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PELVIC GIRDLE MORPHOLOGY IN *STAGONOLEPIS*, WITH REMARKS ON AETOSAUR SYSTEMATICS

Hilde G. B. DESMET [1*], **Mateusz ANTCZAK** [2] **& Adam BODZIOCH** [2]

[1] *European Centre of Palaeontology, University of Opole, ul. Oleska 48, 45-052 Opole, Poland; e-mail: desmethilde@telenet.be*

[2] *Institute of Biology, Laboratory of Palaeobiology, University of Opole, ul. Oleska 22, 45-052 Opole, Poland*

** Corresponding author*

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Abstract: In recent years, the Upper Triassic deposits at Krasiejów (south-west Poland) have yielded several tetrapod taxa, both aquatic and terrestrial. *Stagonolepis olenkae* is one of the terrestrial vertebrates recovered there; a quadrupedal, armoured aetosaur, which belonged to the crocodile-line archosaurs with a characteristic shovel-shaped snout. Several previous studies (osteological, histological and taphonomic) have attempted to understand the mode of life, growth pattern and possible dimorphism of this species and on this basis, to interpret palaeoecological, palaeoclimatic and stratigraphical implications. So far, the pelvic girdle of *S. olenkae* from Krasiejów remained undescribed. Here, the authors record stagonolepid ilia and pubes and a single ischium from collections housed at the University of Opole, and compare these with the pelvic girdles of other aetosaurian taxa. These well-preserved bones have a typical aetosaurian general outline, but also show some peculiar features. For instance, the preacetabular blade of the ilium is short and flattened and does not exceed the pubic peduncle; several small foramina occur dorsally of the supracetabular crest; the number of pubic foramina is two and the pubic symphysis is less than half the length of the pubis. The material is similar to previously known *Stagonolepis robertsoni* from the Elgin area, except for the length of the symphysis. The bones presented here differ between each other in thickness, morphology of the preacetabular blade or attachment of sacral ribs, which may be connected with sexual dimorphism. The pelvic girdle of most aetosaurs is not well known. This is unfortunate, because it is an important element in the study of the evolution of the pelvic girdle and in phylogenetic analyses. Thus, the ilia, pubes and ischium of the present study are valuable examples that may contribute to the discussion of the ontogeny and sexual dimorphism in *Stagonolepis*, as well as to our general knowledge of the Aetosauria.

Key words: Pelvis, ilium, pubis, ischium, Aetosauria, Krasiejów, Upper Triassic.

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INTRODUCTION

Aetosaurs were quadrupedal, fully terrestrial, heavily armoured pseudosuchians that experienced a radiation during the Late Triassic. Their length varied between 1 and 6 m; their limbs were well-developed and the small skull had a shovel-shaped snout (Walker, 1961; Heckert and Lucas, 2000; Desojo *et al*., 2013). Surface ornament, width/length ratios and lateral osteoderm morphology are diagnostic for aetosaurian clades and in some cases, for species (Parker, 2018b). The diagnostic osteoderm morphology has allowed differential diagnoses of several taxa, but species cannot be distinguished solely on the basis of isolated osteoderms (Brust *et al*., 2018; Marsh *et al*., 2020; Czepiński *et al*., 2021).

To date, 30 species of Aetosauria have been described (Brust *et al*., 2018). There are different versions of the phylogenetic trees of aetosaurians, but additional work aimed at clarifying various issues is ongoing. It has been suggested that *Aetosauroides scagliai* is the most basal aetosaur and sister-taxon to all other members of the Aetosauria (Desojo *et al*., 2013; Parker, 2016a; Brust *et al*., 2018).

Aetosaur material has been recorded from Europe, North and South America, Greenland, Morocco and India (Desojo *et al*., 2013; Roberto-da-Silva *et al*., 2014; Parker, 2016a). The presence of these reptiles in South Africa has not yet been confirmed; to date, only footprints (ichnogenus *Brachychirotherium*) have been documented. These may be assigned to Aetosauria (Heckert *et al*., 2010; Lucas and Heckert, 2011; Desojo *et al*., 2013).

Originally, the aetosaurs were considered to have been herbivorous, but there are numerous indications that, in fact, they were omnivorous (Small, 2002; Sulej, 2010). Except for *Aetosaurus ferratus* (Schoch, 2007) and *Stenomyti huangae* (Small and Martz, 2013), the morphology of the shovel-shaped snout indicates that this was used to scratch or dig in the soil to look for roots, insects and small vertebrates (Heckert *et al*., 2010). Examination of the limbs (including, for instance, the short forearm, the radius that is shorter than the humerus, and claw-like fingertips), provides additional arguments for considering these animals to have been adapted for rooting, or even scratching and digging (Heckert *et al*., 2010; Dróżdż, 2018). Studies of jaw biomechanics (Desojo and Vizcaino, 2009) and of the well-developed sense of smell (i.e. large olfactory tracts and bulbs; Sulej, 2010; Antczak, 2016; von Baczko *et al*., 2021) have also indicated that insectivory could have been possible.

Stagonolepis attained overall lengths of up to 3 m (Walker, 1961), with its back, sides, belly and limbs covered with characteristically ornamented osteoderms and with a typical aetosaurian shovel-shaped snout. This upturned premaxillary tip is very prominent in *Stagonolepis* according to Brust *et al*. (2018). *Stagonolepis robertsoni*, found in the neighbourhood of Elgin, Scotland, was the first aetosaur to be described. Some other aetosaur species previously have been assigned to *Stagonolepis*, including *Calyptosuchus wellesi* and *Aetosauroides scagliai* (Parker, 2018b). Sulej (2010) described a new species, *Stagonolepis olenkae*, from Krasiejów, mainly on the basis of cranial material. However, there is still discussion about the status of this form (see Parker, 2016a). In-depth studies by Lucas *et al*. (2007), who considered the original postcranial material, and by Antczak (2016), who evaluated new cranial material, have shown that the differences listed by Sulej (2010) are very small and that *S. olenkae* is in fact synonymous with *S. robertsoni* Agassiz, 1844 from northern Scotland. Also, assigning the postcranial material to the taxa erected on the basis of cranial features is problematic, as stated by e.g., Górnicki *et al*. (2021).

There are several papers on this species from Krasiejów (Lucas *et al*., 2007; Sulej, 2010; Antczak, 2016; Dróżdż, 2018; Górnicki *et al*., 2021), but none of them included a description of the pelvic girdle. The skull, osteoderms and forelimb are better known. The present work offers the first description of the ilium, pubis and ischium of *Stagonolepis* from Krasiejów, on the basis of disarticulated bones of an aetosaur pelvic girdle, contained in the University of Opole collections, that could be assigned to this genus. The main aim of this project was to describe and measure the bones in detail. During this comprehensive study, new features were recognised. A second aspect of this analysis is a comparison of the ilia, pubes and ischium of *Stagonolepis* with the pelvic girdle of other aetosaurs. Resemblances and differences found are described here.

Pelvic girdles have undergone great modifications during the evolution from fish to reptile, with the modifications of reptilian pelves reflecting the change of posture. The orientation of the ilium changed from vertical (sprawling gait), via oblique (semi-erect gait) to horizontal (erect gait) (Rasskin-Gutman and Buscalioni, 2001; Hogervorst *et al*., 2009). Most pseudosuchians had a semi-erect gait, but some did achieve an erect stance, as is seen also in the 'pillar-like' erect posture of rauisuchians (Iijima and Kobayashi, 2014). In aetosaurians, three pelvic morphologies occur. The acetabular region of the ilium is vertically oriented in *Aetosaurus ferratus*, oblique in *Desmatosuchus spurensis* and horizontal in *Aetosauroides scagliai* (Desojo *et al*., 2013). The modification of the gait and concomitant changes in the morphology of pelvis and limbs took place mainly during the Triassic (Hogervorst *et al*., 2009) and the study of osteology and fossil trackways has led to the conclusion that non-dinosauromorph archosaurs also could have had an erect stance (Kubo and Benton, 2009).

GEOLOGICAL SETTING

All material originates from Krasiejów (Upper Silesia, south-west Poland), 20 km east of Opole (Fig. 1), having been collected from Upper Triassic (Keuper) terrestrial deposits. During the Late Triassic, which was a long stable period, the inland of the supercontinent Pangaea was dry, with deposition of the typical nonmarine reddish beds (Ogg *et al*., 2020), while the margins (such as in Poland at that time) were within the realms of a subtropical climate. Palaeogeographically, present-day Upper Silesia was located in the eastern part of the Germanic Basin, which covered an area that now corresponds to the territory extending from France to Poland (Jewuła *et al*., 2019). The bone-bearing deposits at Krasiejów are dated as Carnian on the basis of faunal correlations with other Upper Triassic sites (Dzik and Sulej, 2007, 2016; Lucas, 2015, 2020), while geological data indicate a Norian age, more precisely the base of that stage (Racki and Szulc, 2015; Szulc *et al*., 2015). Litho-, chemo- and climatostratigraphically, the site of Krasiejów belongs to the lowermost Steinmergelkeuper of the German subdivision (Racki and Szulc, 2015; Szulc *et al*., 2015), which corresponds with the Patoka (Marly Mudstone-Sandstone) Member of the Grabowa Formation and correlates with the Arnstadt Formation in Germany.

The site at Krasiejów comprises two bone beds (Fig. 1), the lower (and richest, 10 m below present soil level) and the upper (2 m below that level). The strata consist of siltstones and claystones, containing thin lenses of very fine-grained sandstones and calcareous concretions (Bodzioch and Kowal-Linka, 2012). The detritus appears to have come from higher-lying areas towards the south-west. The deposits of the lower bone bed show alternations of humid (with monsoon-like rainfall) and dry seasons, indicative of a warm, subtropical climate (Bodzioch and Kowal-Linka, 2012) on the edges of Pangaea. Histological research has also demonstrated that the Krasiejów tetrapods lived in a climate with alternating dry and humid periods. Humid periods are represented by obvious bone growth, while dry periods are marked by reduced growth or even temporary halts in growth (LAG, layers of arrested growth; Teschner and Konietzko-Meier, 2019).

The Krasiejów site has yielded numerous fossils, mainly of tetrapods but also of invertebrates, as well as plants. The origin of the bone accumulations, comprising aquatic, semi-aquatic and terrestrial tetrapods, indicates a freshwater environment (e.g., the edge of a shallow, anastomosing

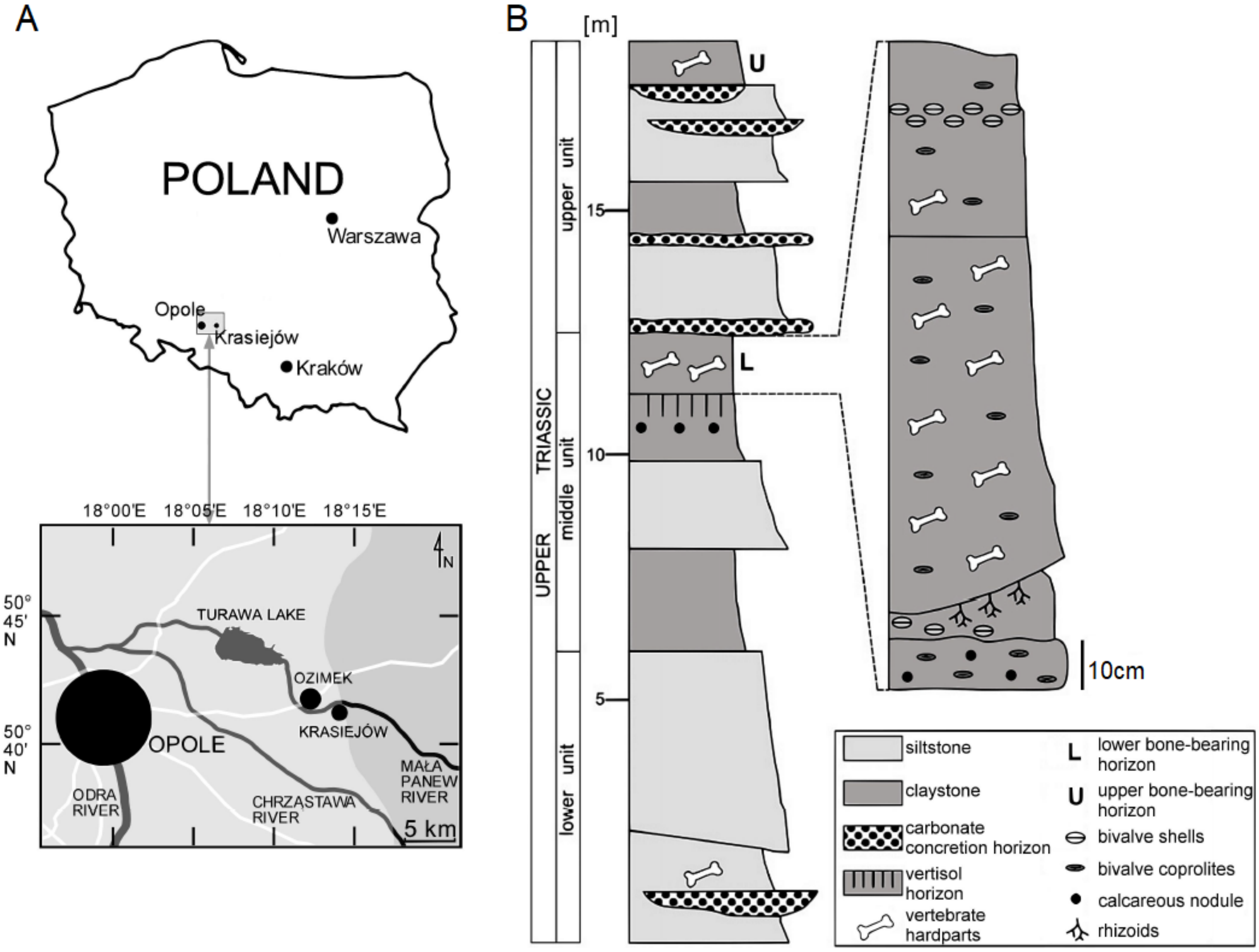

Fig. 1. Location map and investigated section. **A.** Map with the position of the Krasiejów locality in Poland and in Silesia. **B.** Geological section with marked layers containing fossils. L indicates the lower bonebed, where the bones described were found (after Bodzioch and Kowal-Linka, 2012).

river) and event deposition. The bone bed consists of both autochthonous tetrapod remains and bones (already in decay) transported from the surroundings during a high-energy event, such as catastrophic rainfall leading to a flooding event (Bodzioch and Kowal-Linka, 2012). This explains why no complete skeletons occur and why so many bones can be found (Gruntmejer *et al*., 2015). Other authors, e.g., Jewuła *et al*. (2019) have confirmed the climatic seasonality, reflected in the alternation of well-developed vertisols and flood-related deposits. Dzik and Sulej (2007, 2016) suggest that the lower bone-bearing horizon is of lake origin.

MATERIAL AND METHODS

Four ilia, two pubes and a single ischium from the collections of the University of Opole, Institute of Biology, Laboratory of Palaeobiology, have been studied (Tab. 1). In August 2019, one right ilium (UOPB01141), together with two pubes were found, a right (UOPB01143) and a left one (UOPB01144). These 3 bones, found articulated, originate from the lower bone bed in Upper Triassic deposits at Krasiejów. The other 4 bones are isolated bones from various places in the lower bone bed, the horizontal range of all bones being 20 m, the vertical one 60 cm. The lowest finds sit in blue-grey claystone, the higher ones are embedded in reddish claystone with more compact calcareous concretion. The ilia are more or less complete, with the exception of UOPB00149, which lacks the preacetabular blade,

Table 1

Registration numbers of bones of *Stagonolepis* studied herein.

UOPB00148	Right ilium
UOPB00149	Right ilium
UOPB00150	Left ilium
UOPB01141	Right ilium
UOPB01143	Right pubis
UOPB01144	Left pubis
UOPB00154	Left ischium

the pubes are incomplete; however, their morphology can be observed clearly. The ischium is complete.

The present research included the extraction of bones, preparation, morphological analysis (including biometric parameters), photographic documentation and comparative analysis. The tools used for extracting material on site were hammer, chisel and brush. The isolated bones were recovered one by one; no plaster jackets were needed. All matrix was subsequently removed mechanically. The bones were first prepared by using sharp-edged chisels; small chisels were then used to scrape away the more strongly indurated calcium-carbonate matrix and to remove thick layers of less consolidated rock. For removing a thick cover of indurated sediment, chisels were not effective and a hand-drill was used instead. For final preparation, tap water with toothbrushes was used in combination with various dentist tools. During preparation, no chemicals were used, except for cyanoacrylate glues for assembling loose and broken parts.

Morphological analysis included the definition of shape and all other external features of these bones. Photographs were taken with a digital single-lens reflex camera (Nikon D7100) and edited with Paint 3D.

Measurements were taken using a calliper and ruler, with those of the ilium in lateral aspect. The measurements of the ilia (Fig. 2) include the iliac blade length (Lib), iliac height (H), the distance between the pubic and ischiadic peduncles (pp–ip), the width of the neck (neck) and that across the acetabulum (Aac), the supracetabular height (Hsa), the length of the preacetabular blade (Lprab), as well as the projection of the preacetabular blade, relative to the pubic peduncle (papp). For *Stagonolepis*, the last-named is negative because the preacetabular blade (prab) does not precede the pubic peduncle (pp). The iliac projection

Table 2

Dimensions of ilia in millimetres; for abbreviations see Figure 2. Iliac projection: ilp=(d1/(d1+d2))*100, see Figure 3.

Specimen	Lib	H	Aac	Hsa	Lprab	pp-ip	neck	papp	Lib/H	ilp
UOPB00149		151.7	94.1	56.4		127.6	80.7			
UOPB00148	206.0	154.4	92.3	61.8	35.8	137.2	88.7	-18.7	1.33	29
UOPB01141	219.3	168.3	102.9	65.9	46.3	147.4	87.4	-13.1	1.30	29
UOPB00150	231.3	170.5	112.4	62.3	46.5	155.0	93.8	-20.0	1.36	30

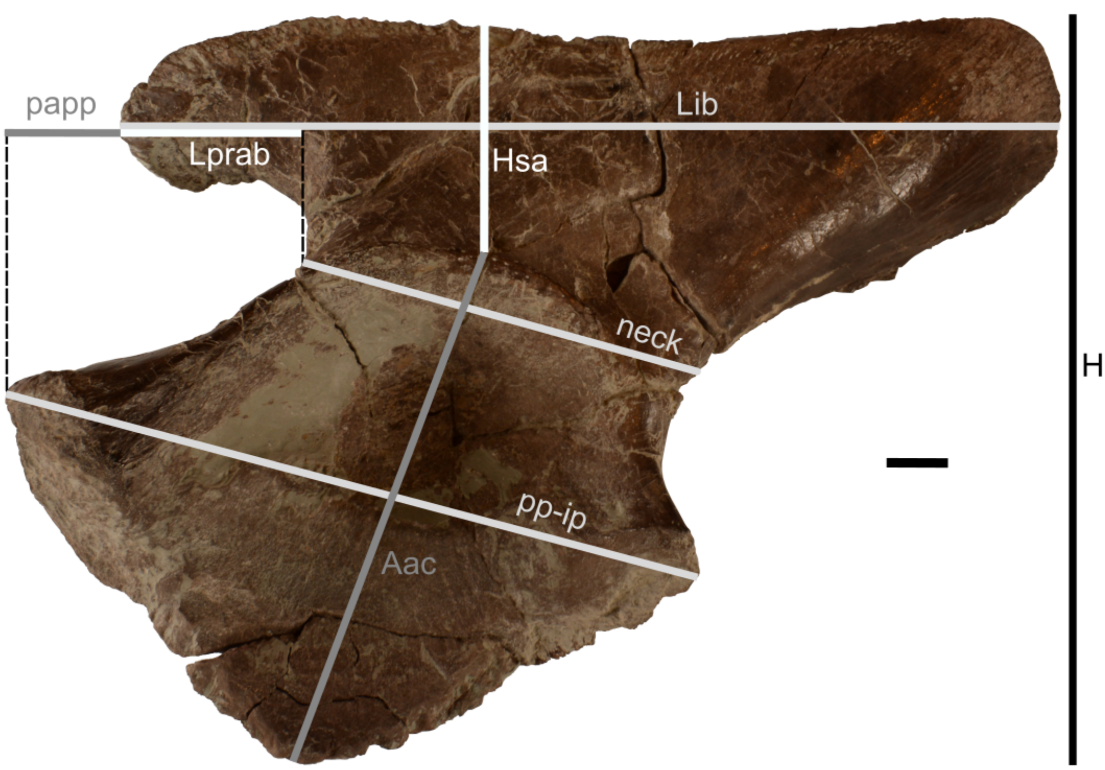

Fig. 2. Measurements of the ilium of *Stagonolepis* in lateral view (UOPB00150). Abbreviations: Aac – across acetabulum; H – height; Hsa – supracetabular height; Lib – iliac blade length; Lprab – preacetabular blade length; neck – breadth of neck; papp – projection of the preacetabular blade anterior of the pubic peduncle; pp-ip – distance between pubic and ischiadic peduncle. Scale bar equals 10 mm.

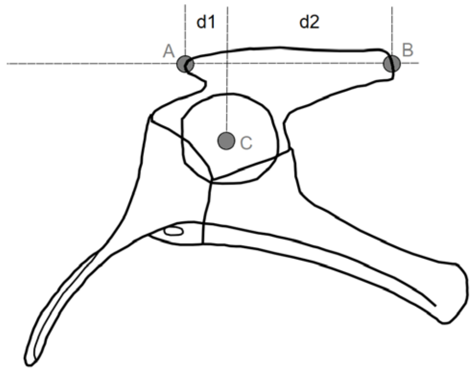

Fig. 3. Ilp, iliac projection modified from Rasskin-Gutman and Buscalioni (2001). **A.** Most anterior part of the iliac blade. **B.** Most posterior part of the iliac blade. **C.** Centre of the acetabulum.

(ilp; see Tab. 2; Fig. 3) and orientation type were defined as and compared to the results discussed by Rasskin-Gutman and Buscalioni (2001) and Iijima and Kobayashi (2014). In addition, the length of the iliac blade/width of the ilium ratio, as mentioned by Kimmig (2013), was assessed (Lib/H in this study). Measurements of the pubis (Fig. 4), taken in anterior aspect, are height (H), width of the narrowest section of the pubic diaphysis (Wn), and width of the widest section of the distal pubis (Wwd). The ratio of the two last-named measurements was used by Claessens and Vickaryous (2012) to compare archosauromorphs and crocodylomorphs. Morphometric parameters were determined on the basis of these measurements. Figure 5 illustrates the dimensions of the ischium, namely height (H) and length (L).

The analysis by the present authors comprises a comparison of the results of their morphological study with all aetosaurian pelvic girdle bones, described in the literature to date (Appendix 1). Unfortunately, not many pelvic girdle dimensions of aetosaurs have been published (Appendix 2), which precluded comparisons with all other species.

The institutional abbreviations are:

DMNH: Denver Museum of Nature and Science, Denver, Colorado, USA;
EM: Elgin Museum, Elgin, Scotland;
GSM: Geological Survey Museum, London, UK;
MCZD: Marischal College, Zoology Department, University of Aberdeen, Scotland;
MNA: Museum of Northern Arizona, Flagstaff, Arizona, USA;
NMMNH: New Mexico Museum of Natural History and Science, Albuquerque, New Mexico, USA;
PEFO: Petrified Forest National Park, Petrified Forest, Arizona, USA;
PVL: Paleontología de Vertebrados, Instituto ‘Miguel Lillo’, San Miguel de Tucumán, Argentina;
R: The Natural History Museum, London, UK;
SMNS: Staatliches Museum für Naturkunde, Stuttgart, Germany;
TMM: Texas Memorial Museum, Austin, Texas, USA;
TTUP: Museum of Texas Tech University, Lubbock, Texas, USA;

Fig. 4. Measurements of the pubis of *Stagonolepis*. Right pubis (UOPB01143) in anterior view showing three measurements. Abbreviations: H – total height; Wn – width of the narrowest section of the pubic diaphysis; Wwd – width of the widest section of distal pubis in mm. Scale bar equals 10 mm.

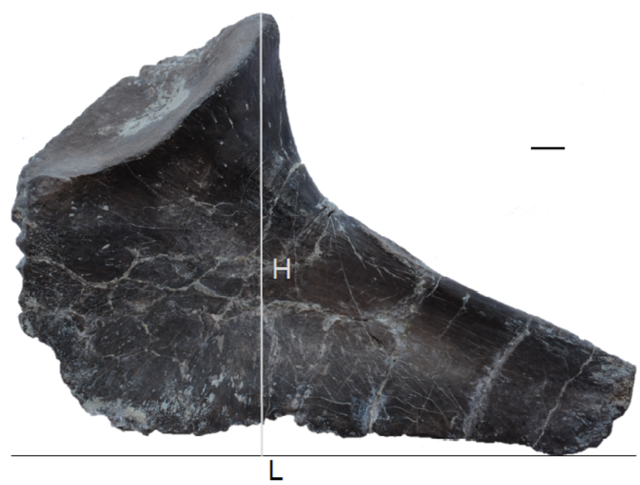

Fig. 5. Measurements of the ischium of *Stagonolepis*. Left ischium (UOPB00154) in lateral view showing two measurements. Abbreviations: H – height; L – length in mm. Scale bar equals 10 mm.

UCMP: University of California, Museum of Paleontology, Berkeley, California, USA;
ULBRA PVT: Universidade Luterana do Brasil, Coleccão de Paleovertebrados, Canoas, Rio Grande do Sul, Brazil;
UMMP: University of Michigan, Museum of Paleontology, Ann Arbor, Michigan, USA;

UOPB: University of Opole, Palaeobiology Department, Opole, Poland.

RESULTS

Description of ilium

The ilium of aetosaurs can be lateroventrally inclined. The ilium, as well as the other bones, will be described here as if there were no inclination so as to permit the use of the terms lateral, medial, ventral and dorsal in an understandable way. The position of the bones were set using the reconstruction of the pelvic girdle of *Stagonolepis robertsoni* Walker (1961), which also was made without inclination. The present authors do not express any opinion about the position of the ilium in the body.

The anterior projection of the ilium, i.e. the preacetabular blade (prab), is triangular in lateral view (Figs 2, 6), slightly pointed ventrally, and does not exceed the pubic peduncle (pp). The preacetabular blade is dorsoventrally flattened and oblique in ventromedial direction, clearly visible in anterior view (Fig. 7). In lateral view, between the preacetabular blade and the pubic peduncle, the anterior margin is curved (Figs 2, 6). The postacetabular blade is longer and much larger than the preacetabular blade, its ventral edge being medially folded (poab-angle), clearly visible in the posterior view (Fig. 8B). The dorsal margin of the iliac blade is striated (muscle attachment area) (Figs 2, 8C). In lateral

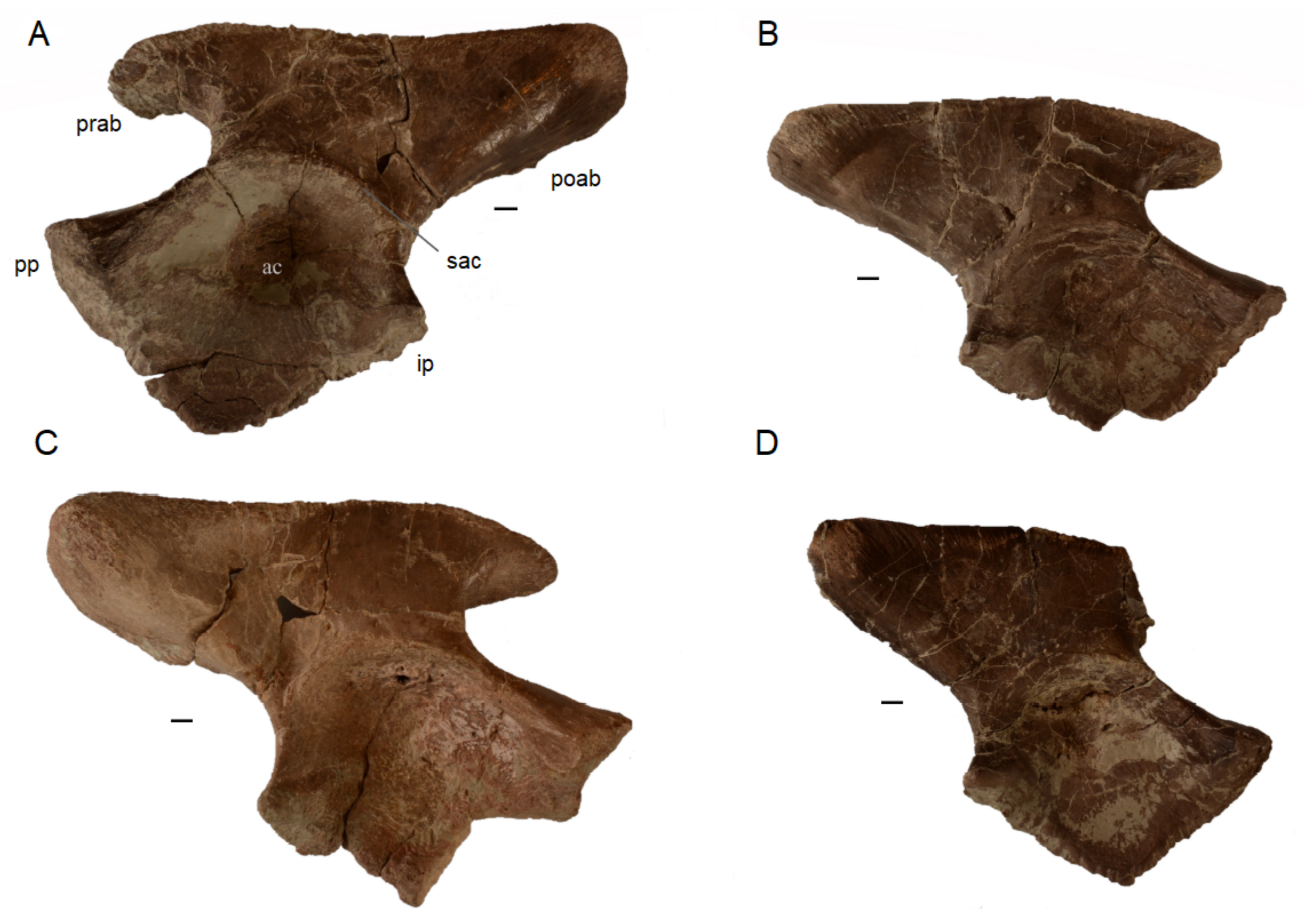

Fig. 6. Ilia of *Stagonolepis* from Krasiejów in lateral view. **A**. UOPB00150 (l). **B**. UOPB00148 (r). **C**. UOPB01141(r). **D**. UOPB00149 (r). (l) – left ilium; (r) – right ilium. Abbreviations: ac – acetabulum; ip – ischiadic peduncle; poab – postacetabular blade; pp – pubic peduncle; prab – preacetabular blade; sac – supracetabular crest. Scale bar equals 10 mm.

Table 3

Seven ratios for ilia of *Stagonolepis*, from small (UOPB00149) to large (UOPB00150), and angle between lateral and ventral sides of the postacetabular blade (poab-angle). For measurements see Figure 2 and Table 2.

Specimen	neck/pp-ip	neck/Lib	Lib/L	Lib/pp-ip	Hsa/Lib	Hsa/Aac	Lprab/Lib	poab-angle
UOPB00149	0.6					0.6		129°
UOPB00148	0.6	0.4	0.9	1.5	0.3	0.7	0.2	120°
UOPB01141	0.6	0.4	0.9	1.5	0.3	0.6	0.2	97°
UOPB00150	0.6	0.4	0.9	1.5	0.3	0.6	0.2	91°

view, the posterior margin is curved. At mid-height, there is a constriction (neck, see Fig. 2). The ratio of the width of the neck to the length of the iliac blade (Lib) is 0.4 (see Tab. 3). The acetabulum (ac) is triradiate, consisting of three parts (portions of ilium, pubis and ischium), although the contribution of the pubis is limited (Lecuona and Desojo, 2012). The ventral margin of the ilium (part of the acetabulum) is convex, indicating an imperforate acetabulum. Dorsally of the acetabulum there is a fine, sharp and pronounced rim, the supracetabular crest (sac). The acetabulum is deep and has a circular bowl shape, the deepest part of the acetabulum being rough and just below the supracetabular crest.

Above the supracetabular crest, there are some small foramina (Fig. 9); these are well-outlined holes measuring between 1 and 3.5 mm in diameter. In UOPB00150, three foramina (diameter 2.5 mm) dorsal to the supracetabular crest (Fig. 9C) are seen; in UOPB01141, there are two foramina of diameter 2 mm (Fig. 9B), in UOPB00148, one large foramen 3.5 mm in diameter and two smaller ellipsoid holes (Fig. 9A), and in UOPB00149, there are four foramina, two close to each other (diameter 2 mm), a smaller one and a small, ellipsoid one (Fig. 9D).

On the anterior and posterior sides of the acetabulum, thick edges widen ventrally to contact the pubis (anteriorly) and the ischium (posteriorly), i.e. the pubic and ischiadic peduncle (pp and ip; see Figs 2, 6, 8). In ventral view, the articular portions of the pubis and ischium are rugose and comma shaped. The pubic peduncle (Fig. 8A) is larger than the ischiadic peduncle, coinciding with their counterparts on the proximal ends of the pubis and ischium.

Medially (Fig. 10), the surface for sacral ribs is strongly rugose. It is mainly at the height of the neck and ventrally from the neck, but also slightly more dorsally. The rugosity continues in the direction of the preacetabular blade, which is convex. The dorsal edge of the iliac blade is striated, as in lateral view. The ventral extremity of the iliac pedestal in medial view is very smooth. In dorsal view (Fig. 8C), the iliac blade is slightly curved, the central part bending in a medial direction. The margin is fine, becoming thicker anteriorly above the preacetabular blade.

A comparison of the four ilia of *Stagonolepis* from Krasiejów shows that differences are related to size (Tab. 2) and curvature of the anterior margin (Fig. 6). The latter feature is most pronounced in the ilia UOPB01141. UOPB00148 and UOPB00149 are smaller and additionally UOPB00149 is very thin mediolaterally. UOPB01141 is more robust, lateromedially thicker and the preacetabular blade is not flattened as in the other ilia. Medially, the attachment to the sacrum is also different. UOPB01141 has clearly two attachment sites for the primordial sacral ribs, while UOPB00148, 00149 and 00150 show a possible third scar, situated more anteriorly and dorsally (Fig. 10).

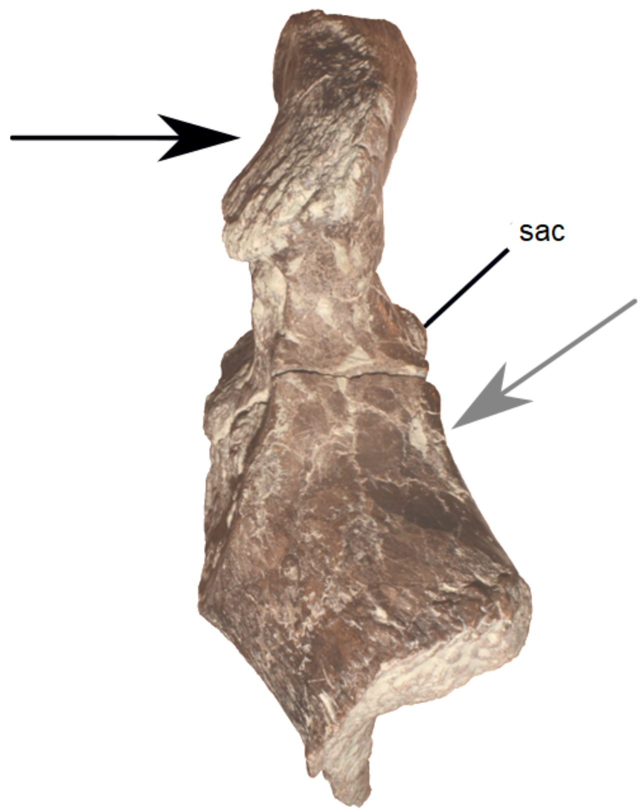

Fig. 7. Left ilium of *Stagonolepis* (UOPB00150) from Krasiejów in anterior view with inclination of the preacetabular blade (black arrow) and curvature of the anterior rim of the acetabulum (grey arrow). Scale bar equals 10 mm.

Description of pubis

Both specimens are of the same animal, as is a right ilium (UOPB01141). The pubes are quite slender and gracile. The right pubis (Figs 11, 12) is more or less complete, while the left one lacks the central part (Fig. 12A). The proximal part of the pubis is oriented anteroposteriorly, robust on the anterior side, becoming thin on the ventroposterior side. In lateral view, on the proximal edge, there is a fold-like buttress (Fig. 11D). The dorsal plane which contacts the ilium is rugose, the broadest side tapers anteriorly to a narrow ridge posteriorly (Figs 11C, 12B). In medial view the proximal part of the pubis is smooth. The distal part is plate like, slightly convex anteriorly, very thin medially and twisted 90° relative to the proximal part, forming the pubic apron. The lateral margin is thicker and forms a shaft, the diaphysis. This lateral shaft slightly widens distally forming a knob at the end (Fig. 11D). In anterior view, the pubic shaft is lateroventrally oriented at an angle of 45° (Fig. 11A). The medial margins of the distal part of the pubis were fused to form the pubic apron. The pubic apron is broad and the symphysis is less than one half of the pubis (Fig. 12A). On the lateral side of the proximal part of the right pubis, two deep depressions are distinguishable (Fig. 11D). The largest one is roundish, ventrally placed close to the anterior edge where the bone is robust. The second one is smaller, oval shaped and situated more posteriorly and dorsally, close to the buttress.

Description of ischium

Specimen UOPB00154 is very well preserved. The bone is plate like, smooth on both sides and slightly

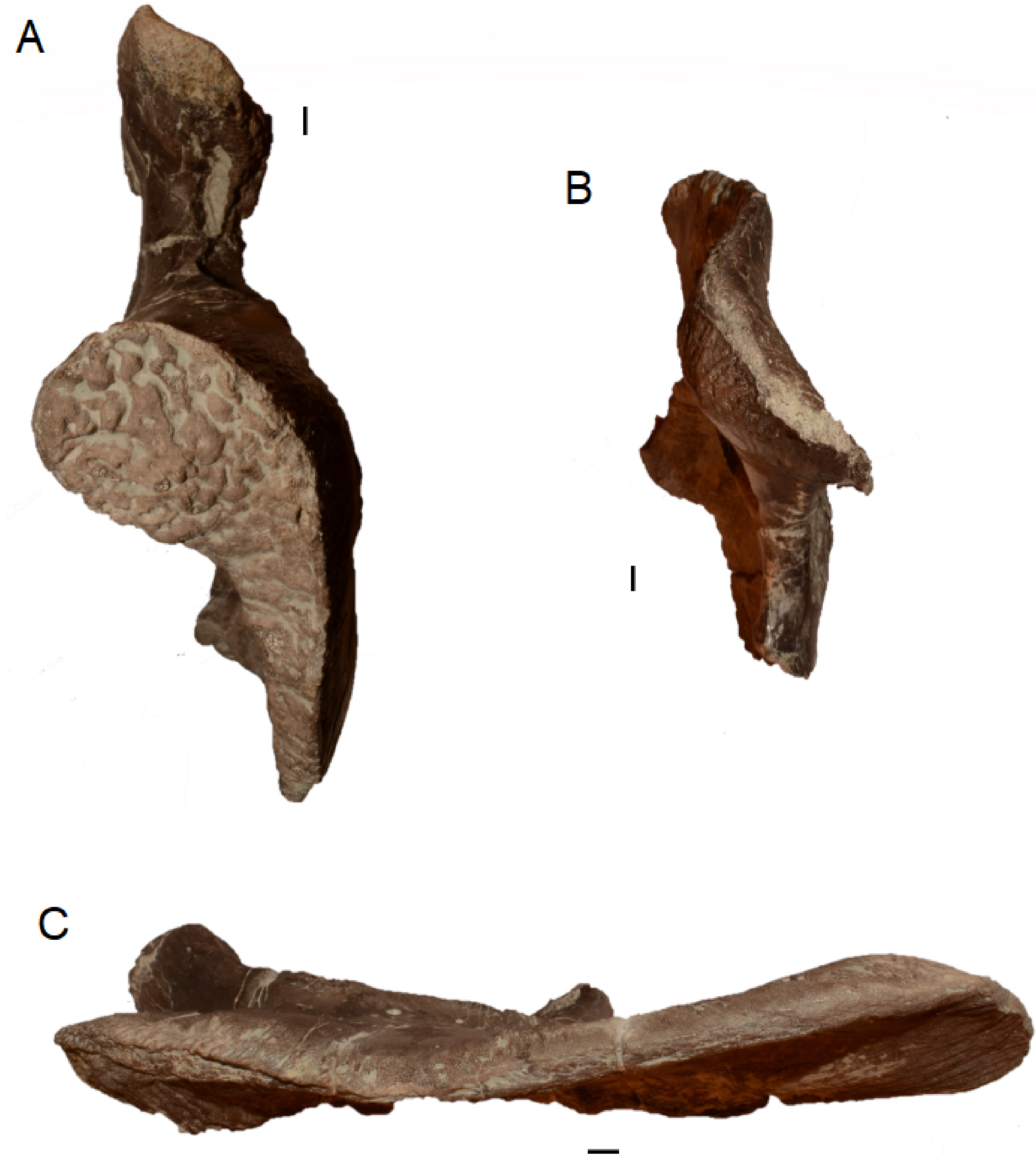

Fig. 8. Ilium UOPB00150 in **A.** Anteroventral, **B.** Posterior and **C.** Dorsolateral view. Scale bar equals 10 mm.

ventrolaterally concave, triangular in shape, and directed posteroventrally. The broadest and thickest part proximally is the contribution to the acetabulum on the lateral side (Fig. 13C) and the rugosity for contact with the ilium on the medial side (Fig. 13E). The ilium and ischium fit together very well. The rugosity of the contact with the ilium continues anteriorly to the contact with the pubis (Fig. 13C). The part of the acetabulum is spindle-shaped and concave, with well-pronounced edges. The dorsal margin of the ischium (Fig. 13A, B) is shaped like a shaft, with the anterior part being curved, the posterior part straight. Walker (1961, p. 150) described the shaft of *Stagonolepis robertsoni* as follows, 'The posterodorsal edge is rounded off, the middle part having a rough area for muscle origin', the same observation as in the material from Krasiejów (compare Fig. 13A, B). The ventral margin of the ischium is straight

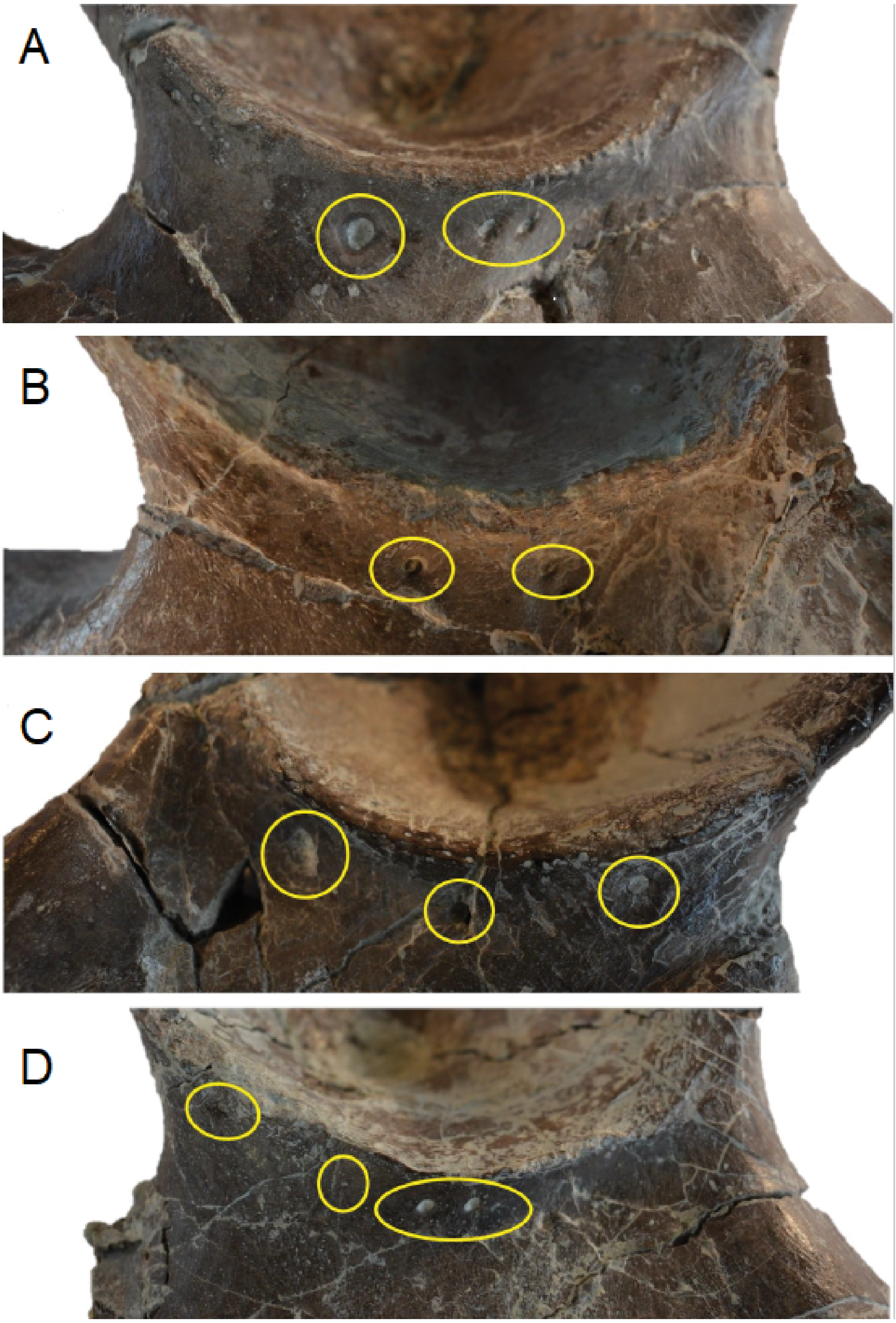

Fig. 9. Detail of the foramina dorsal of the supracetabular crest. **A.** UOPB00148. **B.** UOPB01141. **C.** UOPB00150. **D.** UOPB00149. Pictures taken from dorsal perspective.

and thin. These margins are fused medially to form the ischiadic symphysis; the contact region is a lined rugosity (Fig. 13D).

Measurements of ilium, pubis and ischium

Eight biometric parameters of the ilium were defined (Fig. 2; Tab. 2). Some of these (Lib, H, Aac, Hsa and Lprab) were specifically chosen to permit comparison with some other published measurements of aetosaurian pelvic girdle bones (Small, 1985; Lucas *et al*., 2002; Roberto-da-Silva *et al*., 2014; Parker, 2016b, 2018a), although not many measurements of the pelvis of aetosaurs are available (Appendix 2). Other dimensions were noted, because they appeared relevant to the morphology of the ilium and would allow ratios to be assessed. Table 2 lists these measurements, and the

Fig. 10. Left ilium of *Stagonolepis* (UOPB00150), medial view. Circle shows possible additional attachment for sacrum. Scale bar equals 10 mm.

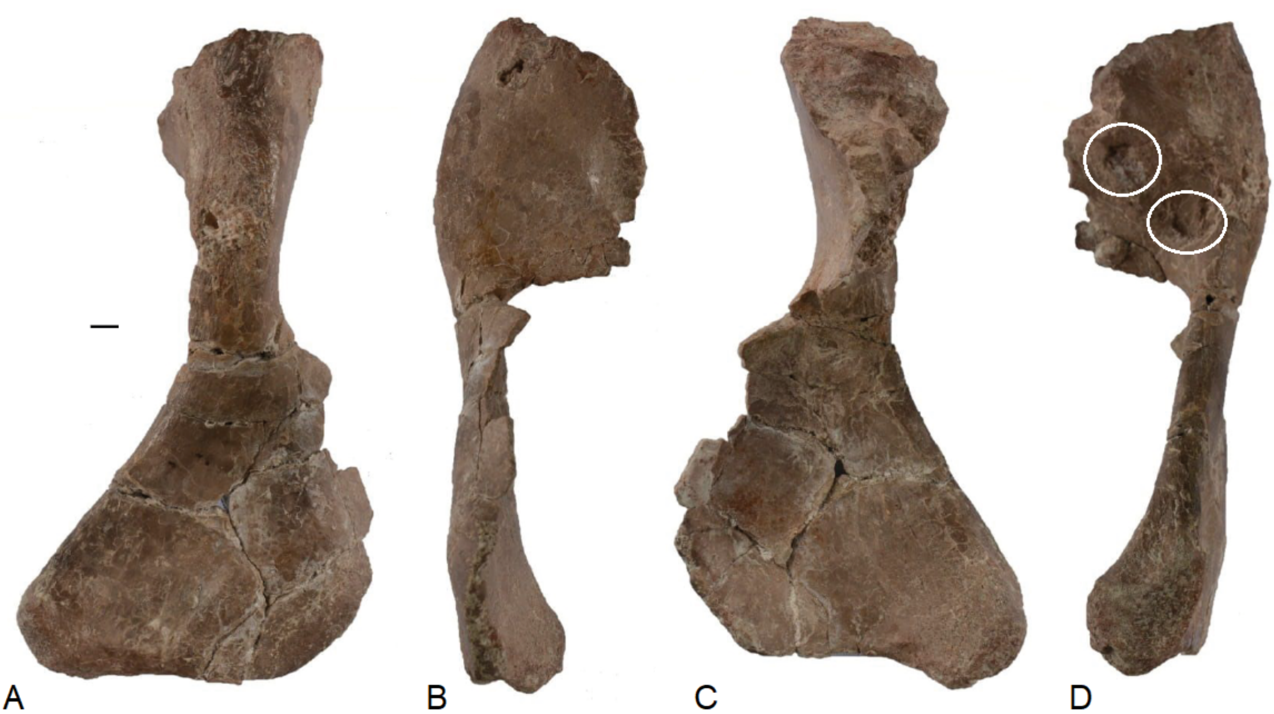

Fig. 11. Right pubis of *Stagonolepis* (UOPB01143). **A.** Anterior view. **B.** Medial view. **C.** Posterior view. **D.** Lateral view. The circles show the pubic foramina. Scale bar equals 10 mm.

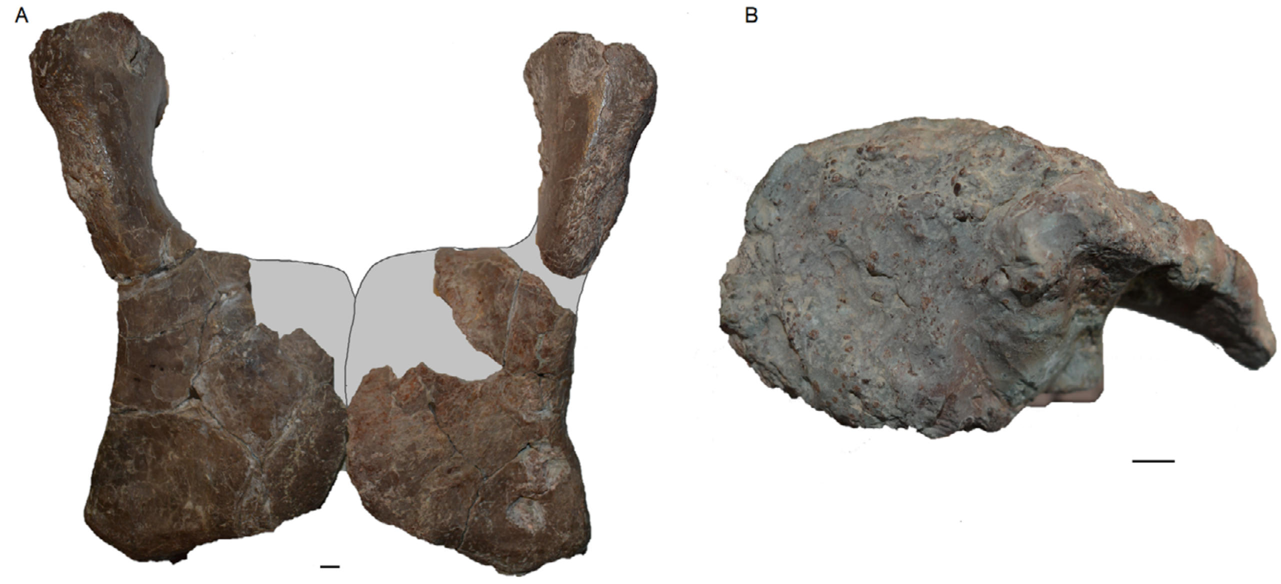

Fig. 12. Pubes of *Stagonolepis*. **A.** Reconstruction of the pubic apron and symphysis (maximum possible extension) in anterior view, UOPB01143 and UOPB01144. **B.** Left pubis UOPB01144 in dorsal view. Scale bar equals 10 mm.

ratio 'length of the iliac blade to height' and ilp; Table 3 adds other ratios and the angle of the postacetabular blade (poab).

All ratios are the same for the three complete ilia and those ratios, for which the preacetabular blade was not needed (i.e. neck/pp–ip and Hsa/Aac), the results match as well. This means that the ilium of *Stagonolepis* has constant proportions, irrespective of size. The angle was measured between the lateral and ventral parts of the postacetabular blade, at one-third of the distance from the end of the blade (poab angle): the smaller the ilium, the larger the angle (Tab. 3).

The three dimensions of the pubis measured (Fig. 4) are height (H), width of the narrowest section of the pubic diaphysis (Wn), and width of the widest section of the distal pubis (Wwd); see Claessens and Vickaryous, 2012. The height of the right pubis (H) is 220 mm, the width of the narrowest section of the pubic diaphysis (Wn) is 25.7 mm and the width of the widest section of the distal pubis (Wwd) is 119 mm. For the ischium, two measurements were taken (Fig. 5): height (H) and length (L). The height of the ischium (H) is 103 mm and the length (L) is 155 mm.

Comparison with other aetosaurs

To date, 30 species of aetosaurians are known (Brust *et al*., 2018). Different versions of the aetosaurian phylogenetic tree exist, but the search for clarity is not yet over. It has been suggested that *Aetosauroides scagliai* was the most basal and the sister-taxon of all other members of the Aetosauria (Desojo *et al*., 2013; Parker, 2016a; Brust *et al*., 2018). Out of the 30 aetosaur species, only 15 pelvic girdles have been (in part) described and/or illustrated. In addition to the bones used here, this amounts to 16 pelvic girdles for comparison (Appendices 1, 2). The original nomenclature of the papers used has been adapted. One species, *Desmatosuchus haplocerus*, is a *nomen dubium*; material was reassigned to *Desmatosuchus spurensis* (see Parker, 2008, 2018a), but in view of the fact that this particular ilium (UMMP7322) is markedly different from that of the other two species, *D. spurensis* and *D. smalli*, the present authors decided to treat this pelvic girdle separately and use the name '*D. haplocerus*'. Here, the authors discuss only the morphology of the ilium, pubis and ischium of aetosaurs, but not the size. In the literature not many measurements have been published, which makes comparison difficult. Known measurements are listed in Appendix 2.

Ilium

In fourteen aetosaur taxa, the ilium is more or less completely preserved and its morphology can be assessed, although in some cases only a drawing is available. The one that is the most important for the present case, *Stagonolepis robertsoni* of Scotland, is a reconstruction based on three specimens (GSM 90849, EM 46 R and R 4789/4790). The drawing provided by Walker (1961) is still the leading representation of the pelvic girdle of Aetosauria. The pictures or drawings of the ilium of *Aetosauroides scagliai* (Heckert and Lucas, 2002), *S. robertsoni* (Walker, 1961), *Polesinesuchus aurelioi* juvenile (Roberto-da-Silva *et al*., 2014), *Neoaetosauroides engaeus* (Desojo and Báez, 2005), *Calyptosuchus wellesi* (Case, 1922; Long and Murry, 1995), *Longosuchus meadei* (distorted), *Lucasuchus hunti, Desmatosuchus* '*haplocerus*', *Typothorax coccinarum* (damaged; Long and Murry, 1995), *Desmatosuchus spurensis* (distorted; Parker, 2008) and *Aetosaurus ferratus* (Schoch, 2007) are compared with the ilia of *Stagonolepis* from Krasiejów (UOPB01141, UOPB00148, UOPB00149

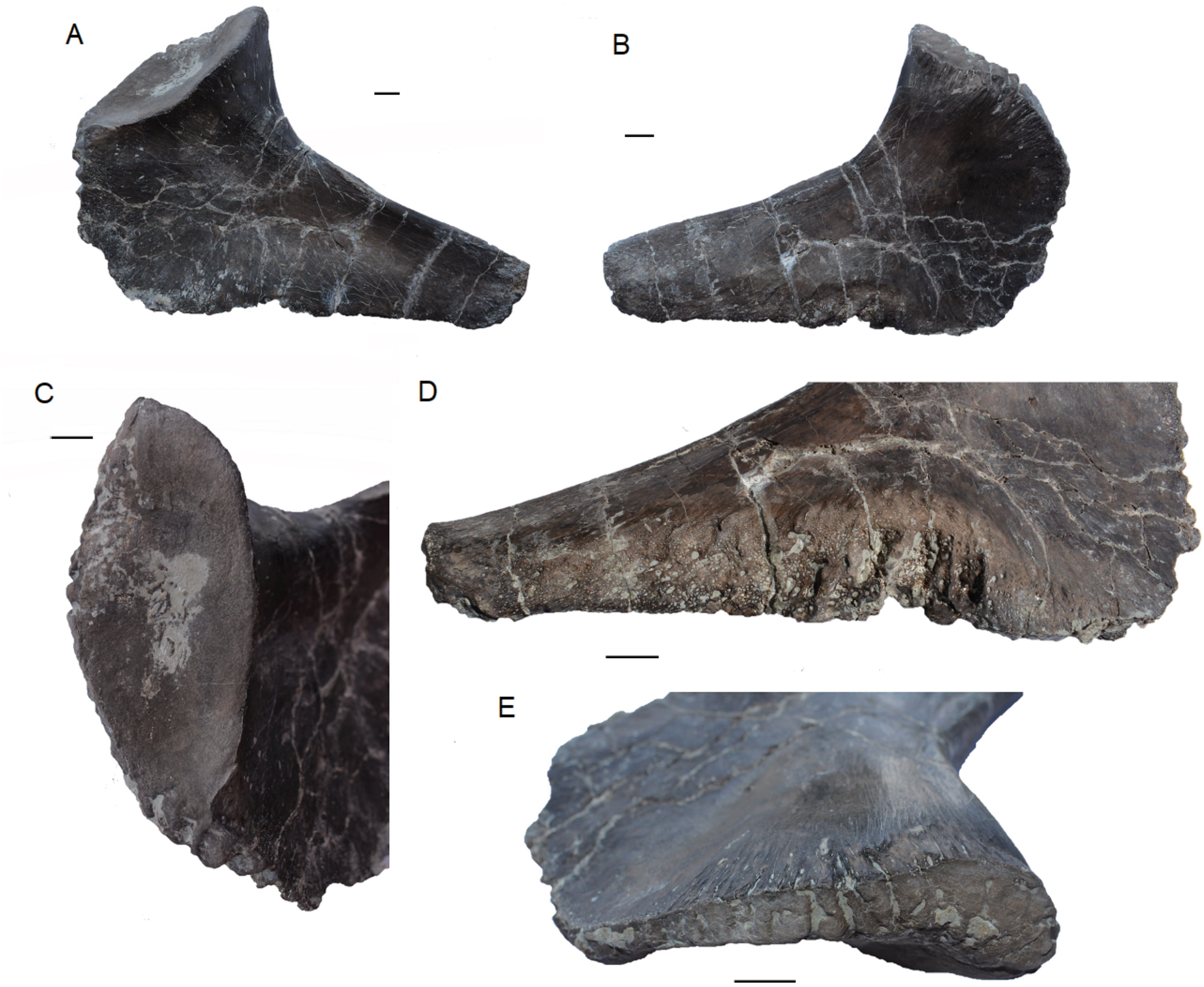

Fig. 13. Left ischium of *Stagonolepis* (UOPB00154). **A.** Ventrolateral view. **B.** Medial view. **C.** Detail acetabular contribution. **D.** Detail of surface of ischiadic symphysis. **E.** Detail contact with ilium. Scale bar equals 10 mm.

and UOPB00150). The ilium DMNH 9938, mentioned by Long and Murry (1995) as belonging to *Paratypothorax*, is not considered further because of the uncertainty about its status. Collection numbers of all ilia, plus pertinent references, are listed in Appendices 1 and 2.

Numerous details of the ilium, seen in lateral view, are available, but pictures or drawings of other views are scarce. All ilia of aetosaurs are three-pronged and have a convex, ventral margin, a feature of most pseudosuchians and primitive reptiles. The acetabulum continues into the proximal end of the pubis and the ischium (Walker, 1961, fig. 16). At first sight, most ilia of aetosaurs look alike, but closer inspection yields several differences. The height of the ilia in *Stagonolepis* is smaller (or equal) dorsal of the supracetabular crest (Hsa) than ventral (the pedestal). Most ilia of aetosaurs have this morphology, but those of *Aetosaurus ferratus* (Schoch, 2007, fig. 11), a juvenile (Schoch and Desojo, 2016), *Neoaetosauroides engaeus* (Desojo and Báez, 2005, fig. 2) and *Desmatosuchus spurensis* (Parker, 2008, fig. 20), which is much larger, appear to be the exceptions. In the last-named and in *Typothorax coccinarum* (Long and Murry, 1995, fig. 106; Heckert *et al*., 2010), the ilia are the most dorsoventrally stretched. The most dorsoventrally compressed ilia are those of *Polesinesuchus aurelioi* (Roberto-da-Silva *et al*., 2014, fig. 22) and *Aetosaurus ferratus*. The preacetabular blade of all ilia is smaller than the postacetabular blade, but the form of the former differs: triangular and pointing slightly downwards in *Stagonolepis* from Krasiejów (Figs 2, 6), *S. robertsoni* (Walker, 1961, fig. 16) and *Calyptosuchus wellesi* (Fig. 14B), triangular, but long and fine in *Lucasuchus hunti* (Long and Murry, 1995, fig. 66) and *Desmatosuchus* '*haplocerus*' (Long and Murry, 1995, figs 91, 92), or sharp, but shorter and pointing in an anterior direction in *Polesinesuchus aurelioi*. The preacetabular blade is long and slender and points strongly anteroventrally in *Aetosaurus ferratus*, *Aetosauroides scagliai* (Fig. 14A) and *Neoaetosauroides engaeus*. The same holds true for *Typothorax coccinarum*, but in this species the preacetabular blade is blunt (Long and Murry, 1995, figs 106, 107). The preacetabular blade of

Neoaetosauroides is the one that exceeds the pubic peduncle furthest, while those in *Polesinesuchus* and *Calyptosuchus* only slightly do so. Most preacetabular blades do not exceed the pubic peduncle, this is the case for *Stagonolepis, Longosuchus meadei* (Long and Murry, 1995, fig. 63) and *Desmatosuchus smalli* (Small, 1985, fig. 9). Walker (1961, p. 150) described the preacetabular blade of *Stagonolepis robertsoni* as, '…flattened above and below.'. This is the same for the ilia of the *Stagonolepis* from Krasiejów (Figs 2, 6, 7). This fact has not been mentioned by any subsequent author, nor is it observable in drawings or photographs. The anterior margin of the ilium in lateral view is mostly curved as in *Stagonolepis*; in some species the curvature is small, as in *Aetosauroides scagliai* (Fig. 14A) and *Aetosaurus ferratus*, but in *Polesinesuchus* curvature of the anterior margin is very small and angulated. The posterior edge of the ilium of *Stagonolepis*, *Calyptosuchus wellesi* (Fig. 14B) and *Lucasuchus hunti* is well curved, while it is straighter and more upright in *Aetosauroides* (Fig. 14A), *Neoaetosauroides*, *Desmatosuchus* '*haplocerus*' and *Aetosaurus ferratus*, which means that the postacetabular blade rises in a posterodorsal direction. The posterior edge of the ilium in lateral view of *Polesinesuchus* is most angulated. Some postacetabular blades are long and triangular, having a mediolaterally inclination as in *Stagonolepis, Aetosauroides scagliai, Polesinesuchus aurelioi, Lucasuchus hunti* and *Desmatosuchus* '*haplocerus*', while the shape is rather bulbous and rectangular in *Neoaetosauroides engaeus*, *Calyptosuchus wellesi* (Fig. 14B) and *Longosuchus meadei* (Long and Murry, 1995, fig. 63). The postacetabular blade in *Typothorax coccinarum* is relatively short. The iliac blade is generally slightly concave and smooth, for example in *Stagonolepis* and *Calyptosuchus* (Long and Murry, 1995). The thickest iliac blades are those of *Longosuchus meadei* and *Desmatosuchus spurensis* (Long and Murry, 1995). The ilium of *Typothorax coccinarum* has a pronounced depression above the supracetabular crest (Long and Murry, 1995), whereas that of *Aetosauroides scagliai* has moderate depressions (Heckert and Lucas, 2002). Two ilia have a remarkable, unique character on the iliac blade: *Scutarx deltatylus* has a fossa, dorsal to the supracetabular crest on the posterior portion of the iliac blade (Parker, 2016b, fig. 20A) and *Aetosaurus ferratus* has an oblique ridge between the supracetabular crest and preacetabular blade (Schoch, 2007). Both autapomorphies are distinct from the rauisuchian thick vertical crest dorsally of the supracetabular crest (Nesbitt, 2011). The dorsal margin of the iliac blade in lateral view can be straight as in *Stagonolepis, Polesinesuchus* and *Desmatosuchus* '*haplocerus*' or undulate as in *Aetosauroides* (Fig. 14A), *Calyptosuchus* (Fig. 14B) and *Lucasuchus*. The edge in dorsal view is remarkably thick in *Aetosauroides scagliai* (Heckert and Lucas, 2002), *Lucasuchus hunti, Calyptosuchus wellesi* and *Desmatosuchus* '*haplocerus*' (Case, 1922; Long and Murry, 1995).

A very characteristic feature is the constricted neck in *Desmatosuchus spurensis* and *Typothorax coccinarum.* The neck is remarkably wide in *Aetosauroides* (Fig. 14A), *Neoaetosauroides* and *Aetosaurus*. A large part of the pedestal is the acetabulum, dorsally bordered by the supracetabular crest. The acetabulum is shallow in *Polesinesuchus aurelioi* (Roberto-da-Silva *et al*., 2014) and deep in *Neoaetosauroides engaeus* (Desojo and Báez, 2005), *Scutarx deltatylus* (Parker, 2016b) and *Desmatosuchus smalli* (Small, 1985). Case (1922) described the acetabulum of *Desmatosuchus* '*haplocerus*' (UMMP7322) as very deep. The supracetabular crest is thin, yet pronounced, in *Stagonolepis, Aetosaurus ferratus* and *Aetosauroides scagliai* (Fig. 14A) and swollen in *Calyptosuchus wellesi* (Fig. 14B), *Desmatosuchus* '*haplocerus*' and *Longosuchus meadei.* There is no pronounced supracetabular crest present in the ilium of *Neoaetosauroides* (Desojo and Báez, 2005). The orientation of the ischiadic peduncle is mostly downwards, more or less vertical in lateral view, as in *Stagonolepis* (Fig. 6), this being pointed posteriorly in

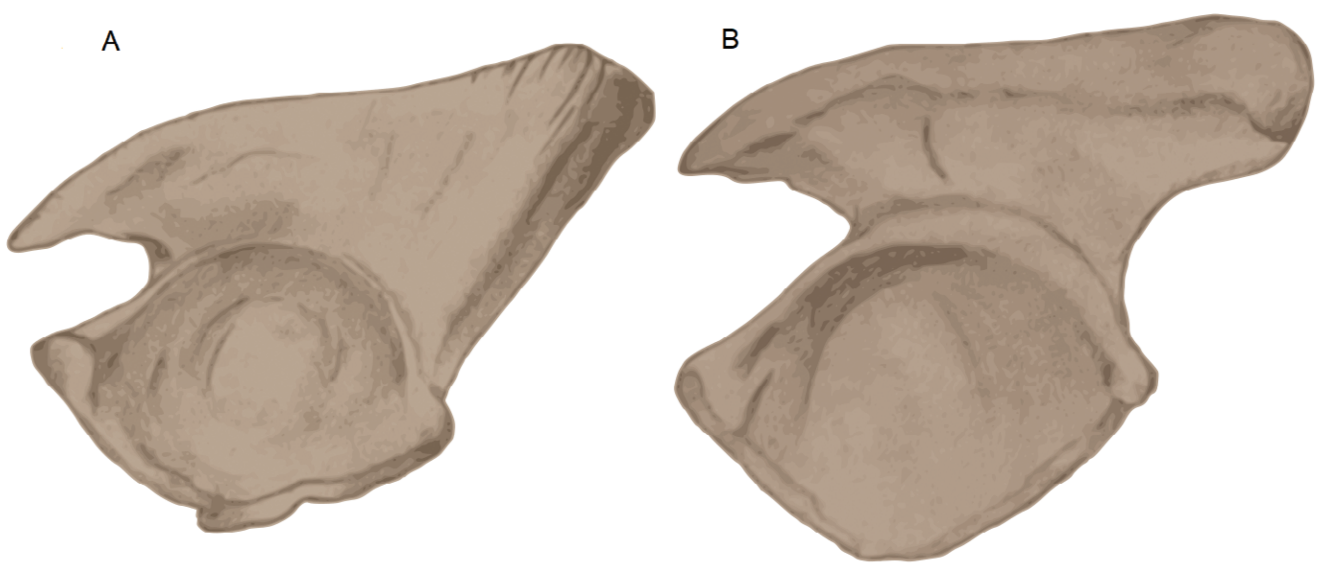

Fig. 14 Drawings of ilia of Aetosauria, lateral view. **A.** *Aetosauroides scagliai*. **B.** *Calyptosuchus wellesi*. Not to scale. Copyright Titia Nerinckx.

Lucasuchus hunti. *Polesinesuchus aurelioi* is the most aberrant form, in that it has an ischiadic peduncle pointing anteriorly. In all aetosaurs, the pubic peduncle is larger than the ischiadic peduncle, except in *Lucasuchus hunti* and *Scutarx deltatylus* (Parker, 2016b).

The medial side shows the attachment of the sacral ribs in the region of the neck. The area above is slightly concave. Medially, *Stagonolepis* (Fig. 10) closely resembles *Calyptosuchus wellesi*, the portion of the rugose region for attachment of the sacral ribs being equal. Long and Murry (1995) described the attachments of the sacral ribs as being anteroposteriorly very elongated in *Typothorax coccinarum*. According to Parker (2016b), in *Scutarx deltatylus*, the attachments of the sacral ribs are situated dorsally to the neck, ventrally bordered by a ridge. According to Case (1922), in UMMP7322 (*D.* '*haplocerus*'), these articulations were situated lower than in other ilia.

Not all ilia are complete and undistorted but judging by available pictures and descriptions, the ilia of *Stagonolepis* resemble that of *Lucasuchus hunti* most closely; however, the preacetabular blade of the latter is longer and much sharper at the tip. *Calyptosuchus wellesi* is also similar, but its postacetabular blade is much more bulbous and the preacetabular blade more triangulate (Fig. 14B).

Table 2 and Figure 3 illustrate the iliac projection, i.e. the relative anterior projection of the ilium. Here, three complete ilia of *Stagonolepis* are compared with data supplied by Rasskin-Gutman and Buscalioni (2001) and Iijima and Kobayashi (2014). Rasskin-Gutman and Buscalioni (2001) measured the ilp of *Stagonolepis robertsoni*, while Iijima and Kobayashi (2014) did so for *Stagonolepis robertsoni* and *Longosuchus meadei*. The ilp of *Stagonolepis* from Krasiejów (UOPB00148, UOPB00150 and UOPB01141) is equal to or slightly less than 0.3 (Tab. 4). The ilp of *Longosuchus* is slightly larger. The equation in Table 4 is ilp = d1/(d1+d2).

Table 4

Iliac projection (ilp) of six ilia of Aetosauria. * data from Rasskin-Gutman and Buscalioni (2001); ° data from Iijima and Kobayashi (2014). See Figure 3.

Specimen	Ilp
UOPB00148	0.286
UOPB00150	0.297
UOPB 01141	0.290
*Stagonolepis robertsoni**	0.300
Stagonolepis robertsoni°	0.293
Longosuchus meadei°	0.311

Pubis

Of all aetosaurs described, only eight (including, as presented here, *Stagonolepis* from Krasiejów) have a more or less completely preserved pubis. Of seven other species, only proximal fragments are available (see overview in Appendices 1 and 2). Most fragments are too small or too poorly preserved for certain features to be recognised. Even when described, often not much attention was paid to it, unless it concerned the foramina.

All aetosaurian pubes are fused to form the pubic apron, but the symphyseal portion differs and all have the typical pseudosuchian twist (Walker, 1961). The pubes of *Stagonolepis* from Krasiejów (Figs 11, 12) and *S. robertsoni* (Walker, 1961, figs 16, 17) are similar, including proportions, such as length relative to the ilium, the dimensions and the rate of twisting between the proximal and distal part, the morphology and rugosity of the contact with the ilium and the knob at the distal end in lateral view. Similar, in anterior view, is the pubis of *Aetosauroides scagliai* (Heckert and Lucas, 2002, fig. 3). The pubis of *Stenomyti huangae* is comparatively shorter, having different proportions and with the distal blade broader and more undulate (Small and Martz, 2013, fig. 10). Because of this undulating morphology, this pubis is obviously different in lateral and medial views. The contact with the ilium is more elongate and does not show the buttress that is seen in *Stagonolepis* (Small and Martz, 2013). The pubis of *Typothorax coccinarum* (Long and Murry, 1995, fig. 108) is more robust and more dorsoventrally compressed and possesses a buttress on the proximal part (Martz, 2002) as in *Stagonolepis.* The proximal part is larger than the distal and the main shaft ends in a more pronounced knob than in *Stagonolepis*. The reconstruction of this pubis in anterior view shows a broad pubic apron (Long and Murry, 1995, fig. 108). The distal blade is thin, as in *Stagonolepis*. The most elongated pubis is that of *Desmatosuchus smalli* (Small, 1985, fig. 9), whereas that of *Aetosaurus ferratus* is shorter and stouter than in *Stagonolepis* (Schoch, 2007, fig. 11). According to Parker (2016b), the pubis of *Scutarx deltatylus* is also dorsoventrally short, as are those of *Polesinesuchus aurelioi* (Roberto-da-Silva *et al.*, 2014), *Calyptosuchus wellesi* (Parker, 2018a) and *Typothorax coccinarum* (Long and Murry, 1995). The incomplete pubis of *Desmatosuchus spurensis* (Parker, 2008, fig. 20) is comparable, in lateral view, to that of *Stagonolepis* although the distal knob is slightly thicker.

The medial margins of the distal parts of the pubis fuse to a symphysis, the pubic symphysis (Fig. 12). The symphyseal portion in UOPB01143 and UOPB1144 is shorter than half of the pubis length (see above). According to Small and Martz (2013), the symphysis of *Stenomyti* is one half of the total length of the pubis. No other author has ever mentioned these proportions, because the distal part of most pubes is not preserved and, moreover, certainly the medial part of the blade is absent because it is extremely thin. Drawings or pictures show the symphysis of *Aetosaurus* (Schoch, 2007, fig. 11) and *Typothorax coccinarum* (Long and Murry, 1995, fig. 108; Martz, 2002, fig. 4.12) to be short, and that of *Desmatosuchus smalli* (Small, 1985, fig. 10) to be long. Walker (1961, fig. 17) also provided a drawing with the symphysis visible but did not mention the proportions in the text. Parker (2016a) stipulated that the symphysis of *Stagonolepis robertsoni* equalled more than half of the pubis length. The dorsal view of the pubis of *Stagonolepis* from Krasiejów (Figs 11, 12B) shows a narrower end on the posterior side. This could be the same morphology as the one described by Roberto-da-Silva *et al.* (2014) as a 'tongue' in

Polesinesuchus aurelioi. The dorsal plane of *Calyptosuchus wellesi* has more or less the same form (Parker, 2018a, fig. 10), but this bone is not as long as in *Stagonolepis*.

Most pubes of Aetosauria described in literature are not well preserved or are covered by a mineral layer, which precludes additional preparation (see Appendix 1) to document the number, one or two, of pubic foramina. Moreover, in those cases where authors mentioned a single pubic foramen, the pubis may have been incomplete, lacking the part with the second foramen. Only in one species is the presence of two foramina very clear: *Scutarx deltatylus* (Parker, 2016b, fig. 21), which has two distinct holes. Walker (1961), who described two foramina in the pubis of *S. robertsoni*, based this on a reconstruction of two incomplete pubes (R4793 and MCZD4). For a long time, *Stagonolepis* from Elgin was the sole known aetosaur with two foramina. There are two holes in the described pubis of *Stagonolepis* from Krasiejów (see above), although not as pronounced as in *Scutarx deltatylus.* Small and Martz (2013) presumed the presence of two foramina in the pubes of *Stenomyti huangae*, because the edges were visible; those authors designated these as two obturator notches, but these could actually be two foramina. *Neoaetosauroides engaeus* has one well-marked foramen (Desojo and Báez, 2005), as does *Longosuchus meadei* (Sawin, 1947). Small (1985) drew only one in his reconstruction of the pelvic girdle of *Desmatosuchus smalli*, then described as *D. haplocerus*. The fragment of the pubis of *Calyptosuchus wellesi* has one foramen, but this piece is too small for detection of a possible second one (Case, 1922). With regard to the pubis of *Desmatosuchus spurensis*, Parker (2008, p. 18, fig. 20E) did show the region where the foramen should be, but 'the regions that should contain the obturator foramina are broken and incomplete, so the morphology of the foramina is indeterminate.'. It should be noted that Parker (2018a) described one foramen in the same pubis (MNAV9300).

On the basis of original descriptions and drawings/pictures, three species, maybe four *(Stenomyti huangae*) have probably two foramina and three with (most probably) one obturator foramen. However, Parker (2016a) listed in his tables for phylogenetic analysis (see below), four additional species with one foramen and one species with two foramina (Appendix 2), although the specimens he used are the same as the ones listed here. This information cannot be confirmed from the literature.

Ischium

Aetosaurian ischia are rare. In only ten species, a more or less complete ischium has been described. The morphology of this part of the pelvic girdle is the most uniform among aetosaurians. The general outline of ischium UOPB00154 of *Stagonolepis* (Fig. 13) is elongated and triangular, as in *Stagonolepis robertsoni*, *Aetosauroides scagliai* and *Aetosaurus ferratus*. However, the posteroventral blade in the latter is more concave (Schoch, 2007). The ischium of *Calyptosuchus wellesi* is shorter and thicker than the ischium of *Stagonolepis* and curves posterodorsally (Parker, 2018a). The curvature of the dorsal shaft of *Scutarx deltatylus* (Parker, 2016b) is also continuous from proximal to distal ends, while that of the ischium in *Stagonolepis* occurs only in the anterior part and continues as a straight shaft more posteriorly to the rugose region for muscle attachment. This rugose region is also visible in *Stagonolepis robertsoni* (Walker, 1961) and *Calyptosuchus wellesi* (Parker, 2018a). Also different is the ischium of *Polesinesuchus aurelioi*, which is more L-shaped (Roberto-da-Silva *et al*., 2014), while according to Heckert *et al*. (2010), the ischia of *Typothorax coccinarum* 'are strikingly short and somewhat gracile relative to the ilium', however, the rugose contact with the ilium (Fig. 13E), resembling that of *Stagonolepis robertsoni* (Martz, 2002). The most elongated aetosaurian ischium known is that of *Desmatosuchus smalli* (Small, 1985). All ischia are thicker dorsally than ventrally. The spindle shape of the acetabular contribution (Fig. 13C) is the same as in *Stagonolepis robertsoni*, while in *Polesinesuchus aurelioi* and *Calyptosuchus wellesi* this is more oval (Roberto-da-Silva *et al*., 2014; Parker, 2018a) and more rounded in *Scutarx deltatylus* (Parker, 2016b). The ischiadic symphysis of *Calyptosuchus wellesi* is not straight as in *Stagonolepis*, but sigmoidal (Case, 1922).

DISCUSSION

In lateral view, the orientation of the bones of the pelvis in *Stagonolepis* are 'ilium projected posteriorly, pubis vertical and ischium retroverted.' (Rasskin-Gutman and Buscalioni, 2001, p. 63). This type of orientation occurs in Archosauriformes and Crurotarsi. The ilium of *Stagonolepis* (Fig. 2, 6) is 'three-pronged' with an elongate preacetabular blade; this is a character that is peculiar to post-Early/Middle Triassic Archosauriformes, but not yet present in Early Triassic proterosuchids (Benton, 2015). The contact between ilium and pubis is a feature which disappears among basal crocodyliforms (Claessens and Vickaryous, 2012).

For the present study, four ilia were analysed, of two different sizes (see Tab. 2). The most distinctive difference, and an interesting character, is the angle between the lateral and ventral side of the postacetabular blade (poab-angle). This angle shows a dependence on the size of the ilium: the larger the ilium, the smaller the poab-angle (Tab. 3). There are no literature data on this angle, although the same character can be seen in pictures and drawings of ilia of other aetosaurs, for instance, in *Stagonolepis robertsoni* (Walker, 1961, fig. 15b), *Aetosauroides scagliai* (Fig. 14A), *Lucasuchus hunti* (Long and Murry, 1995, fig. 66I) and *Typothorax coccinarum* (Long and Murry, 1995, fig. 107). This angle is less clear in *Aetosaurus ferratus*, *Calyptosuchus wellesi* (Fig. 14B) and *Desmatosuchus* '*haplocerus'*. The difference in size and, thus also the poab-angle, could represent sexual dimorphism. However, it is more probable that these four ilia represent an ontogenetic series.

The two large ilia also differ from each other. UOPB01141 is thicker and more robust (Fig. 6), the morphology of the preacetabular blade (prab) is different, i.e. it is not flattened as in the three other ilia and as described by Walker (1961). This could be an expression of sexual dimorphism. Another difference lies in the attachment regions of the sacral ribs. The ilia UOPB00150 (Fig. 10), UOPB00149 and

UOPB00148 have an irregularity anteriorly and slightly more dorsally, i.e. a scar, which is not seen in UOPB01141. This could be another attachment area for a dorsosacral, in addition to the two primordial sacral ribs, in analogy to the morphology seen in the phytosaur *Smilosuchus adamanensis* (Griffin *et al*., 2017). Parker (2008) mentions the presence of fused dorsals in *Desmatosuchus*, *Longosuchus* and *Lucasuchus* and only two unfused sacrals in *Calyptosuchus*, *Neoaetosauroides* and *Typothorax*. Already in 2007, Parker insinuates fusion of the last presacral vertebra or not, can be due to sexual dimorphism.

A similar possible sexual dimorphism previously has been observed in cranial material by Antczak (2016), e.g., different shapes of lateral line remnants, distance from the dentary symphysis to the first tooth, character of the lateral surface of the mandible, tubercules at the posterior part of the parietals. Sexual dimorphism of the pelvic girdle has also been observed in many extant sauropsids. Except for size differences (females are usually larger than males) in some turtles, skeletal shape deformation and size of the pelvic aperture can be different in females, compared to males (Cordero, 2018). The different depth/width ratio of the pelvic canal between sexes has been described in recent crocodiles and been suggested to be synapomorphy of all archosaurs (Prieto-Marquez *et al*., 2007).

The description of the pelvic girdle of *Stagonolepis* in the present study is also of importance for phylogenetic analyses. In archosaur evolution, the skull and pelvis are key elements. Nesbitt (2011) analysed the early evolution of archosaurs, using 412 characters, 35 of which (8.5%) concern the pelvic girdle. Three species of Aetosauria are included in that analysis: *Stagonolepis robertsoni, Aetosaurus ferratus* and *Longosuchus meadei.* The pelvic characters of the three species are always equal. The bones used in the present study were compared with characters (where possible) listed in Nesbitt's analysis (2011) and those are the same as the characters of the species analysed. Thus, the distinctive features of the ilia, pubes and ischia of *Stagonolepis* from Krasiejów are the same as those of *Stagonolepis robertsoni, Aetosaurus ferratus* and *Longosuchus meadei* in a phylogenetic analysis of archosaurs.

The general morphology of the three bones, forming the pelvic girdle of *Stagonolepis* from Krasiejów, is identical to that of *Stagonolepis robertsoni*. There are no arguments for distinguishing two species on the basis of the pelvic girdle, nor on the basis of the skull (Antczak, 2016); a similar conclusion was reached after restudying specimens in the Warsaw collections (Lucas *et al*., 2007).

On the other hand, there are phylogenetic analyses of the Aetosauria. Here, differences with other aetosaurs were present because the characters are chosen to find out the relationship and affinities within the Aetosauria. Most phylogenetic analyses of aetosaurs (Desojo *et al*., 2012; Roberto-da-Silva *et al*., 2014; Schoch and Desojo, 2016; Hoffman *et al*., 2018) are based on the analysis of Parker (2007); unfortunately they include almost no axial and appendicular skeleton characters. The most comprehensive phylogenetic analysis is that of Parker (2016a), who compared 27 taxa, using 83 characters: 34 cranial, 16 axial/appendicular and 33 osteoderm. Only three characters concern the pelvis (3.6%). This phylogenetic study is the only one wherein *Stagonolepis olenkae* is mentioned. For *Stagonolepis olenkae,* two of the three characters are scored as unknown in his analysis. The first (50) is the number of foramina in the pubis (one or two). The upper foramen is the obturator foramen, the lower, more ventrally placed foramen, is the thyroid fenestra (Walker, 1961). Claessens and Vickaryous (2012, p. 1194) noted that, 'during the transition from basal archosauromorphs to crocodylomorphs, the obturator foramen/incisure for passing the obturator nerve is gradually lost'. Unfortunately, those authors did not consider aetosaurians in their description of the evolution of the pelvis. The second character ('51.) is the length of the symphysis more than one-half of the pubis length or shorter' (Parker 2016a). In phylogenetic analyses of archosaurs, these two characters are not applicable. Character 50, the number of foramina, can be filled in as being (1): two foramina. Character 51, the length of the symphysis, or the length of the medial fusion of the distal pubic blades, in *Stagonolepis* of present study*,* is shorter than one-half of the pubis length, thus (1), although Parker (2016a) stated this character to be (0) for *Stagonolepis robertsoni* (i.e. longer than one-half of the pubis length). This can have three reasons. This feature is not correctly interpreted, or it is an expression of sexual dimorphism reflecting another gender than considered in the present study. The third possibility is a single, effective difference between the pelvic girdles of *Stagonolepis robertsoni* of the Elgin area and *Stagonolepis* found in Krasiejów. Hitherto, no differences in the male and female pelvis of aetosaurians have been described.

The osteological description of the ilia and pubes of *Stagonolepis* from Krasiejów revealed a few other interesting characters. In general, the outline of the ilium and pubis is comparable to that of other aetosaurs, representing an intermediate morphology, except for the length of the preacetabular blade (Fig. 2), which is shorter than that of other aetosaurs. A property that had not yet been described in the group of Aetosauria is the presence of small foramina, dorsal of the supracetabular crest, measuring between 1 and 3.5 mm in diameter (Fig. 9). These foramina, which could be ligament attachments or nutrient foramina, have never been mentioned in descriptions of the ilia of aetosaurs. Either they do not occur in other aetosaurs and are thus taxon-specific, or are not visible (distortion, covering layer). Lastly, previous authors did not consider it worthwhile to report them.

The fine state of preservation and detailed preparation have revealed two pubic foramina (Fig. 11D) in the proximal part of the pubis, corresponding to the pubes of *Stagonolepis robertsoni* and *Scutarx deltatylus*, other aetosaurs of which the pubis is preserved reveal only a single foramen.

CONCLUSIONS

The skeletal material of the aetosaurs is comparatively poorly known. On the basis of the present study, the authors have a better understanding of both the genus and the group of the Aetosauria. Many studies of these reptiles have focused on the skull and osteoderms, but as in other Triassic archosaurs, there also are important traits and differences in the pelvic girdle, mainly in the ilium (Heckert and Lucas, 2002). Within the Aetosauria, the ischium is the bone with the most uniform outline.

The morphology of the pelvic girdle of *Stagonolepis* from Krasiejów is identical to that of *S. robertsoni*, which raises the questions of whether there are enough differences to distinguish *S. olenkae* as a separate species and the validity of ascribing postcranial material to species, established on the basis of cranial bones (Górnicki *et al*., 2021). In detail, the ilia and pubes of *Stagonolepis* from Krasiejów are different from those of aetosaurs from other localities, although comparisons are difficult because of a lack of complete aetosaurian pubes. Only the morphology of the ischia of different aetosaurs is more or less the same.

The results of the present study may contribute to the analysis of the phylogenetic tree. Two question marks (see Parker, 2016a) now can be removed for *Stagonolepis* from Krasiejów (*S. olenkae* in Parker's analysis): the number of pubic foramina, namely two, and the symphysis length, shorter than half of the total length of the pubis.

The description presented here raises important questions about sexual dimorphism and ontogeny in the aetosaurs. More research is needed in order to decide whether the differences in the poab-angle reflect growth stages or constitute differences between males and females. Differences in morphology of the ilia may illustrate sexual dimorphism. Additional data are needed to confirm the presence of the two foramina on pubis and the pubes symphysis length.

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Appendix 1

Published descriptions of aetosaurian pelvic girdle bones. Abbreviations: S. Am. – South America; EU – Europe; N. Am. – North America.

Species	Group	Conti-nent	Country/state	Author	Description of pelvis by	Ilium	Pubis	Ischium	Preser-vation	Synonymy
Aetosauroi-des scagliai	Most basal species	S. Am.	Argenti-na, Brazil	Casa-miquela (1960)	Heckert and Lucas (2002)	x	x	x	good, articula-ted	Identical to *Stagonole-pis robertsoni* (smaller specimens) and *S. wellesi* (larger ones), according to Heckert and Lucas (2002).
Polesinesu-chus aurelioi	Desmato-suchinae basal group	S. Am.	Brazil	Rober-to-da-Silva *et al.* (2014)	Rober-to-da-Silva *et al.* (2014)	x	part	x		
Stagonolepis robertsoni		EU	Scotland	Agassiz (1844)	Walker (1961); Parker (2018b)	parts	parts	x	casts made from natural moulds	
Stagonolepis from Krasie-jów		EU	Poland		Present paper	x	x	x	good	Described by Sulej (2010) as *S. olenkae* sp. nov., possibly synonym with *S. robertsoni.*
Neoaeto-sauroides engaeus		S. Am.	Argentina	Bonapar-te (1969)	Desojo and Báez (2005)	x	part	part		
Calyptosu-chus wellesi		N. Am.	Arizona, Texas	Long and Ballew (1985)	Long and Murry (1995); Parker (2018a)	x		parts	good	Alternative generic attribution: *Stagonolepis wellesi.*
					Case (1922); Parker (2018a)	x	part	x	good	
Scutarx deltatylus		N. Am.	Arizona	Parker (2016b)	Parker (2016b)	x	x	x	covered with he-matite	Initially (2011) assi-gned to *Calyptosuchus wellesi.*
Longosuchus meadei	Desma-tosuchini (spinose)	N. Am.	Texas	Sawin (1947)	Sawin (1947); Long and Murry (1995)	x	part	part	not well pre-served and slightly distor-ted	Alternative generic attribution: *Typothorax meadei.*
Lucasuchus hunti		N. Am.	Texas	Long and Murry (1995)	Long and Murry (1995)	x	part	parts		Heckert and Lucas (1999) suggested synonymy with *Longosuchus.*
Desma-tosuchus spurensis		N. Am.	Texas, Arizona, New Mexico	Case (1920)	Parker (2008)	x	x	x	thin crust of miner-als and slightly crushed	

Species	Group	Conti-nent	Country/state	Author	Description of pelvis by	Ilium	Pubis	Ischium	Preser-vation	Synonymy
(D. haplocerus)					Case (1922); Long and Murry (1995)	x				*D. haplocerus* is synonymous with *D. spurensis*. Form of ilia differ.
Desmatosuchus smalli		N. Am.	Texas	Parker (2005)	Small (1985)	x	x	x		Described as *D. haplocerus,* since Parker (2005) *D. smalli*.
Stenomyti huangae	Aetosaurinae basal group	N. Am.	Colorado	Small and Martz (2013)	Small and Martz (2013)		x		good	
Aetosaurus ferratus		EU	Germany, Italy, Greenland	Fraas (1877)	Schoch (2007)	x	x	x	well preserved, foramen not exposed	*Aetosaurus crassicauda* is a synonym.
Coahomasuchus kahleorum		N. Am.	Texas and North Carolina	Heckert and Lucas (1999)	Heckert and Lucas (1999)		part	part	half pubis, incomplete ischium	
Typothorax coccinarum	Paratypothoracini	N. Am.	New Mexico	Cope (1875)	Long and Murry (1995); Martz (2002)	x	x	part	quite good	
					Heckert *et al.* (2010)	part	part	part	in articulated skeleton	
(Typothorax antiquum)		N. Am.	New Mexico	Lucas *et al.* (2002)	Lucas *et al.* (2002)	x		x		Synonym of *Typothorax coccinarum.*
Paratypothorax sp.		N. Am.	Arizona, Texas		Long and Murry (1995)	part			broken	

Appendix 2

Summary of collection numbers and measurements of published aetosaurian pelvic bones. All measurements in mm. () – distorted; * – incomplete thus estimated. ? – number of foramina according to Parker (2016a). Symphysis length (Parker, 2016a) – long, more than one-half (0); short, less than one-half of the element length (1).

Species	Body length [m]	Ilium								Pubis							Ischium			Remarks
		Catalogu-enumber	Prab exceeds pp?	Lib	H	Aac	Hsa	Prab	Neck	Catalogue number	L	Width prox. expan-sion	Wn	Wwd	# Fo-ramina	Symphisis acc. to Parker, 2016a / authors	Catalogue number	L	H	
Aetosau-roides scagliai	1–2.5	PVL 2073	yes?							id.					1?	0/long	id.			Obturator foramen in pubis not visible (dam-aged).
Polesine-suchus aurelioi		ULBRA-PVT003	slightly	50.5		19.5	10.4			id	(50)	(20.5)		15*	2?	1/short	id	37	22*	Juvenile. Rober-to-da-Silva *et al*. (2014) writes that foramen is not visible.
Stago-nolepis robertsoni	2.7	GSM 90849 + EM 46R	no	207	146				80	R 4793 + MCZD 4	195			77	2	0/long	GSM 90851 + R 4804		108	Obturator foramen and thyroid fenestra. Drawings pelvis composed of a lot of incom-plete parts.
	2.1	R4789		159	118				62	MCGD2	146						R4790		82	
Stagono-lepis from Krasiejów		UOPB 01141	no	223	170	105	65	42		UOPB 01143	220	65.5	25.7	119	2	? /short	UOPB 00154	155	76	
Neoaeto-sauroides engaeus	2.5?	PVL 3525	yes							id					1	?	id.			
Calyptosu-chus wellesi	3	UCMP A 269/32422	slightly	180			52	50		UCMP 32150						0/long	UCMP A269/ 32148	110	97	Pubis, obturator flange broken away.
		UMMP 7470	equal							id							Id.			Case (1922) writes about 1 pubic foramen.
Scutarx deltatylus		PEFO 34919	no	196			66.8									0/long				
		PEFO 31217	no	188.6		116.5	67.4			id					2		PEFO 31217	183		
Longosu-chus meadei	3	TMM 31185–40	no							id					1	? /long	id			Info of foramen in Sawin (1947).
Lucasu-chus hunti	3.5	TMM 31100–1	no							TMM 31100–313						?	id			
Desmato-suchus spurensis		MNA V 9300	yes							id					1?	0/long	id			Regions with foramen are broken (Parker, 2008).
(described as *D. 'haplo-cerus'*)	4–5	UMMP 7322	equal							/							/			Ilia of *D. spurensis* and *D. haplocerus* does not resemble.
Desmato-suchus smalli	5	TTUP 9172	no	270	170	100				id	330	145		75	1	?/long	id			Described as *D. haplocerus*. Small (2002) does not write something about foramina but the author draws 1. Drawing made of 2 incomplete pubes.

Species	Body length [m]	Ilium								Pubis							Ischium			Remarks
		Catalogu-enumber	Prab exceeds pp?	Lib	H	Aac	Hsa	Prab	Neck	Catalogue number	L	Width prox. expan-sion	Wn	Wwd	# Fo-ramina	Symphisis acc. to Parker, 2016a / authors	Catalogue number	L	H	
		TTUP 9024	no	250	170	100				id	330	145		75			id	310	175	
Stenomyti huangae		/								in DMNH 34565					2	?/0.5	/			2 obturator not-ches. Although the proximal part of the thin posterior edge seems to be complete, there is no evidence of single or paired obturator fenestrae.
Aetosaurus ferratus	1.5	SMNS 5770								id						1/ short	id			Foramen not exposed.
Coahoma-suchuska-hleorum	<1	/								in NMMNH P–18496						?	Id.			
Typothorax coccina-rum	2–3	UCMP V2816 122683								UCMP V2816 34248					1?	1/ short	TTUP 9214			Region with foramina not preserved.
		NMMNH P–12964								id.							id.			
Typothorax antiquum		NMMNH P–36075		125	98	45											id			Ilium does not look like *T. coccinarum*.
?Paratypo-thoraxsp.		DMNH 9938	equal							/							/			Long and Murry (1995) are not sure of species.