Osteology of a forelimb of an aetosaur *Stagonolepis olenkae* (Archosauria: Pseudosuchia: Aetosauria) from Krasiejów locality in Poland and its probable adaptations for a scratch-digging behaviour

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Abstract

Aetosaurs are armo~~u~~red basal archosaurs that played a significant role in land ecosystems during the Late Triassic (237–201 Ma). The polish species *Stagonolepis olenkae* Sulej, 2010 described from the Krasiejów locality (southern Poland) is one of the oldest known representatives of the group. Abundant and well-preserved material, including partially articulated specimens, allows a detailed description of forelimbs in this species. The forelimbs of *Stagonolepis olenkae* are the most similar to that of large aetosaurs like *Desmatosuchus smalli*, *Desmatosuchus spurensis*, *Longosuchus meadei*, *Typothorax* ~~*cocinarum*~~*coccinarum* or *Stagonolepis robertsoni.* Several characters recognized in the forelimbs of *Stagonolepis olenkae* suggest its adaptation for scratch-digging. The most indicative are: short forearm, carpus, and hands, with the radius shorter than the humerus, carpus and manus shorter than the radius (excluding terminal phalanges); a prominent deltopectoral crest that extends distally on the humerus and a wide prominent entepicondyle, a long olecranon process with well-marked attachment of triceps muscle; hooked, laterally compressed, claw-like terminal phalanges with ornamentation of small pits (indicative of well-developed keratin sheaths).

Stagonolepis olenkae might have used its robust forelimbs to break through the compacted soil with its claws and proceed the digging in search of food in softened substrate with the shovel-like expansion at the tip of its snout. The entire forelimb of *Stagonolepis olenkae* is covered by osteoderms, including the dorsal surface of the hand, which is unusual among aetosaurs and have not been noted for any species up to date.

Key words

Archosauria, Aetosauria, forelimb, manus, carpus, Krasiejów, scratch-digging

Introduction

Aetosaurs are heavily armoured, quadrupedal basal archosaurs cladistically nested within Pseudosuchia, the crocodile lineage of archosaurs (e.g., Brusatte *et al.* 2010; Nesbitt 2011; Desojo *et al.* 2012, 2013). They are medium to large sized animals (1–6 m long) with semi-erect to erect gait (Parrish 1986; Desojo and Baéz 2005; Desojo and Vizcaíno 2009; Padian *et al.* 2010; Desojo *et al.* 2013). Their most characteristic feature is the suit of dermal armour composed of rectangular, plate-like osteoderms, which cover the dorsal and partially the lateral surfaces of their bodies, and in more heavily armoured species also the belly, ventral surfaces of the tail and the limbs (e.g., Walker 1961; Desojo *et al.* 2013,). Presumably, the aetosaurs are considered to be omnivores but their exact mode of life is not clear yet. In most species (with the exception of ~~of~~ *Aetosaurus ferratus*) the triangular skull is equipped with a shovel-like expansion at the tip of tapering snout (e.g., Desojo and Vizcaíno 2009; Sulej 2010; Desojo *et al.* 2013). They probably used this shovel-like expansion to dig their food out of the ground (e.g., Walker 1961; Sulej 2010; Desojo *et al.* 2013), likely utilizing limbs in the process (Heckert *et al.* 2010). Aetosaur~~s’~~ fossil remains are restricted in occurrence to the continental Upper Triassic (Carnian–Rhaetian) (e.g., Heckert and Lucas 2000; Desojo *et al.* 2013). They are known from several localities in Europe, India, Africa, and both Americas, which makes them one of the most widespread groups among pseudosuchians in the Late Triassic (e.g., Desojo *et al.* 2013).

In Poland, ~~the~~ aetosaurs have been reported from two localities in southern part of the country: Krasiejów and Poręba. The material described from Poręba is restricted to few osteoderms and a vertebra, which hampers further studies and attempts of taxonomical affiliations (Sulej *et al.* 2012). In contrast, the aetosaur collection from Krasiejów is very rich and provides several cranial and numerous postcranial specimens of different size and probably different ontogenetic age. Although the material is so abundant, there is some controversy over its taxonomical affiliation. In the detailed description of the skull by Sulej (2010), the aetosaur from Krasiejów has been recognized as a new species, *Stagonolepis olenkae* Sulej, 2010, similar to *Stagonolepis robertsoni* Agassiz, 1844 from Elgin, Scotland. Further work by Książkiewicz (2014) on the postcranium of the Krasiejów species also supported this thesis. However, Antczak (2015) suggested synonymy of *S. olenkae* and *S. robertsoni* based on a new skull material. He argued that previously recognized differences represent intraspecific variations or sexual dimorphism. Quite different results were shown by the cladistic analysis by Parker (2016, 2018), also based on the cranial material. It placed *S. olenkae* and *S. robertsoni* on two distant branches of the tree, implying that they may even represent distinct genera. I also recognized some small differences between those two species, but after personal examination of material assigned to both species I have to admit that differences in the postcranium of those two species are minor in general and difficult in interpretation, mostly due to small amount and incompleteness of the preserved elements in Scottish material and its likely younger ontogenetic age, as suggested by smaller sizes of the specimens and some other indicatives (e.g., lack of fusion between the elements of the axial skeleton or pectoral girdle). Until some more comprehensive taxonomic and ontogenetic study is performed and the definitive answer is found, I follow the division into two species proposed by Sulej (2010) and I assign the aetosaur forelimb elements described in this study to *Stagonolepis olenkae.*

In general, fossils of aetosaur forelimbs are less abundant than those of the hind limbs. In spite of that, the long bones of the forelimbs are recognized and well-described in several species (e.g., Sawin 1947; Walker 1961; Bonaparte 1971; Lucas *et al.* 2002; Schoch 2007; Heckert *et al.* 2010; Roberto-Da-Silva *et al.* 2014). Much less is known about aetosaurs' manus and carpus. In fact, those parts are described in detail only for *Stagonolepis robertsoni*, *Longosuchus meadei*, ~~*Thyphothorax*~~*Typothorax coccinarum* and recently *Stagonolepis olenkae* (Sawin 1947; Walker 1961; Lucas and Heckert 2011; Książkiewicz 2014; this study), but associated metacarpals with elements of carpus are known also for *Aetosaurus ferratus* (Schoch 2007). The material of *Stagonolepis olenkae* currently consists of a several isolated humeri, radii and ulnae, and few specimens with associated forearm, hand and carpal elements. Two of those specimens are illustrated by Książkiewicz (2014) in his doctoral thesis, and four are described and illustrated in this study.

Based on the literature, large and middle size aetosaurs (over 2 m in length), like *Longosuchus meadei*, *Stagonolepis olenkae*, *Stagonolepis robertsoni*, and *Typothorax coccinarum*, have forelimbs more similar to each other than to that the small~~ ones~~er aetosaurs (below 1 m in length), like *Aetosaurus ferratus* and *Polesinesuchus aurelioi* (Sawin 1947; Walker 1961; Schoch 2007; Heckert *et al.* 2010; Roberto-da-Silva 2014). However, in all species the forelimbs are shorter than the hind limbs, robust and strongly-built, with the humerus longer than the forearm bones, and the radius and ulna of comparable length (e.g., Sawin 1947; Walker 1961; Heckert *et al.* 2010; Desojo *et al.* 2013,). The humerus has a wide, well-defined head and a prominent deltopectoral crest (e.g., Heckert *et al.* 2010; Desojo *et al.* 2013). The ulna and radius are straight and the olecranon process of the ulna is usually high (e.g., Desojo *et al.* 2013). In the hand of known species, metacarpals and phalanges are short and wide, and the digits are finished with claw-shaped unguals (e.g., Sawin 1947; Walker 1961; Desojo *et al.* 2013). The probable phalangeal formula is 2-3-4-5-3 (Walker 1961; Desojo *et al.* 2013) with the fifth digit much smaller than the others (Lucas and Heckert 2011). The carpus consists of few (probably four) bony components (Sawin 1947; this study). The most characteristic carpal element that distinguishes aetosaurs' carpus from this of other pseudosuchians, is a large bone adjacent to radius, probably fused radiale and intermedium (Sawin 1947; Walker 1961; Schoch 2007; Książkiewicz 2014, this study).

Probable usage of the forelimbs for digging was already suggested for *Stagonolepis robertsoni* by Walker (1961), based on the presence of short manus and an excavation below the proximal end of the ulna. Adaptations for digging has been more comprehensively discussed by Heckert *et al.* (2010) in respect to *Typothorax coccinarum*, known from almost complete and articulated skeletons. *T. coccinarum* possesses five of eleven characters that, according to Hildebrand (1988), indicate a digging behaviour in modern vertebrates, namely: a low brachial index (radius shorter than humerus), (1) a prominent deltopectoral crest that extends distally on the humerus, (2) a wide entepicondyle, (3) short and wide metacarpals, (4) short and wide phalanges (Heckert *et al.* 2010). In addition they pointed out that compact and strongly articulated foot with a large, curved and laterally compressed unguals could have been used for scratch-digging, as it was suggested for the rhynchosaur *Hyperodapedon* (Heckert *et al.* 2010, Benton 1983). Based on the presence of such digging adaptations in *T.* ~~*coccianrum*~~*coccinarum*, it is suggested that it might have used its limbs to unearth roots or burrowing invertebrates (Heckert *et al.* 2010; Desojo *et al.* 2013). The digging features mentioned for *T.* ~~*coccianrum*~~*coccinarum* are also present in the forelimbs of *Stagonolepis* *olenkae*, but the latter also has other characters that are indicative more specifically for scratch-digging, according to Hildebrand (1983, 1988, Heckert *et al.* 2010).

The postcranial skeleton of *Stagonolepis olenkae*, including forelimbs, has been described by Książkiewicz (2014) in his doctoral thesis. However, the research conducted for my paper was done independently ~~from~~ of his studies, and is based on different material (with exception of hand elements of the specimen ZPAL AbIII/2071, which were only mentioned in his thesis but have not been illustrated). I have personally examined the material used by Książkiewicz, but since he wishes to publish his thesis soon, I will make only necessary references to his work, which have an impact on the subject of my paper. My work contains more detailed description of the *S. olenkae* forelimbs and debate the probable scratch-digging behaviour in this species, which is not discussed by Książkiewicz (2014).

Geological settings

Krasiejów is located at the southern-eastern edge of the fore-Sudetic Homocline in Opole Voivodeship (Upper Silesia), SW Poland. This was the first of the series of Late Triassic localities in Silesia containing bones of large vertebrates discovered near the end of the 1990s, supplemented later by the Lisowice, Poręba, Woźniki, and Marciszów localities in the beginning of the 2000s (Dzik *et al.* 2000, 2008; Dzik 2001; Budziszewska-Karwowska *et al.* 2010; Niedźwiedzki *et al.* 2012; Sulej *et al.* 2012; Szczygielski and Sulej 2016; Szczygielski 2017). The outcrop is located in an unoperational clay pit. The exact age of the beds exposed at Krasiejów is not certain. Originally, a late Carnian age was proposed, based on biostratigraphic evidence (Dzik *et al.* 2000; Dzik and Sulej 2007, 2016; Zatoń *et al.* 2005; Kozur and Weems 2010), but the lithostratigraphic correlations suggest the Norian age (Szulc *et al.* 2015).

Rocks deposited in Krasiejów consist mostly of red to red-brown or gray siltstones and mudstones. Alternating series of red and gray rocks indicate a seasonal climate with dry (red) and wet (gray) periods (Szulc 2005; Gruszka and Zieliński 2008). Lenses of fine-grained sandstone and calcareous concretions (often containing bones) as well as several palaeosol horizons (Szulc 2005) occur in the section. Below the level of the outcrop the presence of gypsum was reported (Szulc 2005).

The Krasiejów locality is one of the ~~biggest~~largest accumulations of fossil vertebrates in central Europe. Specimens gathered from this locality are counted in the thousands. In addition to *Stagonolepis olenkae*, the Krasiejów fauna includes temnospondyls *Metoposaurus krasiejowensis* and *Cyclotosaurus intermedius*, basal archosaurs including a rauisuchian *Polonosuchus silesiacus* and a phytosaur *Paleorhinus* (=*Parasuchus*) sp., a dinosauromorph *Silesaurus opolensis*, a gliding protorosaurid *Ozimek volans*, fishes, and invertebrates (Dzik *et al.* 2000; Dzik 2001, 2003a, 2003b, 2008; Sulej 2002, 2005, 2007, 2010; Sulej and Mayer 2005; Dzik and Sulej 2007, 2016; Brussatte *et al.* 2009; Piechowski and Dzik 2010; Skrzycki 2015). Plant remains are rare (Dzik *et al.* 2000; Dzik 2003b; Dzik and Sulej 2007; Pacyna 2014).

The majority of vertebrate fossils are accumulated in two bone-bearing horizons (e.g., Dzik *et al.* 2000; Dzik and Sulej 2007; Szulc 2007; Bodzioch and Kowal-Linka 2012). The lower bone horizon is about 1 m thick, with a grey bed (about 0.3 m thick) at the bottom that is distinct from the red paleosol series below it, and the red bed in its upper part covered mostly by a layer of calcareous grainstone and fluvial variegated sediments above. Most of the vertebrate fossils are preserved at the boundary of the red and grey sediments within this bone horizon. Horizontal layering of sediments indicates its deposition in open standing water (Dzik *et al.* 2000; Dzik and Sulej 2007; Gruszka and Zieliński 2008). In this bone level, fossils of aquatic vertebrates dominate: *Metoposaurus krasiejowensis, Cyclotosaurus intermedius*, and the phytosaur (Dzik *et al.* 2000; Dzik 2003b; Dzik and Sulej 2007). Remains of terrestrial animals are less frequent, although common (e.g., *Stagonolepis olenkae*, *Silesaurus opolensis*) (Dzik *et al.* 2000; Dzik 2003b; Dzik and Sulej 2007). According to Bodzioch and Kowal-Linka (2012), the lower bone level was deposited by a single short-lived, high energy event, probably a flood, which is contradicted by strictly horizontal intercalations of grainstone.

The upper bone horizon (a few meters above the lower one) is a lenticular red mudstone body within fluvial deposits. In contrast to the lower bone horizon, ~~land~~ terrestrial vertebrates dominate there, whereas aquatic ones are rare (Dzik 2003b, Dzik and Sulej 2007).

Material and methods

Four specimens with elements of forearms, carpus and hand preserved in association as well as several various isolated forelimb bones were examined. All humeri used in this study were found isolated. The studied material comes from both bone bearing horizons at the Krasiejów locality. It is a part of the collection of the Institute of Paleobiology, Polish Academy of Sciences in Warsaw. ~~Complete~~ A complete list of specimens with the description, measurements, photographs and taphonomical notes are provided in supplementary online materials (Appendix online 1-3, supplementary Figures 1-9).

Specimens were recognized as representing aetosaurs based on the general morphology of the long bones, the relative proportions between the different elements, the presence of wide, well-defined head and prominent deltopectoral crest in the humerus, the presence of a long olecranon process in ulna, the presence of fused radiale and intermedium in the carpus, the massive and thick digits, and the presence of osteoderms. Isolated bone elements were

Commented [WGP1]: Parker (2012) discusses how to differentiate aetosaur and phytosaur humeri and ulnae. Parker, W. (2012). Redescription and taxonomic status of specimens of Episcoposaurus and Typothorax, the earliest known aetosaurs (Archosauria: Suchia) from the Upper Triassic of western North America, and the problem of proxy “holotypes”. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh, 103*(3-4), 313-338. doi:10.1017/S1755691013000212 identified based on comparison with specimens preserved in association~~s~~, if possible. All were referred to *Stagonolepis olenkae*, as there is only one species of aetosaur described thus far from Krasiejów.

All specimens were cleaned from the surrounding sediment mechanically (with a pneumatic airscribe,~~r~~ PaleoTools model ME-9100) and chemically (with 5% formic acid). Three dimensional models of five specimens were obtained utilizing photogrammetry method with ~~usage~~ use of several freeware programs (FastStone Photo Resizer, VisualSFM, MeshLab, Texture Stitcher, and DazStudio) and then implemented into .PDF files with Adobe Acrobat (Cignoni *et al.* 2008; Chuang *et al.* 2009; Furakawa and Ponce 2010; Wu 2011; Khazdan and Hoppe 2013). Detailed description of the process and 3D PDFs are provided in the supplementary materials (Appendix online 4-9).

Results: Osteological description of the forelimbs of the aetosaur *Stagonolepis olenkae*

Proportions and general description of the forelimb bones

Forelimb elements of *Stagonolepis olenkae* are ~~usually~~ smaller than the corresponding elements of the hind limbs, therefore the entire forelimb must have been shorter than hind limb (personal observation; Książkiewicz 2014). The humerus (Fig. 1) is two-thirds the length of the femur (Książkiewicz 2014). Although there are no humeri found in articulation with radius and ulna, it can be assumed that humerus in *Stagonlepis olenkae* is longer than each of the forearm bones, based on the comparison of several specimens (personal observation, Ksiażkiewicz 2014). ~~Radius~~ The radius and ulna are orientated parallel to each other (Fig. 2; based on spec. ZPAL AbIII/2407). The ulna is longer than the radius and more massive. The ratio of length between the radius and the ulna in the specimen ZPAL AbIII/2407 is 0.85.

Commented [WGP2]: Which specimens?

~~Proximal~~ The proximal ends of the radius and ulna form a single articulation surface for the humerus. The joint between the radius and ulna is elongated and crescent-shaped (Fig. 3, 4; based on spec~~.~~ imen ZPAL AbIII/3351, 3322), which ~~probably~~ seemingly makes the relative rotation of these two bones impossible. The olecranon process of the ulna is high (Fig. 2, 3; based on spec. ZPAL AbIII/2407, 2014, 3351) and in large specimens of humeri the olecranon fossa is present (Fig. 1; spec. ZPAL AbIII/1175, 257). Based on specimen ZPAL AbIII/2407 (Fig. 2) the manus together with the carpus is shorter than both the ulna and the radius. The carpus consist of at least four bone elements. The largest one of them is probably a fused radiale and intermedium (Fig. 5; spec. ZPAL AbIII/2071, 2407, 3349, 3350). It is connected with the radius and partially with the ulna at the forearm side and the metacarpals I-III and probably IV at palm side. Its arrangement prevents rotation movements of the carpus and restricts moves of the carpal joint only to a one sagittal plane. Metacarpals and phalanges (Fig. 6) are stout, relatively short and wide. Medial digits (II, III, IV) are almost of equal length and they are noticeably longer than digits I and V, while digit I is longer than digit V. Digit I is the most robust in the manus, the medial digits are of similar form and massiveness, while digit V is the tiniest one in the hand~~-~~. The phalangeal formula is probably 2-3-4-5?-3? and at least digits I to III ~~are~~ terminate ~~ended~~ with claw-like unguals (Fig. 6, mostly based on spec. ZPAL AbIII/3349 and 2071). Ungual of the first digit is the largest one and it is much bigger than the rest. Ungual of the second digit is about one-third smaller than the first one, and the sizes of following unguals decrease in the same pattern (Fig. 6; based on spec. ZPAL AbIII/3349, 2071). The dorsal part of the hand, forearm and probably also arm is entirely covered by osteoderms (Fig. 6; based on spec. ZPAL AbIII/2407, 3349, 3350).

Humerus

The humerus of *Stagonolepis olenkae* (Fig. 1), represented in the specimens ZPAL AbIII/257, 1175, 2627, is a massive~~, strongly build~~ bone with a straight shaft and well-defined, wide, proximal and distal head. The shaft is twisted ~~through~~ about 30 degrees, so that the distal end faces backward as well as upward. The proximal head expands into the coronal plane, mostly medially, and is very wide, almost half of the length of the entire bone – the ratio of the medio-lateral width of the humeral head to the entire length of the bone is about 0.54 (spec. ZPAL AbIII/1175, 2627). Its articulation surface is convex and it is covered by multiple irregularly arranged tubercles of random size, which indicate the presence of a well-developed cartilaginous cap (spec. ZPAL AbIII/2627). The medial process of the proximal head forms an internal tuberosity (it is almost as robust as the articular thickening). It is separated from the main articulation surface by a pronounced indentation (spec. ZPAL AbIII/1175, 2627). Below the articulation surface of the proximal head the shaft gently slopes forming a short neck. Under the medial process the neck forms a thin lamina. ~~Deltopectoral~~ The deltopectoral crest is well-developed. It starts below the level of the articulation surface of the humeral head and below the level of the internal tuberosity (spec. ZPAL AbIII/1175, 2627). The shaft in ~~the~~ medial/lateral view remains straight throughout its entire length. In ~~the~~ proximal/ventral view, the medial edge of the humerus forms an arch. The arch is strongly bent, toward the lateral and distal side, in the proximal portion of the shaft, then fluently transits into almost straight line in the middle portion of the shaft, and bends again, toward the medial and distal side, above the medial epicondyle. The shaft expands laterally, in the regions of the deltopectoral crest and the lateral epicondyle, but the expansion is not as significant as on the medial side (spec. ZPAL AbIII/1175, 2627). The wide proximal portion of the shaft is much thinner than the middle and distal section. Its thickness increases gradually from the neck of the proximal head, up to the end of the deltopectoral crest. On the dorsal surface of the shaft, next to the deltopectoral crest, there is an elevation, which in the specimen ZPAL AbIII/2627 is ornamented by delicate grooves. On the dorsal side, distal to the elevation, close to the medial edge, an elongated knob is present. The ventral side of the shaft in the proximal section is smooth (spec. ZPAL AbIII/1175, 2627). The middle section of the shaft, below the deltopectoral crest up to the epicondyles, is close to oval in cross-section and of uniform thickness and width. On the dorso-lateral surface there is a straight furrow that originates in the elevated area next to deltopectoral crest and continues up to the epicondyle (spec. ZPAL AbIII/1175, 2627). The distal head of the humerus is much narrower than the proximal head, being about 0.6 the length of the proximal head and 0.25 the length of the entire bone. The entepicondyle is wide. The ectepicondylar groove on the lateral side is fully exposed and deep (spec. ZPAL AbIII/257, 1175, 2627). The supinator process is thick and prominent (spec. ZPAL AbIII/257). In large specimens the olecranon fossa is present (Fig. 11). In specimens ZPAL AbIII/257 olecranon fossa is not fully enclosed as in spec. ZPAL AbIII/1175. The distal head is eight-shaped in distal view. Its articulation surface is covered by multiple irregularly arranged tubercles of random size, which indicate the presence of well-developed cartilaginous cap (spec. ZPAL AbIII/257, 2627).

Ulna

The ulna of *Stagonolepis olenkae* (Fig. 2, 3) represented by the spec~~.~~imen ZPAL AbIII/2407, 3349, 3350, 1100/1, 1179, 2014, and 3351, is straight and dorso-ventrally flattened. The proximal portion of the shaft is triangular in cross-section and it is wider and thicker than the middle and distal portion. The olecranon process is long (around 0.2 of the total ulna length in the spec~~.~~imen ZPAL AbIII/2407 and 3351), but probably it was even longer as on its top there is a tubercular area, which indicates the presence of well-developed apical cartilage (Fig. 3; ~~spec.~~ ZPAL AbIII/2407, 2014, 3351). The tubercles are of different size and are irregularly arranged. The articular surface for the humerus concaves rapidly behind the tubercular area of olecranon process towards the coronoid process, where it becomes almost flat (Fig. 3; ~~spec.~~ ZPAL AbIII/2407, 2014, 3351). The coronoid process is elongated medially and prominent. The articular surface for the radius (on the dorsal side, below the coronoid process) is elongated and crescent-shaped (Fig. 3; ~~spec.~~ ZPAL AbIII/2014, 3351). The area below the olecranon process is covered by irregularly arranged and strongly marked series of pits and grooves (Fig. 2, 3); ~~spec.~~ ZPAL AbIII/2014, 2407, 3351). In crocodiles, this area is the insertion point for the triceps muscle (Meers 2003). The presence of strongly marked structures in this region suggests that the triceps muscle must have been well-developed in *Stagonolepis olenkae*. There is ~~an~~ another small ornamented area (with an ornamentation of small pits and grooves) on the dorsal side of the ulna, in the proximal part of the shaft, distal to the articular surface for the radius (Fig. 2, 3; ~~spec.~~ ZPAL AbIII/2014). Its ornamentation consists of small pits and grooves. The shaft in the middle section forms two parallel, almost flat surfaces (on the dorsal and ventral side) and (in dorsal/ventral view) slightly tapers symmetrically towards the distal end of the ulna, where a delicate neck can be distinguished (Fig. 3; ~~spec.~~ ZPAL AbIII/1100/1, 1179, 2014, 2407, 3351). The lateral edge of the shaft in the middle section is smooth and rounded. The medial edge of the shaft, in the middle section, ends with a furrow that initiates below the articular surface for the humerus and the radius, continues throughout the middle portion of the shaft and weakens towards the distal end of the ulna. The cross-section of the shaft, in the upper part of the middle section, is similar to irregular pentagon with two parallel sides (dorsal and ventral surfaces of ulna) and sharp edge oriented medially (where the furrow is). The shape of the cross-section changes towards the distal end of the ulna and becomes more oval. On the dorsal side of the ulna, in the middle section of the shaft, two other well marked longitudinal furrows can be recognized (Fig. 2, 3). The first furrow on the dorsal surface, situated next to the lateral edge of the bone, continues almost through the entire length of the shaft and is arched laterally in the dorsal view. The other one, situated next to the medial edge of the bone, is straight and continues only through the middle section of the shaft. The ventral surface of the ulna forms a single flat plane with a small longitudinal depression in the middle. The plane continues through the proximal and the middle section of the shaft. In the distal part, distal to the delicate neck, the shaft slightly expands and gently twists (Fig. 3). In the distal view, the shape of the surface for the wrist bones is regularly oval (Fig. 3; ~~spec.~~ ZPAL AbIII/2407, 3349). Similar to the proximal end, the distal end of the ulna was also partially cartilaginous. Its bony surface is covered by irregularly distributed tubercles, although much smaller than those in the region of the olecranon process (~~spec.~~ ZPAL AbIII/2407, 3349, 3351). Distal to the neck on the ventro-medial side, there is a prominent oval ornamented area (Fig. 3; ~~spec.~~ ZPAL AbIII/3351). Its ornamentation consists of small, irregularly arranged pits and grooves.

Radius

The radius (Fig. 4) represented by the spec~~.~~imen ZPAL AbIII/1628, 2407, 2016/2, 2016/4, 3322, 3349, 3350 is shorter than the ulna and longer than the manus. The ratio of length between the radius and the ulna in the spec~~.~~imen ZPAL AbIII/2407 is 0.85 (Fig. 2). The shaft is straight and of almost uniform thickness throughout its entire length, except for the proximal and the distal ends, where it expands in a funnel-like manner. In the dorsal/ventral view the proximal and distal ends are of the same width (~~spec.~~ ZPAL AbIII/3322).

The articulation surface for the humerus is orientated perpendicular to the shaft and in proximal view it is semi-rounded. Its surface is almost flat, with a tiny depression in the centre and a small process at the lateral edge. The articulation surface for the ulna is crescent shape and extends longitudinally (~~spec.~~ ZPAL AbIII/3322). The middle portion of the shaft is semi-square in cross-section. Two corresponding, sharp, well-marked furrows are present on the dorsal and the ventral side of the shaft (~~spec.~~ ZPAL AbIII/3322). Both furrows are s-shaped, which gives the impression that the shaft is twisted helically. Two furrows of similar pattern, but much less distinct, are also present on the lateral and the medial side of the shaft. The bony surface of the articulation area with the carpus is semicircular in the distal view (~~spec.~~ ZPAL AbIII/2106/2, 2407, 3322). Its surface is covered by irregularly arranged tubercles (~~spec.~~ ZPAL AbIII/2106/2), similar to those present on the olecranon process of the ulna and the humeral heads, but smaller. Presence of the tubercles indicates a well-developed cartilaginous finish.

Carpus

The carpus consists of at least four bony elements, probably oriented in two rows (Fig. 6). The largest carpal bone is the fused radiale and intermedium (Fig. 5), present in the spec~~.~~imen ZPAL AbIII/2407, 3349, 3350, 2071, which probably forms the proximal row with the narrow, square-shaped ulnare, present in the spec~~.~~imen ZPAL AbIII/2407, 3349, 3350, and 2071. The second row consist of at least two bony distal carpals (present in the spec~~.~~imen ZPAL AbIII/2071, 2407 (only one), 3349, and 3350), among which one is larger and crescent-shaped and the second one much smaller and pea-shaped.

The fused radiale and intermedium (Fig. 5) is a thick bone, elongated in the coronal plane. It proximally face the radius and partially the ulna, and was adjacent distally to metacarpals I, II, III, and partially IV (Fig. 6; based on ~~the spec.~~ ZPAL AbIII/2407, 3349). Książkiewicz (2014) described a single specimen (UOBS 02609), in which the radiale and the intermedium are separated, but he suggested that the bone is probably broken. The radiale and intermedium are joined together by a suture (~~spec.~~ ZPAL AbIII/2071). The suture is less significant or totally fades in the ventral and middle portion of the bone, which suggests a continuous process of fusion of both elements. It seems that the two bones initially ossified separately and fused later in ontogeny. For the purpose of further description, the suture will be used as reference point dividing the bone in two sections: the one corresponding to the radiale and the second corresponding to the intermedium. In the proximal/distal view the section corresponding to the radiale is semi-oval or rounded and the section corresponding to the intermedium is rectangular. In this view, the section corresponding to the radiale is much larger than the section corresponding to intermedium. In the dorsal/ventral view the shape of the fused radiale and intermedium is close to rectangular. On the proximal side of the bone (facing the forearm), at the section corresponding to the radiale, the surface forms a prominent ridge surrounding the centre of the section dorsally and laterally (~~spec.~~ ZPAL AbIII/2071). Farther, on the proximal side at the section corresponding to the intermedium, a modest but distinct elevation is present. The elevation originates at the middle of the proximal articulation surface, and continues towards the dorsal edge of the bone forming a process-like structure. On the distal side (facing the metacarpals), at the section corresponding to the radiale, there is a large, prominent tuber (~~spec.~~ ZPAL AbIII/2071). The tuber originates in the middle of the articulation surface, and continues towards the distal edge, covering little less than a half of the section corresponding to the radiale. Excluding the tuber region, the articulation surface of the distal side of the fused radiale and intermedium forms an almost uniform plane, with a modest elevation close to the dorso-lateral edge and in the section corresponding to the intermedium (~~spec.~~ ZPAL AbIII/2071, Fig. 5). On the dorsal surface of the fused radiale and intermedium, two distinct areas are visible, one at the section corresponding to the radiale, and one at the section corresponding to intermedium (Fig. 5, 6; ~~spec.~~ ZPAL AbIII/2071). The area in the section corresponding to the radiale is flat with a small depression in its central part. It continues through the lateral and partially the ventral side of the section. The area in the section corresponding to intermedium forms a deep depression. Opposite to it, on the ventral side of the section corresponding to the intermedium, there is another area that forms depression but it is smaller and shallower (~~spec.~~ ZPAL AbIII/2071). The medial side of the fused radiale and intermedium forms one square-shaped articulation area with prominent tuber in the distal-dorsal corner.

The ulnare is of a ~~cuboid shape~~cube with ~~a~~ square bases and rectangular sides. The width of the sides is half the width of the bases. It was probably arranged in one line with the fused radiale and intermedium, with the bases oriented proximally/distally (based on the spec~~.~~imen ZPAL AbIII/2407, 3349). The bases are almost flat, with delicate depressions in their ~~centre~~centers.

The carpus consist of at least two other (probably distal) carpals. One of them (larger) is elongated and lunar-shaped, and the other one is about five times smaller and pea-shaped. These are probably distal carpals III and IV, and based on the specimens ZPAL AbIII/2407 and 3349 they are arranged adjacent to metacarpal III in the second (distal) row of carpals.

The elongated lunar-shaped bone in spec~~.~~imen ZPAL AbIII/2071, alternatively may be interpreted as a pisiform, based on the comparison with modern scratch-digging mammals, such as badger (Hildebrand 1988). If true, it should be oriented in one line with ulnare. Presence of long pisiform is characteristic for digging mammals (Hiledebrand 1988).

Metacarpals

The metacarpals (Fig. 6) present in the spec~~.~~imen ZPAL AbIII/2071, 2102, 2407, 3349, 3350 and are robust, relatively short, wide and dorso-ventrally flattened ~~dorso-ventrally~~. Their bases are wider than the heads. Their shafts taper towards the distal ends. They match and partially cover each other in the dorsal view. ~~The m~~Metacarpals II, III, and IV are of similar shape and length, and are noticeably longer than ~~the~~ metacarpals I and V, which are about 0.75 their size (based on spec~~.~~imen ZPAL AbIII/2071, 2407, 3349, 3350). ~~The m~~Metacarpal I is slightly longer than ~~the~~ metacarpal V. The relative length between the metacarpals I, II, and III vary among specimens. For example, in ~~the~~ specimen ZPAL AbIII/3349 ~~the~~ metacarpal IV is the longest, but in ~~the~~ specimen ZPAL Ab III/2407 the longest is ~~the~~ metacarpal III. ~~The metacarpal~~ Metacarpal I is the most robust, and ~~the~~ metacarpal V the most gracile. The relationship of robustness can be described as I<II<III<IV<V. The distal articulation surfaces of the metacarpals are slightly asymmetric, each with a larger tuber on the medial side. ~~The metacarpal~~ Metacarpal I is also the ~~most wide~~widest among the metacarpals (Fig. 6; ~~spec.~~ ZPAL AbIII/2071, 2407, 3349, 3350). Its shaft is flat dorsally and rectangular in cross-section. On the ventral surface it has a depression for the subsequent metacarpal. ~~The metacarpals~~ Metacarpals II, III, and IV are of similar shape (Fig. 6; ~~spec.~~ ZPAL AbIII/2071, 2102, 3349, 3350). Their shafts are triangular in cross-section. Like in ~~the~~ metacarpal I, there is a depression on their dorsal surface for the subsequent metacarpal. The shape of ~~the~~ most gracile metacarpal V differs between specimens. In specimen ZPAL AbIII/3349 and 3350 it is wide and flat. Its width is almost uniform throughout the entire length, and the base and the head are not distinct. In the specimens ZPAL AbIII/2071 and 2407 the base and the head are much wider than the shaft and well-developed. The shaft is slender and oval in cross-section.

Phalanges

The phalanges (Fig. 6) are present in the spec~~.~~imen ZPAL AbIII/2407 – all phalanges of the first row, ~~spec.~~ ZPAL AbIII/3349 – all phalanges of the first and second digits, the broken 1st row phalanx of the third digit, the four phalanges of the fourth digit and 1st row phalanx of the fifth digit, ~~spec.~~ ZPAL AbIII/3350 – all phalanges of the first row, spec. ZPAL AbIII/2071 – in the right hand all phalanges of the first, second and third digit, in the left all phalanges of the first and second digit, and ~~spec.~~ ZPAL AbIII/257, 3352, 3353 – isolated phalanges. The probable phalangeal formula for *Stagonolepis olenkae* is 2-3-4-5?-3? (Fig. 6), based mostly on the specimens ZPAL AbIII/3349 and 2071. The number of the phalanges for the first three digits is certain, because they ~~are~~ terminate~~d~~ with claw-like unguals preserved in the first two ~~firsts~~ digits of ~~the spec.~~ ZPAL AbIII/3349, and first three digits of the right manus and the first two of the left of ~~the spec.~~ ZPAL AbIII/2071 (Fig. 6). In ~~the spec~~ ZPAL AbIII/3349 the phalanx of the 4th row of the digit IV ends with an articulation surface, which indicates the presence of another phalanx or an ungual. However ~~due~~ because of ~~to~~ the small size of the preserved 4th phalanx, it is unlikely that there was more than one element following it. As for the fifth digit, the size of the 1st row phalanx, compared to the size of other phalanges in ~~the specimen~~ ZPAL AbIII/3349, suggest that at least two phalanges and an ungual were present. In ~~the specimen~~ UOBS 02834 described by Książkiewicz (2014), containing hand elements preserved in articulation, two phalanges of the fifth digit are present. The phalanges are dorso-ventrally flattened, short, and wide (Fig. 6). The phalanx base is always wider than its head. The shaft narrows towards the distal end. It is rounded at the dorsal side and flat at the ventral side. Both the base and the head are slightly asymmetric. In the heads the tuber on the internal side is always larger than that on the external side and a depression is present on the articulation surface. This feature is more pronounced in the phalanges closer to the metacarpals. Interlocking phalangeal articular surfaces are wide and they extend deep into the shaft. The grooves for ligament attachments are well marked in all phalanges despite the size.

As mentioned above, claw-like unguals are present on at least first three digits (Fig. 6; based on ~~spec.~~ ZPAL AbIII/2071, 3349). The size of the claw-like unguals decreases in more lateral digits. The largest claw-like ungual of the first digit is about one-third longer and more massive than that of the second digit, and the second is longer and more massive than the third one in the same manner (~~spec.~~ ZPAL AbIII/2071). It can be inferred from the size of the preserved phalanges that other claw-like unguals (if present) kept this tendency. The unguals are laterally compressed, with sharp edges at the top and bottom sides (similar to claws of for example armadillos, pangolins, badgers) (Hildebrand 1988). They are tear-shaped in cross section but asymmetric, with a depression on the medial surface (spec. ZPAL AbIII/2071). Longitudinal grooves for ligaments are well-marked on both lateral and medial surfaces. Almost the entire unguals are covered by tiny and very densely distributed perforations (Fig. 6; spec. ZPAL AbIII/2071, 3349). Similar texture can be observed on the bony parts of horns, for example, in modern ~~bovide~~ bovids or in the unguals of armadillos (personal observation). It indicates the presence of a well-developed keratin sheath. Considering the general morphology of the whole hand it is probable that very small claw-like unguals were present on the fourth and the fifth digits. In some species of modern digging animals ~~like~~ such as armadillos, pangolins, or moles ~~in which~~ often one or several digits enlarge and take a blade-like shape useful for a scratch-digging, while the others are considerably smaller, reduced or absent (Beddard 1992, Hildebrand 1988).

Dermal skeleton

Probably the entire forearm of *Stagonolepis olenkae* was covered by numerous appendicular osteoderms (Fig. 6). They are preserved in association with the arm, carpus and ~~hand~~ manus elements in ~~the spec.~~ ZPAL AbIII/2071, 2407, 3349 and 3350. In ~~the specimens~~ ZPAL AbIII/2407, 3349, and 3350 they are accumulated mostly on the dorsal ~~side~~ surface of the ~~hand~~manus. In ~~the spec.~~ ZPAL AbIII/2407 there is also a large cluster of osteoderms, previously recovered arranged in front of the distal end of radius and ulna, but separated during ~~the~~ preparation (not illustrated). The appendicular osteoderms are generally flat, plate-like structures, semi-round to semi-oval in dorsal/ventral view. The edges of the osteoderms can be regular and smooth (mostly in the larger scutes) or irregular and ridged (more often in smaller ones). They are of various sizes, the largest are about 2.5 cm in diameter (~~spec.~~ ZPAL AbIII/2407, separated cluster of osteoderms), the smallest around 0.5 cm in diameter (several osteoderms in ~~the spec.~~ ZPAL AbIII/2407, 3349, and 3350). They are ornamented on their dorsal surface. The ornamentation ~~is gentle and~~ consists of delicate grooves and depressions. The ventral surfaces of the appendicular osteoderms ~~is~~ are smooth. On both the dorsal and ventral side of osteoderms, tiny openings for blood vessels ~~can be noticed~~are present.

The appendicular osteoderms in ~~the spec.~~ ZPAL AbIII/2407, 3349 and 3350 are significantly displaced in regard to their *in vivo* position, likely because of transport~~ation~~ and early diagenesis processes. However, some general observation can be made. The appendicular osteoderms cover the entire dorsal ~~side~~ surface of the carpus and the ~~hand~~ manus (Fig. 6). The osteoderms that occur in this area are of various sizes and shapes, but generally they are semi-round and small to medium (with diameter about 0.5 to 1.5 cm). In more flexible regions, such as the carpus and joints of the digits, the osteoderms are smaller, but in greater number than in more static regions, such as above the metacarpal shafts, where they are larger but less numerous. As for the region of the arm, it is likely that it was entirely covered by appendicular osteoderms in the manner restored for *Aetosaurs ferratus* or *Typothorax coccinarum* (Schoch 2007, Heckert *et al.* 2010). The osteoderms of the arm are larger (up to around 2.5 cm in diameter). Lack of articulation structures on the surfaces of the appendicular osteoderms suggests that they did not overlap with each other (unlike the rectangular osteoderms presents on the back of the animals), but rather ~~lied~~ lay one next to another like the scutes of modern crocodiles and alligators (e.g., Grig and Gans 1993).

Discussion

Comparisons with other aetosaurs

Based on the literature, the forelimbs of *Stagonolepis olenkae* being robust, with the humerus having a prominent wide head and condyles, and well-developed deltopectoral crest, dorso-ventrally flattened ulna with high olecranon process, straight stout radius, and sturdy short digits ending with claw-like unguals, with flattened, wide metacarpals and phalanges, are much more similar to other large and middle size aetosaurs like *Stagonolepis robertsoni*, *Longosuchus meadei*, *Typothorax coccinarum*, *Typothorax antiquum*, *Desmatosuchus smalli*, *Desmatosuchus spurensis*, or *Neoaetosauroides engaeus* (Sawin 1947; Walker 1961; Bonaparte 1971; Small 1985; Long and Murr~~a~~y 1995; Heckert and Lucas 2002; Martz 2002; Parker 2008; Heckert *et al.* 2010; Desojo *et al.* 2013) and differ from the small ones like *Polesinesuchus aureoli* and *Aetosaurus ferratus*, in which the above features are less developed (Roberto-da-Silva *et al.* 2014, Schoch 2007). However *Stagonolepis olenkae* has also unique features in the forelimbs that distinguish it from other species in which they are known, namely (1) presence of dermal amour covering the dorsal part of the manus, (2) presence of enlarged ungual of the first digit in regard to other unguals of the manus, (3) and in having square cross-section of the radius. Detailed comparisons of *S. olenkae* with other aetosaurs as well as notes on their variability are given in the supplementary materials (Appendix online 10, supplementary figures 10-12).

Comment on Stagonolepis robertsoni *and* Stagonolepis olenkae.

I personally studied *S. robertsoni* material and I think that differences in the postcranial skeleton between the *S. olenkae* and *S. robertsoni* are generally minor~~ in general~~, which was first pointed out by Lucas *et al.* (2007). Nevertheless I need to mention that material of *S. robertsoni*, which consist mostly of casts and incomplete specimens, is often difficult to directly compare with *S. olenkae*, as the specimens does not have or have not enough preserved essential parts that could be used in comparisons. On the other hand, Książkiewicz (2014) specified list of differences in post-cranium between those two species, but ~~it~~ does not include any forelimbs characters. Referring to the description of *S. robertsoni* provided by

Walker (1961), I have found another three characters (in spite of those three unique for *S. olenkae*) that may distinguish those two species, namely (1) the presence of an indentation on the humeral head that separates the internal tuberosity and the main articulation surface in *S. olenkae*, (2) a more transversely expanded humeral head in *S. olenkae* (pointed out also by Parker 2016; ~~,~~2018), (3) and a sharp ended coronoid process in *S. olenkae*. It must be, nonetheless, remembered that Walker also based his interpretations on the same incomplete and poorly preserved material, and thus some of his restorations may be speculative or inaccurate.

Probable scratch-digging behaviour in Stagonolepis olenkae

Stagonolepis olenkae has several features significant for scratch-diggers according to Hildebrand (1983, 1985) and Coombs (1983) which are explained in detail in the supplementary material (appendix online 11). Without a doubt, it was able to produce great out-forces with its forelimbs. They are (1) of strong, robust ~~built~~ build (2) with a short radius (shorter than the humerus), (3) have a short carpus, with short, stout metacarpals, and (4) have short, broad phalanges. (5) The deltopectoral crest of the humerus (attachment area of the deltoid muscles) is well-developed and (6) spans almost ~~for the~~ half the length of the bone~~e length~~. In the distal part of the humerus, (7) the medial entepicondyle is prominent and wide (comparable to that of armadillos, pangolins, anteaters, and aardvarks; Hildebrand 1983), and on the lateral side (8) a distinct supinator process is present. (9) The olecranon process of the ulna is long (minimum 0.2 of the total ulna length – the level of scratch-digging ground squirrels (Hildebrand 1988), but for sure it was longer in *S. olenkae*, because of ~~cartilage~~ cartilaginous expansion), and has strong and well-marked insertions of the triceps muscle. Following the criteria used by Heckert *et al.* (2010) in regard to *Typothorax coccinarum*, ~~it~~ *S. olenkae* ~~would~~ bears nine of the eleven characters associated with digging behaviour.

Furthermore, the joints of *Stagonolepis olenkae* are modified for stabilizing the arm. The wrist joint is hinge-like due to the presence of the fused radiale and intermedium. The radius and the ulna are oriented parallel to each other and are immovable relative to each other ~~in~~ at the elbow joint. The head of the humerus is very expanded medio-laterally which suggests that it had higher mobility in the horizontal plane than in the vertical plane. In the autopodium, the joints between the metacarpals and the phalanges are almost flat-ended, the joints between phalanges are slightly V-shaped, and the surfaces of more proximal phalanges ~~is~~ are not larger than those of the distal ones. The second-to-last phalanges in the first, second, and third digits have enlarged distal ends with a great ~~radius of~~ curvature radius. The autopodial bones of *S. olenkae* did not have bony stops and I ~~did~~ do not recognize sesamoids, however the whole hand was covered by osteoderms that ~~may~~ might stiffen it. In modern crocodiles, dorsal osteoderms together with dorsal muscles form a complex structure that strengthens the vertebral column (Frey 1988). ~~Small~~ The small number of free phalanges (one in the first digit and two in the second digit), obviously helped in the digging process, however, it is a typical condition in crocodiles and among many basal archosaurs (for example *Postosuchus*, *Parasuchus*, *Riojasuchus*) (Bonaparte 1971; Szarski 1976; Chatterjee 1978; Peyer *et al.* 2008; Weinbaum 2013).

The hands of *Stagonolepis olenkae* were also adapted for breaking ~~a~~ compacted soil. Its unguals are laterally compressed, claw-like, and elongated in the manner of modern armadillos, pangolins, echidnas, or moles (Hildebrand 1983). Their surface ornamentation is similar to that on the unguals of, for example, armadillos (Hildebrand 1983), or on the bony surface of Bovidae horns (personal observation), which indicates the presence of a strong keratin sheath. In addition, the ungual of the first digit in *S. olenkae* is enlarged in respect to the others, similar to what is found in some pangolins and armadillos in which the primary digging digit become enlarged (Beddard 1902; Hildebrand 1983, 1988; Gaudin *et al.* 2016).

Implications for the ~~Stagonolepis olenkae~~ mode of life in Stagonolepis olenkae

Sulej (2010), based on the presence of a skull endocast with a very large olfactory tract and bulbous, large nares, and the shape of teeth, considered *Stagonolepis olenkae* to be an omnivorous animal relaying mostly on smell in its search for food and using its shovel-like snout to extract invertebrates and plants from under the ground, ~~and compared~~ comparing its lifestyle to modern wild boars. Considering several adaptations for scratch-digging recognized here for *S. olenkae*, it safe to assume that it probably started digging with its forelimbs to break and loosen the soil, and then proceeded with its snout. Modern scratch-diggers (as armadillos, pangolins, and aardvarks) can balance their body with hind limbs and long tail to apply additional strength for a breaking strike (Hildebrand 1988), which is also expected in *S. olenkae*, due to its relatively large size and long tail (a feature characteristic ~~for~~ of aetosaurs, Desojo *et al.* 2013, described also for *S. olenkae* by Książkiewicz 2014).

~~Presence~~ The presence of specialized claws together with the dermal armo~~u~~r covering the entire forelimb suggests an analogy to the insectivorous mode of life of armadillos or pangolins, considered by some authors to be modern analogues of aetosaurs (e.g., Bonaparte 1978; Small 2002; Desojo *et al.* 2013). The armo~~u~~r protects them against the insects (ants, termites or beetles) they mostly feed on, as well as larger predators they cannot outrun (for example ~~lions~~ leopards or ~~tigers~~hyena in the case of pangolins) (e.g., Talmage and Buchanan 1954; Deligne *et al.* 1981; Yang *et al.* 2013; Wang *et al.* 2016). A few beetle ~~elytrons~~ elytra have been reported from Krasiejów (Dzik and Sulej 2007) and the diet of, for example, the nine-banded armadillo may consist of even ~~in~~ 40% of coleopterans (Talmage and Buchanan 1954). Several authors ~~Therefore~~suggest therefore that ~~the~~ beetles could be the important source of food for aetosaurs (Small, 2002); ~~However~~however, it is hard to imagine ~~the~~ an animal ~~being~~ almost as long as a ~~middle~~ mid-sized ~~car~~ automobile to base its diet mostly on insects. Therefore, the wild boar analogy seems more appropriate because of ~~the~~ *S. olenkae*'s overall size. Besides, the wild boar’s omnivorous diet includes roots, tubers, bulbs, nuts, seeds, bark, insects, and other smaller animals, and also includes scavenging, but the majority of its food consists of items dug from the ground (Heptner *et al.* 1988). This covers every kind of feeding behaviour ~~which~~ that has ever been suggested for aetosaurs (Desojo *et al.* 2013). Enlarged osteoderms forming an extensive dermal carapace are most likely a result of a selective pressure from large predators, rather than protection against small arthropods. The upper size range of aetosaurs is comparable to ~~the~~ associated rauisuchids, which possibly hunted them (Drymala and Bader 2012) and in Krasiejów, *S. olenkae* is the only large land animal of a size comparable to the local predator *Polonosuchus silesiacus* (e.g., Dzik and Sulej 2007). Still, *S. olenkae* is the only known aetosaur with the osteoderms covering the dorsal surface of the hand. As the osteoderms take part in thermoregulation (Farlow *et al.* 2010) and may buffer ~~the~~ lactic acid (Jackson *et al.* 2003), their presence may support *S. olenkae*’s warming up or giving up ~~the~~ heat generated by the intense work of the forelimb~~s~~ muscles, and help to longer sustain ~~the~~ high activity of the forelimbs.

During the sedimentation of bone bearing horizons in Krasiejów, the climate ~~in~~ was semi-tropical with distinct seasonal wet and dry periods (Gruszka and Zieliński 2008). In modern tropical areas during the dry season the plants protect themselves against dehydration by losing their photosynthetic organs ~~reaching~~ that are situated above the ground and by developing resting underground organs rich in storage polysaccharides and proteins (Bullock and Solis-Magallanes 1990). *Stagonolepis olenkae* may have temporarily relied on such a source of food. A s~~S~~imilar climate with distinct seasonal wet and dry periods was also recognized in Upper Triassic Chinle ~~formation~~ Formation in the USA (e.g., Dubiel 1984, 1987; Simms and Ruffell 1990), from ~~witch~~ which several aetosaur~~s~~ species have been

Commented [WGP3]: What kinds of plants?

described (e.g., *Desmatosuchus*, *Typothorax, Paratypothorax, Calyptosuchus, Scutarx*; Desojo et al. 2013; Parker 2016, 2018).

Probable scratch-digging in other aetosaur~~s~~ species

Although the possible ability to dig was previously proposed only for *Stagonolepis robertsoni* and *Typothorax coccinarum* (Walker 1961; Heckert *et al.* 2010), many features associated with the scratch-digging behavio~~u~~r can also be recognized ~~also~~ in the forelimbs of other ~~middle~~ mid- and large sized aetosaurs. Namely (1) robust forelimb bones, with (2) the humerus having a prominent, well-developed deltopectoral crest, and (3) a wide entepicondyle (*Aetobarbakinoides brasiliensis, Argentinosuchus bonapartei*, *Desmatosuchus smalli, Desmatosuchus spurensis, Longosuchus meadei, Neoaetosauroides engaeus, Typothorax coccinarum*, *Typothorax antiquus*, *Stagonolepis robertsoni*), (4) marked supinator process (*S. robertsoni)*, (5) long and marked olecranon process of ulna (*D. smalli, L. meadei, N. engaeus, T. coccinarum, T. antiquus*, *S. robertsoni*), (6) short and stout metacarpals, (7) short and broad phalanges (*L. meadei, T. coccinarum, S. robertsoni*), and (8) the fused radiale and intermedium in the carpus (*L. meadei* and *S. robertsoni*) (Sawin 1947; Walker 1961; Small 1985; Long and Murry 1995; Lucas *et al.* 2002; Heckert and Lucas 2002; Martz 2002; Lucas and Heckert 2011; Desojo *et al.* 2012). Many of the ~~middle~~ mid- ~~and~~ to large sized aetosaurs also have the shovel-like expansion at the end of the snout (e.g. *D. smalli, D. spurensis, L. meadei, N. engaeus, T. coccinarum, S. robertsoni*) (Sawin 1947; Walker 1961; Small 2002; Parker 2005, 2008; Desojo and Baéz 2007; Heckert *et al.* 2010; Desojo *et al.* 2013). Therefore, it is probable that many of them could also perform scratch-digging, and had a similar mode of life as *Stagonolepis olenkae*.

Despite the lack of many characters typical for diggers, the forelimbs of the ~~small~~ diminuative *Aetosaurus ferratus* have proportions usual for the digging animals with the radius shorter than the humerus, and the palm shorter than the radius (Schoch 2007). *Aetosaurus ferratus* also has a prominent supinator process and transversely elongated element in the carpus (radiale), but lacks the shovel expansion in the snout (Schoch 2007). ~~It~~ This suggests that it could also perform scratch-digging with the forelimbs (probably even better than contemporary animals), but not ~~at~~ to the degree of larger aetosaurs species.

Conclusions

The forelimbs of *Stagonolepis olenkae* have an anatomy characteristic for large and middle sized aetosaurs (over 2 m long, ~~like for example~~such as *Desmatosuchus, Typothorax, Longosuchus*) and differs much from the smaller ones (below 1 m long, such as *Aetosaurus, Pol~~i~~sinesuchus*). *Stagonolepis olenkae*, also has ~~also~~ a few features that have not been described thus far for any other aetosaur, namely (1) presence of ~~the~~ dermal armour covering the dorsal part of the manus, (2) the presence of an enlarged ungual of the first digit, (3) and having a square cross section of the radius.

It appears that some of the features observed in the forelimbs of all aetosaurs, like the transverse expansion of the humeral head, transverse expansion of the condyles, elongation of the olecranon process ~~in~~ of the ulna and general increase of bone robustness, are associated with the increase of size of ~~the~~ certain species. However, to fully understand complexity of this process among aetosaurs, further studies on ontogeny and intraspecific variation are needed.

~~Total number of six~~ Six characters that distinguish *Stagonolepis olenkae* and *Stagonolepis robertsoni* have been recognized in this study (in addition to three unique for *S. olenkae* (4) more transversely expanded humeral head in *S. olenkae*, (5) distinct greater trochanter (internal tuberosity) in *S. olenkae*, and (6) sharp ended coronoid process of ulna in *S.*

olenkae). In addition some specimens of *S. olen~~a~~kae* have ~~the~~ an olecranon fossa that is not present in *S. robertsoni*. ~~Found~~ These differences may furthermore ~~prove~~ support the distinction of those two species, therefore supporting the establishment of new species for the Polish material. However, this statement needs to be treated with caution, because the intraspecific variation and particularly the ontogeny of both species is not well known yet, and the described material of *S. robertsoni* usually does not allow for the detailed comparisons due to the poor state of preservation.

Stagonolepis olenkae was an effective scratch-digger. It has several adaptations associated with producing great forces against hard substrates, stabilizing the joints and breaking compacted soils. It probably started digging with its forelimbs to loosen and shatter the earth, and then proceeded with its shovel-expansion at the tip of the snout, in search for food underground.

Characters connected with scratch-digging can be recognized also in forelimbs of other species, and in most of them they are associated with the presence of the shovel-like expansion in the skull. Therefore the scratch-digging behavio~~u~~r proposed here for *S. olenkae* was probably much more common among aetosaurs.

Possible digging behavio~~u~~r in aetosaurs could have co-evolved in an environment with seasonal dry and wet periods like that present during the ~~sedimentation~~ deposition of the Krasiejów strata. In such environments, many plants develop underground resting organs of high dietary ~~value, that~~value, which could serve as a source of energy during drought.

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Supporting materials online:

Additional supporting information and supplementary figures can be found in the online version of this article.

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Appendix online 1. List of forelimb specimens of *Stagonolepis olenkae* with the description.

- **ZPAL AbIII/2407** (manuscript Figure 2, supplementary Figure 1) – Specimen contains elements of the right forelimb: the ulna; the radius; three carpal elements: fused radiale and intermedium, ulnare, one distal carpal; ten elements of the manus: all metacarpals and all phalanges of the 1st row and numerous small osteoderms. The ulna and radius, are preserved in entirety and are located parallel to each other, almost as in ~~the~~ life position. The carpus and manus are rotated at 90º in respect to the forearm bones. Most of the osteoderms are located on the dorsal side of the manus. The specimens includes also a separated cluster of osteoderms previously arranged in front of the distal end of radius and ulna (not illustrated).
- **ZPAL AbIII/3349** (manuscript Figure 6, supplementary Figure 2) – Specimen contains elements of the right forelimb: distal end of the ulna; distal end of the radius; four carpal elements: fused radiale and intermedium, ulnare, two distal carpals (probably the distal carpals III - smaller and IV - larger); sixteen elements of the manus: all metacarpals, all phalanges of the digit I (1st row phalanx and ungual), all phalanges of the digit II (two phalanges and ungual), broken 1st row phalanx of the digit III, four phalanges of the fourth digit IV (1st, 2nd, 3rd and 4th row phalanges), 1st row phalanx of the fifth digit; and numerous small osteoderms. The ulna and radius are preserved close to each other. The manus is rotated at 90º in respect to ulna, similar to specimen ZPAL AbIII/2407. The carpus elements are disarticulated. The fused radiale and intermedium is rotated in respect to its anatomical position (the surface visible on the dorsal side of specimen in natural arrangement should face towards the metacarpals. Rotation of this bone must have occurred when the skin still covered the limbs, as indicated by the presence of osteoderms over its surface for metacarpals. Hand elements are preserved in articulation. The metacarpal of the III digit is pathologically enlarged and thicker in respect to other metacarpals of this individual and in comparison with other specimens with hands preserved in association. Most of the osteoderms are preserved on the dorsal side of the manus and in the sediment associated with remains of the ulna and radius.
- **ZPAL AbIII/3350** (supplementary Figure 3) – Specimen contains elements of the left forelimb: distal end of the ulna; distal end with part of the shaft of the radius; three carpal elements: fused radiale and intermedium and two other carpals (they cannot be identified properly due to poor state of preservation); ten elements of the manus: all metacarpals and five phalanges (probably 1st row phalanx of the digit III, 1st and 2nd row phalanges of the digits IV and V); numerous small osteoderms. All elements are disarticulated. It appears that at the moment of burial, the joints of the hand were pushed towards the forelimbs, which eventually caused disarticulation of the digits and displacement of its elements. On the lateral side of the fused radiale and intermedium is an unnatural hole with the rugose surface. This deformation could be caused by the decomposition process before ~~the~~ burial. The phalanges are in chaotic disorder and because of that it is difficult to recognize them. Most of the osteoderms are located in the sediment between the long bones and manus and in the sediment associated with the long bones (over the dorsal side of the metacarpals).
- **ZPAL AbIII/2071** (manuscript Figure 5, supplementary Figure 4) – Specimen contains elements of the left and right limbs: four carpal elements of the right limb: the fused radiale and intermedium, ulnare, two other carpals (larger crescent shaped and smaller garlic shaped); fourteen elements of the right manus: all

metacarpals, all phalanges of the digit I (phalanx and ungual), all phalanges of the digit II (1st, 2nd row phalanges and ungual), and probably all phalanges of the digit III (1st, 2nd, 3rd row phalanges and ungual); two carpal elements of the left limb: the fused radiale and intermedium and crescent shaped carpal; eight elements of the left manus: metacarpals I, II and IV, all phalanges of the digit I (1st row phalanx and ungual), all phalanges of the digit II (1st, 2nd row phalanges and ungual). The specimen should contain elements originally preserved in association and separated later during the preparation process. However, the preparation was done several years ago and it could be a mixture of several animals. Based on the state of preservation, it seems that elements of the right limb and probably the left fused radiale and intermedium belong to one animal. The elements of the left limb are much darker than those of the right, but they are of corresponding size to those of right. Exception is the crescent shaped carpal of the left limb, which have much different colour from other left hand elements corresponding more to those of the right, but it's size does not compare to similar element of the right hand.

- **ZPAL AbIII/ 257,1175, 2627** (supplementary Figure 5) - isolated humeri
- **ZPAL AbIII/1100/1, 1179, 2014, 3351** (supplementary Figure 6) - isolated ulnae
- **ZPAL AbIII/2106/2, 2106/4, 1628, 3322** (supplementary Figure 7) - isolated radii
- **ZPAL AbIII/2102** (supplementary Figure 8) - isolated metacarpal of the digit IV
- **ZPAL AbIII/267, 3352, 3353** (supplementary Figure 8) - isolated phalanges

Appendix online 10. Detailed comparisons of forelimbs of the aetosaur *Stagonolepis olenkae* from Krasiejów locality in Poland, with other aetosaur species.

Humerus

The overall shape and robustness of the humerus of *Stagonolepis olenkae* is most similar to large humeri of *Desmatosuchus smalli*, *Desmatosuchus spurensis* and *Longosuchus meadei* (Sawin 1947; Small 1985; Long and Murry 1995; Parker 2008; sup. Fig. 10A, B). In *S. olenkae*, like in *D. smalli*, *D. spurensis* and *L. meadei*, the humeral head is strongly medially expanded, with the internal tuberosity separated from the main articulation surface by a pronounced indentation, and the epicondyle is very widened medially, the shaft has similar outline in the proximal/distal view, with a distinct section of the humeral head and the base, and a relatively slim straight medial section (Sawin 1947; Small 1985; Long and Murry 1995). Similar conditions are present also in humerus of *Aetobarbakinoides brasiliensis* (Desojo et al. 2012; sup. Fig. 10H). In *Typothorax coccinarum* the humeral head is proportionally less expanded medially than in *S. olenkae*, and the internal tuberosity is not separated by any indentation from the main articular surface (it smoothly continues along the proximal edge of the head) (Long and ~~Murray~~ 1995; Martz 2002; Heckert et al. 2010; Sup. Fig. 10F). Also the middle section of the shaft appears to be proportionally longer than in *S. olenkae* (Long and ~~Murray~~ 1995; Martz 2002; Heckert et al. 2010). Based on the restoration of the humerus of *S. robertsoni* (fig. 14a, b in Walker 1961; sup. Fig. 10D) the general shape and proportions are almost identical ~~like in~~ *S. olenkae*, but the humeral head in *S. robertsoni* is negligibly less expanded than in *S. olenkae* (*S. robertsoni* ratio of humeral head medio-lateral width to the entire length of humerus is about 0.58 and in *S. olenkae* 0.54) (Walker 1961; Parker 2016, 2018). The proximal articulation surface of the humerus in *S. robertsoni* is continuous, so there is no distinction of the internal tuberosity similar to *T. coccinarum* (Walker 1961; sup. Fig. 10D). The restored humerus of *S. robertsoni* does not have an olecranon fossa, as large as the humeri of *S. olenkae*~~, spec.~~ ZPAL AbIII/1175 and 257 (sup. Fig. 5A, C) (Walker 1961; sup. Fig. 10D). However, smaller humerus of *S. olenkae* ~~spec.~~ ZPAL AbIII/2627 (sup. Fig. 5B) (and comparable in size to *S. robertsoni*) also does not have the olecranon fossa. Large humeri of "*Argentinosuchus bonapartei*" (spec. PVL 2091) and *Neoaetosauroides engaeus* have proximal heads strongly expanded medially like in *S. olenkae*, but there is no indentation between the internal tuberosity and proximal articulation like in *T. coccinarum* (Casamiquela 1960; Bonaparte 1971; Heckert and Lucas 2002; Desojo et al. 2012; sup. Fig. 10). The shafts of "*A. bonapartei*" and *N. engaeus* seem to be more robust than in *S. olenkae* (Casamiquela 1960; Bonaparte 1971; Heckert and Lucas 2002; Desojo et al. 2012; Sup. Fig. 10). The olecranon fossa present in large specimens of *S. olenkae*, can occur also in *N. en-*

gaeus (Bonaparte 1971; sup. Fig. 10). In comparison to *S. olenkae*, the humeri of *Aetosauroides scagliai* (spec. PVL 2073) and *Polesinesuchus aurelioi*, apart from being much smaller (about 0.40 the length of the spec. ZPAL AbIII/1175 for *A. scagliai* and 0.25 for *P. aurelioi*) are less robust, their humeral heads and condyles are less expanded medially and laterally, and their deltopectoral crest is less developed (Heckert and Lucas 2002; Desojo and Ezcurra 2011; Roberto-da-Silva et al. 2014; sup. Fig. 10I, J). The humeri of *Aetosaurus ferratus* strongly differ from *S. olenkae* and other large aetosaurs in having slender proximal and distal portions, weakly developed deltopectoral crest and condyles of equal size (Schoch 2007; sup. Fig. 10K). The ectepicondylar groove in *S. olenkae* is fully exposed like in most aetosaurs, but unlike in *D. smalli*, *D. spurensis*, *L. meadei*, *T. coccinarum* and *N. engaeus* in which it is closed by bone and forms a foramen (Sawin 1947; Bonaparte 1971; Small 1985; Long and Murry 1995; Martz 2002; Desojo et al. 2013; sup. Fig. 10 A, B, F, G). *S. olenkae* have prominent supinator process. Marked supinator process is also present in *S. robertsoni* and *A. ferratus* (Walker 1961; Schoch 2007; sup. Fig. 10 D, K).

Ulna

The ulna of Stagonolepis olenkae has a shape typical for most aetosaurs, ~~having~~ well-developed proximal part with high olecranon process and the shaft being wide mediolaterally and flattened dorso-ventrally (e.g[illegible]win 1947; Walker 1961; Schoch 2007; Roberto-Da-Silva et al. 2014; sup. Fig. 11D). The olecranon process is partially cartilaginous, which is suggested also for *Longosuchus meadei* (Sawin 1947) and *Polesinesuchus aureolii* (Roberto-Da-Silva et al. 2014) and was pointed as well for *S. olenkae* by Książkiewicz (2014). ~~Height~~ of the olecranon process in *S. olenkae* (around 0.2 in proportion to the entire length of the bone) is comparable to that of *Stagonolepis robertsoni*, *Typothorax antiquus*, *Typothorax coccinarum* and *Neoaetosauroides engaeus* (Sawin 1947; Walker 1961; Bonaparte 1971; Lucas et al. 2002; Heckert et al. 2010; sup. Fig. 11E–H). ~~Olecranon~~ process is higher than in *S. olenkae*, in *L.* ~~*medei*~~ and *D. smalli* (being around 0.25 of the entire ulna length in *L.* ~~*medei*~~ and 0.3 in *D. smalli*) (based on fig. 4c, d in Sawin 1947; and fig. 8 c, d in Small 1985; sup. Fig. 11A, B). In *Aetosaurus ferratus*, *P. aureolii*, and *Aetosauroides scagliai* (spec. PVL 2073) the olecranon process is shorter than in *S. olenkae* (being around of the entire ulna length 0.15 in *A. ferratus*, 0.14 in *A. scagliai* and 0.10 in *P. aureolii* (based on fig. 3-3, 4 in Heckert and Lucas 2002; fig. 10G in Schoch 2007; fig. 21 in Roberto-Da-Silva et al. 2014; sup. Fig. 11I–K). The coronoid process in *S. olenkae* is elongated medially, pronounced and with a sharp end (spec. ZPAL AbIII 2014, 3351, fig. 6C, D), similar to ~~*D. spurensis*~~ and "*Argentinosuchus bonapartei*" (spec. PVL 2091) (Small 1985; Heckert and Lucas 2002). In *L. meadei*, *T. coccinarum*, *T. antiquus*, and *S. robertsoni* the coronoid process is also elongated medially, but its end is smooth (Sawin 1947; Walker 1961; Lucas et al. 2002; Heckert et al. 2010; sup. Fig. 11B, E–H). In *A. ferratus*, *P. aureolii*, and *A. scagliai* (spec. PVL 2073) the coronoid process is much less developed than in S. olenkae (Heckert and Lucas 2002; Schoch 2007; Desojo and Ezcurra 2011; Roberto-Da-Silva et al. 2014; sup. Fig. 11I–K).

Radius

The radius of *Stagonolepis olenkae* is similar to known aetosaurs in having a straight shaft with equally expanded proximal and distal ends (e.g., Sawin 1947; Walker 1961; Lucas et al. 2002; Schoch 2007). The level of expansion of the proximal and distal end in *S. olenkae* (in proportion to the entire length of the radius) is comparable to *Stagonolepis robertsoni*, *Typothorax antiquus*, and *Typothorax coccinarum* (Walker 1961; Lucas et al. 2002; Heckert et al. 2010; sup. Fig. 11E, G, H). In *Aetosaurus ferratus* and *Aetosauroides scagliai* (spec. PVL 2073) the proximal and distal ends of radius are less expanded (Heckert and Lucas 2002; Schoch 2007; Desojo and Ezcurra 2011; Sup. Fig. 11I, K). The square cross-section of the shaft of the radius of *S. olenkae* is a character that distinguishes it from other known aetosaurs, including *S. robertsoni*, *L. meadei*, *A. ferratus*, and *T. antiquus*, in which the cross section is oval (Sawin 1947; Walker 1961; Schoch 2007; Lucas et al. 2002).

Carpus

Stagonolepis olenkae is one of few aetosaurs with known carpal elements, along with the *Aetosaurus ferratus*, *Longosuchus meadei*, *Stagonolepis robertsoni*, and *Typothorax coccinarum* (Sawin 1947; Walker 1961; Schoch 2007; Lucas and Heckert 2011; sup. Fig. 12). The number of carpals in *S. olenkae* is four, which is similar to *L. meadei* and *T. coccinarum* (~~spec.~~ MCZ 1487) (Sawin 1947, Lucas and Heckert 2011). Książkiewicz (2014) speculated that in *S. olenkae* could be up to five carpals, but there is no specimen with more than four carpal bones preserved. In *S. robertsoni* and *A. ferratus* two carpals are recognizable, but in some individuals of A. ferratus more could be preserved (Walker 1961, Schoch 2007). In *S. olenkae*, *S. robertsoni*, *A. ferratus*, and *L. meadei* the dominant carpal bone is the large fused radiale and intermedium (Sawin 1947, Walker 1961, Schoch 2007). Książkiewicz (2014) described one specimen of *S. olenkae* (UOBS 02830) with those two bones separated, but as he suggested, the fused radiale and intermedium in this case is most likely broken. In *Typothorax coccinarum* (spec. MCZ 1487) the carpal bones are of comparable size, but the rounded bone opposite to the radius seems to be little larger than others and its shape is corresponding to the lateral side of the fused radiale and intermedium of *S. olenkae*, therefore it could also be a fused radiale and intermedium (based on fig. 4a, b in Lucas and Heckert 2011). The fused radiale and intermedium in *S. robertsoni* seems to be smaller than its homologue in *S. olenkae*, as it reaches only to the metacarpal III, while in *S. olenkae* it is adjacent to the metacarpal III and also part of the metacarpal IV (Walker 1961; Sup. Fig. 12F).

I propose the arrangement of the carpal elements in *Stagonolepis olenkae* in two rows, first consisting of the fused radiale and intermedium with the ulnare and the second consisting of two distal carpals. In *Longosuchus meadei*, the only other aetosaur species in which the arrangement of carpals is proposed, the fused radiale and intermedium forms a single row with the other three carpals (Sawin 1947; sup. Fig. 12A). However Sawin (1947), when preparing his restoration of *L. meadei*, did not have ~~in~~ his disposal any articulated carpus and was able to identify only the fused radiale and intermedium, already known to occur in *A. ferratus*. He wrote ~~himself~~ that the arrangement of the other carpal elements in one row was only his best assumption (Sawin 1947). Ksiażkiewicz (2014) also suggest arrangement of the carpal bones in a single row for S. olenkae, but he as well did not have any specimens with articulated carpus. The arrangement of carpals in two rows for *S. olenkae* is strongly supported by ~~the spec.~~ ZPAL AbIII/2407 (sup. Fig. 1), in which the carpus and hand bones are preserved the closest to their anatomical position among studied specimens. In this specimen the fused radiale and intermedium form one row with the ulnare, and another (distal) carpal is preserved in front of them, towards metacarpals. Similar condition could be observed also in ~~the spec.~~ ZPAL AbIII/3349 (sup. Fig. 2), in which the distal carpals are preserved in front of the ulnare, opposite to the third metacarpal. However, in this specimen the fused radiale and intermedium is not preserved in articulation and it is not certain how much the position of other carpals changed in respect to their original setting. The arrangement of carpals in two rows is also recognized in *Postosuchus alisonae* – rauisuchid closely related to aetosaurs (Peyer et al. 2008). The longer side of the ulnare in ~~the spec.~~ ZPAL AbIII/2407 (sup. Fig. 1) faces the metacarpals and forearms. In this setting, the medial side of the ulnare seems to be disproportionally narrow in comparison to the corresponding surface on the fused radiale and intermedium (manuscript Fig. 6C). Nevertheless, in ornithosuchians, other basal archosaurs closely related to aetosaurs, a huge disproportion in size between the radiale and the intermedium is possible (Bonaparte 1971; Von Baczko and Ezcurra 2013). The carpus of modern crocodilians consist of both bony and cartilaginous elements (e.g. Buscalioni et al. 1997) and since the preserved carpal bones does not fit perfectly with the metacarpals and long bones, it is probable that also in *S. olenkae* the carpus could consist of cartilage elements or at last the amount of cartilage covering the bones was significant.

Manus

Palm bones, similarly as carpals, are also known for only a few aetosaurs apart of S. olenkae. The others are *Aetosaurus ferratus, Longosuchus meadei*, *Stagonolepis robertsoni*, *Hypothorax coccinarum* (Sawin 1947; Walker 1961; Schoch 2007; Lucas and Heckert 2011; Sup. Fig. 12). The metacarpals and phalanges of *S. olenkae* are robust, short, and dorso-ventrally flattened similarly to *L. meadei*, *S. robertsoni*, and *T. coccinarum* (Sawin 1947; Walker 1961; Lucas and Heckert 2011; sup. Fig. 12A, D, F). The manus of *A. ferratus* seems to be more slender than that of *S. olenkae* and other known aetosaurs (Schoch 2007; sup. Fig. 12C). Unfortunately, none of the described specimens of aetosaur~~s~~ manus ~~has~~ complete set of phalanges, so the phalangeal formula proposed for aetosaurs remains hypothetical (Sawin 1947, Walker 1961, Schoch 2007, this study). In *S. olenkae* none of the studied specimens preserve all of the distal phalanges of digits IV and V. Considering the number of phalanges in the preserved specimens and their size, the most simple phalangeal formula for S. olenkae is 2-3-4-5-3, the same as for *S. robertsoni* (Walker 1961). The same number of phalanges was ~~recognized~~ by Książkiewicz (2014). The phalangeal formula proposed for *L. meadei* (2-3-4-5-2) cannot be applied to *S. olenkae* because in the spec. UOBS 02834 described by Ksiażkiewicz (2014) the fifth digit has two phalanges even though the ungual is not preserved. Need to be mentioned that the phalangeal formula proposed by Sawin (1947) could be a mistake, because the restoration of manus of *L. meadei* (fig. 3c in Sawin 1947) shows two phalanges and small ungual on the fifth digit. Thus based on the Sawin's restoration, the phalangeal formula of *L. meadei* should be 2-3-4-5-3, which is consistent with proposed formulas of *S. olenkae* and *S. robertsoni* (Sawin 1947; sup. Fig. 12A, B, F). In *A. ferratus* the phalangeal formula cannot be determined (Schoch 2007). The claw-like unguals in *S. olenkae* are present on at least first three digits (based on spec. ZPAL AbIII/2071, Fig. 4), similarly to *S. robertsoni* (Walker 1961; sup. Fig. 12F). In *L. meadei* they are preserved on the first two digits (Sawin 1947; Sup. Fig. 12A). In *S. olenkae* the size of unguals decreases in regular pattern with the second ungual being one–third the length of the first, and the third being one-third the length of the second. Middle digits (II, III, IV) are almost of equal length in *S. olenkae*, while the external digits are much shorter, about 0.75 the length of the middle digits. The same pattern of digit length characterizes *S. robertsoni*, but Walker (1961) suggested that the digit III was probably the longest one and the same proportions are also established for *L. meadei* and *T. coccinarum*, as both Sawin (1947) and Lucas and Heckert (2011) indicated the digit III is a little longer than the II and IV. Furthermore, the lengths of digits in *T. coccinarum* are also inferred to be III>II>IV>I>V, based on the probable correspondence of tracks of *Brachychirotherium* to this species (Lucas and Heckert 2011). In *S. olenkae*, as in *S. robertsoni*, *L. meadei*, and *T. coccinarum*, the first digit is the most robust and the fifth digit is the tiniest and reduced (Sawin 1947, Walker 1961, Lucas and Heckert 2011, Książkiewicz 2014, this study). It is probable that in *S. olenkae* the fifth digit was not functional in stepping, as was probably the case in *T. coccinarum* (Lucas and Heckert 2011). The fifth metacarpal of *S. olenkae* in the spec. ZPAL AbIII/3349 (sup. Fig. 2), 3350 (sup. Fig. 3) is dorso-ventrally flattened, very wide (as wide as the metacarpal IV) and its proximal head is not distinct, however in the spec. ZPAL AbIII/2071 (sup. Fig. 4) and 2407 (sup. Fig. 1) the fifth digit is thin, oval in cross section and with a distinct proximal head. The latter conditions are similar to *S. robertsoni*, *L. meadei*, and *T. coccinarum* (Sawin 1947, Walker 1961, Lucas and Heckert 2011). Differences in shape of the fifth metacarpal in S. olenkae may be due to intraspecific variation, dimorphism or ontogeny, since the spec. ZPAL AbIII/3349 (sup. Fig. 2) and 3350 (sup. Fig.3) belong to larger individuals than ZPAL AbIII/2071 and 2407.

Dermal ~~armour~~

Probably the entire arm, carpus, and hand of *Stagonolepis olenkae* were covered by osteoderms at least dorsally. The osteoderms covering the arms and forearms are larger than those of the manus and carpus, and it is probable that they were arranged in rows, similar ~~like in~~ *Aetosaurus ferratus* and *Typothorax coccinarum* (Schoch 2007; Heckert et al. 2010). The presence of osteoderms ~~on~~ arms and forearms is also reported for *Stagonolepis robertsoni* (Walker 1961) and it is probable that they were also present in "*Argentinosuchus bonapartei*", since the appendicular osteoderms are found in the sediment associated with humerus (~~spec.~~ PVL 2091) (Heckert and Lucas 2002). *S. olenkae* is the only known aetosaur in which the osteoderms cover the carpus and manus region. In modern crocodiles each osteoderm corresponds to a keratinous scale of similar shape (Burns et al. 2013). The presence of such scales can be expected also in ~~the~~ aetosaurs.

Increase of size as a probable explanation of some variability in aetosaurs forelimbs

The studies conducted by Bonnan *et al.* (2013) on the changes of the shape of long bones of archosaurs and mammals, showed that expansion of long bone joints, associated with an increase of cartilage volume, are typical features connected with the escalation of size in archosaurs. The increase of bone robustness, increase of transverse length of distal and proximal heads of the humerus, as well as increase of length of the olecranon process, and expansion of proximal and distal parts of the radii, correlated with an increase of the animal size can be easily observed in transition from small to large aetosaur species (Sawin 1947; Walker 1961; Small 1985; Lucas et al. 2002; Heckert and Lucas 2002; Martz 2002; Schoch 2007; Parker 2008; Desojo and Ezcurra 2011; Desojo et al. 2012; Lucas and Heckert 2011;

Roberto-Da-Silva et al. 2014; sup. Fig. 10, 11). Considering the research of Bonnan *et al.* (2013) I think that evolutionary increase of size might be a major factor determining at least the above mentioned variability between aetosaurs, but further studies are needed to additionally support this statement.

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Appendix online 11. Explanation of features and ~~adaptations characteristic~~ for scratch-diggers.

Scratch-digging is the method of digging in which by alternate flexing and extending the limbs the animal cuts and loosens the soil with its claws and pushes or flings it to the rear (=for example as a dog trying to bury the bone) (Hildebrand 1988). The most powerful modern scratch-diggers are armadillos, the pangolins, and the aardvark, but several other animals dig this way, including some frogs, some tortoises, some birds, fossorial marsupials, most badgers, a ratel, ground squirrels and variety of other mammals (some with scant structural adaptations for it, like canids) (Hildebrand 1983, 1988).

The digging requires enormous strength, therefore the limbs of specialized scratch-diggers are modified to be able to apply a great force against the hard, solid substrate (Hildebrand 1988). During the process, most scratch-diggers extend the forefeet to the earth and then draw the claws downward, toward or under the body (Hildebrand 1988). In this case the arm works as a lever in which the in-force (F_i) is applied to the olecranon process being the lever arm (power arm) and the out-force (F_o) is produced at the end of the hand, while the forearm and the hand (with exception of the olecranon process) are the out lever arm (load arm) (Hildebrand 1988). Considering that $F_o=\frac{Fi*li}{lo}$ (l_i - length of the power arm, l_o - length of the load arm), there are three major ways to increase the out-force (F_o) (Hilderand 1988). The first way is to reduce the length of the out lever arm (l_o). As a result, the limbs of specialized diggers in general have relatively short distal segments: the radius is shorter than the humerus (low brachial index), the manus is shorter than the radius (exclusive of terminal phalanges and their claws), the carpus is short, the metacarpals and phalanges are short and wide, with proximal phalanges often broader than long (Coombs 1983, Hildebrand 1983, 1988, Heckert *et al.* 2010). The second way to increase the out-force (F_o) is to increase the related in-lever (l_i). Due to that, the muscles used in digging tend to insert far from the joints they turn (Hildebrand 1988). Accordingly, the insertions of the deltoid muscles (deltoid crest) in diggers commonly extends more than halfway of the humerus, the median epicondyle of the humerus is wide (feature of all scratch-diggers, origin of forearm pronator and manual flexors), the origin of the supinator muscle on the humerus (the supinator crest) is proximally extended, and the pisiform is elongated (insertion of the flexor carpi ulnaris muscle) (Hildebrand 1988, Coombs 1983, Heckert *et al.* 2010). For the same reason, the olecranon process of ulna in diggers is usually long (Coombs 1983, Hildebrand 1988, Heckert *et al.* 2010). ~~Third~~ way to increase the out-force (F_o) is to increase the in-force (F_i). Consequently the muscles connected to the digging ~~behaviour~~ are exceptionally well-developed in diggers, and to accommodate such muscles, their insertions and origins are enlarged (Hildebrand 1988). As a result, the bones of diggers are usually rugged and rough (Hildebrand 1988). The medial epicondyle of humerus (origin of flexors of digits) and the deltoid crest (insertion of the deltoids) are particularly prominent, as well as the acromion process of the scapula (origin of deltoid musculature) and posterior angle of a scapula (origins of the teres major and the long head of the triceps) (Hildebrand 1988, Coombs, 1983, Heckert *et al.* 2010).

~~Appliance of a~~ relatively great force puts the joints of the diggers under much higher stress then in other animals, therefore they are usually better adapted in several ways to resist hyperextension, dislocation, and counterproductive deflection (Hildebrand 1983). The motion of joints that in less specialized animals ~~allow~~ for moves in several planes, in digging animals tend to become limited to a single plane: the wrist joint becomes hinge-like (permitting only flexion and extension), the head of the humerus may has a greater radius of curvature in horizontal than in vertical plane (limiting or preventing adduction and abduction), and the acromion process is long (also limiting adduction and abduction) (Hildebrand 1983). Likewise, joints that usually permit motion, are modified to allow little or no motion: joints between the phalanges and joints between the digits and metacarpals may be flat-ended, V-shaped, multiangled or provided with a peg and a socket, and the surfaces of the distal phalanges cover the surfaces of the proximal ones (preventing sliding movements) (Hildebrand 1983). Rigidity may also be achieved by loss and fusion of bones (Hildebrand 1983). For example, the number of phalanges preceding the unguals decreases in digging mammals (usually to two or one), in some few digits may be modified into digging tools and others may be lost or reduced, the metacarpals and proximal phalanges may be fused, and some elements of the carpus may be horizontally fused (Hildebrand 1983, 1988). Furthermore, joints that normally provide for motion in one plane tend to become strengthened against dislocation: distal ends of the ones preceding the terminal phalanges are enlarged with relatively great radius of curvature (increasing the surface contact between the bones), palm bones develop structures that resist dislocation (for example vertical splines and compatible grooves in metacarpals and phalanges), large sesamoid bones may be present under the joints (their presence functionally bond the distal phalanges to the proximal ones, they also brace joints against motion, and guide or serve as attachments for tendons) (Hildebrand 1983). Diggers also commonly have bony stops between phalanges, and metacarpals and phalanges, that work as a passive mechanism to prevent hyperextension of hinge joints (Hildebrand 1983, 1988).

Scratch-diggers often need to excavate in a dry, compacted soil, therefore in addition to being able to produce great force, they usually have ~~an~~ impressive elongated terminal phalanges changed into blade-like or pick-like structures, and covered by strong keratin sheath (Hildebrand 1983, 1988). Claws allow them to concentrate the delivered force into small, restricted area which makes it much easier to break the hard, consolidated substrate (Hildebrand 1988).

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Appendix online 3. Taphonomical notes on forelimb specimens of *Stagonolepis olenkae* from Krasiejów locality in Poland.

The detailed studies on the taphonomy and origin of Krasiejów assemblage were conducted by Bodzioch and Kowal-Linka (2012) and general comments on the taphonomy and sedimentation of Krasiejów deposits are also included in the review of Krasiejów biota by Dzik and Sulej (2007).

Bodzioch and Kowal-Linka (2012) proposed that early diagenesis of aquatic animals from Krasiejów (*Paleorhinus=Parasuchus* and *Metoposaurus krasiejowensis*) occurred in freshwater environment while early diagenesis of terrestrial *Stagonolepis olenkae* occurred ~~in~~ arid terrestrial environment.

Rich bone-bearing horizons in Krasiejów contain bones of different animals which are usually mixed together (e.g. Dzik and Sulej 2007; Bodzioch and Kowal-Linka 2012). The character of this locality makes it often difficult to determine which remains belong to a single animal and due to that the bone elements not found in articulation must be interpreted as isolated. The bones are mostly preserved in three dimensional anatomical shape. They may be more or less deformed due to compaction of soft siltstone and mudstone, however the resulting changes of proportions of the bones are negligible and the original shape in most cases can be easily recognized.

The most common deformation among aetosaurs bones is dorso-ventral compression along their whole length. In the more fragile parts of the bones the external surface is often pushed inside the shaft forming deep dents. Those dents occur often in the long bones in the region behind the proximal and/or distal head. The pattern is often similar in the bones of the same type. In humeri, the dents occur usually on the ventral side behind the proximal head (see spec. ZPAL AbIII/2627, sup. Fig. 5B), in ulnae the dents occur usually on the ventral side behind the olecranon process (see spec. ZPAL Ab/III 2407, sup Fig. 1B; and ZPAL Ab/III 1179, 2014, 3351, sup. Fig. 6B–D), and in radii the dents occur usually in the regions behind the both proximal and distal heads at the dorsal and ventral side (see spec. ZPAL Ab/III 2407, sup. Fig. 1A; and ZPAL Ab/III 1628, 2106/4, 2106/2, 3222, sup. Fig. 7 A–D). In ulnae spec. ZPAL Ab/III 1100/1 and 1179 the proximal and distal heads are abraded ~~missing~~ olecranon ~~process~~ and significant ~~part of the proximal section~~. This damage could be an effect of decomposition in the terrestrial environment in the early stage of diagenesis before burial, according to hypothesis proposed by Bodzioch and Kowal-Linka (2012). In the specimens ZPAL Ab/III 2407, 3349, 3350 (sup. Fig. 1–3) the osteoderms are grouped closely with hand elements preserved in association. In living animals the osteoderms are attached to the skin within which they develop and grow (e.g. Vickaryous and Hall 2008). Their close arrangement with articulated hand bones indicates early burial of the individuals with hands still covered by the skin. Dislocation of the bones in the specimens preserved in association (ZPAL Ab/III 2407, 3349, 3350, sup. Fig. 1–3) could be caused by the impact with the bottom of the water basin before burial. Similar arrangement of the bones was observed due to the impact with the bottom of the water pool in the taphonomical experiment conducted by Syme and Salisbury (2014) on the bodies of juvenile *Crocodylus porosus*.

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Appendix online 4. ~~Detail~~ description of the method used to generate 3D models of the forelimb bones of *Stagonolepis olenkae* ~~from~~ Krasiejów locality in Poland.

Part 1. List of the programs used for generation of the 3D models, with the respective links to download them (if they are free to use):

1. **FastStone Photo Resizer, ver. 3.8**
   http://www.faststone.org/FSResizerDetail.htm
2. **VisualSFM**
   http://ccwu.me/vsfm/
3. **MeshLAB, 64bit, ver. 1.3.4 BETA**
   (currently newer version 2016.12 is available)
   http://www.meshlab.net/
4. **Texture Stitcher**
   (author: Michel Khazdan, Johns Hopkins University)
   http://www.cs.jhu.edu/~misha/Code/TextureStitcher/
5. **Daz Studio**
   https://www.daz3d.com/home
6. **Adobe Acrobat**

Part 2. Detail description of the method used to obtain 3D models:

1. Obtaining pictures for further processing

Photogrammetry allows reconstruction of the 3D shape of photographed objects from a set of photographs taken from different angles. The selected specimens of the aetosaur *Stagonolepis olenkae* were photographed with a 24,2 mega-pixels digital single-lens reflex (DSLR) Nikon D-3300 camera, mounted with AF-S DX Nikkor 18-105 mm f/3.5-5.6G ED VR lens. Each specimen was placed on a small desk (easy to walk around), at the centre of a piece of paper (A4 format) with continuous block of text printed (to ensure proper convergence of the orientation algorithm). Each specimen was photographed from two sides – dorsal and ventral, around 100 photos each. The models for both the ventral and the dorsal side were later scaled and digitally reassembled into a single object. Most of the images covered the entire surface of the specimen, and each overlapped with other photographs. The photographs were taken from 8 spots (in more or less regular intervals of approximately 45°), from different vertical angles (about 8, approximately form 0° to 90°), and from different distances. The images were acquired in the area with a constant, abundant, diffused light source to reduce glares and harsh shadows on the object. They were saved by the camera as .JPG files with the resolution of 6000x4000 px and later scaled down with the freeware program FastStone Photo Resizer to the resolution of 3200x2400 px, to speed up the photogrammetric processing.

2. Generation of dense point clouds in VisualSFM

Each dorsal and ventral sets of scaled images were imported into the freeware program VisualSFM (Wu 2011). VisualSFM allows to perform keypoint detection (unambiguous feature-points in each image) through SIFT algorithms (i.e. Scale Invariant Feature Transforms; Lowe 1999; Wu 2007), tie-points matching (matching points between pairs of photographs), sparse 3D points generation (Wu 2013; Wu *et al.* 2011) and finally to reconstruct high-resolution 3D point-clouds by dense correlation through CMVS-PMVS algorithms (i.e. Clustering Views for Multi-view Stereo and Patch Based Multi-view Stereo Software; Furukawa and Ponce 2010). For each specimen, two dense point clouds were generated (for dorsal and ventral surface) and saved as .PLY files.

3. Creation of the models in MeshLAB

Each of the generated files was imported into the freeware program MeshLAB (Cignoni *et al.* 2008). MeshLAB provides several tools for work with the 3D models, including cleaning, scaling, measuring, moving, and joining objects (Cignoni *et al.* 1998, Ranzgulia *et al.* 2012, Pietroni *et al.* 2010, Tarini *et al.* 2010, Vergne *et al.* 2010), as well as allows building triangulated meshes out of point clouds with Poisson Surface Reconstruction algorithm (Kazhdan and Hoppe 2013), and creates textures for the finished models (Ranzuglia *et al.* 2013). For each specimen, after manually cleaning unsubstantial points, two triangulated meshes and their respective textures were generated, and saved as .PLY files. Models of ventral and dorsal surface were aligned using the alignment tool (point based gluing) in MeshLAB. Then unsubstantial faces were manually cleaned, and both models were joined, using Surface Reconstruction: Poisson filter. The process, however, caused the loss of colour in generated model.

4. ~~Colour~~ restoration with Texture Stitcher. Reduction, and scaling of the model in MeshLAB.

The ~~colouration~~ was restored using Laplace-Beltrami Operator algorithm, with Texture Stitcher program (Chang *et al.* 2009). Texture Stitcher allows to transfer ~~colours~~ from a few different meshes into the model generated from them. For the program to work, it requires transfer of ~~colour~~ from the textures to vertices, and the ~~colouration~~ of the generated model is saved also into the vertices. The generated model is saved as a .PLY file. To properly save the ~~colouration~~, the number of the vertices of the model needs to be increased a few times, and at this point the model is too big to be published. To reduce its size (reduce the number of vertices), the Quadric Edge Collapse Decimation filter was used. To preserve the ~~colour~~ation, the ~~colour~~ from the vertices of the mesh exported by Texture Stitcher was saved to the texture generated for the smaller mesh. The model with smaller number of vertices and assigned texture was scaled to match the dimensions of the real specimen, and then exported as an .OBJ file. For each specimen an .OBJ file was created.

5. Export of the models into .PDF files.

The .OBJ files were imported into the freeware program Blender. This is a well-known tool allowing creation, management, and projection of 3D graphic. The models of each specimen were transformed in the program to match properly the X, Y, Z coordinate axis. Each model was than saved as an .OBJ file, and imported into Daz Studio. Daz Studio is another free to use program to manage and animate the models. The program allows to export textured models into .U3D files, which can be implemented into .PDF files. Exported .U3D files of each specimen were inserted into a .PDF file with Adobe Acrobat.

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