri* is of such length that this dimension of the bone exceeds its height by a ratio of about two and one-half to one'. This ratio would be an interesting character for comparing all the examined theropods; unfortunately COLBERT (1989, 1995) did not mention the exact measurement details leaving the reader unsure if the measurements were taken along the dorsal iliac ridge or not and how height measurement was defined. RAATH (1969, 1977) gives the lengths along the dorsal iliac margin of QG1, QG691 and QG696 ending up with a iliac ratio of minimum 3.4:1 to maximum 4.5:1 composed of dorsal iliac length and preacetabular process (cranial margin of anterior blade) depth. The dorsal margin of the Swiss theropod material is 180 mm in length, whereas the height of the preacetabular process is assumed to be 45 mm resulting in a ratio of 4.9:1. The lengths of the other theropods cannot be established due to either the incompleteness of the findings or due to the lack of description. However, comparing the Swiss theropod material to the portions of the ilia available of *Syntarsus kayentakatae*, the latter is approximately one third smaller in body size (ROWE 1989; TYKOSKI 1998). The lengths of the ilia vary from 148 mm in *Coelophysis rhodesiensis* (QG1; RAATH 1969, 1977) to 370 mm in *Dilophosaurus wetherilli* (UCMP 37302; WELLES 1984). Again, the authors did not mention the exact measurements taken. *Coelophysis bauri* varies intraspecies from 97.4 mm (AMNH 7227) to 155 mm (AMNH 7224) (COLBERT 1989, 1995), whereas *C. rhodesiensis* exhibits a known minimum of 122 mm (QG691) to a maximum of 148 mm (QG1) (RAATH 1969, 1977).

Morphological characters regarding the iliac silhouette as the dorsal margin, the cranial margin of the anterior blade, and the caudal rim of the posterior blade are useful to compare the different examined theropods. The cranial border of the ilium is convex or straight in *Coelophysis bauri, C. rhodesiensis*, and the Swiss theropod material; it is unknown in the other examined theropods (after RAUHUT 2003). The caudal margin of the ilium is '… squared or rounded off when viewed laterally…' (EZCURRA & CUNY 2007: 84) in *Herrerasaurus ischigualastensis*, *Liliensternus liliensterni*, and *Segisaurus halli*, or concave under the same condition in *Coelophysis bauri*, *C. rhodesiensis, Dilophosaurus wetherilli*, and the Swiss theropod material (SERENO et al. 1994; TYKOSKI 1998; EZCURRA & CUNY 2007). The dorsal margin is stated to be straight in *Coelophysis bauri*, *C. rhodesienis, Dilophosaurus wetherilli*, and *Herrerasaurus ischigualastensis,* whereas *Segisaurus halli* and the Swiss theropod material exhibit a slightly convex dorsal border (EZCURRA & CUNY 2007). Thus after EZCURRA & CUNY (2007), one may differentiate the Swiss theropod from *Coelophysis bauri* and *C. rhodesiensis* on at least the basis of the dorsal iliac margin. There is no information about the dorsal margin of the ilia of *Syntarsus kayentakatae* due to the fact that the dorsal border, preacetabular process, and postacetabular process are missing in both elements (ROWE 1989; TYKOSKI 1998). One may assume that the Swiss theropod material shows a slightly different silhouette compared to *Coelophysis bauri* and *C. rhodesiensis* as well as to the other examined theropods. When looking at the cranial and caudal portions along the dorsal margin of the ilium, this bone of the Swiss theropod material increases constantly from its posterior beginning to its anterior end being slightly convex as stated yet. The ilia of *Coelophysis bauri* only exhibit a slightly swelling in the posterior part, getting steeper in the middle part above the acetabulum, before becoming straight horizontal and decreasing most intensely at its anterior portion (COLBERT 1989, 1995). Conversely, the dorsal iliac margin of *Coelophysis rhodesiensis* varies from the Swiss theropod material and *Coelophysis bauri* as well, being even more horizontal from the anterior blade of the ilium to the portion above the posterior border of the open acetabulum; then the margin slightly decreases, only by 5 degrees, into the end of the posterior blade (RAATH 1977). However, although there are slight differences in the shape of the dorsal iliac borders, in almost all of the examined theropods (unknown in *Lophostropheus airelensis,* *Procompsognathus triassicus, Segisaurus halli, Syntarsus kayentakatae*) this rim is declared to be '… relatively linear/angular…' (TYKOSKI 2005: 203). The only known exception is *Herrerasaurus ischigualastensis* showing a dorsally convex and obviously curved dorsal iliac margin after TYKOSKI (2005).

All examined theropods display a thick lip-like swelling above the acetabulum (HUENE 1934a; CAMP 1936; LARSONNEUR & LAPPARENT 1966; WELLES 1984; ROWE 1989; ROWE & GAUTHIER 1990; SERENO & WILD 1992; CUNY & GALTON 1993; TYKOSKI 1998; RAUHUT 2003; TYKOSKI & ROWE 2004; EZCURRA & CUNY 2007). This dorsal roof (supraacetabular crest), which is a characteristic feature in theropods, proceeds in a swelled band (caudal rim) along the ventro-posterior margin of the posterior iliac shelf for the attachment of the M. iliofibularis and reflects archosaurian specialization related particularly to the bipedal mode of locomotion (RAATH 1969, 1977; ROWE 1989; ROWE & GAUTHIER 1990; COLBERT 1989, 1995; TYKOSKI 1998; CARRANO & HUTCHINSON 2002; TYKOSKI & ROWE 2004). Although the caudal rim of *Coelophysis bauri* is not illustrated, and even negated in COLBERT's studies (1964, 1989, 1995), it certainly has to be there as hints for its existence in figures can be seen (TYKOSKI & ROWE 2004: 60, fig. 3.7.: the caudal rim is illustrated only at the most posterior portion of the posterior blade; the rim proceeds upwards along the dorso-ventral margin of the latter, and vanishes subsequently again along the dorsal iliac border). This assumption has been confirmed by TYKOSKI. He stated that the *Coelophysis bauri* specimens found in the Ghost Ranch Quarry '… are very flattened, and usually in a medio-lateral direction. Therefore, the lateral expansion of the posterior part of the ilium is often crushed flat' (TYKOSKI, pers. communication). This means, that even though the specimens of *Coelophysis bauri* are flattened, they still display flaring on the posterior iliac shelf. The Swiss theropod material also shows this feature and as in the *Coelophysis bauri* specimens, it is flattened in the medio-lateral direction as a consequence of diagenesis. Therefore, flaring was originally likely to have been pronounced in both the *Coelophysis bauri* specimens and the Swiss theropod material. The caudal rim is also known in *Coelophysis rhodesiensis*, but not in *Syntarsus kayentakatae* due to the incompleteness of preservation (RAATH 1969, 1977; ROWE 1989; TYKOSKI 1998). RAATH (1977) was able to study over 30 individuals of *Coelophysis rhodesiensis* recognizing variation in the lateral iliac flaring behind the acetabulum (caudal rim). 'The majority of pelvises from mature adults are broadly flared as in the type, while others are more slender. Whether this reflects true dimorphism or is simply a result of individual variation or compression is not possible to state at this stage of the study. Juveniles tend to show narrow pelvises with relatively unflared ilia. The hood-like roof over the acetabulum is consistently well developed in both juveniles and adults' (RAATH 1977: 50, 1990). Thus, the Swiss theropod material, *Coelophysis bauri*, *C. rhodesiensis*, and probably also *Syntarsus kayentakatae* are derived in possession of this distinct, caudally rimmed fossa for the M. iliofemoralis on the postacetabular process of the ilium as thought by RAATH (1969, 1977), ROWE & GAUTHIER (1990), HUTCHINSON (2001), and TYKOSKI & ROWE (2004). However, the caudal rim on the postacetabular process is better interpreted as the insertion area for the M. iliofibularis as stated by CARRANO & HUTCHINSON (2002), rather than for the M. iliofemoralis externus. The lateral surface of the caudal end of the ilium is smooth in *Dilophosaurus wetherilli*, *Herrerasaurus ischigualastensis*, and *Liliensternus liliensterni* (HUENE 1934a; WELLES 1984; NOVAS 1993; EZCURRA & CUNY 2007).

In *C. rhodesiensis* and *S. kayentakatae* the supraacetabular crest of the ilium is flared to probably the same extent as seen in *C. bauri* and the Swiss theropod material (RAATH 1969, 1977; ROWE 1989; TYKOSKI 1998). Nevertheless, the supraacetabular flaring of *Syntarsus kayentakatae* seems to be not as extreme as seen in *Coelophysis rhodesiensis* (TYKOSKI, pers. communication). The supraacetabular crest sometimes forms a continuous well developed lamina with the ventro-lateral margin of the brevis fossa (posteroventat arch of the ilium, sensu WELLES 1984). This morphological feature can be seen in *Coelophysis bauri*, *C. rhodesiensis, Dilophosaurus wetherilli*, *Liliensternus liliensterni*, and the Swiss theropod material. *Dilophosaurus wetherilli* and *Liliensternus liliensterni* exhibit a '… weakly developed continuous ridge …' (EZCURRA & CUNY 2007: 84), whereas a '… continuous well developed ridge with a non-distinct notch …' (EZCURRA & CUNY 2007: 84) between the supraacetabular crest and the ventro-lateral margin of the postacetabular blade can be seen in *Coelophysis rhodesiensis*, *Lophostropeus airelensis,* and the Swiss theropod material. In *Coelophysis bauri* this character is bivariate being either as in *Liliensternus liliensterni* or as in *C. rhodesiensis* (RAUHUT 2003; EZCURRA & CUNY 2007). EZCURRA & CUNY (2007:84) state the presence of this lamina '… differs from that of basal Dinosauriformes, where the supraacetabular crest is well separated from the lateral margin of the brevis shelf …' as seen in *Herrerasaurus ischigualastensis,* and *Segisaurus halli*. This chaining of the supraacetabular crest to the brevis fossa is not known in *Procompsognathus triassicus* and *Syntarsus kayentakatae* (FRAAS 1913; OSTROM 1981; ROWE 1989; CHATTERJEE 1993; TYKOSKI 1998; EZCURRA & CUNY 2007).

The Swiss theropod material shares the following morphological feature with *Dilophosaurus wetherilli* (contra TYKOSKI 2005: this author states the brevis fossa of *D. wetherilli* as posteriorly broad), *Herrerasaurus ischigualastensis*, *Lophostropheus airelensis*, and *Liliensternus liliensterni*: medial and lateral margins of the brevis fossa stand sub-parallel to each other resulting in a rather narrow and lengthened outline of the whole area when seen ventrally (RAUHUT 2003). In contrast, the medial and lateral borders of the brevis fossa in *Coelophysis bauri*, *C. rhodesiensis*, and *Segisaurus halli* are very strongly caudally expanded (RAUHUT 2003; MOLNAR et al. 1990; EZCURRA & CUNY 2007; TYKOSKI 2005).

Lophostropheus airelensis is the only one of the examined theropods showing a vertical ridge on the iliac blade above the acetabulum (LARSONNEUR & LAPPARENT 1966; MOLNAR et al. 1990; CUNY & GALTON 1993; EZCURRA & CUNY 2007).

'The pubic peduncle of the ilium bears a single large ventrally directed facet for contact with the pubis in most basal theropods' as in *Herrerasaurus ischigualastensis*. 'There are two distinct socket-like facets on the distal end of the ilium's pubic peduncle in coelophysoid theropods' as well as in the Swiss theropod material (TYKOSKI 2005: 210).

In *Coelophysis bauri*, *Dilophosaurus wetherilli*, *Herrerasaurus ischigualastenis, Liliensternus liliensterni* and *Lophostropheus airelensis* no pubo-ischiadic plate has been found (HUENE 1934a; LARSONNEUR & LAPPARENT 1966; WELLES 1984; COLBERT 1989, 1995; NOVAS 1993; CUNY & GALTON 1993; EZCURRA & CUNY 2007). The Swiss theropod material shows several indicators for possessing this plate such as the obturator process, which is confluent with the proximo-cranial margin of the ischium, and the posterior expansion of the proximal pubic plate. In contrast, the proximal portions of the pubes and ischia in *Coelophysis rhodesiensis* and *Syntarsus kayentakatae* were definitely connected by a bony plate (RAATH 1969, 1977; ROWE 1989; TYKOSKI 1998). The proximal part of each pubis is very thin and delicate in the Swiss theropod material, as it is reported in all other theropods examined. In conclusion, the possibility of preservation of this thin structure is very low, and thus, the original presence of this plate is assumed for *Coelophysis bauri* (COLBERT 1989, 1995) and the Swiss theropod material.

9.4.2.2. Pubis

Long pubes are characteristic particularly for theropod dinosaurs. Their lengths are suitable for muscle attachments facilitating bipedalism which is the typical gait of these dinosaurs (ROMER 1974; RAATH 1977; COLBERT 1989).

The pubes of the Swiss theropod material are disarticulated, lying upon each other at their most distal portions. This state of preservation supports the assumption that the individual is of juvenile to subadult age.

The pubic lengths measured along their dorsal borders are very similar in *Coelophysis bauri, C. rhodesiensis*, *Syntarsus kayentakatae*, and the Swiss theropod material despite their different ontogenetic stages: the pubes of one adult specimen of *C. bauri* (AMNH 7224) add up to 233 mm, the ones of an adult of *C. rhodesiensis* (QG1) measure 204 mm in length (COLBERT 1989, 1995; RAATH 1969, 1977), whereas the corresponding of subadults of *S. kayentakatae* (TR 97/12) and of the Swiss theropod material measure 232 mm and 256 mm, respectively (ROWE 1989; TYKOSKI 1998). Thus, the pubis length of the Swiss theropod material exceeds its correspondings of *Syntarsus kayentakatae*, *Coelophysis rhodesiensis,* and *Coelophysis bauri*, although those of the latter are widely ranged (139 mm of AMNH 7228 to 233 mm of AMNH 7224; COLBERT 1989). The known pubic lengths of *Dilophosaurus wetherilli* (UCMP 37302), *Herrerasaurus ischigualastensis* (PVL 2566), and *Liliensternus liliensterni* (MB.R. 2175, small individual) are all much longer measuring 485 mm, 430 mm, and 410 mm, respectively (HUENE 1934a; WELLES 1984; NOVAS 1993). However, the ontogenetic stages of *D. wetherilli* and *L. liliensterni* are still poorly defined (TYKOSKI 1998), and data for an adult individual of *Syntarsus kayentakatae* and the Swiss theropod material is not available (ROWE 1989; TYKOSKI 1998). The estimated pubes lengths of *Segisaurus halli*, which represents an individual of subadult ontogenetic stage, measure 110 mm (CARRANO, HUTCHINSON & SAMPSON 2005).

The proximal portion of the pubis (pubic plate) of the Swiss theropod material consists of very delicate and thin material. This approximately one millimetre thin sheet most likely formed a pubo-ischiadic plate with the dorso-cranial part of the ischium. However, the original construction of such a plate appears feasible, but is not confirmed, because of the lack of preservation in the Swiss theropod material. In addition, there is another very delicate element best visible in the right pubis: the pubic apron, which is typical for coelophysoids (TYKOSKI 1998) expands proximal from the dorso-medial margin of this element to an uncertain distal end, only penetrated at its upper beginning by the pubic fenestrum, whose posterior border was probably not yet ossified due to the juvenile to subadult ontogenetic state of the specimen. The pubic apron seems to range to the dorsal edge at the distal tip of the pubis as seen in *Coelophysis bauri, C. rhodesiensis*, *Herrerasaurus ischigualastensis*, *Liliensternus liliensterni*, *Procompsognathus triassicus*, *Segisaurus halli*, and *Syntarsus kayentakatae* (RAATH 1977; COLBERT 1989, 1995; ROWE 1989; TYKOSKI 1998; RAUHUT 2003; EZCURRA & CUNY 2007). In *Dilophosaurus wetherilli* the pubic apron exhibits a medial opening just above the pubic boot (WELLES 1984; RAUHUT 2003; EZCURRA & CUNY 2007).

Compared to the findings of *Coelophysis bauri* and *Syntarsus kayentakatae,* the pubes of the Swiss theropod material are very well preserved (COLBERT 1989, 1995; ROWE 1989; TYKOSKI 1998). In general, the pubo-ischiadic plate and the pubic apron are rarely available due to either diagenesis affecting preservation state, or due to the hindered conditions of recovery. In *Coelophysis bauri* the presence of a pubo-ischiadic plate, as well as the presence of the obturator foramen and pubic fenestrum is only assumed, because COLBERT (1989, 1995) had neither illustrated, nor described any openings or plate-like structures between the ischia and pubes. However, it should be noted that he did not state an absence of the elements mentioned either. COLBERT (1989, 1995) neglected the fact ROMER (1956) had written in his book: 'the presence of an obturator foramen is plesiomorphic for archosaurs …, and derived tetanuran theropods that lose this character as an enclosed opening still retain an obturator notch'. In 2000, DOWNS re-examined several individuals of COLBERT's *Coelophysis bauri* from the Ghost Ranch Quarry and published inter alia the following statement: 'all the *Coelophysis* pelves that I have prepared or examined in various blocks from Ghost Ranch have an obturator foramen if overlying bones do not obscure the proximal pubes. Most *Coelophysis* pelves from the Ghost Ranch do not exhibit a pubic fenestra, but this is apparently due to breakage of the very thin pubo-ischiadic plate' (DOWNS 2000: 34). In contrast to COLBERT, RAATH (1969) and CAMP (1936) have recognized the two openings in the pubes of *Coelophysis rhodesiensis* and *Segisaurus halli.* RAATH identified the upper smaller opening as homologous with the obturator foramen in *Coelophysis bauri*, but named this the thyroid fenestrum (RAATH 1969, 1977). The larger second opening, which is located ventrally to the smaller 'thyroid fenestra', was described as the actual obturator foramen, although ROMER (1956) stated the thyroid fenestra to be absent in archosaurs (RAATH 1969, 1977). Later, ROWE & GAUTHIER (1990) adjusted the names of the openings in *Coelophysis bauri* and *C. rhodesiensis*. In *Syntarsus kayentakatae* (TR 97/12), 'the pubes were found complete, including the delicate pubic apron typical of coelophysoids. Drying of the surrounding matrix prior to preparation caused the sediment to shrink, shattering the apron. Some of it was salvaged, but most of it bordering the midline was lost. The extremely thin pubo-ischiadic plate suffered the same fate as the pubic apron' (TYKOSKI 1998: 90). Thus, evidence for the presence of the pubic apron, the pubic plate with the foramina and fenestra, and the pubo-ischiadic plate, was destroyed before measuring. An obturator foramen is present in all examined theropods except for *Dilophosaurus wetherilli* whose foramen is absent in the proximal portions of the pubes (HUENE 1934a; LARSONNEUR & LAPPARENT 1966; WELLES 1984; SERENO & WILD 1992; CUNY & GALTON 1993; NOVAS 1993; HOLTZ 1994; RAUHUT 2003; CARRANO, HUTCHINSON & SAMPSON 2005; EZCURRA & CUNY 2007). The pubic fenestra is absent in *Dilophosaurus wetherilli*, *Herrerasaurus ischigualastensis*, and *Liliensternus liliensterni* (RAUHUT 2003; WELLES 1984; ROWE & GAUTHIER 1990; NOVAS 1993; TYKOSKI & ROWE 2004). In contrast, TYKOSKI (1998) stated the following in his master thesis: 'Neither HUENE (1934a) nor WELLES (1984) figured a pubic fenestra in *Liliensternus liliensterni* or *Dilophosaurus wetherilli* also a likely result of non-preservation of the pubo-ischiadic plate'.

The pubic shafts are straight in *Herrerasaurus ischigualastensis* and nearly straight in *Dilophosaurus wetherilli* and *Liliensternus liliensterni* when seen in lateral or medial view (HUENE 1934a; WELLES 1984; NOVAS 1993; SERENO 1999; TYKOSKI 2005; EZCURRA & CUNY 2007). The pubes of the Swiss theropod material are compressed medio-laterally and thus, the shafts' curvatures are not really affected by diagenetic compaction. However, the shafts of the Swiss theropod material are very slightly convex as seen amongst other things in *Coelophysis bauri*, and *C. rhodesiensis* (RAATH 1969, 1977; COLBERT 1989, 1995). Only the shape of the pubes of the two latter from illustrations and photographs can be judged. It seems the curvature of the pubis shaft of *Coelophysis bauri* and *C. rhodesiensis* is constantly convex, bent along the whole length as in the Swiss theropod material. However, there seems to be variation in the achievement of this shape in *C. bauri* (COLBERT 1990) and *C. rhodesiensis*: the specimen YPM 41197 of *C. bauri* exhibits a pubis which is more strongly bowed caudally in its distal portions (COLBERT 1989), whereas there are pubes of *C. rhodesiensis* exhibiting rather straight shafts. In *Coelophysis rhodesiensis* (QG1), the pubic shaft seems to be straighter in its distal half than those of *C. bauri* (RAATH 1969). In *Segisaurus halli* (UCMP 32101) and *Syntarsus kayentakatae* (TR97/12) the pubis shafts are also convex seen laterally or medially, but are as strongly bowed in their cranial portion as seen in *Coelophysis bauri* (contra SERENO 1998, 1999) (HUENE 1934a; ROWE 1989; SERENO & WILD 1992; TYKOSKI 1998; EZCURRA & CUNY 2007). The pubic shaft of *Syntarsus kayentakatae* is much abraded, and thus any comparison is rather difficult (TYKOSKI 1998). However, it seems that the pubes are more similar in *Syntarsus kayentakatae*, and the Swiss theropod material, comparing them to the other examined theropods: the dorso-proximal part of the pubes of *S. kayentakatae* is slightly concave; its shaft bends distinctly convex (compared to slightly convex to straight in the Swiss theropod material) behind the pubic fenestrum. Only the distal half of the shaft bears the most visible difference to the Swiss theropod material: while the appropriate portions of the pubes of *Syntarsus kayentakatae* are strongly bent posteriorly (ROWE 1989; TYKOSKI 1998), the correspondings (approximately the distal 20 mm of the shaft) of the Swiss theropod material are straight proceeding into the pubic boot or distal knob. In conclusion, the curvature of the pubic shafts of the Swiss theropod material appears to be a mixture of the conditions found in *Coelophysis rhodesiensis* and *Syntarsus kayentakatae*: the distal portions of the pubic shaft and the dorsal rim of the pubic boot are almost as straight as those of the former, whereas the dorsal margin of the pubic plate is concave as seen in the latter.

The pubes of all examined theropods end distally in a slightly and only posteriorly expanded pubic boot (FRAAS 1913; HUENE 1934a; RAATH 1969, 1977; OSTROM 1981; WELLES 1984; GAUTHIER 1986; COLBERT 1989, 1995; SERENO & WILD 1992; NOVAS 1993; SERENO 1999; RAUHUT 2003; EZCURRA & CUNY 2007). The only differences of this morphological feature can be observed in its shape and size: the distal knob of the Swiss theropod material resembles an almost isosceles triangle when viewed laterally. ROWE (1989) and TYKOSKI (1998: 93) describe the distal portion of *Syntarsus kayentakatae* as '… rounded, teardrop-shaped knobs'. COLBERT (1989: 101, 1995) has documented the shape of the pubic boot of *Coelophysis bauri* as well: 'the distal end of the pubis is expanded moderately into a rounded, ball-like protuberance'. The same rounded-off shape of the pubic boot was described by RAATH (1977) within the specimens of *Coelophysis rhodesiensis*, but his drawings illustrate knobs rather structures resembling the isosceles appendages of the Swiss theropod material. In ventral view, the pubic boot is subtriangular *in Coelophysis bauri, Dilophosaurus wetherilli, Liliensternus liliensterni*, and the Swiss theropod material. In contrast, the pubic boot of *Herrerasaurus ischigualastensis, Segisaurus halli,* and *Syntarsus kayentakatae* is narrow with subparallel margins when seen from the same position (i.e. rectangular or subequant after TYKOSKI 2005). This feature is either not preserved or not documented in any study for the other theropods (RAATH 1969, 1977; HOLTZ 1994; RAUHUT 2003; TYKOSKI 2005). In addition, COLBERT describes and illustrates conjoined pubes which are only separated distally in *Coelophysis bauri* (1989, 1995). TYKOSKI (1998) also reports the separation of the two knobs by a median notch in *Syntarsus kayentakatae* and CARRANO, HUTCHINSON & SAMPSON (2005: 839) write about the distal portion of the pubes in *Segisaurus halli* that 'there is a median gap below the pubic apron as in *Procompsognathus* (SERENO, 1999) and many other coelophysoids (including *Dilophosaurus*, *Syntarsus kayentakatae*, and *Liliensternus liliensterni*; HUENE 1934a; TYKOSKI, pers. communication)'. RAATH (1977) does not mention this distal condition in *Coelophysis rhodesiensis,* and it its existence cannot be determined in the Swiss theropod material either due to the extent of medio-lateral compression during diagenesis.

9.4.2.3. Ischium

TYKOSKI (1998) was able to observe the grade of fusion during ontogenetic stages in the subadult *Syntarsus kayentakatae* specimen TR97/12: in early ontogenetic event (stage 1), all sacral elements such as centra, neural arches, ribs, and modified transverse processes fuse together. Almost isochronous, the unification of the pelvic bones begins in stage 2. At last, after the complete unification of the pelvic bones, the sacral ribs and modified transverse processes attach to the inner wall of the ilia (stage 3), as already noted for *Tyrannosaurus rex* by ERICKSON et al. (2006) and PADIAN et al (2001).

In the Swiss theropod material, the only totally fused elements of the pelvis are the two ischia. This similarity to TYKOSKI's observations in *Syntarsus kayentakatae* consolidates the theory of having different fusion stages in theropod dinosaurs. The Swiss theropod material exhibits sacral transverse processes, ribs, and neural arches which are partially fused to each other, whereas the sacral centra, pubes, and ilia show no signs of fusion or maximally partial fusion between each other. This constitution of fused, only partially coalesced and non fused elements support the assumption the Swiss theropod material representing a juvenile to subadult specimen between stage 1 and 2. The transition between these two ontogenetic stages is not clear, because they chronologically overlap each other (TYKOSKI 1998). In the Swiss theropod material all the sacral elements exhibit a minimal fusion and the dorsal centra are often disarticulated from their neural arches on one hand (stage 1). On the other hand only the ischia are firmly attached to each other (stage 2). All these morphological features fit into very early ontogenetic stages reflecting a rather juvenile nature.

The total length of the ischium measured along its dorsal border adds up to 150 mm in the Swiss theropod material. The length cannot be established exactly, because the mid portions of both ischia are still hidden in the sediment. The ischium lengths of *Coelophysis bauri* (AMNH 7224) measure 142 mm (COLBERT 1989, 1995), those of *C. rhodesiensis* add up to 130 mm (QG1) and 125.5 mm (QG691) (RAATH 1969, 1977), whereas the ischia of *Syntarsus kayentakatae* (TR97/12) are 151.5 mm in length (ROWE 1989; TYKOSKI 1998). The smaller individual of *Liliensternus liliensterni* (MB.R. 2175) displays an ischiadic length of 270 mm (HUENE 1934a; WELLES 1984), *Herrerasaurus ischigualastensis* (PVL 2566) exhibits 330 mm in length (NOVAS 1993), and *Dilophosaurus wetherilli* (UCMP 37302; ischia lengths restored) defies all with a length of 340 mm (WELLES 1984). *Segisaurus halli* displays the smallest ischia lengths which are estimated at 96 mm (CARRANO, HUTCHINSON & SAMPSON 2005).

The ischia are shorter than the pubes in the Swiss theropod material resulting in an ischia-pubes ratio of 0.58 to 1. COLBERT's *Coelophysis bauri* data includes an ischia-pubes ratio of 0.61 to 1 (AMNH 7224; COLBERT 1989). TYKOSKI (1998) also recorded *Syntarsus kayentakatae* (TR97/12) as displaying an ischia-pubes ratio not exceeding 0.65 to 1. In addition, RAATH (1969, 1977) measured the ischia and pubes length of the holotype QG1 of *Coelophysis rhodesiensis* counting up to a ratio of 0.64 to 1. In conclusion, *Coelophysis bauri*, *C. rhodesiensis*, *Syntarsus kayentakatae,* and the Swiss theropod material all show a similar ischia-pubes ratio. However, this result is surely affected by the fact that *Syntarsus kayentakatae* (TR 97/12) and the Swiss theropod material are immature individuals (ROWE 1989; TYKOSKI 1998) and due to the respective grade of preservation. The ischia-pubes ratio is 0.66 to 1 in *Liliensternus liliensterni* and thus, very similar to the Coelophysidae (HUENE 1934a; WELLES 1984). In contrast, *Dilophosaurus wetherilli, Herrerasaurus ischigualastensis,* and *Segisaurus halli* exhibit another ratio-value of 0.7 to 1, 0.77 to 1, and 0.87 to 1 (WELLES 1984; NOVAS 1993; CARRANO, HUTCHINSON & SAMPSON 2005).

The ischia of the Swiss theropod material are assumed to conjoin for almost all of their lengths and only part proximally for extending dorsally and laterally, forming articulation areas for making contact with the ischiadic peduncles of the ilia and with the pubes. The contact of the ischia of *Syntarsus kayentakatae* is restricted to the distal half as seen in the Swiss theropod material (TYKOSKI 1998). The ischia of *Coelophysis bauri* are '… conjoined distally for about half of their lengths' (COLBERT 1989: 104, 1995). RAATH (1969, 1977) only mentioned the lack of symphysial articulation between the two ischia of *Coelophysis rhodesiensis*, but did not report anything about the conjunction along the ischia lengths. However, he published dorsal-view drawings of the ischia and illustrated them together with the ischia of *Coelophysis bauri*, and *Elaphrosaurus bambergi* (RAATH 1977). It seems that the conjunction of the ischia of *Coelophysis rhodesiensis* range from their distal tips to less than two thirds of the ultimate ischia lengths (RAATH 1977).

In contrast to the pubes, the ischia shafts are very straight and resemble slender rods in *Coelophysis bauri, C. rhodesiensis, Herrerasaurus ischigualastensis, Liliensternus liliensterni*, *Syntarsus kayentakatae* and the Swiss theropod material (RAATH 1969, 1977; COLBERT 1989, 1995; ROWE 1989; NOVAS 1993; TYKOSKI 1998). Controversely, the ischia of *Dilophosaurus wetherilli* are straight, but along the distal one third bowed cranially (WELLES 1984).

The paired '… cross-sectional shapes of the ischial mid-shafts …' also differ in the examined theropods (SERENO 1999; EZCURRA & CUNY 2007: 84): *Dilophosaurus wetherilli* and *Herrerasaurus ischigualastensis* exhibit an oval outline, while *Coelophysis bauri* and *Liliensternus liliensterni* display heart-shaped cross-sections. In addition, *C. rhodesiensis*, *Lophostropheus airelensis*, and *Syntarsus kayentakatae* exhibit a sub-rectangular shape. The cross-section of the ischia of the Swiss theropod material is unknown. The abrupt swelling on the lateral sides in the distal part of the ischia rather results from processes during diagenesis or from a fracture adhered during lifetime than being morphological fact.

Distally, the ischia end in a foot with a ball-like shape when viewed from lateral position, and a sub-triangular outline in posterior aspect in *Syntarsus kayentakatae*, *Coelophysis bauri*, *C. rhodesiensis*, and the Swiss theropod material (RAATH 1969, 1977; COLBERT 1989, 1995; ROWE 1989; TYKOSKI 1998). COLBERT (1989, 1995), RAATH (1969, 1977), ROWE (1989), and TYKOSKI (1998) always emphasized the presence of an only slightly expanded ischiadic knob, but all authors gave no detailed measurements. In contrast, COLBERT (1989: 103; 1995) states '… distally, the ischium shows a moderate expansion roughly equivalent in size to the distal expansion of the pubis', and TYKOSKI (1998: 169) reports that the '… distal ischium is only slightly expanded or not at all'. The statement of the latter author also fits the morphology found in *Herrerasaurus ischigualastensis* and *Segisaurus halli* (CAMP 1936; NOVAS 1993; CARRANO, HUTCHINSON & SAMPSON 2005). In the Swiss theropod material, the ischiadic distal knob is not equivalent in size to the pubic boot as seen in the Family Coelophysidae; the ischiadic boot is much larger than the pubic one. *Liliensternus liliensterni* and *Dilophosaurus wheterilli* also have an ischiadic boot that is greater than its distal pubic expansion (HUENE 1934a; WELLES 1984; TYKOSKI &

ROWE 2004). COLBERT (1989: 101, fig. 76) reports a very similar condition in one individual of *Coelophysis bauri* which he states to be an exception for this taxon. He found a specimen (YPM 41197) with an extremely curved ischium (as seen in *Dilophosaurus wetherilli*) probably caused during fossilization and a much greater expansion at its distal end than ever seen in other *Coelophysis bauri*. He regarded these extraordinary ischia as a result of individual variation in pelvic structure of *Coelophysis bauri*. Nevertheless, the ischia fit the description of the Swiss theropod material with the exception of the curved shaft.

9.5. Excursus D: geographical and chronological distribution of the Coelophysidae

The fossil record for the genera *Coelophysis* (*C. bauri* and *C. rhodesiensis*) and *Syntarsus* (*S. kayentakatae*) indicates the success of the Family Coelophysidae sensu HOLTZ (1994) (i.e. *C. bauri*, *C. rhodesiensis*, *S. kayentakatae* and all the descendants of their most recent common ancestor) within the Coelophysoidea sensu HOLTZ (1994), accepted inter alia by SERENO (1998); EZCURRA & CUNY (2007) (i.e. Coelophysidae plus *Dilophosaurus wetherilli, Liliensternus liliensterni, Lophostropheus airelensis,* ?*Procompsognathus triassicus,* ?*Segisaurus halli*). SERENO (1998) specified HOLTZ's definition of the Coelophysoidea and stated that this group comprises all theropods which are closer to *Coelophysis bauri* than to *Ceratosaurus nasicornis* (accepted inter alia by EZCURRA & CUNY 2007). Chronologically, the Coelophysoidea are reported from Late Carnian to the end of the Pliensbachian (RAATH 1969, 1977; COLBERT 1989, 1990, 1995; BENTON 1983; ROWE 1989; ROWE & GAUTHIER 1990; CUNY, DOUBINGER & RAUSCHER 1991; BENTON 1993; PROBST & WINDOLF 1993; GRADSTEIN et al 1995; GLUT 1997, 2003; HECKERT & LUCAS 1998; TYKOSKI 1998; MEYER & THÜRING 2003; TYKOSKI & ROWE 2004). The members of the Coelophysoidea are known so far to have lived in Arizona, New Mexico (United States of America), South Africa, as well as in England, Scotland, and Wales (United Kingdom), Yunnan Province (China), Germany, and now also Switzerland (HUENE 1908, 1921, 1926; SCHMIDT 1928, 1938; COLBERT 1947, 1964, 1989, 1990; KUHN 1956, 1968, 1971, 1974; RAATH 1969, 1977, 1980; CLARK & FASTOVSKI 1986; PAUL 1988; HU 1993; BENTON et al. 1995; CARPENTER 1997; MUNYIKWA & RAATH 1999; MUNTER 1999; WERNEBURG 1999; RAUHUT & HUNGERBÜHLER 2000; LUCAS & HECKERT 2001; TYKOSKI & ROWE 2004; CARRANO 2004; IRMIS 2004; WEISHAMPEL et al 2004; CLARK 2005; LUCAS 2005; MILNER 2005). To this day, the fossil record of the Coelophysoidea and thus also of the Coelophysidae is immense, but still quite incomplete, leaving many questions unanswered regarding the genera *Coelophysis* and *Syntarsus*.

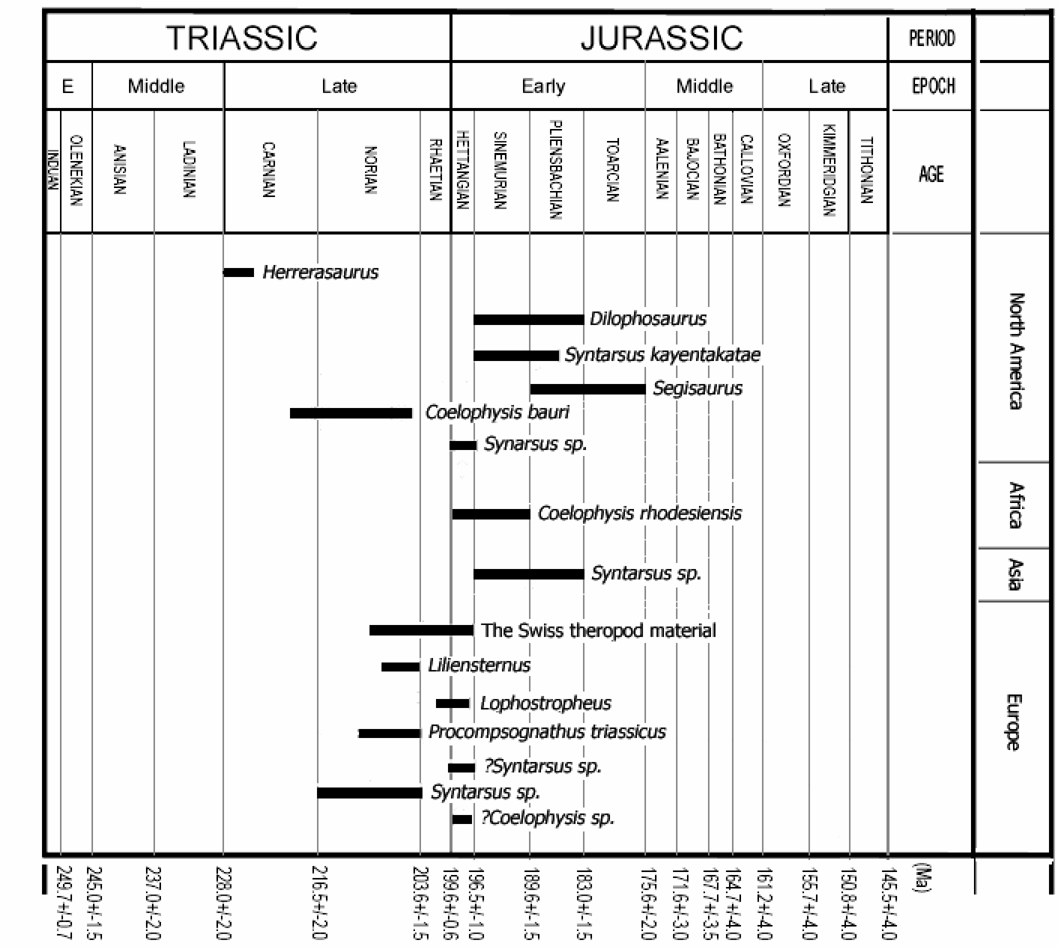

Figure 38: modified after TYKOSKI 2005; geographic and temporal distribution of coelophysoid taxa. The time ranges are relative and not absolute. The table shows various *Syntarsus* and *Coelophysis sp.* which are not definitely assigned to these genera, since *Syntarsus rhodesiensis* become a member of the genus *Coelophysis*. Now, these taxa have to be re-examined and successively certified belonging either to *Coelophysis bauri*, *C. rhodesiensis* or to *Syntarsus kayentakatae.* For further details regarding only the distribution of Coelophysidae see «11.3. Completion to chronological and geographical distribution» table 6, in appendix.

The oldest known representative of the Family Coelophysidae is *Coelophysis bauri*, which has been found in America at the Ghost Ranch Quarry, New Mexico (Fig.38). The American findings of the Coelophysidae document a geographical range from Arizona to Utah and New Mexico within the time span from Late Carnian to Middle Pliensbachian. The youngest record of the Coelophysidae is represented by three specimens of *Syntarsus kayentakatae* that lived during the Sinemurian to the Middle Pliensbachian of Arizona (ROWE 1989; TYKOSKI 1998). In Africa, there is no *Coelophysis* material reported originating from the time before the Hettangian (RAATH 1969, 1977, 1980). In contrast, the specimens found in Europe had lived during the Norian until the end of the Hettangian (BENTON et al. 1995; RAUHUT & HUNGERBÜHLER 2000; CLARK 2005).

Currently, it seems that the ancestor of the coelophysid theropods lived in America. During the Late Triassic prior to the break-up of Pangaea, emigrations from America towards Europe, Asia and Africa were still possible (BLOOS 1999; FASTOVSKI & WEISHAMPEL 2005). At the beginning of the Early Jurassic, Pangaea began to split into Gondwana and Laurasia. The break-up gradually separated North America, Europe, and Asia from South America, and Africa. In the Early Jurassic, the Central Atlantic Ocean had functioned as a barrier between North and South America, and between North America and Africa. However, only the Northern area of West Africa was separated from North America, thus emigrations were possible along the Southern part of the West shore of Africa (FASTOVSKI & WEISHAMPEL 2005). Hence the African coelophysid populations that are only represented from the Hettangian, may have risen from either packs that emigrated from North America or from populations originating from Europe (England, Switzerland, and China). The American *Syntarsus* population could either be a successor of the American *Coelophysis* population or may have been founded by emigrants of the African or European continent.

Material from across the global range of the group provides evidence that the radiation of the genera *Coelophysis* and *Syntarsus* had began during the Late Triassic, and continued into the Early Jurassic (HUENE 1908, 1921, 1926; SCHMIDT 1928, 1938; COLBERT 1947, 1964, 1989, 1990; KUHN 1956, 1968, 1971, 1974; RAATH 1969, 1977, 1980; CLARK & FASTOVSKI 1986; PAUL 1988; HU 1993; BENTON et al. 1995; CARPENTER 1997; MUNYIKWA & RAATH 1999; MUNTER 1999; WERNEBURG 1999; RAUHUT & HUNGERBÜHLER 2000; LUCAS & HECKERT 2001; TYKOSKI & ROWE 2004; CARRANO 2004; IRMIS 2004; WEISHAMPEL et al 2004; CLARK 2005; LUCAS 2005; MILNER 2005).

Syntarsus kayentakatae is the only member of the Coelophysidae which lived up to the Middle Jurassic outliving all other members of its group (except the rather unknown *Syntarsus sp.* found in Yunnan Province, China, see figure 38) (ROWE 1989; ROWE & GAUTHIER 1990; HU 1993; TYKOSKI 1998; TYKOSKI & ROWE 2004; TYKOSKI 2005).

10. Conclusion

Although the material of the Swiss theropod is incomplete, it can be recognized as juvenile to subadult, probably deriving from a gracile male individual (LUI UNTERRASSNER, pers. communication). The assignment of the Swiss specimen to the Family Coelophysidae can be confirmed unambiguously. The close relationship of the Swiss theropod material to *Coelophysis bauri, C. rhodesiensis*, and *Syntarsus kayentakatae* is reflected in all available material, for example by the presence of a caudal rim on the posterior blade of the ilium or the expanded articular faces of the sacral vertebrae (see «9.4.2.1. Ilium» and «9.4.1.3. Sacral Region»). However, *S. kayentakatae* is shown to be the closest relative of all. It shares one autapomorphy with the Swiss theropod material namely a deep fossa on the lateral sides of sacral 2 (TYKOSKI 2005). The absence of this fossa is not really confirmed in the other taxa studied due to a lack of urgently requested re-description of the material of *C. bauri* and *C. rhodesiensis*. On one hand, there are many synapomorphies the Swiss theropod material shares with the three Coelophysid theropods (*Coelophysis bauri, C. rhodesiensis*, and *Syntarsus kayentakatae*), on the other hand, the Swiss remains show unique morphological features such as an antero-proximally located process on the chevrons and a large distal ischiadic knob both also seen in *Dilophosaurus wetherilli* (WELLES 1984; TYKOSKI 2005; see «9.4.1.4. Caudal Region» and «9.4.2.3. Ischium»). Furthermore, there are differences in size of the members of the Family Coelophysidae. Although the size is not a good character for differentiating species, it is nevertheless helpful if one knows the ontogenetic state of an individual (see «2. Abbreviations», and «11.2. Measurements» table 2 to 5, in appendix). For example, *Syntarsus kayentakatae* (MNA V2623) represents a subadult specimen, as well as the Swiss theropod material, but is approximately one third smaller than the latter. The adult *Coelophysis bauri* (AMNH 7224) is of similar size as the Swiss theropod, whereas the adult *C. rhodesiensis* (QG1) is less than one fifth smaller.

These morphological observations are supported by the results of the phylogenetic analysis, which confidently places the Swiss theropod material within the Coelophysidae with a reliability of 77 percent (Jackknife) in both full heuristic and branch-and-bound method searches. The ingroup relationship was rather strongly supported by stabilities over 70 between *Syntarsus kayentakatae* and the Swiss theropod material, although there are rather high amounts of missing data, especially for the Swiss specimen (64.2% Swiss theropod material, 27.3% *Syntarsus kayentakatae*).

In conclusion, the material found in the Quarry Gruhalde in Frick (Canton Aargau) that represents the first theropod skeleton of Switzerland is considered as a juvenile to subadult male individual, most closely related to the American *Syntarsus kayentakatae.*

11. APPENDIX

11.1. Phylogenetic Analysis

11.1.1. Character description

1. Skull length (premaxilla-quadrate condyle) versus skull height (articular condyle of quadrate to dorsalmost edge of parietal): less than 3 times (0); equal or more than 3 times (1) (FORSTER, 1999; SERENO, 1999; TYKOSKI, 2005).

2. Angle between rostral margin and alveolar margin of premaxilla: equal or more than 70° (0); less than 70° (1); equal or less than 40° (2) (modified from RAUHUT, 2003; unordered).

3. Height:length ratio of premaxilla below external naris: 0.5—1.25 (0); <0.5 (1); > 1.25 (2) (HOLTZ, 1994, 2000; unordered).

4. Main body of the premaxilla: lacks or shows few neurovascular foramina (0); laterally perforated by a moderate sized pit at the base of the premaxillary nasal process above the level of the second maxillary alveolus (1); laterally perforated by multiple neurovascular foramina (2) (reversed and modified from TYKOSKI, 1998; TYKOSKI & ROWE, 2004; ordered).

5. Premaxilla nasal process: less than or equal to half of the rostrodorsal narial border (0); forms more than half the rostrodorsal narial border (1) (reversed from HOLTZ, 2000).

6. Ventral process at the caudal end of premaxillary body: absent (0); present (1) (RAUHUT, 2003).

7. Serrations on premaxillary teeth: not substantially different from other teeth (0); serrations or denticles on premaxillary teeth greatly reduced or absent (1) (TYKOSKI, 1998).

8. Premaxilla union to maxilla: firmly attached (0); loosely attached with the capability of passive kinesis, without a terminal rosette on the premaxilla (1) (TYKOSKI, 1998; SERENO 1999).

9. Sub-narial foramen: present (0); absent (1) (GAUTHIER, 1986; SERENO et al., 1993).

10. Subnarial gap: absent (0); present (1) (GAUTHIER, 1986).

11. Constriction between articulated premaxillae and maxillae: absent (0); present (1) (RAUHUT, 2003).

12. Angle between the dorsoventral margin of the maxilla and the alveolar margin: equal or more than 75° (0); less than 75° (1) (EZCURRA & NOVAS, in press).

13. Rostral process of maxilla: between 10% and 25% of total maxilla length (0); equal or less than 10% of total maxilla length (1); equal or more than 25% or total maxilla length (2) (TYKOSKI, 2005; unordered).

14. Ventral border of rostral tip of maxilla: relatively straight, contacts ventral edge of premaxilla, and tooth row continuous (0); ventral border of rostral-most maxilla sharply curves dorsally to meet the maxillary process of the premaxilla (1) (ROWE, 1989; TYKOSKI, 1998).

15. Rostromedial process of maxilla: dorsoventrally deep and short to moderate in length, being slightly visible in lateral view (0); rostrocaudally long and dorsoventrally low, being well rostrally extended and far visible in lateral view (1) (EZCURRA & NOVAS, in press).

16. Medial surface of rostromedial process of maxilla: smooth (0); bears longitudinal ridges (1) (SERENO et al., 1998).

17. Antorbital fossa, rostral end, in late ontogeny: caudal to caudal end of external naris (0); ventral to caudal end of external naris (1) (modified from SERENO, 1999).

18. Rostral margin of maxillary antorbital fossa: rounded or pointed (0); squared (1). (RAUHUT, 2003)
19. Promaxillary foramen: absent (0); present (1) (CARPENTER, 1992).

20. Lateral surface of maxillary antorbital fossa at the base of the ascending process: smooth (0); with deep, large, and subcircular or oval blind pockets (1) (modified from CARRANO et al., 2002).

21. Ventral rim of the antorbital fossa: parallel to tooth row (0); ventrally sloped in its caudal part (1) (SERENO, 1986).

22. Dorsoventrally compressed ridge on lateral surface of maxilla, forming the ventral border of the antorbital fossa: absent (0); present (1) (ROWE & GAUTHIER, 1990).

23. Maximum length of internal antorbital fenestra: less than 25% of skull premaxilla-quadrate length (0); 25% or more than maximum skull premaxilla-quadrate length (1) (ROWE, 1989).

24. Ascending process of the maxilla: confluent with rostral rim of maxillary body and gently sloping caudolaterally (0); offset from the rostral rim of maxillary body, with rostral projection of maxillary body shorter than high (1); offset from rostral rim of maxillary body, with rostral projection of maxillary body as long as high or longer (2) (SERENO et al., 1996; RAUHUT, 2003; ordered).

25. Ascending process of maxilla angulation: between 35° and 50° (0); less than 35° (1); more than 50° (2) (TYKOSKI, 2005; unordered).

26. Number of maxillary tooth in the adulthood: 18 or less (0); more than 18 (1) (EZCURRA & NOVAS, in press).

27. Maxillary tooth row caudal extension: extends caudally to approximately half the length of the orbit (0); completely antorbital, tooth row ends rostral to the vertical strut of the lacrimal (1) (GAUTHIER, 1986; RAUHUT, 2003).

28. Pronounced lateral rims of the nasals and dorsolateral margins of lacrimal: absent (0); conforming a low and laterally projected pair of crests (1) (modified from RAUHUT, 2003).

29. Nasal fenestrae: absent (0); present (1) (ROWE & GAUTHIER, 1990).

30. Lacrimal rostral ramus: subequal or shorter than the ventral ramus in length and width (0); bonger than the ventral ramus (1); absent (2) (modified from SERENO et al., 1996; unordered).

31. Lateral lamina of bone in the lacrimal: almost covering most of the bone (0); with no interruption of the lacrimal antorbital fossa and restricted to the caudal margin of the ventral ramus along its dorsoventral extension (1); only interrupting the lacrimal antorbital fossa near the proximal end of the ventral ramus and ventrally restricted to caudal margin of the ventral ramus (2) (EZCURRA & NOVAS, in press; ordered).

32. Lacrimal antorbital pneumatic recess (into central body of lacrimal) absent (0); present (1) (MOLNAR et al., 1990; NOVAS, 1992).

33. Lateral ridge longitudinally traversing the rostral and caudal processes of the jugal absent (0); present (1) (SERENO & NOVAS, 1993; TYKOSKI, 1998; TYKOSKI & ROWE 2004).

34. Rostral process of jugal contributes to the caudoventral margin of the internal antorbital fenestra (0); excluded from the internal antorbital fenestra (1); expressed at the rim of the internal antorbital fenestra and with a distinct process that extends rostrally underneath it (2) (HOLTZ, 1994; RAUHUT, 2003; unordered).

35. Sublacrimal part of jugal tapering (0); bluntly squared rostrally (1); expanded (2) (modified from RAUHUT, 2003; ordered).

36. Angle between ascending process and caudal process of jugal right or obtuse (0); acute with an ascending process strongiy dorsocaudadlly oriented (1) (EZCURRA & NOVAS in press).

37. Orbit length subequal to or longer than internal antorbital fenestra length (0); shorter than internal antorbital fenestra length (1) (HOLTZ, 2000).

38. Frontal process of the postorbital sharply upturned (0); at about the same level as or slightly higher than the squamosal process resulting in a T-shaped postorbital (1) (CURRIE, 1995).

39. Quadratojugal process of the squamosal broad and usually somewhat expanded (0); tapering (1) (reversed from RAUHUT, 2003).

40. Quadrate foramen developed as a distinct opening between the quadrate and quadratojugal (0); almost entirely enclosed in the quadrate (1); absent (2) (Holtz, 2000; RAUHUT, 2003; unordered).

41. Infratemporal fenestra shape: rostrocaudally wide (0); strongly rostrocaudally compressed (1); strongly widen, resulting in its length being 1.5 times the length of the orbit (2) (modified from RAUHUT, 2003; unordered).

42. Ventral border of infratemporal fenestra in lateral view: mostly constituted by the jugal or equal participation of both jugal and quadratojugal (0); mostly constituted by the quadratojugal (1) (EZCURRA & NOVAS, in press).

43. Prefrontal: widely exposed on the rostrodorsal rim of the orbit in lateral view with a slender ventral process along the mediocaudal rim of the lacrimal (0); reduced, with little participation on the rostrodorsal rim of the orbit in lateral view, being displaced caudally and/or medially, ventral process absent (1) (modified from RAUHUT, 2003).

44. Frontal: elongated triangular (0); square shaped (1) (reversed from HOLTZ, 1994).

45. Supratemporal fossa, postorbital participation: present (0); absent (1) (SERENO, 1999).

46. Ventral process of squamosal: tapering (0); broad, and usually somewhat expanded (1) (RAUHUT, 2003).

47. Squamosal caudal process: short and not well caudally extended (0); strongly caudally extended and longer than the rostral process, sometimes exceeding the caudal level of the quadrate condyle in lateral view (1) (EZCURRA & NOVAS, in press).

48. Squamosal-quadratojugal contact: present, but small contact between the bones (0); present, broad contact (1); absent (2). (reversed from HOLTZ, 1994; unordered).

49. Dorsal ramus of the quadratojugal: longer than the rostral ramus (0); of the same length, or shorter, than the rostral ramus (1) (SERENO, 1986; LANGER, 2004; unordered).

50. Caudal curvature of the proximal end of quadrate: absent or slight, proximal half of quadrate almost straight (0); present, with quadrate head caudodorsally oriented (1) (EZCURRA & NOVAS, in press).

51. Basisphenoid between basal tubera and basipterygoid processes: approximately as wide as long, or wider (0); significantly elongated, at least 1,5 times longer than wide (1) (RAUHUT, 2003).

52. Lateral surface of basisphenoid: penetrated by a small foramen for passage of internal carotid, below the crista prootica (0); penetrated by a large pneumatic foramen, partially covered by the crista prootica (1) (TYKOSKI, 1998).

53. Basisphenoid fontanelle: present (0); absent (1) (SERENO, 1999).

54. Ectopterygoid: slender, without ventral fossa (0); expanded, with a deep ventral depression medially (1); as above, but with a deep groove excavated into the body of the ectopterygoid from the medial side (2) (GAUTHIER, 1986; SERENO et al., 1996; RAUHUT, 2003; unordered).

55. Exit of nerve V in lateral view: positioned at the level of the caudal half of the basisphenoid (0); positioned at the level of the rostral half of the basisphenoid (1) (EZCURRA & NOVAS, in press).

56. Exit of nerves X and XI: laterally through the jugular foramen (0); caudally through a foramen lateral to the exit of the nerve XII and the occipital condyle (1) (CHATTERJEE, 1993; RAUHUT, 2003).

57. Exit of mid-cerebral vein: included in trigeminal foramen (0); vein exils braincase through a separate foramen rostrodorsal to the trigeminal foramen (1) (RAUHUT, 2003).

58. Mandibular joint: approximately straight below the quadrate head (0); significantly caudal to the quadrate head (1) (RAUHUT, 2003).

59. Ventral rim of the basis of the paroccipital processes: above or level with the dorsal border of the occipital condyle (0); situated at mid-height of occipital condyle or lower (1) (RAUHUT, 2003).

60. Occipital condyle size: subequal or smaller than foramen magnum diameter (0); larger than foramen magnum diameter (1) (EZCURRA &NOVAS, in press).

61. Rostral end of dentary dorsoventrally expanded: absent (0); present (1) (GAUTHIER, 1986).

62. Mediolateral width of anterior end of dentary: equal to that of caudal part (0); expanded (1) (CARRANO et al., 2005).

63. Caudoventral process of dentary: extends further caudally than caudodorsal process (0); subequal in length to caudodorsal process (1) (SERENO, 1999).

64. Caudal end of splenial: straight (0); forked (1) (SERENO et al., 1996).

65. Angular reaches caudal end of mandible, blocking surangular from ventral margin of the jaw in lateral view: absent (0); present (1) (TYKOSKI, 2005).

66. Retroarticular process of the mandible: narrow and rod-like (0); broad with muscle scar (1) (SERENO et al., 1996; HARRIS, 1998; RAUHUT, 2003).

67. Enlarged fang-like mesial dentary teeth: absent (0); present (1) (GAUTHIER, 1986).

68. Dentary tooth count: 18 or less (0); 20-29 (1); more than 29 (2) (modified from RUSSELL & DONG, 1993; unordered).

69. Postaxial centra pneumatization: not pneumatized (0); pneumatized by a single pair of fossae, that does not penetrate into the centra (1); pneumatized by two pair of fossae, that does not penetrate into the centra (2); pneumatized by two pair of foramina, that penetrate into the centra resulting in a pneumatic camerae within it (3); pneumatized by a single pair of foramina, that penetrate into the centra resulting in a pneumatic camerae within it (4) (modified from GAUTHIER, 1986 & BRITT, 1993; ordered).

70. Axial intercentrum length-axial centrum length ratio: 25-40% (0); 40-70% (1) (SERENO, 1999).

71. Axial neural spine: broad and blade-shaped (0); laterally invaginated and craniocaudally reduced and rod-like (1) (modified from MOLNAR et al., 1990).

72. Axial diapophysis: absent (0); present (1) (reversed from ROWE & GAUTHIER, 1990).

73. Axial parapophysis: strongly reduced or absent (0); well developed (1) (reversed from ROWE & GAUTHIER, 1990).

74. Axial pleurocoels: absent (0); present (1) (note: can substitute "pneumatic foramen" or "fossa" for "pleurocoel" (TYKOSKI, 1998)) (reversed from ROWE & GAUTHIER, 1990).

75. Cranial articular facet of cranial cervical vertebrae: approximately as high as wide or higher (0); significantly wider than high (1); wider than high and higher laterally than medially (kidney-shaped) (2) (Gauthier, 1986, modified by RAUHUT, 2003; EZCURRA & CUNY, 2007; unordered).

76. Cranial face of cervical and cranial dorsals: amphiplatyan or amphicoelous (0); slightly convex (1); strongly convex, having ball-like articulations (2) (GAUTHIER, 1986; EZCURRA & CUNY, 2007; ordered)

77. Mid-cervical (C3-C6) centrum proportions: equal or less than 3 times the height of the cranial articular surface (0); more than 3 times the height of the cranial articular surface (1); more than 4 times the height of the cranial articular surface (2) (SERENO, 1999; EZCURRA & CUNY, 2007; ordered).

78. Ventral keel in anterior cervicals: present (0); absent (1) (RAUHUT, 2003)

79. Ventral lamina, from the diapophyses to the ventral rim of the caudal end of the vertebral centra in cervical centra: absent (0); present (1) (CUNY & GALTON, 1993; RAUHUT, 2003; EZCURRA & CUNY, 2007).

80. Lamina protracted from the diapophyses in cervical vertebrae: absent (0); postzygapophyseal lamina, reaches the postzygapophyses (1); centrodiapophyseal lamina reaches the dorsocaudal corner of the centrum (2) (EZCURRA & CUNY, 2007; unordered).

81. Lateral arch lamina craniolateral to postzygapophysis is solid (0), or there is a large, caudally opening entrance craniolateral to the postzygapophysis, that leads into a large pneumatic cavity within the lateral arch lamina of post-axial cervical vertebrae (1) (TYKOSKI, 1998)

82. Cervical lateral arch laminae caudomedial to postzygapophysis is solid (0), ort there is a pneumatic foramen in cervical lateral arch laminae, caudomedial to postzygapophysis (1) (TYKOSKI, 1998).

83. Broad ridge from the diapophyses to the ventral rim of the posterior end of the vertebral centra in cervical vertebrae: absent (0); present (1) (RAUHUT, 2003)

84. Prezygapophyses in anterior cervicals: transverse distance between prezygapophyses less than width of neural canal (0); prezygapophyses situated lateral to the neural canal (1) (RAUHUT, 2003)

85. Prezygapophyses in anterior postaxial cervicals: straight (0); anteroposteriorly convex, flexed ventrally anteriorly (RAUHUT, 2003, modified from GAUTHIER, 1986)

86. Epipophyses in anterior cervical vertebrae: absent or poorly developed (0); well-developed (1); pronounced, strongly overhanging the postzygapophyses (2) (RAUHUT, 2003, modified from GAUTHIER, 1986; ordered)

87. Cranial cervical epipophyses: low and blunt (0); long, thin and not well developed (1); long and well developed (2); craniocaudally lengthened and extremely developed (3) (NOVAS, 1992; EZCURRA & CUNY, 2007; ordered).

88. Transverse process shape of caudal cervical and dorsal vertebrae: subrectangular (0); subtriangular (1) (SERENO, 1999; EZCURRA & CUNY, 2007).

89. Postaxial cervical neural spines: dorsoventrally tall (0); extremely low (1) (EZCURRA & CUNY, 2007).

90. Cervical centra lack pleurocoels (0), or possess single pair of pleurocoels (0), or two pairs of pleurocoels in each cervical centrum (2) (note: can substitute 'pneumatic foramen' or 'fossa' for 'pleurocoel') (GAUTHIER, 1986; TYKOSKI, 1998; unordered).

91. Cervical pleurocoels developed as: deep depressions (0); foramina (1) (RAUHUT, 2003).

92. Interior pneumatic spaces in cervicals: absent (0); present, structure camerate (1); present structure camellate (2) (BRITT, 1993; RAUHUT, 2003; unordered).

93. Cervical ribs: stout, and less than three centra long (0); very thin, and extend caudally at least three centra behind their vertebra of origin (1) (HOLTZ, 1994; EZCURRA & CUNY, 2007).

94. Cranial and mid-dorsal centrum length: subequal to centrum height (0); more than 2 times centrum height (1) (EZCURRA & CUNY, 2007).

95. Caudal dorsal vertebrae: strongly shortened, centrum length less than 1.33 times the height of the cranial articular surface (0); relatively short, centrum length equal or more than 1.33 times the height of the cranial articular surface (1); significantly elongated, centrum length equal or more than 2 times the height of the cranial articular surface (2) (RAUHUT, 2003; TYKOSKI, 2005; EZCURRA & CUNY, 2007; ordered).

96. Shape of dorsal centra in anterior view: subcircular or oval (0); significantly wider than high (1) (RAUHUT, 2003).

97. Dorsal centra lengths: the centra are more or less constant in length along the dorsal series (0); the centra increase their lengths caudally the series (1); the centra decrease their lengths caudally the series (2); the centra vary with the lengths independent from their position (3) (HUGI; unordered).

98. Transverse processes of the dorsal vertebrae: craniocaudally narrow (0); broad, extending to lateral margin of the prezygapophyses (1); broad, extending not to lateral margin of the prezygapophyses (2) (ROWE & GAUTHIER, 1990; EZCURRA & CUNY, 2007; unordered).

99. Transverse processes craniocaudally short and not strongly backswept (0), or transverse processes of dorsal vertebrae meet neural arches over a long craniocaudal contact, have (strongly) backswept cranial edges, and are triangular when viewed dorsally (1) (TYKOSKI, 1998).

100. The transverse processes of dorsals stand horizontally to the longitudinal axis of the centra (0); the transverse processes of dorsals are bent dorsally at least about 25 degrees (1); the transverse processes of dorsals are bent ventrally (2) (HUGI; unordered).

101. The caudal margin of the dorsal transverse processes stands in a right angle to the longitudinal axis of the centrum (0); the caudal edge is bent forwards the dorsal series at least 10 degrees (1); the caudal margin is bent backwards the dorsal series, overlapping the posterior articular face (2) (HUGI; unordered).

102. Neural spines of caudal dorsals: broadly rectangular and approximately as high as long (0); high rectangular, significantly higher than long (1); high rectangular, significantly longer, than high (2) (modified from RAUHUT, 2003; EZCURRA & CUNY, 2007; unordered).

103. Neural spine in posterior dorsals: of subequal length throughout its height or tapering dorsally (0); significantly expanded dorsally, fan-shaped (RAUHUT, 2003).

104. Height of neural spine in dorsals: the height of the dorsal neural spines is more or less constant heading caudally (0); the height of the dorsal neural spines increases heading caudally (1); the height of the dorsal neural spines decreases heading caudally (2) (HUGI; unordered).

105. Laminae in neural arch of dorsals: there are no laminae underneath the transverse processes of dorsals (0); there are laminae present in at least one dorsal vertebrae underneath its transverse processes (1) (HUGI).

106. Hyposphene-hypantrum articulation in dorsal vertebrae: absent (0); present (1) (GAUTHIER, 1986; RAUHUT, 2003).

107. Shape of hyposphene-hypantrum articulation: hyposphene developed as a single sheet of bone (0); hyposphene wide, formed by the ventrally bowed medial parts of the postzygapophyses, and only connected by a thin horizontal lamina of bone (1) (RAUHUT, 2003).

108. Hypapophyses in anterior dorsals: absent or poorly developed (0); strongly pronounced (1) (GAUTHIER, 1986; RAUHUT, 2003).

109. Ventral keel in anterior dorsals: absent or very poorly developed (0); pronounced (1) (RAUHUT, 2003).

110. Parapophyses in posteriormost dorsals: on the same level as transverse process (0); distinctly below transverse process (1) (RAUHUT, 2003).

111. Fossae in dorsal vertebrae: absent (0); present in anterior dorsals ('pectorals') (1); present in all dorsals (2) (HOLTZ, 1994; modified from RAUHUT, 2003; ordered).

112. Fusion of sacral centra: do not fuse, or they remain distinct from one another (0); extensively fused to one another, obliterating all sutures by adulthood (1) (TYKOSKI, 1998; EZCURRA & CUNY, 2007).

113. Sacral ribs and ilia: remain separate throughout ontogeny (0); fuse to medial wall of ilia late in ontogeny (1) (TYKOSKI, 1998; EZCURRA & CUNY, 2007).

114. Sacral transverse processes, sacral ribs, neural arches, and neural spines remain separate throughout ontogeny (0), or fuse to one another (1) (TYKOSKI, 1998).

115. Sacral transverse processes in the adulthood: slender and well separated (0); very massive and strongly expanded (1); forming a more or less continuous sheet in ventral or dorsal view (2) (ROWE and GAUTHIER, 1990; RAUHUT, 2003, reversed by EZCURRA & CUNY, 2007; unordered).

116. Number of sacral vertebrae: two (0); three (1); more than three (2); more than five (3) (RAUHUT, 2003, modified from GAUTHIER, 1986; ordered).

117. Sacral centra comparable in size to other post-cervical vertebrae (0), or diameter of sacral centra greatly reduced relative to other post-cervical vertebrae (1) (TYKOSKI, 1998).

118. Sacrum arched only slightly or not arched (0), or sacrum strongly arched dorsally (1) (TYKOSKI, 1998).

119. Sacral centra: rounded or keeled ventrally (0); flattened ventrally (1) (RAUHUT, 2003).

120. Diameter of mid-sacral centra approximately the same (0); or substantially smaller than posterior dorsals and anterior caudals (1); or substantially larger than posterior dorsals and anterior caudals (2) (modified from HOLTZ, 1994; TYKOSKI, 2005; unordered).

121. Pleurocoels in sacral vertebrae: absent (0); present with at least one fossa (1) (modified from HOLTZ, 1994; RAUHUT, 2003).

122. Ventral groove in anterior caudals: absent (0); present (1) (ROWE & GAUTHIER, 1990; RAUHUT, 2003).

123. Ventral surface of anterior caudal vertebrae: smooth or weakly grooved longitudinally (0); at least some caudal vertebrae with narrow, sharply defined, longitudinal, ventral groove (1) (ROWE & GAUTHIER, 1990; TYKOSKI, 1998; EZCURRA & CUNY, 2007).

124. Number of caudal vertebrae: 41 or more (0); fewer than 41 (1); fewer than 36 caudals (2) (RAUHUT, 2003; ordered).

125. Caudal centra lengths: the centra are constant in length for at least the anterior caudals along the series (0); the centra increase their lengths caudally the series (1); the centra decrease their lengths caudally the series (2) (HUGI; unordered).

126. Shape of anterior caudal centra: oval (0); subrectangular and box-like (1) (GAUTHIER, 1986; RAUHUT, 2003).

127. Caudal transverse processes I: the transverse processes of the anterior caudals stand horizontally to the longitudinal axis of the centra (0); the transverse processes of the anterior caudals are bent dorsally (1) (HUGI).

128. Caudal transverse processes II: the transverse processes of the anterior caudals are standing in a right angle to the longitudinal section of the centrum (0); the transverse processes of the anterior caudals are back-swept (1) (HUGI).

129. Zygapophyses of anterior caudal vertebrae: prezygapophyses and postzygapophyses are not overlapping the cranial or caudal centrum face (0); prezygapophyses and postzygapophyses are cranially and caudally elongated overlapping the centrum faces (1); only the prezygapophyses are elongated (2); only the postzygapophyses are elongated (3) (HUGI; unordered).

130. Laminae in caudals: the anterior caudals exhibit no laminae underneath the basis of transverse process (0); the anterior caudals exhibit two laminae underneath the base of transverse process (1) (HUGI).

131. Anterior process on proximal end of chevrons absent (0); or small tubercules (1); or large and projecting (2) (CARRANO et al 2002; TYKOSKI 2005; unordered)

132. Pleurocoels in caudals: There is no groove proceeding along the longitudinal axis of the centra underneath the neurocentral suture (0); there is a longitudinal groove underneath the neurocentral suture (1) (HUGI).

133. Pelvic girdle: separate elements throughout ontogeny (0); fused together by late ontogeny (1) (ROWE & GAUTHIER, 1990; EZCURRA & CUNY, 2007).

134. Supraacetabular crest of ilium: present as a weakly developed ridge (0); present as a well developed raised shelf (1); flares lateroventrally to form a hood-like overhang that hides craniodorsal half of acetabulum in lateral view (2) (LANGER, 2004; TYKOSKI, 2005; EZCURRA, 2006; unordered).

135. Articulation of iliac blades with sacrum: vertical, well separated above sacrum (0); strongly inclined mediodorsally, almost contacting each other of sacral neural spines at the midline (1) (HOLTZ, 1994; RAUHUT, 2003).

136. Preacetabular part of ilium: significantly shorter than postacetabular part (0); subequal in length to postacetabular part (1); significantly longer than postacetabular process (RAUHUT, 2003; HUTCHINSON, 2001a).

137. Preacetabular part of ilium: approximately as high as postacetabular part (excluding the ventral expansion) (0); significantly higher than postacetabular part (1) (RAUHUT, 2003).

138. External lateral surface of caudal end of ilium: smooth (0); distinct caudal rim on ilium for M. Iliofibularis (1) (ROWE & GAUTHIER, 1990, modified by EZCURRA & CUNY, 2007).

139. Dorsal margin of iliac blade: straight (0); strongly convex (1); slightly convex (2) (modified from EZCURRA & CUNY, 2007; unordered).

140. Preacetabular process strongly cranioventrally oriented, thus it closely approaches the iliac pubic peduncle at the base of the process: absent (0); present (1) (Ezcurra & Cuny, 2007).

141. Pronounced ventral hook on cranial expansion of ilium: absent (0); present (1) (Gauthier, 1986; Rauhut, 2003; Ezcurra & Cuny, 2007).

142. Cranial rim of ilium: convex or straight (0); distinctly concave dorsally (1) (Rauhut, 2003).

143. Caudal margin of the ilium: squared or rounded off when viewed laterally (0); posteroacetabular process caudal margin concave in lateral view (1) (Sereno et al., 1994; Tykoski, 1998; Ezcurra & Cuny, 2007).

144. Posterior end of ilium: rectangular (0); sloping downwards (1) (Gauthier, 1986).

145. Supraacetabular crest and ventrolateral margin of the postacetabular blade continuity: not continuous (0); continuous by a weakly developed ridge (1); continuous by a well developed ridge, with non-distinct notch between both structures (2) (Ezcurra & Cuny, 2007; unordered).

146. Vertical ridge on iliac blade above acetabulum: absent or poorly developed (0); well-developed (1) (Molnar et al., 1990; Rauhut, 2003).

147. Brevis fossa: narrow and with subparallel margins (0); very strongly caudally expanded (1) (Molnar et al., 1990; Rauhut, 2003; Ezcurra & Cuny, 2007).

148. Articulation facet of pubic peduncle of ilium: facing more ventrally than cranially, and without pronounced kink (0); with pronounced kink and cranial part facing almost entirely cranially (1) (Rauhut, 2003; Ezcurra & Cuny, 2007).

149. Pubic peduncle of ilium: transversely broad and roughly triangular in outline (0); anterioposterorly elongated and narrow (1) (Rauhut, 2003).

150. Pubic peduncle: subequal in length to ischial peduncle (0); significantly longer than ischial peduncle, ischial peduncle tapering ventrally and without clearly defined articular facet (1) (Rauhut, 2003).

151. Anterior margin of pubic peduncle: straight or convex (0); concave (1) (Rauhut, 2003).

152. Ischial obturator notch (or foramen): absent (0); present (1) (Gauthier, 1986; Sereno et al., 1994; Ezcurra & Cuny, 2007).

153. Ventral notch between obturator process or –flange on ischium: absent (0); present (1) (Rauhut, 2003, modified from Sereno et al., 1996)

154. Ischial mid-shaft cross-sectional shape (paired): oval (0); heart-shaped (1); subrectangular (2) (Sereno, 1999; Ezcurra & Cuny, 2007; unordered).

155. Ischium length: at least three-quarters the length of pubis (0); ischium two-thirds or less the length of the pubis (1); ischium less than three-quarters and more than two-thirds the length of pubis (2) (Gauthier, 1986; Rauhut, 2003; modified from Ezcurra & Cuny, 2007; unordered).

156. Posterior process on proximal part of ischium: absent or only developed as a small flange (0); well-developed (1) (Rauhut, 2003)

157. Distal end of ischium: slightly expanded or not at all (0); craniocaudal expansion of distal tip of ischium forms a larger boot than that of the pubis (1) (modified from Tykoski, 1998; Ezcurra & Cuny, 2007).

158. Pubic shaft: slightly concave and strongly bowed caudally (0); nearly straight (1); slightly concave without a caudal bow (2) (Sereno, 1999, modified by/from Ezcurra & Cuny, 2007; unordered).

159. Distal expansion of the pubis: non-expanded or slightly expanded (0); more expanded than ischium boot (1) (modified from Gauthier, 1986, Ezcurra & Cuny, 2007, reversed from Sereno, 1999).

160. Pubic boot in ventral view: broadly triangular (0); narrow, with subparallel margins (1) (Rauhut, 2003, reversed and modified from Holtz, 1994).

161. Pubic boot: more posteriorly than anteriorly expanded (0); more anteriorly than posteriorly expanded (1) (RAUHUT, 2003).

162. Pubic boot: with distinct anterior expansion (0); only expanded posteriorly (1); only expanded posteriorly and posterior expansion more than half the length of the pubic shafts (2) (RAUHUT, 2003, modified from GAUTHIER, 1986; HOLTZ, 1994; ordered).

163. Distal tip of pubis elongate rectangular or subequant (0); or subtriangular (1) in distal view (TYKOSKI, 2005, modified from RAUHUT, 2003).

164. Pubic apron: completely closed (0); with medial opening distally above the pubic foot (1) (RAUHUT, 2003; EZCURRA & CUNY, 2007).

165. Obturator foramen in pubis: completely enclosed (0); open ventrally (1); absent (2) (RAUHUT, 2003, modified from HOLTZ, 1994; ordered).

166. Pubic fenestra below obturator foramen: absent (0); present (1) (GAUTHIER, 1986; RAUHUT, 2003).

167. Furcula: absent (0); present (1) (GAUTHIER 1986).

168. Scapular blade broad and relatively short, ratio of maximum length/minimum breadth < 10 (0), or blade narrow and long, ratio of maximum length/minimum breadth >= 10 (1) (modified from GAUTHIER, 1986; HOLTZ; RAUHUT 2003) (TYKOSKI 2005)

169. Distal end of scapula: expanded (0); not expanded (1) (GAUTHIER 1986).

170. Anterodorsal border of acromion process of scapula protrudes conspicuously (0), or has smooth, continuous, high-angle transition to scapular blade (1) (modified from RAUHUT 2003)

171. Glenoid facet on scapula: facing ventrally (0); facing ventrolaterally (1) (NOVAS & PUERTA 1997).

172. Coracoid: higher than long (0); longer than high (1) (RAUHUT 2003).

173. Shape of coracoid: semicircular (0); subrectangular (1) (GAUTHIER 1986).

174. Distal expansion of scapular blade: marked as a fan-shaped expansion (0); slightly expanded, narrow with subparallel margins or strap-like (1) (CURRIE & ZHAO 1993).

175. Shape of craniodorsal corner of distal scapular blade: rounded (0); acuminate (1) (CARRANO *et al.* 2005).

176. Cranial margin of scapulacoracoid at scapula-coracoid contact in adults: notched (0); continuous and uninterrupted (1) (HOLTZ 2000).

177. Spacing between ventral glenoid and caudoventral coracoid process (= sternal process): more than dorsoventral depth of glenoid (0); less than dorsoventral depth of glenoid (1) (CARRANO *et al.* 2005).

178. Caudoventral process (= sternal process) of the coracoid: rounded and not projected beyond glenoid fossa (0); tapering and projected little beyond the caudal margin of the glenoid fossa (1); tapering and strongly caudally projected well beyond the caudal margin of the glenoid fossa (modified from Sereno *et al.* 1996) (RAUHUT 2003).

179. Distal humeral condyles: rounded (0), flattened (1) (CARRANO *et al.* 2002).

180. Ratio femur/humerus: more than 2.5 (0); between 1.2 and 2.2 (1); less than 1 (2) (RAUHUT 2003; ordered).

181. Outline of proximal articular facet of humerus: broadly oval (more than twice as broad transversely than anteroposteriorly) (0); distinctly rounded (less than twice as broad anteroposteriorly than transversely) (1) (RAUHUT 2003).

182. Shape of internal tuberosity on humerus: triangular, often rounded (0); rectangular (1) (RAUHUT 2003).

183. Humerus with anteroposterior sihmoid curvature (0), or straight (1) in lateral view (SERENO, 1999a; RAUHUT, 2003)

184. Humeral shaft torsion of proximal and distal ends: absent (0); present (1) (HOLTZ 1994).

185. Humeral distal width accounts: for less than, about 0.3 of the total length of the bone (0); more than 0.3 of the total length of the bone (1) (LANGER 2004).

186. Deltopectoral crest: positioned within the proximal 30% of the humerus (0); proximodistally elongate, more than 34% of humeral length (1) (NOVAS 1996).

187. Olecranon process of ulna: well-developed (0); strongly reduced or absent (1) (NOVAS 1998).

188. Radius: more than half the length of humerus (0); less than half the length of humerus (1) (RAUHUT 2003).

189. Large distal carpal, capping Mc I and parts of Mc II: absent (0); present (1); present, showing the shape and morphology of a semilunate carpal in proximal view, but rectangular rather than semilunate in palmar view (2); typical semilunate carpal present (3) (modified from GAUTHIER 1986; ordered) (RAUHUT 2003).

190. Distal carpal 5: present (0); absent (1) (SERENO 1999).

191. Strongly developed dorsal lip proximal to the extensor pit on the distal end of the metacarpals II and III: absent (0); present (1) (EZCURRA 2006).

192. Width of metacarpal I at the middle of the shaft: accounts for less or 0.3 of the total length of the bone (0); between 0.3 and 0.45 of the total length of the bone (1); more than 0.45 of the total length of the bone (2) (BAKKER & GALTON 1974, modified from LANGER 2004; unordered).

193. Metacarpal I shorter than the phalanx I-1: absent (0); present (1) (modified from Rauhut 2003) (EZCURRA 2006).

194. Metacarpal II in relation to metacarpal III: shorter (0); subequal or longer (1) (GAUTHIER 1986).

195. Width of the distal end of the metacarpal II: smaller or subequal to the distal end of the metacarpal III (0); larger than the distal end of the metacarpal III (1) (EZCURRA 2006).

196. Shaft of metacarpal IV in relation to that of metacarpals I-III: about the same width (0), significantly narrower (1) (SERENO *et al.* 1993; LANGER 2004).

197. Metacarpal IV and fourth digit: proximal portion set lateral to Mc III (proximal portion of Mc V also set lateral to Mc IV if it is present) and with more than one phalanx (0); proximal portion set lateral Mc III (idem Mc V) and with only one or lacking phalanges (1); proximal portion at the palmar surface of Mc III (idem Mc V) and with only one or lacking phalanges (2); absent (3) (GAUTHIER 1986, modified from EZCURRA & NOVAS 2006; ordered).

198. Metacarpal V: with phalanges (0); vestigial and lacking phalanges (1); absent (2) (GAUTHIER 1986; ordered).

199. Metacarpus: relatively short and broad (ratio length/width of Mc I-III < 2) (0); slender and elongated (ratio > 2.2) (1) (RAUHUT 2003).

200. Contact between Mc I and Mc II: metacarpals contact each other at their bases only (0); Mc I closely appressed to proximal half of Mc II (1) (GAUTHIER 1986).

201. Distal end of Mc I: condyles more or less symmetrical (0); condyles strongly asymmetrical, the medial condyle being positioned more proximally than the lateral (1) (RAUHUT 2003).

202. Medial side of Mc II: expanded proximally (0); not expanded (1) (RAUHUT 2003).

203. Shaft of Mc III: subequal in width to Mc II (0); considerably more slender than Mc II (less than 70 per cent of the width of Mc II) (1).

204. Proximal articular end of Mc III: expanded and similar in width to Mc I and II (0); not expanded, very slender when compared to Mc I and II (1) (modified from GAUTHIER 1986) (RAUHUT 2003).

205. Proximal outline of Mc III: subrectangular (0); triangular, apex dorsal (1) (RAUHUT 2003).

206. Shaft of Mc III: straight (0); bowed laterally (1) (GAUTHIER 1986).

207. Extent of metacarpal I contact with metacarpal II: <1/3 (0), ½ (1) metacarpal I shaft length (GAUTHIER 1986; HARRIS 1998).

208. Metacarpal I length: >= (0), < (1) 50% of metacarpal II length (GAUTHIER & PADIAN 1985).

209. Manus length: < (0), >= (1) length of arm + forearm (GAUTHIER 1986; SERENO 1999).

210. Manual length (measured as the average length of digits I-III): accounts for less than 0.3 of the total length of the humerus plus the radius (0), more than 0.3 but less than 0.4 of the total length of the humerus plus the radius (1); or more than 0.4 of the total length of humerus plus radius (2) (GAUTHIER 1986; LANGER 2004; unordered).

211. First phalanx of manual digit I: is not the longest non-ungual phalanx of the manus (0); is the longest non ungual phalanx of the manus (1) (GAUTHIER 1986, modified) (EZCURRA 2006).

212. Twisted first phalanx in digit I: absent (0); present (1) (BENTON *et al.* 2000).

213. Manual digit II longer than digit III: absent (0); present (1) (GAUTHIER 1986).

214. Manual digits II-III: with short penultimate phalanx (0); with long penultimate phalanx (1) (GAUTHIER 1986; modified from SERENO *et al.* 1993).

215. Unguals of manual digits II and III: poorly curved (0); trenchant, i.e. strongly curved (1) (GAUTHIER 1986).

216. Ungual phalanx of digit II: the longest of the manus (0); equal in length to the ungual of digit I (1) (GAUTHIER 1986; YATES 2003).

217. Five fingers present (0); fifth finger absent and fourth finger reduced to a metacarpal with only one phalanx (1); fourth finger absent (2) modified from Gauthier 1986; ordered) (RAUHUT 2003).

218. Penultimate phalanx of the second finger: shorter than first phalanx (0); longer than first phalanx (1) and (RAUHUT 2003).

219. Penultimate phalanx of the third finger: as long as, or shorter than, more proximal phalanges (0); longer than each of the more proximal phalanges (1); longer than both proximal phalanges taken together (2) (modified from GAUTHIER 1986; ordered) (RAUHUT 2003).

220. Manual ungual I: less than half the length of the radius (0); more than two-thirds of the length of the radius (1) (modified from SERENO *et al.* 1998) (RAUHUT 2003).

221. Dorsal lip at proximal articular end of manual unguals: absent (0); present (1) (CURRIE & RUSSELL 1988).

222. Flexor tubercle on manual unguals: less than half the height of the articular facet (0); more than half the height of the articular facet (1) (RAUHUT 2003).

223. Mc I: significantly longer than broad (0); very stout, approximately as broad as long (1) (RAUHUT 2003).

224. Femoral dimorphism: absent (0); present, expressed in muscle scars, attachments, and processes (robust versus gracile morphs) (1) (ROWE & GAUTHIER, 1990).

225. Proximal surface of femur: with a transversely extended groove (0); smooth (1) (EZCURRA, in review).

226. Caudal surface of proximal femur: smooth (0); marked by an obturator ridge in robust individuals (1) (RAATH, 1977).

227. Cranial trochanter: absent or poorly developed (0); spike-like or pyramidal prominence (1); broadened ("wing like") (2) (RAUHUT, 2003; ordered).

228. Placement of the cranial trochanter: at distal end of femoral head (0); more proximally placed, but below the greater trochanter (1) (GAUTHIER, 1986; RAUHUT 2003).

229. Tibiofibular crest of distal femur: smoothly continuous with fibular condyle (0); sharply demarcated from fibular condyle by a sulcus or concavity (1) (ROWE, 1989).

230. Femoral popliteal fossa in adults: smooth (0); transversed by infrapopliteal ridge between tibial condyle and tibiofibular crest (1) (TYKOSKI 1998).

231. Craniomedial crest on distal femur: absent (0); proximal to condyles, blend smoothly together (1); an hypertrophied craniomedial crest on the distal femur separates cranial and medial surfaces of femur (2) (HOLTZ, 1994; unordered).

232. Cranial surface of distal femur: strongly convex (0); cranial surface planar or slightly concave, showing a poorly developed cranial intercondylar groove (1); strongly concave, showing an incipient and deep cranial intercondylar groove (2) (modified from RAUHUT, 2003; ordered).

233. Ridge on lateral side of tibia for connection with fibula: absent (0); present, extending from the proximal articular surface distally (1); present, clearly separated from proximal articular surface (2) (GAUTHIER, 1986; RAUHUT, 2003; ordered).

234. Distal tibial lateral malleolus: lobe-shaped (0); polygonal-shaped (1) (SERENO, 1999).

235. Development of lateral malleolus in distal tibia: partially caudally overlaps the distal end of fibula and calcaneum (0); nearly completely overlaps the distal end of fibula and calcaneum (1) (modified from SERENO et al., 1994).

236. Distal articular surface of tibia: subrectangular in outline and slightly wider transversely than craniocaudally (0); subrectangular with small lateral process (1); narrow triangular in outline and strongly mediolaterally expanded (2) (RAUHUT, 2003; ordered).

237. Facet for the reception of the ascending process of the astragalus in the distal tibia: craniocaudally as well as transversely well developed (0); subtriangular, not well developed cranially (1); subrectangular, cranially poorly developed (2); nearly absent (3) (EZCURRA & NOVAS, in press; ordered).

238. Ridge on medial side of proximal end of fibula, that runs anterodistally from the posteroproximal end: absent (0); present (1) (ROWE & GAUTHIER, 1990).

239. Medial surface of proximal fibula: flat or slightly concave (0); caudodistally opening sulcus on medial surface of proximal fibula (1) (ROWE & GAUTHIER, 1990).

240. Astragalus and calcaneum: remain separate elements throughout ontogeny (0); fused to each other by later stages of ontogeny (1) (WELLES & LONG, 1974).

241. Ascending process of astragalus. lower than astragalar body (0); higher than the astragalar body (1) (WELLES & LONG, 1974).

242. Astragalar ascending process thickness: wedge-shaped dorsal margin inserting into tibia (0); low plate, 2—5 times taller than thick craniocaudally at midpoint (1) (GAUTHIER 1986; modified from SERENO et al., 2004; ordered).

243. Deep fossa at the base of the ascending process of the astragalus: absent (0); present (1) (EZCURRA & NOVAS, in press).

244. Horizontal groove across cranial face of astragalar condyles: absent (0); present (1) (WELLES & LONG, 1974).

245. Tibial facet of calcaneum: with no participation of the tibial facet (0); with small participation of the tibial facet on the caudomedial most corner of the bone (1); with large tibial facet, reaching the lateral margin of the bone (2) (modified from RAUHUT, 2003; ordered).

246. Proximal tarsals: remain separate from tibia throughout ontogeny (0); astragalocalcaneum fuses to distal end of tibia in adults to create a functional tibiotarsus (1) (ROWE & GAUTHIER, 1990).

247. Distal tarsal III: remain a separate element throughout life (0); fused to the proximal end of metatarsal III (1) (ROWE & GAUTHIER 1990).

248. Metatarsal 1: contacts the ankle joint (0); reduced, elongated splint-like, attached to Mt II and not reaching the ankle joint (1); broadly triangular and attached to the distal part of Mt II (2) (GAUTHIER 1986; RAUHUT, 2003; ordered).

249. Metatarsals II and III: separate (0); fusion of proximal ends of metatarsals II and III to each other (1) (ROWE & GAUTHIER, 1990).

250. Proximal end of metatarsal III position: does not back to the ventral side of metatarsals II and IV (0); backs metatarsals II and IV ventrally, resulting in a T-shaped proximal profile ("antarctometatarsus") (1) (CARRANO et al., 2002; TYKOSKI, 2005).

251. Metatarsal V: with rounded distal articular facet (0); strongly reduced and lacking distal articular facet (1); short, without articular surface, transversely flattened and cranially bowed distally (2) (GAUTHIER 1986; RAUHUT, 2003; ordered).

252. Posterior margin of scapular blade curves over full length (0), or nearly straight over most of length, curves posteriorly only at distal tip (1) (TYKOSKI, 2005).

253. Anterodorsal border of acromion process of scapula protrudes conspicuously (0), or has smooth, continuous, high-angle transition to scapular blade (1) (modified from RAUHUT 2003) (TYKOSKI, 2005).

254. Humerus proximal head flattened (0), or rounded, bulbuous, subspherical (1) (HOLTZ, 1998; RAUHUT, 2000).

255. Radius and ulna distal articular surfaces not enlarged (0) or large and subhemispherical (1) (TYKOSKI, 2005).

256. Distal ends of metacarpals dorsally rounded, smooth (0), or with deep, well-developed extensor pits (1) (SERENO et al., 1993).

257. Manual digit I proportions normal, with functional phalanges (0), or digit reduced to sub-conical, blocky metacarpal that lacks distal articular condyles and phalanges (1) (TYKOSKI, 2005).

258. Metacarpal IV subequal to metacarpal III (0), or much smaller than metacarpal III (1) or absent (2) (GAUTHIER, 1986; ordered).

1.2. Data Matrix Table 1

Coelophysis	1 2 1 1 0	1 1 1 1 1	1 1 1 1 1	? 1 1 0 1	1 1 1 0 1	1 0 1 0 1	1 0 1 1 ?	1 1 0 1 ?	1 1 0 0 1	0 1 2 0 1
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	0 0 1 1 1	0 0 0 0 0	? 0 1 0 0	1 1 0 0 0	0 0 0 0 1	1 1 2 0 1	0 0 0 1 0	1 0 0 1 1	1 1 1 1 1	1 2 2 0 0
	1 0 ? 0 ?	0 1 0 1 2	1 1 1 1 0	1 1 1 1 0	? 0 0 1 0	1 1 0 0&1 0&1	1 0 1 1 0	1 1 1 1 1	0 0 1 0 0	1 1 1 1 1
	1 1 0 0 0	1 0 1								
Coelopysis	1 2 1 1 0	1 1 1 1 1	1 1 1 1 1	0 1 1 0 1	1 1 1 1 1	1 0 1 0 1	1 0 1 ? 1	1 1 0 1 0	1 1 0 0 1	0 1 2 0 1
rhodesiensis	1 1 1 1 0	0 0 0 0 0	1 ? 1 0 0	0 1 1 2 0	0 0 0 0 ?	0 2 0 ? ?	1 0 0 ? 0	1 1 1 1 2	0 ? 1 1 2	0 0 1 1 1
	2 0 0 0 1	1 0 0 0 0	1 1 1 1 2	2 0 0 1 0	0 1 1 0 1	0 0 1 1 0	1 ? 1 2 0	0 0 1 0 0	0 0 1 0 2	0 1 1 0 0
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	1 1 0 0 0	1 0 1								
Dilophosaurus	1 2 1 2 1	1 1 1 1 1	1 0 2 1 1	1 0 0 1 0	0 0 1 0 0	0 0&1 ? 0 0&1	? 0 0 2 2	0 1 1 0 0	0 0 0 ? 0	1 0 2 1 0
wetherilli	0 0 0 ? 1	1 1 0 0 1	1 1 0 0 1	0 1 0 2 0	0 0 0 0 1	0 0 0 0 0	0 0 0 0 ?	2 1 0 0 2	1 0 ? 0 1	0 3 1 1 ?
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	0 1 0 0 0	0 0 0 1 2	1 1 0 1 1	1 1 1 0 0	0 0 0 0 1	0 0 0 0 0	0 0 0 0 0	0 0 0 0 0	0 0 0 0 0	0 0 0 0 0
	0 1 0 0 0	1 1 1								
Liliensternus	? ? ? ? ?	? ? ? ? ?	? 0 ? ? 1	? ? ? 1 ?	1 1 ? ? ?	? ? ? ? ?	? ? 0 ? 1	? ? 0 0 0	? ? ? ? ?	1 ? ? ? 0
liliensterni	? ? ? 1 ?	? ? 0 ? ?	1 1 ? ? ?	? 1 1 1 ?	? ? ? ? 0	0 1 0 1 1	? 0 1 0 0	1 1 0 1 2	0 0 ? 0 1	0 0 1 1 ?
	? ? 0 0 1	1 0 0 0 0	1 ? ? ? ?	? 0 0 0 0	0 1 1 0&1 0	0 1 ? 2 ?	? ? ? 2 0	0 0 0 ? 0	0 ? 0 0 1	0 0 1 0 0
	0 ? ? 1 1	0 1 1 0 ?	? ? 1 0 0	? ? ? 0 0	0 0 0 0 ?	? 1 0 0 1	0 0 0 1 0	1 0 0 ? ?	1 ? ? ? 1	? ? ? 0 ?
	? 1 ? ? ?	? 1 0 1 ?	? ? ? ? 0	? ? ? ? ?	0 0 ? ? 1	0 1 0 0 1	1 0 1 1 0	1 1 0 1 1	0 0 1 0 0	? ? ? 0 1
	? 1 0 0 0	1 ? ?								
Lophostropheus	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?
airelensis	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?	? ? ? 2 ?	? ? ? ? ?	1 1 ? 1 1&2	? ? 1 0 0	1 1 ? 1 2	0 ? ? ? 1	0 ? 1 ? ?
	? ? ? ? 1	1 0 ? ? ?	0&1 ? ? ? ?	? ? ? 0 ?	0 1 1 ? ?	0 ? ? 0 1	? ? ? 2 ?	? ? ? ? ?	0 ? ? ? 0	1 0 ? 0 0
	0 ? ? 2 ?	? ? ? ? ?	? ? ? 1 0	? ? ? ? ?	? ? ? ? ?	? ? ? 0 ?	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?
	? ? ? ? ?	? 1 0 1 ?	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?
	? ? ? ? ?	? ? ?								
Procompsognathus	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?
triassicus	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?	0 ? ? ? ?	? ? ? ? ?	1 2 1 1 ?	? ? ? 1 2	0 ? 1 1 ?
	? ? ? ? ?	? ? ? ? ?	0&1 ? ? ? ?	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?
	? ? ? ? ?	? ? ? 0 ?	? ? ? 0 0	? ? ? 0 0	? ? 0 ? ?	? ? ? ? ?	? ? ? ? ?	? 0 ? ? ?	? ? ? ? ?	? ? ? 0 ?
	? 0 ? 0 ?	? ? ? ? ?	? ? ? ? ?	1 1 ? ? ?	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?
	? ? ? ? ?	? ? ?								
Segisaurus	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?
halli	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?	? ? 0 ? ?	? ? ? ? 2
	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?	? 1 1 ? ?	0 1 1 0 1	? ? 1 2 ?	? ? ? 2 ?	0 ? 0 ? 0	? 1 ? ? ?
	? ? ? ? 0	0 0 0 ? ?	? ? 0 0 0	1 1 1 0 1	0 0 0 1 1	? 1 2 ? 1	? ? 0 1 0	1 ? ? ? ?	? ? ? ? ?	? ? ? ? ?
	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?	0 0 ? ? 0	? ? ? ? ?	? ? 1 ? ?	? ? ? ? ?	? ? ? ? ?	? ? 1 ? ?
	1 1 1 ? 0	? ? ?								
Swiss theropod	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?
material	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?	? ? 1 1 2	0 1 1 1 0
	1 2 0 1 1	? ? 0 0 0	1 ? 1 ? ?	? 0 1 1 2	1 1 0 ? 1	1 1 0 0 1	2 1 ? 2 ?	0 0 1 2 0	0 0 1 0 2	0 0 1 0 0
	0 0 ? ? 1	? 1 2 0 0	0 1 1 0 0	1 ? 0 0 1	0 0 0 0 1	0 1 1 ? ?	0 0 0 1 0	1 ? 0 1 ?	1 0 1 1 1	1 2 2 0 0
	1 0 1 0 0	0 ? 1 ? ?	1 1 ? 1 1	? 1 1 1 ?	0 0 0 ? ?	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?	? ? ? ? ?
	? 1 1 0 0	1 0 1								
Syntarsus	1 2 1 1 1	? 1 1 1 1	1 1 1 1 1	0 1 1 1 0	1 1 1 1 0	1 0 1 1 1	2 0 1 1 1	0 1 1 0 0	1 1 1 0 1	1 1 0 0 1
kayentakatae	1 1 1 1 1	0 1 1 0 0	1 0 0 0 1	0 1 1 2 1	0 0 0 0 ?	0 2 0 0 2	1 0 0 ? ?	2 1 1 1 2	0 0 1 ? ?	? ? ? 1 0
	? ? ? ? 1	? ? ? ? ?	1 1 ? 1 ?	2 0 0 ? 0	1 1 1 ? 1	? ? ? ? ?	? ? 1 2 ?	? ? ? ? 0	? ? ? ? ?	? ? ? ? ?
	? 0 ? 2 1	1 0 0 0 0	? ? 0 0 0	? 1 0 0 1	0 0 0 0 1	? 1 1 0 1	0 0 ? ? ?	1 0 ? ? ?	? ? ? ? ?	1 2 ? 0 0
	? 0 1 0 0	0 ? ? ? ?	? ? ? 1 0	? 1 ? ? 0	0 0 0 ? 1	1 1 0 1 1	2 0 1 1 0	1 2 1 1 1	0 0 1 0 1	1 1 1 1 1
	1 1 1 0 ?	1 ? 1								

Table 1: shows all the character states of the examined theropods.

11.1.3. Missing data per all informative characters (81):

Coelophysis bauri	4.9%
Coelophysis rhodesiensis	7.4%
Dilophosaurus wetherilli	2.5%
Herrerasaurus ischigualastensis	1.2%
Liliensternus liliensterni	33.3%
Lophostropeus airelensis	79.0%
Procompsognathus triassicus	93.1%
Segisaurus halli	77.8%
Swiss theropod material	64.2%
Syntarsus kayentakatae	27.3%

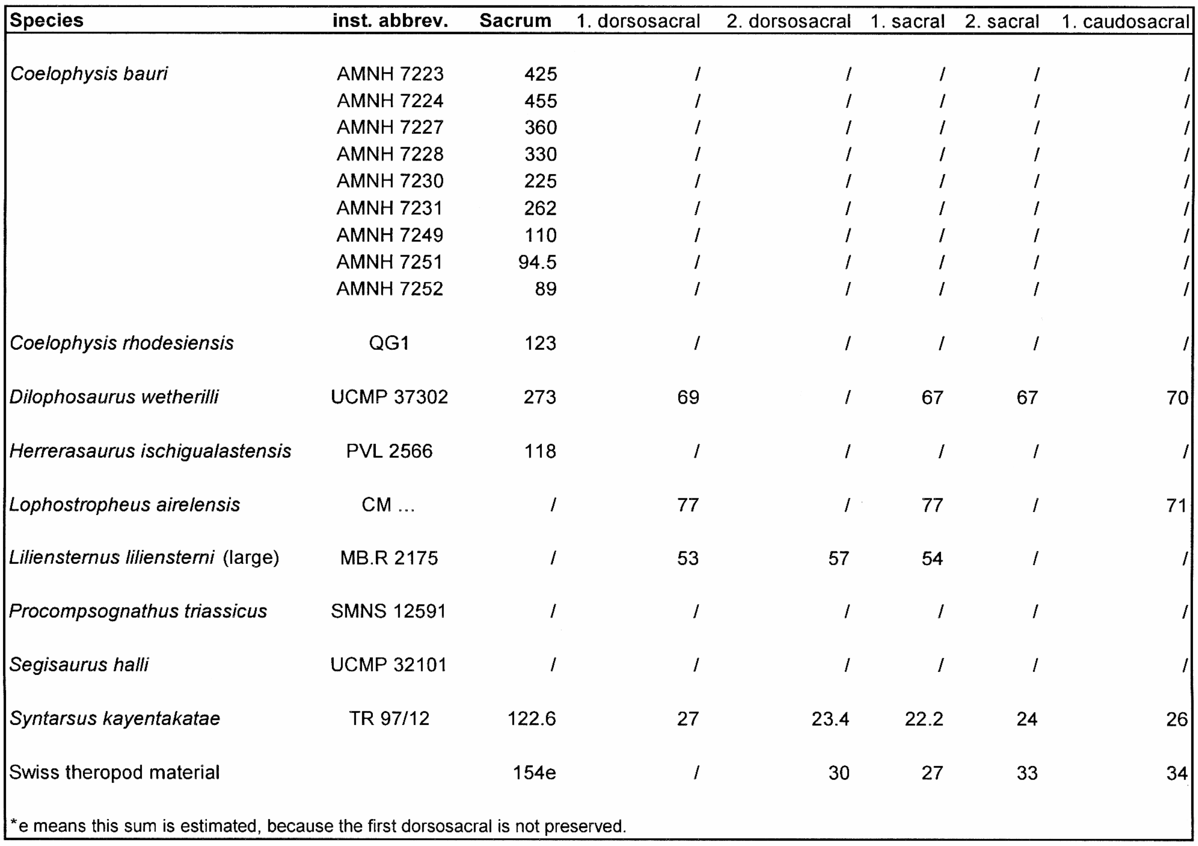
11.2. Measurements

The measurements given in the tables do conclude information about all examined theropods giving only information on the particular skeletal region regarding the existence of the Swiss theropod material. However, the data is often not complete due to missing elements in the other nine theropods. If there are elements twice available (ilia, pubes, and ischia), only the ones which have not been tampered by diagenesis are noted in the table.

All measurements regarding *Coelophysis bauri* are copied from COLBERT 1989; the data of *C. rhodesiensis* comes from RAATH 1969 and 1977; the information about *Syntarsus kayentakatae* is the same as in the studies of ROWE 1989, as well as TYKOSKI 1998. *Liliensternus liliensterni* has been documented by HUENE 1934a, *Lophostropeus airelensis* by CUNY & GALTON 1993, *Dilophosaurus wetherilli* by WELLES 1984, and *Herrerasaurus ischigualastensis* by NOVAS 1993. The measurement data of *Procompsognathus triassicus* and *Segisaurus halli* still is extensively incomplete, because I was not able to get any valuable information.

Species	**inst. abbrev.**	**1. dorsal**	**2. dorsal**	**3. dorsal**	**4. dorsal**	**5. dorsal**	**6. dorsal**	**7. dorsal**	**8. dorsal**	**9. dorsal**	**10. dorsal**	**11. dorsal**
Coelophysis bauri	AMNH 7224	37	36	32	32.5	33	34	35	36.5	38	37.5	38.5
	AMNH 7230	16	14	14	14	16.5	16	17	20	21	18.5	/
Coelophysis rhodesiensis	QG1	/	/	/	/	/	28	29	29	29	32	31
Dilophosaurus wetherilli	UCMP 37302	74	70	78	84	82	88e	87	90	70	70	/
Herrerasaurus ischigualastensis	PVL 2566	/	/	/	/	/	/	50	45	45	45	45
Liliensternus liliensterni (large)	MB.R 2175	70	/	/	/	/	/	/	/	/	/	/
Liliensternus liliensterni (small)	MB.R 2175	/	56	50	/	/	/	/	/	/	/	/
Lophostropheus airelensis	CM …	/	/		/	/	/	/	/	/	/	?75
Procompsognathus triassicus	SMNS 12591											
Segisaurus halli	UCMP 32101											
Syntarsus kayentakatae		/	/	/	/	/	/	/	/	/	/	/
Swiss theropod material		/	31	33	/	36	36	35	38	/	42	/

Table 2: measurement of dorsal vertebrae of the examined theropods.



Species	inst. abbrev.	Sacrum	1. dorsosacral	2. dorsosacral	1. sacral	2. sacral	1. caudosacral
Coelophysis bauri	AMNH 7223	425	/	/	/	/	/
	AMNH 7224	455	/	/	/	/	/
	AMNH 7227	360	/	/	/	/	/
	AMNH 7228	330	/	/	/	/	/
	AMNH 7230	225	/	/	/	/	/
	AMNH 7231	262	/	/	/	/	/
	AMNH 7249	110	/	/	/	/	/
	AMNH 7251	94.5	/	/	/	/	/
	AMNH 7252	89	/	/	/	/	/
Coelophysis rhodesiensis	QG1	123	/	/	/	/	/
Dilophosaurus wetherilli	UCMP 37302	273	69	/	67	67	70
Herrerasaurus ischigualastensis	PVL 2566	118	/	/	/	/	/
Lophostropheus airelensis	CM ...	/	77	/	77	/	71
Liliensternus liliensterni (large)	MB.R 2175	/	53	57	54	/	/
Procompsognathus triassicus	SMNS 12591	/	/	/	/	/	/
Segisaurus halli	UCMP 32101	/	/	/	/	/	/
Syntarsus kayentakatae	TR 97/12	122.6	27	23.4	22.2	24	26
Swiss theropod material		154e	/	30	27	33	34

*e means this sum is estimated, because the first dorsosacral is not preserved.

Table 3: measurements of sacral vertebrae of the examined theropods.

Species	inst. abbrev.	1. caudal	2. caudal	3. caudal	4. caudal
Coelophysis bauri	AMNH 7223	28	30	31	32
	AMNH 7224	28	30	32	31
Dilophosaurus wetherilli	UCMP 37302	70	73	77	/
Herrerasaurus ischigualastensis	PVL 2566	49	45	42	47
Lophostropheus airelensis	CM …	67	/	70	/
Liliensternus liliensterni (small)	MB.R 2175	49	51	51	50
Procompsognathus triassicus	SMNS 12591				
Segisaurus halli	UCMP 32101				
Syntarsus rhodesiensis	QG1	24.5	/	/	/
	QG445	27.5	28	27	28
Syntarsus kayentakatae		/	/	/	/
Swiss theropod material		28	31	31	33

Table 4: measurements of caudal vertebrae of the examined theropods.

Table 5: measurements of the pelvic region of the examined theropods.

Species	inst. abbrev.	Ilium	Pubis	Ischium
Coelophysis bauri	AMNH 7224	155	233	142
	TM 84-63-33	100.3	147.7	111.6
Coelophysis rhodesiensis	QG1	148	204	130
Dilophosaurus wetherilli	UCMP 37302	370	485	340
Herrerasaurus ischigualastensis	PVL 2566	240	430	330e
Lophostropheus airelensis	CM …	/	/	/
Liliensternus liliensterni (small)	MB.R 2175	270	410	270
Procompsognathus triassicus	SMNS 12591			
Segisaurus halli	UCMP 32101			
Syntarsus kayentakatae	TR 97/12	/	232	151.5
Swiss theropod material		180	256	180

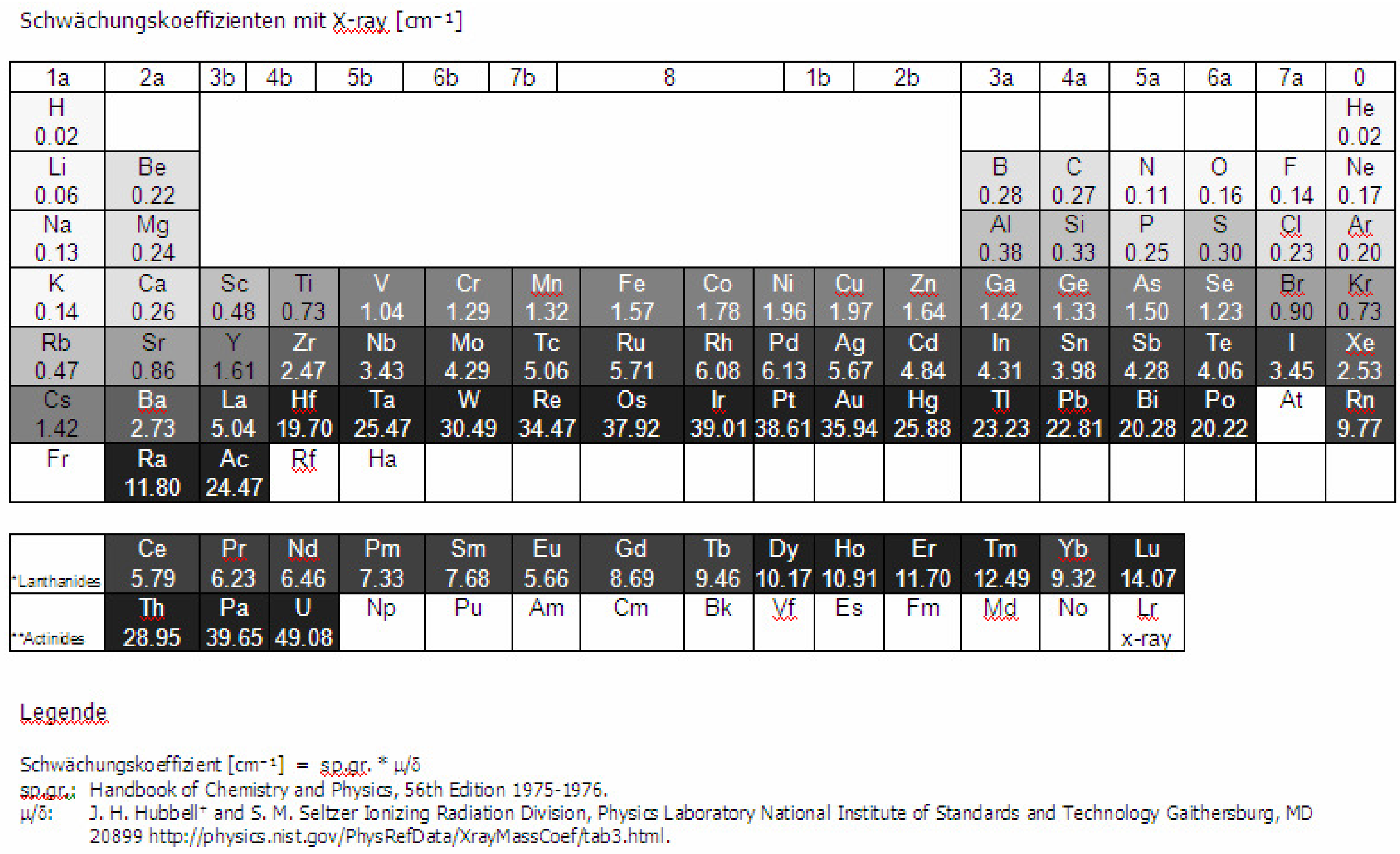
11.3. Completion to chronological and geographical distribution Table 6

specimen	locality	formation	time	material	literature
Syntarsus sp.	Southern Colorado Plateau, USA	Moenave Formation	Hettangian	?body fossil	Lucas 2005
Syntarsus sp.	St. George, Utah, USA	Moenave Formation	Hettangian	approximately 3000 individual claw marks, mostly in sets of three, represent many small swimming theropod dinosaurs. Size ranges and morphology are consistent with the Early Jurassic theropod *Megapnosaurus* (formerly *Syntarsus*) or a *Megapnosaurus*-like dinosaur	Milner 2005
Syntarsus sp.	Arizona, USA	Moenave Formation	?Hettangian	two theropod dinosaur incomplete pelvic regions	Lucas & Heckert 2001
Syntarsus sp.	Huizachal Canyon in Tamaulipas, Mexico, USA	La Boca Formation	?Hettangian	an articulated pelvis and sacrum, and two fragments from the posterior portion of a skull	Munter 1999
Syntarsus kayentakatae	Arizona, USA	Kayenta Formation	Sinemurian to Middle Pliensbachian	one articulated skull and postcranial skeleton (adult), two fragmentary skeletons, one incomplete skeleton	Rowe 1989; Tykoski 1998
Coelophysis rhodesiensis	Zimbabwe, South Africa	Forest Sandstone Formation	Hettangian to ?Sinemurian	so far, there are three localities in the Forest Sandstone which yielded over 30 individuals (fragmentary to almost complete specimens	Raath 1969, 1977, 1990; Munyikwa & Raath 1999
?Syntarsus sp.	Southern Isle of Skye, Scotland, UK	Broadford Beds Formation	Hettangian	partial tibia(→ not precisely determined taxa, but this element conforms to the distal tibiae of coelophysoid taxa such as *Coelophysis, Syntarsus, Liliensternus.* The present specimen is more similar in size to the tibia of *Coelophysis bauri*	Colbert 1989; Benton et al. 1995; Clark 2005
Syntarsus sp.	South Glamorgan, Wales, UK	Pant-y-ffynnon fissure filling	?Norian	articulated left pelvic girdle, including parts of the sacrum, the posteriomost dorsal vertebrae and an associated left femur	Hungerbühler & Rauhut 1998
Coelophysis bauri	New Mexico and Arizona, USA	Chinle Formation/Rock Formation and Chinle Formation/Petrified Forest Formation	Late Carnian to Late Norian	several hundred individuals ranging from juveniles to adults, including nearly complete skeletons	Cope 1887, 1889; Colbert 1964, 1989, 1990
?Coelophysis sp.	Southern Isle of Skye, Scotland, UK	Broadford Beds Formation	Hettangian	one caudal vertebra of a small theropod dinosaur, that appears indistinguishable from *Coelophysis.* *	Clark 2005
Syntarsus sp.	Yunnan Province, China	Lufeng Formation	Lower Jurassic	distal humerus, proximal radius and ulna, fragments of metacarpals and phalanges; right distal tarsals II and III and proximal metatarsals II and III.	Irmis 2005

Table 6: all the known and published *Coelophysis* and *Syntarsus sp.* are displayed in this table, for complement to figure 38 in «9.5. Excursus D: geographical and chronological distribution of the Coelophysidae».

11.4. Investigations at the PSI

11.4.1. Attenuation coefficient of every element Table 7 & 8



Schwächungskoeffizienten mit X-ray [cm⁻¹]

1a	2a	3b	4b	5b	6b	7b	8			1b	2b	3a	4a	5a	6a	7a	0
H 0.02																	He 0.02
Li 0.06	Be 0.22											B 0.28	C 0.27	N 0.11	O 0.16	F 0.14	Ne 0.17
Na 0.13	Mg 0.24											Al 0.38	Si 0.33	P 0.25	S 0.30	Cl 0.23	Ar 0.20
K 0.14	Ca 0.26	Sc 0.48	Ti 0.73	V 1.04	Cr 1.29	Mn 1.32	Fe 1.57	Co 1.78	Ni 1.96	Cu 1.97	Zn 1.64	Ga 1.42	Ge 1.33	As 1.50	Se 1.23	Br 0.90	Kr 0.73
Rb 0.47	Sr 0.86	Y 1.61	Zr 2.47	Nb 3.43	Mo 4.29	Tc 5.06	Ru 5.71	Rh 6.08	Pd 6.13	Ag 5.67	Cd 4.84	In 4.31	Sn 3.98	Sb 4.28	Te 4.06	I 3.45	Xe 2.53
Cs 1.42	Ba 2.73	La 5.04	Hf 19.70	Ta 25.47	W 30.49	Re 34.47	Os 37.92	Ir 39.01	Pt 38.61	Au 35.94	Hg 25.88	Tl 23.23	Pb 22.81	Bi 20.28	Po 20.22	At	Rn 9.77
Fr	Ra 11.80	Ac 24.47	Rf	Ha													

*Lanthanides	Ce 5.79	Pr 6.23	Nd 6.46	Pm 7.33	Sm 7.68	Eu 5.66	Gd 8.69	Tb 9.46	Dy 10.17	Ho 10.91	Er 11.70	Tm 12.49	Yb 9.32	Lu 14.07
**Actinides	Th 28.95	Pa 39.65	U 49.08	Np	Pu	Am	Cm	Bk	Vf	Es	Fm	Md	No	Lr x-ray

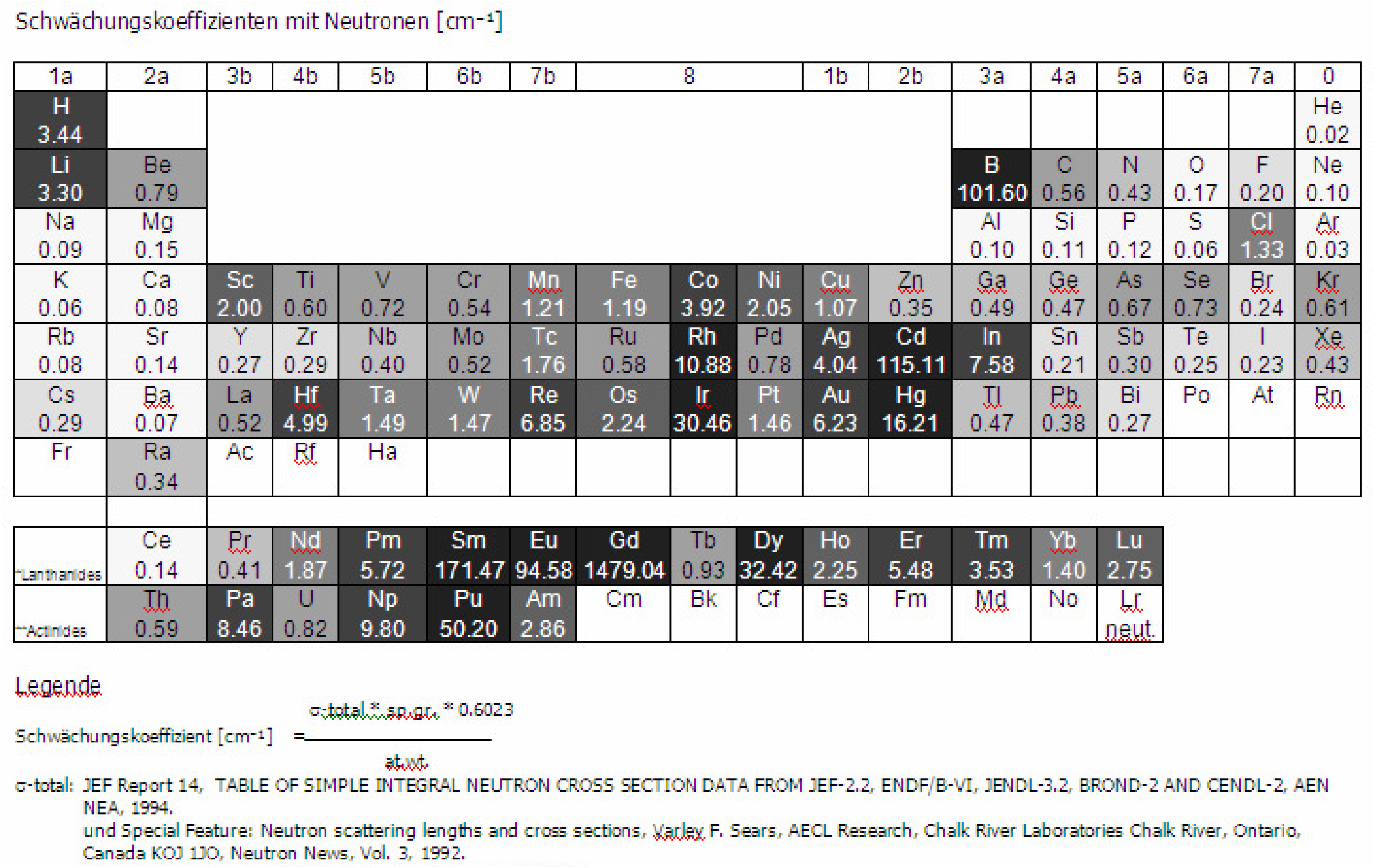
Legende

Schwächungskoeffizient [cm⁻¹] = sp.gr. * μ/δ

sp.gr.: Handbook of Chemistry and Physics, 56th Edition 1975-1976.

μ/δ: J. H. Hubbell⁺ and S. M. Seltzer Ionizing Radiation Division, Physics Laboratory National Institute of Standards and Technology Gaithersburg, MD 20899 http://physics.nist.gov/PhysRefData/XrayMassCoef/tab3.html.

Table 7: the elements with their attenuation coefficient when used on x-rays (Neutron Imaging and Activation Group (NIAG): Neutron Imaging an der Spallations-Neutronenquelle SINQ, Brochure of the Paul Scherrer Institute, Villigen 2006).



Schwächungskoeffizienten mit Neutronen [cm^{-1}]

1a	2a	3b	4b	5b	6b	7b	8			1b	2b	3a	4a	5a	6a	7a	0
H 3.44																	He 0.02
Li 3.30	Be 0.79											B 101.60	C 0.56	N 0.43	O 0.17	F 0.20	Ne 0.10
Na 0.09	Mg 0.15											Al 0.10	Si 0.11	P 0.12	S 0.06	Cl 1.33	Ar 0.03
K 0.06	Ca 0.08	Sc 2.00	Ti 0.60	V 0.72	Cr 0.54	Mn 1.21	Fe 1.19	Co 3.92	Ni 2.05	Cu 1.07	Zn 0.35	Ga 0.49	Ge 0.47	As 0.67	Se 0.73	Br 0.24	Kr 0.61
Rb 0.08	Sr 0.14	Y 0.27	Zr 0.29	Nb 0.40	Mo 0.52	Tc 1.76	Ru 0.58	Rh 10.88	Pd 0.78	Ag 4.04	Cd 115.11	In 7.58	Sn 0.21	Sb 0.30	Te 0.25	I 0.23	Xe 0.43
Cs 0.29	Ba 0.07	La 0.52	Hf 4.99	Ta 1.49	W 1.47	Re 6.85	Os 2.24	Ir 30.46	Pt 1.46	Au 6.23	Hg 16.21	Tl 0.47	Pb 0.38	Bi 0.27	Po	At	Rn
Fr	Ra 0.34	Ac	Rf	Ha													

*Lanthanides	Ce 0.14	Pr 0.41	Nd 1.87	Pm 5.72	Sm 171.47	Eu 94.58	Gd 1479.04	Tb 0.93	Dy 32.42	Ho 2.25	Er 5.48	Tm 3.53	Yb 1.40	Lu 2.75
**Actinides	Th 0.59	Pa 8.46	U 0.82	Np 9.80	Pu 50.20	Am 2.86	Cm	Bk	Cf	Es	Fm	Md	No	Lr neut.

Legende

$$\text{Schwächungskoeffizient } [cm^{-1}] = \frac{\sigma\text{-total} * \text{sp.gr.} * 0.6023}{\text{at.wt.}}$$

σ-total: JEF Report 14, TABLE OF SIMPLE INTEGRAL NEUTRON CROSS SECTION DATA FROM JEF-2.2, ENDF/B-VI, JENDL-3.2, BROND-2 AND CENDL-2, AEN NEA, 1994.
und Special Feature: Neutron scattering lengths and cross sections, Varley F. Sears, AECL Research, Chalk River Laboratories Chalk River, Ontario, Canada KOJ 1JO, Neutron News, Vol. 3, 1992.

Table 8: the elements with their attenuation coefficient when used on neutrons (Neutron Imaging and Activation Group (NIAG): Neutron Imaging an der Spallations-Neutronenquelle SINQ, Brochure of the Paul Scherrer Institute, Villigen 2006).

11.4.2. Neutron computer tomography of PSI

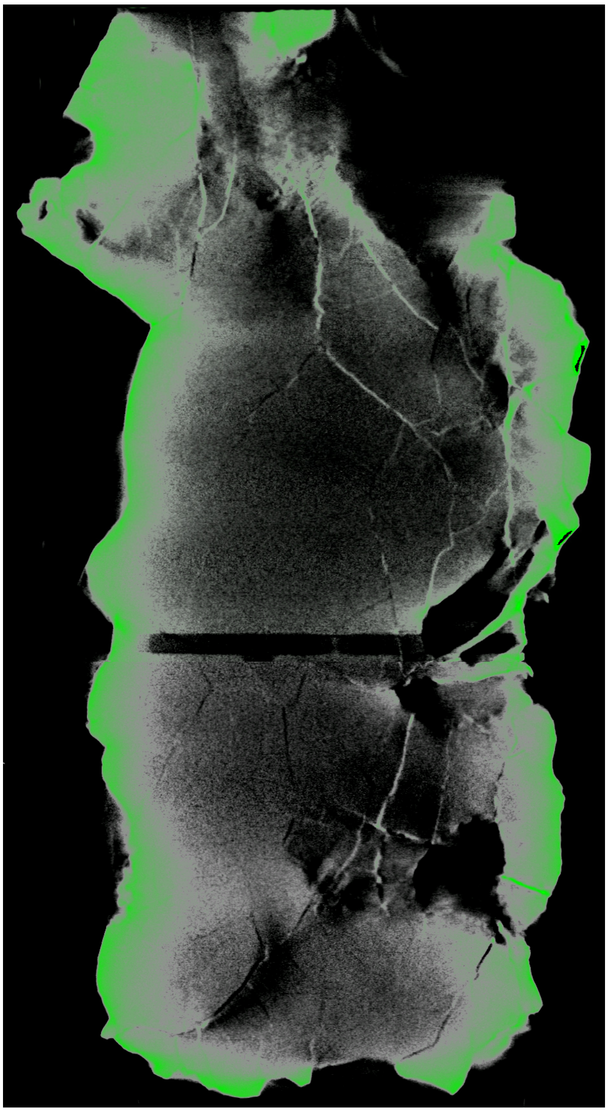


Figure 39: computer tomography based on neutrons invesitigated at the PSI. The green coloured areas point up the depth of penetration of the acrylic resin and varnish which had been used during preparation.

11.5. Sexual Dimorphism in *Tyrannosaurus rex*

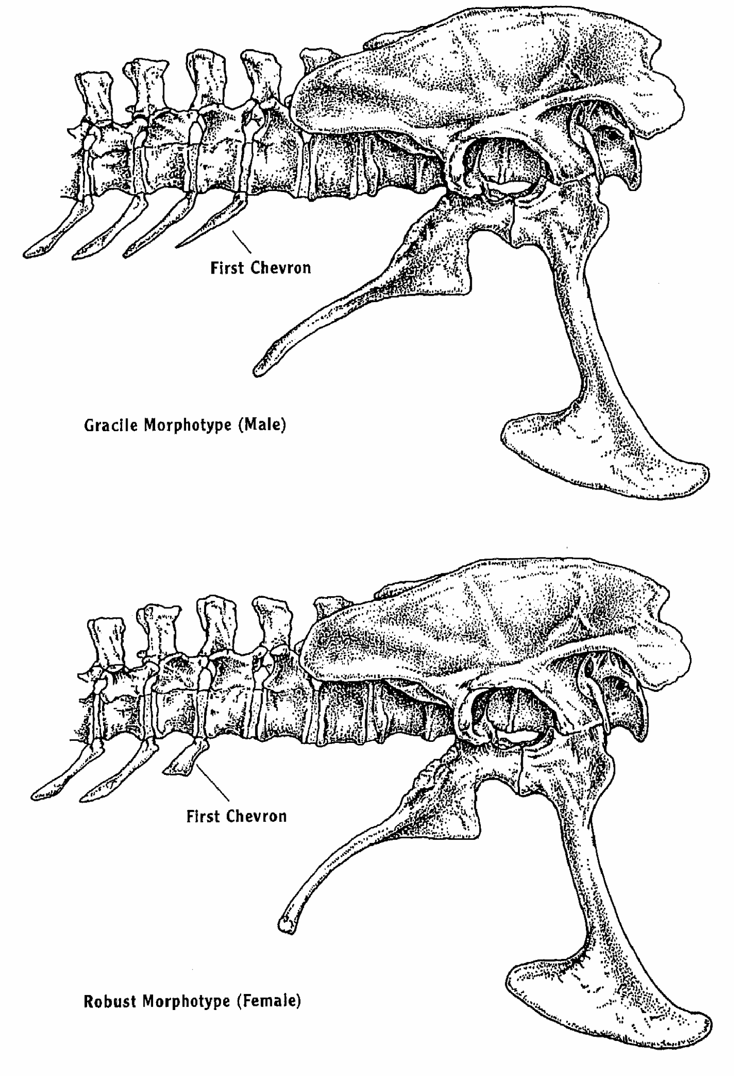


Figure 40: Larson (1995) pictured this figure in his work 'how to sex a rex'. He claimed to distinguish the sexes of *Tyrannosaurus rex* on the basis of skeletal characteristics. Here, the right lateral view of the pelvis and the subsequent anterior right caudal vertebrae are illustrated. The size and the shape of the first chevron indicate whether it is a male (gracile morphotype) or a female (robust morphotype).

11.6. Portrait of the Swiss theropod

Figure 41: represents the possible look of the Swiss theropod; the body is as formed as seen in reconstructions of *Coelophysis bauri*. In addition, the Swiss theropod wears a crest on its head as it is known from *Syntarsus kayentakatae*.

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