Zakład Paleobiologii Ewolucyjnej
Instytut Paleobiologii PAN

Locomotor system of the aetosaur *Stagonolepis olenkae*

(Układ ruchu aetozaura *Stagonolepis olenkae*)

Dawid Dróżdż

Dissertation for the degree of doctor of geology presented
at the Institute of Paleobiology of the Polish Academy of Sciences
conducted under the supervision of Dr. Tomasz Sulej and Dr. Tomasz Szczygielski

Rozprawa doktorska wykonana w Instytucie Paleobiologii PAN
pod kierunkiem Dra hab. Tomasza Suleja oraz Dra Tomasza Szczygielskiego

Warszawa 2022

Dla mojego Taty, który jako pierwszy pokazał mi jak ciekawy może być świat.

For my Dad, who first showed me how fascinating the world could be.

ACKNOWLEDGMENTS

I thank my supervisors Dr. Tomasz Sulej and Dr. Tomasz Szczygielski for their support and constructive comments in regard to the thesis.

Special thanks to Dr. Justyna Słowiak-Morkovina, for her comments and notes on the manuscript; as well as to Dr. Julia Brenda Desojo and Dr. Voltaire Paes-Neto for the great discussions about aetosaurs and for being excellent hosts during my visit in South America, in the Museo de La Plata, Argentina and Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil, respectively; and Prof. Jerzy Dzik for checking the early version of the manuscript about the forelimbs and finding the unique specimen from Woźniki.

Many thanks also to other people that hosted me in the collections, especially Dr. Stig Walsh (National Museum of Scotland, Edinburgh, UK), Janet Trythall, Dave Longstaff, and Dr. Alison Wright (Elgin Museum, Scotland, UK), Dr. Pablo Ortiz (Paleontología de Vertebrados, Instituto 'Miguel Lillo', San Miguel de Tucumán, Argentina), Dr. Ricardo Martinez (División de Paleontología de Vertebrados del Museo de Ciencias Naturales y Universidad Nacional de San Juan, San Juan, Argentina), Prof. Marco Brandalise (Pontifical Catholic University of Rio Grande do Sul, Porto Alegre, Brazil), Dr. Eudald Mujal (Staatliches Museum für Naturkunde, Stuttgart, Germany).

I thank Dr. Paul Tafforeau and Dr. Vincent Fernadez for conducting the scanning in the European Synchrotron Radiation Facility in Grenoble, France; and Martyna Czaja for the virtual segmentation of the slices.

I thank Urszula Chatys, Katarzyna Przestrzelska, Piotr Bajdek, and Antoni Lewczuk for their excellent preparation of the material; as well as Kacper Węgrzyn, Marceli Witasik, and Piotr Gryz for helping with photogrammetry and 3D scanning of some of the specimens:Jakub Jabłoński and Dr. Marek Dec for 3D printing some of the specimens.

I thank Prof. Adam Bodzioch, and Dr. Mateusz Antczak from the University of Opole for they cooperation in the organization of the field works in Krasiejów; as well as the participants of the excavations: Mateusz Bagiński, Magda Samborska, Piotr Kłonowski, Anna Dudek, Kacper Sładkiewicz, Marysia Gajewska, Michalina Biedrzycka, Alicja Pełczyńska, Cezary Ruchlewicz, Fabio Cavaler, Krzysztof Bratek, Leszek Hebda, Patrycja Wiśniewska, Piotr Ulwański.

Many thanks for great scientific discussions to Dr. Mateusz Tałanda, Dr. Rafał Piechowski, Dr. Sergi Lopez-Torres, Wojciech Pawlak, Przemysław Świś, Maciej Pindakiewicz, Dr. Łukasz Czepiński, Adam Rytel, Dr. Daniel Madzia, Dr. Andrzej Wolniewicz, Dr. Grzegorz Niedźwiedzki, Dr. Martin Qvarnström, William Reyes, Elżbieta Teschner, Dr. Bryan Small, Dr. Andrew Heckert, Dr. William Parker.

I also thank the director of the Institute of Paleobiology, PAS, Prof. Jarosław Stolarski, as well as Dr. Przemysław Gorzelak and Dr. Barbara Kremer for their help in solving the difficult situations that arose during my PhD studies.

Finally, I thank my family, especially my brothers Tomasz and Dominik Dróżdż, close friends Michał Zygmut, Dr. Paweł Raźny, Agnieszka Kuc, Klaudiusz Ziemek; and my girlfriend Martyna Kułakowska, for being there for me in my times of trouble.

FINANCING

Excavations in Krasiejów 2017–2020 were financed from the National Center of Science grant of Dr. Tomasz Sulej NCN 2017/27/B/NZ8/01543. The synchrotron scan was financed from the National Center of Science grant of Dr. Tomasz Sulej NCN 2019/33/B/NZ8/01453.

STRESZCZENIE

Dysertacja jest opracowaniem układu ruchu aetozaura *Stagonolepis olenkae* z Krasiejowa i zawiera szczegółowy opis osteologiczny kończyn przednich, obręczy miednicznej i kończyn tylnych, oraz ich interpretację w kontekście postawy, sposobu poruszania, przystosowań i rozwoju osobniczego. Praca zawiera także opis młodocianego aetozaura z Woźnik wstępnie rozpoznanego przez dra hab. Tomasza Suleja jako *Stagonolepis olenkae*.

Aetozaury były opancerzonymi zwierzętami spokrewnionymi z dzisiejszymi krokodylami. Z wyglądu nieco przypominały żyjące dziś łuskowce lub pancerniki, u których pancerz (rogowy, u pancerników też kostny) niemal w całości pokrywa ciało. Znane gatunki aetozaurów osiągały rozmiary od około 1 do 6 metrów długości. Ich zapis kopalny jest ograniczony do osadów kontynentalnych górnego triasu, głównie karniku i noryku (ok. 273–208,5 mln lat temu). Występowały na terytorium niemal całej Pangei, a ich szczątki są znane ze stanowisk paleontologicznych w Europie, Indiach, Afryce i obu Amerykach. Wszystkie były czworonożne i wszystkożerne. Gatunek z Krasiejowa jest najbardziej podobny do znanego ze Szkocji *Stagonolepis robertsoni* i jest jednym ze starszych znanych przedstawicieli grupy.

Morfologia kończyn i obręczy *Stagonolepis olenkae* jest typowa dla średnich i dużych aetozaurów z północnej Pangei. *Stagonolepis olenkae* miał kończyny ustawione pionowo pod tułowiem (ang. „erect gait”), oraz był palcochodny, podobnie do innych współczesnych mu zaawansowanych przedstawicieli Pseudosuchia, z których wywodzą się dzisiejsze krokodyle. Kończyny *Stagonolepis olenkae* były bardzo muskularne i krępe, przystosowane do podtrzymywania ciężkiego pancerza i wykonywania bardzo silnych ruchów w płaszczyźnie strzałkowej, to znaczy wzdłuż długiej osi ciała zwierzęcia. Ostatnie paliczki palców łap przednich i tylnych miały kształt pazurów, a ostatnie paliczki pierwszych palców były znacząco powiększone w proporcji do ostatnich paliczków pozostałych placów. Umiejętność wykonywania silnych ruchów oraz znaczące powiększenie jednego z pazurów w stosunku do pozostałych jest charakterystyczne dla dzisiejszych zwierząt wyspecjalizowanych w kopaniu. Obecność tych cech u *Stagonolepis olenkae* wskazuje na przystosowanie tego gatunku do kopania.

Analiza porównawcza wykazała, że morfologia układu ruchu jest generalnie konserwatywna u aetozaurów. Najmniejsze z nich mają smuklejsze kończyny i dłuższe stylopodia (udo, ramie) w stosunku do zeugopodiów (przedramię, podudzie) co wskazuje na ich większą zwin-

ność i szybkość w porównaniu do dużych form, ale ich kończyny posiadają wszystkie inne cechy charakterystyczne dla aetozaurów, związane z podtrzymywaniem pancerza, możliwością wykonywania silnych ruchów i kopaniem.

Pomimo daleko posuniętej specjalizacji, kończyny tylne aetozaurów, przynajmniej jeśli chodzi o konstrukcję kluczowych dla lokomocji stawów biodrowego („pillar erect") i skokowego, nie różnią się znacznie od innych zaawansowanych triasowych Pseudosuchia (popozaurydów i rauizuchidów). Jednakże w odróżnieniu od aetozaurów, ich układ ruchu ma cechy bardziej charakterystyczne dla zwierząt szybko biegających. Wydaje się więc, że zasadnicza morfologia kończyn była już w pełni ukształtowana u wczesnych Pseudosuchia i wraz z postępującą specjalizacją grup, została zmodyfikowana w drodze doboru naturalnego; u aetozaurów żeby wspierać ciężar ciała i umożliwić wykonywanie silnych ruchów; a u innych triasowych Pseudosuchia by zwiększyć zwinność i szybkość.

Ustalono, że u *Stagonolepis olenkae* w trakcie rozwoju ontogenetycznego kręgi krzyżowe i elementy miednicy zyskiwały na masywności oraz zrastały się. Podobnie zrastały się też kość krucza i łopatka w obręczy barkowej. Proces obliteracji szwów w kręgach krzyżowych wydaje się jednorodny i mógłby być wykorzystany jako wskaźnik stadium ontogenetycznego, gdyby inne metody nie były dostępne. Natomiast fuzje w miednicy nie wydają się mieć wyraźnego wzoru. Zaobserwowano też wyraźną zmianę morfologii powierzchni stawowych kości długich w ontogenezie, która polega na zmniejszeniu frekwencji guzowatości na powierzchniach, co jest związane ze wzrostem kości na długość, co także można wykorzystać do szacowania względnego wieku osobników.

Młodociany aetozaur z Woźnik jest prawdopodobnie pierwszym stwierdzonym młodocianym osobnikiem aetozaura. Jego morfologia jest podobna do innych małych aetozaurów; zgadza się to z sugestiami niektórych badaczy, że te małe formy to nie osobne gatunki, ale osobniki młodociane większych aetozaurów znanych z tych samych stanowisk. Podobnie jest ze stanowiskiem w Woźnikach, gdzie także występowały większe aetozaury.

Jest prawdopodobne, że młode aetozaury były bardziej ruchliwe i zwinne od dorosłych, co pozwalało im na łatwiejszą ucieczkę przed drapieżnikami lub polowanie na szybką zdobycz. Dorosłe osobnik najprawdopodobniej polegały bardziej na pancerzu w celu ochrony przed drapieżnikami. W związku z rozwojem pancerza, zwierzę stopniowo stawało się cięższe, co było kompensowane przez wzrost kości na grubość oraz powiększenie przyczepów mięśniowych.

Być może w rozwoju dochodziło także do zmiany diety, co w przypadku aetozaurów wymagało rozwinięcia umiejętności kopania.

ABSTRACT

The dissertation is a study of the locomotor system of the aetosaur *Stagonolepis olenkae* from Krasiejów and includes a detailed osteological description of the forelimbs, pelvic girdle, and hind limbs, as well as their interpretation in the context of posture, movement, adaptation and ontogeny. It also includes a description of a juvenile specimen from Woźniki initially recognized by Dr. Tomasz Sulej as *Stagonolepis olenkae.*

Aetosaurs were armored animals related to today's crocodiles. In appearance, they slightly resembled the extant pangolins or armadillos, the armor of which (keratinous, in the armadillos also osseous) almost entirely covers their bodies. Described aetosaur species range in size from about 1 to 6 meters in length. Their fossil record is limited to the continental Upper Triassic, mainly Carnian and Norian (approx. 273–208.5 million years ago). They were found across almost the entire Pangea territory, and their remains are known from paleontological sites in Europe, India, Africa, and both Americas. All aetosaurs were quadrupeds and omnivores. The species from Krasiejów is the most similar to *Stagonolepis robertsoni* known from Scotland and is one of the older known representatives of the group.

The morphology of the limbs and girdles of *Stagonolepis olenkae* is typical of medium and large aetosaurs from northern Pangea. *Stagonolepis olenkae* was a digitigrade, pillar-erect gait animal, similarly to other advanced Triassic representatives of the Pseudosuchia (crocodile lineage of the Archosauria). The limbs of *Stagonolepis olenkae* were robust and muscular, adapted to support its heavy armor and to perform strong movements in the sagittal plane (along the long axis of the animal's body). The unguals in both manus and pes were claw shaped, and the last unguals of the first digits were enlarged in proportion to the unguals of the other digits. The ability the ability to perform strong moves and presence of significantly enlarge one of the claw-like unguals compared to other digits is characteristic for today's specialized digging animals. These features of *Stagonolepis olenkae* indicates its adaptation toward scratch-digging.

A comparative analysis showed that the morphology of the locomotor system is generally conservative in aetosaurs. The smallest species have slender limbs and longer stylopodia (femora, humeri) compared to zeugopodia (forearms, lower legs), which indicates their greater agility and speed compared to large forms. However, their limbs have all the other characteristics of aetosaurs related to supporting the weight of armor, the ability to perform strong movements and scratch-digging.

Despite the high specialization of aetosaur hind limbs, the morphology of the acetabulum and ankle joint, most crucial for locomotion, does not differ significantly from other advanced Triassic Pseudosuchia (mostly Poposauroidea and Rauisuchidae). However, unlike aetosaurs, their locomotor system has characteristics more typical of fast-running animals. It thus appears that the essential limb morphology was already fully developed in the early pseudosuchians and, with the progressive specialization of the groups, has been modified by natural selection; in aetosaurs to support the weight of the body and enable the performance of strong movements; and in the other Triassic Pseudosuchia to increase the agility and speed.

The study established that in *Stagonolepis olenkae* the sacral vertebrae and pelvic elements grew in robustness and fused together during ontogeny. Similarly, fused the scapula and coracoid in the pectoral girdle. Suture obliteration in the sacral vertebrae appears to be uniform and could be used as an indicator of the ontogenetic stage if other methods are not available. In contrast, pelvic fusions do not appear to have a clear pattern. There is also a marked ontogenetic change in the morphology of the articular surfaces of long bones, in which observed is the reduction of the frequency of tuberosities on the surface, which is related to bone growth in length. This feature also can be used to estimate the relative age of individuals.

The juvenile aetosaur from Woźniki is probably the first certain juvenile aetosaur individual. Its morphology is the most similar to that of other small aetosaurs. Some researchers suggest that these are not separate species, but juveniles of larger aetosaurs known from the same sites. The same may be true for the Woźniki individual, as larger aetosaurs have also been recognized in the locality.

It is likely that young aetosaurs were more mobile and agile than adults, which allowed them to more easily escape predators or to hunt for a quick prey. The adults likely relied more on their armor to protect themselves from predators. Probably due to the development of the armor, the animals gradually became heavier, which was compensated by the growth of the bones in thickness and the enlargement of the muscle attachments. A change in their diet could also occur, which in the case of aetosaurs required the development of scratch-digging adaptations.

THE AIMS OF THE STUDY

The major aim of the study was to describe the limbs and pelvic girdle of *Stagonolepis olenkae* from Krasiejów in Poland, based on the previously undescribed material, and interpret the results in the context of locomotion and probable ecological adaptations in reference to the current knowledge. The thesis is comprised of results of the author's research on forelimbs (Dróżdż 2018), as well as provides new interpretation of some previously studied material (Lucas et al. 2007; Książkiewicz 2014; Górnicki et al. 2021).

An additional aim was to recognize the ontogenetic changes in the locomotor system of aetosaurs, given the opportunity to study a juvenile aetosaur skeleton from the Woźniki locality, initially recognized by my supervisor, Dr. Tomasz Sulej, as *Stagonolepis olenkae*.

CONTENTS

INTRODUCTION

What are aetosaurs?

Omnivorous armored reptiles

Stagonolepis olenkae is an aetosaur, which were heavily armored, quadrupedal “basal suchian archosaurs” nested within the Pseudosuchia, the crocodile lineage of the Archosauria (e.g., Brusatte et al. 2010*a*; Nesbitt 2011; Desojo et al. 2013; Ezcurra 2016; Parker 2016*a*). They were medium to large animals, with size varying from up to one meter in length in the smallest species *Aetosaurus ferratus,* up to even six meters in the largest forms, *Desmatosuchus* spp. (e.g., Long and Murry 1995; Schoch 2007; Desojo et al. 2013; Roberto-Da-Silva et al. 2014). Their most characteristic feature is the suit of dermal armor composed of rectangular, plate-like osteoderms, that in all species formed four rows that covered the trunk and tail dorsally and partially laterally. In more heavily armored species, the osteoderms formed multiple rows that covered the belly and ventral part of the tail, along with the limbs (e.g., Case 1922; Sawin 1947; Casamiquela 1961; Walker 1961; Bonaparte 1971; Long and Murry 1995; Schoch 2007; Heckert et al. 2010; Desojo et al. 2013). The aetosaurs are considered to be omnivores, but their exact mode of life is not clear. In many species, the triangular skull is equipped with a shovel-like expansion at the tip of the 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; Dróżdż 2018).

Fossil record of aetosaurs

Aetosaur fossil remains are restricted in occurrence to the continental Upper Triassic, mostly Carnian and Norian. A few species from the Redonda Formation in New Mexico could be Rhaetian (e.g., Heckert and Lucas 2000; Desojo et al. 2013). The aetosaurs 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, however, majority of their species, including the most advanced representatives come from the North America (e.g., Long and Ballew 1985; Long and Murry 1995; Parker 2016*a*; Czepiński et al. 2021). The most iconic aetosaur species known from mostly complete and articulated skeletons are *Desmatosuchus* *spurensis* form the Norian Chinle and Tecovas formations in Texas, USA (e.g., Case 1922; Long and Murry 1995; Desojo et al. 2013), *Longosuchus meadei* from the Norian Cooper Canyon Formation in Texas, USA (e.g., Sawin 1947; Desojo et al. 2013), *Typothorax coccinarum* from the Norian Chinle, Trujillo, Copper Canyon, and Bull Canyon formations in Arizona, New Mexico, and Texas, USA (e.g., Heckert et al. 2010; Parker and Martz 2010), *Aetosauroides scagliai* from the Carnian parts of the Ischigualasto Formation in Argentina Santa Maria Formation in Brazil (e.g., Casamiquela 1960, 1961, 1967; Biacchi Brust et al. 2018), *Neoaetosauroides engaeus* from the Norian Los Colorados Formation in Argentina (e.g, Bonaparte 1971), *Stagonolepis robertsoni* from the Carnian Elgin Sandstones in Scotland (e.g., Walker 1961), and *Aetosaurus ferratus* and *Paratypothorax andressorum* from the Norian Löwenstein Formation in Germany (Schoch 2007; Schoch and Desojo 2016); however, the latter one has a cosmopolitan reported range of occurrence, but beside Germany it is known mostly from osteoderms (Lucas et al. 2006). In fact, the majority of known aetosaur fossils are osteoderms, that due to their abundance and high diversity are used as the basic for the aetosaur classification and phylogeny, with some taxa described solely based on the dermal amour (e.g., Long and Ballew 1985; Desojo et al. 2013; Parker 2016*a*; Czepiński et al. 2021).

Stagonolepis olenkae from Krasiejów in southwestern Poland also can be considered an important aetosaur taxon, because the material form the locality is very rich and includes cranial and postcranial remains of several individuals of different sizes and ontogenetic ages, with some skeletons being partially articulated. The Polish species is very similar to the Scottish *Stagonolepis robertsoni*. Beside the generally larger size of the Krasiejów species, the differences appear to be located only in the skull (Antczak 2016; Parker 2016a), therefore, the division of this species has been contested especially when it comes to the postcranium (Antczak 2016; Górnicki et al. 2021).

This work for the first time reports the presence of an aetosaur from Woźniki, Poland. The unambiguous new aetosaur material from this locality comprises an almost complete skeleton of a juvenile aetosaur individual and an ischium of an adult individual. The juvenile aetosaur initially was tentatively referred to *Stagonolepis olenkae* by dr. Tomasz Sulej.

Apart from Krasiejów and Woźniki, aetosaurs have been reported from two other localities in the southern part of Poland: Poręba and Kocury (Sulej et al. 2012; Czepiński et al. 2021). However, the material from both localities is scarce. From Poręba, vertebra and a few osteoderms are known, including a lateral osteoderm with the spike (Sulej et al. 2012); and from Kocury, a maxilla, paramedian osteoderm, and lateral osteoderms are known, which have been described as new species *Kocurypelta silvestris* similar to *Paratypothorax andressorum* (Czepiński et al. 2021).

Aetosaur classification

The first known aetosaur fossil was the natural cast of the ventral osteoderms of *Stagonolepis robertsoni* described by Louis Agassiz (1844). He named it *Stagonolepis* (from Greek words: Σταγόνες (stagones)/drops and λεπίς (lepis)/scale, laminae), as he confused it for a Devonian fish. This mistake was corrected by Thomas Henry Huxley (1875) who redescribed the species as a reptile. Soon after that, Oscar Fraas (1877) described a remarkable block including at least twenty two small, heavily armored, articulated reptiles he recognized as a new genus. He named it *Aëtosaurus* (*Aetosaurus*) due to its specific morphology of skull which reminded him of an eagle (Greek αετός (aetos)), and recognized its similarities to *Stagonolepis robertsoni.* Ever since the validity of the group has never been contested. Historically, under the Linnaean taxonomic system, it was named either Aetosauria or Stagonolepididae (Marsh 1884; Lydekker 1887; Schoch 2007; Parker 2016*a*).

The aetosaurs are considered to be monophyletic, and the advanced forms seem to be divisible into two clear lineages that differ mostly in the morphology of paramedian and lateral osteoderms (e.g., Long and Ballew 1985; Desojo et al. 2013; Parker 2016*a*).

This differences in anatomy were historically (and, informally, still are) used in classification to divide aetosaurs into three groups: the "basal aetosaurs"; advanced aetosaurs more similar to *Typothorax* spp. (Thypothoracisinae in Desojo et al. 2013); and advanced aetosaurs more similar to *Desmatosuchus* spp. (Desmatosuchinae in Desojo et al. 2013). The "basal aetosaurs", such as *Aetosauroides scagliai*, *Stagonolepis* spp., or *Aetosaurus ferratus,* have a slim trunk with narrow paramedian osteoderms and lateral osteoderms without the spikes; in those similar to *Typothorax* spp., the dorsal paramedian osteoderms of the trunk region are significantly expanded transversally, what gives the body of the animal a barrel-like shape; and the remaining advanced forms, such as *Desmatosuchus* spp., those osteoderms are narrower, therefore their body is more slender in comparison to *Typothorax* spp. and its close relatives (e.g., Long and Ballew 1985; Desojo et al. 2013; Parker 2016*a*).

More recent cladistic analyses consequently place the aetosaurs such as *Typothorax* spp. and *Paratypothorax andressorum* within one clade and such as *Desmatosuchus* spp. and *Longosuchus meadei* in another. According to these topologies, however, the "basal aetosaurs" in fact are mostly distributed in the two main lineages with *Aetosauroides scagliai* as the only true basal aetosaur (e.g., Desojo et al. 2013; Parker 2016*a*).

Taxonomical history of *Stagonolepis olenkae*

The first description of the Krasiejów locality mentioned eleven osteoderms, as well as other long bones of aetosaurs and referred this material to Stagonolepididae (Dzik et al. 2000). The same paper (Dzik et al. 2000) mentioned also two dinosaur dentaries (ZPAL AbIII/281, ZPAL AbIII/282), which were later redescribed as belonging to aetosaurs by Dzik (2001). In the latter work, Dzik additionally mentioned an incomplete ilium and osteoderms, as well as indicated that osteoderms are similar as in the genus *Stagonolepis*, although dentaries and ilium were referred simply to an aetosaur (Dzik 2001). Dzik and Sulej (2007) first hinted that both the postcranium and cranium of Krasiejów aetosaur belonged to the same species, but did not make a clear taxonomical statement. They suggested that osteoderms are alike *Stagonolepis robertsoni*, but marked the possibility that Krasiejów material may be a different species based on the morphology of the cranium (Dzik and Sulej 2007). Shortly after, Lucas et al. (2007) assigned undescribed material exhibited in the Museum of Evolution of the Institute of Paleobiology, PAS, in Warsaw to *Stagonolepis robertsoni*. They argumented that it is undistinguishable from *S. robertsoni* (Heckert and Lucas 2000; Lucas et al. 2007), however, their assignment was based solely on the postcranium, with no reference to the cranial material (Lucas et al. 2007). Sulej (2010) assigned the material described by Lucas at el. (Lucas et al. 2007) to the new species, *Stagonolepis olenkae*, but in contrast to Lucas at el. (2007), he based his identification almost solely on the cranium, with no references to the postcranial material, except for poorly specified differences in the tibia distinguishing *S. robertsoni* and *S. olenkae* from *Calyptosuchus* (“*Stagonolepis*“) *wellesi*. In accordance with the statement from Dzik and Sulej (Dzik and Sulej 2007), Sulej (Sulej 2010) pointed several differences between the crania of *S. olenkae* and *S. robertsoni*, though admitted that these two forms are very similar. In his unpublished thesis, Książkiewicz (Książkiewicz 2014), based on the postcranial material, supported the validity of the new species and declared differences in the morphology of dorsal trunk paramedian osteoderms, ventral osteoderms, and calcaneum. Antczak (2016) based on a new cranial material, argued that many of the differences observed between *S. olenkae* and *S. robertsoni* may be explained by intraspecific variation. Although he did not synonymize those two species, he stated that synonymy of *S. olenkae* with *S. robertsoni* seems more reasonable than considering these two as distinct species (Antczak 2016) and he referred the postcranial material from Krasiejów to *S. robertsoni*, following Lucas et al. (Lucas et al. 2007). He additionally supported this referral with, at the time unpublished, data on an aetosaur pes identified by a student, Szymon Górnicki, that, as he claimed, is identical as that of *S. robertsoni* (Górnicki 2015; Antczak 2016). However, in the later paper presenting the material, the pes was referred to Aetosauria indet. (Górnicki et al. 2021). Parker (2016*a*) also stated that the differences between those two species are minor and appear to lay only in the skull. Dróżdż (2018) arbitrary assigned the forelimb material to *S. olenkae* as the most parsimonious and noted few differences with *S. robertsoni*. However, he also pointed that those two forms are very similar and difficult to compare directly due to poor preservation of *S. robertsoni* in comparison to *S. olenkae*. This assignment of the material to *S. olenkae* is kept in this study.

Limbs and locomotion of aetosaurs

Gait evolution in archosaurs

By the time of *Stagonolepis olenkae*, archosaurs were already dominant animals in the terrestrial environments, being highly diversified morphologically and specialized toward various ecological roles (e.g., Bonaparte 1971; Parrish 1986; Long and Murry 1995; Brusatte et al. 2010*b*; Nesbitt 2011; Nesbitt et al. 2013, 2017; Ezcurra 2016). One of the key aspects of archosaur radiations in the Triassic is the evolutionary development of erect gait from sprawling ancestors (e.g., Charig 1972; Parrish 1986; Kubo and Benton 2007; Nesbitt et al. 2017). It was a gradual process that resulted in appearance of various adaptive types of gaits in different archosaur lineages; through semi-erect gait of Middle Triassic stem-archosaurs such as *Euparkeria capensis* (Sookias and Butler 2013; Sookias et al. 2014; Sookias 2016; Demuth et al. 2020); along with distinct types of erect gaits in the Late Triassic in early dinosaurs (buttress erect) and pseudosuchians (pillar erect), from which eventually derived the erect gaits of non-avian dinosaurs and birds, and modified gait of modern crocodiles (e.g., Charig 1972; Parrish 1986, 1987; Benton and Clark 1988; Hutchinson and Gatesy 2000; Hutchinson 2006; Demuth et al. 2020; Piechowski and Tałanda 2020). Several studies focused on biomechanical and functional aspects of this transition and there is an established set of general morphological indicators characteristic for each type of gait. However, a lot of aspects of archosaur locomotion, especially concerning the early forms, is still unsolved (e.g., Charig 1972; Bonaparte 1984; Parrish 1986, 1987; Hutchinson and Gatesy 2000; Hutchinson 2006; Nesbitt et al. 2017; Demuth et al. 2020).

Limbs and girdles of aetosaurs

The perception of aetosaur gait and locomotion evolved over time. An erect gait was first proposed for aetosaurs by Parish (1986) in the context of their pelvic girdle and hind limbs. Previous reconstructions pictured them as sprawling animals (e.g., Case 1922; Sawin 1947; Walker 1961). Parrish (1986) analyzed multiple “Thecodonts” (polyphyletic group including basal Pseudosuchia and Avemetatarsalia). In his analysis, he included at least four aetosaur taxa, namely *Calyptosuchus wellesi*, *Desmatosuchus* spp., *Stagonolepis robertsoni*, and *Typothorax* spp., and proposed an upright position of the hind limbs for all aetosaurs (Parrish 1986). Later studies showed that the aetosaur condition was similar as in other Pseudosuchia and termed pillar erect due to the horizontal orientation of the acetabula to which the femora articulated ventrally, in contrast to vertically oriented acetabula to which the femora could articulate laterally (buttress erect; Benton and Clark 1988). However, Desojo et al. (2013) argued that Parrish (1986) relayed mostly on *Typothorax* spp. which might not be representative for the whole group, and pointed out differences in the orientation of the acetabula between various aetosaurs. Probable differences in the posture between the aetosaurs was shown also by Kubo and Benton (2007), who suggested a more upright position of hind limbs in the aetosaurs from the Placerias Quarry in *Longosuchus meadei*. Therefore Desojo et al. (2013) proposed a range of locomotor capabilities and different types of gait for certain species (erect or semi-erect as proposed by the previous studies; Parrish 1986; Desojo and Báez 2005; Desojo and Vizcaíno 2009; Heckert et al. 2010; Padian et al. 2010).

Previous studies on the gait focus mainly on hind limbs, and there was little attention given to forelimbs, as the researchers tend to search for analogies between pseudosuchians and early Avemetatarsalia that triggered the evolution toward bipedalism (e.g., Charig 1972; Parrish 1986; Kubo and Kubo 2012). However, aetosaurs were heavily built, obligatory quadrupeds (e.g., Desojo et al. 2013) and their pectoral girdle and forelimbs probably played as important role in the locomotion as the hind limbs. Until now, few studies focused on this aspect of aetosaur locomotion. Heckert et al. (2010) proposed a mixed posture for *Typothorax coccinarum*, with erect hind limbs and sprawling forelimbs.

A major difficulty with the studies of limbs and girdles in aetosaurs is due to the rarity of those elements in the fossils record. Moreover, in many articulated specimens they are obscured by osteoderms. The forelimbs are generally less abundant than the hind limbs, probably due to the large disproportion in the size between those elements (the pes is almost three times the size of the manus). However, both the forelimb and hind limb girdles and other elements are overall known for the most complete specimens representing *Aetosaurus ferratus*, *Aetosauroides scagliai*, *Calyptosuchus wellesi*, *Desmatosuchus* spp., *Neoaetosauroides engaeus*, *Typothorax* spp., *Scutarx deltatylus*, and *Stagonolepis robertsoni* (e.g., Sawin 1947; Casamiquela 1961; Walker 1961; Casamiquela 1967; Bonaparte 1971; Long and Murry 1995; Lucas et al. 2002; Desojo and Báez 2005; Schoch 2007; Roberto-Da-Silva et al. 2014; Parker 2016*b*, 2018*a*). The least information is available for the manus and carpus. Those parts are described in detail only for *Stagonolepis robertsoni*, *Longosuchus meadei*, *Typothorax coccinarum*, and *Stagonolepis olenkae* (Sawin 1947; Walker 1961; Lucas and Heckert 2011; Dróżdż 2018), but they are present also in *Aetosaurus ferratus* and *Aetosauroides scagliai* (Casamiquela 1961; Schoch 2007). Little more is known about the pes and, especially, the distal tarsals. Those elements have been recognized in a few more species, including *Aetosaurus ferratus*, *Aetosauroides scagliai*, *Polesinesuchus aurelioi*, *Stagonolepis robertsoni*, *Longosuchus meadei*, *Typothorax* spp., *Neoaetosauroides engaeus*, and *Aetobarbakinoides brasiliensis* (Sawin 1947; Romer 1956; Casamiquela 1961, 1967; Bonaparte 1971; Long and Murry 1995; Martz 2002; Desojo and Báez 2005; Schoch 2007; Heckert et al. 2010; Desojo et al. 2012; Roberto-Da-Silva et al. 2014). It is widely accepted that aetosaurs are the trackmakers of the ichnogenus *Brachychirotherium*, which also gives some insight into the morphology and locomotion of the group (Lucas and Heckert 2011). However, the presence of this ichnogenus is not always accompanied by body fossils (e.g., Avanzini et al. 2007; Desojo et al. 2013).

It is worth noting that the material of *Stagonolepis olenkae* from Krasiejów includes several articulated, relatively complete and exposed from under sediment and osteoderms specimens of both the manus and the pes (among them, four of each are described in this study), while for other mentioned aetosaurs the material is less abundant, in many cases incomplete, or obscured by osteoderms (Zittel 1887; e.g, Walker 1961; Bonaparte 1971; Schoch 2007; Heckert et al. 2010; Lucas and Heckert 2011; Desojo et al. 2012).

Previous works on the limbs of *Stagonolepis olenkae*

Majority of the material, especially when it comes to the pelvic girdle and hind limbs, is described here for the first time. The author already published description of the forelimbs of *Stagonolepis olenkae* and the results of that previous description (Dróżdż 2018) are incorporated into the thesis. However, as the research progressed and new techniques have been applied, the interpretation of some elements changed and was updated in this work.

The postcranial skeleton of *Stagonolepis olenkae* has been described by Książkiewicz (2014) in his unpublished doctoral thesis. However, the research conducted for this work was performed independently from his studies, in majority based on different and previously unpublished material from Krasiejów as well as a wider range of personally studied aetosaur specimens from around the world, and provided different results. The author have personally examined the material used by Książkiewicz, but since he wishes to publish his thesis in a separate paper, only necessary references to his work were provided in this study. This work contains a more detailed description of the forelimbs, pelvic girdle, and hind limbs of *S. olenkae*, and discusses the locomotion, adaptations, and ontogeny of those elements in the aspects that have not been mentioned by Książkiewicz (2014). Some of the specimens used in this study were previously described by Lucas et al. (2007) in a taxonomical context. The pes assigned here to *Stagonolepis olenkae* was described by Górnicki et al. (2021), thus the interpretation of the elements presented by the authors are different from this study.

Aetosaur ontogeny

Majority of the studies about the ontogeny in aetosaurs focus on the osteoderms and skeletochronology, in which the count of the lines of arrested growth (LAGs) is used to determine the probable age of the studied specimens, with little insight into morphological changes in other parts of the skeleton (e.g., de Ricqlès et al. 2003; Parker 2008; Cerda and Desojo 2011; Taborda et al. 2013; Cerda et al. 2018; Hoffman et al. 2019). Taborda et al. (2013) utilized this method of age determination, as well as estimated the total length and body mass for *Aetosauroides scagliai*. They compared the results with other aetosaurs and extant crocodilians, and suggested that the aetosaurs had a slower growth rate compared to pseudosuchians, and the growth rate of various aetosaur taxa was similar in terms of the entire body length, but there was a difference between the slender- and thick-bodied aetosaurs (e.g., *Typothorax* spp.) when it comes to the body mass, which increased faster in the latter. De Ricqlès et al. (2003), based on the long bone histology, suggested that the growth of aetosaurs was rapid in early ontogeny and slowed down in adulthood.

Morphological analysis of *Typothorax coccinarum* osteoderms performed by Martz (2002) suggested that juveniles had narrower bodies then the adults. However, some observation suggest that the general morphology of the osteoderms did not change during the ontogeny (e.g., Parker 2006). Desojo et al. (2013) speculated that the sequence of fusion between the centra and neural arches was similar as in crocodiles and phytosaurs (posteroanterior) (Brochu 1996; Irmis 2007; Desojo et al. 2013). The centra in the presacral region are not fused with the neural arches in *Aetosaurus ferratus*, therefore Schoch (2007) suggested that the known individuals of that species probably did not reach their full body sizes. In addition, Schoch and Desojo (2016), based on a comparison of the skull of *Paratypothorax andressorum* with *Aetosaurus ferratus,* suggested that the latter might represent a juvenile of the former, despite the differences in the osteoderm morphology. A similar situation seems to occur with *Polesinesuchus aurelioi* and *Aetosauroides scagliai* known from the same locality in Brazil. Based on the axial skeleton, Paes-Neto et al. (2021) proposed that the significantly smaller *Polesinesuchus aurelioi* is a juvenile of the larger *Aetosauroides scagliai.*

Adaptations toward strength and probable scratch-digging in aetosaurs

One of the major differences between the limb morphology in aetosaurs and other contemporary Pseudosuchians is that in aetosaurs the limbs are more heavily built, stouter and more muscular, at least when it comes to large and middle-sized species such as *Desmatosuchus* spp., *Stagonolepis* spp., *Longosuchus meadei*, and *Typothorax* spp. Parrish (1986) pointed out that in comparison to other "thecodontians", in the femora of aetosaurs the fourth trochanter is positioned more distally and the shaft is thicker in cross-section, the iliofibularis trochanter is also positioned more distally, and both the tibia and fibula are comparatively thicker in relation to the length. He proposed that this might represent either a graviportal or fossorial adaptation (Parrish 1986). Adaptations for digging have been more comprehensively discussed by Heckert et al. (2010) in respect to *Typothorax coccinarum*. They focused more on the forelimbs and pointed a low brachial index (radius shorter than the humerus), a prominent deltopectoral crest that extends distally on the humerus, a wide entepicondyle, short and wide metacarpals, and short and wide phalanges as being the most indicative. In addition, they pointed out that the compact foot with large, curved, and laterally compressed unguals could have been used for scratch-digging, as it was suggested for the rhynchosaur *Hyperodapedeon* (Benton 1983; Heckert et al. 2010). Both Parrish (1986) and Heckert et al. (2010) used as the basis for their studies the work of Hildebrand (1983, 1988) who specified characters indicating digging behavior in modern vertebrates. Usage of the limbs for digging was also suggested for *Stagonolepis robertsoni* by Walker (1961). Heckert et al. (2010) suggested that *Typothorax coccinarum* might have used its limbs to unearth roots or burrowing invertebrates.

GEOLOGICAL SETTING

Krasiejów

Virtually all of the studied material comes from Krasiejów, which is located at the southern-eastern edge of the fore-Sudetic Homocline in the Opole Voivodeship, southwestern Poland. This was the first discovered locality of the series of the Late Triassic, vertebrate-bearing localities in southern Poland brought to light near the end of the 1990s, supplemented later by the Lisowice, Poręba, Woźniki, Marciszów, and recently Kocury (Dzik et al. 2000, 2008; Dzik 2001; Budziszewska-Karwówska et al. 2010; Sulej et al. 2011, 2012; Niedźwiedzki et al. 2012; Szczygielski and Sulej 2016; Szczygielski 2017; Czepiński et al. 2021). The outcrop is located in a not functioning clay pit.

The age of the beds exposed in Krasiejów is late Carnian but early Norian was also discussed. The late Carnian was proposed originally based on biostratigraphic evidence (Dzik et al. 2000; Zatoń et al. 2005; Dzik and Sulej 2007, 2016; Kozur and Weems 2010), but the lithostratigraphic correlations suggest a Norian age (Szulc et al. 2015).

Rocks deposited in Krasiejów consist mostly of red to red-brown or gray siltstones and mudstones. An alternating series of red and gray rocks indicates 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 paleosol horizons are present in the section (Szulc 2005). In the section below the outcrop level, the presence of gypsum was reported (Szulc 2005).

The Krasiejów locality is one of the largest accumulations of fossil vertebrates in Central Europe. In addition to aetosaurs, the Krasiejów fauna includes temnospondyls *Metoposaurus krasiejowensis* and *Cyclotosaurus intermedius*, other “basal archosaurs” – a rauisuchid *Polonosuchus silesiacus* and a phytosaur *Paleorhinus* (=*Parasuchus*) sp., a dinosauromorph *Silesaurus opolensis*, a gliding archosauromorph *Ozimek volans*, eucynodont *Polonodon woznikiensis*, fishes, microfossils, and invertebrates (Dzik et al. 2000; Dzik 2001, 2003*a*, *b*, 2008; Sulej 2002, 2005, 2007, 2010; Sulej and Majer 2005; Dzik and Sulej 2007, 2016; Brusatte et al. 2009; Piechowski and Dzik 2010; Skrzycki 2015; Kowalski et al. 2019; Sulej et al. 2021). Plant remains are rare (Dzik et al. 2000; Dzik 2003*b*; Dzik and Sulej 2007; Pacyna 2014).

A majority of vertebrate fossils comes from the two “bone-bearing horizons” (e.g., Dzik et al. 2000; Dzik and Sulej 2007; Szulc 2007; Bodzioch and Kowal-Linka 2012). The lower “bone-bearing horizon” is about 1 m thick, with a grey bed (about 0.3 m thick) in the bottom part 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 the lower “bone-bearing horizon”. According to some studies, the horizontal layering of the sediments indicates their deposition in open standing water (Dzik et al. 2000; Dzik and Sulej 2007; Gruszka and Zieliński 2008). However, according to Bodzioch and Kowal-Linka (2012), the lower “bone-bearing horizon” was deposited by a single short-lived, high energy event, probably a mud flood. Recently, Jewuła et al. (2019) proposed a gilgai model of sedimentation for the entire Krasiejów locality, known from modern Australia.

In the lower “bone-bearing horizon”, fossils of aquatic vertebrates dominate: *Metoposaurus krasiejowensis*, *Cyclotosaurus intermedius*, and phytosaurs; terrestrial fauna is less frequent, but nevertheless abundant, including mostly *Stagonolepis olenkae* and *Silesaurus opolensis* (Dzik et al. 2000; Dzik 2003*b*; Dzik and Sulej 2007). The upper “bone-bearing horizon” (a few meters above the lower one) is composed of lenticular red mudstone body within fluvial deposits. In contrast to the lower “bone-bearing horizon”, terrestrial vertebrates are more frequent there, whereas aquatic ones are rare (Dzik 2003*b*; Dzik and Sulej 2007).

Woźniki

The Woźniki locality, where the specimen of a juvenile aetosaur comes from, is also within the area of the Triassic part of fore-Sudetic Homocline in southwestern Poland, but eastward from Krasiejów, in the Silesia Voivodeship, near the city of Częstochowa. The locality is no longer available as the clay-pit of the neighboring brickyard was recently flooded.

The locality is lithologically similar to Krasiejów, with mostly red to red-brown or gray siltstones and mudstones, which also form an alternating series (Sulej et al. 2011). There are no “bone-bearing horizons” as in Krasiejów, but accumulations of bones were usually found within lenses of the of grey-colored sediments of a coarser texture. Lenses of fine-grained sandstone and calcareous concretions also occur in the section. The juvenile aetosaur specimen is preserved in such a concretion. Possibly the gilgai model of sedimentation is also true for Woźniki.

Szulc et al. (2015) proposed the age of the locality to be middle Norian, mostly due to the close proximity of the Woźniki Limestones, which they dated to Norian, and which are present a few kilometers from the outcrop (e.g., Gąsiorowski and Piekarska 1976). However, the Woźniki Limestones are not present within the section of the locality. On the other hand, the fauna implies the Carnian age of the assemblage, due to presence of the conchostracan *Laxitextella* cf. *laxitexta*, basal phytosaurs similar to *Paleorhinus* sp., an eucynodont *Polonodon woznikiensis*, and a dicynodont probably conspecific with a fragmentary specimen from the lower part of the early Carnian Stuttgart Formation of Germany (Szczygielski and Sulej in press; Sulej et al. 2011, 2020, 2021; Schoch 2012).

Beside the juvenile aetosaur skeleton, other aetosaur remains have not been described from the Woźniki locality thus far, but there are a few unnumbered osteoderms, as well as an ischium which can be referred to aetosaurs. From the Woźniki locality, also remains of sharks, a dicynodont, temnospondyls, and dinosauriforms have been described (Sulej et al. 2011).

INSTITUTIONAL ABBREVIATIONS

AMNH, American Museum of Natural History, New York, USA; **CPE2**, Coleção Municipal, São Pedro do Sul, Brazil; **E.M.**, Elgin Museum, Elgin, Scotland, UK**; MCZ**, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; **MCZD**, Marischal College Zoology Department, University of Aberdeen, Aberdeen, Scotland, UK; **NMMNH**, New Mexico Museum of Natural History and Science, Albuquerque, New Mexico, USA; **MNA**, Museum of Northern Arizona, Flagstaff, Arizona, USA; **PEFO**, Petrified Forest National Park, Petrified Forest, Arizona, USA; **PVL**, Paleontología de Vertebrados, Instituto ‘Miguel Lillo’, San Miguel de Tucumán, Argentina; **R**, The Natural History Museum, London, United Kingdom; **R.S.M.**, National Museum of Scotland, Edinburgh, Scotland, UK; **SMNS**, Staatliches Museum für Naturkunde, Stuttgart, Germany; **TMM**, Texas Memorial Museum, Austin, Texas, USA; **TTUP**, Museum of Texas Tech, Lubbock, Texas, USA; **UCMP**, University of California, Berkeley, California, USA; **ULBRAPVT**, Universidade Luterana do Brasil; Coleção de Paleovertebrados, Canoas, Rio Grande do Sul, Brazil; **UMMP**, University of Michigan, Ann Arbor, Michigan, USA; **ZPAL**, Institute of Paleobiology of the Polish Academy of Sciences, Warsaw; Poland.

MATERIAL

The studied material from Poland comes from the collection of the Institute of Paleobiology Institute of Paleobiology Polish Academy of Sciences in Warsaw, where it is housed. A majority of the studied material is described here for the first time or was published by the author in the article that is incorporated in the thesis (Dróżdż 2018). Seven specimens were previously described and pictured by Lucas et al. (2007): ZPAL AbIII/115 (femur), ZPAL AbIII/502/40 (fibula, misnumbered there as ZPAL AbIII/1178), ZPAL 502/52 (left metatarsal of the first digit), ZPAL AbIII/693 (second sacral, misnumbered there as ZPAL AbIII/1693), ZPAL AbIII/1175 (humerus), ZPAL AbIII/1178 (tibia), and ZPAL AbIII/1179 (ulna). Specimens ZPAL AbIII/2531/1 and ZPAL AbIII/2531/2 were mentioned and photographed by Książkiewicz (2014) in his doctoral thesis.

The studied material consists of articulated specimens as well as isolated ones. The material from Krasiejów comes from different parts of the locality and different bone bearing-horizons, and belongs to individuals of various sizes and probably ontogenetic ages. The specimens were selected to provide the most complete information about the morphology. The author considers the most important the articulated ilium and sacrum of ZPAL AbIII/1937; articulated manus ZPAL AbIII/2071; manus and forearm ZPAL AbIII/2407; articulated pelvis, manus, and pes of the association ZPAL AbIII/3349; complete pubis ZPAL AbIII/3266; pes and lower leg ZPAL AbIII/3368; articulated pes ZPAL AbIII/3455; semi articulated skeleton of a juvenile aetosaur ZPAL V. 34/106. The complete list of the specimens used in this study is presented in the Table 1.

The author also makes references to material from other collections. Among those, the author had the privilege to examine in person the material of *Stagonolepis robertsoni* housed in the Elgin Museum (E.M.) and the National Museum of Scotland in Edinburgh (R.S.M.; that contains also casts of specimens from The Natural History Museum in London (R) and the Marischal College Zoology Department, University of Aberdeen (MCZD)), *Aetosaurus ferratus* and *Paratypothorax andressorum* housed in the Staatliches Museum für Naturkunde in Stuttgart, Germany (SMNS); *Aetosauroides scagliai* in the Paleontología de Vertebrados, Instituto ‘Miguel Lillo’, San Miguel de Tucumán in Argentina (PVL), *Polesinesuchus aurelioi* in the Universidade Luterana do Brasil; Coleção de Paleovertebrados, Canoas, Rio Grande do Sul, Brazil (ULBRAPVT), and *Aetobarbakinoides brasiliensis* in the Coleção Municipal, São Pedro do Sul, Brazil (CPE2).

Table 1. List of specimens from ZPAL collection examined for the thesis.

Catalogue no.	Description	Notes	Fig no.	Publications
ZPAL AbIII/115	Femur	Left, brown coloration, not deformed by compaction, the head broken and missing, the lateral condyle damaged anteriorly, possible bite marks present		Lucas et al. 2007
ZPAL AbIII/199	Ilium	Left, dark brown coloration, slightly compacted lateroventrally, anteroventral portion of the acetabulum broken	6, p. 62; 11, p. 70	
ZPAL AbIII/226	Metatarsal V	Left, dark grey coloration, complete, proximal part of the shaft compacted		
ZPAL AbIII/239	Femur	Left, light beige coloration, not deformed by compaction, only the head preserved		
ZPAL AbIII/246	Tibia	Left, only the distal portion preserved, probably part of the same tibia as ZPAL AbIII/294, light beige coloration, not deformed by compaction	15, p. 87	
ZPAL AbIII/249	Tibia	Left, only the proximal portion preserved, probably part of the same tibia as ZPAL AbIII/294, light beige coloration, not deformed by compaction	15, p. 87	
ZPAL AbIII/251	Tibia	Left, proximal portion only, dark brown coloration, probable bite marks or postmortem decay, anteroposteriorly compacted		
ZPAL AbIII/257	Humerus	Right, distal portion with the condyles and supinator process, brown coloration		Dróżdż 2018
ZPAL AbIII/267	Phalanx (manus)	Left, 2nd row phalanx of digit III, dark grey coloration		Dróżdż 2018
ZPAL AbIII/341	Phalanx (pes)	Left, 1st row phalanx digit II, light pink coloration		
ZPAL AbIII/502/12	Astragalus	Left, part of the association ZPAL AbIII/502, light pink coloration, complete	18, p. 98	
ZPAL AbIII/502/23	Pubis	Left, part of the association ZPAL AbIII/502, light pink coloration, ilium peduncle damaged, pubic flange broken and absent, obturator foramen not preserved, distal knob damaged		
ZPAL AbIII/502/40	Fibula	Right, part of the association ZPAL AbIII/502, light pink coloration, slightly compacted transversally	16, p. 90	Lucas et al. 2007
ZPAL AbIII/502/52	Metatarsal I	Left, part of the association ZPAL AbIII/502, light pink coloration, complete		Lucas et al. 2007
ZPAL AbIII/502/62	Tibia	Left, part of the association ZPAL AbIII/502, light pink coloration, slightly compacted anteroposteriorly, proximal portion damaged, scavenging?		
ZPAL AbIII/502/65	Phalanx (pes)	Right, part of the association ZPAL AbIII/502, light pink coloration		
ZPAL AbIII/502/68	Metatarsal V	Left, part of the association ZPAL AbIII/502, light pink coloration, slightly compacted anteroposteriorly		
ZPAL AbIII/553/28	Ungual	Left, ungual of digit I or II, part of the association ZPAL AbIII/553, beige coloration		

ZPAL AbIII/553/36	Metatarsal V	Right, part of the association ZPAL AbIII/553, beige coloration, compacted anteroposteriorly		
ZPAL AbIII/690	Calcaneum	Left, complete, undeformed, dark brown coloration, hole on the ventral side on the articulation surface for distal tarsals, probable bite mark?	19, p. 100	
ZPAL AbIII/691	Femur	Left, light pink coloration, compacted anteroposteriorly, lateral portion of the head broken, probably part of the association ZPAL AbIII/502 (based on the field notes)		
ZPAL AbIII/693	II sacral vertebra	Light pink coloration, ventral portion of the centrum broken	10, p. 67	Lucas et al. 2007
ZPAL AbIII/1100/1	Ulna	Left, light beige coloration, proximal and distal articulation surfaces damaged	2, p. 50	Dróżdż 2018
ZPAL AbIII/1175	Humerus	Right, light beige coloration, complete	1, p.48; 33, p.175	Lucas et al. 2007, Dróżdż 2018
ZPAL AbIII/1177	Femur	Right, light pink coloration, anteroposteriorly compacted, head and condyles damaged, possible bite marks present, preserved similarly to the tibia ZPAL AbIII/1178 (possibly of the same individual?)		
ZPAL AbIII/1178	Tibia	Left, light pink coloration, preserved in its entirety, anteroposteriorly compacted, probable bite marks on the proximal portion near the articulation surface, preserved similarly to the femur ZPAL AbIII/1177 (possibly of the same individual?)		Lucas et al. 2007
ZPAL AbIII/1179	Ulna	Left, light pink coloration, proximal and distal articulation surfaces damaged		Lucas et al. 2007; Dróżdż 2018
ZPAL AbIII/1624	Fibula	Right, preserved in its entirety, proximal portion of the shaft broken, dark grey/brown coloration, laterally compacted		
ZPAL AbIII/1625	Fibula	Right, preserved in its entirety, iliofibularis trochanter damaged, laterally compacted, dark brown coloration, similarly preserved to the tibia ZPAL AbIII/1626 and the calcaneum ZPAL AbIII/1627 (possibly single individual?)		
ZPAL AbIII/1626	Tibia	Right, dark brown coloration, preserved in its entirety anteroposteriorly compacted, similarly preserved to the fibula ZPAL AbIII/1625 and the calcaneum ZPAL AbIII/1627 (possibly single individual?)	33, 175 p.	
ZPAL AbIII/1627	Calcaneum	Right, dark brown coloration, complete, significantly compacted dorsoventrally, similarly preserved to the fibula ZPAL AbIII/1625 and the tibia ZPAL AbIII/1626 (possibly single individual?)		
ZPAL AbIII/1628	Radius	Right, dark brown coloration, proximal part compacted anteroposteriorly, distal part missing		Dróżdż 2018
ZPAL AbIII/1629	Fibula	Left, brown coloration, preserved in its entirety, slightly compacted laterally		
ZPAL AbIII/1937	Ilium and sacrum	Articulated specimen, light beige coloration, not damaged by compaction, neural spines broken, spine table of II sacral separate from the neural arch, anterior portion of sacral ribs in I sacral and posterior portion of sacral ribs in II sacral broken, pre- and postacetabular portion of the iliac blade broken and absent	8, p. 64; 31, p. 170	

ZPAL AbIII/1942	Femur	Left, dark brown coloration, compacted anteroposteriorly, preserved in its entirety	14, p. 79	
ZPAL AbIII/1981	Ungual (pes)	Right, ungual of digit I, dark grey coloration, anterior tip broken		
ZPAL AbIII/2014	Ulna	Right, dark grey coloration, distal part broken, compacted laterally		Dróżdż 2018
ZPAL AbIII/2071	Manus	Left and right; right manus: 4 carpal elements (fused radiale and intermedium, ulnare, two distal carpals), 14 elements of the manus (complete digits I-III and metacarpals IV and V); left manus: 2 carpals (fused radiale and intermedium, crescent-shaped distal carpal IV), 8 elements of the manus (complete digits I-II and metacarpal IV); right manus and the left fused radiale and intermedium similarly preserved, of brown coloration; left manus elements of dark grey coloration, despite the corresponding size, probably belong to a different animal; the crescent-shaped distal carpal IV of light coloration, much smaller from the homologous element of the right hand, probably a third animal mixed in this specimen	4, p. 54; 5, p. 57; Supp. fig. 4, p. 200	Dróżdż 2018
ZPAL AbIII/2102	Metacarpal IV	Right, dark grey coloration, complete		Dróżdż 2018
ZPAL AbIII/2106/2	Radius	Right, dark brown coloration, only distal part preserved		Dróżdż 2018
ZPAL AbIII/2106/4	Radius	Right, dark brown coloration, compacted anteroposteriorly, distal end missing		Dróżdż 2018
ZPAL AbIII/2407	Manus + forearm	Right, dark grey coloration, elements articulated, ulna and radius complete; carpus and manus rotated about 90º in respect to the forearm; in the carpus preserved: fused radiale and intermedium, ulnare, at least one distal carpal; in the manus preserved: metacarpals I-V and 1st row phalanges I-V, associated with appendicular osteoderms	Supp. fig. 1, p. 197	
ZPAL AbIII/2410	Pubis	Left, light pink coloration, slightly compacted anteroposteriorly, anterior part of the ilium peduncle damaged, dorsal portion of the pubic flange broken and absent, obturator foramen partially preserved, pubic apron almost complete, slightly damaged medially and ventrally, distal knob damaged anteriorly		
ZPAL AbIII/2411	Phalanx (pes)	1st phalanx of digit I, right, light pink coloration		
ZPAL AbIII/2412	Pubis	Right, distal portion of pubic rami with sharp lateral margin of pubic apron and pubic knob, light pink coloration		
ZPAL AbIII/2508	Pes and lower leg	Right, articulated lower leg, ankle joint and pes, with associated appendicular osteoderms, belly osteoderm and two proximal ends of ribs, specimen compacted anteroposteriorly (in relation to the tibia and fibula), dark grey coloration, phalanges broken from the joints and positioned parallel to the metatarsals, V metatarsal broken		
ZPAL AbIII/2531/1	I sacral vertebra	Part of the association ZPAL AbIII/2531, dark grey coloration, compacted anteroposteriorly	6, p. 62; 10, p. 67;	Książkiewicz 2014
ZPAL AbIII/2531/2	II sacral vertebra	Part of the association ZPAL AbIII/2531, dark grey coloration, slightly compacted anteroposteriorly	6, p. 62; 10, p. 67; 31, p. 170	Książkiewicz 2014
ZPAL AbIII/2568	Tibia	Right, dark grey coloration, compacted anteroposteriorly, preserved in its entirety		

ZPAL AbIII/2570/2	Tibia	Left, preserved in its entirety, brown coloration, anteroposteriorly compacted		
ZPAL AbIII/2627	Humerus	Right, dark brown coloration, complete	33, p. 175;	Dróżdż 2018
ZPAL AbIII/2629	Fibula	Left, grey coloration, complete	34, p. 176	
ZPAL AbIII/2630	Femur	Left, dark grey coloration, preserved in its entirety, compacted anteroposteriorly, fourth trochanter damaged		
ZPAL AbIII/2641	Tibia	Right, preserved in its entirety, dark grey coloration, anteroposteriorly compacted		
ZPAL AbIII/2738	II sacral vertebra	Dark grey coloration, compacted anteroposteriorly and dorsoventrally, posterior part of the left sacral rib broken	31, p. 170	
ZPAL AbIII/3303	Femur	Right, dark brown coloration, compacted anteroposteriorly, lateral portion of the head and shaft broken and missing		
ZPAL AbIII/3304	Femur	Right, light pink coloration, preserved in its entirety, compacted anteroposteriorly		
ZPAL AbIII/3305	Femur	Left, only the distal part preserved (almost entire shaft and head broken off and missing), light brown coloration, not deformed by compaction		
ZPAL AbIII/3308	Femur	Right, light pink coloration, slightly compacted anteroposteriorly, head and condyles damaged, bite marks present		
ZPAL AbIII/3309	Femur	Right, dark grey coloration, preserved in its entirety, compacted anteroposteriorly		
ZPAL AbIII/3266	Pubis	Right, light beige coloration, not deformed by compaction, preserved in its entirety, middle portion of the pubic flange slightly damaged	6, p. 62; 12, p. 73; 30, p. 152	
ZPAL AbIII/3322	Radius	Left, dark grey coloration, shaft broken in several places	3, p. 52	Dróżdż 2018
ZPAL AbIII/3323/1	Metatarsal III	Right, complete, part of the association of pes elements ZPAL AbIII/3323, dark grey coloration, compacted dorsoventrally		
ZPAL AbIII/3323/2	Metatarsal IV	Right, part of the association of pes elements ZPAL AbIII/3323, mostly complete (distal lateral tip broken), dark grey coloration, compacted dorsoventrally		
ZPAL AbIII/3323/3	Distal tarsal IV	Left, part of the association of pes elements ZPAL AbIII/3323, dark grey coloration, compacted laterally, damaged dorsally		
ZPAL AbIII/3349/1	Manus + forearm	Right, dark grey coloration, elements semi articulated, part of the association ZPAL AbIII/3349, complete forearm, carpus and almost complete manus (no unguals of digits III–V, only one phalanx in the digit V), compacted dorsoventrally, manus rotated about 90º in respect to forearm, numerous appendicular osteoderms; at the moment of the description the rest of the forearm was lost, therefore, it is not presented in the figures	Supp. fig. 2, p. 198	Dróżdż 2018
ZPAL AbIII/3349/2	Arm + interclavicle	Arm: left, dark grey coloration, part of the association ZPAL AbIII/3349, semi articulated humerus, forearm, carpus, and manus, associated with numerous appendicular osteoderms and interclavicle, the elements are mostly complete; in the manus 5 metacarpals and 5 phalanges are preserved (1st row phalanges of digits III–V, 2nd row phalanges of digits IV and V); at the moment of the description the elements that connected the parts of the arm were lost, therefore, they are not presented in the figures	Supp. fig. 3, p. 199	Dróżdż 2018

ZPAL AbIII/3349/3	Pes	Left, articulated, associated with appendicular osteoderms, part of the association ZPAL AbIII/3349, dark grey collation, significantly compacted dorsoventrally, complete metatarsals I–IV and V broken at the base, preserved phalanges and unguals of the I to V digit: 2-2-2 (2nd broken)-3? (1st broken)-0, both distal tarsals complete		
ZPAL AbIII/3349/4	Astragalus + calcaneum	Left, articulated, part of the association ZPAL AbIII/3349, associated with appendicular osteoderms, dark grey coloration, significantly compacted	17, p. 96	
ZPAL AbIII/3349/5	Pelvis	Articulated pelvis, part of the association ZPAL AbIII/3349, dark grey coloration, compacted dorsoventrally and laterally, neural spines broken, ventral portion of the puboischiadic plate broken	7, p. 63; 32, p. 172	
ZPAL AbIII/3350	Tibia	Left, dark grey coloration, anteroposteriorly compacted, preserved in its entirety		
ZPAL AbIII/3351	Ulna	Left, dark grey coloration, complete, compacted laterally	2, p. 50	Dróżdż 2018
ZPAL AbIII/3352	Phalanx (manus)	Right, 2nd row phalanx of digit II, dark grey coloration, complete		Dróżdż 2018
ZPAL AbIII/3353	Phalanx (manus)	Left, 3rd row phalanx of digit III, dark grey coloration		Dróżdż 2018
ZPAL AbIII/3355/1	Astragalus	Right, complementary to the calcaneum ZPAL AbIII/3355/2, brown coloration, complete	17, p. 96; 18, p. 98	
ZPAL AbIII/3355/2	Calcaneum	Right, complementary to the astragalus ZPAL AbIII/3355/1, brown coloration, complete	17, p. 96; 19, p. 100	
ZPAL AbIII/3356	Metatarsal V	Left, anterior part broken, dark brown coloration, compacted dorsoventrally		
ZPAL AbIII/3362	Femur	Right, brown coloration, preserved in its entirety, not deformed by compaction, anterior portion of the condyles damaged, possible bite marks present, found near the femur ZPAL AbIII/3363 and tibia ZPAL AbIII/3367		
ZPAL AbIII/3363	Femur	Left, brown coloration, preserved in its entirety, slightly damaged around head and condyles, possible bite marks present, found near the femur ZPAL AbIII/3362 and tibia ZPAL AbIII/3367	14, p. 79; 34, p. 176	
ZPAL AbIII/3364	Femur	Right, dark grey coloration, preserved in its entirety, compacted anteroposteriorly		
ZPAL AbIII/3365/1	Femur	Left, part of the association ZPAL AbIII/3365, dark grey coloration, preserved in its entirety, compacted anteroposteriorly and laterally		
ZPAL AbIII/3365/2	Ischium	Left, part of the association ZPAL AbIII/3365, dark grey coloration, preserved in its entirety, slightly compacted laterally, minor damage in the anterior portion	6, p. 62; 13, p. 76	
ZPAL AbIII/3366	Tibia	Right, light beige coloration, not deformed by compaction, middle portion of the shaft not preserved, proximal and distal ends broken and missing, scavenging?	15, p. 87	
ZPAL AbIII/3367	Tibia	Left, brown coloration, preserved in its entirety, not deformed by compaction, found near the femora ZPAL AbIII/3362, ZPAL AbIII/3363	33, p. 175; 34, p. 176	
ZPAL AbIII/3368	Pes and lower leg	Right, articulated lower leg, ankle joint, pes, and partially osteoderms covering them, dark grey coloration, compacted anteroposteriorly (in relation to zeugopodium)	21, p. 107	

ZPAL AbIII/3378	Ischium	Left, dark grey coloration, anterior and distalmost portion broken and missing	
ZPAL AbIII/3380	Phalanx (pes)	Right, 2nd row phalanx of the digit III or IV, dark grey coloration	
ZPAL AbIII/3381	Phalanx (pes)	Right, 1st row phalanx digit II, dark grey coloration	
ZPAL AbIII/3382	Fibula	Left, preserved in its entirety, slightly compacted laterally, dark grey coloration	16, p. 90
ZPAL AbIII/3383	Calcaneum	Right, brown coloration, associated with appendicular osteoderms and some bone fragments, complete, significantly compacted anteroposteriorly	
ZPAL AbIII/3384	Metatarsal I	Right, preserved in its entirety, beige coloration	
ZPAL AbIII/3385	Phalanx (pes)	Right, 1st phalanx of digit I, dark grey coloration	
ZPAL AbIII/3386	Phalanx (pes)	Right, 3rd row phalanx of digit IV, dark grey coloration	
ZPAL AbIII/3387	Fibula	Left, preserved in its entirety, proximal portion damaged, laterally compacted, dark brown coloration	
ZPAL AbIII/3388	Fibula	Left, preserved in its entirety, slightly compacted laterally, dark grey coloration	
ZPAL AbIII/3394/1	Pubis	Left, part of the association 3394, dark grey coloration, compacted anteroposteriorly, dorsal portion of the pubic flange partially broken, medioventral side covered by sediment	9, p. 65
ZPAL AbIII/3394/2	Ilium	Left, part of the association ZPAL AbIII/3394, dark grey coloration, anterior portion of the ilium covered by sediment	9, p. 65
ZPAL AbIII/3394/3	Ischium	Left, part of the association ZPAL AbIII/3394, dark grey coloration, anteriormost portion damaged, medial portion not visible	9, p. 65
ZPAL AbIII/3394/4	Ischium	Right, part of the association ZPAL AbIII/3394, dark grey coloration, preserved in its entirety, lateral portion not visible	9, p. 65
ZPAL AbIII/3396	Tibia	Left, dark brown coloration, only the proximal portion preserved, anteroposteriorly compacted, probable bite marks or postmortem decay	
ZPAL AbIII/3397	Fibula	Left, only distal portion preserved, laterally compacted, dark brown coloration	
ZPAL AbIII/3455	Pes + astragalus	Right, dark coloration, all elements articulated, complete digits I-IV and metatarsal V, phalanx associated with the metatarsal V probably not from the same specimen, both distal tarsals present, specimen slightly compacted dorsoventrally, associated with appendicular osteoderms	21, p. 107
ZPAL AbIII/3456	Fibula	Right, only proximal and distal portions preserved, brown coloration, compacted transversally	
ZPAL V. 34/106	Semi-articulated skeleton	Complete skeleton of a juvenile individual from Woźniki preserved in a concretion	22 – 28, pp. 114 – 122; 34, p. 176

TAPHONOMIC NOTES

Krasiejów

Examined material (ZPAL) is significantly varied in preservation. The author, being aware that some of those changes may impact interpretation of the studied specimens, considered it important to recognize at least some of these variations as taphonomic deformation. Based on his personal field observations from the excavation seasons 2017–2020, available documentation, and examinations of specimens in the collection, the author recognizes three major types of preservation that seems to correlate with the position in the geological section. However, these divisions are only superficial as an entire taphonomic spectrum can be observed in the locality and further studies on taphonomy are needed.

(1) The first type of preservation applies to bones that come from the most bottom part of the "lower fossiliferous layer" (uniform grey siltstones) often preserved in a close association or articulation (for example, ZPAL AbIII/3349 – association of pelvis, scapula, tibia, humerus, ribs, osteoderms, and other elements; ZPAL AbIII/3368 – articulated autopodium and zeugopodium; ZPAL AbIII/3394 – associated pelvis, vertebrae, ribs and osteoderms; or ZPAL AbIII/3455 – articulated pes); that are not preserved in concretions; usually they are compacted (for example, the pelvis ZPAL AbIII/3349/5, tibia ZPAL AbIII/3350, or femur ZPAL AbIII/3364), frequently of a dark coloration, varying from black to brown, and lack damage that could be connected with predation, scavenging, or transport. Additionally, limbs are preserved with osteoderms, which indicate that at the moment of burial, they were still covered by the skin, which kept them together during burial, as in, for example, ZPAL AbIII/3368 or ZPAL AbIII/3349/1 (Dróżdż 2018). The level of articulation in the associated specimens matches the results of the experiments on decaying *Crocodylus porosus* conducted by Syme and Salisbury (2014, fig. 9). It would suggest that the burial happened in an aquatic environment of low energy, and prior to the burial the carcasses of the animals were bloating and floating in the water, until they sunk and were gently covered by the sediment (Syme and Salisbury 2014).

(2) The second type of preservation applies to bones that come from the upper part of the "lower fossiliferous layer" below the section with bivalves. They are usually preserved in concretions, therefore, they are mostly not deformed by compaction, preserving the natural

three dimensional anatomical shape. Specimens of this group are brown or dark brown in coloration, and often with visible signs of scavenging (for example, the femora ZPAL AbIII/115, ZPAL AbIII/3362, ZPAL AbIII/3363). At the part of the locality where the excavations took place in 2016-2020, aetosaur bones were preserved across a larger area and with larger distances between each other than those from the first group. No aetosaur association was documented there. It thus seems that the bones of this type were transported or mechanically distributed over a larger area prior to the burial than those from the first group. The presence of carbonate concretions indicates a high concentration of dissolved carbonate in the sediment porewater at the moment of burial (Mccoy et al. 2015). Decaying bones may act as a nucleus which started the formation of the concretion. Their decomposition may have started on the land as proposed by Bodzioch and Kowal-Linka (2012).

(3) The third type of preservation applies to bones that come from the "upper fossiliferous level", which represents a riverine system of sedimentation (Dzik and Sulej 2007; Gruszka and Zieliński 2008). In the documented associations, aetosaurs are preserved together with phytosaurs, but no articulation, unlike in the first type of preservation, was documented. Some of the specimens are surrounded by a thin cover of lithified sediments. Some specimens are much compacted (e.g., the femur ZPAL AbIII/691 and the tibia ZPAL AbIII/502/62), but not to the level visible in the specimens from the first group), and others are preserved in their anatomical or close to the anatomical shape (for example, the humerus ZPAL AbIII/1175 or the fibula ZPAL AbIII/502/40). Their coloration varies from beige to pink. Bite marks caused by scavenging are visible in some specimens (for example, ZPAL AbIII/3308). Aetosaur bones of this type of preservation were most likely exposed for a long time for scavenging and decayed on the land or in a shallow water, and then were transported across a short distance by the river system.

Woźniki

The specimen ZPAL V. 34/106 consists of an aetosaur skeleton preserved inside a carbonate concretion. Therefore, the supposed model of preservation is similar to the second type observed in the Krasiejów locality, with the decaying body of the animal acting as the nucleus that started the formation of the concretion (Mccoy et al. 2015).

The skeleton is semi-articulated, with most elements of the axial skeleton, limbs and dermal amour preserved in an arrangement close to their position *in vivo*. It is almost complete.

It lacks only the anterior part of the skull, right pes, and the distal end of the tail. No skeletal elements that can be attributed to other animals have been detected. The skeleton seems to be crushed from the sides, causing the ventral surfaces of the dorsal paramedian osteoderms, normally forming double rows along the back of the animal (e.g., Desojo et al. 2013) to be turned to face their contralateral counterparts. A similar direction of compaction is observed also in the femur. A majority of the bones are cracked in several places, but the parts remain in a close proximity to each other.

Most of the dorsal paramedian osteoderms are also preserved in articulation, however, due to compaction they are displaced in relation to their natural orientation. The appendicular skeleton is more distorted than the axial skeleton, however, the limb elements are generally preserved in their respective order and position in reference to other bones. The tail seems to be severed form the body.

METHODS

Excavations

The studied specimens from Krasiejów were excavated over several seasons from 2000 to 2020. The author personally directed the excavations in the years 2017–2020. The author mapped the position of the specimens in the field, as well as in the geological section. These observations were used in the section concerning the taphonomy. To avoid damaging specimens during transportation, they were collected with the surrounding sediment, or preserved in a gypsum jacket. The skeleton from Woźniki was found by prof. Jerzy Dzik (University of Warsaw/Institute of Paleobiology, PAS) during a routine checkup of the locality in 2009.

Mechanical preparation

The specimens were cleaned from the surrounding sediment mechanically (with a pneumatic airscribe) and chemically (with 5% formic acid). The preparation was done mostly by the technicians of the Institute of Paleobiology, PAS in Warsaw, but some of the preparation, especially of the forelimbs, was conducted by the author himself.

Synchrotron scan

The small aetosaur ZPAL V. 34/106 was scanned in the European Synchrotron Facility in Grenoble (ESRF) in the beamline ID 19. Two types of scans were performed. First, the entire specimen was scanned for gross anatomical examination in a resolution of about 13 µm per pixel; secondly, scans of the femur, humerus, and an osteoderm were performed for virtual histology with 0.7–1.4 µm pixel size. The scans were performed by the synchrotron facility crew.

Visualizations and reconstructions

3D models were obtained utilizing photogrammetry with the program Agisoft Metashape v. 1.8.3. Other operations, including visualization and modifications of the 3D models, such as the arrangement of the models into reconstructions or simplification of the model surfaces, were done in MeshLab 2022.02 (Cignoni et al. 2008).

Reconstructions in the form of technical drawings were made in GIMP 2.10.22. In the case of the forelimbs, they were based mostly on photographs of the selected parts of the specimens, which were arranged and drawn in the program filling in the missing parts. For hind limbs, the author based the reconstructions also on the 3D models.

The volume reconstruction of the limb elements from the small aetosaur ZPAL V. 34/106 were performed in Drishti v2.7 by a person hired form outside of the Institute of Paleobiology, PAS. Those volumetric reconstructions were used for figures.

SYSTEMATIC PALEONTOLOGY

Krasiejów species

Archosauria Cope 1869 *sensu* Gauthier and Padian 1985

Pseudosuchia Zittel 1887-1890 *sensu* Gauthier and Padian 1985

Aetosauria Marsh 1884 *sensu* Parker 2007

Desmatosuchia Case 1920 *sensu* Parker 2016a

Stagonolepininae Huene 1936 *sensu* Heckert and Lucas 2000

Stagonolepis olenkae Sulej 2010

2000: Aetosauria indet.; Dzik et al., p. 233
2001: *Stagonolepis* sp.; Dzik, p. 625, fig. 2c–f
2007: *Stagonolepis robertsoni*; Lucas et al., p. 249, figs. 3–7
2010: *Stagonolepis olenkae*; Sulej, p. 879, figs. 1–7, 8 a, 9 c
2011: *Stagonolepis robertsoni* (partim); Desojo and Ezcurra, p. 599
2011: *Stagonolepis olenkae* (partim); Desojo and Ezcurra, p. 605
2013: *Stagonolepis olenkae*; Desojo et al., p. 207, fig. 4e, f
2016: *Stagonolepis robertsoni*; Antczak, p. 781, fig. 2–5
2016a: *Stagonolepis olenkae*; Parker, p. 33
2018b: *Stagonolepis olenkae*; Parker, p. 5, fig. 9b
2018: *Stagonolepis olenkae*; Dróżdż 2018, p. 2, fig. 1–6, app. online 5–9, sup. fig. 1–8
2021: Aetosauria indet.; Górnicki et al., p. 4, fig. 2b, app. online 2

Assignment of the material to the Aetosauria

Specimens were recognized as representing aetosaurs based on their general similarity in morphology with those of other aetosaurs and associations with aetosaur-like osteoderms. Isolated bone elements were identified based on comparisons with specimens preserved in associations, if possible.

In addition, the author recognized the specific combination of characters that can be attributed to aetosaurs; in reference to general proportions anatomical structure: robust, stout pelvis and limbs; very short forearms and crus in proportion to the humerus and femur, respectively (Long and Murry 1995; Desojo et al. 2013).

In the forelimbs: presence of a well-defined humeral head; well-developed deltopectoral crest; presence of a long olecranon process in the ulna; presence of fused radiale and intermedium in the carpus (Sawin 1947; Walker 1961; Long and Murry 1995; Desojo et al. 2013).

In the sacrum: sacral vertebrae with massive neural arches and especially neural spines; neural spines of the sacral vertebrae with expanded apices (spine tables); sacral ribs entirely ossified with the centrum of vertebra and transverse processes; sacral ribs transversally and anteroposteriorly expanded and broadly attached to the ilium (e.g., Casamiquela 1961; Bonaparte 1971; Long and Murry 1995; Lucas et al. 2002; Desojo and Báez 2005; Parker 2008).

In the pelvis: ilia with a high, horizontally pointed iliac blade; distinct, prolonged preacetabular process; deep, ventrolaterally oriented acetabulum (Sawin 1947; Casamiquela 1961; Walker 1961; Bonaparte 1971; Small 1985; Parrish 1986; Long and Murry 1995; Heckert and Lucas 2002; Martz 2002; Desojo and Báez 2005; Schoch 2007; Parker 2018*a*, *b*, 2008, 2016*b*; Heckert et al. 2010; Desojo et al. 2013; Roberto-Da-Silva et al. 2014); and short pubic ramus (length roughly twice the acetabulum width); wide pubic flange (of width comparable to the width of the acetabulum) that forms broad pubic aprons in the anterior section; buttress on the lateral edge of the pubic apron (in the place of the pubic foot) (Walker 1961; Small 1985; Long and Murry 1995; Martz 2002; Desojo et al. 2013); as well as ischium short in relation to the pubis and ilium; high ischiadic blade, ventral to the acetabulum (Casamiquela 1961; Walker 1961; Bonaparte 1971; Long and Murry 1995; Small 1998; Lucas et al. 2002; Martz 2002; Desojo and Báez 2005; Desojo et al. 2013; Roberto-Da-Silva et al. 2014).

In the hind limbs: femora of a sigmoidal shape in the craniocaudal direction, with well-defined, medially developed proximal head and a hypertrophied fourth trochanter (Long and Murry 1995; Martz 2002; Desojo et al. 2013); and tibiae thicker than the fibulae, with the proximal portion of the shaft strongly expanded transversely; pronounced intercondylar ridge on the dorsal articulation surface of the femur; as well as well-defined "saddle-shaped" articulation facet for the astragalus; fibula with a hypertrophied iliofibularis trochanter (Parrish 1986; Long and Murry 1995; Desojo et al. 2013); and "crocodile normal" tarsus with four elements: astragalus, calcaneum, and two distal tarsals of different size (one much larger than the other); tarsi with the astragalus and calcaneum of roughly similar size; astragali with well-defined "saddle-shaped" articulation facet for the tibia and distinct articulation facet for the fibula (relatively small in area); well-developed ball for the calcaneum. Calcanei with: deep socket for the astragalus ball; sustentacular joint oriented perpendicularly to the long axis of calcaneum; wide, potent, posteriorly projecting calcaneal tuber (Parrish 1986; Desojo et al. 2013). Transversely expanded pes with five digits, in which the first four metatarsals are positioned in one line, slightly overlapping each other, while the fifth "hook-shaped" metatarsal is oriented posteriorly to them, digits ended with claw-shaped unguals (Parrish 1986; Sereno 1991; Desojo et al. 2013).

Justification of the taxonomy

Despite being a relatively recently described species, *Stagonolepis olenkae* already has a complicated taxonomical history, and its status was debated by several authors (Dzik and Sulej 2007; Lucas et al. 2007; Antczak 2016; Parker 2016*a*; Dróżdż 2018; Górnicki et al. 2021). Part of the confusion is caused by the separate treatment of the cranial and postcranial material by the previous authors (Lucas et al. 2007; Sulej 2010; Antczak 2016; Dróżdż 2018) and lack of overlap between the type material of *S. olenke* and *S. robertsoni*. Sulej (2010) designated the skull roof ZPAL AbIII/466/17 as the holotype of *S. olenkae* and referred all other cranial and postcranial material from Krasiejów to the new species. The status of the material beyond the holotype, in regard to the Krasiejów species, is therefore similar as in the case of the non-holotype material of *Stagonolepis robertsoni*, the type specimen of which is a cast of articulated ventral osteoderms, EM 27 (Agassiz 1844), not associated with other postcranial or cranial material (Walker 1961; Parker 2018*b*).

The holotype of *S. robertsoni* has been recently reexamined by Parker (2018*b*) and recognized as being autapomorphic due to the rectangular shape of the osteoderms, with ornamentation composed of randomly arranged, oblong pits. Ventral osteoderms that match this morphology are present in the association of *S. olenkae* ZPAL AbIII/3349 (with articulated pelvis). Książkiewicz (2014), the only other author that examined this part of the skeleton of *S. olenkae*, also reported this morphology in the Krasiejów species, but only for ventral osteoderms from the cloacal region. Although he might have mistaken some of the ventral osteoderms for dorsal paramedian caudal ones, and interpreted ventral osteoderms of a larger size, with more elongated pits, as a different morphotype (Książkiewicz 2014).

The previous assignments of the material to *S. robertsoni* sensu Heckert and Lucas (2000) cannot be considered valid any longer as this taxon was proven to be polyphyletic by several authors (Parker and Martz 2010; Desojo and Ezcurra 2011; Parker 2016*a*, 2018*b*, *a*). It was based on the similarities of morphology of dorsal trunk paramedian osteoderms and vertebrae, and united a few previously separate species, including *Aetosauroides scagliai* and *Calyptosuchus wellesi*, proven to be separate by later studies (Parker and Martz 2010; Desojo and Ezcurra 2011; Biacchi Brust et al. 2018). Moreover, other studies on the aetosaurs showed that *Aetosaurus ferratus*, *Aetosauroides scagliai*, *S. robertsoni*, and *Stenomyti huangae*, despite sharing almost the same dorsal trunk paramedian osteoderm morphology, differ significantly in the skull (Walker 1961; Schoch 2007; Small and Martz 2013; Biacchi Brust et al. 2018; Parker 2018*b*). Similar dependence may be also true for the widespread *Paratypothorax andressorum* (see Czepiński et al. 2021). Therefore, regardless of the similarity between the osteoderms of *Stagonolepis olenkae* and *Stagonolepis robertsoni*, the differences in the skull should be consider more informative for species differentiation, if they are indeed beyond what should be considered an intraspecific variation as proposed by Sulej (2010). Unfortunately, the matter is complicated by the fact that all the cranial and endoskeletal postcranial material of *S. robertsoni* is also merely attributed to that species, therefore necessitating a chain of assumptions and attributions between the holotype of *S. robertsoni* (osteodermal), hypodigm of *S. robertsoni* (cranial and postcranial), holotype of *S. olenkae* (cranial), and paradigm of *S. olenkae* (postcranial and osteodermal), which are currently accepted by at least some authors (and are also accepted herein) but were never rigorously tested. This calls for a comprehensive, specimen-level revision and reconsideration of all the material currently attributed to the genus *Stagonolepis* – a massive undertaking which lies beyond the scope of this work, but for which this dissertation will hopefully serve as a foundation, and which will be attempted in the future by the author.

The postcranial skeleton currently attributed to *Stagonolepis olenkae* seems indeed undistinguishable from *Stagonolepis robertsoni* as suggested by other authors (Lucas et al. 2007; Antczak 2016; Parker 2016*a*). Although the author recognized some minor differences between the species in regard to forelimbs, pelvis, and hind limbs, they are not sufficient to support division of the new species and may be a result of an ontogenetic age difference or incompleteness and worse preservation of the Scottish material (Dróżdż 2018; this study). Górnicki et al. (2021) described fragments of an aetosaur pes and stated that due to its plesiomorphic morphology it cannot be described as *Stagonolepis* spp. However, no significant difference between the material described here and the one described by Górnicki et al. (2021) was noticed in this study. The UOPB material is poorly preserved and vastly deformed, however, shares the general morphology with the articulated specimens of *Stagonolepis olenkae* described in this study, especially ZPAL AbIII/3349, which also contains partially articulated elements of the axial skeleton, pectoral girdle, forelimbs, pelvis, hind limbs, and associated osteoderms.

Woźniki juvenile skeleton ZPAL V. 34/106

Archosauria Cope 1869 *sensu* Gauthier and Padian 1985

Pseudosuchia Zittel 1887-1890 *sensu* Gauthier and Padian 1985

Aetosauria Marsh 1884 *sensu* Parker 2007

Aetosauria indet.

Justification of the taxonomy

The general body plan and morphology of the skeletal elements of the specimen from Woźniki are considered to be plesiomorphic for aetosaurs and correspond with, e.g., *Stagonolepis* spp., *Aetosauroides scagliai* and *Polesinesuchus aurelioi*, *Aetosaurus ferratus*, *Coahomasuchus* spp., or *Stenomyti huangae*, especially in regards to the postcranium (Casamiquela 1961; Heckert and Lucas 1999; Schoch 2007; Sulej 2010; Desojo et al. 2013; Small and Martz 2013; Roberto-Da-Silva et al. 2014; Heckert et al. 2017; Dróżdż 2018; Paes-Neto et al. 2021).

Due to the young age of the individual, the skull of the Woźniki specimen is significantly underdeveloped and morphologically different in comparison to adult aetosaurs (e.g., Case 1922; Walker 1961; Parrish 1994; Long and Murry 1995; Sulej 2010; Desojo et al. 2013; Schoch and Desojo 2016; Biacchi Brust et al. 2018): e.g., the skull it is noticeably larger in proportion to postcranium, the bones of the skull roof are not fused, the skull roof is convex – not flat, orbits are enlarged in proportion to rest of the skull elements. The lack of the anterior part of the skull makes it additionally difficult to assign the individual to any particular species, because a lot of taxonomically important features relate to this region (e.g., Case 1922; Long and Murry 1995; Small 2002; Schoch 2007; Sulej 2010; Desojo et al. 2013; Parker 2016*a*). The bulbous shape of the teeth seems to exclude at least *Aetosauroides scagliai* (see Biacchi Brust et al. 2018) but the possibility of an ontogenetic variability of tooth shape (Estes and Williams 1984; Buckley and Currie 2014; Gignac and Erickson 2014; D’Amore 2015; Kosch and Zanno 2020) resulting, e.g., from changing food preferences during ontogeny cannot be refuted with complete certainty.

Presence of a double obturator foramen is a characteristic feature that has been only described for *Stagonolepis robertsoni* (see Walker 1961) and apparently is not present in the studied material of *Stagonolepis olenkae*. The original material of *Stagonolepis robertsoni* is not clear when it comes to this feature, and the examination of the Scottish specimens shows that most likely that it is an artifact of preservation. Therefore, the presence of additional obturator foramen in Woźniki specimen is even more surprising. Potentially, this feature may be ontogenetic (and thus absent in larger individuals) and consequently taxonomically uninformative.

The only other aetosaur material known from the locality is left ischium (ZPAL V. 34/100) with a characteristic comb-like pattern recognized also in *Stagonolepis olenkae* from Krasiejów. However, given that the presence of this structure might be also the feature that develop in the ontogeny, the taxonomic value of this character is dubious. Summarizing the juvenile specimen from Woźniki (ZPAL V. 34/106) have to be strictly formally referred to Aetosauria indet.

Problematic aetosaur species

In some of the recent studies, two small species, *Aetosaurus ferratus* and *Polesinesuchus aurelioi*, have been considered juveniles (and, thus, junior synonyms) of, respectively, *Paratypothorax andressorum* and *Aetosauroides scagliai* (Schoch and Desojo 2016; Paes-Neto et al. 2021). Although the author is fond of those ideas, there is still an ongoing debate on the status of those taxa. Therefore, all the names have been used in the thesis and the species are treated as possibly separate entities.

OSTEOLOGY

Forelimbs

Proportions and general description of the forelimb bones

Forelimb elements of *S. olenkae* are smaller than the corresponding elements of the hind limbs, therefore the entire forelimb must have been shorter than hind limb (Dróżdż, pers. obs., 2018; Książkiewicz 2014). The humerus is about two-thirds the length of the femur (Książkiewicz 2014). The length ratio of the humerus ZPAL AbIII/2369 to the femur ZPAL AbIII/691 is 0.69 (the specimens possibly belong to a single animal, because they have been found close to each other in the same assemblage). Although there are no humeri found in articulation with radius and ulna, it can be assumed that humerus in *S. olenkae* is longer than each of the forearm bones, based on the comparison of several specimens (Książkiewicz, 2014). Possibly the ulna ZPAL AbIII/1179 belongs to the same animal as the humerus ZPAL AbIII/2369, because of their similar taphonomic condition and relatively close position in the sediment at the moment of recovery. The length ratio of the ulna ZPAL AbIII/1179 to the humerus ZPAL AbIII/2369 is 0.79. The radius and ulna are orientated parallel to each other (Fig. 2; based on specimen 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. 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 (based on ZPAL AbIII/3351, ZPAL AbIII/3322), which seemingly makes the relative rotation of these two bones impossible. The olecranon process of the ulna is high (based on ZPAL AbIII/2407, ZPAL AbIII/2014, ZPAL AbIII/3351), and in large specimens of humeri the olecranon fossa is present (ZPAL AbIII/1175, ZPAL AbIII/257). Based on specimen ZPAL AbIII/2407 the manus together with the carpus is shorter than both the ulna and the radius. The carpus consists of at least four bone elements. The largest one of them is probably a fused radiale and intermedium (ZPAL AbIII/2071, ZPAL AbIII/2407, ZPAL AbIII/3349/1, ZPAL AbIII/3349/2). 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 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 (relative length of digits II~III~IV>I>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 terminate with claw-like unguals (mostly based on ZPAL AbIII/3349/1 and ZPAL AbIII/2071). The ungual of the first digit is the largest one, and it is much bigger than the rest. The 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 (based on ZPAL AbIII/3349/1, ZPAL AbIII/2071). The dorsal part of the hand, forearm and probably also upper arm is entirely covered by osteoderms (based on ZPAL AbIII/2407, ZPAL AbIII/3349/1, ZPAL AbIII/3349/2).

Humerus

The humerus of *S. olenkae* (Fig. 1), examined here in the specimen ZPAL AbIII/257, ZPAL AbIII/1175, ZPAL AbIII/2627, is a massive, strongly built bone with a straight shaft and well-defined, transversely 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 (Figs. 1A–1B; ZPAL AbIII/1175, ZPAL AbIII/2627). Its articulation surface is convex and covered by multiple irregularly arranged tubercles of random size, which indicate the presence of a well-developed cartilaginous cap (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 (ZPAL AbIII/1175, ZPAL AbIII/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. 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 (ZPAL AbIII/1175, ZPAL AbIII/2627). The shaft in the medial/lateral view remains straight throughout its entire length. In the dorsal/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

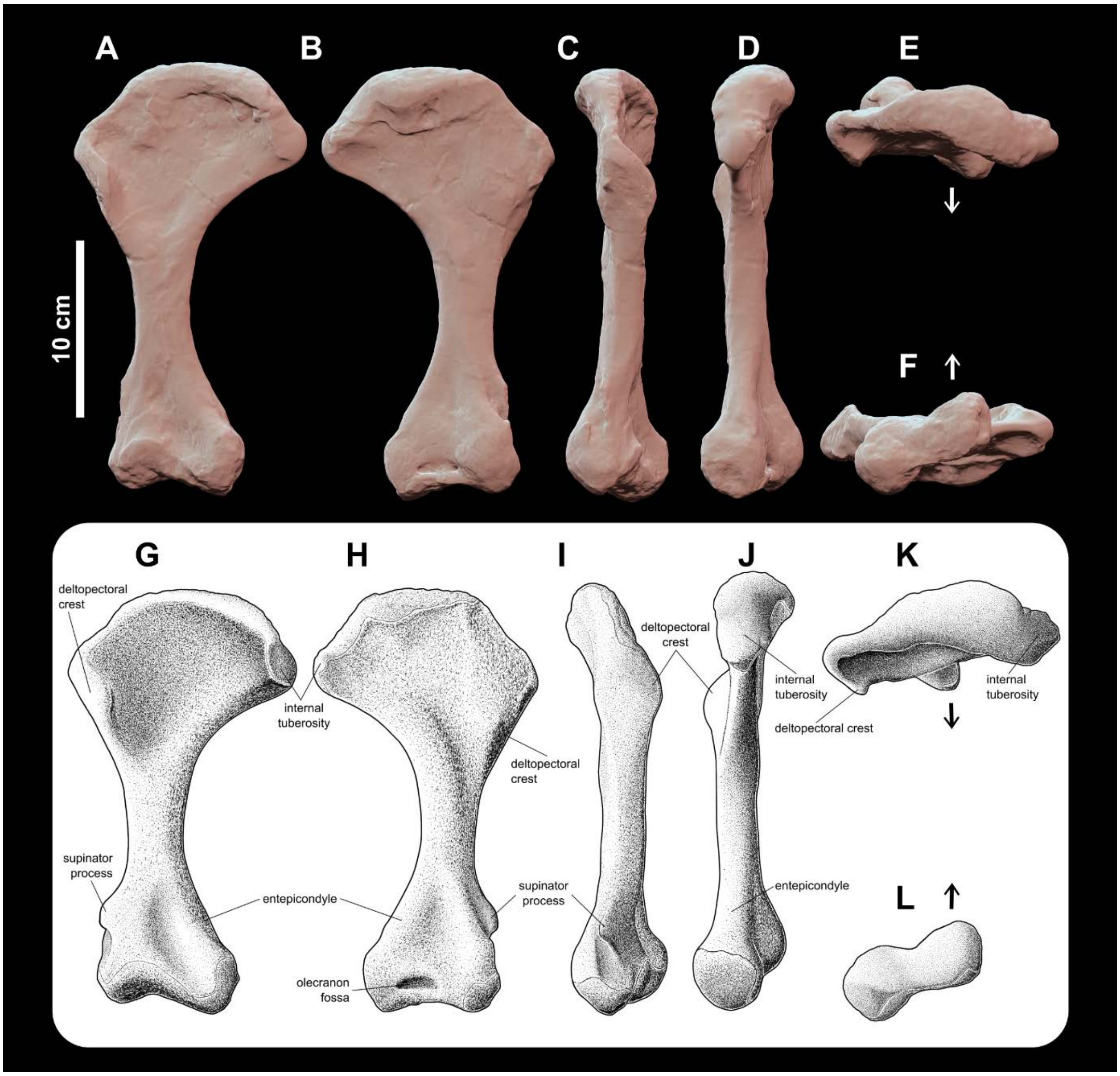


Figure 1. Right humerus of *Stagonolepis olenkae*. ZPAL AbIII/1175 (A–F) and reconstruction (G–L), in anterior (A, G), posterior (B, H), lateral (C, I), medial (D, J), proximal (E, K), and distal view (F, L). The arrows indicate the cranial direction.

the lateral epicondyle, but the expansion is not as significant as on the medial side (ZPAL AbIII/1175, ZPAL AbIII/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 (ZPAL AbIII/1175, ZPAL AbIII/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 dorsolateral surface there is a straight furrow that originates in the elevated area next to deltopectoral crest and continues up to the epicondyle (ZPAL AbIII/1175, ZPAL AbIII/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 (ZPAL AbIII/257, ZPAL AbIII/1175, ZPAL AbIII/2627). The supinator process is thick and prominent (ZPAL AbIII/257). In large specimens the olecranon fossa is present. In smaller one (ZPAL AbIII/257) the olecranon fossa is not fully enclosed as in specimen ZPAL AbIII/1175. In distal view, the distal head is transversely elongated, with pronounced narrowing in its center. The articulation surface of the distal head is covered by multiple irregularly arranged tubercles of random size, which indicate the presence of well-developed cartilaginous cap (ZPAL AbIII/257, ZPAL AbIII/2627).

Ulna

The ulna of *S. olenkae* (Fig. 2) represented by the specimen ZPAL AbIII/2407, ZPAL AbIII/3349/1, ZPAL AbIII/3349/2, ZPAL AbIII/1100/1, ZPAL AbIII/1179, ZPAL AbIII/2014, and ZPAL AbIII/3351, is straight and dorsoventrally 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 specimen ZPAL AbIII/2407 and ZPAL AbIII/3351; Figs. 3A–3D), but it was probably even longer as on its top there is a tubercular area (Fig. 3B, 3D–3E), which indicates the presence of well-developed apical cartilage (ZPAL AbIII/2407, ZPAL AbIII/2014, ZPAL AbIII/3351). The tubercles are of different size and are irregularly arranged. The articular surface for the humerus falls rapidly behind the tubercular area of olecranon process towards the coronoid process, where it becomes almost flat (Figs. 3A–3B; ZPAL AbIII/2407, ZPAL AbIII/2014, ZPAL AbIII/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. 3A; ZPAL AbIII/2014, ZPAL AbIII/3351). The area below the olecranon process is covered by an irregularly arranged and strongly marked series of pits and grooves (Figs. 2E, 3A–3B, 3D; ZPAL AbIII/2014, ZPAL AbIII/2407, ZPAL AbIII/3351). There is another small ornamented area (with an ornamentation of small pits and grooves) on the dorsal side of the ulna, in the proximal

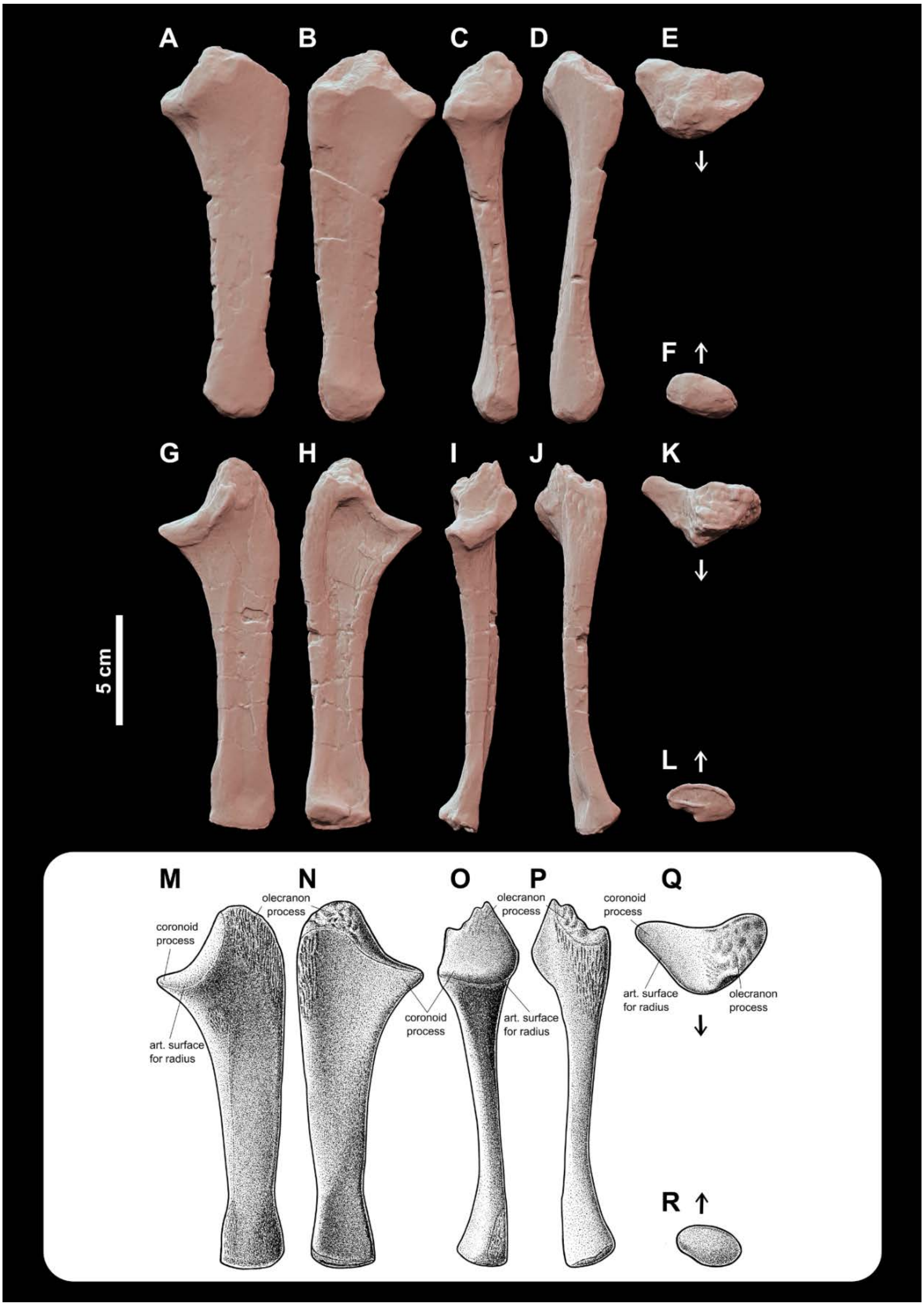


Figure 2. Left ulna of *Stagonolepis olenkae*. ZPAL AbIII/1100/1 (A–F), ZPAL AbIII/3351 (G–L) and reconstruction (M–R), in anterior (A, G, M), posterior (B, H, N), medial (C, I, O), lateral (D, J, P), proximal (E, K, Q), and distal view (F, L,R). The arrows indicate the cranial direction.

part of the shaft, distal to the articular surface for the radius (Figs. 2E, 3A; 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 (Figs. 3A–3B; ZPAL AbIII/1100/1, ZPAL AbIII/1179, ZPAL AbIII/2014, ZPAL AbIII/2407, ZPAL AbIII/3351). The lateral edge of the shaft in the middle section is smooth and rounded (Fig. 3D). 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 (Fig. 3C). The cross-section of the shaft, in the upper part of the middle section, is similar to an 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 (Figs. 2E, 3A). 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 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 (Fig. 3B). 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 (Figs. 3C–3D). In distal view, the shape of the surface for the wrist bones is oval (Fig. 3F; ZPAL AbIII/2407, ZPAL AbIII/3349/1). 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 (ZPAL AbIII/2407, ZPAL AbIII/3349/1, ZPAL AbIII/3351). Distal to the neck on the ventromedial side, there is a prominent oval ornamented area (Figs. 3A, 3C; ZPAL AbIII/3351). Its ornamentation consists of small, irregularly arranged pits and grooves.

Radius

The radius (Fig. 3) represented by the specimen ZPAL AbIII/1628, 2407, 2016/2, 2016/4, 3322, 3349/1, 3349/2 is shorter than the ulna and longer than the manus. The ratio of length between the radius and the ulna in the specimen ZPAL AbIII/2407 is 0.85. The shaft is straight and of almost uniform thickness throughout its entire length, except for the proximal or distal ends, where it expands in a funnel-like manner. In dorsoventral view the proximal and distal ends are of the same width (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

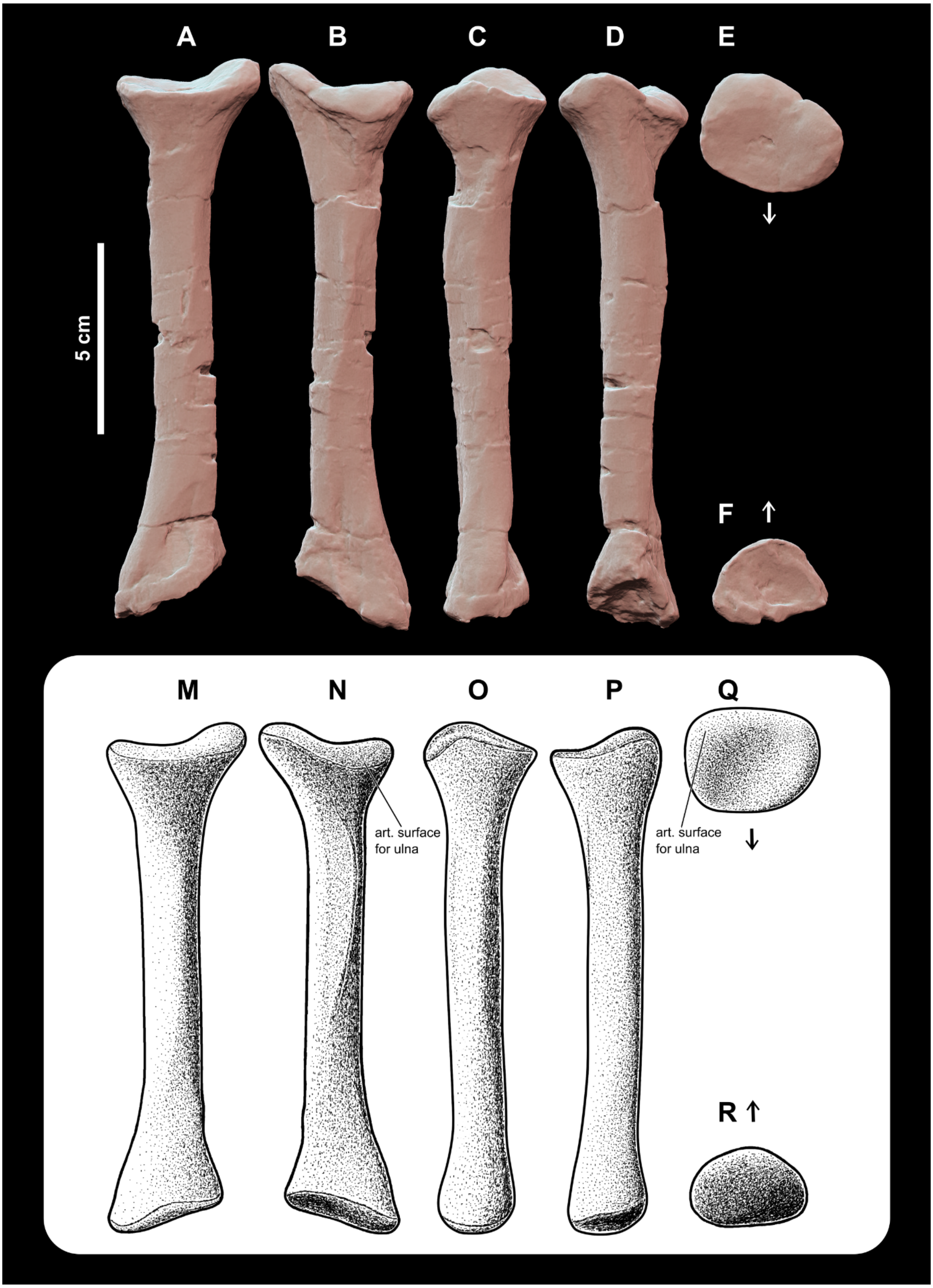


Figure 3. Left radius of *Stagonolepis olenkae*. ZPAL AbIII/3322 (A–F) and reconstruction (M–R), in anterior (A, M), posterior (B, N), medial (C, O), lateral (D, P), proximal (E, Q), and distal view (F, R). The arrows indicate the cranial direction.

almost flat, with a tiny depression in the center and a small process at the lateral edge. The articulation surface for the ulna is crescent-shaped and extends longitudinally (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 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 distal view (ZPAL AbIII/2106/2, ZPAL AbIII/2407, ZPAL AbIII/3322). Its surface is covered by irregularly arranged tubercles (ZPAL AbIII/2106/2), similar to those present on the olecranon process of the ulna and the humeral heads, but smaller. The presence of the tubercles indicates a well-developed cartilaginous finish.

Carpus

The carpus (Fig. 4) consists of at least four bony elements, the author initially proposed that they were oriented in two rows (Dróżdż 2018). However thanks to the new data from the specimen ZPAL AbIII/2071 the author was able to reinterpret the arrangement of carpus elements and it seems that previous interpretation was wrong and instead the elements were oriented in a single row. The largest carpal bone is the fused radiale and intermedium (Fig. 5), present in ZPAL AbIII/2407, ZPAL AbIII/ 3349/1, ZPAL AbIII/3349/2, 2071. It was followed laterally by the small pea-shaped second carpal (third distal carpal in Dróżdż 2018), to which articulate much larger crescent shaped third carpal (ZPAL AbIII/2407, ZPAL AbIII/3349/1, ZPAL AbIII/3349/2, and 2071) (fourth distal carpal in Dróżdż 2018). The crescent shape carpal covered the smaller carpal ventrally, which is probably why it is not visible in the specimen ZPAL AbIII/2407. The flattened and square-shaped ulnare, articulated horizontally to the larger carpal. The metacarpals articulated directly ventrally, metacarpal I and II to fused radiale and intermedium, metacarpal III partially to fused radiale and intermedium and middle carpals, metacarpal IV to crescent shape third carpal and partially to ulnare, metacarpal V to ulnare only. Radius articulated directly dorsally to the fused radiale and intermedium and ulna articulated with all there lateral carpals.

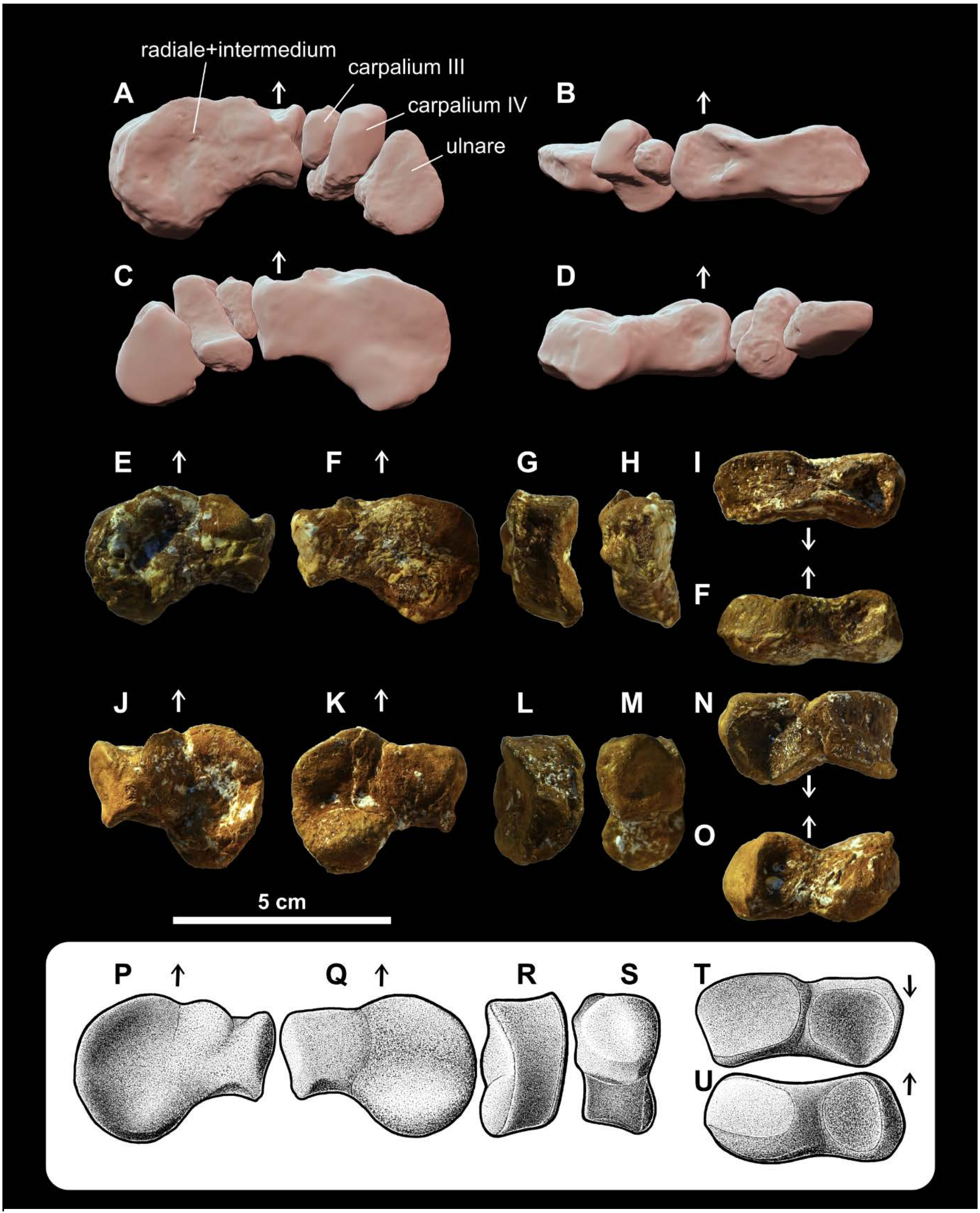


Figure 4. Right carpus of *Stagonolepis olenkae* ZPAL AbIII/2071 (A–D), right fused radiale and intermedium ZPAL AbIII/2071 (E–F), left fused radiale and intermedium ZPAL AbIII/2071 (J–O) and reconstruction this bone (P–U), in dorsal (A, E, J, P), anterior (B, I, N, T), ventral (C, F, K, Q), lateral (G, L, R), medial (H, M, S), and posterior view (D, F ,O ,U). The arrows indicate the cranial direction in (A, C, E, F, J, K, P, Q) and proximal direction in (B, D, I, F, M, N).

The fused radiale and intermedium is a thick bone, elongated in the coronal plane. Proximally it articulates with the radius and partially the ulna, and is adjacent distally to metacarpals

I, II, III, and partially IV (based on ZPAL AbIII/2407, ZPAL AbIII/3349/1). 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 (ZPAL AbIII/2071, ZPAL AbIII/3349/1). The suture is less pronounced, 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 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 dorsoventral aspect, the shape of the fused radiale and intermedium is close to rectangular. On the proximal side of the bone, at the section corresponding to the radiale, the surface forms a prominent ridge surrounding the center of the section dorsally and medially (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, at the section corresponding to the radiale, there is a large, prominent tuber (ZPAL AbIII/2071). The tuber originates in the middle of the articulation surface, and continues towards the distal edge, covering a little less than 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 dorsomedial edge and in the section corresponding to the intermedium (ZPAL AbIII/2071). 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 (ZPAL AbIII/2071, ZPAL AbIII/3349/1). The area in the section corresponding to the radiale is flat with a small depression in its central part. It continues through the medial and part of the ventral side of the section. The area in the section corresponding to the 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 (ZPAL AbIII/2071). The lateral side of the fused radiale and intermedium forms one square-shaped articulation area with a prominent tuber in the distal-dorsal corner.

The ulnare is a cube with 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 specimen ZPAL AbIII/2407, ZPAL AbIII/3349/1). The bases are almost flat, with slight depressions in their centres.

The carpus consists 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 ZPAL AbIII/3349/1 they are arranged adjacent to metacarpal III in the second (distal) row of carpals.

Metacarpals

The metacarpals (Fig. 5) present in the specimen ZPAL AbIII/2071, ZPAL AbIII/2102, ZPAL AbIII/2407, ZPAL AbIII/3349/1, ZPAL AbIII/3349/2 and are robust, relatively short, wide and dorsoventrally flattened. Their bases are wider than the heads. Their shafts taper towards the distal ends. They match and partially cover each other in dorsal view. Metacarpals II, III, and IV are of similar shape and length, and are noticeably longer than metacarpals I and V, which are about 0.75 their size (based on ZPAL AbIII/2071, ZPAL AbIII/2407, ZPAL AbIII/3349/1, ZPAL AbIII/3349/2). Metacarpal I is slightly longer than metacarpal V. The relative length between the metacarpals I, II, and III vary among specimens. For example, in specimen ZPAL AbIII/3349/1, metacarpal IV is the longest, but in specimen ZPAL AbIII/2407 the longest is metacarpal III. Metacarpal I is the most robust, and 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. Metacarpal I is also the widest among the metacarpals (ZPAL AbIII/2071, ZPAL AbIII/2407, ZPAL AbIII/3349/1, ZPAL AbIII/3349/2). Its shaft is flat dorsally and rectangular in cross-section. On the ventral surface it has a depression for the subsequent metacarpal. Metacarpals II, III, and IV are of similar shape (Fig. 6E; spec. ZPAL AbIII/2071, ZPAL AbIII/2102, ZPAL AbIII/3349/1, ZPAL AbIII/3349/2). Their shafts are triangular in cross-section. Like in metacarpal I, there is a depression on their dorsal surface for the subsequent metacarpal. The shape of most gracile metacarpal V differs between specimens. In specimen ZPAL AbIII/3349/1 and ZPAL AbIII/3349/2 it is wide and flat. Its width is almost uniform throughout the entire length,

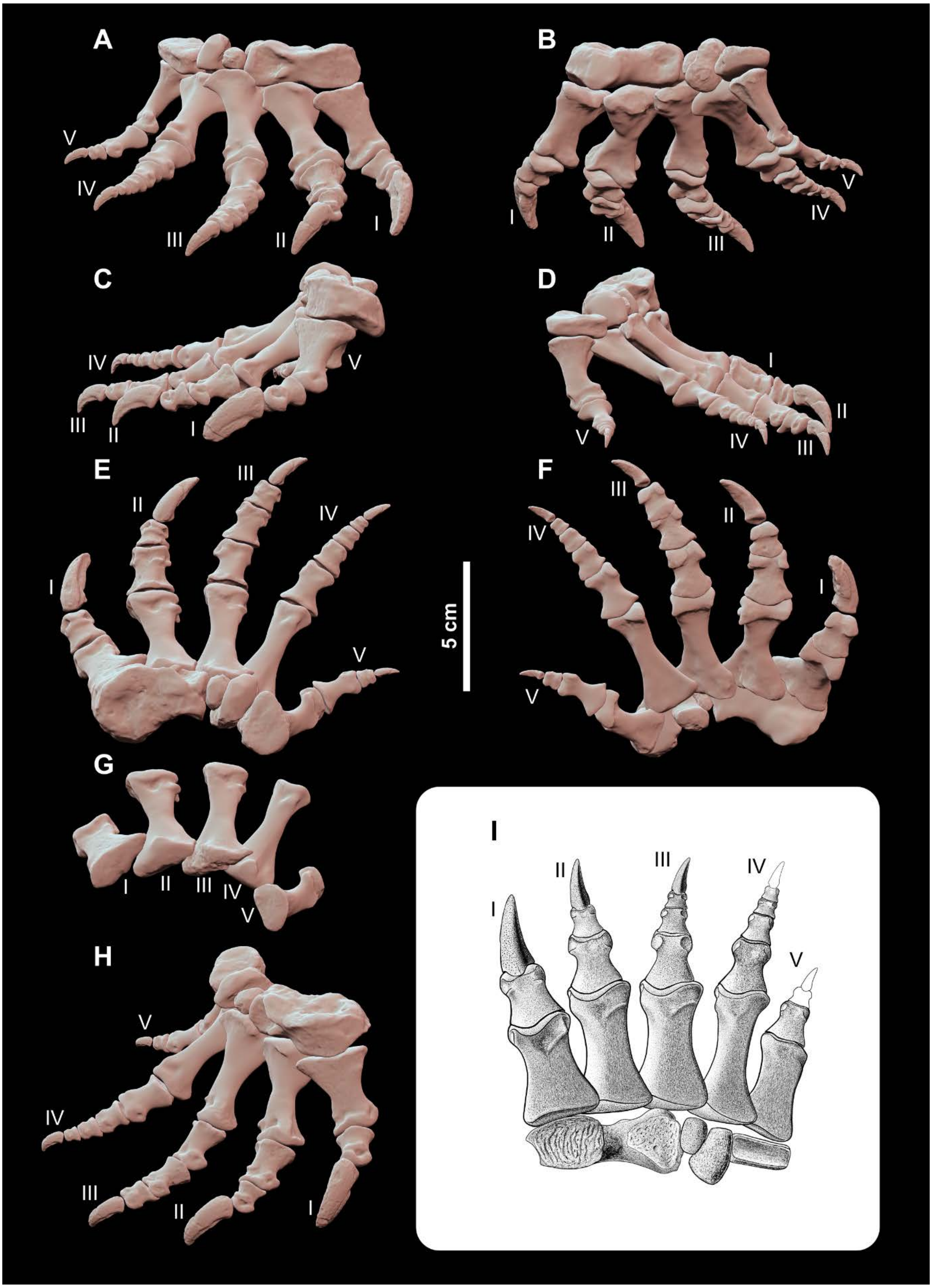


Figure 5. Reconstruction of the right manus of *Stagonolepis olenkae* ZPAL AbIII/2071 in anterior (A), posterior (B), medial (C), lateral (D), dorsal (E), ventral (F), and anterodorsomedial view (H). Right metacarpals of ZPAL AbIII/2071 in dorsal view (G), reconstruction of the right manus in dorsal view (I) based on specimen ZPAL AbIII/3349/1.

and the base and the head are not distinct. In the specimens ZPAL AbIII/2071 and ZPAL

AbIII/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. 5) are present in the specimen ZPAL AbIII/2407 – all phalanges of the first row, ZPAL AbIII/3349/1 all phalanges of the first and second digit, broken 1st row phalanx of the third digit, the four phalanges of the fourth digit and 1st row phalanx of the fifth digit, ZPAL AbIII/3349/2—all phalanges of the first row, 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 ZPAL AbIII/257, ZPAL AbIII/3352, ZPAL AbIII/3353—isolated phalanges. The probable phalangeal formula for *S. olenkae* is 2-3-4-5?-3?, based mostly on the specimens ZPAL AbIII/3349/1 and ZPAL AbIII/2071. The number of the phalanges for the first three digits is certain, because they terminate with claw-like unguals preserved in the first two digits of ZPAL AbIII/3349/1, and first three digits of the right manus and the first two of the left of the spec. ZPAL AbIII/2071. In ZPAL AbIII/3349/1 the phalanx of the fourth row of the digit IV ends with an articulation surface, which indicates the presence of another phalanx or an ungual. However, because of the small size of the preserved fourth phalanx, it is unlikely that there was more than one element following it. As for the fifth digit, the size of the first row phalanx, compared to the size of other phalanges in ZPAL AbIII/3349/1, suggests that at least two phalanges and an ungual were present. In UOBS 02834 described by Książkiewicz (2014), containing hand elements preserved in articulation, two phalanges of the fifth digit are present. The phalanges are dorsoventrally flattened, short, and wide (Fig. 6E). 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 their size.

As mentioned above, claw-like unguals are present on at least the first three digits (based on ZPAL AbIII/2071, ZPAL AbIII/3349/1). 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 (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 (ZPAL AbIII/2071). Longitudinal grooves for ligaments are well-marked on both lateral and medial surfaces. Almost the entire surface of the unguals is covered by tiny and very densely distributed perforations (Figs. 6A–6B, 6E; ZPAL AbIII/2071, ZPAL AbIII/3349/1). Similar texture can be observed on the bony parts of horns, for example, in modern bovids or in the unguals of armadillos (personal observation, Hildebrand, 1983). 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 such as armadillos, pangolins, or moles 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, 1902; Hildebrand, 1988).

Dermal skeleton

Probably the entire forearm of *S. olenkae* was covered by numerous appendicular osteoderms. They are preserved in association with the arm, carpus and manus elements in ZPAL AbIII/2071, ZPAL AbIII/2407, ZPAL AbIII/3349/1, and ZPAL AbIII/3349/2. In the specimens ZPAL AbIII/2407, ZPAL AbIII/3349/1, and ZPAL AbIII/3349/2 they are accumulated mostly on the dorsal side of the hand. In the spec. ZPAL AbIII/2407 there is also a large cluster of osteoderms, previously recovered in front of the distal end of radius and ulna, but removed during 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 (ZPAL AbIII/2407, separated cluster of osteoderms), the smallest around 0.5 cm in diameter (several osteoderms in ZPAL AbIII/2407, ZPAL AbIII/3349/1, and ZPAL AbIII/3349/2). They are ornamented on the dorsal surface. The ornamentation consists of delicate grooves and depressions. The ventral surfaces of the appendicular osteoderms are smooth. On both dorsal and ventral side of osteoderms, tiny openings for blood vessels are present.

The appendicular osteoderms in ZPAL AbIII/2407, ZPAL AbIII/3349/1, and ZPAL AbIII/3349/2 are significantly displaced in regard to their in vivo position, likely because of transportation and early diagenesis processes. However, some general observation can be made. The appendicular osteoderms cover the entire dorsal surface of the carpus and the manus (Fig. 6F). 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 *Aetosaurus 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). The 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 lay one next to another like the scutes of modern crocodiles and alligators.

Pelvic girdle and sacrum

Pelvis structure

The pelvis (Fig. 6, Fig. 7, Fig. 8) of *Stagonolepis olenkae* is transversely broad and robustly build. The sacrum is positioned far caudally in relation to the pubis. It is composed of two vertebrae, which is characteristic for pseudosuchians and phytosaurs (e.g., Romer 1956; Parrish 1986; Nesbitt 2011). Sacral vertebrae are large in the proportion to the ilia. They are entirely fused to the transverse processes and vertebral centra, and form thick, transversely elongated rami, which expand in height and width towards the ilia (ZPAL AbIII/693, ZPAL AbIII/1937, ZPAL AbIII/2531/1, ZPAL AbIII/2531/2, ZPAL AbIII/3349/5, ZPAL AbIII/3394/5). In anteroposterior view, the rami descend at an acute angle towards the iliac blades (ZPAL AbIII/1937, ZPAL AbIII/2531/1, ZPAL AbIII/2531/2, ZPAL AbIII/2738, ZPAL AbIII/3349/5).

The pelvis is triradiate, with the pubis directed anteroventrally and ischium directed posteroventrally. The ilia are tilted so their outer surfaces face ventrolaterally. High iliac blades ascend laterally and engage the sacral ribs in a near horizontal plane (ZPAL AbIII/1937, ZPAL AbIII/3349/5). The anterior processes of the iliac blades are well-developed and elongated anteroposteriorly (ZPAL AbIII/199, ZPAL AbIII/3349/5).

The posterior portion of the pubis and the anterior portion of the ischium are broadly expanded ventromedially, forming a puboischiadic plate. Ventral concavity between the pubis and ischium, usually conspicuous in other archosaurs, is poorly developed in *S. olenkae*, which is typical for aetosaurs (Romer 1956). An unossified notch in the ventral margin of the puboischiadic suture most likely was filled with cartilage in life, therefore the pelvis was fully closed in ventral view, with obturator foramens being the only perforations. Only a single obturator foramen is present (ZPAL AbIII/3266), not two as proposed by Walker (1961) for *Stagonolepis robertsoni*.

The arrangement of the pubes in *S. olenkae* is different from what is generally proposed for the group. In the anteroposterior aspect, the lateral outline of the pubes descends medially (ZPAL AbIII/502/23, ZPAL AbIII/2410, ZPAL AbIII/3266, ZPAL AbIII/3349/5), not vertically; in side view the pubes descend cranially at an angle of about 45° in relation to the iliac blades (ZPAL AbIII/3349/5, ZPAL AbIII/1937 – based on the orientation of the pubic peduncle), not at a right angle; the pubes are twisted so the pubic knobs (buttresses, feet) and their

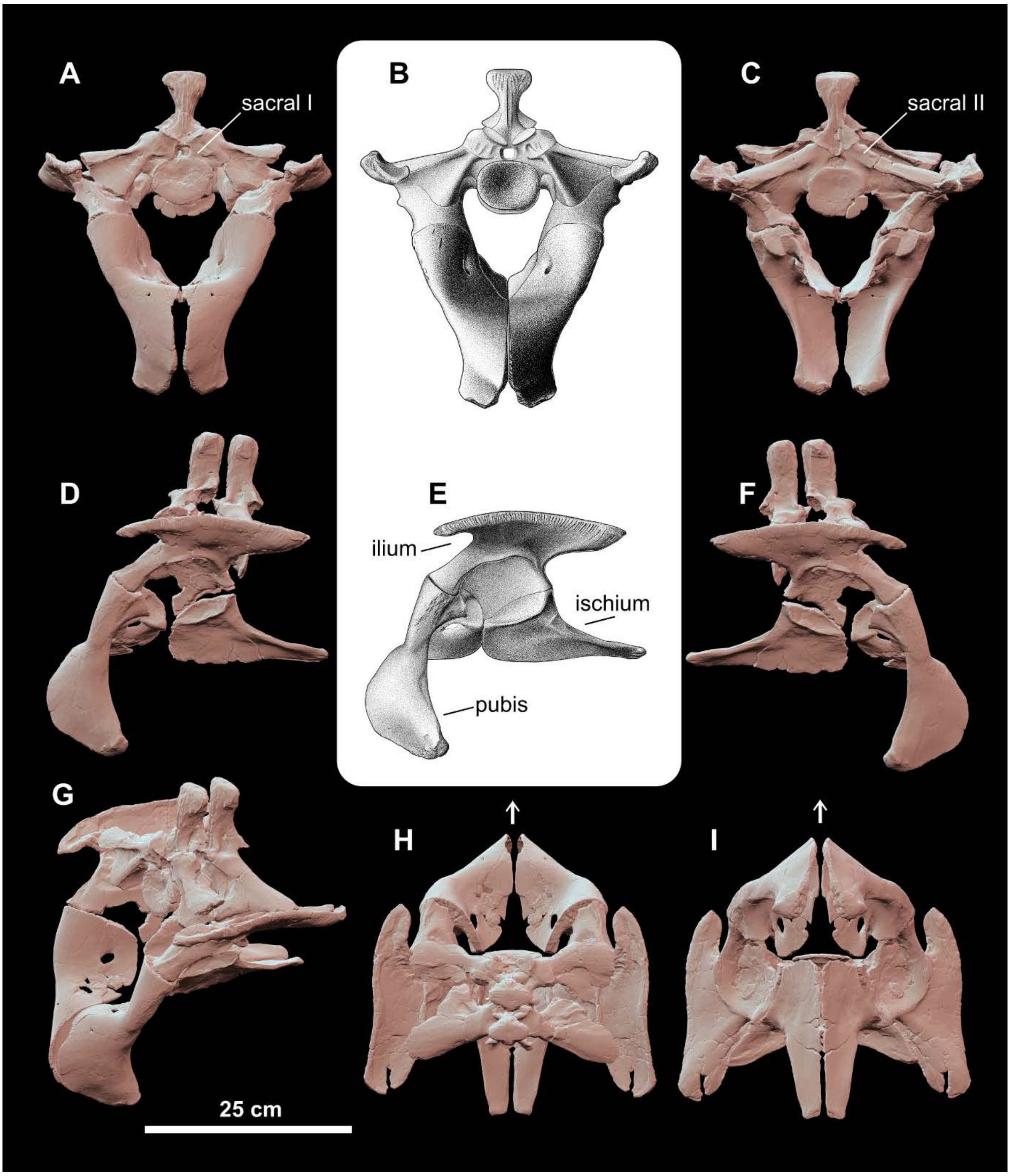


Figure 6. Reconstruction of the pelvis of *Stagonolepis olenkae* based on sacrals ZPAL AbIII/2351/1 and ZPAL AbIII/2351/2, ilium ZPAL AbIII/199, pubis ZPAL AbIII/3266, and ischium ZPAL AbIII/3365/2 in anterior (A, B), posterior (C), lateral (D–F), lateral (G), dorsal (H), and ventral view (I). The arrows indicate the cranial direction.

lateral margins are directed caudolaterally (ZPAL AbIII/502/23, ZPAL AbIII/2410, ZPAL AbIII/3266, ZPAL AbIII/3349/5), not laterally; and the laminae of the pubic aprons in *S. olenkae* form an acute angle with each other in a coronal plane (ZPAL AbIII/3349/5, ZPAL

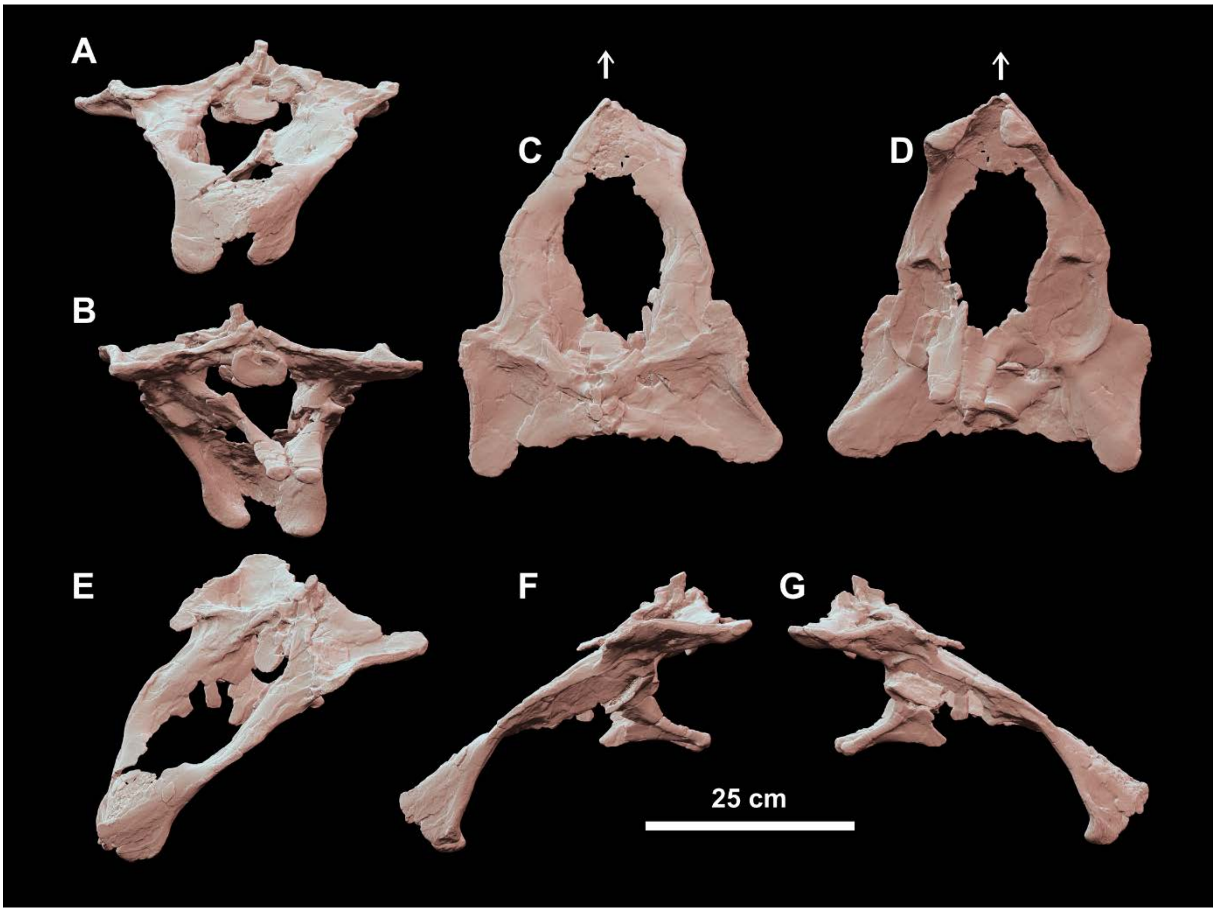


Figure 7. Pelvis of *Stagonolepis olenkae*. ZPAL AbIII/3349/5 in anterior (A), posterior (B), dorsal (C), ventral (D), antero dorsal side view (E), and side views (F–G). The arrows indicate the cranial direction.

AbIII/3266), they are not parallel and do not form a single plane with each other (Walker 1961; Small 1985; Long and Murry 1995; Martz 2002; Schoch 2007; Desojo et al. 2013).

The ischia of *S. olenkae* project caudally. In lateral view, their ventral margins are oriented almost parallel to the dorsal margins of the iliac blades. In anteroposterior aspect, they descend medially at an angle of roughly 45° (ZPAL AbIII/3349/5). The anterior portion of the ischium is high (ZPAL AbIII/3365/2, ZPAL AbIII/3394/3, AbIII/3394/4) and thin (2 mm thick in ZPAL AbIII/3365/2). The posterior portions of the ischia twist laterally and form a horizontal shelf with each other (ZPAL AbIII/3349/5) similar to *Aetosauroides scagliai* (PVL 2073), *Desmatosuchus spurensis* (MNA V9300), *Lucasuchus hunti* (TMM 31100-313), and *Typothorax antiquum* (NMMNH P-36075). Ischia end caudally with buttresses that face ventrally (ZPAL AbIII/3349/5, ZPAL AbIII/3365/2, ZPAL AbIII/3394/3, ZPAL AbIII/3394/4).

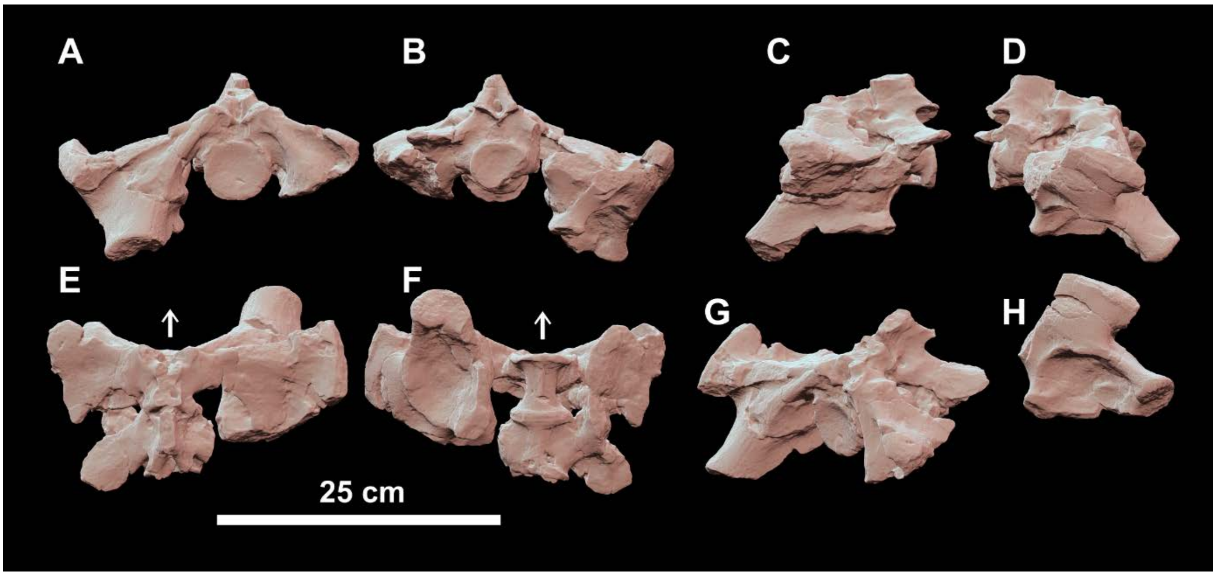


Figure 8. Right ilium and sacrum of *Stagonolepis olenkae*. ZPAL AbIII/1937 in anterior (A), posterior (B), lateral(C, D), dorsal (E), ventral (F), and anterodorso view (G); ilium in ventrolateral view (H). The arrows indicate the cranial direction.

Acetabulum

The acetabulum is fully closed, deep (Parrish 1986), and oriented obliquely in a vertical plane (Desojo et al. 2013) (ZPAL AbIII/1937). A distinct supraacetabular crest, with laterally pointing supraacetabular buttress is present in all preserved ilia (ZPAL AbIII/199, ZPAL AbIII/1937, ZPAL AbIII/ 3349/5, ZPAL AbIII/3394/2). The acetabulum is composed mainly by the ilium (about 90% of entire acetabulum) with a minor area contributed by the pubis and ischium. The ventral curvature of the acetabulum is parabolic with the topmost point placed medially to the supracetabular buttress, forming a socket for the femoral head (ZPAL AbIII/199, ZPAL AbIII/1937).

Sutures and medial symphysis

Sutures and symphyses formed broad areas of attachment and developed interlocking structures or were obliterated, which enhanced stiffness of the pelvis. Sacral vertebrae form a vertical suture between each other in their anterior and posterior-most portions (ZPAL AbIII/2531/1, ZPAL AbIII/2531/2, ZPAL AbIII/2738). These sutures are completely obliterated in ZPAL AbIII1937. The area of the iliosacral suture is of comparable size to the iliac portion of the acetabulum and in anteroposterior aspect, follows general curvature of the ilium and descends medially, towards the sacral vertebrae centra (ZPAL AbIII/1937, ZPAL AbIII/2531/1, ZPAL AbIII/2531/2, ZPAL AbIII/2738, ZPAL AbIII/3349/5). It is stiffened by four ridges on the ilium, which match corresponding grooves on the sacral vertebrae (ilia: ZPAL

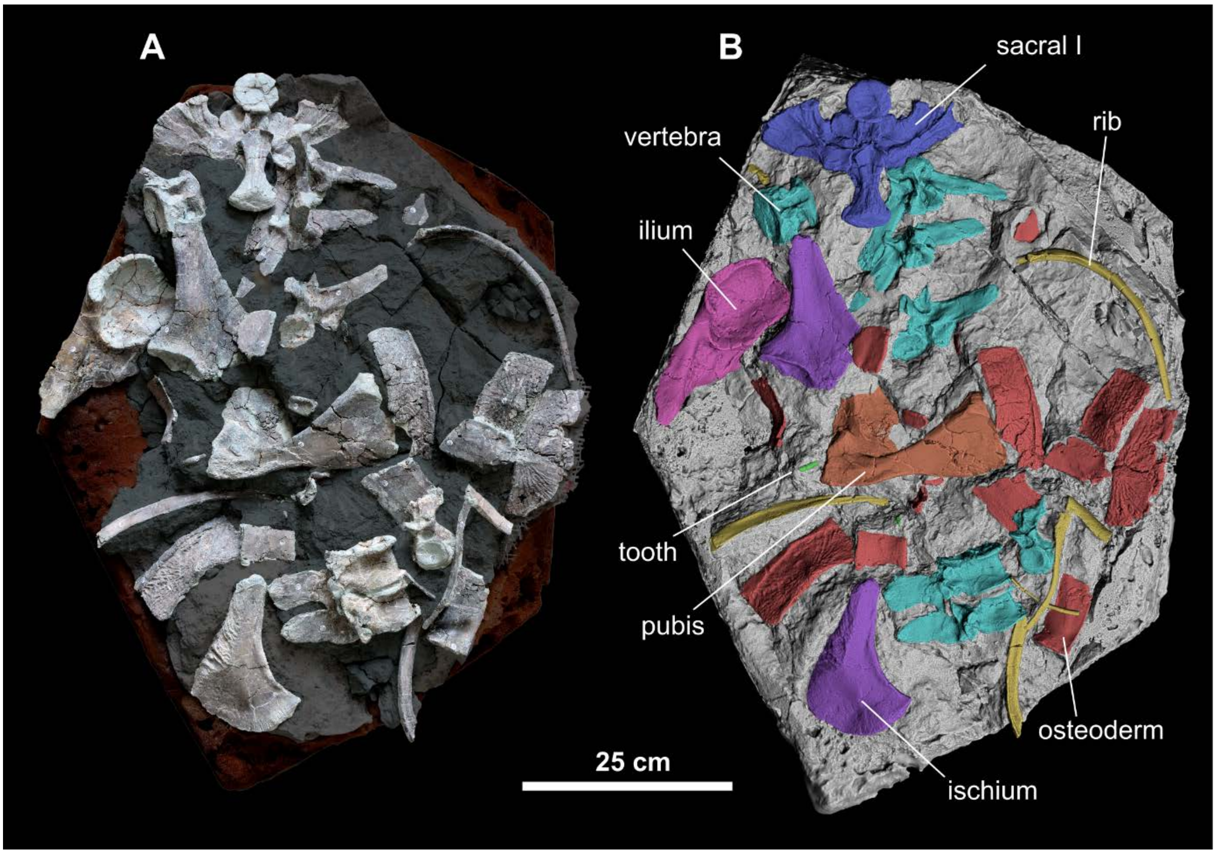


Figure 9. *Stagonolepis olenkae*, association ZPAL AbIII/3394, the photograph (A), and colorized 3D model (B).

AbIII/199, sacrals: ZPAL AbIII/2531/1, ZPAL AbIII/2531/2, ZPAL AbIII/2738). In most specimens the sacroiliac suture is not ossified, although at least partial fusion may be present in ZPAL AbIII/1927 and ZPAL AbIII/3349/5. The ventral (median) symphysis starts at the anterior tip of the pubes and continues along the medial axis, till the posterior end of the ischia. In ZPAL AbIII/3349/5, the anterior portion of the pubic symphysis and the puboiliac suture are fully ossified. The ischiadic symphysis in its anterior portion forms a series of alternating ridges and grooves stiffening it and preventing ischia from dislocation (ZPAL AbIII/3365/2, ZPAL AbIII/3394/4, ZPAL AbIII/3378).

Proportions of the pelvic elements

Stagonolepis olenkae has the pubes longer than the ilia and the ilia longer than the ischia (ZPAL AbIII/3349/5 (Fig. 7) and ZPAL AbIII/3394 (Fig. 9). Relative proportions of the preserved pelvis elements in ZPAL AbIII/3349/5 suggest that the pubes are longer in proportion to the ischia than in ZPAL AbIII/3394. However, this is an estimation, because the anterior portions of the ischia are damaged in ZPAL AbIII/3349/5, and for the same reason exact measurements are not given here.

Sacral vertebrae

Sacral vertebrae (Fig. 10) are present in six specimens: ZPAL AbIII/693 (2nd), ZPAL AbIII/1937 (1st and 2nd), ZPAL AbIII/2531/1 (1st), ZPAL AbIII/2531/2 (2nd), ZPAL AbIII/2738 (2nd), ZPAL AbIII/3349/5 (1st and 2nd), and ZPAL AbIII/3394/5 (1st).

Neural spines are higher than the vertebral centra (ZPAL AbIII/693, ZPAL AbIII/2531/1, ZPAL AbIII/2531/2, ZPAL AbIII/2738). The spine table is the same width as the caudal surface of the vertebral centrum in the 1st sacral and the cranial surface of the vertebral centrum in the 2nd sacral (ZPAL AbIII/1937, ZPAL AbIII/ 2531/1, ZPAL AbIII/2531/2, ZPAL AbIII/2738). Dorsally, it forms a flat surface with a small indentation in the middle (ZPAL AbIII/693, ZPAL AbIII/2531/1, ZPAL AbIII/2531/2). In ZPAL AbIII/2738 the indentation is more indicated, giving the entire transverse expansion a heart-shaped appearance. The spine table is thick and high, being roughly one fourth of the entire neural spine height (ZPAL AbIII/693, ZPAL AbIII/2531/1, ZPAL AbIII/2531/2,ZPAL AbIII/2738, ZPAL AbIII/3394/5) similar as in *Desmatosuchus spurensis* (MNA V9300)(Parker 2008). It is distinguished form the rest of the neural spine by rugosities that cover it ventrally to the dorsal surface (ZPAL AbIII/2531/1, ZPAL AbIII/2531/2, ZPAL AbIII/2738). It gradually decreases in width towards the middle part of the neural spine (ZPAL AbIII/693, ZPAL AbIII/2531/1, ZPAL AbIII/2531/2, ZPAL AbIII/2738). On both anterior and posterior side of the neural spine two prominent vertical laminae are present. At each side they are parallel to each other and there is a shallow groove between them. They originate ventrally to the spine table and continue along the entire neural spine till postzygapophyses or hypantrum (ZPAL AbIII/693, ZPAL AbIII/2531/1, ZPAL AbIII/2531/2, ZPAL AbIII/2738, ZPAL AbIII/3394/5). In ZPAL AbIII/2531/1 and ZPAL AbIII/2531/2 on the posterior and anterior surfaces of the neural spine, accessory laminae are present, positioned laterally to the main two. On the ventral part of the neural spine there are depressions on the lateral surfaces, between the pre- and postzygapophyses.

The prezygapophyses and postzygapophyses are expanded laterally to the degree comparable to that of the spine table (ZPAL AbIII/693, ZPAL AbIII/2531/1, ZPAL AbIII/2531/2,

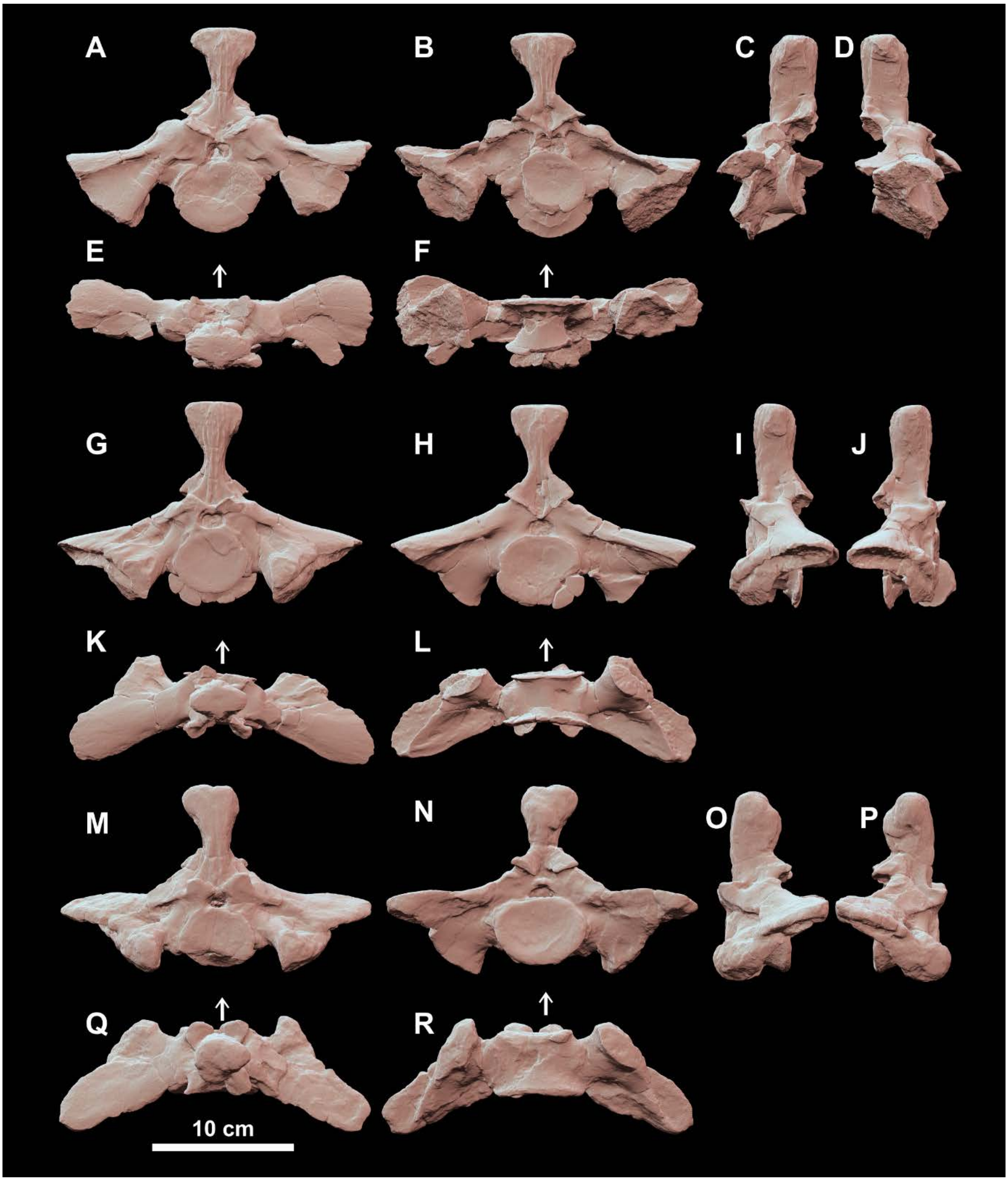


Figure 10. Sacral vertebrae of *Stagonolepis olenkae*. The first sacral ZPAL AbIII/2531/1 (A–F), the second sacral ZPAL AbIII/2531/2 (G–L), the second sacral ZPAL AbIII/693 (M–R); in anterior (A, G, M), posterior (B, H, N), lateral (C, D, I, J, O, P), dorsal (E, K, Q), and ventral view (F, L, R). The arrows indicate the cranial direction.

ZPAL AbIII/2738). There are no prezygapophyseal laminae (ZPAL AbIII/693, ZPAL AbIII/1937, ZPAL AbIII/2531/1, ZPAL AbIII/2531/2, ZPAL AbIII/2738, ZPAL AbIII/3349/5, ZPAL AbIII/3394/5). Postzygapophyseal laminae start around the middle part of the neural spine and are well developed in both sacrals (ZPAL AbIII/693, ZPAL AbIII/1937, ZPAL AbIII/2531/1, ZPAL AbIII/2531/2, ZPAL AbIII/2738, ZPAL AbIII/3349/5, ZPAL

AbIII/3394/5). Hyposphene-hypantrum articulations are present between the last dorsal vertebrae, sacrals, and the first caudal vertebrae (ZPAL AbIII/1937, ZPAL AbIII/2531/1, ZPAL AbIII/2531/2, ZPAL AbIII/2738, ZPAL AbIII/3394/5). It seems that in ZPAL AbIII/1937 pre- and postzygapophyses are partially co-ossified with each other.

The neural canal is square in anterior view (ZPAL AbIII/1937, ZPAL AbIII/2531/1, ZPAL AbIII/2531/2, ZPAL AbIII/2738, ZPAL AbIII/3349/5). The sutures between the neural arch and transverse processes with the vertebral centra and sacral ribs are completely obliterated and there is no clear anatomical distinction between them (ZPAL AbIII/693, ZPAL AbIII/1937, ZPAL AbIII/2531/1, ZPAL AbIII/2531/2, ZPAL AbIII/2738, ZPAL AbIII/3349/5, ZPAL AbIII/3394/5). However, in both sacrals there is a furrow which most likely is a remnant of a suture between the sacral ribs and transverse processes. It is particularly well visible dorsally, where it forms an elongated tuber on both sacrals, but less indicated in the sacral II (I sacrals: ZPAL AbIII/1937, ZPAL AbIII/2531/1, ZPAL AbIII/3349/5, ZPAL AbIII/3394/5, II sacrals (ZPAL AbIII/693, ZPAL AbIII/1937, ZPAL AbIII/2531/2, ZPAL AbIII/3349/5).

In the second sacral ZPAL AbIII/2738, dorsally there is a suture in the place of the furrow observed in other specimens. The suture continues posteriorly, although obliterated, where it forms s-shaped furrows positioned laterally to the neural canal. The furrows' shape may indicate the initial border between the sacral ribs, transverse processes, and the neural arch. It is unclear if presence of that suture indicates the younger ontogenetic age of ZPAL AbIII/2738 or intraspecific variation, because in the comparably sized ZPAL AbIII/693, ZPAL AbIII/2531/2, and ZPAL AbIII/1937 the surface is smooth in the place of the furrow of ZPAL AbIII/2738.

A furrow of probably similar origin (that might be a remnant of an initial border between the sacral ribs, transverse process, and neural arch) is visible anteriorly in the first sacral ZPAL AbIII/2531/1. It originates from the dorsal furrow, continues near vertically at the anterior side and then forms a horizontal shelf positioned ventrally and parallel to the prezygapophyses. Two distinct fossae are present around the shelf: one obliquely oriented positioned dorsally to the shelf, and one ventrally to it formed between ventral margin of the shelf and dorsal margin of the fused centrum. In ZPAL AbIII/3349/5 the furrow is conspicuous, but the fossae are moderately developed. In the first sacral of ZPAL AbIII/1937 there is no furrow, and the fossae are less developed than in both ZPAL AbIII/2531/1 and ZPAL AbIII/3349/5.

The centra of the vertebrae are amphicoelous. The anterior surface is larger and more concave than posterior one in the first sacral, opposite in the second sacral (ZPAL AbIII/693, ZPAL AbIII/2531/1, ZPAL AbIII/2531/2, ZPAL AbIII/3349/5). In both sacrals the anterior and posterior surfaces are roughly round (ZPAL AbIII/1937, ZPAL AbIII/2531/1, ZPAL AbIII/2531/2, ZPAL AbIII/2738, ZPAL AbIII/3394/5). It seems that the larger surfaces are slightly more expanded laterally then the smaller ones (ZPAL AbIII/693, ZPAL AbIII/2531/1, ZPAL AbIII/2531/2, ZPAL AbIII/3349/5). It appears that in ZPAL AbIII/1937 the posterior part of the first sacral centrum and the anterior part of the second sacral centrum are dorsally partially fused together. Ventrally, the centra are hourglass-shaped as in, e.g., *Typothorax antiquum* (Lucas et al. 2002). A well-indicated sharp keel is present on the first sacral of ZPAL AbIII/1937, and a marked medial elevation is present on the second sacral of the same specimen. A similar elevation is visible also on the first sacral ZPAL AbIII/2531/1/, ZPAL AbIII/2531/2, and second sacral of ZPAL AbIII/3349/5. There is no such structure in ZPAL AbIII/2738.

Sacral ribs articulating with the first sacral vertebra are thinner in their middle part than laterally. They attach to the centrum only in the anterior middle and anterior dorsal part of the centrum (ZPAL AbIII/1937, ZPAL AbIII/2531/1, ZPAL AbIII/3349/5, ZPAL AbIII/3394/5). In ZPAL AbIII/2531/1 there is a furrow in the place of a possible suture laterally to the middle part of the centrum. The transverse rami of the sacral ribs expand in height laterally. Anteriorly, they form a deep conical fossa which is dorsally restricted by a shelf-like projection and ventrally by a pronounced furrow (ZPAL AbIII/1937, ZPAL AbIII/2531/1, ZPAL AbIII/3349/5). In anterior view, the ventral margin of the sacral ribs is around the level of the ventral margin of centrum. Posteriorly, the transverse rami are deeply depressed (ZPAL AbIII/1937, ZPAL AbIII/2531/1, ZPAL AbIII/3349/5, ZPAL AbIII/3394/5). The depression is dorsally restricted by a shelf-like projection that covers the posterior part of the centrum and suture area for the second sacral (ZPAL AbIII/2531/1). The shelf is broadly expanded laterally and anteroposteriorly. Posteriorly, it reaches out to the anterior portion of the second sacral rib pair. The posterior margin of the shelf forms a bow-shaped indentation. This indentation forms an opening between the posterior margin of the first sacral rib and anterior margin of the second sacral rib (ZPAL AbIII/1937, ZPAL AbIII/3349/5) in a similar manner as in *Typothorax antiquum* (NMMNH P-36075) and *Aetosauroides scagliai* (PVL 2073) (Casamiquela 1961; Heckert and Lucas 2002; Lucas et al. 2002). The suture areas between the sacral ribs of both sacrals and between the sacral ribs and the ilium are rugose, composed of multiple small tubers (ZPAL AbIII/2531/1).

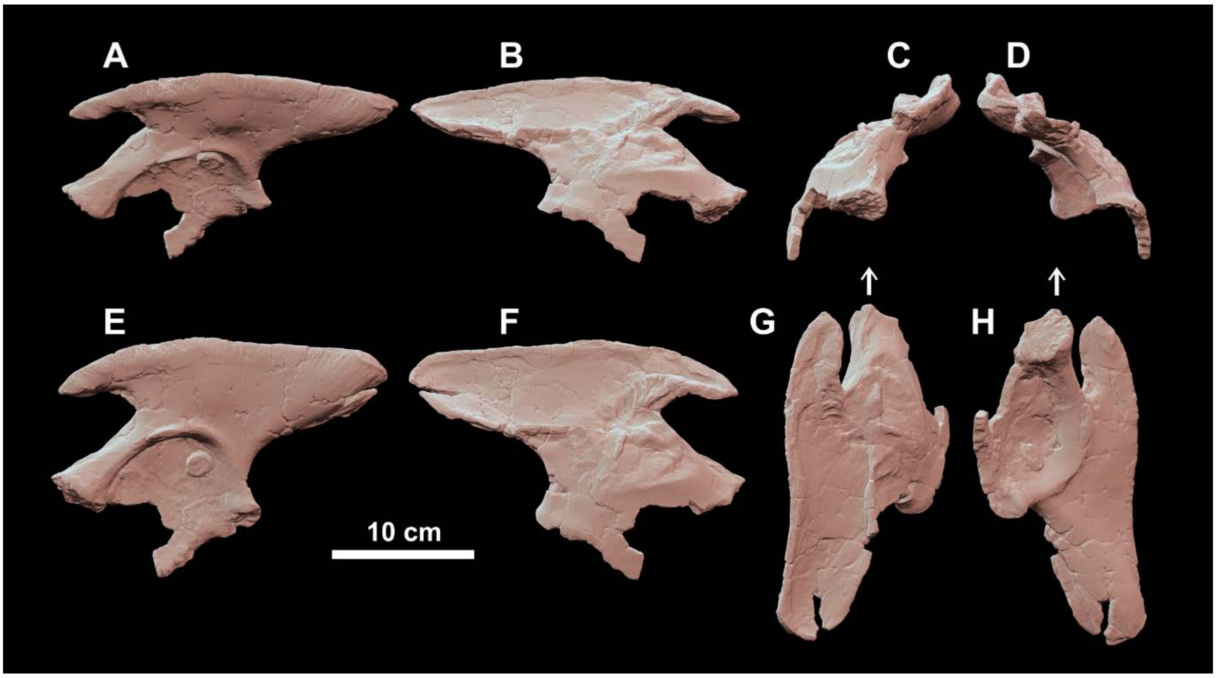


Figure 11. Left ilium of *Stagonolepis olenkae* ZPAL AbIII/199, in lateral (A), medial (B), anterior (C), posterior (D), ventrolateral (E), dorsomedial (F), dorsal (G), and ventral (H) view. The arrows indicate the cranial direction.

It seems that in ZPAL AbIII/1937 the suture between both the sacral rib pairs is completely obliterated.

The sacral ribs articulating with the second sacral vertebra, in contrast to the ribs of the first sacral vertebra, are attached to the centrum at their almost entire width. They also expand in height laterally. However, they do not increase in thickness anteroposteriorly, but obliquely ascend posteriorly, which is well visible in lateral view. Anteriorly, lateral to the neural canal, conspicuous fossae are present (ZPAL AbIII/2531/1, ZPAL AbIII/2738). Posteriorly, a shelf-like projection is formed on the dorsal portion of the sacral ribs' rami. It continues caudally and ends in a sharp furrow (ZPAL AbIII/693, ZPAL AbIII/2531/2, ZPAL AbIII/2738, ZPAL AbIII/3349/5). A deep fossa for the posterior ridge of the ilium continues along the entire posteriorly elongated suture area between the sacral ribs and the ilium (ZPAL AbIII/693, ZPAL AbIII/2531/2, ZPAL AbIII/2738). The suture area is rugose, composed of multiple small tubers (ZPAL AbIII/2531/2).

Ilium

The ilia (Fig. 11) are preserved in four specimens: ZPAL AbIII/199, ZPAL AbIII/1937, ZPAL AbIII/3349/5, and ZPAL AbIII/3394/2. Their morphology is most similar to *Stagonolepis robertsoni* (Walker 1961). The proportions of the most complete ilium, ZPAL AbIII/199, are as follows: the height of the iliac blade is 0.5 of the diameter of the acetabulum; the length of the preacetabular process is 0.7 of the length of the pubic peduncle and 0.25 of the length of the entire iliac blade; the length of the postacetabular process is 1.1 of the diameter of the acetabulum; and the acetabulum diameter is 0.5 of the length of the entire iliac blade.

The iliac blades are oriented obliquely in a vertical plane (ZPAL AbIII/1937, ZPAL AbIII/199). A near horizontal orientation of the iliac blades in ZPAL AbIII/3349/5 is most likely due to compaction. The lateral outline of the iliac blades is s-shaped in dorsal view (ZPAL AbIII/199, ZPAL AbIII/3349/5). ZPAL AbIII/1937 has a much thicker iliac blade, proportionally twice the thickness of the iliac blades in other specimens. The lateral margin of the iliac blade is rugose along its entire length (ZPAL AbIII/199, ZPAL AbIII/3349/5, ZPAL AbIII/3394/2). The rugosities consist of irregularly arranged, vertically oriented ridges. The degree of its development is variable: in ZPAL AbIII/199 it is clearly visible on both the ventral and dorsal surface (but less clear on the dorsal surface), in ZPAL AbIII/3349/5 and ZPAL AbIII/3394/2 it is visible only on the ventral surface (and less indicated than in ZPAL AbIII/199). The thick iliac blade of ZPAL AbIII/1937 lacks this feature entirely. Similar ornamentation can be recognized in *Polesinesuchus aurelioi* (ULBRAPVT003), *Calyptosuchus wellesi* (UCMP 25941, UCMP 32150) (Roberto-Da-Silva et al. 2014; Parker 2018*a*). Rugosities at the posterior section of the iliac blade were also reported for *S. robertsoni* (Walker 1961: R 4804, fig. 16).

The preacetabular process of the iliac blade is shorter than the pubic peduncle ZPAL AbIII/119, ZPAL AbIII/3349/5) to the exact same degree as in *Stagonolepis robertsoni* (R 4789)(Walker 1961; Parker 2018*b*). It is flattened vertically, and recurved ventrally (ZPAL AbIII/199, ZPAL AbIII/3349/5) as in *S. robertsoni* (R 4789/4790) (Walker 1961; Parker 2018*b*). In dorsal view the outline of the process ends sharply (ZPAL AbIII/199) like in *S. robertsoni* (R 4789, dorsomedial cast). In ventrolateral view the anterior process of the iliac blade is triangular (ZPAL AbIII/199), similar as in, e.g., *Aetosauroides scagliai* (PVL 2073, left ilium) (Casamiquela 1961; Heckert and Lucas 2002), *Calyptosuchus wellesi* (UCMP 25941)(Parker 2018*a*), and *S. robertsoni* (R 4790, ventrolateral cast) (Walker 1961), contra Parker (Parker 2018*b*) who recognized the shape of the preacetabular as being autapomorphic in *S. robertsoni* (based on R 4789). On the lateral side of the preacetabular process, close to its anterior edge, a prominent tuber is present in ZPAL AbIII/199, visible also in *S. robertsoni* (R 4790, ventrolateral cast).

The postacetabular process of the iliac blade is elongated in comparison to *Typothorax coccinarum* (UCMP V2816/122683: (Long and Murry 1995; Martz 2002)) and *Typothorax antiquum* (NMMNH P-36075; (Lucas et al. 2002)), however, its length in proportion to the width of the acetabulum is comparable as in most of other aetosaurs (Sawin 1947; Casamiquela 1961; Bonaparte 1971; Small 1985; Long and Murry 1995; Desojo and Báez 2005; Schoch 2007; Parker 2008; Roberto-Da-Silva et al. 2014). The end of the postacetabular process is squared-off (ZPAL AbIII/199, ZPAL AbIII/3349/5, ZPAL AbIII/3394/2, the same as in, e.g., *Aetosauroides scagliai* (PVL 2073) (Casamiquela 1961; Heckert and Lucas 2002) and most other aetosaurs including *S. robertsoni* (E.M. 46 R), contra Parker (Parker 2018*b*) who interpreted the posterior end in this species as being acute.

The acetabulum faces ventrolaterally. A distinct supracetabular crest is present in all studied specimens (ZPAL AbIII/199, ZPAL AbIII/1937, ZPAL AbIII/3349/5, ZPAL AbIII/3394/2). The edge of the supracetabular crest is sharp, it originates posteriorly near to the anterior end of the postacetabular blade and continues dorsally over the acetabulum and towards the pubic peduncle (ZPAL AbIII/199, ZPAL AbIII/1937, ZPAL AbIII/3349/5, ZPAL AbIII/3394/2), similar as in, e.g., *Stagonolepis robertsoni* (R 4789), *Calyptosuchus wellesi* (UCMP 25941), *Aetosauroides scagliai* (PVL 2073), *Polesinesuchus aurelioi* (ULBRAPVT003) (Casamiquela 1961; Walker 1961; Roberto-Da-Silva et al. 2014; Parker 2018*a*). Dorsally to the deepest portion of the acetabulum, the supracetabular crest expands laterally forming a well-developed supracetabular buttress in ZPAL AbIII/199 and ZPAL AbIII/3394/2, moderately expanded in ZPAL AbIII/3349/5, and almost inconspicuous in the thick acetabulum of ZPAL AbIII/1937.

The pubic peduncle is thicker than the ischiadic peduncle (ZPAL AbIII/199, ZPAL AbIII/3349/5), in a similar manner as in, e.g., *Stagonolepis robertsoni* (Walker 1961), *Calyptosuchus wellesi* (UCMP 25941), *Aetosauroides scagliai* (PVL 2073), *Polesinesuchus aurelioi* (ULBRAPVT003) (Casamiquela 1961; Walker 1961; Roberto-Da-Silva et al. 2014; Parker 2018*a*). The dorsal surface of the pubic peduncle is flat (ZPAL AbIII/199, ZPAL AbIII/1937, ZPAL AbIII/3394/2. In ventrolateral view, the pubic peduncle expands towards the pubic symphysis (ZPAL AbIII/199, ZPAL AbIII/1937, ZPAL AbIII/3349/5). The area of the pubic and ischiadic suture is rugose, composed of multiple irregularly arranged grooves and cusps (ZPAL AbIII/199, ZPAL AbIII/1937). In ZPAL AbIII/3349/5 the ilium-pubis suture is fully ossified.

Figure 12. Right pubis of *Stagonolepis olenkae* ZPAL AbIII/3266 in anterior (A), posterior (B), medial (C), lateral (D), dorsal (E), and ventral view (F). The arrows indicate the cranial direction.

The iliosacral suture area is broad, matching the respective area on the sacral ribs. The area is rugose in a manner similar as in *Stagonolepis robertsoni* (Walker 1961) or *Calyptosuchus wellesi* (UCMP 25941) (Parker 2018*a*). The suture is additionally stiffened by distinct ridges that match the corresponding grooves on the sacral ribs. There are three short ridges in the area of suture with the first sacral rib. The most dorsal one is on the preacetabular process of the iliac blade. It originates at the level of the pubic peduncle, continues parallel to the medial edge of the process, and fades at the end of the rugose suture area (it does not continue towards the end of the process; ZPAL AbIII/199). A similar structure can be recognized in *S. robertsoni* (Walker 1961). The other two ridges originate in the middle of the suture area with the first sacral rib and are directed towards the pubic and ischiadic peduncles (ZPAL AbIII/199). A single long, posteriorly directed ridge is present on the suture area with the second sacral rib (ZPAL AbIII/199), similar as in other aetosaurs (Walker 1961; Long and Murry 1995; Roberto-Da-Silva et al. 2014; Parker 2018*a*).

Pubis

The pubis (Fig. 12) is preserved in six specimens: ZPAL AbIII/502/23, ZPAL AbIII/2410, ZPAL AbIII/2412, ZPAL AbIII/3266, ZPAL AbIII/3349/5, and ZPAL AbIII/3394/1. The morphology of the best preserved specimen, ZPAL AbIII/3266, is most similar to *Stagonolepis robertsoni* (R 4793, medioventral cast) (Walker 1961).

The iliac peduncle is massive in proportion to the rest of the pubis. In ZPAL AbIII/3266 it is 3.5 times thicker than the thickness of the lateral margin of the pubic apron, and twice the thickness of the pubic knob (buttress). On the anterolateral surface of the iliac peduncle a rugose area is present which continues dorsoventrally across the entire ilium peduncle (ZPAL AbIII/502/23, 2410, 3266, 3349/5, 3394/1).

The anteroventral portion of the acetabulum forms a pronounced acetabular buttress (ZPAL AbIII/502/23, ZPAL AbIII/3266, ZPAL AbIII/3349/5). Between the acetabular buttress and the pubic flange, there is a deep, obliquely oriented open canal (ZPAL AbIII/2410, ZPAL AbIII/3266, ZPAL AbIII/3349/5). It is developed similar as in, e.g., *Polesinesuchus aurelioi* (ULBRAPVT003), *Aetosauroides scagliai* (2073-18), *Stagonolepis robertsoni* (R 4793, medioventral cast), and different than in *Scutarx deltatylus* (PEFO 31217), in which the canal is closed. In ZPAL AbIII/3266, distally to the canal there is another buttress formed on the ventral side of the pubic flange that forms the ventral-most border of the acetabulum.

The pubic flange is of equal width throughout the entire length of the pubis (ZPAL AbIII/3266). Medially it descends obliquely and forms a flat, horizontal shelf at the end of the iliac peduncle, then twists laterally and abruptly descends in a near vertical plane at the pubic apron (ZPAL AbIII/502/23, ZPAL AbIII/2410, ZPAL AbIII/2412,ZPAL AbIII/3266, ZPAL AbIII/3349/5). The dorsal-most portion of the pubic flange is very thin, especially in the part ventral to the iliac peduncle (~1–3 mm; ZPAL AbIII/2410, ZPAL AbIII/3266, ZPAL AbIII/3349/5).

There is only a single obturator foramen positioned ventrally and parallel to the acetabular canal (ZPAL AbIII/2410, ZPAL AbIII/3266, ZPAL AbIII/3349/5, ZPAL AbIII/3394/1), similar as in, e.g., *Stagonolepis robertsoni* (R 4793: presence of two foramina postulated by Walker (1961) is a mistake) and *Desmatosuchus spurensis* (MNA V9300) (Parker 2008). The obturator foramen is oval with its anterior part squared-off (*S. olenkae:* ZPAL AbIII/3266), similar as in *S. robertsoni* (R 4793).

The surfaces of the pubic aprons are directed caudolaterally and form an acute angle with each other, which can be deduced based on the fully preserved symphysis of ZPAL AbIII/3266 and articulation of the pubes in ZPAL AbIII/3349/5. The lateral edge of the pubic apron ends with a thick, sharp crest (ZPAL AbIII/502/23, ZPAL AbIII/2410, ZPAL AbIII/2412, ZPAL AbIII/3266, ZPAL AbIII/3349/5, ZPAL AbIII/3394/2), similar as in, e.g., *Stagonolepis robertsoni* (R 4793) and *Aetosauroides scagliai* (PVL 2073-18). The distal part of the pubic apron, medially to the pubic knob (buttress), is not ossified entirely, as proposed for *S. robertsoni* (R 4793) (Walker 1961), but obliquely ascends towards the pubic symphysis (ZPAL AbIII/3266).

The distal knob (buttress) is tear-shaped and it slightly projects medioposteriorly (ZPAL AbIII/2410, ZPAL AbIII/3266, ZPAL AbIII/3349/5, ZPAL AbIII/3394/1) similar as in *Desmatosuchus spurensis* (MNA V9300) and *S. robertsoni* (R 4793) (Walker 1961; Parker 2008). In *Typothorax coccinarum* (UCMP V28I6 34248) this projection seems to be more pronounced (Martz 2002).

The area of puboiliac suture is rugose in a way similar to the corresponding area on the ilium (*Stagonolepis olenkae*: ZPAL AbIII/3266). The pubic symphysis is s-shaped in medial view (ZPAL AbIII/3266). The surface of the pubic symphysis is oriented vertically and almost flat (ZPAL AbIII/3266). It is covered by multiple tiny grooves and tubers (ZPAL AbIII/3266).

Ischium

The ischium of *Stagonolepis olenkae* (Fig. 13) is preserved in five specimens: ZPAL AbIII/3349/5, ZPAL AbIII/3365/2, ZPAL AbIII/3378, ZPAL AbIII/3394/3, and ZPAL AbIII/3394/4. Their morphology is similar as in the other known aetosaurs (Casamiquela 1961; Walker 1961; Bonaparte 1971; Long and Murry 1995; Small 1998; Lucas et al. 2002; Martz 2002; Desojo and Báez 2005; Desojo et al. 2013; Roberto-Da-Silva et al. 2014).

The ischiadic blade descends medially at a similar angle as the iliac blades (ZPAL AbIII/3349/5). The ischiadic portion of the acetabulum extends laterally from the ischiadic blade (ZPAL AbIII/3349/5, ZPAL AbIII/3365/2, ZPAL AbIII/3378, ZPAL AbIII/3394/3, ZPAL AbIII/3394/4). Lateroventrally, there is a marked fossa that distinguishes the acetabulum from the rest of the ischium surface (ZPAL AbIII/3349/5, ZPAL AbIII/3365/2, ZPAL AbIII/3378, ZPAL AbIII/3394/3). Mediodorsally, the ischiadic blade is flat, with a depression in the anterior-most part (ZPAL AbIII/3365/2, ZPAL AbIII/3378 3394/4; *Stagonolepis robertsoni*: R 4790). The anterior-most part of the ischiadic blade is very thin (~2–3 mm; ZPAL AbIII/3365/2, ZPAL AbIII/3378).

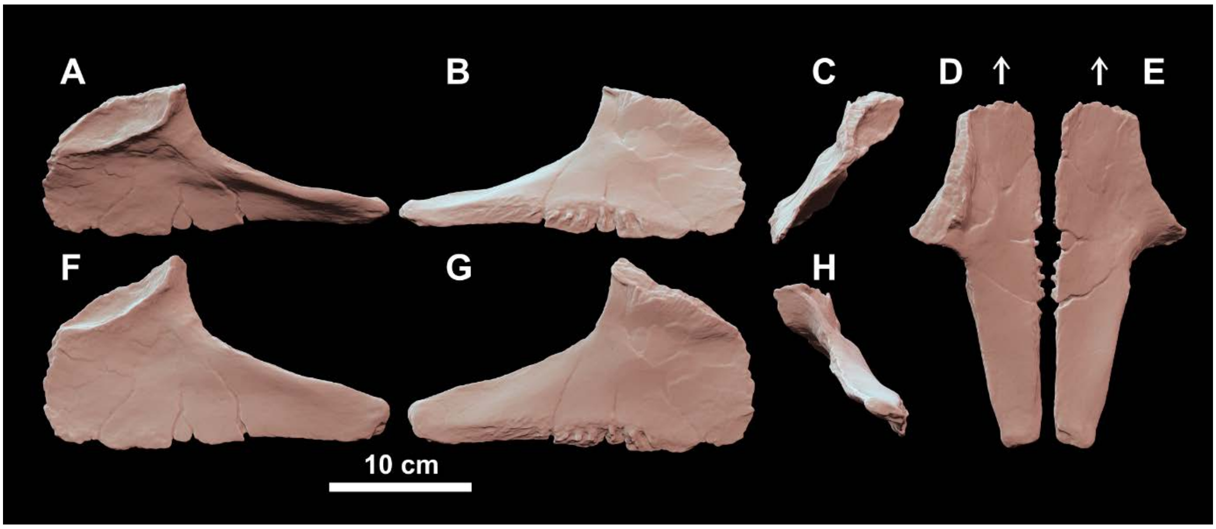


Figure 13. Left ischium of *Stagonolepis olenkae* ZPAL AbIII/3365/2 in lateral (A), medial (B), anterior (C), dorsal (D), ventral (E), ventrolateral (F), dorsomedial (G), and posterior view (H). The arrows indicate the cranial direction.

The postacetabular process of the ischium is twisted laterally, so its distal-most part forms a horizontally oriented shelf (ZPAL AbIII/3349/5, ZPAL AbIII/3365/2, ZPAL AbIII/3378, ZPAL AbIII/3394/3, 3394/4) similar as in, e.g., *Aetosauroides scagliai* (PVL 2073), *Desmatosuchus spurensis* (MNA V9300), and *Typothorax antiquum* (NMMNH P-36075) (Casamiquela 1961; Heckert and Lucas 2002; Lucas et al. 2002; Parker 2008). The postacetabular process ends with a small buttress, which is rugose ventrally (ZPAL AbIII/3349/5, ZPAL AbIII/3365/2). The lateral margin of the postacetabular process forms a sharply ended crest (ZPAL AbIII/3349/5, ZPAL AbIII/3365/2, ZPAL AbIII/3378, ZPAL AbIII/3394/3, 3394/4).

The ilioischiadic suture surface is rugose in a manner similar to the puboiliac suture (ischia: ZPAL AbIII/3365/2, ZPAL AbIII/3394/3, ZPAL AbIII/3394/4). The rugosity is composed of irregularly arranged groves and tubers.

The ischiadic symphysis surface is broad and bowed (ZPAL AbIII/3365/2, ZPAL AbIII/3378, ZPAL AbIII/3394/4). Numerous openings for blood vessels are present along the entire symphysis (ZPAL AbIII/3365/2, ZPAL AbIII/3378, ZPAL AbIII/3394/4). The surface of the symphysis is rugose, but smooth like the rest of the ischiadic blade surface, not harsh as the surface of the ilioischiadic suture and the surface of the acetabulum. Along the entire surface of the symphysis, vertically oriented ridges are present (ZPAL AbIII/3365/2, ZPAL AbIII/3378, ZPAL AbIII/3394/4). They are larger and more prominent in the middle and anterior parts of the symphysis, and smaller and more irregularly arranged than in the posterior part (ZPAL AbIII/3365/2, ZPAL AbIII/3378, ZPAL AbIII/3394/4). The development of the anterior part of ischium symphysis might be unique for *Stagonolepis olenkae* as similar structure have not been recognized for other aetosaurs.

Hind limbs

Proportions of long bones

None of the available femora was found in articulation with the zeugopodial bones. However, the right femur ZPAL AbIII/3362, the left femur ZPAL AbIII/3363, and the left tibia ZPAL AbIII/3367 were found in close proximity to each other. Although the length difference between ZPAL AbIII/3362 (37 cm) and ZPAL AbIII/3363 (34 cm) seems too big to recognize them as belonging to the same individual, it is probable that tibia ZPAL AbIII/3367 belongs to one of them. The length proportion between the tibia ZPAL AbIII/3367 (21.5 cm) and femur ZPAL AbIII/3363 (34 cm) is 0.63, while between ZPAL AbIII/3367 and ZPAL AbIII/3362 (37 cm) it is 0.58.

Similar proportions, with tibia being around 0.6 length of the femur, is present in other probable associations: femur ZPAL AbIII/691 and tibia ZPAL AbIII/502/62; femur ZPAL AbIII/1177 and tibia ZPAL AbIII/1178. However, the specimens are damaged and the available field documentation is not clear in regard to their respective position at the moment of excavation. In comparison to other known aetosaur proportions of long bones in *Stagonolepis olenkae* seems to be the most similar to *Longosuchus meadei* (Sawin 1947; Long and Murry 1995).

The fibula is slightly longer than the tibia. In the articulated ZPAL AbIII/2508, the proportion of the tibia (23 cm) to the fibula (24 cm) is 0.96; and in the articulated ZPAL AbIII/3368 the proportion of the tibia (20.5 cm) to the fibula (21.5 cm) is 0.95.

Femur

The femur (Fig. 14) is preserved in 14 specimens. Among them 9 are preserved in their entirety: ZPAL AbIII/691, ZPAL AbIII/1942, ZPAL AbIII/2630, ZPAL AbIII/3304, ZPAL AbIII/3308, ZPAL AbIII/3309, ZPAL AbIII/3362, ZPAL AbIII/3363, ZPAL AbIII/3364, ZPAL AbIII/3365/1; and 5 are preserved partially ZPAL AbIII/115, ZPAL AbIII/239, ZPAL AbIII/1177, ZPAL AbIII/3303, ZPAL AbIII/3305.

ZPAL AbIII/3362 is the largest complete available femur and measures 37 cm in length, which is comparable to mid-sized aetosaurs like, for example, *Calyptosuchus wellesi* (34 cm: left femur UCMP 25918), *Longosuchus meadei* (33.9 cm: right femur TMM 31185-84a, 33.4

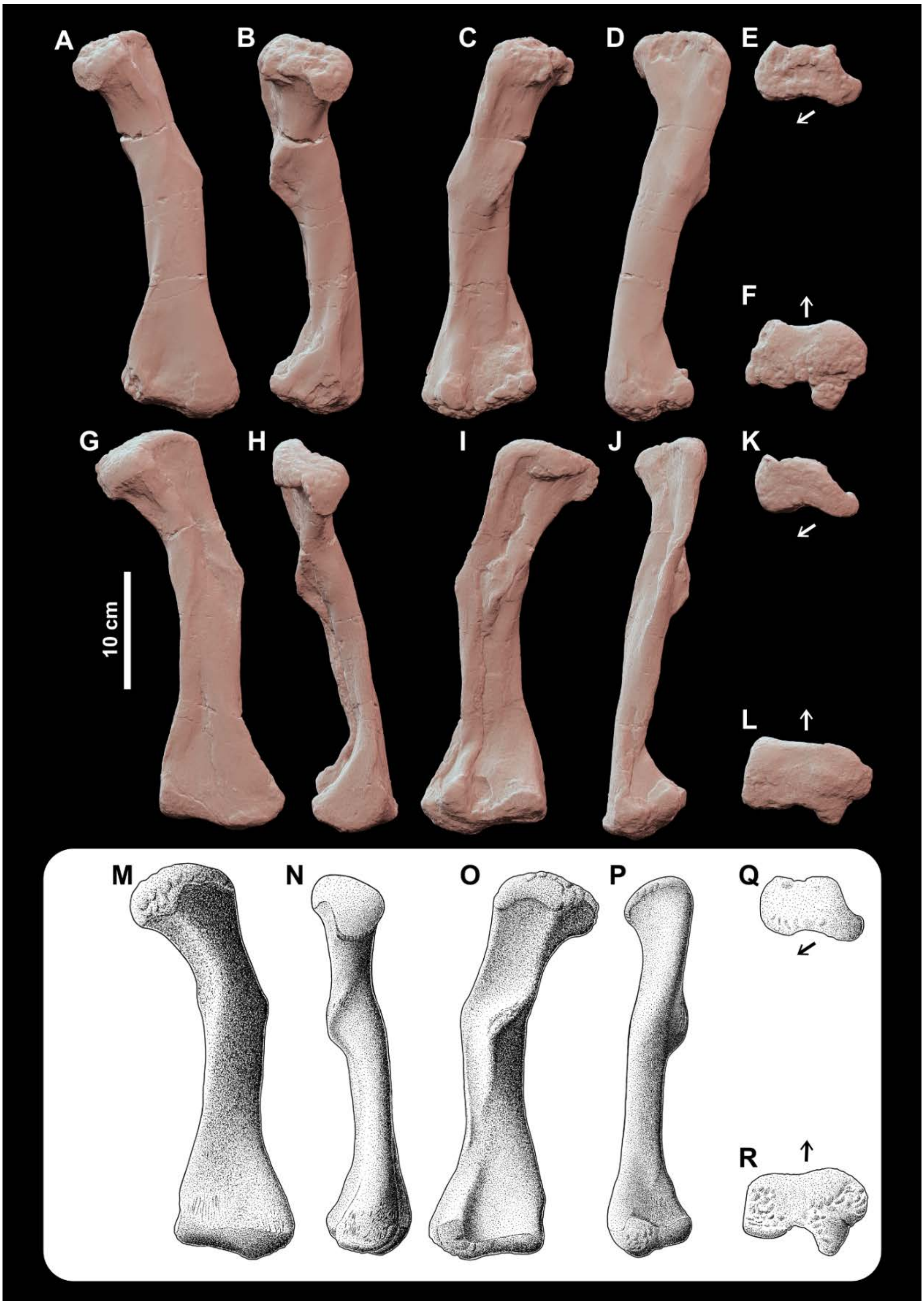


Figure 14. Left femur of *Stagonolepis olenkae*. ZPAL AbIII/3363 (A–F), ZPAL AbIII/1942 (G–L), and reconstruction (M–R), in anterior (A, G, M), medial (B, H, N), posterior (C, I, O), lateral (D, J, P), dorsal (E, K, Q), and ventral (F, L, R). The arrows indicate the cranial direction.

cm: left femur TMM 31185-84a, 32.8: left femur TMM 31185-84b) and *Stagonolepis robertsoni* (30 cm: left femur in the block E.M. 46) (Sawin 1947; Walker 1961; Long and Murry

1995; Parker 2018*a*). Slightly larger (42.2 cm) is the aetosaur femur UMMP 3396, which my belong to *Desmatosuchus spurensis* although described as dinosaur; Case 1922: fig. 32).

The femur of *Stagonolepis olenkae* is distinctly sigmoidal in the sagittal plane (ZPAL AbIII/115, ZPAL AbIII/3308, ZPAL AbIII/3362, ZPAL AbIII/3363) and bent medially in the frontal plane at an angle of approximately 55° (ZPAL AbIII/115, ZPAL AbIII/691, ZPAL AbIII/1177, ZPAL AbIII/1942, ZPAL AbIII/2630, ZPAL AbIII/3304, ZPAL AbIII/3309, ZPAL AbIII/3362, ZPAL AbIII/3363, ZPAL AbIII/3364, ZPAL AbIII/3365/1). The bending starts at about two thirds of the bone length at the level of the distal portion of the fourth trochanter.

Anterolaterally, on an elevation at which the bending starts, a prominent tuber is present (best-preserved in ZPAL AbIII/115, ZPAL AbIII/3362, and ZPAL AbIII/3363). The tuber extends laterally and breaks the lateral outline of the shaft in anterior/posterior view, giving an impression of the medial bending beginning abruptly (ZPAL AbIII/115, ZPAL AbIII/691, ZPAL AbIII/1177, ZPAL AbIII/1942, ZPAL AbIII/2630, ZPAL AbIII/3304, ZPAL AbIII/3309, ZPAL AbIII/3362, ZPAL AbIII/3363, ZPAL AbIII/3364, ZPAL AbIII/3365/1). From the tuber originates a distinct furrow ascending at an angle of about 45° (ZPAL AbIII/115, ZPAL AbIII/1947, ZPAL AbIII/2630, ZPAL AbIII/3309, ZPAL AbIII/3362, ZPAL AbIII/3363, ZPAL AbIII/3364, ZPAL AbIII/3365/1). A similar structure was described for *Typothorax coccinarum* (e.g., UCMP 34255 70/U80, TTUP 9214), and has been referred as homologous to the lesser trochanter of dinosaurs (Long and Murry 1995; Martz 2002).

The femoral head of *Stagonolepis olenkae* is oriented craniomedially and twisted at about 40° in relation to the condyles (ZPAL AbIII/115, ZPAL AbIII/3362, ZPAL AbIII/3363). It projects far medially in the frontal plane (ZPAL AbIII/691, ZPAL AbIII/1942, ZPAL AbIII/2630, ZPAL AbIII/3304, ZPAL AbIII/3308, ZPAL AbIII/3309, ZPAL AbIII/3362, ZPAL AbIII/3363, ZPAL AbIII/3364). Its shape is characteristic for aetosaurs, with distinct, well-developed anterolateral, anteromedial, and posteromedial tubers (ZPAL AbIII/239, ZPAL AbIII/1942, ZPAL AbIII/3362, ZPAL AbIII/3363; e.g. Casamiquela 1961; Bonaparte 1971; Small 1985; Long and Murry 1995; Martz 2002; Roberto-Da-Silva et al. 2014). The dorsal surface of the head is highly rugose (ZPAL AbIII/239, ZPAL AbIII/1942, ZPAL/AbIII/2630, ZPAL AbIII/3304, ZPAL AbIII/3309, ZPAL AbIII/3362, ZPAL AbIII/3363, ZPAL AbIII/3364, ZPAL AbIII/3365/1).

The rugosities are composed of multiple randomly arranged tubers of various size. A shallow, oblong depression (sulcus) originates from the area medial to the greater trochanter and continues medially, parallel to the anterolateral margin of the head (ZPAL AbIII/289, ZPAL AbIII/1942, ZPAL AbIII/2630, ZPAL AbIII/3304, ZPAL AbIII/3309, ZPAL AbIII/3362, ZPAL AbIII/3363, ZPAL AbIII/3364, ZPAL AbIII/3365/1). The depression seems to be less indicated in ZPAL AbIII/289 and ZPAL AbIII/1942.

In the region of the posteromedial tuber, the rugose area expands more distally than in the other parts of the head. It forms there a distinct, almost flat surface, oriented perpendicularly to the dorsal surface of the femoral head. In specimens ZPAL AbIII/3304, ZPAL AbIII/3362, and ZPAL AbIII/3365/1, there is a marked depression which surrounds this area medially, distally, and laterally, forming a short neck-like structure, which is most prominent posteriorly and distally. The structure is less indicated in ZPAL AbIII/1942 and ZPAL AbIII/3362, and not present in ZPAL AbIII/239. It seems to be also less developed in ZPAL AbIII/2630, ZPAL AbIII/3309, and ZPAL AbIII/3364, but it is not clear due to compaction.

Faint striations oriented subparallel to the long axis of the bone, are present distally to the rugose area on the posteromedial and anterolateral sides of the head (best preserved in ZPAL AbIII/3309, ZPAL AbIII/3363, and ZPAL AbIII/3364, less developed in ZPAL AbIII/239).

In ZPAL AbIII/3363, distally to the anterolateral tuber, there is a pronounced, crescent shape furrow with a sharp edge, that forma a laminar structure in anterolateral view. The structure is noticeable also in ZPAL AbIII/239, ZPAL AbIII/1942, ZPAL AbIII/2630, ZPAL AbIII/3364, and ZPAL AbIII/3365/1, but in ZPAL AbIII/3304 and ZPAL AbIII/3363 the rugose area is present in that position.

The laterodistal portion of the femoral head smoothly changes into the greater trochanter, which is roughly half as thick as the femoral head (ZPAL AbIII/239, ZPAL AbIII/3308, ZPAL AbIII/3362, ZPAL AbIII/3363). The dorsal surface of the greater trochanter is smooth, in contrast to the rugose main body of the head (ZPAL AbIII/289, ZPAL AbIII/1942, ZPAL AbIII/2630, ZPAL AbIII/3304, ZPAL AbIII/3309, ZPAL AbIII/3362, ZPAL AbIII/3363, ZPAL AbIII/3364, ZPAL AbIII/3365/1). The trochanteric flange continues distally till the level of the fourth trochanter. Its lateral edge forms a smooth-ended, distally pointing crest (ZPAL AbIII/289, ZPAL AbIII/691, ZPAL AbIII/1942, ZPAL AbIII/2630, ZPAL AbIII/3304, ZPAL AbIII/3308, ZPAL AbIII/3309, ZPAL AbIII/3362, ZPAL AbIII/3363, ZPAL AbIII/3364, ZPAL AbIII/3365/1). In specimens ZPAL AbIII/3362 and ZPAL AbIII/3363, on the laterodistal side of the trochanteric flange and proximally to the fourth trochanter there is a clear rugose area which seems to be a muscle or tendon attachment. Though this structure is not present in ZPAL AbIII/3309 and in the remaining specimens the area is not preserved.

The fourth trochanter is developed similarly as in other aetosaurs, being enlarged and positioned far distally in comparison with other Pseudosuchia (Casamiquela 1961; Walker 1961; Bonaparte 1971; Small 1985; Parrish 1986; Long and Murry 1995; Lucas et al. 2002; Martz 2002; Desojo and Báez 2005; Schoch 2007; Desojo et al. 2013; Roberto-Da-Silva et al. 2014). Anteroposteriorly, it is as thick as the shaft. It is a little shorter that one fourth of the length of the entire femur. It originates slightly proximally to the distal end of the greater trochanter flange and fades distally near the origin point of the medial bending, but its peak is at about two thirds of the femur length (ZPAL AbIII/115, ZPAL AbIII/691, ZPAL AbIII/1177, ZPAL AbIII/1942, ZPAL AbIII/2630, ZPAL AbIII/3003, ZPAL AbIII/3304, ZPAL AbIII/3308, ZPAL AbIII/3309, ZPAL AbIII/3362, ZPAL AbIII/3363, ZPAL AbIII/3364, ZPAL AbIII/3365/1). A prominent furrow of somewhat sigmoidal shape goes through the middle of the fourth trochanter and divides its surface into medial and lateral facets, the medial facet concave and the lateral one convex (ZPAL AbIII/115, ZPAL AbIII/691, ZPAL AbIII/1177, ZPAL AbIII/1942, ZPAL AbIII/2630, ZPAL AbIII/3003, ZPAL AbIII/3304, ZPAL AbIII/3308, ZPAL AbIII/3309, ZPAL AbIII/3362, ZPAL AbIII/3363, ZPAL AbIII/3364, ZPAL AbIII/3365/1). Both the ridge of the furrow and the trochanteric facets are delicately rugose, with multiple small sulci, especially on the proximal portion of the lateral surface (insertion of the muscle coccygeo-femoralis brevis; Romer 1923; Rowe 1986; Martz 2002) and proximal and middle portion of the medial surface (insertion of the muscle caudofemoralis longus; Romer 1923; Rowe 1986; Martz 2002) (ZPAL AbIII/115, ZPAL AbIII/691, ZPAL AbIII/1177, ZPAL AbIII/1942, ZPAL AbIII/2630, ZPAL AbIII/3003, ZPAL AbIII/3304, ZPAL AbIII/3309, ZPAL AbIII/3362, ZPAL AbIII/3363, ZPAL AbIII/3364, ZPAL AbIII/3365/1).

Mid-shaft distal to the fourth trochanter is straight in the coronal plane and of almost equal width lateromedially (ZPAL AbIII/115, ZPAL AbIII/691, ZPAL AbIII/1177, ZPAL AbIII/1942, ZPAL AbIII/2630, ZPAL AbIII/3308, ZPAL AbIII/3309, ZPAL AbIII/3362, ZPAL AbIII/3363, ZPAL AbIII/3364). Based on relatively undeformed ZPAL AbIII/115, ZPAL AbIII/3362, and ZPAL AbIII/3363, it seems that the shaft is slightly thinner anteroposteriorly than lateromedially, however, the difference is much less severe than one could expect based on other, compacted specimens (ZPAL AbIII/691, ZPAL AbIII/1177, ZPAL AbIII/2630, ZPAL AbIII/3304, ZPAL AbIII/3308, ZPAL AbIII/3309, ZPAL AbIII/3364). The posterior side is slightly concave (nearly flat) and the anterior side is slightly convex (ZPAL AbIII/115, ZPAL AbIII/3362, ZPAL AbIII/3363).

The mid-shaft cross-section, distally to the fourth trochanter is subcircular with distinct flat surface posteriorly, which seems more rectangular in compacted specimens. This shape is characteristic for aetosaurs among other pseudosuchians (e.g. Walker 1961; Bonaparte 1971; Parrish 1986; Long and Murry 1995; Martz 2002; Roberto-Da-Silva et al. 2014). This outline is indicated by the presence of the four distinct longitudinal elevations that form more or less clear corners anteromedially, anterolaterally, posteromedially, and posterolaterally (ZPAL AbIII/115, ZPAL AbIII/691, ZPAL AbIII/1177, ZPAL AbIII/1942, ZPAL AbIII/2630, ZPAL AbIII/3308, ZPAL AbIII/3309, ZPAL AbIII/3362, ZPAL AbIII/3363, ZPAL AbIII/3364). The level of development of those structures varies between studied specimens. The most prominent posterolateral elevation is very clear in all studied specimens with preserved mid-shaft (ZPAL AbIII/115, ZPAL AbIII/691, ZPAL AbIII/1177, ZPAL AbIII/1942, ZPAL AbIII/2630, ZPAL AbIII/3303, ZPAL AbIII/3304, ZPAL AbIII/3308, ZPAL AbIII/3309, ZPAL AbIII/3362, ZPAL AbIII/3363, ZPAL AbIII/3364, ZPAL AbIII/3365/1). It has a characteristic shape recognized as “pinching” or ridge by Martz (2002) and probably can be referred as the “primary adductor scar”, which separates the longitudinal insertions of the muscle femoro-tibialis externus and the branches of the muscle adductor femoralis (Romer 1923; Martz 2002). It originates distally to the fourth trochanter and continues straight along the mid-shaft and on the elevation of the tibiofibular crest turns anteriorly (ZPAL AbIII/115, ZPAL AbIII/691, ZPAL AbIII/1177, ZPAL AbIII/3362, ZPAL AbIII/3303, ZPAL AbIII/3309, ZPAL AbIII/3363, ZPAL AbIII/3364, ZPAL AbIII/3365/1). The second most prominent is the anteromedial elevation, which continues along almost the entire length of the shaft and forms a distinct scar in its proximal and middle part. Proximally, the elevation originates distally to the lamina-like structure (or rugose area) positioned near the anterolateral tuber of the femoral head, then continues straight distally along the mid-shaft, and turns medially in the distal portion of the shaft following the curvature of the medial condyle (ZPAL AbIII/115, ZPAL AbIII/691, ZPAL AbIII/1942, ZPAL AbIII/3304, ZPAL AbIII/3305, ZPAL AbIII/3308, ZPAL AbIII/3362, ZPAL AbIII/3363, ZPAL AbIII/3364). Both the posteromedial and anterolateral elevation are much less indicated than the previous two. In most specimens they do not form clear scars, except in the largest ZPAL AbIII/1942 (only the anterolateral one) and ZPAL AbIII/3362. They are also well recognizable in the uncompacted ZPAL AbIII/115 and ZPAL AbIII/3363. The anterolateral elevation originates distally to the “lesser trochanter” structure, slightly bends medially and in the distal portion it fades out before reaching the lateral condyle (ZPAL AbIII/115, ZPAL AbIII/1942, ZPAL AbIII/3362, ZPAL AbIII/3363). The posteromedial elevation forms a smooth edge that originates on the elevation of the proximal tip of the fourth trochanter and continues till the proximal portion of the medial condyle (ZPAL AbIII/115, ZPAL AbIII/3362, ZPAL AbIII/3363).

The distal end of the femur is strongly expanded transversally in a manner typical for other aetosaurs (Sawin 1947; Casamiquela 1961; Walker 1961; Bonaparte 1971; Small 1985; Long and Murry 1995; Martz 2002; Desojo and Báez 2005; Schoch 2007; Roberto-Da-Silva et al. 2014; Parker 2018*a*). The shape and surface features of the distal end are best-preserved in ZPAL AbIII/3305. The lateral condyle is bulbous in shape and enlarged in proportion to medial condyle, being about three fourth of the distal end’s transverse width (e.g., ZPAL AbIII/115, ZPAL AbIII/3305, ZPAL AbIII/3362, ZPAL AbIII/3363). Anteriorly, there is a shallow depression that divides the condyles (ZPAL AbIII/3305, ZPAL AbIII/3363). Posteriorly, both the tibiofibular crest and the posterior projection of the medial condyle are well-developed. They are of almost equal length anteroposteriorly and reach about half of the anteroposterior thickness of the shaft (ZPAL AbIII/115, ZPAL AbIII/3362, ZPAL AbIII/3363). Popliteal fossa between them is deep and well indicated (e.g., ZPAL AbIII/115, ZPAL AbIII/3305, ZPAL AbIII/3362, ZPAL AbIII/3363, ZPAL AbIII/3364, ZPAL AbIII/3365/1). A pronounced tuber is present on the medial surface of the medial condyle (ZPAL AbIII/115, ZPAL AbIII/3304, ZPAL AbIII/3305, ZPAL AbIII/3362, ZPAL AbIII/3363 ZPAL AbIII/3364). Faint striations are present around the condyles proximally to the rugose area, most of them accumulated anteriorly (ZPAL AbIII/1942, ZPAL AbIII/2630, ZPAL AbIII/3304, ZPAL AbIII/3305, ZPAL AbIII/3363, ZPAL AbIII/3364). There is a clear border between the main body of the shaft and the rugose articular surface, which most likely indicates the extent of the cartilaginous cap (e.g., ZPAL AbIII/1942, ZPAL AbIII/3305, ZPAL AbIII/3309, ZPAL AbIII/3364). Anteriorly, the articulation surface reaches higher proximally than posteriorly and is smooth (ZPAL AbIII/3303, ZPAL AbIII/3305, ZPAL AbIII/3309, ZPAL AbIII/3364). Except for the anterior part, the articulation surface is covered by numerous randomly arranged tubers, similar to those on the dorsal surface of the femoral head (ZPAL AbIII/2630, ZPAL AbIII/3305, ZPAL AbIII/3364, ZPAL AbIII/3365/1). Ventrally, there is a clear sulcus between the bulbous lateral condyle and the area corresponding to the tibiofibular crest (ZPAL AbIII/115, ZPAL AbIII/240, ZPAL AbIII/1942, ZPAL AbIII/2630, ZPAL AbIII/3303, ZPAL AbIII/3304, ZPAL AbIII/3305, ZPAL AbIII/3309, ZPAL AbIII/3362, ZPAL AbIII/3363, ZPAL AbIII/3364, ZPAL AbIII/3365/1). In specimens ZPAL AbIII/3303 and ZPAL AbIII/3309 the sulcus continues medially beyond the tibiofibular crest, forming a transverse depression along almost the entire mediolateral width of the distal end.

Tibia

The tibia (Fig. 15) is preserved in 15 specimens; 10 preserved in their entirety, including two in articulation with other limb elements (ZPAL AbIII/2508, ZPAL AbIII/3368) and eight isolated ones (ZPAL AbIII/502/62, ZPAL AbIII/1626, ZPAL AbIII/1178, ZPAL AbIII/2568, ZPAL AbIII/2570/2, ZPAL AbIII/2641, ZPAL AbIII/3350, ZPAL AbIII/3367); and five isolated and preserved partially (ZPAL AbIII/246 and ZPAL AbIII/249 – probably parts of the same bone, ZPAL AbIII/251, ZPAL AbIII/3366, ZPAL AbIII/3396). The best-preserved specimen is ZPAL AbIII/3367, being relatively undamaged and undeformed.

The tibia is straight with transversely expanded proximal and distal portions and slender mid-shaft (e.g., ZPAL AbIII/1178, ZPAL AbIII/2568, ZPAL AbIII/2570/2, ZPAL AbIII/3350, ZPAL AbIII/3367). It is thicker and slightly shorter than the fibula (ZPAL AbIII/2508, ZPAL AbIII/3368). In life position it was rotated in a way that the transversely widest surfaces were facing anteromedially and posterolaterally (ZPAL AbIII/2508, ZPAL AbIII/3368), so in the proximal/distal view the longest axis of the bone was oriented in anterolateral to posteromedial direction diagonally to traditional planes used in anatomical descriptions. It will be called “the longest diagonal axis” in the following description.

The transverse expansion of the proximal part of the shaft is very prominent (about 2.5 times of the mid-shaft width in the narrowest part and about 1.5 times of the distal portion (ZPAL AbIII/1178, ZPAL AbIII/2568, ZPAL AbIII/2570/2, ZPAL AbIII/3350, ZPAL AbIII/3367), which is characteristic for aetosaurs, compared other pseudosuchians (Parrish 1986). In the proximal part, the shaft gradually narrows down in “the longest diagonal axis”, till about one third of the bone’s entire length (ZPAL AbIII/1178, ZPAL AbIII/2568, ZPAL AbIII/2570/2, ZPAL AbIII/3350, ZPAL AbIII/3367). The narrowing is asymmetrical, with the posteromedial side being slightly more expanded than the anterolateral one. At the same time, the shaft decreases in width in the axis perpendicular “the longest diagonal axis”, but the ratio is less significant than in the case of “the longest diagonal axis” (about 2 times in ZPAL AbIII/249 and ZPAL AbIII/3367).

The outline of the proximal end is semicircular in proximal view, forming an almost straight line posterolaterally and being prominently convex anteromedially (ZPAL AbIII/249, ZPAL AbIII/3367). This semicircular shape continues in the cross-section along almost the entire length of the tibia (ZPAL AbIII/246, ZPAL AbIII/249, ZPAL AbIII/3366, ZPAL AbIII/3367).

The articulation surface appears to be more or less flat, with two shallow depressions (fossae), divided by a faint ridge in the middle of the articulation plane (best-preserved in ZPAL AbIII/249 and ZPAL AbIII/3367, but well discernible also in ZPAL AbIII/1178, ZPAL AbIII/2568, ZPAL AbIII/2570/2, and ZPAL AbIII/3350). According to Martz (2002) and Parrish (1986), these fossae housed menisci that met the femoral condyles and reinforced the knee. The fossae are of almost even size, the medial one being slightly larger than the lateral one (ZPAL AbIII/249, ZPAL AbIII/1178, ZPAL AbIII/2568, ZPAL AbIII/2570/2, ZPAL AbIII/3350). In the posterior part, the lateral fossa slopes posteriorly more steeply than the medial fossa and forms a distinct notch, crescent-shaped in posterior view – the articulation surface for the fibula (ZPAL AbIII/249, ZPAL AbIII/251, ZPAL AbIII/1178, ZPAL AbIII/1626, ZPAL AbIII/2507/2, ZPAL AbIII/2508, ZPAL AbIII/2641, ZPAL AbIII/3350, ZPAL AbIII/3367, ZPAL AbIII/3368). Anterolaterally, the articulation surface abruptly slopes distally, forming a triangular rugose surface, transversally of a size comparable to the lateral fossa (ZPAL AbIII/249, ZPAL AbIII/1626, ZPAL AbIII/2568, ZPAL AbIII/2570/2, ZPAL AbIII/2641, ZPAL AbIII/3350, ZPAL AbIII/3367). On that surface, laterodistally, a faint tuber is present (ZPAL AbIII/249, ZPAL AbIII/1178, ZPAL AbIII/2568, ZPAL AbIII/3367).

The articulation surface is rugose in the manner similar to articulation surfaces of the femur, with numerous randomly arranged tubers (e.g., ZPAL AbIII/249, ZPAL AbIII/1626, ZPAL AbIII/2507/2, ZPAL AbIII/3350). The development of tubers show some gradation among studied specimens: in ZPAL AbIII/2568 and ZPAL AbIII/2570/2, they are feeble and seem to be present only at the edges of the medial fossa (other surfaces are smooth); in ZPAL AbIII/3350 the tubers are more clear than in ZPAL AbIII/2568 and ZPAL AbIII/2570/2, they are present on both medial and lateral fosse, and (less pronounced) at the fibular articulation surface and anterolateral surface; in ZPAL AbIII/1626 the tubers are smaller and more clear

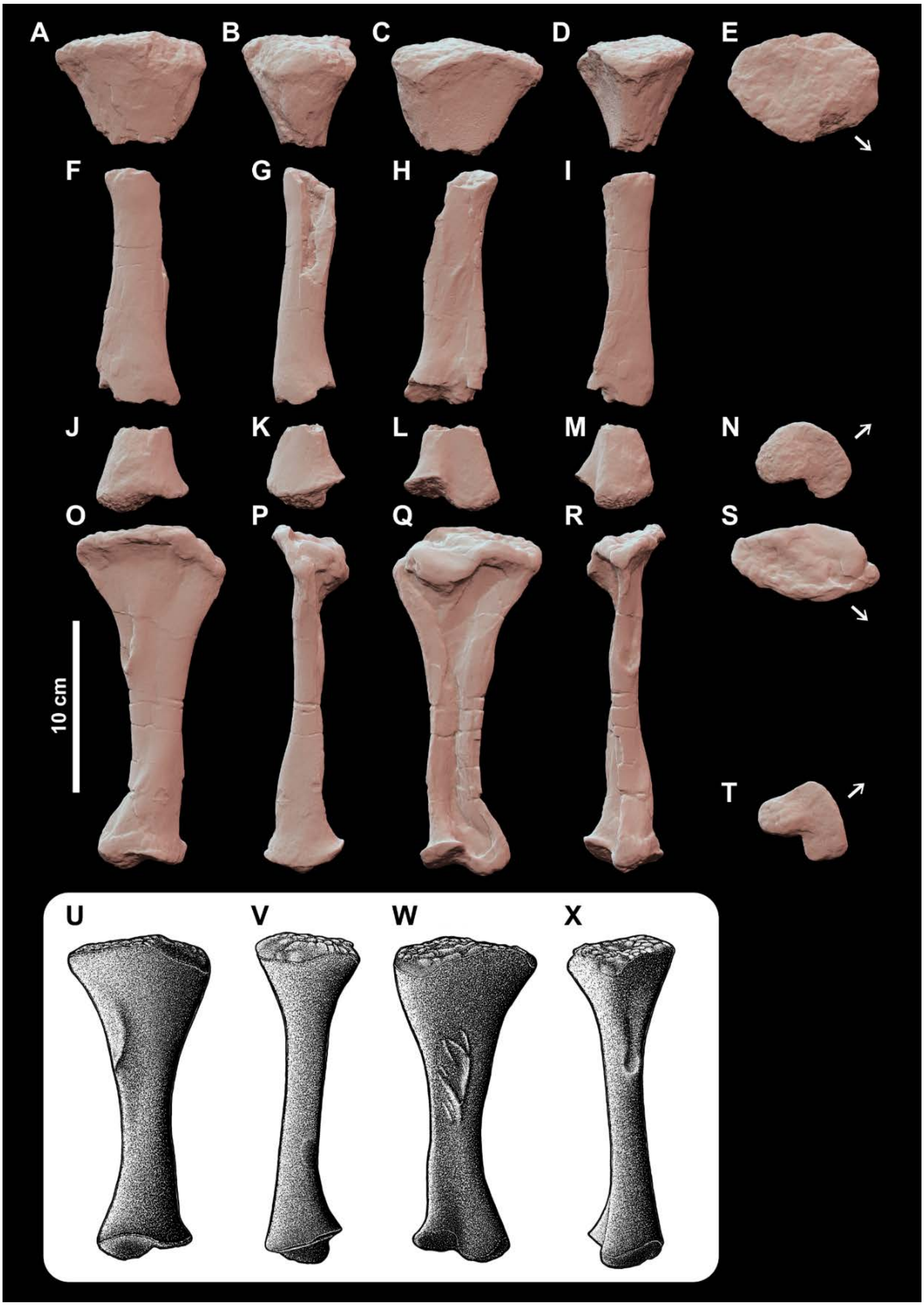


Figure 15. Left tibia of *Stagonolepis olenkae*. ZPAL AbIII/249 (A–E), ZPAL AbIII/3366 (F–I), ZPAL AbIII/246 (J–N), ZPAL AbIII/2570/2 (O–T), and composite reconstruction (U–X), in anterior (A, F, J, O, U), lateral (B, G, K, P, V), posterior (C, H, L, Q, W), medial (D, I, M, R, X), dorsal (E, S), and ventral view (N, T). The arrows indicate the cranial direction.

than at the previously mentioned specimens and covers almost entire articulation surface with almost equal intensity.

Medially to the crescent-shaped projection, at the posterolateral surface, close to the border with the articular surface starts a depression, that gently slopes down distally and forms a flat surface which continues till the articulation surface for the astragalus (ZPAL AbIII/249, ZPAL AbIII/3367). Proximally, at the anteromedial side, there is a well-defined rugose area spanning from the middle of the anterior surface, continuing laterally, and fading anterolaterally around the crescent-shaped expansion of the lateral fossa (best-preserved in ZPAL AbIII/3367, well-visible also in ZPAL AbIII/502/62, ZPAL AbIII/1178, ZPAL AbIII/2508, ZPAL AbIII/2570/2, and ZPAL AbIII/3396).

Anterolateral and anteromedial sides of the proximal shaft of tibia are asymmetrically developed. Anterolaterally, the transition between the anterolateral and posteromedial surfaces is round and smooth (ZPAL AbIII/249, ZPAL AbIII/3367), while posteromedially the shaft is pinched and forms a prominent ridge (ZPAL AbIII/249, ZPAL AbIII/502/62, ZPAL AbIII/2568, ZPAL AbIII/2570/2, ZPAL AbIII/3350, ZPAL AbIII/3367). The ridge at the posteromedial side continues distally, and at about one third of the tibia's length forms a shelf-like structure, laterally restricted by a vertically oriented furrow and distally ended by oval fossa. The structure faces medioposteriorly and is not visible in anterior view (ZPAL AbIII/2508, ZPAL AbIII/3368). It is very clear in all studied specimens. Comparing its morphology and position to the dinosauriform *Silesaurus opolensis* and crocodiles, it seems that it is an attachment for the muscle gastrocnemius internus (Allen et al. 2014; Klinkhamer et al. 2017; Piechowski and Tałanda 2020).

In the middle part, the shaft continue to narrow down distally in diagonal axis, from about one third till about three fourth of the tibia's length, but the narrowing is less significant than in the proximal part of the shaft and more distally it becomes almost straight (ratio between the proximal and distal portions of the mid-shaft is about 1.33, compared to about 1.9 of the same ratio in the proximal part of the shaft; e.g., ZPAL AbIII/1178, ZPAL AbIII/2568, ZPAL AbIII/2570/2, ZPAL AbIII/3350, ZPAL AbIII/3367). The thickness of the mid-shaft perpendicularly to the widest surfaces remains almost the same throughout its entire length. Anteriorly, there is a marked elevation that originates in the middle of the shaft's length, continues straight distally along the mid-shaft, turns medially in the distal portion of the shaft, and continues till the articulation surface for the astragalus (ZPAL AbIII/1178, ZPAL AbIII/2568, ZPAL AbIII/2570/2, ZPAL AbIII/3350, ZPAL AbIII/3367). At the end of this elevation, a rugose area is present. It covers the medial and anteromedial surfaces of the distal part of the shaft (ZPAL AbIII/246, ZPAL AbIII/502/62, ZPAL AbIII/1178, ZPAL AbIII/2568, ZPAL AbIII/2570/2, ZPAL AbIII/2641, ZPAL AbIII/3350, ZPAL AbIII/3367). It is developed similarly as the rugose area distal to the lateral fossa in the proximal part of the shaft. The posterolateral surface ends anteriorly with a sharp ridge which originates around the middle of the tibia’s length, at the same level as the elevation on the anteromedial side (ZPAL AbIII/502/62, ZPAL AbIII/1178, ZPAL AbIII/3350 ZPAL AbIII/3366, ZPAL AbIII/3367). The ridge ends abruptly in the distal portion of the shaft, around the origin point of the posterolateral projection crest (ZPAL AbIII/502/62, ZPAL AbIII/1178, ZPAL AbIII/3350 ZPAL AbIII/3366, ZPAL AbIII/3367). At its end there is also a small rugose area (about 2 cm^2) similar to that on the anterior and anteromedial surfaces in the distal portion of the shaft (ZPAL AbIII/502/62, ZPAL AbIII/2568, ZPAL AbIII/2570/2, ZPAL AbIII/3350, ZPAL AbIII/3366, ZPAL AbIII/3367). A prominent V-shaped muscle scar is present on the mid-shaft on the posterior surface of ZPAL AbIII/502/62, ZPAL AbIII/1178, ZPAL AbIII/3366, and ZPAL AbIII/3367. The structure is the clearest in ZPAL AbIII/3366. It seems to be less developed in ZPAL 502/62, ZPAL AbIII/1178, and ZPAL AbIII/3367. In ZPAL AbIII/1626 a faint elevation of similar shape is present in the same area.

Distally the shaft expands in both “the longest diagonal axis” (anterolateral/posteromedial axis) and in the axis perpendicular to “the longest diagonal axis”, at about three fourth of the tibia’s length. The distal part of the shaft is less expanded than the proximal part in “the widest diagonal axis” (about two third thickness of the proximal part), and is also asymmetrically developed with a little more pronounced posterior side (ZPAL AbIII/246, ZPAL AbIII/1178, ZPAL AbIII/502/62, ZPAL AbIII/2568, ZPAL AbIII/2570/2, ZPAL AbIII/3350, ZPAL AbIII/3367). Expansion of the shaft in the axis perpendicular to “the diagonal axis” is about the same thickness as in the proximal part of the shaft (ZPAL AbIII/3367).

The articulation surface for astragalus form a curving facet spiraling posterolaterally (best preserved in ZPAL AbIII/246, ZPAL AbIII/3367). The facet originates from a prominent tuberosity at the posteromedial part of articulation surface and ascends posterolaterally, forming a distinct projection oriented in the same direction (ZPAL AbIII/246, ZPAL AbIII/2568, ZPAL AbIII/2570/2, ZPAL AbIII/3350, ZPAL AbIII/3367). In life position the surface fits perfectly with a contemporary saddle-shaped facet at the astragalus, forming a tightly articulated tibio-astragalar column (Parrish 1986). It is rugose at the same manner as the proximal articulation surface, with multiple randomly arranged and shaped tubers. Those rugosities are restricted mostly to the area of the posteromedial tuberosity, while the curving surface at the posterolateral side remain smooth (e.g. ZPAL AbIII/2568, ZPAL AbIII/2570/2, ZPAL AbIII/3350). It seems

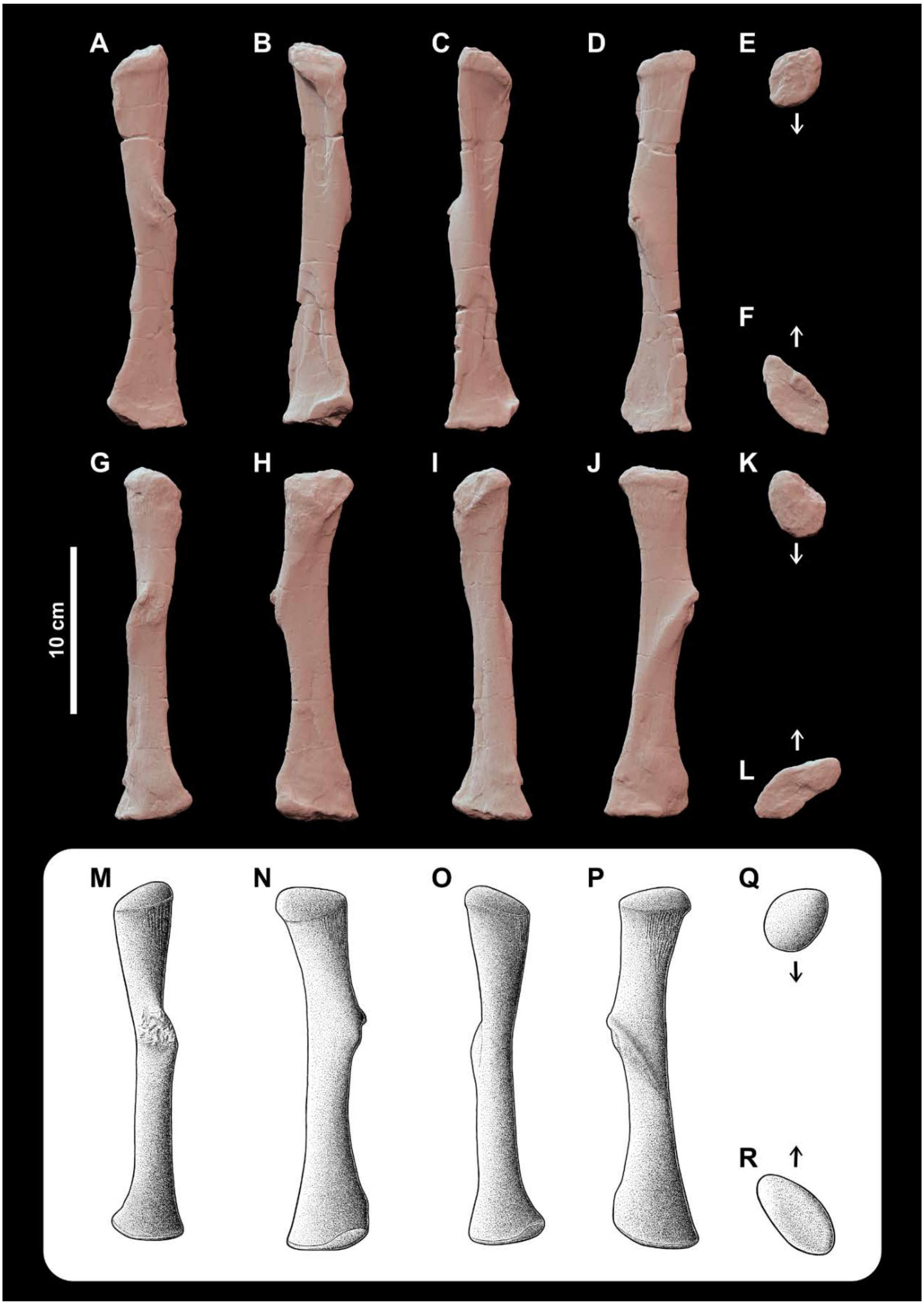


Figure 16. Fibula of *Stagonolepis olenkae*. ZPAL AbIII/3382 (left, A–F), ZPAL AbIII/502/40 (right, G–L), and reconstruction (left, M–R) in anterior (A, G, M), medial (B, H, N), posterior (C, I, O), lateral (D, J, P), dorsal (E, K, Q), and ventral (F, L, R). The arrows indicate the cranial direction.

that the frequency and morphology of tubers change between specimens, in the same manner as with proximal surface; from only large and small indicated tubers in ZPAL AbIII/2568 and

ZPAL AbIII/2570/2; medium indicated and more frequent tubers in ZPAL AbIII/3350; multiple small and very clear tubers in ZPAL AbIII/1626).

Fibula

The fibula (Fig.16) is preserved in 11 specimens: eight are preserved in their entirety, including two in articulation with other hind limbs elements (ZPAL AbIII/2508, ZPAL AbIII/3368) and seven isolated (ZPAL AbIII/502/40, ZPAL AbIII/1624, ZPAL AbIII/1625, ZPAL AbIII/2629, ZPAL AbIII/3382, ZPAL AbIII/3387, ZPAL AbIII/3388), and three preserved partially (ZPAL AbIII/242, ZPAL AbIII/3397, ZPAL AbIII/3456). Overall, the best-preserved are ZPAL AbIII/502/20 and ZPAL AbIII/2629, and ZPAL AbIII/3382, which are relatively less compacted than the remaining specimens.

The fibula is straight with anteroposteriorly expanded proximal and distal ends and hypertrophied and positioned far distally iliofibularis trochanter, which is characteristic for aetosaurs (e.g. Long and Murry 1995; Desojo et al. 2013). It is slightly longer than the tibia and much less robust (ZPAL AbIII/2508, ZPAL AbIII/3368). The shaft is wider anteroposteriorly than transversally (ZPAL AbIII/2629). Except for the area of the iliofibularis trochanter, it forms two major flattened surfaces parallel to the longest axis (ZPAL AbIII/502/40, ZPAL AbIII/1624, ZPAL AbIII/1625, ZPAL AbIII/2629, ZPAL AbIII/3382, ZPAL AbIII/3387). In the anatomical position, the fibula was rotated in a manner similar to the tibia, so the surfaces faced anterolaterally and posteromedially, so the longest axis in proximal/distal view is oriented in anteromedial to posterolateral direction, diagonally to traditional planes used in anatomy, and perpendicularly to “the longest diagonal axis” of tibia (ZPAL AbIII/2508, ZPAL AbIII/3368). The Iliofibularis trochanter faced anteriorly (ZPAL AbIII/2508, ZPAL AbIII/3368).

The proximal end is noticeably shorter anteroposteriorly than the distal end, but this difference is minor (slightly less than one fourth of the distal part length; ZPAL AbIII/502/40, ZPAL AbIII/1624, ZPAL AbIII/1625, ZPAL AbIII/2629, ZPAL AbIII/3382, ZPAL AbIII/3387, ZPAL AbIII/3388). It projects slightly posteriorly in side view (e.g., ZPAL AbIII/2629, ZPAL AbIII/3382, ZPAL AbIII/3388). In proximal view, the outline of the articulation surface appears to be oval, symmetrical along its longest axis (ZPAL AbIII/502/40, ZPAL AbIII/3382, ZPAL AbIII/3388). It forms two distinct surfaces divided along the sagittal plane: medial for articulation with the tibia and lateral for articulation with the femur (ZPAL AbIII/242, ZPAL AbIII/502/40, ZPAL AbIII/1624, ZPAL AbIII/1625, ZPAL AbIII/2629, ZPAL AbIII/3382, ZPAL AbIII/3387, ZPAL AbIII/3388). The lateral surface is larger than the medial one (e.g., ZPAL AbIII/502/40, ZPAL AbIII/2629, ZPAL AbIII/3382). In larger specimens it descends anteriorly, because the posterior end is at a higher (more proximal) elevation than the anterior one (ZPAL AbIII/242, ZPAL AbIII/502/40, ZPAL AbIII/2508, ZPAL AbIII/2629, ZPAL AbIII/3382, ZPAL AbIII/3387, ZPAL AbIII/3388), while in smaller specimens the surface is oriented more horizontally (ZPAL AbIII/1624, ZPAL AbIII/1625, ZPAL AbIII/3456). The articulation surface for the tibia forms a flat, roughly triangular surface that descends medially at a roughly 45° angle (e.g., ZPAL AbIII/502/40, ZPAL AbIII/ 1624, ZPAL AbIII/1625, ZPAL AbIII/3382, ZPAL AbIII/3388, ZPAL AbIII/3456).

The entire proximal articulation surface is rugose in a manner similar as in other long bones of *S. olenkae*. The rugosities are composed of numerous randomly arranged tubers (e.g., ZPAL AbIII/1625, ZPAL AbIII/1624, ZPAL AbIII/3382). The tubers are more frequent in the posteriormost portion of the articulation areas. As in other long bones, there is a gradation in the degree of those structures' development: in ZPAL AbIII/242, ZPAL AbIII/2629, ZPAL AbIII/3382, and ZPAL AbIII/3387, ZPAL AbIII/3388, a few faint tubers are present only in the distalmost portion of the lateral surface, while its anterior part and the medial surface are smooth; in ZPAL AbIII/3456, apart from a few clear tubers on the posterior lateral surface, feeble tuberosities are present in the middle part of the lateral surface; and in ZPAL AbIII/1624 and ZPAL AbIII/1625 small tubers cover the entire articulation surface.

Proximally, posteromedially, the shaft forms a concave surface, ascending distally till about one eight of the shaft length (ZPAL AbIII/502/40, ZPAL AbIII/2629, ZPAL AbIII/3382). The surface is restricted posteriorly by a marked elevation that abruptly originates distally to the articulation surface, continues straight along the mid-shaft, where it strengthens up forming a ridge, and fades at the level of the distal part of the iliofibularis trochanter (ZPAL AbIII/242, ZPAL AbIII/1624, ZPAL AbIII/1625, ZPAL AbIII/2629, ZPAL AbIII/3382). Anteriorly to the concave surface, there is a triangular rugose area that reaches distally about as far as the ascending part of the facet (ZPAL AbIII/502/14, ZPAL AbIII/ 1624, ZPAL AbIII/1625, ZPAL AbIII/2629, ZPAL AbIII/3382, ZPAL AbIII/3387, ZPAL AbIII/3388, ZPAL AbIII/3456). The area has a similar texture as the articulation facets, however, the rugosities are formed of irregular, vertically orientated striations rather than tubers (ZPAL AbIII/1624, ZPAL AbIII/1625, ZPAL AbIII/3382, ZPAL AbIII/3388, ZPAL AbIII/3456). Around the distal end of this rugose area, originates another ridge that continues till the iliofibularis trochanter forming the anterior edge of the proximal part of the shaft (e.g., ZPAL AbIII/1625, ZPAL AbIII/3382, ZPAL

AbIII/3388). Anteroposteriorly, the shaft is slightly convex in the proximal portion (ZPAL AbIII/502/40, ZPAL AbIII/2629, ZPAL AbIII/3382). Ornamentation is visible in the middle and posterior parts of the anteroposterior surface. In specimens ZPAL AbIII/242, ZPAL AbIII/1624, ZPAL AbIII/1625, ZPAL AbIII/3382, ZPAL AbIII/3388 and ZPAL AbIII/3456, the ornamentation is composed of faint vertically oriented ridges, while in ZPAL AbIII/2629 and ZPAL AbIII/3387 it is more clear and composed of small tuberosities.

An enlarged iliofibularis trochanter projects anteriorly and anterolaterally. It reaches about 1/3 of the fibula’s length, and in the most expanded point nearly doubles the horizontal thickness of the shaft (ZPAL AbIII/502/40, ZPAL AbIII/2629, ZPAL AbIII/3382, ZPAL AbIII/3388). The shaft around the iliofibularis trochanter is triangular in cross section (e.g., ZPAL AbIII/502/40, ZPAL AbIII/2629, ZPAL AbIII/3382, ZPAL AbIII/3388). The trochanter forms a clear edge which divides the anterolateral surface of the fibula into two more or less even facets, oriented anteriorly and posteriorly (e.g., ZPAL AbIII/502/40, ZPAL AbIII/1624, ZPAL AbIII/3382). There is an oval rugose surface in the anteriormost part the trochanter (e.g., ZPAL AbIII/242, ZPAL AbIII/502/40, ZPAL AbIII/1624, ZPAL AbIII/3382, ZPAL AbIII/3387, ZPAL AbIII/3388).

The anterior rugose surface faced cranially in life position (ZPAL AbIII/2508, ZPAL AbIII/3368). In anterior view, it is oriented diagonally form proximomedial to distolateral direction following curvature of the trochanter’s edge (e.g., ZPAL AbIII/242, ZPAL AbIII/502/40, ZPAL AbIII/1624, ZPAL AbIII/3382). Its distal end is around the middle of the fibula’s length (ZPAL AbIII/502/40, ZPAL AbIII/1624, ZPAL AbIII/1625, ZPAL AbIII/2629, ZPAL AbIII/3382, ZPAL AbIII/3387, ZPAL AbIII/3388). There is a deep sulcus in the middle of the rugose area (e.g., ZPAL AbIII/242, ZPAL AbIII/502/40, ZPAL AbIII/1624, ZPAL AbIII/3382, ZPAL AbIII/3388). Two well-indicated ridges are present parallel to the sulcus, at the lateral and medioventral border of the rugose facet (e.g., ZPAL AbIII/502/40, ZPAL AbIII/3382, ZPAL AbIII/3387, ZPAL AbIII/3388). The lateral ridge (which also forms the lateral edge of the entire trochanter) is bigger and forms a distinct lateral appendix (ZPAL AbIII/502/40, ZPAL AbIII/1624, ZPAL AbIII/3382, ZPAL AbIII/3388). The medial ridge forms a marked tuberosity in the ventralmost part (e.g., ZPAL AbIII/242, ZPAL AbIII/502/40, ZPAL AbIII/3382, ZPAL AbIII/3387, ZPAL AbIII/3388). The extent of the development of the rugosities, depth of the sulcus, and robustness of the ridges vary between specimens; those features are poorly indicated in ZPAL AbIII/1624, ZPAL AbIII/1625, medium-developed in

ZPAL AbIII/242, and very prominent in ZPAL AbIII/502/40, ZPAL AbIII/2629, ZPAL AbIII/3382, ZPAL AbIII/3387).

The lateral edge of the iliofibularis trochanter is delicately s-shaped in anterolateral view (ZPAL AbIII/242, ZPAL AbIII/502/40, ZPAL AbIII/1624, ZPAL AbIII/1625, ZPAL AbIII/2629, ZPAL AbIII/3382, ZPAL AbIII/3388). It starts proximally at about 1/4 of the shaft length with a faint vertically oriented ridge (e.g., ZPAL AbIII/1624, ZPAL AbIII/3382, ZPAL AbIII/3388). At the level of the rugose area (at about 1/3 of the shaft length, proximally) it abruptly turns posteriorly and starts to diagonally descend, from anteroproximal to dorsoposterior direction, till about 2/3 of the shaft length (e.g., ZPAL AbIII/1624, ZPAL AbIII/2629, ZPAL AbIII/3382). In anterior view, in the same area the trochanter's edge rapidly expands transversely, forming a thin appendix on the lateral border of the rugose area – the most laterally expanded part of the trochanter (e.g., ZPAL AbIII/502/40, ZPAL AbIII/1624, ZPAL AbIII/3382, ZPAL AbIII/3387, ZPAL AbIII/3388). Distally to the appendix, the edge of the trochanter forms a uniformly thick ridge (e.g., ZPAL AbIII/502/40, ZPAL AbIII/1624, ZPAL AbIII/2629, ZPAL AbIII/3382). The edge of the ridge is rugose. The rugosities are less defined than in the anterior rugose area, but their development varies between specimens in a similar way, being poorly indicated in ZPAL AbIII/1624 and ZPAL AbIII/1625, medium-developed in ZPAL AbIII/242, ZPAL AbIII/3382, and ZPAL AbIII/3456, and very intense in ZPAL AbIII/2629 and ZPAL AbIII/3387, ZPAL AbIII/3388.

Distally to the iliofibularis trochanter, the shaft starts to expand anteroposteriorly and transversally. Its shape becomes teardrop like in cross-section, with slim, pinched anterior part, and thick posterior part which could be either rounded (ZPAL AbIII/2629, ZPAL AbIII/3387) or also pinched; however, the latter state could be induced by compaction (ZPAL AbIII/502/40, ZPAL AbIII/1624, ZPAL AbIII/1625, ZPAL AbIII/3382, ZPAL AbIII/3397). The anterior edge forms a clear ridge that originates distally to the rugose area of the iliofibularis trochanter and ends with a tuberosity, slightly proximally to the distal articulation surface (ZPAL AbIII/502/40, ZPAL AbIII/1624, ZPAL AbIII/1625, ZPAL AbIII/2629, ZPAL AbIII/3382, ZPAL AbIII/3387). It seems that there is another ridge posteriorly, taking form of an extension of the iliofibularis trochanter (ZPAL AbIII/2629), but this part is apparently deformed in all studied fibulas.

The distal articulation surface of the fibula forms two well-defined surfaces for the astragalus and calcaneum. Anteriorly positioned, the triangular articulation surface for the astragalus is much smaller than the articulation surface for calcaneum. It ascends medially, forming a convex vertically oriented projection that matched the corresponding concave surface of the astragalus, and probably formed a tight immovable joint (ZPAL AbIII/502/40, ZPAL AbIII/1624, ZPAL AbIII/1625, ZPAL AbIII/2629, ZPAL AbIII/3382, ZPAL AbIII/3387, ZPAL AbIII/3388, ZPAL AbIII/3397). This ascension is especially well well-marked in anterolateral view, in which an acute projection is formed at the border, between the articulation surfaces for the astragalus and calcaneum (ZPAL AbIII/502/40, ZPAL AbIII/1624, ZPAL AbIII/1624, ZPAL AbIII/1625, ZPAL AbIII/2508, ZPAL AbIII/2629, ZPAL AbIII/3368, ZPAL AbIII/3382, ZPAL AbIII/3387, ZPAL AbIII/3388, ZPAL AbIII/3397). The larger articulation surface for the calcaneum is oriented horizontally. It is oval and has a deep depression in the middle (ZPAL AbIII/502/40, ZPAL AbIII/1624, ZPAL AbIII/1625, ZPAL AbIII/3382, ZPAL AbIII/3387, ZPAL AbIII/3388 ZPAL AbIII/3397).

The distal articulation surface is rugose in exactly the same manner as the proximal one. Numerous small tubers cover the entire articulation surface in ZPAL AbIII/1624 and ZPAL AbIII/1625, larger and less frequent tubers are present mostly on the calcaneum articulation surface in ZPAL AbIII/3397, and few faint tubers are present around the external border of the calcaneum articulation surface in ZPAL AbIII/2629, ZPAL AbIII/3382, ZPAL AbIII/3387 and ZPAL AbIII/3388 (the surface for the astragalus is smooth).

Tarsus

The tarsus (Fig. 17 – 20) was composed of four elements: massive astragalus and calcaneum, as well as two smaller distal tarsals – 3rd and 4th (ZPAL AbIII/2508, ZPAL 3323/3, ZPAL AbIII/3349/3, ZPAL AbIII/3349/4, ZPAL AbIII/3368, ZPAL AbIII/3455). Morphology of these elements is highly similar as in other aetosaurs, with transversally broad astragalus and calcaneum, characteristic spiral dorsal surface of the astragalus, enlarged calcaneal tuber projecting posteriorly in relation to the main body of the calcaneum, and hemispherical dorsal surface and a deep socket of the calcaneum (e.g., ZPAL AbIII/3349/4, ZPAL AbIII/3355/1, ZPAL AbIII/3355/2; e.g., Sawin 1947; Casamiquela 1961; Long and Murry 1995; Martz 2002; Desojo et al. 2013; Roberto-Da-Silva et al. 2014). The distal tarsals form a wedge-like structure. The lateral one (4th) is significantly larger than the medial one (3rd; ZPAL AbIII/3323, ZPAL AbIII/3349/3, ZPAL AbIII/3455).

The calcaneum was oriented parasagittally, and the astragalus articulated dorsally and perpendicularly to the calcaneum (ZPAL AbIII/3349/4, ZPAL AbIII/3355/1, ZPAL AbIII/3355/2, ZPAL AbIII/3368). The distal tarsals articulated dorsally with the ventral flat

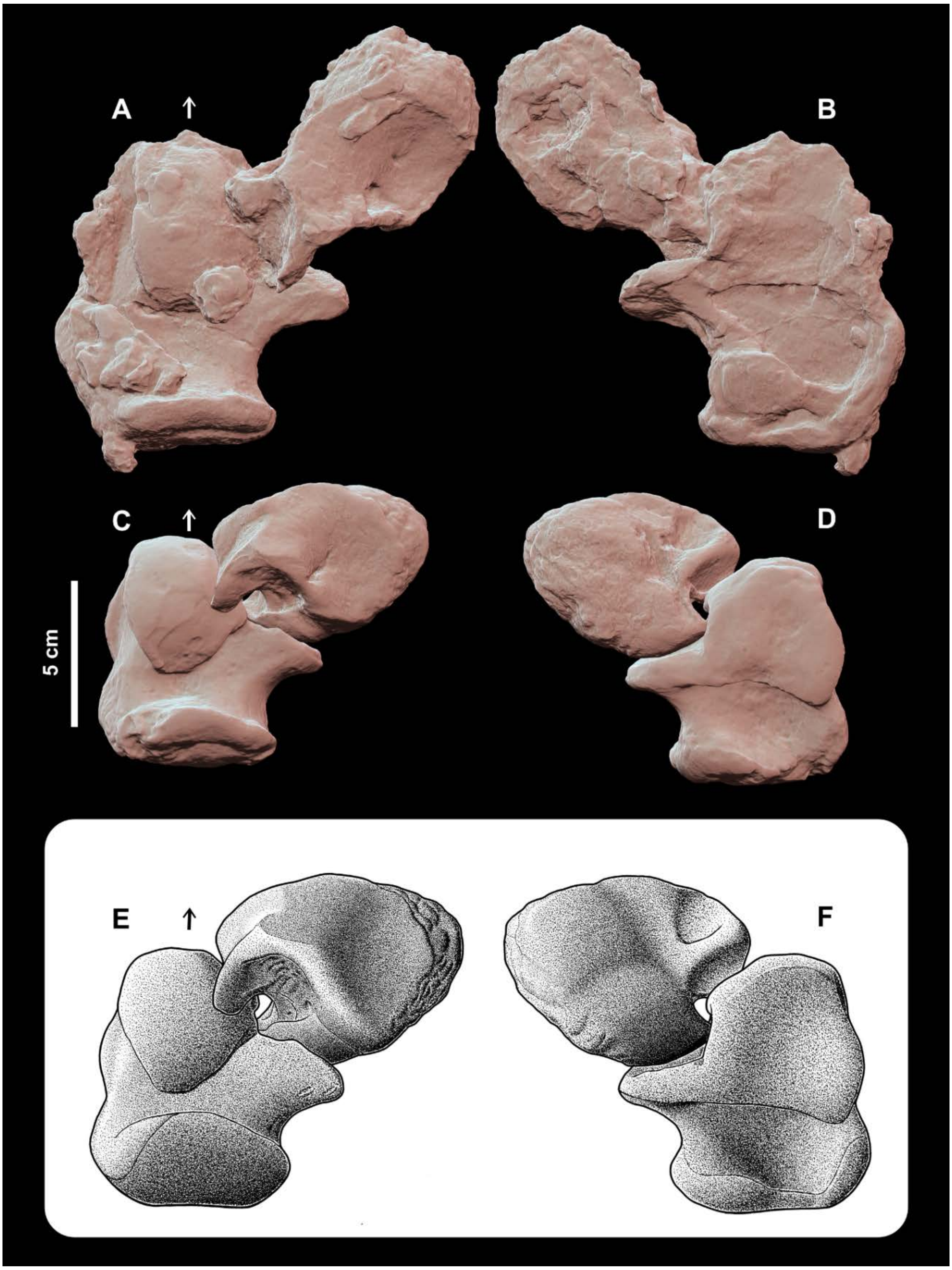


Figure 17. Left astragalus and calcaneum of *Stagonolepis olenkae*. Articulated ZPAL AbIII/3349/4 in dorsal (A) and ventral view (B). Arranged astragalus ZPAL AbIII/3355/1 and calcaneum ZPAL AbIII/3355/2 in dorsal (C) and ventral view (D). Reconstruction of astragalus and calcaneum in dorsal (E) and ventral view (F). The arrows indicate the cranial direction.

surface of the calcaneum (ZPAL AbIII/2508, ZPAL AbIII/3368, ZPAL AbIII/3455). It seems that the metatarsals articulated with the astragalus or distal tarsals, as follows: 1st metatarsal with astragalus, 2nd metatarsal with astragalus and partially with 3rd distal tarsal, 3rd metatarsal with 3rd distal tarsal and partially 4th distal tarsal, 4th and 5th metatarsals with 4th distal tarsal (4th metatarsal proximally and 5th laterally; ZPAL AbIII/2508, ZPAL AbIII/3349/3, ZPAL AbIII/3455). However, it is not entirely clear because in all articulated specimens the tarsals and metatarsals are slightly dislocated.

Tarsus has a crocodile normal rotary ankle joint (with two astragalo-calcaneal articulation surfaces: ventral consisting of a peg on the astragalus that fitted into a socket on the calcaneum, and dorsal sliding joint in which the process from the astragalus slid over a hemispherical surface of the calcaneum). During movement, the astragalus was fixed, because both joints of the tibia and fibula had a very restricted mobility (almost immovable), so the only mobile element in the ankle joint was calcaneum (ZPAL AbIII/2508, ZPAL AbIII/3349/4, ZPAL AbIII/3355/1, ZPAL AbIII/3368). Movement in the ankle joint was restricted to the parasagittal plane.

Astragalus

The astragali (Fig. 18) are preserved in six specimens. All of them are complete, five are articulated or have been found in articulation with other pes elements: ZPAL AbIII/2508, ZPAL AbIII/3349/4, ZPAL AbIII/3355/1, ZPAL AbIII/3368, ZPAL AbIII/3455; and one is isolated: ZPAL AbIII/502/12. The best-preserved specimen is ZPAL AbIII/3355/1.

The astragalus is of comparable size and massiveness to the calcaneum (ZPAL AbIII/3349ZPAL AbIII/3355/1, ZPAL AbIII/3355/2). It has a compact main body, from which laterally extends a dorsal process that slid over the calcaneum hemisphere, and a ventral peg that articulated with a socket of the calcaneum. Its complicated structure is defined by marked articulation surfaces and grooves where the muscles attached. The largest articulation facet for the tibia covers about 80% of the astragalus dorsal surface and is wide anteroposteriorly in proportion to that of other pseudosuchians, as typical for aetosaurs (e.g., Parrish 1986; Long and Murry 1995). It forms a single surface that descends and twists posteriorly, from oblique anterodorsally oriented plane in the anterior part, to near horizontal alignment in the posterior part. It is strongly saddle-shaped and forms a depression in the posterior part. It formed a tight articulation with the corresponding surface of the tibia. Its morphology indicates a near vertical orientation of the latter bone (Parrish 1986). At the lateral edge of the tibias articulation surface, around the middle part, there is a distinct pit (the astragal fossa, Martz 2002; ZPAL AbIII/502/12, ZPAL AbIII/3349/4, ZPAL AbIII/3355/1). The articulation surface for the fibula is clearly demarcated from the articulation surface for the tibia by an s-shaped ridge present

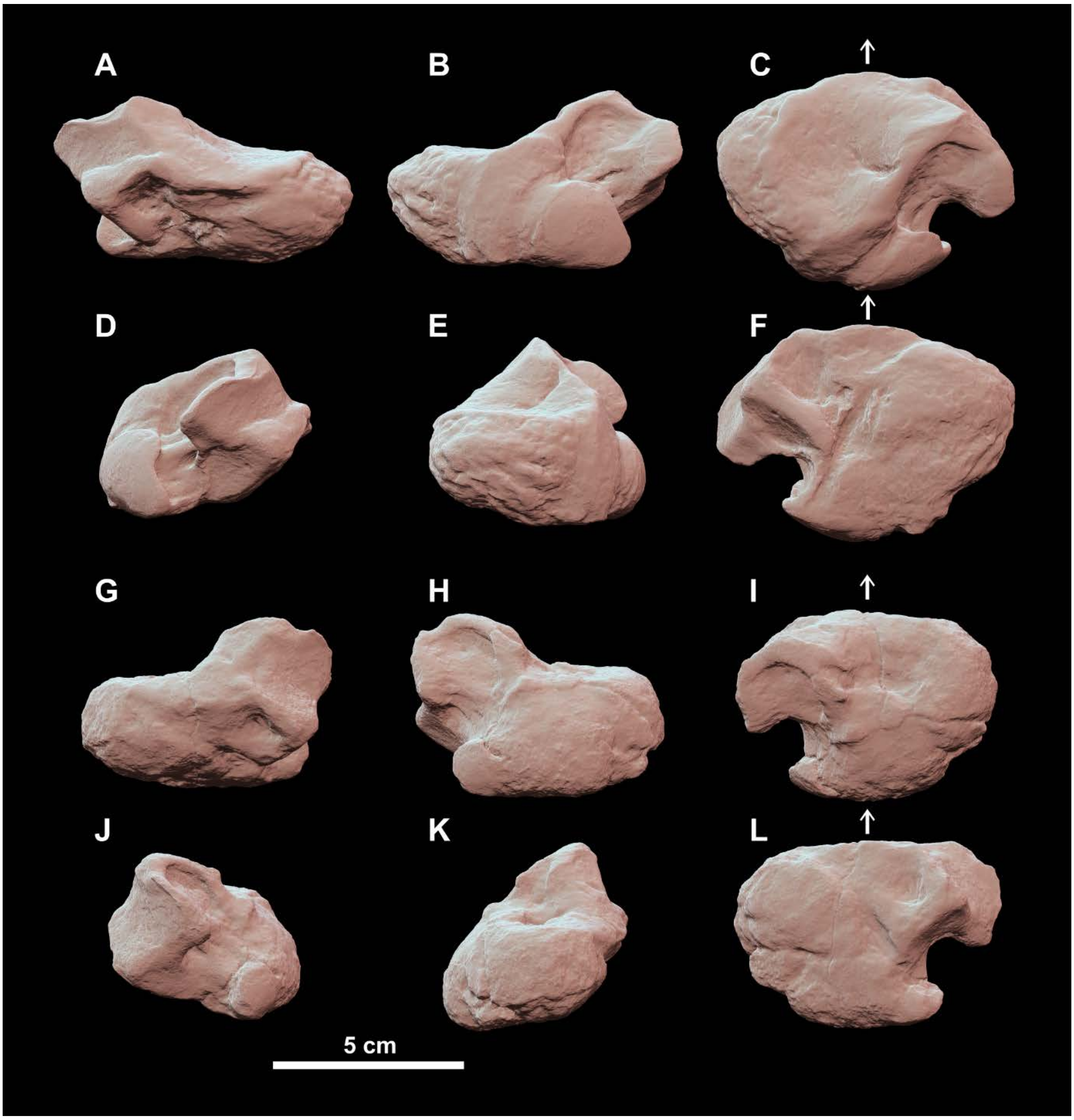


Figure 18. Astragalus of *Stagonolepis olenkae*. ZPAL AbIII/3355/1 (right, A–F) and ZPAL AbIII/502/12 (left, G–L) in anterior (A, G), posterior (B, H), dorsal (C, I), lateral (D, J), medial (E, K), and ventral view (F, L). The arrows indicate the cranial direction.

dorsally between the facets (ZPAL AbIII/502/12, ZPAL AbIII/3349/4, ZPAL AbIII/3355/1). It develops on the lateral surface of the dorsal process. The surface is of rhomboid outline in lateral view and is prominently saddle-shaped (ZPAL AbIII/502/12, ZPAL AbIII/3349/4, ZPAL AbIII/3355/1). It faces directly laterally and is near vertically oriented. The articulation surface for the dorsal sliding joint with the calcaneum is positioned directly ventrally on the dorsal process. It is demarcated from the fibular facet by a ridge similar to that separating the articulation facets dorsally (ZPAL AbIII/502/12, ZPAL AbIII/3355/1). It has a triangular outline in ventral view and is faintly concave (ZPAL AbIII/502/12, ZPAL AbIII/3355/1). Its curvature matches exactly the dorsal surface of the calcaneum hemisphere. The ventral peg is pointed laterally. The articulation surface for the calcaneum covers only its distal part and is prominently convex (ZPAL AbIII/3355/1, ZPAL AbIII/502/12). In ZPAL AbIII/3355/1, the lateral and dorsal edges of the surface form a thin ridge that extends over the posterior groove. In the same specimen, distally there is a depression, which forms a shallow neck around the articulation facet. The articulation surface for the metatarsals (distal roller *sensu* Martz, 2002) faces anteroventrally. A transverse depression in the middle of this surface divides its area into two roughly equal parts (ZPAL AbIII/502/12, ZPAL AbIII/3355/1). The area positioned anteriorly (probably articulation surface for the 1st metatarsal) is delicately convex, while the distal area (probably for articulation with the 2nd metatarsal) is flat (ZPAL AbIII502/12, ZPAL AbIII/3355/1).

In ventral view, anterolaterally to the 1st metatarsal articulation area, there is a triangular depression that expands anteroposteriorly towards the dorsal process. At the level of the dorsal process (in the area neighboring the articulation facets for the fibula and calcaneum) it forms a deep hemispherical concavity (the anterior hollow *sensu* Martz, 2002) (ZPAL AbIII/502/12, ZPAL AbIII/3349/4, ZPAL AbIII/3355/1). Posteriorly to the anterior hollow, there is another deep longitudinal depression, parallel to the lateral edge of the distal roller (ZPAL AbIII/502/12, ZPAL AbIII/3349/4, ZPAL AbIII/3355/1). The posterior groove distinctly twists spirally toward the ventral peg. Ventrally, within the area of the posterior grove, between the ventral peg and the dorsal process, there is a structure composed of two deep, narrow pits divided by a thick ridge (ZPAL AbIII/502/12, ZPAL AbIII/3355/1).

Medially, the astragalus forms a rugose, bulbous edge, which contrasts with smooth articulation surfaces (ZPAL AbIII/502/12, ZPAL AbIII/3349/4, ZPAL AbIII/3355/1, ZPAL AbIII/3368). The rugosities are composed of randomly arranged tubers of similar morphology to those on the articulation surfaces of the long bones.

Calcaneum

The calcaneum (Fig. 19) is preserved in six specimens: three are preserved in articulation or associated with other hind limb elements: ZPAL AbIII/3349/4, ZPAL AbIII/3355/2, ZPAL AbIII/3368; and four have been found in isolation: ZPAL AbIII/690, ZPAL AbIII/1627, ZPAL AbIII/3383. All of them are complete. Best-preserved are ZPAL AbIII/690 and ZPAL AbIII/3355/2, being relatively not compacted and undamaged.

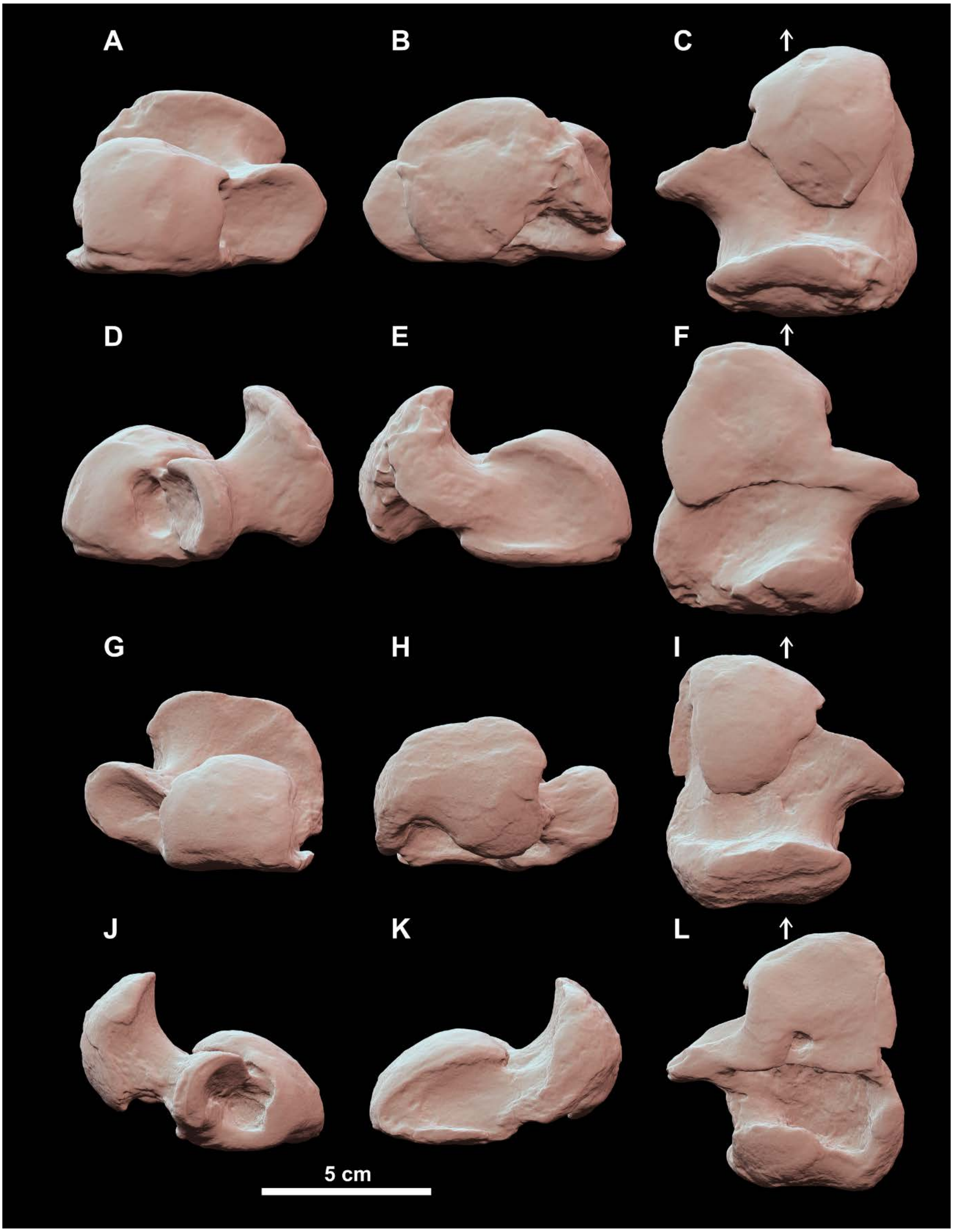


Figure 19. Calcaneum of *Stagonolepis olenkae*. ZPAL AbIII/3355/2 (right, A–F) and ZPAL AbIII/690 (left, G–L) in anterior (A, G), posterior (B, H), dorsal (C, I), medial (D, J), lateral (E, K), and ventral view (F, L). The arrows indicate the cranial direction.

The calcaneum is of comparable size and massiveness to the astragalus (ZPAL AbIII/3349/4, ZPAL AbIII/3355/1, ZPAL AbIII/3355/2, ZPAL AbIII/3368). It has a deep socket for the astragalus and elongated sustentaculum, that forms a medially projecting lip; hemispherical ball-like dorsal articulation surface, and flat ventral articulation surface; and longitudinally short calcaneal tuber that projects directly posteriorly, and has a profound depression at the ventral side (ZPAL AbIII/690, ZPAL AbIII/3349/4, ZPAL AbIII/3355/2).

Typically for aetosaurs, the socket for the peg on the astragalus is very deep in comparison to that of other pseudosuchians (ZPAL AbIII/690, ZPAL 1627, ZPAL AbIII/3355/2), probably for increased stability in the ankle joint (Parrish 1986). The outline of the opening is square like in medial view (ZPAL AbIII/690, ZPAL AbIII/3355/2). Anteriorly, the outline forms a distinct s-shaped notch that corresponds with the curved shape of the ridge on the astragalus peg, additionally indicating a tight match between those two bones (ZPAL AbIII/3355/1, ZPAL AbIII/3355/2). The sustentaculum reaches one fourth of the transverse length of the entire calcaneum (ZPAL AbIII/690, ZPAL AbIII/1627, ZPAL AbIII/3349/4, ZPAL AbIII/3355/2, ZPAL AbIII/3368, ZPAL AbIII/3383). It protrudes directly medially from the posterior edge of the socket, forming a broad concave (u-shaped) articulation surface for the astragalus (ZPAL AbIII/690, ZPAL AbIII/1627, ZPAL AbIII/3355/2). At the end of the projection, a round elevation is formed prior to the external margin of the extension, that gives the tip a characteristic lip-like shape (ZPAL AbIII/690, ZPAL AbIII/1627, ZPAL AbIII/3355/2). Although the articulation area for the astragalus faces directly anteriorly, the projection appears to be descending posteriorly in the dorsoventral aspect, due to the dorsal and ventral margins of the projection extending farther anteriorly in the area closer to the main body of the calcaneum, as well as the tip of the projection being slightly twisted posteriorly (ZPAL AbIII/690, ZPAL AbIII/3349/4, ZPAL AbIII/3355/2).

The ball-like hemispherical dorsal articulation surface is about half the anteroposterior length and three fourth of the transverse length of the calcaneum (ZPAL AbIII/690, ZPAL AbIII/3349/4, ZPAL AbIII/3355/2). Its facet is divided into two distinct sliding areas; the smaller medial surface for the ventral articulation of the astragalus and the larger lateral surface for the fibula. Faint longitudinal ridge is present at the borderline between those facets (ZPAL AbIII/690, ZPAL AbIII/1627, ZPAL AbIII/3349/4, ZPAL AbIII/3355/1). In dorsal view, the articulation surface is semicircular. It forms an almost straight lateral margin parallel to the longitudinal plane of the bone. The anterior and posterior margins curve medially and meet dorsally, above the socket opening. The angle of the curvature slightly changes at the transition between the facets, being more acute medially (e.g., ZPAL AbIII/690, ZPAL AbIII/3355/2). The articulation area extends over the non-articulation surface of the calcaneum laterally and posteriorly, forming a roof-like structure (ZPAL AbIII/690, ZPAL AbIII/1627, ZPAL AbIII/3355/2). It seems that in ZPAL AbIII/3355/2 and ZPAL AbIII/3383 the dorsal surface is more convex than in ZPAL AbIII/690.

The dorsal articulation surface continues onto the ventral side and meets with the ventral articulation surface anteriorly and anteromedially. In ZPAL AbIII/3355/1 and ZPAL AbIII/3368, a well-defined groove is present at the transition between the ventral and dorsal facets, while in ZPAL AbIII/3383 this area is smooth with no depression, and in ZPAL AbIII/690, a faint indentation is present in its place. In ZPAL AbIII/1627, the groove is visible only in the anteriormost part. In this specimen, ventrally to the groove, there is a small rugose area. The rugosities are composed of a few clear tubers, similar to those on the articulation areas of long bones. Similar tubers, but less developed, are present in the analogical position in ZPAL AbIII/3355/2.

The ventral articulation surface forms a flat, horizontally oriented plane with a faint depression in the middle (ZPAL AbIII/3355/2) and distinct facet around the socket area, probably for the articulation with the smaller 3rd distal tarsal (ZPAL AbIII/690, ZPAL AbIII/3355/2). The facet originates from a round elevation laterally to the socket opening and ascends medially (ZPAL AbIII/690, ZPAL AbIII/3355/2). It is lunar-shaped and partially covers the medial projection of the calcaneum (ZPAL AbIII/690, ZPAL AbIII/3355/2). In ventral view it has a semicircular outline generally similar to the outline of the hemispherical dorsal surface, but slightly more expanded and with differently shaped lateral and posterior margins (ZPAL AbIII/690, ZPAL AbIII/3349/4, ZPAL AbIII/3355/2). Its lateral margin distinctly extends from the main calcaneal body forming a longitudinal shelf-like projection, that widens posteriorly (ZPAL AbIII/690, ZPAL AbIII/3355/2). The posterior margin is oriented perpendicularly to the long axis of the bone. It is roughly straight, in alignment with the sustentaculum, with a slight turn posteriorly around the depression on the ventral articulation surface (ZPAL AbIII/690, ZPAL AbIII/3355/2). It marginally extends over the calcaneal tuber groove and roofs it ventrally (ZPAL AbIII/690, ZPAL AbIII/3355/2).

Characteristically for aetosaurs, the calcaneal tuber is very short, being roughly half of the longitudinal length of the calcaneum (ZPAL AbIII/690, ZPAL AbIII/3349/4, ZPAL AbIII/3355/2; e.g., Casamiquela 1961; Bonaparte 1971; Parrish 1986; Long and Murry 1995; Schoch 2007; Desojo et al. 2013; Roberto-Da-Silva et al. 2014). It is positioned directly posteriorly to the main body of the calcaneum and ascends dorsoposteriorly at an angle of about 30º to the ventral articulation surface (e.g., ZPAL AbIII/690, ZPAL AbIII/3349/4, ZPAL

AbIII/3355/2). Posteriorly, it forms a broad, delicately convex surface, that continues onto the ventral side of the tuber. The dorsalmost part of the surface forms a lip-like structure distinctly pointing anteriorly. In the middle part of the surface, there is a transverse depression, very distinct in ZPAL AbIII/3355/2, and less indicated in ZPAL AbIII/690 and ZPAL AbIII/3349/4. The ventral part of the surface medially forms a rounded tuberosity, that partially roofs the ventral fossa. Its facet has a different texture than the rest of the surface, consisting of sublongitudinal striations, while the rest of the surface has a texture similar to that of the hemispherical and ventral articulation surfaces (ZPAL AbIII/690, ZPAL AbIII/3349/4, ZPAL AbIII/3355/2). Laterally, the ventral surface of the tuber expands anteriorly, forming an elongated tuberosity on the bottom of the lateral wall of the tuber's fossa (ZPAL AbIII/690, ZPAL AbIII/3355/2, ZPAL AbIII/3349/4). The neck of the tuber is deeply concave ventrally. The concavity forms a broad fossa that widens and deepens laterally (ZPAL AbIII/690, ZPAL AbIII/3355/2).

Distal tarsals

Distal tarsals (Fig. 20) are present in four specimens ZPAL AbIII/2507, ZPAL AbIII/3349/3, ZPAL AbIII/3368, ZPAL AbIII/3455. In all of the above specimens they are articulated with other hind limb elements. They are best preserved in ZPAL AbIII/3455. No isolated specimens have been recognized.

Like in most archosaurs, only two (3rd and 4th) distal tarsals are present. They have a complex shape. Together they form a wedge-like structure that is wide laterally and narrows down medially (e.g., Parrish 1986).

The larger, 4th distal tarsal (the lateral one) is of pyramidal shape with a flat, horizontally oriented base and dorsally pointing apex (ZPAL AbIII/3349/3, ZPAL AbIII/3455). The base is trapezoid. Its texture is different than that of the articulation facets in having longitudinal striations (like rugosities on the ventral part of the calcaneal tuber), while the articulation surfaces are smooth, similar to the articulation facets on other ankle elements (ZPAL AbIII/3349/3, ZPAL AbIII/3455). There are at least four distinct articulation facets: for the 5th metatarsal (facing laterally), for the 3rd and 4th metatarsals (facing anteriorly), for the 3rd distal tarsal (facing anteromedially), and for the calcaneum (facing posterodorsally). The articulation facets for the 5th metatarsal, 3rd distal tarsal, and calcaneum appear to be close to triangular in shape, and are significantly larger in size than the base (ZPAL AbIII/3349/3, ZPAL AbIII/3455). The articulation surfaces for the metatarsals are not entirely visible nor well preserved in any of the studied specimens. Part of these surfaces is preserved in ZPAL AbIII/3349/3.

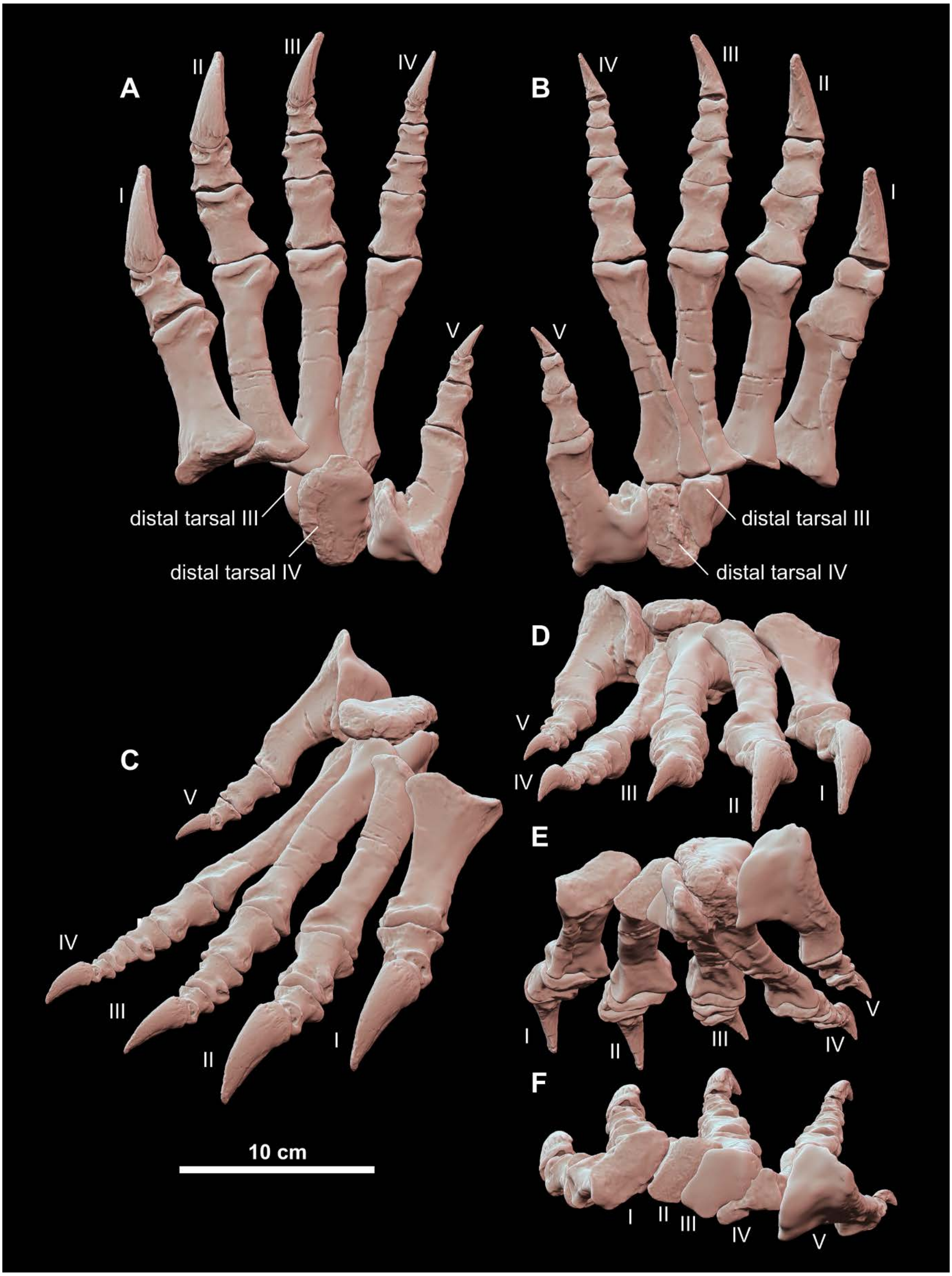


Figure 20. Reconstruction of the right pes of *Stagonolepis olenkae* in dorsal (A), ventral (B), anterodorsolateral (C), anterior (D), posterior (E), and posterior without the distal tarsals (F) view.

The third distal tarsal (the medial one) is about two times smaller than the lateral one. It is of similar form to the 4th distal tarsal, having a horizontally oriented base and ascending surfaces. Its body is longer transversely than anteroposteriorly. The texture of the base is rugose in the same manner as in the 4th distal tarsal. It forms two major articulation surfaces for the 4th distal tarsal (facing posterolaterally) and parallel to it for the metatarsals (facing anteromedially) (ZPAL AbIII/3349/3, ZPAL AbIII/3455). It appears that this surface articulated partially with the 2nd and 3rd metatarsal (ZPAL AbIII/3349/3, ZPAL AbIII/3455).

Pes

The pes (Fig. 20, Fig. 21) is much larger than the manus, being about 3 times the manus longitudinal length (ZPAL AbIII/3349/1, ZPAL AbIII/3349/2, ZPAL AbIII/3349/3; Dróżdż 2018). This huge disproportion between the forelimb and hind limb autopodia is typical for pseudosuchians, and well documented for aetosaurs based on fully articulated skeletons as well as tracks (Casamiquela 1961, 1967; Long and Murry 1995; Schoch 2007; Heckert et al. 2010; Lucas and Heckert 2011; Desojo et al. 2013).

The morphology of the pes is very similar to the manus (Dróżdż 2018): the robustness of the digits decreases laterally, the 1st digit being the most stout one and the 5th one being the most gracile (ZPAL AbIII/1974, ZPAL AbIII/2508, ZPAL AbIII/3349/3, ZPAL AbIII/3357, ZPAL AbIII/3368, ZPAL AbIII/3455); the middle digits (2nd, 3rd, 4th) are of comparable length, and the 1st and 5th are significantly shorter, but the 1st is longer than the 5th (ZPAL AbIII/3368, ZPAL AbIII/3455); at least the first four digits ended with claw-like unguals of the same morphology as those of the manus (ZPAL AbIII/3368, ZPAL AbIII/3455; the 5th ungual is not preserved in any specimen); the first ungual is very large, being one third of the entire digit length (ZPAL AbIII/2508, ZPAL AbIII/ZPAL AbIII/3368, ZPAL AbIII/3455); the size of the unguals decreases in the successive lateral digits (at least in the first four), with each more lateral ungual being one third shorter than the preceding one (ZPAL AbIII/2508, ZPAL AbIII/3349/3, ZPAL AbIII/3357, ZPAL AbIII/3368, ZPAL AbIII/3455). The phalangeal formula is 2, 3, 4, 5, 3? (ZPAL AbIII/3368, ZPAL AbIII/3455), which is the same as in the manus (Dróżdż 2018) and consistent with other aetosaurs in general (e.g., Desojo et al. 2013). In the 5th digit of ZPAL AbIII/3368 there are two articulated phalanges. They are of comparable size and robustness to the last phalanges of the 4th digit, which is ended with the ungual, therefore presence of an ungual on the 5th digit at the 3rd phalanx position is probable (ZPAL AbIII/3368). Fifth metatarsal is characteristically L-shaped and positioned posteriorly to the other metatarsals (ZPAL ABIII/3368 ZPAL AbIII/3455), which is typical for aetosaurs and other pseudosuchians with the erect gait (Parrish 1986).

Metatarsals

In total, 31 metatarsals (Fig. 20, Fig. 21) have been studied: 23 are preserved in articulated or semi articulated pedes (from 1st to 5th in ZPAL AbIII/2508, ZPAL AbIII/3349/3, ZPAL AbIII/3368, ZPAL AbIII/3455; from 1st to 3rd in ZPAL AbIII/1974, ZPAL AbIII/3357); 3rd and 4th associated with other pes elements in ZPAL AbIII/3323; 7 have been found in isolation (two 1st metatarsals: ZPAL AbIII/502/52 and ZPAL AbIII/3384; four 5th metatarsals: ZPAL AbIII/226, ZPAL AbIII/502/68, and ZPAL AbIII/553/36, ZPAL AbIII/3356).

The relative length of the metatarsals can be described as follows: V<I<II<IV<III. It does not entirely reflect the relative length of the digits, because despite the noticeable difference in the length between the 2nd and the 3rd as well as 4th metatarsals, the digits II, III, and IV are of comparable length (ZPAL AbIII/3368, ZPAL AbIII/3455). Although the 3rd metatarsal is the longest one, the differences in the length between the 3rd and 4th metatarsals is minor (a few millimeters; e.g., ZPAL AbIII/3368, ZPAL AbIII/3455).

The metatarsals, especially 1st to 4th one, share a similar form with the metacarpals (Dróżdż 2018), being robust, dorsoventrally flattened, their shaft tapering towards the distal end, and having well-developed, transversely wide and flat trochlea, which dorsally forms an asymmetrical tongue-shaped notch (ZPAL AbIII/502/52, ZPAL AbIII/1052/1, ZPAL AbIII/1974, ZPAL AbIII/2508, ZPAL AbIII/2149, ZPAL AbIII/3349/3, ZPAL AbIII/3357, ZPAL AbIII/3368, ZPAL AbIII/3384, ZPAL AbIII/3455).

Except for the 5th metatarsal positioned distally and laterally to the first four, they also partially overlap with each other in the proximal part (e.g., ZPAL AbIII/3349/3, ZPAL AbIII/3368, ZPAL AbIII/3455). Except for the 5th metatarsal, the distal articulation surface is twisted medially in relation to the trochlea. The twisting is more significant in subsequent lateral metatarsals (ZPAL AbIII/1974, ZPAL AbIII/3357, ZPAL AbIII/3455).

Isolated metatarsals can be easily distinguished from the metacarpals, if not for their overwhelmingly larger size, then by having a comparably longer and more slender shaft (longitudinal length of the metatarsal in proportion to the transverse width of the distal articulation surface for the phalanges); as well as more distinctly developed fovea for collateral ligaments (e.g., ZPAL AbIII/3368, ZPAL AbIII/3357, ZPAL AbIII/1974).

The 1st metatarsal is the most robust and transversely widest (ZPAL AbIII/2508, ZPAL AbIII/3349/3, ZPAL AbIII/3455). Its proximal articulation surface with the astragalus curves

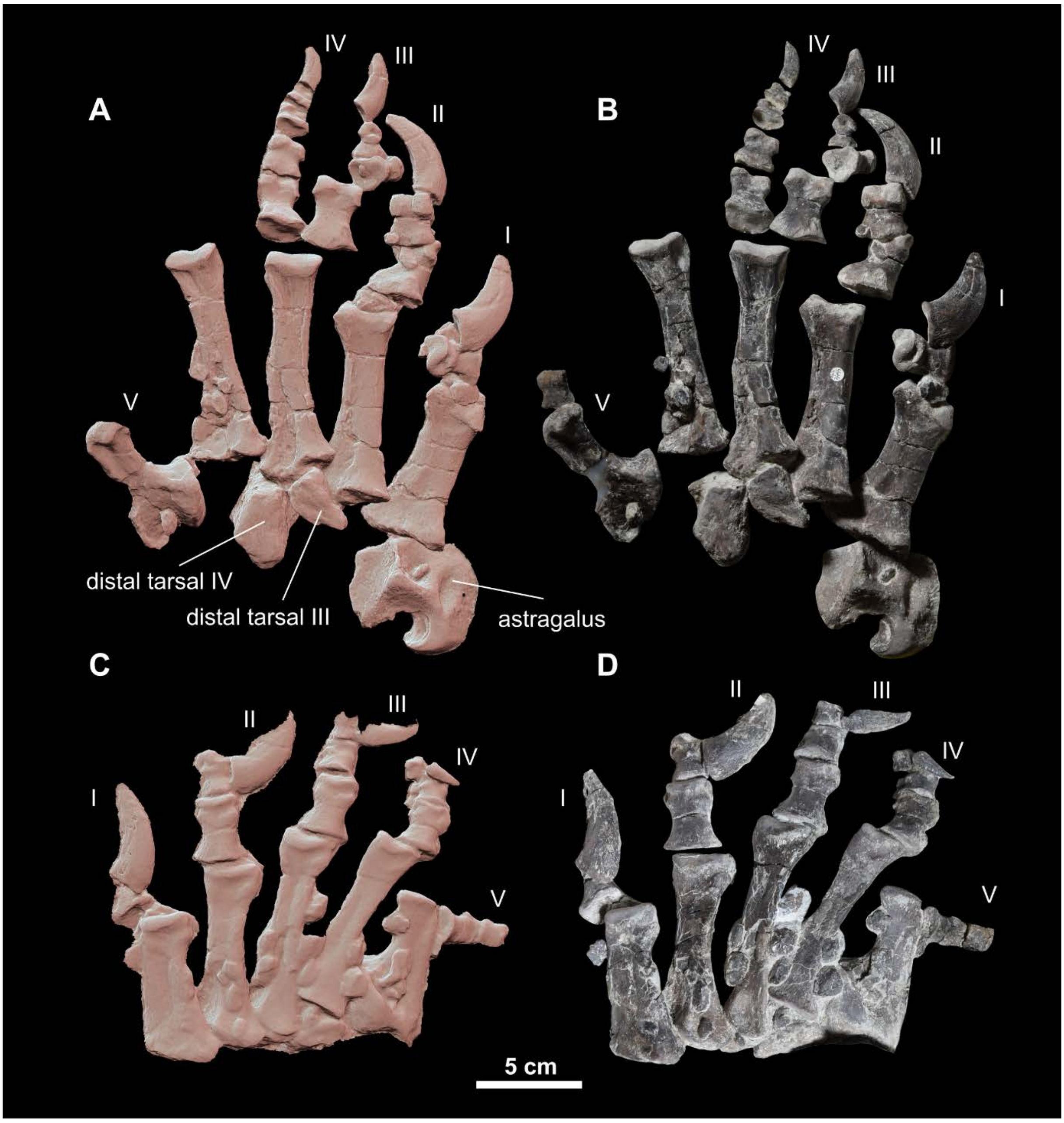


Figure 21. Right pes of *Stagonolepis olenkae*. ZPAL AbIII/3455, 3D model (A) and photograph (B), in ventral view. ZPAL AbIII/3368, 3D model (C) and photograph (D) in dorsal view.

dorsally, forming a lip-like notch in the proximalmost part of the shaft (ZPAL AbIII/502/12, ZPAL AbIII/1974, ZPAL AbIII/3384). The shaft is convex dorsally and flat ventrally (e.g., ZPAL AbIII/502/12, ZPAL AbIII/1974, ZPAL AbIII/3384). In the horizontal plane, it is noticeably wider proximally than distally, and clearly tapers towards the distal end. A few prominent longitudinal sulci are present ventrally on the shaft (ZPAL AbIII/502/12, ZPAL AbIII/1947, ZPAL AbIII/3384). The trochlea is distinctly asymmetrical with the lateral tuberosity extending more distally in relation to the medial tuberosity (ZPAL AbIII/502/12, ZPAL AbIII/1947/1, ZPAL AbIII/3349/3, ZPAL AbIII/3384).

The 2nd metatarsal is less robust than the 1st, but thicker than the remaining ones (e.g., ZPAL AbIII/3349/3, ZPAL AbIII/3368, ZPAL AbIII/3455). Its proximal part is twisted medially at a higher angle than that of the 1st metatarsal (ZPAL AbIII/1974/2, ZPAL AbIII/3357). The proximal articulation surface is of parallelogram shape in proximal view (ZPAL AbIII/1974/2, ZPAL AbIII/3357). The surface extends dorsally and forms a lip-like structure similar to that of the 1st metatarsal but positioned more laterally (ZPAL AbIII/1974/2). As in the 1st metatarsal, the proximal part is noticeably more expanded transversally than the trochlea. The shaft is tapering towards the distal end. Similar to the 1st metatarsal, proximally the lateral side of the shaft is slightly more expanded laterally than the medial side (ZPAL AbIII/1974/2, ZPAL AbIII/3357). The trochlea is symmetrically developed (ZPAL AbIII/1974/2, ZPAL AbIII/3357).

In both the 3rd and 4th metatarsals, the proximal end is proportionally less expanded than in the 1st and 2nd (being of comparable width to the trochlea in the 3rd metatarsal; slightly more expanded in the 4th metatarsal; ZPAL AbIII/3455); their shafts are twisted medially similar to the 2nd metatarsal; in both the proximal articulation areas do not curve dorsally as in 1st and 2nd metatarsals, but form flat surfaces oriented somehow perpendicularly the long axes of the shafts (ZPAL AbIII/1974/3, ZPAL AbIII/3357, ZPAL AbIII/3455); the shafts in both taper only in the proximal parts and the tapering is not as significant as in the 2nd and 1st metatarsals (ZPAL AbIII/1974/3, ZPAL AbIII/3357, ZPAL AbIII/3368, ZPAL AbIII/3455); the trochleae in both are developed symmetrically in the same manner as in the 2nd metatarsal (ZPAL AbIII/1974/3, ZPAL AbIII/3357, ZPAL AbIII/3368, ZPAL AbIII/3455).

The difference between the 3rd and 4th metatarsal is that the proximal part of the shaft in the 3rd metatarsal is distinctly turned medially in relation to the distal part (ZPAL AbIII/1974, ZPAL AbIII/3323/1, ZPAL AbIII/ 3357, ZPAL AbIII/3455), while in the 4th metatarsal the shaft is straight (ZPAL AbIII/3323/2, ZPAL AbIII/3349/3, ZPAL AbIII/3368, ZPAL AbIII/3455). In addition, in the third metatarsal ZPAL AbIII/1937/3, in the middle part of the shaft, there is a laminar process projecting medially.

The 5th metatarsal is distinctly L-shaped in transverse plane (ZPAL AbIII/226, ZPAL AbIII/502/68, ZPAL AbIII/553/36). It is positioned laterally and posteriorly to the other metatarsals (e.g., ZPAL AbIII/3368, ZPAL AbIII/3455), which is typical for aetosaurs and other pseudosuchians with erect gait (Parrish 1986). The medial articulation surface for the 4th distal tarsal is about twice the dorsoventral thickness of the mid-section of the shaft (ZPAL AbIII/226, ZPAL AbIII/3356, ZPAL AbIII/3455). In lateral view, the articulation surface for the distal tarsal is nearly square (ZPAL AbIII/3356, ZPAL AbIII/3455). It is concave and more distally it forms a depression distinct from the rest of the surface (ZPAL AbIII/226, ZPAL AbIII/3356, ZPAL AbIII/3455). The morphology of the shaft is similar as in the 5th metacarpal: in both, the ventral and dorsal surfaces of the shaft are distinctly flat; the trochleae are convex without the depression in the middle and tongue-shaped projection dorsally; proximally both the 5th metatarsal and metacarpal form a medially pointing projection (Dróżdż 2018; ZPAL AbIII/226, ZPAL AbIII/502/68, ZPAL AbIII/553/36). Ventrally, there is a longitudinal rugose area that continues along the entire lateral margin of the shaft (ZPAL AbIII/226, ZPAL AbIII/502/68, ZPAL AbIII/553/36). Dorsally, parallel to the lateral margin, there is a straight ridge that originates proximally to the attachment for the ligament and continues along the entire length of the shaft.

Phalanges

In total, 63 phalanges (Fig. 20, Fig. 21) have been studied, 54 in articulated specimens (13 in ZPAL AbIII/2508, 10 in ZPAL AbIII/3357, 16 in ZPAL AbIII/3368, and 15 in ZPAL AbIII/3455), and 9 isolated: two 1st row phalanges of the 1st digit (ZPAL AbIII/2411, ZPAL AbIII/3385); two 1st row phalanges of the 2nd digit (ZPAL AbIII/341, ZPAL AbIII/3381); single 1st row phalanx of the 3rd digit (ZPAL AbIII/502/65); single 2nd row phalanx of the 3rd or 4th digit (ZPAL AbIII/3380); single 3rd row phalanx of the 4th digit (ZPAL AbIII/3886); and two unguals, the first of the 1st or 2nd digit (ZPAL AbIII/1981), and the second of the 1st or 2nd digit (ZPAL AbIII/553/28). In the most complete specimens ZPAL AbIII/3368 and ZPAL AbIII/3455, the phalanges are fully articulated and preserved close to their anatomical orientation.

The minimum phalangeal formula is 2-3-4-5-3?. Presence of additional phalanx at digit 5 was proposed by Walker (1961) for *Stagonolepis robertsoni* (phalangeal formula 2-3-4-5-4), but the fifth digit is also not present entirely in the Scottish species. Comparing the portions of the preserved phalanges of the digit V to phalanges of the digit IV in ZPAL AbIII/3368, the first two phalanges of the digit IV seem to be comparable in size to the first phalanges of the digit V. Therefore, it could be that at least one more phalanx was present in the digit V. The phalanx associated with the 5th metatarsal in ZPAL AbIII/3455 is similar to the phalanges preceding the unguals. However, it appears that it belongs to the left pes, while the rest of the pes of ZPAL AbIII/3455 is right, and it seems that it erroneously was glued on to the to the specimen at some point during excavation or mechanical preparation along with another bone fragment.

Characteristically for aetosaurs, the phalanges are significantly shorter than the metatarsals (e.g., Long and Murry 1995; Nesbitt 2011). The proportion of the first metatarsal to the 1st row phalanges, from the 1st to 5th digit, is, respectively: 0.33 (I), 0.35 (II), 0.29 (III), 0.27 (IV), 0.25 (V) in ZPAL AbIII/3368 and in ZPAL AbIII/3455. The relative length of the 1st row phalanges in respective digits is, as follows: II>III> IV>I>V (ZPAL AbIII/3368, ZPAL AbIII/3455). Except for the unguals, more distal phalanges are about one third shorter than the preceding ones (ZPAL AbIII/3368, ZPAL AbIII/3455). The unguals are about twice the size of the last preceding phalanges (ZPAL AbIII/3357, ZPAL AbIII/3368, ZPAL AbIII/3455). The 1st ungual is exceptionally large in comparison with other pseudosuchians, being about 80% of the first metatarsal and one third of the entire digit length (ZPAL AbIII/3357, ZPAL AbIII/3368, ZPAL AbIII/3455; e.g., Long and Murry 1995; Nesbitt 2011).

The phalanges of the pes are similar to the phalanges of the manus in being short, flattened, transversely wide and robust, all features characteristic for aetosaurs among the contemporary pseudosuchians (e.g., ZPAL AbIII/3368, ZPAL AbIII/3455; e.g., Long and Murry 1995; Lucas and Heckert 2011; Dróżdż 2018). The distal articulation surfaces extend far dorsally and the trochleae are much more indicated than in the metatarsals.

The phalanges of the pes differ from the phalanges of the manus mainly in their significantly larger size, especially those of the 1st and 2nd row (e.g., ZPAL AbIII/3349/3, ZPAL AbIII/3368, ZPAL AbIII/3357, ZPAL AbIII/3455). In ZPAL AbIII/3349, the phalanges of the pes (except for the unguals) are about 3 times longer than the phalanges of the same row in the manus, and the ungual of the 1st digit of the pes is about one third longer than the ungual of the 1st digit in the manus (Dróżdż 2018). Beside the size, all phalanges of the pes differ from the phalanges of the manus in being more asymmetrically developed, with the medial part more expanded than the lateral one (ZPAL AbIII/341, ZPAL AbIII/502/65, ZPAL AbIII/2411, ZPAL AbIII/2508, ZPAL AbIII/3349/3, ZPAL AbIII/3357, ZPAL AbIII/3368, ZPAL AbIII/3380, ZPAL AbIII/3381, ZPAL AbIII/3385, ZPAL AbIII/3386 and ZPAL AbIII/3455; Dróżdż 2018).

Due to significant differences in the development of each digit, all phalanges, except for the unguals, have a somewhat unique shape and at least 1st row phalanges can be precisely recognized even if not associated. In contrast, the ungual of each digit, apart from the size, seems to be of exactly the same anatomy (ZPAL AbIII/3368, ZPAL AbIII/3455, ZPAL AbIII/2508). The most distinctive is the morphology of the trochleae and fovea for collateral ligaments, which is connected with the substantial variation in the size of the unguals (ZPAL AbIII/341, ZPAL AbIII/502/65, ZPAL AbIII/2411, ZPAL AbIII/2508, ZPAL AbIII/3349/3, ZPAL AbIII/3357, ZPAL AbIII/3368, ZPAL AbIII/3380, ZPAL AbIII/3381, ZPAL AbIII/3385, ZPAL AbIII/3386 and ZPAL AbIII/3455). This is best visible in the morphology of the 1st row phalanges, in which those structures decrease in prominence in more lateral digits and, therefore, could be relatively easily recognized

Additional morphological features that allow recognition of the isolated phalanges of the 1st row are: in the phalanx of the 1st digit (directly articulating with the largest ungual), the asymmetrical development and distinctly triangular shape of the trochlea in proximal view; the distal articulation surface longitudinally thick and extending far ventrally in comparison to the other 1st row phalanges; the fovea for collateral ligaments very deep, continuing dorsally onto the top of phalanx; the base of the phalanx of a distinct triangular shape, with dorsal apex extending medially in one line with the medial tuberosity of the trochlea (ZPAL AbIII/2411, ZPAL AbIII/3349/3, ZPAL AbIII/3357, ZPAL AbIII/3385); in the 1st phalanx of the 2nd digit the trochlea is asymmetrically developed (but less peculiar than in the 1st row phalanx of the 1st digit), markedly expanded transversely – comparably to the base of the phalanx, and forming distinct side projections in dorsal view; well-indicated, deep depression posteriorly to the trochlea on the dorsal surface of the phalanx; the base of the phalanx close to triangular in shape, with the dorsal apex extending laterally (ZPAL AbIII/341, ZPAL AbIII/3357, ZPAL AbIII/3381); in the 1st row phalanx of the 3rd digit, the trochlea is almost symmetrically developed; the transverse width of the trochlea is noticeably shorter than the transverse width of the base of the phalanx; dorsally the tongue-like notch of the trochlea is positioned directly in the middle; the depression posterior to the trochlea is distinct, but shallow in comparison with the 1st row phalanx of the 2nd digit; the base of the phalanx is close to triangular with the dorsal apex extending directly dorsally (in the middle of the shaft; ZPAL 502/65, ZPAL AbIII/3357, ZPAL AbIII/3368); in the 1st row phalanx of the 4th digit the dorsal tongue-shaped notch as well as the depression behind the trochlea is poorly indicated; the base is semicircular in proximal view without the distinct dorsal apex (ZPAL AbIII/3368, ZPAL AbIII/3445); in the 1st phalanx of the 5th digit the distal articulation surface of the tongue-shaped notch is not present and the surface is generally similar in shape to the distal articulation surface of the 5th metatarsal; in dorsal view its surface descend laterally, obliquely to the longitudinal axis of the phalanx; the fovea for the medial ligament is placed within the projection of a similar shape as in the 1st phalanx of the 2nd digit (ZPAL AbIII/3368).

The last phalanges before the unguals have the trochlea developed in the same manner as the 1st phalanx of the 1st digit, being distinctly triangular, asymmetrical, and more robust than in other phalanges (ZPAL AbIII/3357, ZPAL AbIII/3368, ZPAL AbIII/3455). The 2nd row phalanx of the 5th digit seems to have a very poorly developed fovea and appears to be flatter in comparison with other phalanges.

The claw-like unguals of the first four digits are identically developed and seem to have exactly the same morphology as the unguals of the manus (Dróżdż 2018): they are asymmetrically developed; proximally, they are tear-shaped in cross-section, with concave medial and convex lateral side; in dorsal view, they slightly curve laterally; they form a sharp-ended ridge dorsally; and the foveae for collateral ligaments are elongated and continue along almost the entire length of the unguals; their surface is covered by numerous small pits indicating the presence of a well-developed keratinous sheet (ZPAL AbIII/553/28, ZPAL AbIII/1981, ZPAL AbIII/3349/3, ZPAL AbIII/3357, ZPAL AbIII/3368, ZPAL AbIII/3455). The only difference between each of the unguals as well as between them and the unguals of the manus is size. It appears that the largest ungual of the manus is about the size of the middle digit ungual of the pes (Dróżdż 2018).

Appendicular osteoderms

The appendicular osteoderms are present in all articulated specimens of pes and crus (ZPAL AbIII/2508, ZPAL AbIII/3349/3, ZPAL AbIII/3349/4, ZPAL AbIII/3357, ZPAL AbIII/3368, ZPAL AbIII/3455). They are preserved in semi articulated position in ZPAL AbIII/3368.

It seems that the entire thigh and crus, tarsus and dorsal part of the pes was covered by osteoderms was covered by appendicular osteoderms (ZPAL AbIII/2508, ZPAL AbIII/3368).They are of similar morphology of appendicular osteoderms of manus (Dróżdż 2018). They vary in size and shape depend on the covered part of the body. The ones around pes and tarsus are semicircular or oval in shape, with the diameter varying from around 5 to 15 millimeters (ZPAL AbIII/2508, ZPAL AbIII/3349/3, ZPAL AbIII/3349/4, ZPAL AbIII/3357, ZPAL AbIII/3368, ZPAL AbIII/3455). It appears that osteoderms covering the tarsus are slightly smaller and more elongated than those covering the pes (ZPAL AbIII/3349/3, ZPAL AbIII/3349/4), possibly to not restrict mobility in the ankle joint.

Osteoderms covering the crus are larger. They are of distinctly ellipse shape with major axis varying from about 15 mm – 30 mm and minor axis from about 10 mm – 20 mm (ZPAL AbIII/2508 ZPAL AbIII/3368). As indicated by specimen ZPAL AbIII/3368 in life position they were arranged in longitudinal rows and did not cover each other.

Majority of appendicular osteoderms is flat from both ventral and dorsal side, especially those at the dorsal side of the pes (ZPAL AbIII/2508, ZPAL AbIII/3349/3, ZPAL AbIII/3368). At least some osteoderms at the tarsus and crus side developed distinct longitudinally oriented keels or sharply ended eminences (ZPAL AbIII/2508, ZPAL AbIII/3349/4, ZPAL AbIII/3455). The ventral side of osteoderms is smooth, the dorsal sides is delicately ornamented with the shallow randomly arranged canal and small pits. The margins of osteoderms is irregular unlike the margins of dorsal and ventral osteoderms (ZPAL AbIII/2508, ZPAL AbIII/3368, ZPAL AbIII/3349/3, ZPAL AbIII/3349/4, ZPAL AbIII/3455).

Skeleton of a juvenile aetosaur from Woźniki

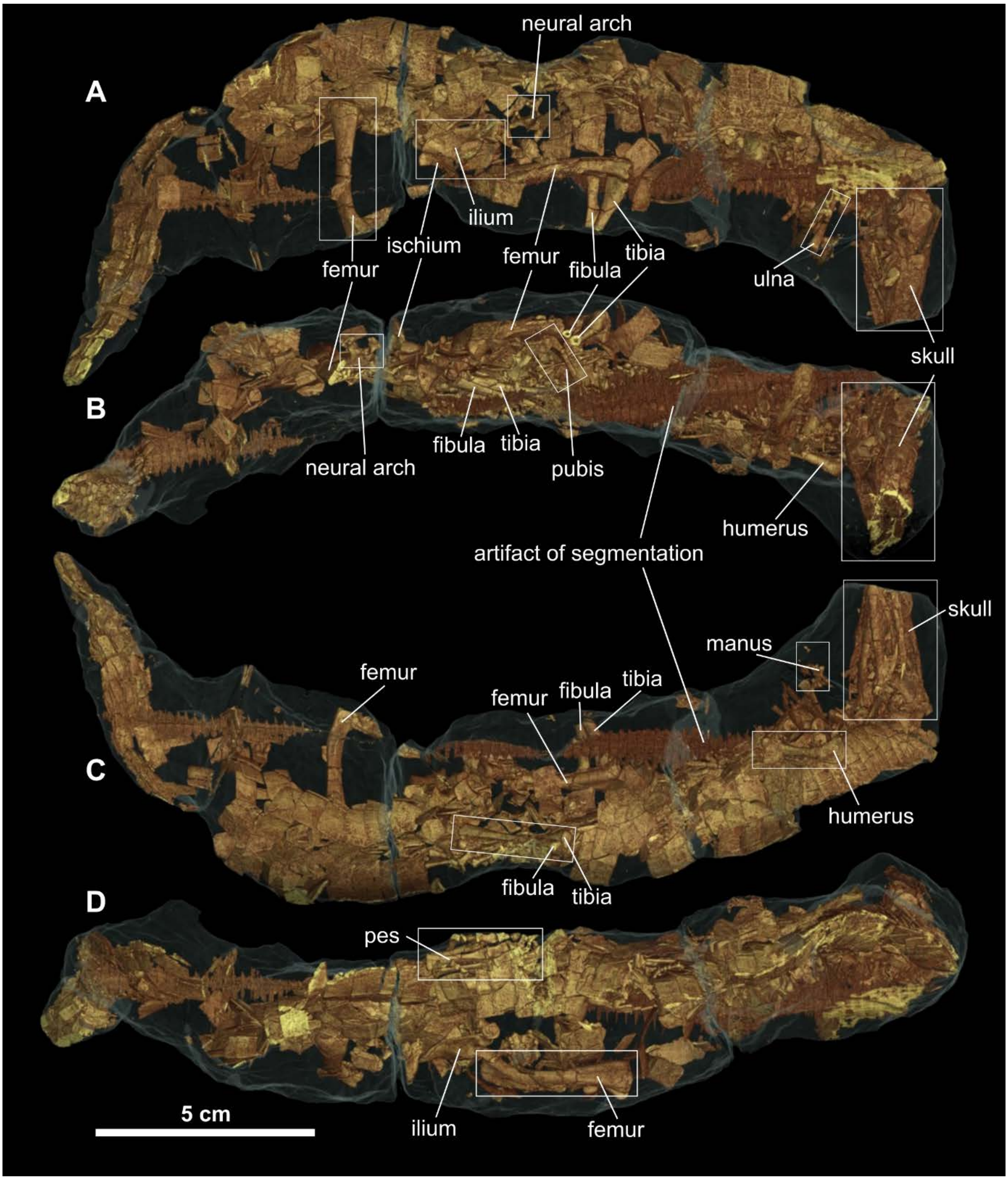


Figure 22. Juvenile aetosaur ZPAL V.34/106, visualization in lateral (A, C), ventral (B), and dorsal view (D). There is an artifact of segmentation running along the long axis of the specimen.

Axial skeleton

The skull (Fig. 22) lacks the anteriormost part, missing completely the premaxilla, almost entire nasals, and large parts of the maxillae, as well as most of the dentary, splenial, and

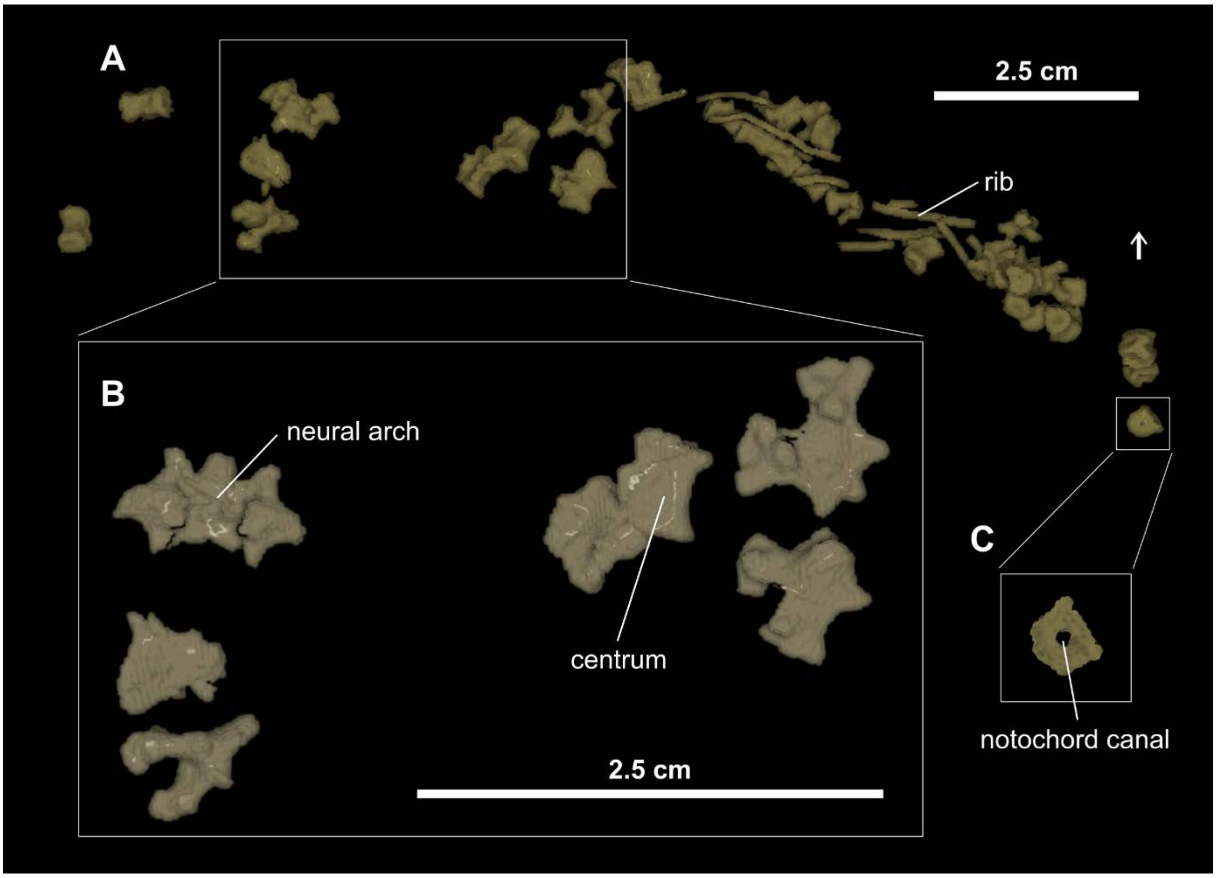


Figure 23. The anterior and middle part of the vertebral column of ZPAL V. 34/106. (A) General view; (B) close up of the sacral region; (C) close up of cervical vertebra. The arrow indicates the cranial direction.

angular. All other elements are present and semi-articulated. Several bulbous teeth are preserved in the maxillae. It seems that the complete skull was longer than the femora. Unlike in most aetosaurs, the elements of the skull roof are not fused together and the roof is not flat, but convex, without thick rugose areas. The orbits seem to be much larger in proportion to maxilla, frontals, and parietals (e.g., Case 1922; Walker 1961; Parrish 1994; Long and Murry 1995; Sulej 2010; Desojo et al. 2013; Schoch and Desojo 2016; Biacchi Brust et al. 2018). There is a distinct ridge over the orbitals on the frontal, similar to *Aetosauroides scagliai* (Casamiquela 1961; Biacchi Brust et al. 2018).

The vertebral column (Fig. 23) seems to be mostly complete. At least five cervical vertebrae, twelve dorsal vertebrae, and two sacral vertebrae have been identified, but it seems that all of the trunk vertebrae are preserved as some parts of the trunk are covered by osteoderms and not exposed. At least three tail vertebrae form the anterior part have been detected, but majority of the tail is entirely covered by osteoderms, therefore, until the segmentation of the specimen is complete, the exact number of preserved tail vertebrae cannot be given. Compared

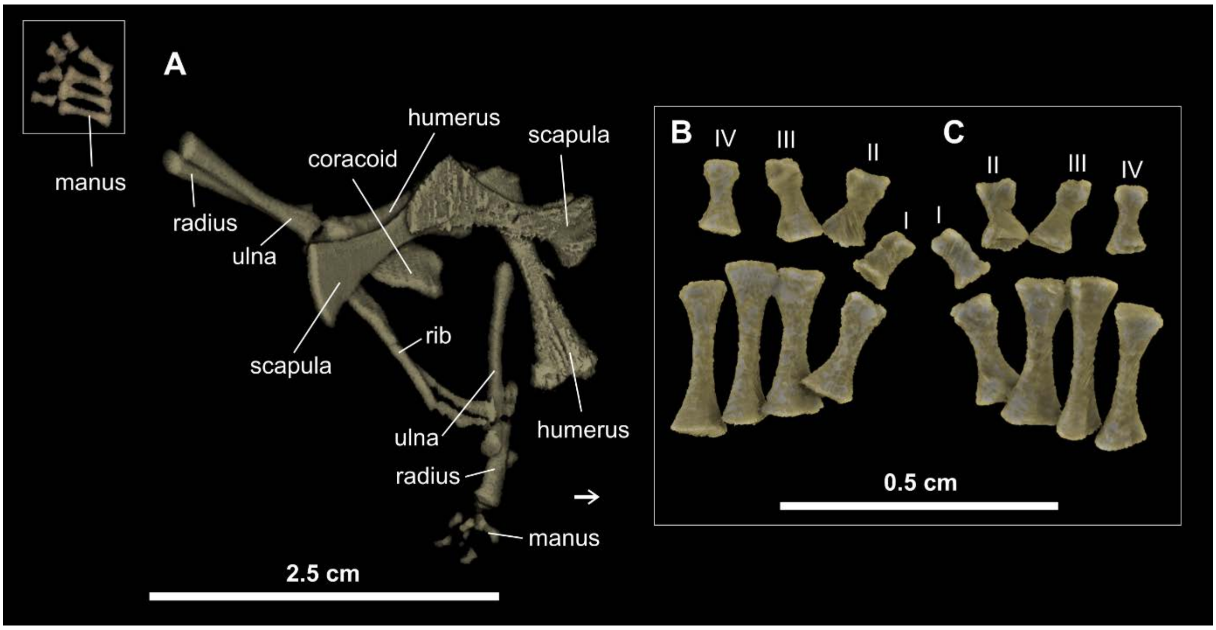


Figure 24. Pectoral girdle and forelimbs of ZPAL V. 34/106. (A) General view; (B) close up of the left manus in dorsal view; (C) close up of the left manus in ventral view. The arrow indicates the cranial direction.

to the articulated *Aetosaurus ferratus* (see Schoch 2007) the missing part of the tail seems to be at least one third of the entire tail length.

The centra are completely separate from the neural arches in the cervical region, trunk, sacrum, and at least anterior part of the tail. In the cervical vertebrae centra have an open canal for the notochord. The ribs are disarticulated, but it appears that most of the rib cage is preserved. In the sacrum, different from other known aetosaurs, the transverse processes are not fused with the sacral ribs and spinous processes does not form a spine table. Also in the sacral neural arches, the neural canal seems to be enlarged in proportion to the transverse processes and spinous processes (e.g., Sawin 1947; Walker 1961; Long and Murry 1995; Lucas et al. 2002; Parker 2008).

Pectoral girdle

Both left and right scapula and coracoid are present (Fig. 24). The clavicles and interclavicle have not been recognized yet. The general shape of the pectoral girdle elements is the most similar to those of *Stagonolepis* spp., *Polesinesuchus aurelioi*, *Aetosaurus ferratus* (Walker 1961; Lucas et al. 2007; Schoch 2007; Roberto-Da-Silva et al. 2014). The scapula and coracoid are not fused together in the Woźniki specimen, which is generally characteristic for smaller aetosaurs such as *Aetosaurus ferratus*, *Polesinesuchus aurelioi*, and *Stagonolepis robertsoni* (Walker 1961; Schoch 2007; Roberto-Da-Silva et al. 2014). In larger aetosaurs, e.g., *Longosuchus meadei*, *Desmatosuchus* spp., and *Typothorax* spp. the elements are usually fused together forming the scapulocoracoid. In *Stagonolepis olenkae*, the fusion between the scapula and coracoid is present in large specimens (e.g., ZPAL AbIII/694, Lucas et al. 2007; ZPAL AbIII/3349; UOBS 02060, Książkiewicz 2014), but in smaller, e.g., ZPAL AbIII/2546 (Książkiewicz 2014), the scapula and coracoid are separate.

Forelimbs

Both the left and right humeri, as well as both ulnae and radii are present, as well as elements of both the right and left carpus and manus (Fig. 24). The left manus is more complete in having four metacarpals associated with the first row phalanges. The humerus is only slightly longer than the ulna and radius, with the ulna being about 80% of the humerus length, a proportion similar as in *Polesinesuchus aurelioi* and *Aetosaurus ferratus* (Schoch 2007; Roberto-Da-Silva et al. 2014). Morphology of the forelimb long bones is also similar as in those aetosaurs, with both the proximal and distal ends poorly developed. In the Woźniki specimen, the proximal part of the humerus is expanded transversally only to the width of the distal condyles, and the humeral head is flat in dorsal view (similarly as in *P. aurelioi* and *A. ferratus*); while in larger species (for example, *Typothorax* spp., *Stagonolepis* spp., *Desmatosuchus* spp., or *Longosuchus meadei*), the proximal part of the humerus is noticeably extended compared to the distal part and the femoral head is prominently convex. Similarly, the olecranon process of ulna is much shorter, as in *Polesinesuchus* and *Aetosaurus*, in opposition to larger species (Sawin 1947; Small 1985; Long and Murry 1995; Lucas et al. 2002; Martz 2002; Schoch 2007; Heckert et al. 2010; Roberto-Da-Silva et al. 2014; Dróżdż 2018).

No significant differences between the manus of the Woźniki specimen and other aetosaurs (Sawin 1947; Walker 1961; Long and Murry 1995; Martz 2002; Heckert et al. 2010; Lucas and Heckert 2011; Dróżdż 2018) have been detected. They seem to be the most similar to those of *Aetosaurus ferratus* and *Aetosauroides scagliai*, because they are more gracile in comparison to the heavily built manus of larger species, such as *Longosuchus meadei* or *Typothorax* spp. (e.g., Sawin 1947; Casamiquela 1961; Schoch 2007; Heckert et al. 2010; Lucas and Heckert 2011)

Pelvic girdle

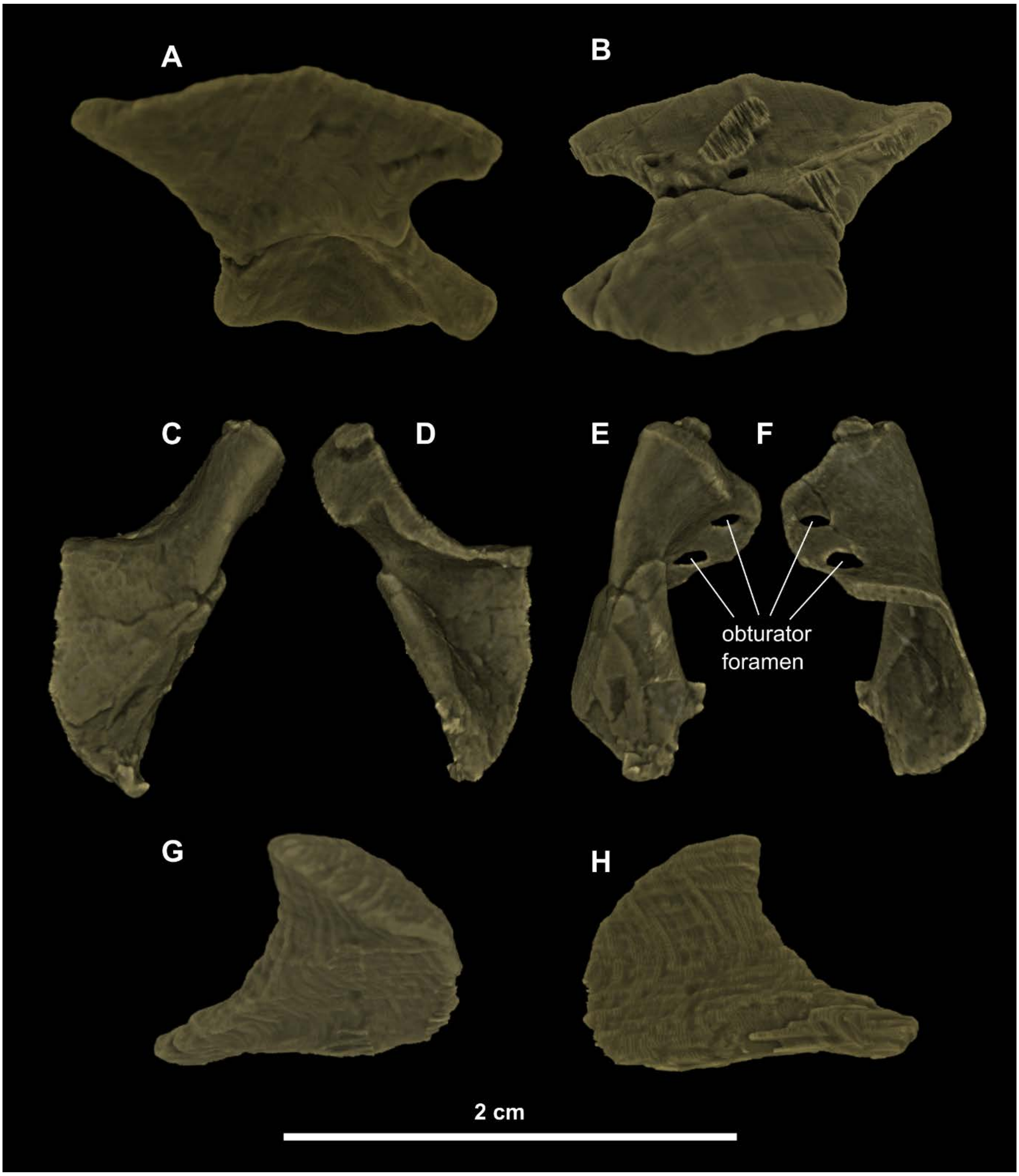


Figure 25. Pelvis elements of ZPAL V. 34/106. Right ilium in lateral (A) and medial (B) view; left pubis in anterior (C), posterior (D), lateral (E), and medial (F) view; right ischium in lateral (G) and medial (H) view.

Both the left and right ilium, pubis, and ischium are present. The elements of the pelvis are disarticulated (Fig. 22). Elements of the right side are well exposed and clearly visible in the scans. Elements of the left side are partially covered by osteoderms. The ilium (Fig. 25 A, B) is developed similarly as in one of the smallest skeletons of *Aetosaurus ferratus* (SMNS 5770, S-20; fig. 11a in Schoch 2007). It has a triangular preacetabular process that is equal in length to the pubic peduncle and a short postacetabular process. The pubis (Fig. 25 C – F) is developed in a similar manner as in *Stagonolepis olenkae* ZPAL AbIII/3266. It seems that it has a double obturator foramen, in the way proposed for *Stagonolepis robertsoni* by Walker (1961). The ischium (Fig. 25 G, H) takes a form typical for other aetosaurs, with the shape similar to, e.g., *Stagonolepis* spp., *Calyptosuchus wellesi*, or *Aetosaurus ferratus* (Walker 1961; Schoch 2007; Parker 2018*a*).

Hind limbs

Figure 26. The femur (A–F); tibia (G–L), and fibula (M–R) of ZPAL V. 34/106 in anterior (A, G, M), medial (B, H, N), posterior (C, I, O), lateral (D, J, P), proximal (E, K, Q) and distal (F, L, R) view. The arrows indicate the cranial direction.

The hind limbs (Fig. 26, Fig. 27) are less complete and more disarticulated than the forelimbs. The right femur (Fig. 26 A – F) is preserved in its entirety and associated with the

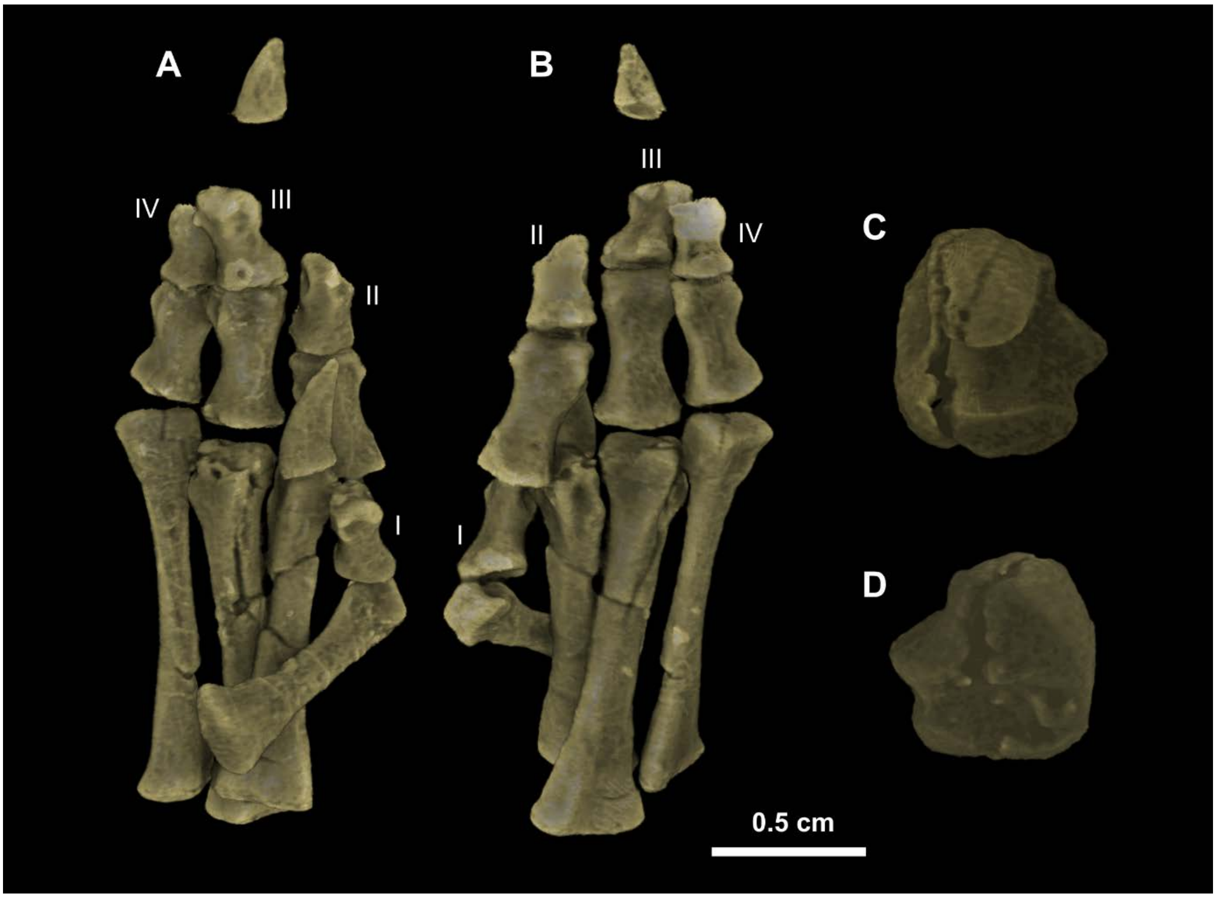


Figure 27. Pes (A–B) and calcaneum (C–D) of ZPAL V. 34/106 in dorsal (A, C) and ventral (B, D) view.

right ilium and the proximal parts of the tibia and fibula (Fig. 22). The latter two are broken at about half of their entire length and slightly displaced from their natural position. The right pes is missing. The left femur is positioned distally and filliped in relation to its natural position so the condyles are oriented toward the specimen’s body. Its head is broken off and not preserved in the specimen. The left tibia and fibula (Fig. 26 G – R) are preserved closer to the pelvis elements. They are complete and preserved in an association with the left pes (Fig. 27), which is partially articulated.

Proportions of the long bones are, as in the forelimbs, similar as in *Aetosaurus ferratus* and *Polesinesuchus aurelioi,* with the tibia and the fibula being about 80% of the femur length (Schoch 2007; Roberto-Da-Silva et al. 2014). They are much longer than those of larger forms such as *Stagonolepis* spp., *Longosuchus meadei*, *Typothorax* spp., or *Desmatosuchus* spp., in which the proportion of the crus to the femur is about 60% (e.g., Sawin 1947; Walker 1961; Long and Murry 1995; Heckert et al. 2010).

The development of the bones is also similar as in *Aetosaurus ferratus* and *Polesinesuchus aurelioi.* The bones are gracile compared to large aetosaur species and their proximal and distal articulation surfaces are poorly developed (e.g., Sawin 1947; Walker 1961; Long and Murry 1995; Schoch 2007; Heckert et al. 2010; Roberto-Da-Silva et al. 2014).

Only the calcaneum (Fig. 27 C, D) was recognized from the ankle joint. It is the most similar to *Polesinesuchus aurelioi*, because of the poor development of the ventral fossa on the calcaneal tuber; however, the calcaneum has a conservative morphology among the aetosaurs (e.g., Sawin 1947; Casamiquela 1961; Long and Murry 1995; Roberto-Da-Silva et al. 2014).

The morphology of the pes in the Woźniki specimen is the most similar to that of *Aetosaurus ferratus*, with the metatarsals and the phalanges being gracile and elongated compared to larger aetosaurs such as *Stagonolepis* spp., *Typothorax* spp., or *Longosuchus meadei* (e.g., Sawin 1947; Long and Murry 1995; Schoch 2007; Lucas and Heckert 2011). The preserved unguals belong to the first and the second digit. Their proportional size and shape is comparable as in other aetosaurs such as *Stagonolepis* spp., *Typothorax* spp., *Aetosauroides scagliai* and *Polesinesuchus aurelioi,* or *Longosuchus meadei* (e.g., Sawin 1947; Casamiquela 1961; Long and Murry 1995; Lucas and Heckert 2011; Roberto-Da-Silva et al. 2014).

Osteoderms

The osteoderms are mainly preserved in articulation and their position mostly reflects their natural arrangement, though the specimen is badly compacted. The dermal armor seems to be fairly complete in the trunk region as well as in the preserved part of the tail (including both dorsal and ventral osteoderms). The osteoderms are the most disarticulated around the area of the pelvis.

The osteoderms have a simple morphology characteristic for the “basal forms” such as *Aetosauroides scagliai*, *Stagonolepis* spp., *Aetosaurus ferratus*, and *Calyptosuchus wellesi* (Casamiquela 1961, 1967; Walker 1961; Long and Murry 1995; Schoch 2007). The dorsal paramedian osteoderms are of rectangular shape, have a radial ornamentation pattern, and are significantly shorter transversally than the osteoderms of *Typothorax* spp. and *Paratypothorax andressorum* (e.g., Long and Ballew 1985; Long and Murry 1995; Martz 2002; Heckert et al. 2010). The lateral osteoderms do not have spikes. The ventral osteoderms are square. No appendicular osteoderms have been detected.

Skeletochronology

In all three performed histological sections: the femur (Fig. 28 A, B), the humerus (Fig. 28 C, D), and the osteoderm (Fig. 28 E, F), at least three distinct growth marks (GM) can be detected. This results strongly implies the age of the individual as the three years old, with the margin of error being plus, minus one year. However, the assumption is that growth marks were formed in the same manner as in modern crocodiles, the closest living relative of Pseudosuchia (e.g., Brusatte et al. 2010*a*; Nesbitt 2011; Ezcurra 2016), in which the method proved to provide valid results (Tucker 1997). The long bone of Woźniki specimen lack the external fundamental system (EFS), which indicate that the animal was still growing and certainly does not reach the skeletal maturity at the moment of death (Woodward et al. 2011).

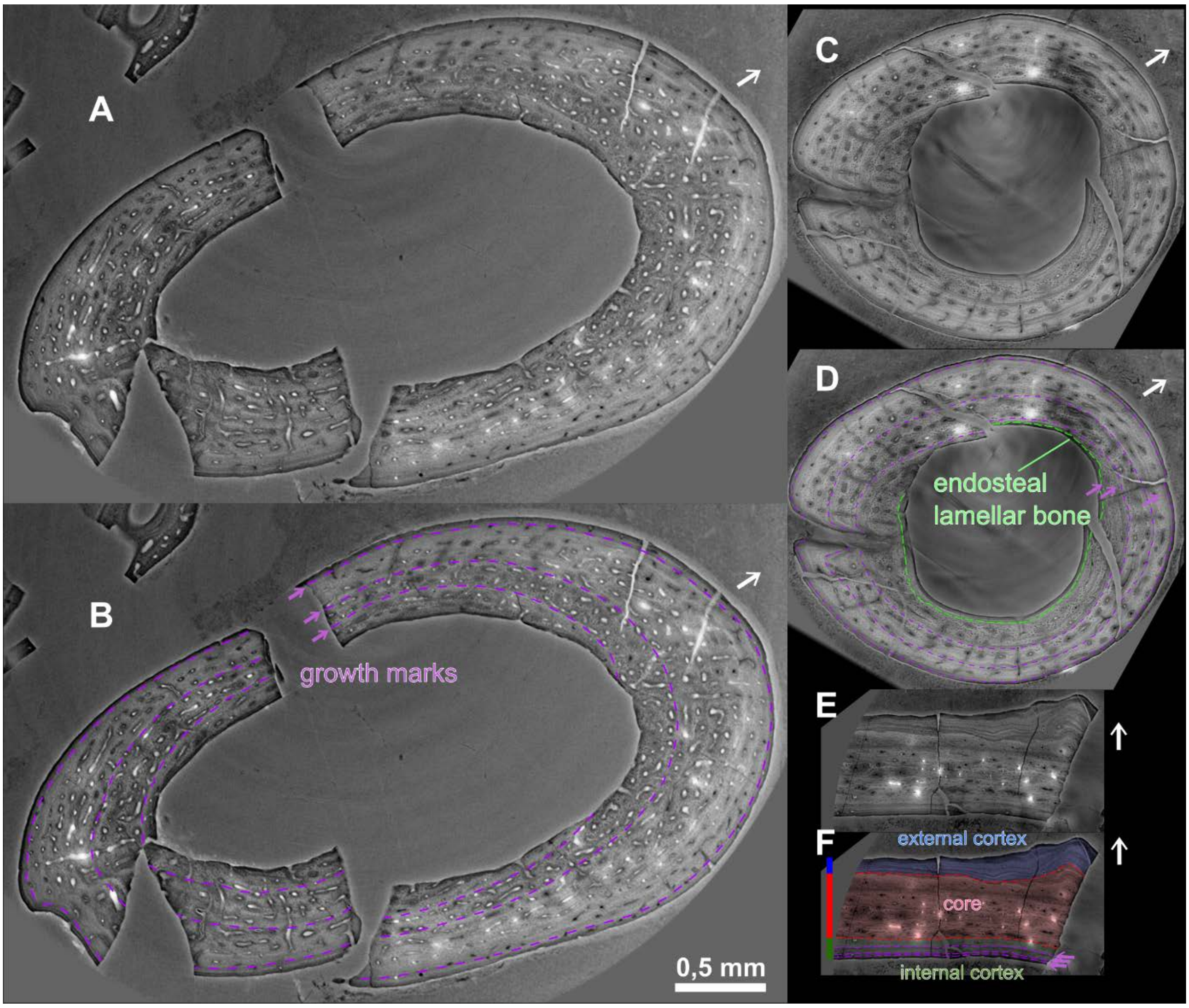


Figure 28. ZPAL V. 34/106, histological CT section of the femur (A, B), humerus (C, D), and dorsal paramedian osteoderm (E, F). The arrows indicate the cranial direction in A–D, and the dorsal direction in E, F).

STAGONOLEPIS OLENKAE AND OTHER AETOSAURS

Summary on the morphology of *Stagonolepis olenkae* in the context of other aetosaurs

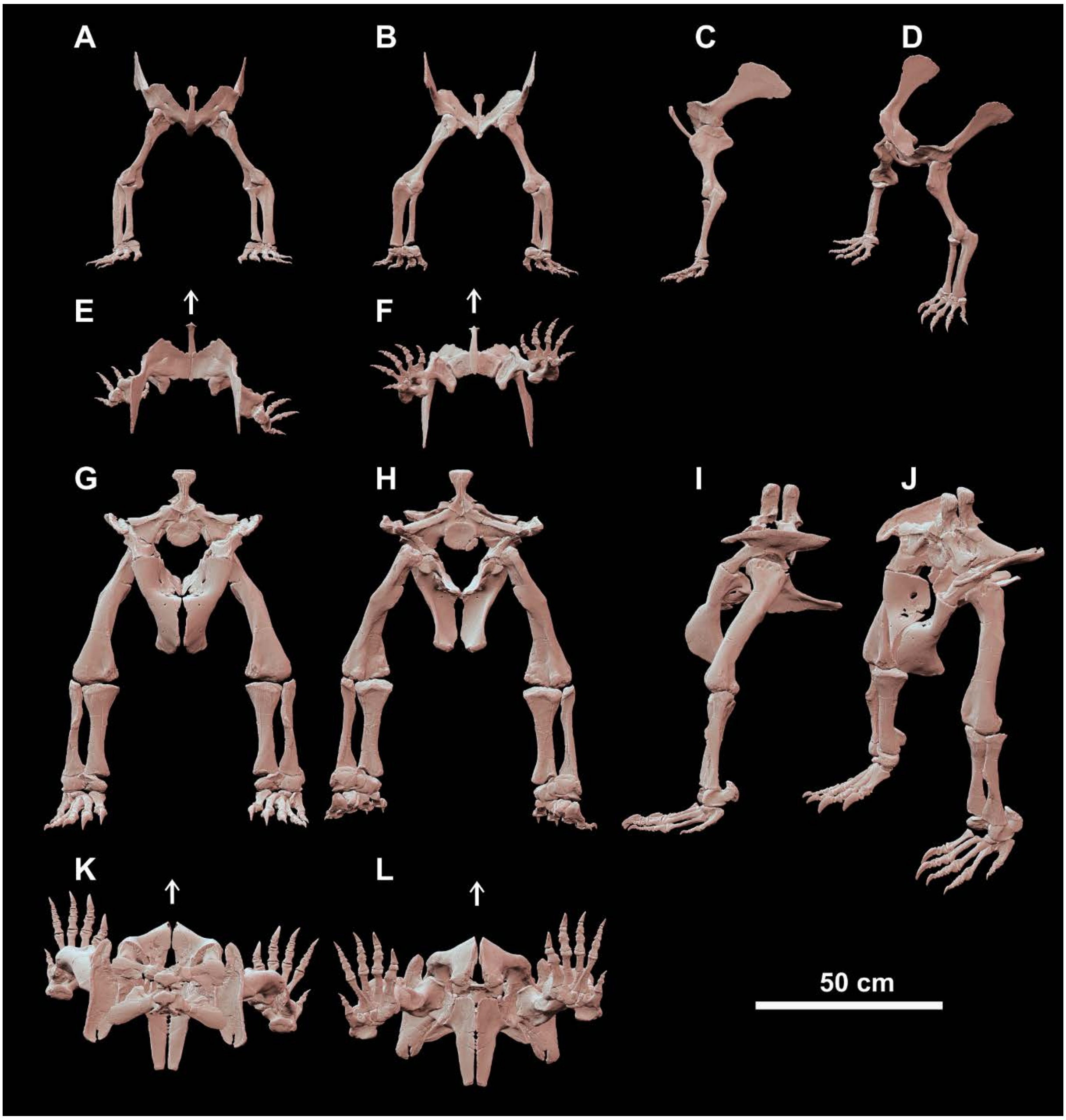


Figure 29. Reconstructions of the pectoral girdle and forelimbs (A–F) and pelvic girdle and hind limbs (G–L) of *Stagonolepis olenkae* in anterior (A, G), posterior (B, H), lateral (C, I), anterodorsolateral (D, J), dorsal (E, K), and ventral view (F, L). The arrows indicate the anterior direction.

Forelimbs

The forelimbs (Fig. 29 A – F) of *Stagonolepis olenkae* are robust, with the humerus having a prominent wide head and condyles, well-developed deltopectoral crest; dorsoventrally flattened ulna with high olecranon process; straight, stout radius, and sturdy short digits ending with claw-like unguals; with flattened, wide metacarpals and phalanges. Based on the literature and personal observations they are alike other large and middle size aetosaurs for example *Stagonolepis robertsoni, Longosuchus meadei, Typothorax spp., Desmatosuchus spp.,* or *Neoaetosauroides engaeus* (Sawin 1947; Walker 1961; Bonaparte 1971; Small 1985; Long and Murry 1995; Lucas et al. 2002; Martz 2002; Parker 2008; Heckert et al. 2010; Desojo et al. 2013). In small aetosaurs *Polesinesuchus aurelioi* and *Aetosaurus ferratus* the above features are less developed, and the forelimbs are more gracile (Schoch 2007; Roberto-Da-Silva et al. 2014). As both of the small species have been suggested to be juveniles (Schoch and Desojo 2016; Paes-Neto et al. 2021), the mentioned features could develop in ontogeny. Morphology of these small aetosaurs is also consistent with the small aetosaur form Woźniki.

Stagonolepis olenkae has some unique features in forelimbs that seem to distinguish it from other aetosaurs namely: presence of dermal amour covering the dorsal part of the manus; presence of enlarged ungual of the first digit in regard to other unguals of the manus; and in having square cross-section of the radius. However, these parts are poorly known in other species.

Pelvic girdle

Morphology of pelvic girdle and limbs (Fig. 29 G – L) recognized here for *Stagonolepis olenkae* is consistent with the other known aetosaurs and could be consider typical for the group. Observed differences are minor and do not affect any crucial aspects of anatomy that could have significant effect on stance, locomotion, as well as probable adaptations toward support of the heavy amour or scratch-digging. In some crown aetosaurs like *Typothorax* and *Desmatosuchus* these adaptations seem to be even enhanced in comparison to *S. olenkae* (Long and Murry 1995; Martz 2002; Heckert et al. 2010).

The degree of lateral inclination of iliac blades as well as orientation of acetabulum recognized in *S. olenkae* seems no different than what is present in most aetosaur e.g., *Desmatosuchus spurensis*, *Longosuchus meadei, Polesinesuchus aurelioi* (juvenile *Aetosauroides scagliai*), *Neoaetosauroides engaeus*, *Scutarx deltatylus* and *Calyptosuchus wellesi* (Case 1922; Sawin 1947; Bonaparte 1971; Small 1985; Long and Murry 1995; Parker 2008, 2016*b*, 2018*a*; Roberto-Da-Silva et al. 2014; Paes-Neto et al. 2021). The orientation of acetabulum present in those aetosaurs and referred as oblique to differentiate the vertical orientation prosed for *Aetosaurus ferratus* and horizontal orientation proposed for *Aetosauroides scagliai* and *Typothorax coccinarum* is functionally the same as the horizontal orientation of acetabulum, characteristic for pillar erect gait rauisuchians (Bonaparte 1984; Benton and Clark 1988; Desojo et al. 2013). However, the examination of the *Aetosaurus ferratus* (SMNS 5770) did not confirm any difference in this aspect relative to other mentioned aetosaurs. Similarly extreme lateral inclination in both *Aetosauroides scagliai* (PVL 2073, PVL 2052/14) as well as *Typothorax* (NMMNH P-36075) seem to be a taphonomical artefact caused by compaction rather than natural anatomical arrangement of those bones (Casamiquela 1961, 1967; Lucas et al. 2002). It seems that there is also no significant difference in anatomy of hind limbs which would support that change in acetabulum orientation.

Short anterior processes of the iliac blades, similar to *Stagonolepis olenkae* and *Stagonolepis robertsoni* are present at least in *Longosuchus meadei* (Sawin 1947; Long and Murry 1995), and larger individuals of *Aetosaurus ferratus* (Schoch 2007). It seems that mentioned species have also proportionally longer posterior process of iliac blade. Their morphology contrast most with *Typothorax coccinarum* in which the anterior process is probably longest among aetosaur exceeding pubic peduncle and shortest posterior process (Long and Murry 1995; Martz 2002). In most other aetosaurs the anterior process are equally long as the pubic peduncle (e.g., Casamiquela 1961, 1967; Long and Murry 1995; Parker 2016*b*, 2018*a*). Elongation of the anterior process as well as shortening of the posterior process could be beneficial for protraction of femur (Parrish 1986), therefore extreme elongation of the anterior process of *Typothorax* may be an evolutionary enhancement for more effective movement of limbs.

Arrangement of pubes with distally directed lateral edges of the pubic aprons, narrowing the lower part of the pelvis can be recognized in articulated specimens of *Scutarx deltatylus*, *Lucasuchus hunti*, *Desmatosuchus spurensis* (Long and Murry 1995; Parker 2008, 2016*b*). The same morphology suggesting this orientation can be recognized also in *Aetosauroides scagliai*, *Stagonolepis robertsoni*, *Aetosaurus ferratus* and *Typothorax coccinarum* (Casamiquela 1961, 1967; Walker 1961; Long and Murry 1995; Martz 2002; Schoch 2007).

Double obturator foramina seems to be not present in any currently known species in sense proposed by Walker (1961) including *Stagonolepis robertsoni*. However, the second obturator foramen is present in the small individual form Woźniki (Fig. 25 E –F), which suggest that it might be present at early stages of the ontogeny and close later.

The rugose pattern on the ischiadic symphysis similar to *Stagonolepis olenkae* can be recognized at least in *Stagonolepis robertsoni*, and weekly in *Polesinesuchus aurelioi* (juvenile of *Aetosauroides scagliai*), but the comb pattern is clearly present only in *Stagonolepis olenkae* (in *Stagonolepis robertsoni* the laminae are less developed, and do not form such a clear pattern). The feature is not mentioned or visible in other aetosaurs. In probable ischium of *Paratypothorax* (SMNS) symphysis is differently developed and does not form compound laminae present in both S. *olenkae* and *S. robertsoni* (Long and Murry 1995). Presence of the laminae and comb like structure in *S. olenkae* indicate that possibly the ischiadic symphysis were not fused together but there was cartilage bridge between and at least in *Desmatosuchus* and *Typothorax* the ischiadic symphysis was reported to be fused together at least in some specimens (Long and Murry 1995; Lucas et al. 2002; Parker 2008).

It seem that fusions between the pelvic girdle elements are relatively often among aetosaurs (e.g., Sawin 1947; Lucas et al. 2002; Parker 2008). They probably strengthen the pelvis to oppose external stress mostly generated by limbs. It seems that at least in *Stagonolepis olenkae* there is no strict pattern for appearance of those fusion in ontogeny as well as which elements will became fused. On the other hand, it appears that they are more likely to be present in large and presumably older individuals. They are not present in smallest aetosaurs *Polesinesuchus aurelioi* and *Aetosaurus ferratus* (Schoch 2007; Roberto-Da-Silva et al. 2014). None was recognized as well in *S. robertsoni* (Walker 1961)

Hind limbs

Distinctly medially bend shaft of femur is present in all known aetosaur species. In most aetosaurs similarly to *Stagonolepis olenkae* the pronounced medial shift of the shaft starts at one third of the femur height at the level of the middle part of the fourth trochanter e.g., *Longosuchus meadei*, *Desmatosuchus*, *Stagonolepis robertsoni*, *Aetosauroides scagliai* and *Polesinesuchus aurelioi*, *Aetosaurus ferratus* (Sawin 1947; Casamiquela 1961; Walker 1961; Small 1985; Long and Murry 1995; Schoch 2007; Roberto-Da-Silva et al. 2014). However in *Typothorax* and *Neoaetosauroides engaeus* the bending starts more proximal to the shaft at the top of the fourth trochanter (Bonaparte 1971; Martz 2002; Heckert et al. 2003)

Crus of *Stagonolepis olenkae* is short in portion to femur (Fig. 29 G – J), with dimensions similar for the most of the middle and large aetosaur e.g., *Desmatosuchus, Longosuchus, Typothorax, Neoaetosauroides, Aetosauroides, Calyptosuchus* (Sawin 1947; Casamiquela 1961; Bonaparte 1971; Long and Murry 1995; Martz 2002; Desojo and Báez 2005; Parker 2018*a*). In smallest aetosaurs *Aetosaurus* and *Polesinesuchus* the crus is longer being of equal length of the femur, which may indicate their better ability to run compared to other aetosaur (Hildebrand 1988; Schoch 2007; Roberto-Da-Silva et al. 2014).

The robustness of the long bones seems to differ between aetosaur species which is especially well visible in the crus. The thickness of the crus bones in *Stagonolepis olenkae* is comparable to middle size aetosaurs for example *Calyptosuchus*, *Neoaetosauroides*, and *Typothorax* (e.g., Bonaparte 1971; Long and Murry 1995; Lucas et al. 2002; Martz 2002; Desojo and Báez 2005; Heckert et al. 2010). Largest aetosaur *Desmatosuchus* seems to be more heavy built (e.g., Long and Murry 1995) and the smallest in *Aetosaurus* and *Polesinesuchus* the seem to be more gracile (Schoch 2007; Roberto-Da-Silva et al. 2014). Slender and more gracile tibiae compared to *S. olenkae* are also present in *Aetosauroides* and *Aetobarbakinoides* (Casamiquela 1961; Desojo et al. 2012). As expected, the increase of robustness seems to be correlated with overall mass of the animals. The robustness of the bones may also increase during ontogeny, as demonstrated at least for the pelvis of *S. olenkae*, but more data is needed to confirm that.

The well-developed gastrocnemius crest on tibia of *Stagonolepis olenkae* formed as deep as in *Stagonolepis olenkae* is another feature that has not been mentioned for other aetosaurs, thus it may be another feature unique for *Stagonolepis olenkae.* However, similar structures are present at least in the tibiae of *Polesinesuchus* and *Longosuchus* (Sawin 1947; Roberto-Da-Silva et al. 2014). Therefore, it is possible that it was present in other aetosaurs.

Compared to *Stagonolepis olenkae* iliofibularis trochanters is positioned more distally at least in *Desmatosuchus*, *Typothorax* and *Longosuchus* – the crown members of Aetosauria (e.g., Sawin 1947; Long and Murry 1995; Martz 2002; Parker 2016*a*). Distal migration of the iliofibularis trochanter would increase the maximum force available during flexion which would be beneficial in for example scratch digging. Therefore, it may indicate the progressive evolution toward this behavior. At least for *Desmatosuchus* more distal position of the iliofibularis trochanters is consistent with much better developed olecranon process compared to *S. olenkae* (Small 1985; Long and Murry 1995; Dróżdż 2018).

There is no significant difference in development of the ankle joint and pes between known aetosaurs. The phalangeal formula 2-3-4-5-3 seems to be the most accurate for currently known species. Large claw like unguals also can be recognized in several species regardless of their size.

Notes on the osteology of forelimbs

Morphology of the humerus

The overall shape and robustness of the humerus of *Stagonolepis olenkae* is most similar to large humeri of *Desmatosuchus smalli*, *D. spurensis*, and *Longosuchus meadei* (Sawin 1947; Small 1985; Long and Murry 1995; Parker 2008). 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* (see 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 Murry 1995; Martz 2002; Heckert et al. 2010). Also the middle section of the shaft appears to be proportionally longer than in *S. olenkae* (Long and Murry 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 as 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*, ZPAL AbIII/1175 and ZPAL AbIII/257 (Walker 1961). However, the smaller humerus of *S. olenkae* ZPAL AbIII/2627 (and comparable in size to *S. robertsoni*) also does not have the olecranon fossa. Large humeri of "*Argentinosuchus bonapartei*" (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). 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). The olecranon fossa present in large specimens of *S. olenkae* is comparable to that in *N. engaeus*

(Bonaparte 1971). In comparison to *S. olenkae*, the humeri of *Aetosauroides scagliai* (PVL 2073) and *Polesinesuchus aurelioi*, apart from being much smaller (about 0.40 the length of 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). 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). The ectepicondylar groove in studied specimens of *S. olenkae* is fully open 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). *S. olenkae* has a prominent supinator process. A marked supinator process is also present in *S. robertsoni* and *A. ferratus* (Walker 1961; Schoch 2007).

Morphology of the ulna and radius

The ulna of *Stagonolepis olenkae* has a shape typical for most aetosaurs, having a well-developed proximal part with high olecranon process and the shaft being wide mediolaterally and flattened dorsoventrally (e.g., Sawin 1947; Walker 1961; Schoch 2007; Roberto-Da-Silva et al. 2014). The olecranon process is partially cartilaginous, which is suggested also for *Longosuchus meadei* (Sawin 1947) and *Polesinesuchus aureolii* (Roberto-Da-Silva et al. 2014) The 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*, *T. coccinarum*, and *Neoaetosauroides engaeus* (Sawin 1947; Walker 1961; Bonaparte 1971; Lucas et al. 2002; Heckert et al. 2010). The olecranon process is lower in *S. olenkae* than in *L. meadei* and *Desmatosuchus smalli* (being around 0.25 of the entire ulna length in *L. meadei* 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* (PVL 2073) the olecranon process is shorter than in *S. olenkae* (being around 0.15 of the entire ulna length 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-DaSilva et al. 2014). The coronoid process in *S. olenkae* is elongated medially, pronounced, and with a sharp end (ZPAL AbIII/2014, 3351, fig. 6C, D), similar to *D. smalli* and "*Argentinosuchus bonapartei*" (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). In *A. ferratus*, *P. aureolii*, and *A. scagliai* (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).

The radius of *Stagonolepis olenkae* is similar as in other 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 ends in *S. olenkae* (in proportion to the entire length of the radius) is comparable as in *Longosuchus meadei*, *Stagonolepis robertsoni*, *Typothorax antiquus*, and *Typothorax coccinarum* (Sawin 1947, Walker 1961; Lucas et al. 2002; Heckert et al. 2010). In *Aetosaurus ferratus* and *Aetosauroides scagliai* (PVL 2073), the proximal and distal ends of the 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).

Morphology of the carpus

Stagonolepis olenkae is one of few aetosaurs with known carpal elements, along with *Aetosaurus ferratus*, *Longosuchus meadei*, *S. robertsoni*, and *Typothorax coccinarum* (Sawin 1947; Walker 1961; Schoch 2007; Lucas and Heckert 2011). The number of carpals in *S. olenkae* is four, which is similar to *L. meadei* and *T. coccinarum* (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* (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).

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, similar to *S. olenkae* (Sawin 1947). However, they are ranged differently - from largest to smallest. Although Sawin (1947), when preparing his restoration of *L. meadei*, did not have at 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 that the arrangement of the other carpal elements in one row was only his best assumption (Sawin 1947). Książkiewicz (2014) also suggest an arrangement of the carpal bones in a single row for *S. olenkae*, but he as well did not have any specimens with an articulated carpus. The previous arrangement of the carpals in two rows was indicated by ZPAL AbIII/2407 and ZPAL AbIII/3349/1, and the author was under the impression that the two carpals associated with III and IV metacarpals are in front of the radiale and intermedium, as well as ulnare. However as the author obtained 3D models of the specimen ZPAL AbIII/2071, and tried to arrange those in the proposed way he realized that there is no physical possibility to fit all carpal elements in proposed way and match them with metacarpals. It became clear that in contrary to initial predictions of the author the elements in ZPAL AbIII/2407 and ZPAL AbIII/3349/1 have been dislocated from their natural position. Therefore the author proposed new more plausible arrangement of carpal elements that is also acceptable with what is seen in ZPAL AbIII/2407 and ZPAL AbIII/3349/1.

Morphology of the manus

Palm bones, similarly as carpals, are also known for only a few aetosaurs apart from *Stagonolepis olenkae*. The others are *Aetosaurus ferratus*, *Longosuchus meadei*, *S. robertsoni*, *Typothorax coccinarum* (Sawin 1947; Walker 1961; Schoch 2007; Lucas and Heckert 2011). The metacarpals and phalanges of *S. olenkae* are robust, short, and dorsoventrally flattened similarly as in *L. meadei*, *S. robertsoni*, and *T. coccinarum* (Sawin 1947; Walker 1961; Lucas and Heckert 2011). The manus of *A. ferratus* seems to be more slender than that of *S. olenkae* and other known aetosaurs (Schoch 2007). Unfortunately, none of the described specimens of aetosaur manus has a 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 preserves all of the distal phalanges of the digits IV and V. Considering the number of phalanges in the preserved specimens and their size, the simplest 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 suggested by Książkiewicz (2014). The phalangeal formula proposed for *L. meadei* (2-3-4-5-2) cannot be applied to *S. olenkae* because in UOBS 02834, described by Książkiewicz (2014), the fifth digit has two phalanges even though the ungual is not preserved. It needs to be mentioned that the phalangeal formula proposed by Sawin (1947) could be a mistake, because the restoration of the manus of *L. meadei* (fig. 3c in Sawin 1947) shows two phalanges and a 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). In *A. ferratus*, the phalangeal formula cannot be determined (Schoch 2007). The claw-like unguals in *S. olenkae* are present on at least the first three digits (based on spec. ZPAL AbIII/2071), similarly as in *S. robertsoni* (Walker 1961). In *L. meadei,* they are preserved on the first two digits (Sawin 1947). In *S. olenkae*, the size of unguals decreases in a 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 the 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 *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, Ksiąkiewicz 2014, this study). It is probable that in *S. olenkae* the fifth digit was not functional during stepping, as was probably the case in *T. coccinarum* (Lucas and Heckert 2011). The fifth metacarpal of *S. olenkae* in ZPAL AbIII/3349, 3350 is dorsoventrally flattened, very wide (as wide as the metacarpal IV) and its proximal end is not distinct, however, in ZPAL AbIII/2071 and 2407 the fifth digit is thin, oval in cross section, and with a distinct proximal end. 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 ZPAL AbIII/3349 and ZPAL AbIII/3350 belong to larger individuals than ZPAL AbIII/2071 and ZPAL AbIII/2407.

Appendicular osteoderms in the forelimbs of other aetosaurs

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 as in *Aetosaurus ferratus* and *Typothorax coccinarum* (Schoch 2007; Heckert et al. 2010). The presence of osteoderms on the arms and forearms was also reported for *Stagonolepis robertsoni* (Walker 1961) and it is probable that they were also present in "*Argentinosuchus bonapartei*", since the appendicular osteoderms were found in the sediment associated with the humerus (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 a similar shape (Burns et al. 2013). The presence of such scales can be expected also in aetosaurs.

Notes on the osteology of the pelvic girdle

Proportions of the pelvic elements

Aetosaur ilia, pubes and ischia are generally of comparable length (Casamiquela 1961; Walker 1961; Small 1985; Long and Murry 1995; Martz 2002; Desojo et al. 2013; Parker 2016*b*, 2018*a*). As a result, pubes and ischia are comparatively shorter than in most other pseudosuchians, especially those with well-developed erect gait (Parrish 1986; Nesbitt 2011; Desojo et al. 2013). It seems that in the pelvis of *Stagonolepis olenkae* ZPAL AbIII/3349/5 the pubis is elongated to a degree similar as in *Desmatosuchus smalli* (TTU P-9024, TTU P-9172), *D. spurensis* (MNA V9300), and *Lucasuchus hunti* (TMM 31100-313) (Small 1985; Long and Murry 1995; Parker 2008). However, the association of *S. olenkae* ZPAL AbIII/3394 shows proportions similar as in *Stagonolepis robertsoni,* in which the differences in the length between the pelvic elements (especially proportions of the pubis and ischium) are smaller, although the pubis is still longer than the ilium and ischium, and the ischium is shorter than the ilium (Walker 1961). *Aetosaurus ferratus* and *Typothorax coccinarum* (Martz 2002; Schoch 2007), have the pubes and ischia of a corresponding length, shorter than the ilium. Heckert et al. (2010) particularly noted that the ischia of *T. coccinarum* NMMNH P-56299 are “strikingly short” in relation to the ilium. From the author’s personal experience, while preparing the restoration of the pelvis based on disarticulated and isolated material, it is difficult to properly set the size of the ischium, due to its minor contribution to the acetabulum. There is a tendency to oversize the ischium to match the acetabular part of the ilium, which might be misleading while restoring proportions. On the other hand, the length of the ischia might be variable, as the complete ischium of *S. olenkae* ZPAL AbIII/2265/2 (used for reconstruction) is proportionally longer and lower than, for example, the complete ischium ZPAL AbIII/3394/4. Elongated ischia in proportion to the ilium are present in *Aetosauroides scagliai* (Casamiquela 1961), but they are still shorter than the pubes, probably to a degree comparable with *S. olenkae* ZPAL AbIII/3394 and *S. robertsoni*. However, it seems that both pubes in *A. scagliai* PVL 2037 come from the left side of the body (in different individuals), and it seems that there is a substantial difference in their length (PVL 2073-17 is 9 cm and PVL 2073-18 is 7.5 cm – although it is not complete). To summarize, it seems safe to assume that in aetosaurs the pubes are expected to be longer than the ischia. However, the material of *S. olenkae* suggests that exact proportions between the pelvic elements might be highly variable, therefore, it is discouraged to use this character for taxonomical purposes. It seems interesting though, that in larger aetosaurs the pubes appears to be more elongated than in the smaller ones, which is accurate also for ZPAL AbIII/3349/5 and ZPAL AbIII/3394.

Specific morphology of the iliac blade

Iliac blade is considered specific among aetosaurs and often used for species discrimination, and cladistics analysis (e.g., Long and Murry 1995; Martz 2002; Parker 2008, 2016*a*, *b*, 2018*b*, *a*). However, as indicated by the material of *Stagonolepis olenkae*, there is a much higher variation in regard to the development of this structure than anticipated, therefore, its use for systematic purposes must be treated with caution.

Apparently, in *Stagonolepis olenkae* the pelvis increased its robustness during ontogeny, which has its impact on the thickness of the iliac blade. Similarly, the lack of ornamentation on the lateral side of the iliac blade in the most robust ZPAL AbIII/1937 might also be an effect of ontogeny, as the tendon attachment area might have been incorporated within the growing lateral margin of the iliac blade, almost not indicated in other *S. olenkae* specimens.

Ontogenetic change in the morphology of the anterior and posterior processes is suggested also for *Aetosaurus ferratus* (Schoch 2007) (mentioned as an example of a morphology similar as in *S. robertsoni* by Parker (2018*b*)). Among the two ilium specimens of SMNS 5770, in the larger SMNS 5770 S-22 the preacetabular process is curved dorsally and seems to be thin and short in the proportion to the pubic peduncle, while in SMNS 5770 S-20 the preacetabular process reaches the anterior margin of the pubic peduncle and is triangular (Schoch 2007). The postacetabular process in SMNS 5770 S-22 is much longer and more acutely angled than in SMNS 5770 S-20 (Schoch 2007).

Additionally, much of the comparable material is highly deformed due to the preservation or taphonomic factors (e.g., Casamiquela 1961, 1967; Walker 1961; Bonaparte 1971; Long and Murry 1995; Lucas et al. 2002; Desojo and Báez 2005). For example, the autapomorphic shapes of the pre- and postacetabular processes in *Stagonolepis robertsoni* recognized by Parker (2018*b*) appear to be artifacts of the poorly preserved ilium R 4789, while in fact (beside the length), the morphology of those processes in both *S. olenkae* and *S. robertsoni* is similar as in most other aetosaurs (Sawin 1947; Casamiquela 1961, 1967; Bonaparte 1971; Long and Murry 1995; Lucas et al. 2002; Desojo and Báez 2005; Parker 2018*b*).

An extremely elongated anterior iliac process of *Typothorax coccinarum* may indicate a better ability to protract the femur than in other aetosaurs species (Parrish 1986; Long and Murry 1995; Martz 2002). However, its adaptive function is difficult to determine without a biomechanical analysis.

The S-shaped morphology of the lateral margin of the iliac blade in *Stagonolepis olenkae* seems to be a normal aetosaur state. It has the same form as in, for example, *Aetosauroides scagliai* (PVL 2073, PVL 2054), *Desmatosuchus spurensis* (MNA 9400), *Polesinesuchus aurelioi* (ULBRAPVT003), *Calyptosuchus wellesi* (UCMP 25941), and *Typothorax antiquum* (NMMNH P-36075) (e.g., Casamiquela 1961, 1967; Long and Murry 1995; Lucas et al. 2002; Parker 2008, 2018*a*; Roberto-Da-Silva et al. 2014)

Orientation of the acetabulum

Desojo et al. (2013) pointed out three possible orientations of the acetabulum in aetosaurs: vertical (as in *Aetosaurus ferratus*), oblique (as in *Desmatosuchus spurensis* and *Neoaetosauroides engaeus*), and horizontal (as in *Aetosauroides scagliai*, *Typothorax antiquum*, and *Typothorax coccinarum*). Based on this variability, they speculated that that aetosaurs were very diversified in the terms of locomotion (Desojo et al. 2013).

Articulated pelves of *Stagonolepis olenkae* can be assigned into two of the above categories: horizontal (ZPAL AbIII/3349/5) and oblique (ZPAL AbIII/1937). However, because ZPAL AbIII/3349/5 is clearly compacted dorsoventrally and laterally, the oblique orientation of the acetabulum in stouter ZPAL AbIII/1937 is more probable for *S. olenkae*.

Casamiquela (1961, 1967) proposed a subhorizontal orientation for *Aetosauroides scagliai*, however, he was well aware of the deformations in both PVL 2054/14 and PVL 2073, and left the problem open until new findings are described. It seems that the pelvis of *A. scagliai* (PVL 2073) suffered a similar deformation as ZPAL AbIII/3349/5. The dorsoventral and lateral compaction of *A. scagliai* PVL 2073 is suggested by an oblique position of its neural spines, deformed shape of the centrum in the second vertebrate, and unequal shape of the right and left ilium, as well as the rotation of the ischia toward the left lateral side. Therefore, an oblique orientation of the acetabulum is more likely for this species.

It is probable that the pelvis of *Typothorax antiquum* (NMMNH P-36075) is as well compacted dorsoventrally and laterally deformed toward its right lateral side, as the neural spine in the second sacral is slightly oblique toward the right lateral side, and right ilium and pubes are shifted toward the right lateral side in a manner similar as in *A. scagliai* PVL 2073 and *S. olenkae* ZPAL AbIII/3349/5 but that is not as clear as in the latter two.

As for *Aetosaurus ferratus*, the anatomy of the ilium in this species is overall similar to that of other aetosaurs, especially in having a high iliac blade (Schoch 2007). The pelves of *A. ferratus* are only partially articulated and the ilia are not twisted as in *Aetosauroides scagliai* and *Typothorax antiquum* (Schoch 2007). A horizontal orientation and lateral expansion of the iliac blades (high iliac blades) in aetosaurs were interpreted by Parrish (1986) as an adaptation for supporting the weight of the posterior end of the armor as in ankylosaurs, armadillos, and glyptodonts. If this feature is indeed connected with the presence of the amour in aetosaurs, it is more likely that the position of the acetabulum in *A. ferratus* was oblique. In the reconstruction proposed by Schoch (2007), the ilia are oriented similar as in *S. olenkae*.

Considering the above, the horizontal and vertical orientations of the acetabulum observed in some aetosaurs might be artificial. Furthermore, in all known aetosaurs there is a marked supracetabular shelf, which is present also in *Aetosaurus ferratus*, *Aetosauroides scagliai*, and *Typothorax antiquum*, although variably developed (Casamiquela 1961; Walker 1961; Bonaparte 1971; Long and Murry 1995; Lucas et al. 2002; Desojo and Báez 2005; Schoch 2007; Parker 2008, 2016*b*, 2018*a*; Roberto-Da-Silva et al. 2014). The structure works as a bony stop preventing excessive femoral abduction, and is also present in, e.g., poposaurids with a pillar erect gait (Parrish 1986). However, its function would be dubious in the case of both the vertical and horizontal orientations of the acetabulum.

A compactive deformation proposed at least for *S. olenkae* (ZPAL AbIII/3349/5) and *Aetosauroides scagliai* (PVL 2073) might appear, because the effective pressure of the sediment on the iliac blades was higher than the pressure on the sacral vertebrae and ischia. If an aetosaur pelvis was buried in an anatomical orientation, the high and laterally pointing iliac blades form a much larger surface, than the sacrals. Therefore, if the pressure of the sediment was applied dorsally, the cumulative force of the sediment acting on the iliac blades would be higher than the force acting on the sacrals. That can be compared with a simple lever of equal arms on the verge of breaking. However, as it was made of a strong material with limited plastic properties (such as bone), instead of breaking, it curved towards ground. This would explain the unusual position of the ilia in *S. olenkae* (ZPAL AbIII/3349/5), *A. scagliai* (PVL 2073), and *T. antiquum* (NMMNH P-36075), and lack of this kind of deformation in more stout specimens such as *S. olenkae* ZPAL AbIII/1937. It would be worth checking experimentally.

Arrangement of the pubes

Position and orientation of the pelvic girdle elements in *Stagonolepis olenkae* are similar as in other aetosaurs, with the exception of the pubes (Casamiquela 1961; Walker 1961; Bonaparte 1971; Small 1985; Long and Murry 1995; Lucas et al. 2002; Martz 2002; Desojo and Báez 2005; Parker 2008; Heckert et al. 2010; Desojo et al. 2013). In most publications, the pubes were pictured as projecting ventrally and with the pubic aprons directed laterally (Casamiquela 1961; Walker 1961; Small 1985; Martz 2002; Heckert et al. 2010; Desojo et al. 2013), while in *S. olenkae* the pubes projected anteroventrally and the pubic aprons were directed posterolaterally. However, the arrangement of the pubes recognized in *S. olenkae* is most likely the natural position of the pubes in aetosaurs, not a special feature of this species.

The anterior projection of the pubes is indicated by the complete pelvis ZPAL AbIII/3349/5. Though ZPAL AbIII/3349/5 is deformed by compaction, if compared with the better preserved ilium ZPAL AbIII/199, ilium and sacrals ZPAL AbIII/1937, and pubis ZPAL AbIII/3266, it seems that this deformation had a minor influence on this aspect of the anatomy. Furthermore, the puboiliac suture is fully ossified in the pelvis ZPAL AbIII/3349/5, therefore, there is no doubt about the direction of articulation of these elements. Anteriorly projecting pubes, as in *S. olenkae,* can be also recognized in the pelvis of *Scutarx deltatylus* (PEFO 31217) and, to a lesser degree, in *Lucasuchus hunti* (TMM 31100-313) (Long and Murry 1995; Parker 2016*b*). It seems probable that the pubes were also more anteriorly directed in *Desmatosuchus spurensis* (MNA V9300), but as the specimen is anteroposteriorly compacted, it is difficult to determine (Parker 2008). Anteroventrally projecting pubes were also reconstructed by Schoch (2007) for *Aetosaurus ferratus* and by Casamiquela (1961) for *Aetosauroides scagliai*. This orientation of the pubes for *Aetosauroides* (PVL 2073) is also confirmed by the reconstruction made in this study.

The posterior direction of the pubic aprons is indicated mostly by the shape of the pubic symphysis in the pubis ZPAL AbIII/3266 and arrangement of the pubes in the pelvis ZPAL AbIII/3349/5. The middle and dorsal portion of the articulation surface of the symphysis in ZPAL AbIII/3266 is oriented in the sagittal plane, uniformly developed, and continues without spaces toward the iliac peduncle. If the pubic aprons were directed laterally, that would create a large opening in the dorsal portion of the symphysis, which seems unlikely because complete aetosaur pelves are rather compact structures (Long and Murry 1995; Lucas et al. 2002; Parker 2008, 2018*b*). This development of the pubic symphysis in *Stagonolepis olenkae* results in the pubic aprons directed posteriorly as in the pelvis ZPAL AbIII/3349/5, and this arrangement is present also in articulated pelves of *Desmatosuchus spurensis* (MNA V9300), *Lucasuchus hunti* (TMM 31100-313), and *Scutarx deltatylus* (PEFO 31217) (Long and Murry 1995; Parker 2008, 2016*b*). Unfortunately, in the other known pubes of aetosaurs, the middle and dorsal portions of the pubic flange are not preserved, or at least not entirely (Casamiquela 1961; Long and Murry 1995; Martz 2002; Parker 2008; Roberto-Da-Silva et al. 2014). In the reconstruction of *Aetosauroides scagliai* pelvis published by Casamiquela (1961), the pubic aprons are also directed posteroventrally, however, aside of this element, their position is pictured entirely differently. Nonetheless, as shown in the 3D reconstruction of the *A. scagliai* pelvis PVL 2073 with the pubis PVL 2073-18, a similar morphology and arrangement as in *S. olenkae* can be recognized in this species. Furthermore, comparison of the relative positions of the pubic distal knob in regard to the iliac peduncle in *A. scagliai* (PVL 2073-17), as well as development of the pubic symphysis (PVL 2054/14) (Casamiquela 1961, 1967) suggest a posterolateral orientation of the pubic aprons, just as in *S. olenkae*. The orientation of the pubes proposed for *S. robertsoni* by Walker (1961) was done based on disarticulated material. Furthermore, the crucial area of the middle and dorsal portions of the pubic symphysis is not preserved in the pubis of *S. robertsoni* R 4793. Therefore, considering the overall similarities of *S. olenkae* and *S. robertsoni*, the same arrangement of the pubes is expected also in the latter species.

The arrangement of the pubes recognized in *Stagonolepis olenkae* has biomechanical benefits over the previously proposed position. The pubes are the areas of attachment of muscles responsible for protraction and retraction of the femur (Parrish 1986; Piechowski and

Tałanda 2020). A more anterior projection and elongation of the pubes would increase the strength of those moves by elongating the in-lever arm of the muscles causing them (Hildebrand 1988). This effect caused by an elongation of the pubis is observed in pseudosuchians with an erect gait (Parrish 1986). The posterior orientation of the pubic aprons in *S. olenkae* significantly narrows the lower portion of the pelvis, which is also beneficial in an erect or semi erect gait, as it makes more space for parasagittal movements of the femur, therefore enabling longer steps and reducing the distance between the limbs, making the animal posture more stable (Parrish 1986; Hildebrand 1988).

Obturator foramen

The idea of aetosaurs having two obturator foramina was introduced by Walker (1961), and for a time being this character became one of the key features that distinguished aetosaurs from other contemporary groups (Long and Murry 1995). However, it seems that Walker (1961) incorrectly interpreted the specimen R 4793 (Fig. 30: fig. 16 in Walker's description, the specimen has two casts that show the medial and lateral portions of the pubis). The medial margin of the pubic flange is not preserved in R 4793, which is why for the rest of the specimen Walker used the outline of MCZD 4 (Walker 1961). Most likely, he deduced the presence of a second foramen based on the lateral cast of R 4793, in which, ventrally to the obturator foramen, there is an artificial projection that imitates a margin of another opening, and that could mislead him (Walker 1961). The surface of the area of the opening is flat and uniform with the rest of the specimen, and beside the projection, there is no other feature that could indicate the presence of an additional foramen (R 4793, lateral cast). On the medial cast of R 4793, the portion of the pubic flange with the supposed foramen is not preserved. Moreover, the medial cast of R4793 has a nearly identical morphology to *S. olenkae* ZPAL AbIII/3266, in which the presence of the second foramen can be clearly excluded.

Although both *Stagonolepis robertsoni* and *S. olenkae* have only a single obturator foramen, the presence of two foramina was described in the pubis of *Scutarx deltatylus* (PEFO 31217) (Parker 2016*b*). However, one of the foramina in *Scutarx deltatylus* is positioned within the acetabular ring of the pubis. Most likely, it can be referred to an open canal between the acetabular buttress and the pubic flange (e.g., *S. olenkae* ZPAL AbIII/3266), which is closed in *Scutarx deltatylus* (PEFO 31217). A similar condition may be present also in *Longosuchus meadei*, which is suggested by an illustration of the pelvis (Sawin 1947 fig. 5 a, University of

Texas 31185-84a) that seems to have the foramen within the acetabulum at an analogical position as *Scutarx deltatylus* (PEFO 31217).

Ischiadic symphysis

The ischia of *Stagonolepis olenkae* are developed in a similar manner as in most aetosaurs (e.g., Sawin 1947; Casamiquela 1961; Walker 1961; Casamiquela 1967; Bonaparte 1971; Long and Murry 1995; Martz 2002; Schoch 2007; Parker 2008, 2016*b*, 2018*a*; Roberto-Da-Silva et al. 2014). A different development of the ischiadic symphysis in comparison to other pelvic sutures suggests a limited movement between the ischia. Unusual, vertically oriented ridges, most indicated in the anterior part, forming there a comb-like structure, are present across the entire surface of the ischiadic symphysis in *S. olenkae*. They were most likely complementary between the contralateral ischia and stiffened the symphysis, restricting movements of the ischia and preventing them from dislocation. Similar structures are present in the ischia of *S. robertsoni* (R 4790, left and right ischium), *Polesinesuchus aurelioi* (ULBRAPVT003), and *Aetosauroides scagliai* (PVL 2052/14) (Walker 1961; Casamiquela 1967; Roberto-Da-Silva et al. 2014). The most conspicuous laminae-like ridges in the anterior part of the ischium of *S. olenkae* may result from the progressive ossification of cartilage and/or fibrous connection between the contralateral ischia, and therefore, the morphology might have been connected with ontogeny and more advanced ontogenetic age of the studied individuals from Krasiejów.

Notes on the osteology of hind limbs

Shape of the femur

The proximal end of the femur in *Stagonolepis olenkae* is formed in a way characteristic for pseudosuchians. It seems that there is a small difference of the head torsion degree between *Stagonolepis olenkae* and other aetosaurs, such as *Aetosauroides scagliai* (PVL 2073), *Desmatosuchus smalli* (TTUP 9024), *Longosuchus meadei* (TMM 31185-84a), or *Typothorax coccinarum* (UCMP V2816 34248 70/G7) (Sawin 1947; Casamiquela 1961; Small 1985; Parrish 1986; Long and Murry 1995; Carrano 2000; Martz 2002).

Distinct femoral head in *Stagonolepis olenkae* projects far medially (ZPAL AbIII/115, 3362, 3363, 3364, 3304, 3309, 2630) in a manner typical for archosaurs with erect posture, similar as in other aetosaurs, such as *Desmatosuchus smalli* (TTUP 9024), *Typothorax coc-*

cinarum (UCMP V2816 34248 70/G7, UCMP V2816 34225 70/U80, TTUP 9214), *Longosuchus meadei* (TMM 31185-84a, 31185-84b), or *Neoaetosauroides engaeus* (PVL 3525) (Sawin 1947; Bonaparte 1971; Small 1985; Parrish 1986; Long and Murry 1995; Martz 2002; Desojo and Báez 2005). Variation in the development of the medial tip of the head, with or without a pronounced articular surface, has not been reported for other species.

Distinct medial bend of the femur in *Stagonolepis olenkae* is similar as in most aetosaurs, such as *Aetosauroides scagliai* (PVL 2073-2), *Polesinesuchus aurelioi* (ULBRAPVT003), and *S. robertsoni* (MCGD 1, E.M. 46) (Casamiquela 1961; Walker 1961; Roberto-Da-Silva et al. 2014). It seem to be different from *Neoaetosauroides engaeus* (PVL 3525) and *Typothorax coccinarum* (UCMP V2816/122674, UCMP V2816/122673, UCMP V2816 34248 70/G7), because in those species the medial shift of the femur starts more proximally, closer to the femoral head (at about 0.7 of the bone length measured from the distal end), above the fourth trochanter, and therefore their femora seem to be straighter (Bonaparte 1971; Long and Murry 1995; Martz 2002).

The shaft of *Stagonolepis olenkae* is subcircular in cross-section, forming a flat surface posteriorly. However, the cross section may seem more rectangular in specimens that are crushed anteroposteriorly. Exactly the same deformed morphology can be observed also at least in *S. robertsoni* (MCGD 1), but compaction along the long axis of long bones is observed in a lot of aetosaurs (e.g., Casamiquela 1961, 1967; Bonaparte 1971; Long and Murry 1995; Lucas et al. 2002).

It seems that there are no significant differences in the development of the distal part of the femur between *Stagonolepis olenkae* and other known aetosaurs (e.g., Sawin 1947; Casamiquela 1961; Bonaparte 1971; Small 1985; Long and Murry 1995; Lucas et al. 2002; Martz 2002; Roberto-Da-Silva et al. 2014).

Morphology of the crus

The crus of *Stagonolepis olenkae* seems to be of moderate robustness compared to middle-sized aetosaurs, such as *Calyptosuchus wellesi* (UCMP 25887) and *Typothorax antiquum* (NMMNH P-36075) (Lucas et al. 2002; Parker 2018*a*); greater than in smaller aetosaurs such as *Aetobarbakinoides brasiliensis* (CPE2 168, fig. 13 in Desojo et al. 2012; tibia described there as a femur), *Aetosaurus ferratus* (SMNS 5770), *Aetosauroides scagliai* (PVL 2073), *Polesinesuchus aurelioi* (ULBRAPVT003); less indicated than in *Desmatosuchus spurensis* (UCMP A269/25886 ,UCMP 25877, UCMPA269/25880).

The tibia of *Stagonolepis olenkae* is developed typically for the group with a prominently transversally expanded head, straight shaft, saddle-shaped distal end forming a prominent tuber medially (e.g., Casamiquela 1961; Bonaparte 1971; Long and Murry 1995; Lucas et al. 2002; Martz 2002).

The ridge on the posteromedial side of the tibia ending with an oval fossa, recognized here as the m. gastrocnemius attachment, is probably the same as the structure described by Sawin (1947) for *Longosuchus meadei* (TMM 31185-84b) as an oval rugosity at one third of the proximal bone length. Examination of the material shows that a similar structure is present also in *Polesinesuchus aurelioi* (ULBRAPVT003) but it is much less developed than in *Stagonolepis olenkae*. Due to poor preservation, it cannot be recognized in *Aetosauroides scagliai* (PVL 2073), *Neoaetosauroides engaeus* (PVL 3535), and *Aetobarbakinoides brasiliensis* (CPE2 168). Its presence is not visible in *Aetosaurus ferratus* (SMNS 5770). The literature does not mention it for other aetosaurs.

The Y-shaped scar on the posterior surface of the tibial shaft in *Stagonolepis olenkae* is not mentioned in aetosaur literature, neither was it recognized during examination of other aetosaur specimens. This character is not observable in *S. robertsoni*, therefore, it could be a unique feature of *Stagonolepis*.

Another interesting feature is that when compared fibulae of other aetosaurs to *Stagonolepis olenkae*, it seems that the iliofibularis trochanter in *Typothorax* (e.g., UCMP V2816 34248 70/G6, NMMNH P-36075), *Desmatosuchus* (UCMPA269/32392), as well as *Longosuchus* is positioned more distally; while in *Aetosaurus ferratus* (SMNS 5770), *Aetosauroides scagliai* (PVL 2073), *Neoaetosauroides engaeus* (PVL 3525), and *Polesinesuchus aurelioi* (ULBRAPVT003) it is positioned at the same height as in *S. olenkae* (Casamiquela 1961; Bonaparte 1971; Long and Murry 1995; Lucas et al. 2002; Martz 2002; Schoch 2007; Roberto-Da-Silva et al. 2014). M. iliofibularis flexes the knee, therefore the iliofibularis trochanter is an analogical structure to the olecranon process in the forelimb (e.g., Piechowski and Tałanda 2020). Its more distal migration might be a specialization to scratch digging, as it would make the flexion easier and allow to produce larger forces at the tip of the pes (Hildebrand 1983, 1988).

Morphology of the ankle joint

Morphology of the ankle joint of *Stagonolepis olenkae*, as well as its individual bones, is generally the same as in other aetosaurs (e.g., Sawin 1947; Casamiquela 1961, 1967; Bonaparte 1971; Long and Murry 1995; Lucas et al. 2002; Martz 2002; Heckert et al. 2010; Lucas and Heckert 2011; Roberto-Da-Silva et al. 2014). It seems that there is little difference in the development of those elements between the species.

Calcaneum of *Stagonolepis olenkae* having a transversally wide ball and wide, short calcaneal tuber compared to other pseudosuchians, shares the shape with that of, e.g., *Neoaetosauroides engaeus* (PVL 3525), *Polesinesuchus aurelioi* (ULBRAPVT003), *Aetosauroides scagliai* (PVL 2073), *Desmatosuchus* (UCMP A269/34483, NMMNH P-33931), *Typothorax* (AMNH 2713, NMMNH P-36075, C-4638, cast of NMMNH P-12964, UCMP V2816/122228 Fa53, UCMP V2816/34255 70/U80), *Longosuchus meadei* (TMM 31185-84a), *Calyptosuchus wellesi* (UCMP A269/34481), and *Lucasuchus hunti* (TMM 31100-498) (Sawin 1947; Casamiquela 1961; Bonaparte 1971; Long and Murry 1995; Lucas et al. 2002; Martz 2002; Heckert et al. 2003, 2010). Walker (1961: fig. 19f) proposed a slightly different shape of the calcaneum for *S. robertsoni*, which he based on *Aetosaurus ferratus*, but examination of the Elgin Museum specimen (E.M. 30 W) revealed that it is undistinguishable from that of *S olenkae*. Although Schoch's (2007) illustrations of the calcaneum of *A. ferratus* seem to present a different morphology than in *S. olenkae*, during examination of the specimen SMNS 5770 also no significant differences were spotted. The calcaneum of *Polesinesuchus aurelioi* (ULBRAPVT003), compared to *S. olenkae* and other larger aetosaurs, has a very shallow fossa on the ventral side of the calcaneal tuber. However, according to Paes-Neto et al. (2021), *Polesinesuchus* is a juvenile *Aetosauroides scagliai* (PVL 2073), in which the fossa is significantly deeper, therefore it could be an ontogenetic change.

The astragalus of *Stagonolepis olenkae*, being transversally wide, with enlarged saddle-shaped dorsal surface for the tibia, as well as having a distinct peg and stout, pronounced dorsal process, is similarly developed as in other aetosaurs, such as *Typothorax* (NMMNH P-36075, NMMNH P33934, TTUP 9214), *Longosuchus meadei* (TMM 31185-84a), *Desmatosuchus* (NMMNH P-33932, UCMPA269/ 34472), *Calyptosuchus wellesi* (UCMP A269/34485), *Polesinesuchus aurelioi* (ULBRAPVT003), *Aetosauroides scagliai* (PVL 2073), and *Neoaetosauroides engaeus* (PVL 3525) (e.g., Sawin 1947; Casamiquela 1961; Bonaparte 1971; Long and Murry 1995; Martz 2002; Heckert et al. 2003; Roberto-Da-Silva et al. 2014).

The structure called the ‘distal roller’ in the literature (e.g., Martz 2002; Roberto-Da-Silva et al. 2014) is recognized here as the articulation surface for the metatarsal I and II, and it did not take part in the rotation of the ankle join. The articulation surface for the medial projection of the calcaneum is restricted only to the posterior and ventral parts of the peg (ZPAL AbIII/3355/1).

Stagonolepis olenkae has a rugose tuberosity projecting medially on astragalus, distinct form the dorsal articulation surface for the tibia, and articulation surfaces for metatarsals (ZPAL AbIII/3355/1, ZPAL AbIII/3349/4; respectively, close to 7 and 8 cm in width). The pattern of the rugosity is similar to the pattern observed in the long bones, therefore, the projection was probably finished in cartilage and thus its osseous extent could extend in length during the ontogeny. It seems that it could also be the case in *Typothorax coccinarum*; for example, in the small specimen TTUP 9214 (around 4 cm wide) the structure is not indicated, and in the larger NMMNH P33934 (close to 7 cm) it is well-developed, however, it seems that it is also present in NMMNH P-36075 (*Typothorax antiquum*) comparable in size to TTUP 9214 (Long and Murry 1995; Lucas et al. 2002; Heckert et al. 2003). The tuberosity is also not developed in *Polesinesuchus aurelioi* ULBRAPVT003 (2.5 cm in width), but the state of preservation of *Aetosauroides scagliai* (PVL 2073) makes it impossible to check the presence of this feature in this presumably older individual (Paes-Neto et al. 2021).

The distal tarsals of aetosaurs are poorly described in the literature. A similar morphology as in *Stagonolepis olenkae* can be recognized in *Typothorax coccinarum* (MCZ 1488, 4th distal tarsal described as an astragalus), *Neoaetosauroides engaeus* (PVL 3525), and *Longosuchus meadei* (TMM 31185-84a) (Sawin 1947; Bonaparte 1971; Lucas and Heckert 2011). In all four species, the 3rd distal tarsal is significantly smaller than the 4th distal tarsal, and the 4th distal tarsal is of a pyramid shape. At least in *S. olenkae* and *N. engaeus*, the 3rd distal tarsal is flattened transversally and close to square in side view. Sawin (1947) reported a lunar shape of that bone for *L. meadei*. The arrangement of the distal tarsals in *S. olenkae* is the same as proposed by Sawin (1947) for *L. meadei*. Both distal tarsals of *S. olenkae* were arranged at the same plane as the metatarsals and possibly could touch the ground during the step, as was proposed by Heckert et al. (2010) for *T. coccinarum.*

The presence of two distal tarsals, a smaller medial one (3rd distal tarsal) and a larger lateral one (4th distal tarsal) was reported by Walker (1961) for *Stagonolepis robertsoni* (MCZD

13). Although Walker (1961) was not able to recognize details of their morphology, he presented the arrangement of those elements similarly as proposed here for *S. olenkae* and *Longosuchus meadei* (Sawin 1947).

Distal tarsal IV was reported also for *Aetobarbakinoides brasiliensis* (CPE2 168) (Desojo et al. 2012). *Aetobarbakinoides brasiliensis* material is significantly deformed, and although the bone generally matches the morphology of other species, it is too small to form articulation surface for both the 3rd and 4th metatarsal as in *S. olenkae* and *Longosuchus meadei* (Sawin 1947). Therefore, it is probable that it is the 3rd distal tarsal not the 4th one.

Bone fragments from Krasiejów interpreted as a calcaneum of an aetosaur by Górnicki et al. (2021) do not have any characteristics that would allow to recognize them as parts of this bone. Larger parts could represent the distal tarsals or at least parts of them (UOPB-01141, UOPB-01142, UOPB-01143, UOPB-01145).

The astragalus (UOPB-01140) described by Górnicki et al. (2021) is compacted dorsoventrally, its surface is significantly damaged with no anatomical details recognizable, especially at the part of peg and the dorsal process, which seem to additionally suffer from overpreparation (Appendix 2 in Górnicki et al. 2021). The differences in the anatomy recognized by Górnicki et al. (2021) are not confirmed here. Despite the state of preservation, the morphology of the specimen is consistent with the material described here and contra Górnicki et al. (2021) the specimen is here assigned to *Stagonolepis olenkae*.

Some details of anatomy visible in *Stagonolepis olenkae,* but not visible or mentioned for other aetosaurs, particularly those associated with the development of the surface (e.g., the presence of the rugose area on the medial side of the astragalus (ZPAL AbIII/3355/1); presence of longitudinal fossae at the neck of the dorsal projection of the astragalus (ZPAL Ab III/502/12, ZPAL AbIII/3355/1); and presence of the shelf-like structure at the tip of the astragalus peg (ZPAL AbIII/3355/1)), can be treated as species specific, but it seems that the lack of those features is due to worse preservation of other material rather than to biological signal.

Among the two supposed distal tarsals described by Książkiewicz (2014), only ZPAL AbIII/2569 is an aetosaur bone, and its morphology matches the 4th distal tarsal. The other one (UOBS 01848) is a left calcaneum of a phytosaur.

Morphology of the pes

Shape, proportions, and arrangement of the pes elements in *Stagonolepis olenkae* are alike other known aetosaurs, such as *Longosuchus meadei* (TMM 31185-84a), *Typothorax* (NMMNH P-56299, C-4638, cast of NMMNH P-12964, MCZ 1488, NMMNH P-36075, TTUP 9214, UCMP V2816/34255, UCMP V2816/34248), *Aetosauroides scagliai* (PVL 2073, PVL 2052), *Neoaetosauroides engaeus* (PVL 3525), *Stagonolepis robertsoni* (MCZD 10 a, b; MCZD 13, R 4792), *Polesinesuchus aurelioi* (ULBRAPVT003), and *Aetosaurus ferratus* (SMNS 5770, SMNS 18554) (Sawin 1947; Casamiquela 1961; Walker 1961; Casamiquela 1967; Bonaparte 1971; Long and Murry 1995; Lucas et al. 2002; Martz 2002; Schoch 2007; Heckert et al. 2010; Roberto-Da-Silva et al. 2014).

Minimal phalangeal formula for *Stagonolepis olenkae* is 2-3-4-5-3?, which is consistent with *Aetosaurus ferratus* (2-3-4-5-3?) and similar as proposed for *Typothorax coccinarum* (2-3-3?-4?-3?), *Longosuchus meadei* (2-3?-4?-4?-3?), and *Stagonolepis robertsoni* (2-3-4-5-4?) (Sawin 1947; Walker 1961; Heckert et al. 2010; Lucas and Heckert 2011; Desojo et al. 2013). The unguals and distal phalanges are usually not preserved, making the formulae uncertain. Unfortunately, so far in the available material of *S. olenkae* there is no articulated specimen in which the V digit would be preserved entirely (ending with the ungual). The presence of an additional phalanx in the last digit is plausible based on comparison with the relative size of phalanges of other digits, especially the fourth one. Probably because of that, Walker (1961) proposed four phalanges in the last digit for *S. robertsoni*. However, in the examined MCZD 10 a, and MCZD 10 b, only one phalanx can be recognized in the 5thdigit and the rest is not preserved. Therefore, for now the most probable phalangeal formula for the pes of *Stagonolepis,* and possibly aetosaurs as a whole, seems to be 2-3-4-5-3.

An enlarged first ungual of similar proportions as in *Stagonolepis olenkae* can be recognized in most other aetosaur species regardless of their size, it is present at least in *Aetosaurus ferratus* (SMNS 5770), *Neoaetosauroides engaeus* (PVL 3525), *Polesinesuchus aurelioi* (ULBRAPVT003), *Typothorax coccinarum* (MCZ 1488, UCMP V2816/34248), *S. robertsoni* (MCZD 10 a, MCZD 10 b), and *Longosuchus meadei* (TMM 31185-84a). The shape of the first ungual as well as other unguals seems to be the same as in *S. olenkae*. Due to overall similarity in the development of the pes between the species, it seems that the size of the unguals decreases proportionally in more distal digits in the same manner as in *S. olenkae* which could be seen also in *S. robertsoni* (MCZD 10 a and b) and *Typothorax* (UCMP V2816/3424). Presence of claw-like unguals at least in the first four digits is strongly indicated also by *Brachychirotherium* tracks in which the claw markings are usually distinct (Lucas and Heckert 2011; Klein and Lucas 2021).

The morphology of the metatarsals and phalanges is alike other known aetosaurs, especially *Typothorax* spp. (UCMP V2816/3424, MCZ 1488), *Stagonolepis robertsoni* (MCZD 10 a and b; MCZD 13, R 4792), *Longosuchus meadei* (TMM 31185-84a), *Neoaetosauroides engaeus* (PVL 3525), and *Aetosauroides scagliai* (PVL 2073, PVL 2052) (Sawin 1947; Walker 1961; Casamiquela 1967; Bonaparte 1971; Long and Murry 1995; Desojo and Báez 2005; Lucas and Heckert 2011). The metatarsals and phalanges of *Aetosaurus ferratus* seem to be more gracile (SMNS 5770, SMNS 18554).

Curios are the distinct medial bend of the shaft of *Stagonolepis olenkae* (ZPAL AbIII/1974/3, ZPAL AbIII/3357, ZPAL AbIII/3455) and the presence of medially projecting laminae (ZPAL AbIII/1974/3) in the III metatarsal. Although the laminae might be a pathology, the distinct shape of the shaft in the metatarsal III repeat itself in few specimens and seems to be an unique feature of *S. olenkae*. In all other known aetosaurs the shaft of the metatarsal III is straight (Sawin 1947; Casamiquela 1967; Bonaparte 1971; Long and Murry 1995; Desojo and Báez 2005; Schoch 2007; Heckert et al. 2010; Lucas and Heckert 2011; Desojo et al. 2012). The feature cannot be examined in *S. robertsoni* because the mentioned part of the shaft is not preserved in any of the described specimens (MCZD 10 a and b; MCZD 13, R 4792).

The morphology of the metatarsal V in *Stagonolepis olenkae* is the same as in most other known aetosaurs, such as *Longosuchus meadei* (TMM 31185-84a), *Typothorax* (UCMP V2816/3424, MCZ 1488), *Neoaetosauroides engaeus* (PVL 3525), *Aetosauroides scagliai* (PVL 2073), and *Polesinesuchus aurelioi* (ULBRAPVT003). A different, hooked shape of the distal end of the metatarsal V in *S. robertsoni* (fig. 19f in Walker 1961) cannot be confirmed. In MCZD 13 the distal end of the V metatarsal is not well exposed, but the general shape of the proximal part is similar to morphology of *S. olenkae* recognized here.

The metatarsals, phalanges, and unguals described by Górnicki et al. 2021 (appendix 2 therein) (UOPB-01124-UOPB-01139) present the same morphology as the material described here. However, the specimens are very badly preserved, being significantly compacted, broken, and glued in several places, especially the metatarsals, therefore, they are not the best example of a typical morphology of the species. It seems that the authors confused the order of the metatarsals and described the metatarsal II as the metatarsal IV (UOPB-01136), the metatarsal III as the metatarsal II (UOPB-01139) and the metatarsal IV as the metatarsal III (UOPB-01138). When placed in the correct order (mt I - UOPB-01137, mt II - UOPB-01136, mt III - UOPB-01139, mt IV - UOPB-01138), the relative length and robustness of the metatarsals is no different than in the material described here. No distinct shift of the shaft in the metatarsal III is recognizable in UOPB-01139 but the specimen is severely damaged.

Appendicular osteoderms in other aetosaurs

Appendicular osteoderms covering almost the entire limb, beside *Stagonolepis olenkae,* have been reported at least for *Aetosaurus ferratus*, *Stagonolepis robertsoni*, and *Typothorax coccinarum* (Walker 1961; Schoch 2007; Heckert et al. 2010). Although they were not mentioned for the pes itself, osteoderms of a similar shape are recognizable in *S. robertsoni* (Walker 1961). Appendicular osteoderms, especially those covering the pes, are generally very small and are probably the first to be disconnected and washed up. They would also be easy to overlook or destroy during traditional excavation or preparation. It seems safe to assume that they were also present in other aetosaurs.

Stagonolepis olenkae* and *Stagonolepis robertsoni

***Stagonolepis robertsoni* within the variance of *Stagonolepis olenkae*?**

The author personally studied material of *Stagonolepis robertsoni* and examination show that differences in the postcranial skeleton between *S. olenkae* and *S. robertsoni* are generally minor, which was first pointed out by Lucas et al. (2007). The material of *S. robertsoni* consist mostly of casts and incomplete specimens often difficult to directly compare with *S. olenkae*, as the specimens of the former often lack essential parts that could be used for comparisons. In addition, many of the individuals of the Scottish aetosaurs are likely of a younger ontogenetic age, as suggested by their smaller sizes and other characters such as incomplete fusion between the neural arches and centra in the axial skeleton (Walker 1961; Brochu 1996).

Nevertheless, the author, referring to the description of *Stagonolepis robertsoni,* have found a few characters that may distinguish those two species, namely: the presence of an indentation on the humeral head that separates the internal tuberosity and main articulation surface in *S. olenkae,* a more transversely expanded proximal end in *S. olenkae* (pointed out also by Parker, 2016; Parker, 2018), and (3) a sharp-ended coronoid process in *S. olenkae*. However, these characters fit ontogenetic development patterns observed in other reptiles, and thus may also be of ontogenetic nature.

Morphology of the pelvic girdle and hind limbs of *Stagonolepis olenkae* seems to be nearly identical as in *S. robertsoni,* as pictured by Walker (1961). In the studied material of *S. olenkae* there are some bones the anatomy of which matches exactly the homologues of *S. robertsoni,* for example, the ilium ZPAL AbIII/119, pubis ZPAL AbIII/3266, or ischium ZPAL AbIII/3394/4. Therefore, it seems that at least for the pelvis and hind limbs, the intraspecific variance recognized for *S. olenkae* includes the morphotypes observed in *S. robertsoni,* which is consistent with the previous observations by other authors (Lucas et al. 2007; Antczak 2016; Dróżdż 2018).

Sacral vertebrae

Morphology of the sacral vertebrae in *Stagonolepis olenkae* is much alike *S. robertsoni,* although in the latter they are preserved worse. *S. robertsoni* has circular articular facets of vertebral centra; the junctions between the sacral ribs and the transverse processes are marked by a longitudinal ridge; sacral ribs of the first sacral vertebra are attached anteriorly and the sacral ribs of the second sacral vertebra are attached in the middle of the centrum (Walker 1961) – all those features are as in *S. olenkae*. Furthermore, the outline of the sacral ribs in dorsal/ventral view in *S. robertsoni* G.S.M. 90884 (Walker 1961: fig. 9 b,c) is closely similar as in *S. olenkae*. The position of fossae, development of bony projections, and thickness of certain parts of the sacrals in *S. robertsoni* seem to match those described here for *S. olenkae.* The only difference seems to be that the spine tables are taller in *S. olenkae* than in *S. robertsoni* G.S.M. 90884 (Walker 1961), but the dorsal portion of the neural spine seems to be deformed in this specimen.

Autapomorphic ilium?

Parker (2018a) described the morphology of *Stagonolepis robertsoni* ilium as being autapomorphic, based on the examination of the ilium R 4789 (dorsomedial cast of the ilium). He recognized as autapomorphies the dorsoventral thinness and ventrally hooked shape of the anterior process of the iliac blade, its short length in proportion to the pubic peduncle, and acutely angled tip of the posterior process of the iliac blade (Parker 2018*b*). However, those parts in the specimen examined by Parker (2018*b*) are damaged and cannot be used to accurately determine anatomy, which was also indicated by Walker (1961: fig. 15 a), at least for the posterior process.

The morphology of the iliac blade recognized in this study is different form Parker's observations in both *S. olenkae* and *S. robertsoni*.

The proportions and form of *S. olenkae* ilium ZPAL AbIII/199 are the same as in *S. robertsoni*, as pictured by Walker (1961). The shape of the preacetabular process in ZPAL AbIII/199 is nearly identical as in R 4789/4790, being dorsoventrally thin, sharply ended, having a tuber laterally, and a ridge for the depression on the sacral rib ventrally. The postacetabular process in ZPAL AbIII/199 is squared-off as in E.M. 46R. Rugosities mentioned by Walker (1961) on the distal portion of the iliac blade based on R 4804, most likely can be referred to lateral rugosities in ZPAL AbIII/199. The supracetabular crest of ZPAL AbIII/199 is also similarly developed as in the cast R 4790. Therefore, as demonstrated, ZPAL AbIII/199 poses all features of the combined ilium reconstruction by Walker (1961: fig. 16).

The anterior process in both *Stagonolepis robertsoni* (R 4789) and *S. olenkae* (ZPAL AbIII/119, ZPAL AbIII/3349/5) is much shorter than in most aetosaurs, however, there are some exceptions such as *Aetosaurus ferratus* S-22, *Longosuchus meadei* TMM 31185-40, and probably *Desmatosuchus smalli* TTUP 9024, TTUP 9172, fig. 9 in Small 1985) (Sawin 1947; Casamiquela 1961; Walker 1961; Small 1985; Long and Murry 1995; Heckert and Lucas 2002; Martz 2002; Desojo and Báez 2005; Schoch 2007; Roberto-Da-Silva et al. 2014; Parker 2016*b*, 2018*b*, *a*).

The shape of the anterior process is triangular in both *Stagonolepis olenkae* and *S. robertsoni*, similar as in most other aetosaurs (e.g. Bonaparte 1971; Long and Murry 1995; Desojo and Báez 2005; Roberto-Da-Silva et al. 2014; Parker 2018*a*, *b*). This triangular outline in ventrolateral view is often indicated by a thin expansion or lamina at the base of the process, which is present in both *S. robertsoni* R 4790 and *S. olenkae* ZPAL AbIII/199. The shape of the anterior tip of the process in both *S. olenkae* and *S. robertsoni* is similar as in, e.g., *Calyptosuchus wellesi* (UCMP 25941) (Parker 2018*a*). It seems similar also as in *Aetosauroides scagliai* (PVL 2073, left ilium) and *Neoaetosauroides engaeus* (PVL 3525) although the latter two are poorly preserved in comparison to ZPAL AbIII/199 (Casamiquela 1961; Bonaparte 1971; Heckert and Lucas 2002; Desojo and Báez 2005).

The anterior process is thin in most specimens of *S. olenkae* (ZPAL AbIII/199, ZPAL AbIII/3349/5) and *S. robertsoni* (R 4789/4790) (Walker 1961; Parker 2018*b*), but robust in the ilium ZPAL AbIII/1937. Due to its thickness, the less pronounced supracetabular crest and lack of lateral rugosities of the iliac blade, it is much more similar to, for example, *Desmatosuchus* *spurensis* (MNA V9300) (Parker 2008). However, the morphology of the sacral vertebrae in ZPAL AbIII/1937 is consistent with other known sacrals of *S. olenkae.* Advanced fusions between the ilium and sacral ribs, fusions between the sacral centra, as well as features indicating strong remodeling (e.g., lack of nodules between the centra and transverse processes in the second sacral), may indicate more advanced age of the individual.

To summarize, although unusual due to having a very short anterior process of the iliac blade, the morphology of the ilium in both *Stagonolepis olenkae* and *S. robertsoni* cannot be considered autapomorphic as proposed by Parker (2018*b*). The increase of ilium thickness observed in ZPAL AbIII/1937 is most likely due to ontogeny, sexual or intraspecific variation and it seems that at least among aetosaurs it not a good character for species discrimination.

Different pubis and ischium?

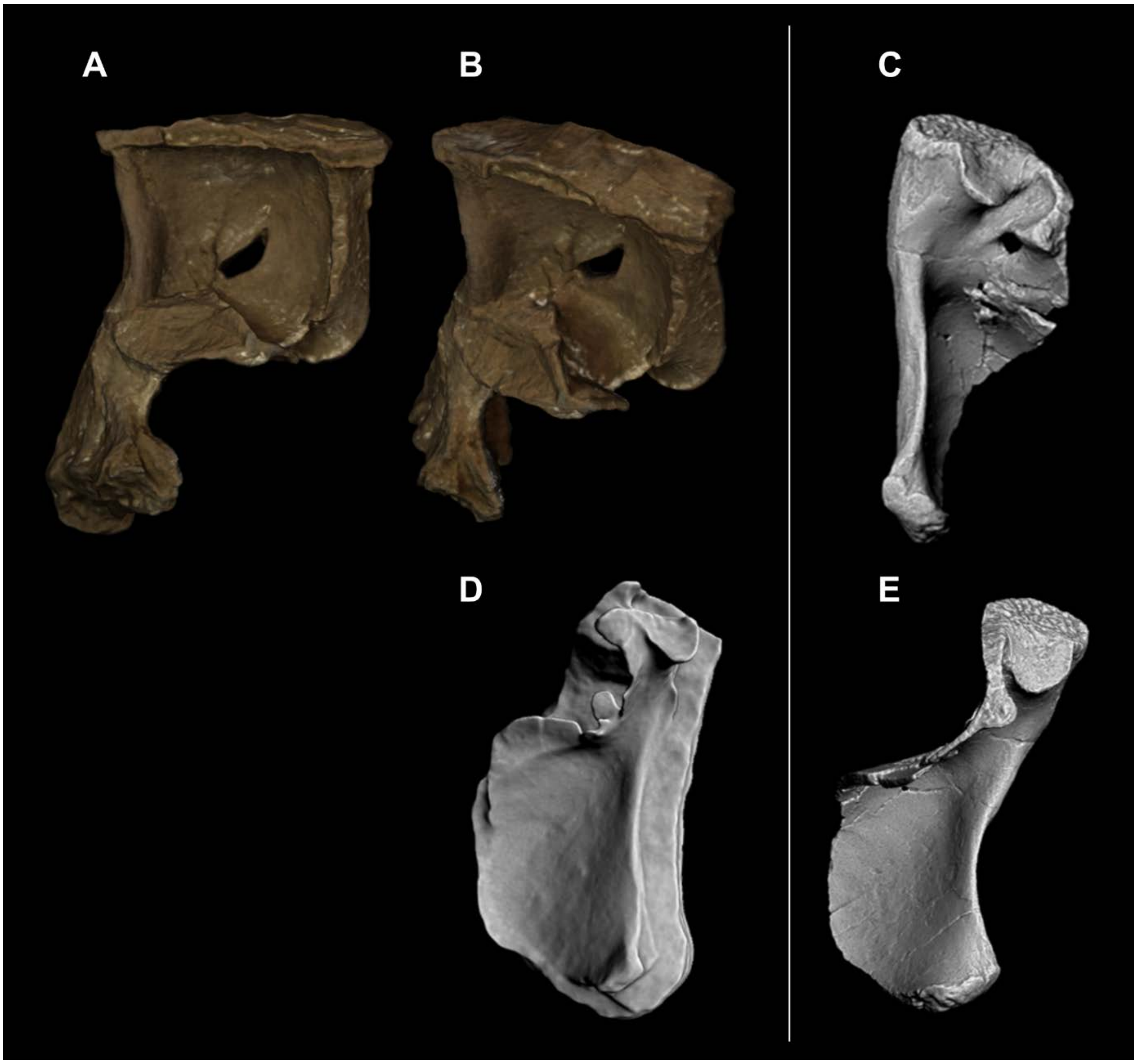


Figure 30. Pubis of *Stagonolepis robertsoni* R 4793 (A, B, D); lateral cast (A, B) and medial cast (D) in comparison to the pubis of *Stagonolepis olenkae* ZPAL AbIII/3266 in medial (C) and posterior (E) view. Specimens not to scale.

Morphology of the pubis in *Stagonolepis olenkae* seems to be nearly identical as in *S. robertsoni* (R 4793: Fig. 30 A, B, D; MCZD 4) (Walker 1961). The most striking is the comparison of ZPAL AbIII/3266 with the medioventral cast of R 4793, which, beside the size, are literally the same. Similarly, the ischia of *S. olenkae* are nearly identical as in *S. robertsoni* (R 4790, fig. 15d and 16 in Walker 1961). The only possible difference is the lack of prominent laminae in the anterior part forming the comb-like pattern. However, the lack of this structure can be explained by the worse preservation of the Scottish specimens or ontogeny, as the Elgin material is significantly smaller. Nevertheless, the morphology of the ischium is generally conservative among aetosaurs, with little difference between species (Casamiquela 1961; Walker

1961; Bonaparte 1971; Long and Murry 1995; Small 1998; Lucas et al. 2002; Martz 2002; Desojo and Báez 2005; Desojo et al. 2013; Roberto-Da-Silva et al. 2014).

The pubes of *S. olenkae* have a single obturator foramen (ZPAL AbIII/3266, ZPAL AbIII/3349/5, ZPAL AbIII/3394/1), not a paired one as it was described for *S. robertsoni* (Walker 1961; Parker 2018*b*). However, this character is most likely invalid for *S. robertsoni*. The reexamination of the pubis R 4793, based on which this character was restored (Walker 1961), shows that the medial edge of the pubic apron (where the second obturator foramen should be positioned), is not preserved in this specimen. There is a gutter-like structure visible in R 4793, most likely interpreted as the second foramen by Walker (1961), however, considering how fragile this part of the pubis is and that no paired obturator foramina are present in any other aetosaur (i.e., according to phylogenetic bracketing), it could be interpreted more parsimoniously as a crack or a taphonomic structure.

LOCOMOTION AND FUNCTION

Posture and mobility

Erect gait of *Stagonolepis olenkae*

Stagonolepis olenkae was an erect gait animal. Its pelvic girdle and hind limbs possess all features that can be attributed to an erect gait according to Parrish (1986, 1987); namely: (1) deep acetabulum; (2) marked medially-extending femoral head; (3) tightly articulating surfaces of the knee and ankle joints preventing marked long axis rotation of the limb – e.g., the presence of menisci on the proximal end of tibia, immovable saddle joint between the tibia and astragalus, distinct astragalar and calcaneal facet on the distal end of the fibula; (4) well-developed musculature responsible for the flexion and extension of the limbs – e.g., distinct posteriorly-projecting condyles divided by deep fossae, enlarged iliofibularis trochanter; (5) reduced musculature responsible both for the long axis rotation of limb segments and femoral adduction – e.g., long anterior projection of the ilium; (6) femur without marked twist of the shaft (around 40º in *S. olenkae*); (7) crus projecting vertically from the proximal tarsus; (8) calcaneal tuber projecting posteriorly from the tarsus, perpendicular to the axis of rotation of the calcaneum; (9) anteriorly directed pes without the divergent 5th digit – the 5th digit is reduced in relation to other digits, the 5th metatarsal is positioned distally relative to other metatarsals and directed anteriorly (L-shaped with a marked medial projection).

The state present in *Stagonolepis olenkae* is a variation of the pillar-erect gait, in which the femur articulated directly ventrally into the horizontally positioned and downward-facing acetabulum, that completely covered the femoral head (Bonaparte 1984; Benton and Clark 1988); this condition was originally proposed to differ the erect gait of ‘rauisuchians’ (mostly Poposauroidea and Rauisuchidae) from those of birds, non-avian dinosaurs, and mammals (buttress-erect gait), in which the femur articulates from the side, via a medially extending head, with a subvertically positioned acetabulum (Bonaparte 1984; Benton and Clark 1988; Ezcurra 2016; Nesbitt et al. 2017). However, the pelvis and hind limbs of *S. olenkae* substantially differ from those of contemporary ‘rauisuchians’, such as *Poposaurus* and *Postosuchus* (e.g., Chatterjee 1985; Long and Murry 1995; Peyer et al. 2008; Schachner et al. 2011; Weinbaum 2013; Demuth et al. 2020).

Comments on the pectoral girdle and forelimbs

A semi-horizontal orientation of articulation surfaces for both forearms and metacarpals suggest a vertical position of forearm bones and an upright orientation of metacarpals. Although the author did not describe the pectoral girdle in detail, some elements were scanned and the author was able to reconstruct the position of the pectoral girdle elements and humerus. It seems that glenoids were oriented more ventrally than laterally and therefore the humerus was oriented more upright than in the reconstructions of Walker (1961) and Heckert et al. (2010). It appears that the general form of the pectoral girdle is similar to that of the pelvis, and allowed a pillar erect or at least a semi-erect rather than sprawling orientation of the limbs.

Anatomical differences between *Stagonolepis olenkae* and ‘rauisuchians’

‘Rauisuchians’, especially the Late Triassic representatives such as *Poposaurus* and *Postosuchus,* have significantly modified pelves and hind limbs compared to stem-archosaurs, which is related with the evolutionary enhancement of the pillar-erect gait and probably gradual development of at least facultative bipedal mode of locomotion similar to that of dinosaurs (e.g., Charig 1972; Bonaparte 1984; Chatterjee 1985; Kubo and Benton 2007; Gauthier et al. 2011; Schachner et al. 2011, 2020; Kubo and Kubo 2012; Weinbaum 2013; Farlow et al. 2014). The most notable modifications of the pelvis are the outstandingly expanded anterior and posterior processes of the iliac blade, horizontal orientation of the acetabulum with laterally pronounced supracetabular crest, transversally narrow lower pelves with long and slender pubes; presence of a marked pubic foot; as well as elongated and slender ischia (e.g., Charig 1972; Bonaparte 1984; Parrish 1986, 1987).

The morphology of the pelvis recognized in *Stagonolepis olenkae* is less derived. Compared to *Poposaurus* and *Postosuchus*, the ilium of *S. olenkae* has proportionally shorter pre- and postacetabular processes; the supracetabular buttress is not developed; the acetabulum is oriented more obliquely and the supracetabular crest does not form a defined lateral projection (e.g., Chatterjee 1985; Long and Murry 1995; Schachner et al. 2011; Weinbaum 2013). The ventral part of the pelvis in *S. olenkae* preserved the shape characteristic for stem archosaurs such as *Euparkeria,* with short pubes and ischia; transversally expanded distal portion of the pubes forming wide and pronounced pubic apron, without the pubic foot; well-developed puboischiadic plate; not indicated ventral concavity; distally pointing ischia, with high ischiadic blade (e.g., Romer 1956; Ezcurra et al. 2013; Sookias and Butler 2013; Demuth et al. 2020).

On the other hand, the morphology of the hind limbs of *Stagonolepis olenkae* is generally consistent with that of 'rauisuchians'. *S. olenkae* presents an 'advanced' state characteristic for erect archosaurs, having a fully vertically oriented crus and the movement in the knee and ankle joint restricted to parasagittal plane (e.g., Parrish 1986). However, it seems that orientation of the femora in *S. olenkae* was more oblique (subvertical) in comparison to 'rauisuchians', because the femora of *S. olenkae* distinctly bend medially in contrast to the relatively straight femora of *Poposaurus* and *Postosuchus* (Schachner et al. 2011, 2020; Weinbaum 2013); consequently, the femoral head of *S. olenkae* articulated with the acetabulum at a more acute angle and are more expanded medially. Another big difference is in the development of the pes, which in *S. olenkae* is distinctly asymmetrical with a specialized massive first digit ending with a proportionally enlarged claw-like ungual, while in *Poposaurus* and *Postosuchus* the pes is more bilaterally symmetrical, with the middle digit being the most massive and significantly reduced medial and lateral ones (e.g., Chatterjee 1985; Nesbitt 2003; Peyer et al. 2008; Gauthier et al. 2011; Schachner et al. 2011; Weinbaum 2013). Other differences relative to 'rauisuchians' would be the generally increased thickness of bones and enlarged muscular attachments in *S. olenkae* (e.g., the forth trochanter, iliofibularis trochanter, gastrocnemius crest of the tibia); as well as shorter crus in proportion to the femur; transversely wider elements of the pes, especially the calcaneum (e.g., Parrish 1986; Gauthier et al. 2011; Schachner et al. 2011, 2020; Weinbaum 2013).

Functional differences between *Stagonolepis olenkae* and 'rauisuchians'

Stagonolepis olenkae had a fully developed pillar-erect gait, functionally the same as that of 'rauisuchians' despite anatomical differences, arising from diverging in these groups. The heavily-built pelvic girdle and hind limbs of *S. olenkae* were adapted to perform better in (1) supporting of the high weight of the body and (2) strong movements of the limbs in a parasagittal plane (Parrish 1986; Hildebrand 1988; Heckert et al. 2010). The 'rauisuchians' in general were more cursorial, with their pelvic girdles and hind limbs adapted more for speed rather than strength (e.g., Charig 1972; Coombs, 1978; Kubo and Kubo 2012; Schachner et al. 2020).

Because of biomechanical constraints, in animals that can perform strong movements, the ability to run fast decreases, mostly since the lower parts of the limbs (crus/forearms) became shorter in proportion to the femur/humerus, which significantly reduces the length of the step (Hildebrand 1988). Adaptations for strength in the hind limbs (very short crus in proportion to the femur; enlarged muscles; and far away positioned muscular attachments which increase the input force – e. g., distal migration of the forth trochanter on the femur, distal migration of the iliofibularis trochanter), probably made *Stagonolepis olenkae*, and potentially other aetosaurs, unable to outrun potential ‘rauisuchian’ predators such as *Polonosuchus*, the compensation for which was the heavy armor (Parrish 1986; Hildebrand 1988; Brusatte et al. 2009). Broken and healed aetosaur osteoderms are present in the Krasiejów material.

Functional morphology of the pelvis of *Stagonolepis olenkae*

In the mentioned context, the lateral inclination of the iliac blades (high iliac blades), exceptional for aetosaurs among the Pseudosuchia, is an adaptation to supporting the armor rather than an evolutionary advancement of the erect gait. Similar transversely wide pelves are present in other heavy armored animals, such as *Doswellia*, ankylosaurs, glyptodonts, or armadillos (e.g., Parrish 1986). The more oblique orientation of the acetabulum and femora results in a broader spacing between the limbs, which would make the animal more stable while standing, and more difficult to overturn by the potential predator (Hildebrand 1988).

The acetabulum of *S. olenkae* is probably effectively the same as those of ‘rauisuchians’, although the supracetabular crest, an indicator of the pillar-erect gait, is less pronounced and does not form an extended lateral projection, being comparable as in semi-erect *Euparkeria* (Bonaparte 1984; Demuth et al. 2020). The pronounced lateral extension of the supracetabular crest in ‘rauisuchians’, e.g., *Poposaurus* and *Postosuchus*, expands the acetabulum laterally, probably to maintain the necessary stability of the hip (e.g., Chatterjee 1985; Weinbaum 2013; Farlow et al. 2014; Schachner et al. 2020). The pelves of the ‘rauisuchians’ are more slim, which is beneficial for cursoriality as it grants grater maneuverability (Hildebrand 1988). The feature probably is not as significantly developed in *S. olenkae* because its pelvis is already broadened transversally, with the acetabulum wide enough to form a stable joint with the femur.

Shorter preacetabular process of the iliac blade in *Stagonolepis olenkae* also does not necessarily indicate a less developed erect gait. The presence of a long preacetabular process in erect archosaurs is connected with the restriction of the long axis rotation of the femur (Parrish 1986, 1987); accordingly, the process is short and not marked in sprawling forms like phytosaurs, proterosuchids or semi-erect *Euparkeria* (e.g., Chatterjee 1978; Parrish 1986; Ezcurra et al. 2013; Sookias and Butler 2013; Bronowicz 2017; Demuth et al. 2020). The preacetabular process in *S, olenkae* is longer and more conspicuous than in the mentioned sprawling forms, however, much shorter than in ‘rauisuchians’ – half the length of the pubic peduncle, while in *Poposaurus* and *Postosuchus* it significantly exceeds its length (e.g., Chatterjee 1985;

Schachner et al. 2011, 2020; Weinbaum 2013). The moderate length of the process in *S. olenkae* might be considered a progressive feature towards a more vertical orientation of the limbs, but not to the extent present in ‘rauisuchians’. It is worth nothing that in many derived members of the Aetosauria, e.g., *Typothorax* and *Desmatosuchus*, the process can be significantly longer than in *S. olenkae* (Case 1922; Long and Murry 1995; Heckert et al. 2010). On the other hand, anterior processes similar to that of *S. olenkae* in shape and length in proportion to the pubic peduncle are present in the ilia of multiple doubtlessly erect dinosaurs, especially basal sauropodomorphs such as *Plateosaurus* (e.g., Bonaparte 1971; Mallison 2010*a*, *b*; Müller et al. 2018; Nau et al. 2020; Novas et al. 2021).

Interestingly, except for the lack of the opening in the acetabulum, the general shape of the ilium in *Stagonolepis olenkae* is very similar to that in basal sauropodomorphs due to similar proportions and shape of the iliac blade processes, similar anteroventral direction of the pubic peduncle in relation to the iliac blade, as well as the continuation of the supracetabular crest towards the end of the pubic peduncle (e.g., Charig 1972; Mallison 2010*a*, *b*; Nau et al. 2020).

In contrast, despite the generally less derived structure of the lower pelvis, the pubes of *Stagonolepis olenkae* show a distinct adaptation towards an erect gait in forming caudally directed pubic aprons, which makes the lower pubis slenderer and grants more space for movements of the vertically oriented femur. It differs from the condition in sprawling forms, such as phytosaurs, which also form wide pubic aprons, but in which the edges of the pubic apron point directly laterally; similar to marine reptiles such as nothosaurs (e.g., Chatterjee 1978; Parrish 1986; Diedrich 2012, 2013; Bronowicz 2017). It seems that the condition in *S. olenkae* is somehow universal for terrestrial pseudosuchians because the lateral margins of the pubic aprons are directed caudally also in the pubes of the ‘rauisuchians’, e.g., *Poposaurus* and *Postosuchus* (e.g., Chatterjee 1985; Schachner et al. 2011, 2020; Weinbaum 2013). A contrasting morphology of the ‘rauisuchians’ with a very slim pubic apron and vast elongation of the pubes would be an effect of their specialization towards a more cursorial behavior (Kubo and Kubo 2012). Compared to *Euparkeria*, as pictured by Demuth et al. (2020), the lateral edges of the pubic aprons are directed more laterally.

Stagonolepis olenkae does not have a pubic foot comparable to that of ‘rauisuchians ‘and dinosaurs. Well-developed pubic foot in non-avian theropod dinosaurs was proposed by Carrier and Farmer (2000) as an improvement of the cuirassal breathing mechanism. In the cuirassal breathing, the ischiotruncus muscle (that attaches to the ischium and the medial aspect of gastralia), by pulling gastralia caudally, increases the volume of the abdominal cavity

(Carrier and Farmer 2000). According to Carrier and Farmer (2000), in non-avian theropod dinosaurs the pubic foot “acted as a guide to direct the force of the (ischiotruncus) muscle”. Due to the morphological similarity, it probably played the same role in ‘rauisuchians’ such as *Poposaurus* and *Postosuchus* (Gauthier et al. 2011; Schachner et al. 2011; Weinbaum 2013). Likewise, the very long pubes and ischia of ‘rauisuchians’, roughly comparable in length to those of non-avian theropods, would improve their ventilation system indirectly supporting their more cursorial mode of life (Carrier and Farmer 2000). By analogy, short and less-specialized pubes, more similar as in stem-archosaurs like *Euparkeria*, indirectly suggest a less active mode of life for *S. olenkae* (Romer 1956; Sookias and Butler 2013; Demuth et al. 2020).

Functional morphology of the hind limbs of *Stagonolepis olenkae*

Pronounced medial bend of the femora in addition to an extended lateral positioning of the acetabulum cause an increased transverse spacing between the hind limbs of *Stagonolepis olenkae* (compared to the erect ‘rauisuchians’, e.g., *Poposaurus* and *Postosuchus*; e.g., Chatterjee 1985; Gauthier et al. 2011; Schachner et al. 2011; Weinbaum 2013), but without disturbing of the vertical orientation of the lower leg. The greater distance between the hind limbs, as well as a high robustness of the hind limb bones can be interpreted as an adaptation to enhance the ability to support the weight of the trunk and tail (e.g., Parrish 1986; Hildebrand 1988).

The enhanced ability to perform strong movements with hind limbs in *Stagonolepis olenkae* (compared to contemporary ‘rauisuchians’ e.g., Chatterjee 1985; Parrish 1986; Gauthier et al. 2011; Schachner et al. 2011; Weinbaum 2013) is indicated by its shorter crus in proportion to the femur; larger and more distally positioned muscular attachment areas that take part in locomotion; and high robustness of the bones (e.g., Parrish 1986; Hildebrand 1988). In the pes, the very well-developed deep excavated attachments for flexors and extensors of the pes, dorsally the extensor digitorum longus and brevis, and ventrally the gastrocnemius, can also be recognized as a morphology enhancing the strength of movements. Pronounced transverse expansion of the pes and ankle elements in *S. olenkae*, compared to that in ‘rauisuchians’, e.g., *Poposaurus* and *Postosuchus* (e.g., Chatterjee 1985; Parrish 1986; Gauthier et al. 2011; Schachner et al. 2011; Weinbaum 2013), especially of the calcaneal tuber and metatarsals, would also contribute in producing a greater strength by increasing the muscle attachments areas (e.g., Hildebrand 1988). Similarly, comparably shorter phalanges in proportion to the metatarsals in *S. olenkae* compared to ‘rauisuchians’ can be interpreted as an adaptation to increasing the strength of the flexion and extension of the digits (e.g., Hildebrand 1988; Gauthier et al. 2011; Weinbaum 2013; Schachner et al. 2020).

It seems that movements of the knee and ankle joints were restricted to the parasagittal plane and there is no difference in general mobility of those joints between *Stagonolepis olenkae* and ‘rauisuchians’, e.g., *Poposaurus* and *Postosuchus* (e.g., Chatterjee 1985; Gauthier et al. 2011; Schachner et al. 2011; Weinbaum 2013). The articulation surface between the metatarsals and phalanges as well as between the phalanges and unguals (especially in the first and second digit) is deeply concave in comparison with ‘rauisuchians’, which may serve as an additional stabilization for the joints (Hildebrand 1988).

The major differences between *S. olenkae* and ‘rauisuchians’, e.g., *Poposaurus* and *Postosuchus,* the distinct asymmetry in the robustness between the medial and lateral digits, as well as the presence of comparably enlarged unguals, morphologically identical to the unguals of the manus, could be an effect of specialization to scratch-digging (Hildebrand 1983, 1988; Dróżdż 2018) and is consistent with described above adaptations towards an increase of movements strength. Laterally decreasing robustness of the digits in the pes as well as the presence of large unguals in *S. olenkae* are similar to basal sauropodomorph dinosaurs (e.g., Charig 1972; Nau et al. 2020).

Digitigradity vs plantigradity in *Stagonolepis olenkae*

In the modern megafauna, the plantigradity is characteristic for animals that seldomly run, such as bears, opossums, or raccoons. They have usually a lower brachial index, shorter metatarsals, and anteroposteriorly shorter calcaneal tuber compared to cursorial digitigrade and unguligrade animals (Hildebrand 1988). Therefore, the heavily built skeleton of *Stagonolepis olenkae* with short crus and metatarsals, and its short calcaneal tuber compared to contemporary pseudosuchians suggest the plantigradity.

However, in a majority of the *Brachychirotherium* tracks referred to aetosaurs (Lucas and Heckert 2011; Desojo et al. 2013), the proximal part of the pes leaves no complete impression, although there are a few examples, such as *B. eyermani*, in which the back of the foot is entirely preserved (Klein and Lucas 2021). This may indicate that during planting of the foot, the digits were the first to touch the ground, unlike in plantigrades in which the heel strikes the ground first during the stride (Hildebrand 1988). This means that mechanics of the stepping in

S. olenkae were similar as in digitigrades, which is plausible considering that digitigradity was proposed for some ‘rauisuchians’ such as *Poposaurus* and *Postosuchus*, and could be treated as an adaptation towards more effective running (e.g., Chatterjee 1985; Hildebrand 1988; Peyer et al. 2008; Gauthier et al. 2011; Schachner et al. 2011, 2020). The impressions of the proximal part of the pes in some tracks could mean that the metatarsals and calcaneal tuber were positioned in a near horizontal orientation and could leave impressions in more boggy ground or appear only during slow walking peace or while standing.

Therefore, it seems plausible that *Stagonolepis olenkae* has at least semi-digitigrade hind limbs and the more horizontal position of its metatarsals and calcaneal tuber, being modification of an ancestral pseudosuchian state, could be an adaptation towards a better support of the heavy body.

It is worth noting that the morphology of the carpus recognized in this study, strongly implies the digitigradity for the forelimbs. In addition, the *Brachychirotherium* tracks of the forelimbs lack palm impressions which also suggest the digitigradity of the manus (Lucas and Heckert 2011; Klein and Lucas 2021).

Increased strength and scratch-digging

Adaptive characteristics of scratch-diggers

Scratch-digging is a 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, pangolins, and the aardvark, but several other animals dig this way, including some frogs, some tortoises, some birds, fossorial marsupials, most badgers, the ratel, ground squirrels and a variety of other mammals (some with scant structural adaptations for it, like canids) (Hildebrand 1983, 1988).

The digging requires an enormous strength, therefore, the limbs of specialized scratchdiggers 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 such a case, the arm works as a lever in which the in-force (Fi) is applied to the olecranon process being the lever arm (power arm) and the out-force (Fo) is produced at the end of the hand, while the forearm and the hand (with the exception of the olecranon process) are the out lever arm (load arm) (Hildebrand 1988). Considering that Fo = (Fi * li) / lo (li = length of the power arm, lo = length of the load arm), there are three major ways to increase the out-force (Fo) (Hilderand 1988). The first way is to reduce the length of the out lever arm (lo). 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 (Fo) is to increase the related in-lever (li). To do 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 extend farther than halfway of the humerus, the median epicondyle of the humerus is wide (feature of all scratch-diggers, origin of the 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). For the same reason, the olecranon process of ulna in diggers is usually long (Coombs 1983, Hildebrand 1988). The third way to increase the out-force (Fo) is to increase the in-force (Fi). Consequently, the muscles connected with the digging behavior 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 the humerus (origin of digit flexors) and the deltoid crest (insertion of the deltoids) are particularly prominent, as is the acromion process of the scapula (origin of the deltoid musculature) and posterior angle of the scapula (origins of the teres major and the long head of the triceps) (Coombs 1983; Hildebrand 1983, 1988).

Application of a relatively great force puts the joints in diggers under a much higher stress than 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 movements in several planes, in digging animals tends to become limited to a single plane: the wrist joint becomes hinge-like (permitting only flexion and extension), the head of the humerus may develop a greater radius of curvature in the horizontal than in vertical plane (limiting or preventing adduction and abduction), and the acromion process grows longer (also limiting adduction and abduction) (Hildebrand 1983). Likewise, joints that usually permit motion, become modified to allow little or no motion: joints between the phalanges and joints between the digits and metacarpals may become flat-ended, V-shaped, multiangled, or develop a peg and a socket, and the surfaces of the distal phalanges may 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 animals several digits may be modified into digging tools and others may be lost or reduced, the metacarpals and proximal phalanges may fuse, and some elements of the carpus may fuse horizontally (Hildebrand 1983, 1988). Furthermore, joints that normally provide motion in one plane tend to become strengthened against dislocation: distal ends of the ones preceding the terminal phalanges are enlarged with a 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 develop under the joints (their presence functionally bonds 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 between 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 a great force, they usually have impressive, elongated terminal phalanges modified into blade-like or pick-like structures, and covered by strong keratin sheaths (Hildebrand 1983, 1988). Claws allow them to concentrate the delivered force in a small, restricted area, which makes it much easier to break the hard, consolidated substrate (Hildebrand 1988).

In summary, the limbs of specialized scratch-digging animals like pangolin, armadillo, or aardvark are adapted to straightening of the arm with the maximum possible force (out-force) that can be used for breaking through a hard substrate with well-developed claws (Hildebrand 1983, 1988). The limb works like a lever, so to increase the out-force, the limbs of scratch-diggers have very short autopodia and zeugopodia (shortening of the out-lever arm), and the muscles used for digging inserting far from the joints they turn (elongation of the in-lever arm) and well-developed (increasing the in-force) (Hildebrand 1983, 1988). Enormous claws of scratch-diggers work like pickaxes and reduce the area to which the force is applied (Hildebrand 1983, 1988). Additionally, the limbs of scratch-diggers usually have their mobility reduced to the parasagittal plane only, to avoid damaging the joints and more effectively apply large forces into the substrate (Hildebrand 1983, 1988).

Although modern specialized scratch-diggers, such as pangolins, armadillos, or aardvarks, usually use their forelimbs as the primary digging unit, the principles of the anatomic design are the same for both fore and hind limbs, therefore, digging with hind limbs is also common (Hildebrand 1983, 1988). For example, many turtles use their hind limbs to dig up their nests (e.g., Fowler and Hall 2011).

Scratch-digging in *Stagonolepis olenkae*

Stagonolepis olenkae shares several features with modern scratch-diggers. Without a doubt, it was able to produce great out-forces with both its forelimbs and hind limbs. The forelimbs are of strong, robust build with short radius (shorter than the humerus), short carpus, short, stout metacarpals, and short, broad phalanges. The deltopectoral crest of the humerus (attachment of the deltoid muscles) is well-developed and spans almost half the length of the bone. In the distal part of the humerus, the medial entepicondyle is prominent and wide (comparable to that of armadillos, pangolins, anteaters, and aardvarks (Hildebrand, 1983) and laterally a distinct supinator process is present. The olecranon process of the ulna is long (minimum 0.2 of the total ulna length, as preserved — the level of scratch-digging ground squirrels (Hildebrand, 1988), but for sure it was longer in *S. olenkae*, because of the unpreserved cartilaginous expansion), and has strong and well-marked insertions of the triceps muscle.

Furthermore, the joints in forelimb 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 the elbow joint. The proximal end of the humerus is strongly expanded mediolaterally which suggests that it had a higher mobility in the horizontal 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 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 curvature radius. The autopodial bones of S. *olenkae* did not have bony stops and the author did not recognize definitive sesamoids, however, the whole hand was covered by osteoderms that might have stiffened it and in some cases it may be difficult to distinguish small, morphologically simple osteoderms from sesamoids. In modern crocodiles, dorsal osteoderms together with dorsal muscles form a complex structure that strengthens the vertebral column (Frey, 1988). 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 many other archosauromorphs (for example *Postosuchus*, *Parasuchus*, *Riojasuchus*) (Bonaparte, 1971; Chatterjee, 1978; Peyer et al., 2008; Weinbaum, 2013). The manus of *S. olenkae* was also adapted for breaking compacted soil. Its unguals are laterally compressed, claw-like, and elongated in a 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), , 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 (Hildebrand 1983, 1988; Gaudin et al. 2016).

As demonstrated above, in the section 'Functional morphology of the hind limbs of *Stagonolepis olenkae*', *S. olenkae* was able to perform strong movements with its hind limbs, possessed modifications restricting joint mobility to the parasagittal plane, as well as large claw-like unguals, which in the hind limbs are developed to an even greater degree than in the forelimbs. It is safe to assume that *Stagonolepis olenkae* performed scratch-digging with its hind limbs as well as the forelimbs. Due to the larger size of the hind limbs in relation to the forelimbs, it could produce much greater forces, and therefore dig through a harder material if necessary.

Probable scratch-digging in other aetosaurs

Although the possible ability to dig with limbs was previously proposed only for *Stagonolepis robertsoni* and *Typothorax coccinarum* (Walker, 1961; Heckert et al., 2010), many features associated with scratch-digging can also be recognized in the forelimbs and hind limbs of other mid-sized and large aetosaurs. Namely, robust forelimb bones, with the humerus having a prominent, well-developed deltopectoral crest, and a wide entepicondyle (*Aetobarbakinoides brasiliensis*, *Argentinosuchus bonapartei*, *Desmatosuchus* spp., *Longosuchus meadei*, *Neoaetosauroides engaeus*, *Typothorax* spp., *S. robertsoni*), marked supinator process (*S. robertsoni*), long and marked olecranon process of ulna (*D. smalli*, *L. meadei*, *N. engaeus*, *Typothorax* spp., *S. robertsoni*), short and stout metacarpals, short and broad phalanges (*L. meadei*, *T. coccinarum, S. robertsoni*), and the fused radiale and intermedium in the carpus (*L. meadei* and *S. robertsoni*) (Sawin, 1947; Walker, 1961; Small, 1985, unpublished data; Long and Murry, 1995; Lucas, Heckert and Hunt, 2002; Heckert and Lucas, 2002; Martz, 2002, unpublished data; Lucas and Heckert, 2011; Desojo, Ezcurra and Kischlat, 2012).

The same goes for the hind limbs, which in large and middle-sized forms are exceptionally robust, with short crus, hypertrophied distally positioned fourth trochanter in the femur, hypertrophied and distally positioned iliofibularis trochanter in the fibulae (*Desmatosuchus* spp., *Stagonolepis* spp., *Longosuchus meadei*, and *Typothorax* spp.) (e.g., Sawin 1947; Small 1985; Parrish 1986; Lucas et al. 2002; Martz 2002), as well as stout and short phalanges in the pes and large claw like unguals at least in the first digits (*Longosuchus meadei*, *Typothorax coccinarum*, *Stagonolepis robertsoni*) (Sawin 1947; Walker 1961; Martz 2002; Lucas and Heckert 2011).

The small *Aetosaurus ferratus*, due to its lighter build lacks many characters typical for diggers, however, the forelimbs have proportions typical for digging animals, with the radius shorter than the humerus, and the palm shorter than the radius, and it has a prominent supinator process and transversely elongated element in the carpus (radiale) (Schoch, 2007). In the hind limbs, it has a much longer crus compared to the femur but has all the other typical characters of aetosaurs that may indicate scratch-digging, including hypertrophied trochanters in the femur and fibula, and large claw-like unguals (Schoch 2007). Similar is true for the small *Polesinesuchus aurelioi* (see Roberto-Da-Silva et al. 2014). This suggests that these small forms could perform scratch-digging with the forelimbs (probably even better than most other contemporary animals), but not to the degree of the larger aetosaur species.

Implications for the mode of life of *Stagonolepis olenkae* and other aetosaurs

Sulej (2010), based on the very large olfactory tract, bulbous, large nares, and the shape of teeth, considered *S. olenkae* to be an omnivorous animal relaying mostly on the smell in its search for food and using its shovel-like snout to extract invertebrates and plants from under the ground, and comparing its lifestyle to modern wild boars.

Considering several adaptations for scratch-digging recognized here for *S. olenkae*, it is 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 (such as armadillos, pangolins, and aardvarks) can balance their body with their 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 of aetosaurs; Desojo et al., 2013, described also for *S. olenkae* by Książkiewicz, 2014). The presence of specialized claws, together with the dermal armor 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, 1971; Small, 2002; Desojo et al., 2013). The armor protects them against the insects (ants, termites or beetles) they mostly feed on, as well as larger predators they cannot outrun (for example, leopards or hyenas in the case of pangolins) (e.g., Talmage and Buchanan 1954; Deligne et al. 1981; Yang et al. 2012; Wang et al. 2016). A few beetle elytra have been reported from Krasiejów (Dzik and Sulej, 2007) and the diet of the nine-banded armadillo may consist in even 40% of coleopterans (Talmage and Buchanan, 1954). Several authors suggested, therefore, that beetles could be an important source of food for aetosaurs (e.g., Small, 2002); however, it is hard to imagine an animal being almost as long as a mid-sized automobile to base its diet mostly on insects. Accordingly, the wild boar analogy seems more appropriate because of *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. 1989). This covers every kind of feeding behavior 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 with 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 documented osteoderms covering the dorsal surface of the manus and pes, however, osteoderms of similar morphology are present also in *Stagonolepis robertsoni* (Walker 1961). As in modern crocodiles, the osteoderms take part in thermoregulation (e.g., Farlow et al. 2010) and may buffer lactic acid (Jackson et al. 2003), their presence might have supported *S. olenkae*'s warming up or giving up heat generated by the intense work of limb muscles, and help to sustain a longer heightened activity.

Many of mid-sized and large aetosaurs have limbs of a similar morphology as *Stagonolepis olenkae*, as well as a shovel-like expansion at the end of the snout (e.g., *Desmatosuchus* spp., *Typothorax* spp., *N. engaeus*, *L. meadei*, *S. robertsoni*) (Sawin, 1947; Walker, 1961; Small, 2002; Parker, 2005; Parker, 2008; Desojo and Báez, 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 *S. olenkae*.

During the deposition of bone-bearing horizons in Krasiejów, the climate was semi-tropical with distinct seasonal wet and dry periods (Gruszka and Zieliński 2008). In modern tropical areas during the dry season, deciduous plants (including trees, shrubs, herbaceous) protect themselves against dehydration by losing their foliage, and some of them develop resting underground organs rich in storage polysaccharides and proteins (e.g., Bullock and Solis-Magallanes 1990). *S. olenkae* may have temporarily relied on such sources of food. A similar climate with distinct seasonal wet and dry periods was also recognized in the Upper Triassic Chinle Formation in the USA (Dubiel and Survey 1987; Simms and Ruffell 1990), from which several aetosaur species, including some of the mentioned above, have been described (Long and Ballew 1985; Long and Murry 1995; Heckert and Lucas 2000; Desojo et al. 2013; Parker 2016*b*, 2018*a*).

ONTOGENY

Ontogenetic changes in the sacral vertebrae in mature individuals

In all known aetosaurs, the sacral ribs are fused together with the sacral centra and transverse processes, forming elongated, near horizontally oriented rami (Casamiquela 1961; Walker 1961; Bonaparte 1971; Small 1985; Lucas et al. 2002; Parker 2008). In the studied material of *S. olenkae*, the area of the closed suture is clearly indicted by bony cusps on both the dorsal and ventral sides (e.g., ZPAL AbIII/1937, ZPAL AbIII/2531/1, ZPAL AbIII/2531/2). It appears that these areas change during ontogeny, which is well visible in the series of the second sacrals ZPAL AbIII/2738, ZPAL AbIII/2531/1, and ZPAL AbIII/1937. In probably the ontogenetically youngest adult ZPAL AbIII/2738, the sutures between the sacral ribs and transverse processes are still present and the cusp on the dorsal surface is not yet developed, while on the ventral surface the cusp indicating the suture line is clear and convex. In the probably ontogenetically older ZPAL AbIII/2531/1, the suture is fully obliterated, with moderately developed cusps on the dorsal side, while on the ventral side the cusps are less marked than in ZPAL AbIII/2738 and partially remodeled. In probably the ontogenetically oldest ZPAL AbIII/1937, the suture area on both sides is fully remodeled, and besides tiny palpable elevations, the surface of the transverse rami is uniformly developed. Moreover, an older ontogenetic age of the ZPAL AbIII/1937 is indicated by partial fusions of the ilium with the sacral ribs, as well as a partial fusion of the sacral vertebral centra and zygapophyses, separate in most other specimens (ZPAL ABIII/2531, ZPAL AbIII/2738, ZPAL AbIII/3394).

Additionally, in the proposed series, the shape of the spine table changes from heart-like in ZPAL AbIII/2738 to flat in ZPAL AbIII/2531/1 and the keel-like medial elevation on the ventral surface of the centrum gradually develops, being absent in ZPAL AbIII/2738, moderately indicated in ZPAL AbIII/2731/1, and enlarged in ZPAL AbIII/1937. A similar change of centra morphology is visible in the first sacrals, in which a slender keel-like elevation in ZPAL AbIII/2531/1 changes into a regular keel with sharp edge in ZPAL AbIII/1937. However, because the sample is small, the change of those features can alternatively explain by intraspecific variation.

Similar development of the sacrum as in ZPAL AbIII/1937 has been reported for the pelvis of *Desmatosuchus spurensis* (MNA V9300), in which the sacral ribs also form uniform rami with transverse process fused with the ilia, and the sacral vertebrae are fused with each

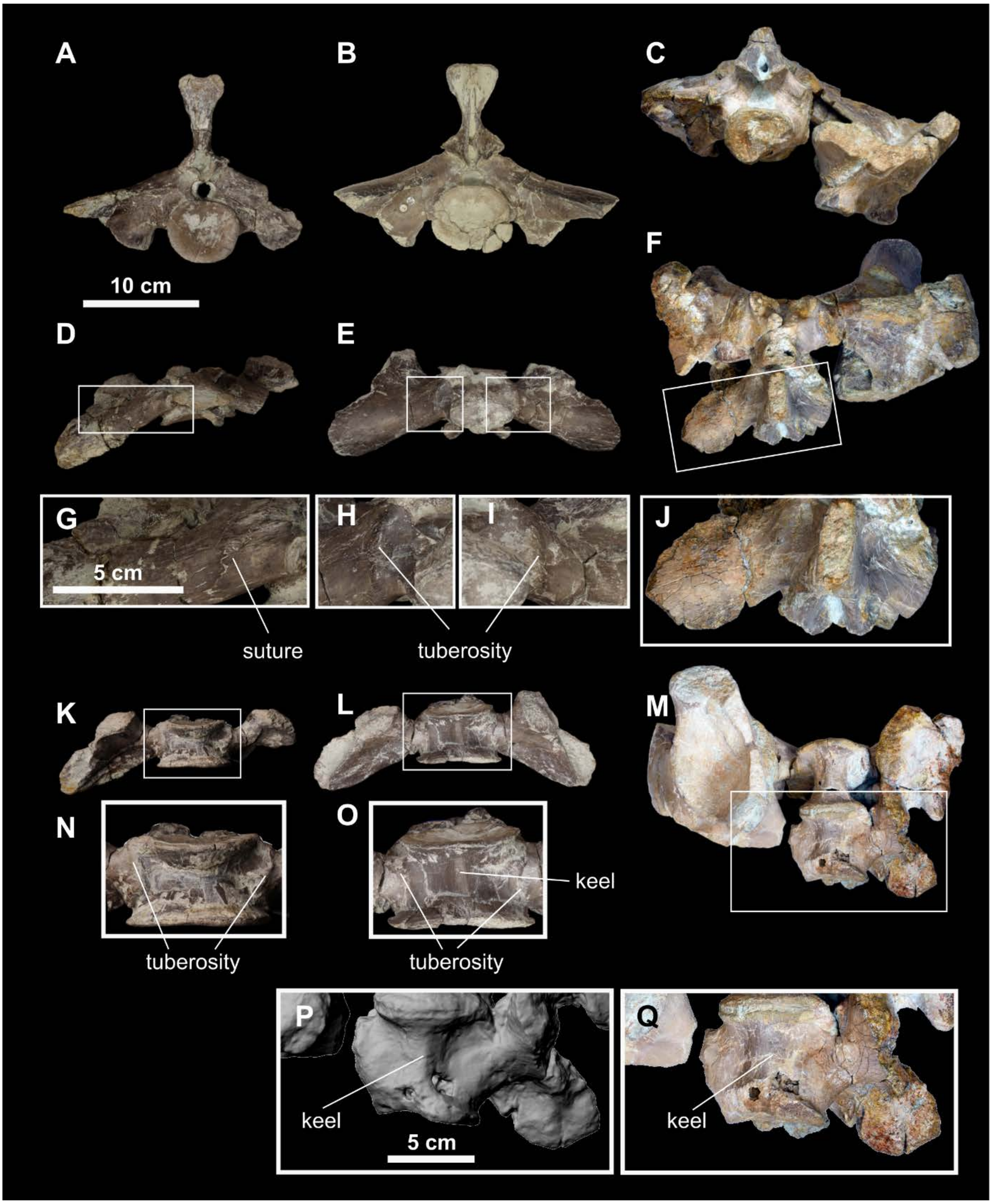


Figure 31. Probable ontogenetic series of the second sacral vertebra: ZPAL AbIII/2738 (A, D, G, K, N), ZPAL AbIII/2531/2 (B, E, H, H, I, L,O); ZPAL AbIII/1937 (C, F, J, M, Q). Specimens shown in posterior (A–C), dorsal (D–J), and ventral view (K–Q). Views A–F and K–M are in the same scale (10 cm); views G, H, I, J and N–Q are in the same scale (5 cm).

other (Parker 2008). However, in *D. spurensis* the fusions are even more advanced, as along with the sacral vertebrae also the last dorsal and the first caudal vertebrae are fused together. Sacral ribs are fused with the ilia also in *Aetosauroides scagliai* (PVL 2052/14, PVL 2073)

(Casamiquela 1961, 1967; Heckert and Lucas 2002) and *Typothorax antiquum* (NMMNH P-36075) (Lucas et al. 2002).

Increase of pelvis thickness during ontogeny in mature individuals?

Supposedly the oldest ZPAL AbIII/1937 is much more heavily built in comparison with the rest of the studied pelvic elements. Its increased thickness is best visible in the lateral margin of the iliac blades (in ZPAL AbIII/1937 25 mm thick, compared to 15 mm in ZPAL AbIII/199 and 12 mm in both ilia of ZPAL AbIII/3349/5).

Higher robustness affects the morphology of the supracetabular buttress, which in more lightly build ilia (ZPAL AbIII/199, ZPAL AbIII/3349/5, ZPAL AbIII/3394/2) markedly extends laterally from the iliac blade, dorsally forming a distinct concavity. In ZPAL AbIII/1937 the iliac blade abruptly ascends dorsally from above the acetabulum, and the supracetabular buttress is poorly developed.

A similar increase of robustness is present in largest pubis ZPAL AbIII/3266. The difference in thickness is most visible in the dorsal portion of the pubic flange (~3 mm in ZPAL AbIII/3266, ~1–2 mm in ZPAL AbIII/2410 and ZPAL AbIII/3349/5). Probably due to this increased robustness, ZPAL AbIII/3266 is the only specimen with this part preserved entirely. ZPAL AbIII/3266 might be of a similar ontogenetic age as ZPAL AbIII/1937, which is suggested by the similar size of the puboiliac suture area in both specimens.

Bone fusions in the pelvis

In the pelvis ZPAL AbIII/3349/5 (Fig. 7, Fig. 32) the pubes and ilia are fused together, and this is the only studied specimen in which such a state occurs. It seems that the development of those fusions cannot be easily correlated with the aging of the animal, because ZPAL AbIII/3349/5 is probably ontogenetically younger than the comparable in size ZPAL AbIII/1937, which is suggested by its lesser robustness and less advanced fusions in the sacrum (comparable as in ZPAL AbIII/2531). Similarly, the most robust pubis ZPAL AbIII/3266 was also not fused with either ilium or the other pubis. Therefore, it seems that the bony fusion of the puboiliac suture and pubic symphysis in *Stagonolepis olenkae* is intraspecifically variable or an expression of sexual dimorphism.

The ischia in ZPAL AbIII/3349/5 are dislocated in a way that indicates that they were not fused with the ilia at the moment of burial, and in ZPAL AbIII/1937 the ilioischiadic suture

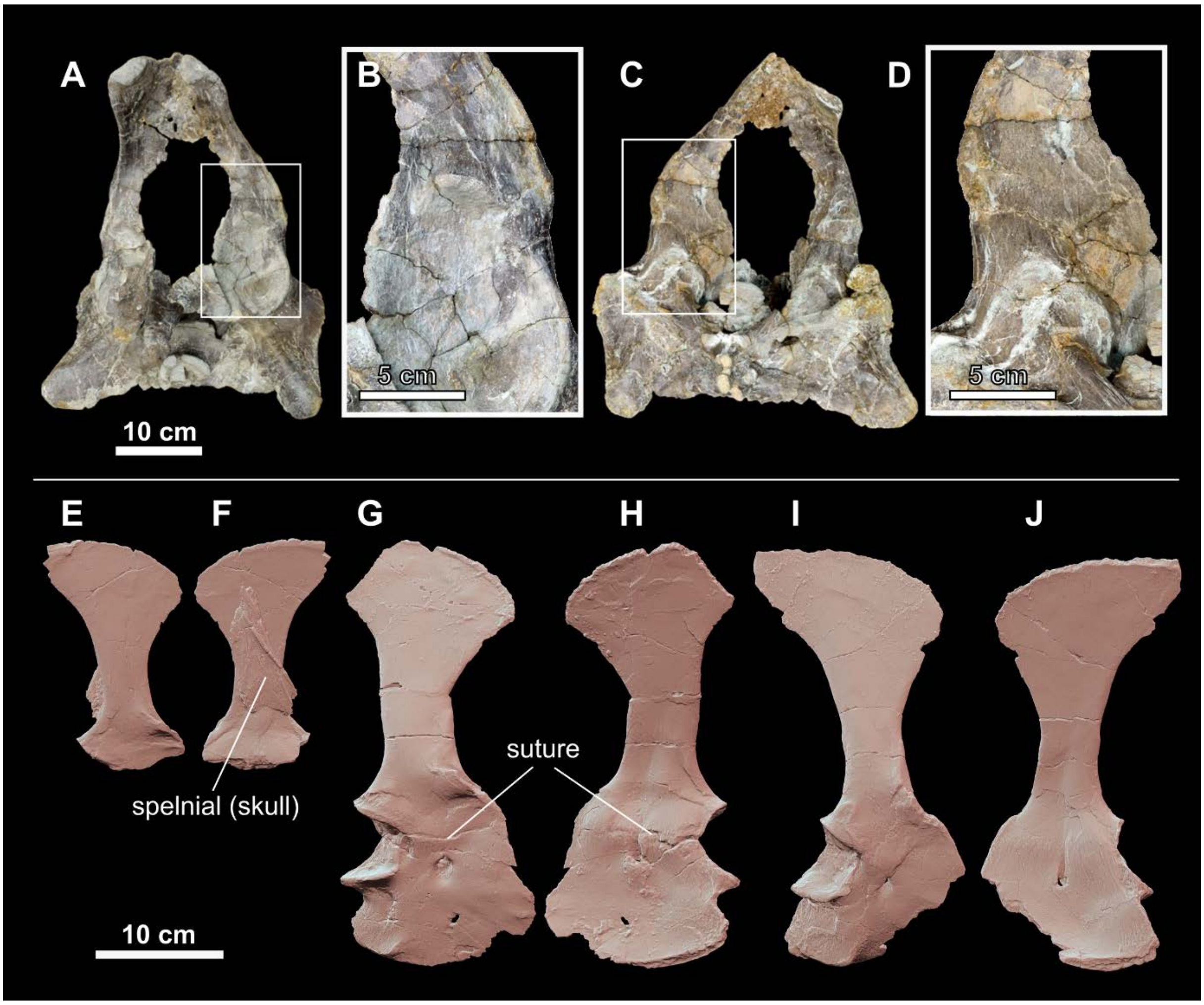


Figure 32. Fused suture between the ilium and the pubis of *Stagonolepis olenkae* ZPAL AbIII/3349/5 (A–D). Specimen visible in ventral view (A, B) and dorsal view (C, D); and fusion between the scapulae and coracoids: ZPAL AbIII/2546 (E, F): scapula separate form coracoid; ZPAL AbIII/2776 (G, H): suture partially fused; ZPAL AbIII/2624 (I, J): suture completely obliterated. Specimens visible in lateral (E, G, I) and medial (F, H, J) view.

was also filled with cartilage. On the other hand, a similar development of the surface of the ilioischiadic suture and puboiliac suture may indicate that eventual merging of those elements was possible. The area of the ischiadic symphysis is developed differently than the latter two: it has numerous openings for blood vessels and its surface is smooth contrary to harsh areas of other sutures. It suggests a different type joint than other pelvis sutures and the pubic symphysis, and possibly did not fuse during ontogeny.

Similar to *Stagonolepis olenkae*, bony fusions between the contralateral pubes and the pubes and ilia have been described in *Desmatosuchus spurensis* (MNA V9300) and *Scutarx deltatylus* (PEFO 31217) (Parker 2008, 2016*b*), while in both species separated pubes and ilia are also known (Long and Murry 1995; Parker 2016*b*). Additionally, in *Desmatosuchus spurensis* (MNA V9300), *Scutarx deltatylus* (PEFO 31217), and *Typothorax antiquum* (NMMNH P-

36075), the ischia are fused with the pubes and ilia (Long and Murry 1995; Lucas et al. 2002; Parker 2016*b*). In *Aetosauroides scagliai*, in both PVL 2052/14 and PVL 2073, despite the fact that the sacral ribs are completely fused, no fusions between other elements have been recognized (Casamiquela 1961, 1967). In most other described aetosaurs, pelvis and sacral elements are not fused (Walker 1961; Long and Murry 1995; Martz 2002; Schoch 2007; Desojo et al. 2013; Roberto-Da-Silva et al. 2014)

Different proportions of long bones in smaller (younger) aetosaurs

The proportion between the thigh and crus recognized in *Stagonolepis olenkae* (ratio around 0.6) is similar as in large and middle-sized aetosaurs such as *Desmatosuchus smalli*, *Neoaetosauroides engaeus*, *Longosuchus meadei*, or *Typothorax coccinarum* (Sawin 1947; Bonaparte 1971; Small 1985; Long and Murry 1995; Heckert et al. 2010), while small aetosaurs (*Aetosaurus ferratus* and *Polesinesuchus aurelioi*) have a noticeably longer crus in proportion to the femur (around 0.8) (Schoch 2007; Roberto-Da-Silva et al. 2014). The limbs of *A. ferratus* and *P. aurelioi* also appear to be more slender in comparison with larger aetosaurs, but have all the features characteristic for the group, especially a hypertrophied iliofibularis trochanter in the fibula and marked and well-developed, distinct, far distally positioned attachment for the *m. gastrocnemius* in the tibia (in *P. aurelioi*, not visible in *A. ferratus*). Similar proportion and development of long bones was recognized in the juvenile specimen from Woźniki.

According to Hildebrand (1988), if the limb is be perceived as a lever (out-lever being the lower leg and pes and in-lever being the femur), a short crus would indicate an increase of the output force of the leg by reduction of the length the out-lever. This feature, among others, is a common adaptation for specialized scratch-digging animals (Hildebrand 1988), and a well-developed ability to scratch-dig has been proposed for aetosaurs as well (Walker 1961; Parrish 1986; Heckert et al. 2010; Dróżdż 2018). However, while the reduction of the out-lever is beneficial in generating a larger output force, it diminishes the ability to run fast (and escape from predators), because of the reduction of the length of the leg and reduction of the mass around the pes (longer, distally heavy leg can achieve larger angular velocity – rotate faster in the hip joint) as well as by shortening of the steps.

Small aetosaurs like *Aetosaurus ferratus* and *Polesinesuchus aurelioi*, despite an extensive protective armor, presumably were still an easy target for the predators. Therefore, it seems plausible that a longer crus in proportion to the femur was an adaptation compensating for their tiny size, which enhanced their ability to run and to prevented them from being hunted.

Recently some authors contested the distinctiveness of those small aetosaur species, and instead proposed that they are early ontogenetic forms of larger aetosaurs: *Aetosauroides scagliai* (for *Polesinesuchus aurelioi*) and *Paratypothorax andressorum* (for *Aetosaurus ferratus*) (Schoch and Desojo 2016; Paes-Neto et al. 2021). In this scenario, the change in proportions could develop through the ontogeny, possibly to improve the strength of the legs, which would be beneficial in activities such as scratch-digging. While the animals grew, the danger of being hunted would gradually decrease due to their larger size and thicker armor, while at the same time the animals would probably need greater amount of food to sustain themselves and remain in good condition. If scratch-digging was a crucial ability in search for food, the development of a shorter crus would be more beneficial for adults than younger individuals and that would explain the ontogenetic change of this feature. Unfortunately, presently the material of *Stagonolepis olenkae* is insufficient for adequate verification of this hypothesis.

Ontogenetic changes in the development of articular surfaces of long bones

In the studied series of long bones of both the forelimbs and hind limbs, articulation surfaces of smaller bones appear to be thinner, the pattern of tuberosities on both the proximal and distal ends is clearer, the irregularities are more frequent, and cover a broader area in comparison to larger bones (Fig. 33). In addition, the articulation surfaces of smaller bones of the series usually form marked, somewhat transversally oriented depressions, mostly absent or shallow in larger specimens.

These changes of morphology are most likely connected with the continuous growth of bones and are caused by the reduction of hyaline cartilage at the bone ends, that progressed during the ontogeny (Holliday et al. 2010; Tsai and Holliday 2015). Long bones, just like all endoskeletal elements, first appear as cartilage that ossifies later during ontogeny (e.g., Romer 1956). Replacement of the cartilage (endochondral ossification) starts within the center of shaft and expands longitudinally, eventually forming structure with a bony center (metaphysis) and cartilaginous ends (e.g., Romer 1956). After this stage, the bone continues to grow in length by deposition of new cartilaginous tissue in growth plates at both ends of the metaphysis, which in time would also ossify (e.g., Romer 1956). The term ‘articular surface’ traditionally used in paleontology to describe bone ends actually refers to the metaphyseal growth plate surface (following the nomenclature of Tsai and Holliday 2015). Therefore, the observed reduction of irregular rugosities, shallowing of the transverse depressions, as well as increase of the articulation surface thickness in larger specimens of *Stagonolepis olenkae* long bones is most likely

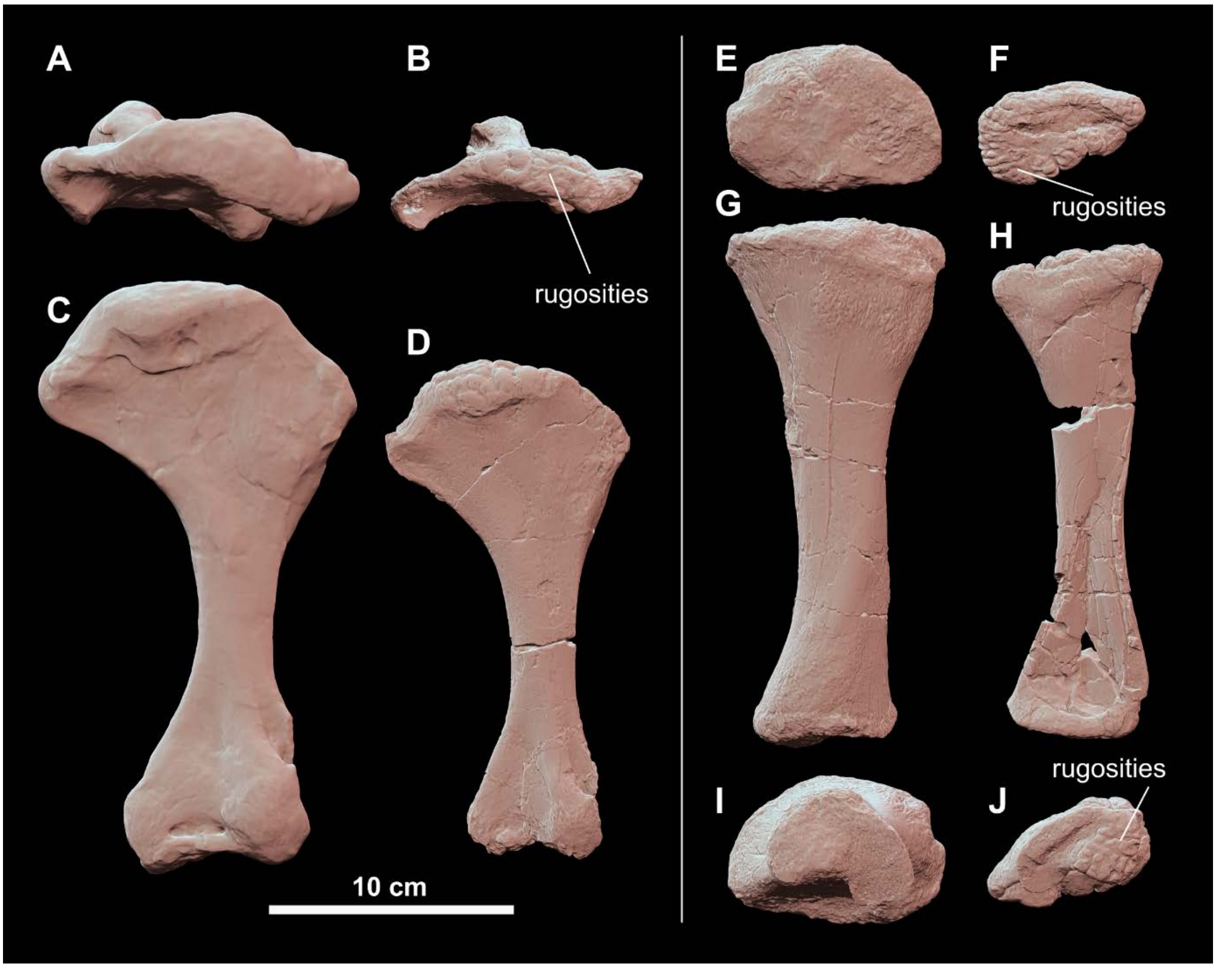


Figure 33. *Stagonolepis olenkae*, humeri ZPAL AbIII/1175 (A, C) and ZPAL AbIII/2627 (B, D) in proximal (A, B) and dorsal (C, D) view; tibiae ZPAL AbIII/3367 (E, G, I) and ZPAL AbIII/1626 in proximal (E, F), anterior (G, H), and distal (I, J) view.

due to progressive ossification of the epiphyseal cartilage, as the cartilaginous cap becomes proportionally thinner compared to the length of the bone (Tsai and Holliday 2015). Similar irregular rugosities are present in long bones of immature non-avian dinosaurs, birds, and lepidosaurs (Holliday et al. 2010; Tsai and Holliday 2015). More pronounced rugosities indicate an intense growth of the bone, therefore indirectly can be used to determine a younger age of the individual by comparison with other specimens in the series.

Differences between the juvenile from Woźniki and *Stagonolepis olenkae*

Compared to adults of *Stagonolepis olenkae* from Krasiejów, the juvenile from Woźniki has a more gracile morphology of its girdles and limbs. There is no fusion between the girdle elements, scapulae, coracoids, and elements of the pelvis are separate. The sacral ribs are not fused with the neural arches and centra. In long bones, the proximal and distal parts are poorly developed, which is the best visible when the development of the proximal end of the humerus

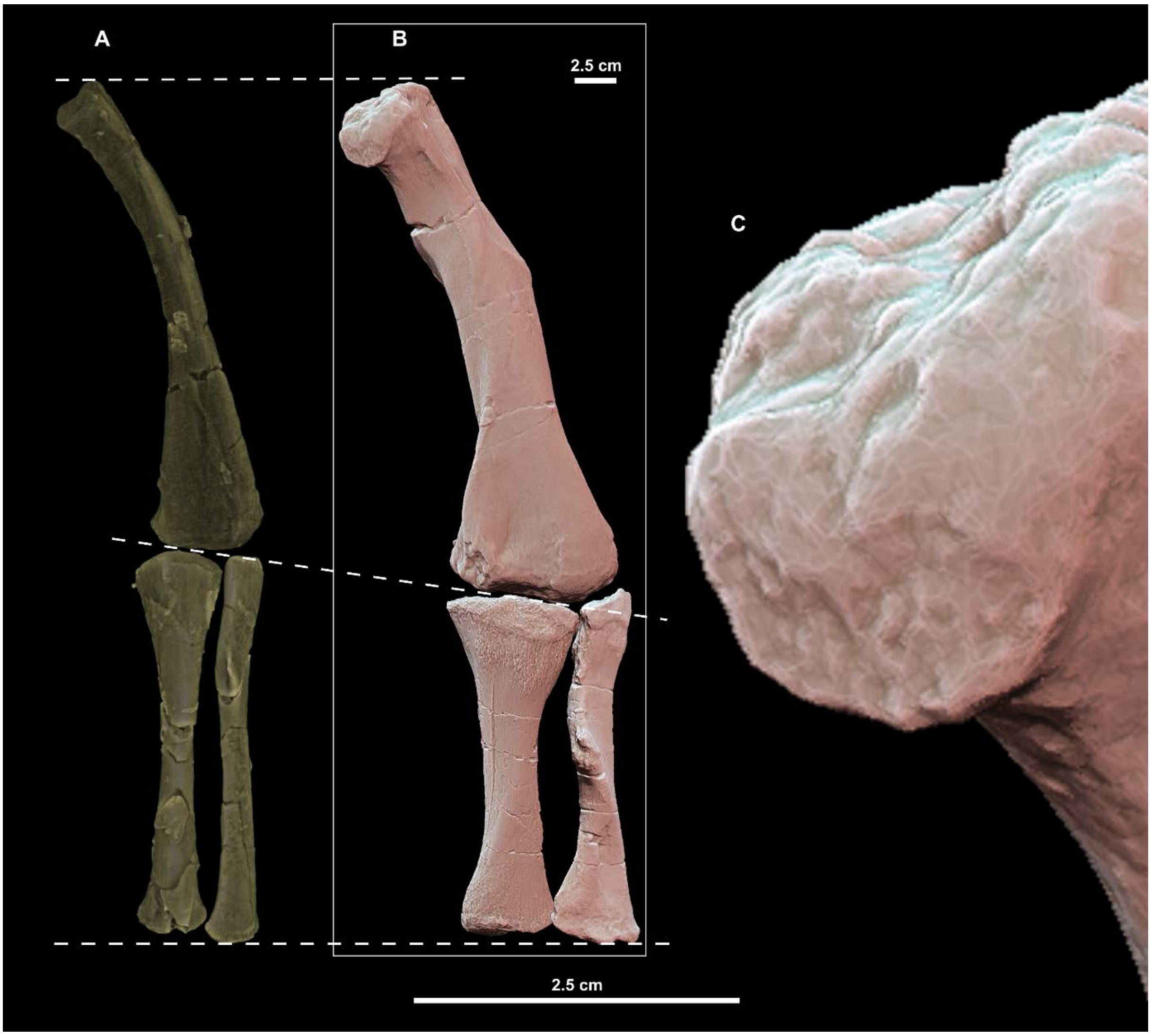


Figure 34. Femur and crus of the juvenile aetosaur ZPAL V. 34/106 (A) compared to the reconstruction of the femur and crus of *Stagonolepis olenkae* based on ZPAL AbIII/3363 (femur), ZPAL AbIII/3367 (tibia), and ZPAL AbIII/2629 (fibula) scaled to the same length. (C) The femoral head of ZPAL AbIII/3363 in the real scale compared to ZPAL V. 34/106. In B the femur and tibia were not scaled, but retain original proportions between the specimens and ZPAL AbIII/2629 was scaled accordingly.

and femoral head are compared, proportionally significantly less expanded in the Woźniki specimen. The olecranon process in ulna is nearly absent. The proportions of the long bones are also different (Fig. 34). The juvenile specimen has proportionally longer forearms and crus in proportion to the humerus and femur.

Despite those differences, the elements of the limbs and girdles of the juvenile skeleton have at least some of the important features discussed in the context of their probable adaptations for strength and scratch-digging including hypertrophied muscle attachments (fourth trochanter of the femur, iliofibularis trochanter, larger deltopectoral crest in the humerus) or enlarged claw-like unguals in the pes; however, these features are developed to a lesser degree than in the adults of *Stagonolepis olenkae*.

Probable model of morphological changes in the locomotor apparatus during ontogeny in aetosaurs

In general, the morphology of the juvenile aetosaur from Woźniki is the most similar to the small species of aetosaurs *Aetosaurus ferratus* and *Polesinesuchus aurelioi*, postulated to be the juveniles of, respectively, *Paratypothorax andressorum* and *Aetosauroides scagliai* (Schoch and Desojo 2016; Paes-Neto et al. 2021). Also in Woźniki larger aetosaur material was found.

If those small aetosaurs would be recognized as the juvenile of the mentioned species, it would indicate that the aetosaur musculoskeletal system would go through a significant transformation during ontogeny form relatively lightly built juveniles into very heavy built adults.

The longer forearm and cruses in the juveniles, along with their more gracile built, and less stiff skeleton indicate that they were more agile and mobile than adults (Hildebrand 1988), but at the same time most of the characters associated with adaptations toward increased strength and possible scratch-digging were already developed, but to a lesser extent then in adults.

This is expected as, despite having the dermal armor, due to their size, the juveniles would not be able to face most of the predators, therefore, their capability to move faster and turn quicker if necessary would be mandatory to survive the early stages of life. Similar adaptions are common in a lot of animals in which the younglings are adapted for an independent life from a very early ontogenetic stages, such as juvenile crocodiles or young antelopes. It is also possible that the juveniles of aetosaurs were not able to feed from the same food sources as adults and were hunting some presumably fast prey, such as insects, which is also observed in many animals.

As the juvenile aetosaurs matured, their limbs would gradually become thicker, the muscle attachments expanded, the forearms and crus shortened, and the pelvic and pectoral girdles started to fuse to gain more stability, therefore, the animals would become slower, but would be able to perform activities that require more strength, such as scratch-digging. At this point of ontogeny, the ability to move fast would have a lesser meaning as mature aetosaurs would rely on their armor to protect themselves against the predators and they would be significantly larger, which would reduce the possible amount of predators capable to hunt them. Therefore, the priority would be to sustain themselves, which probably was related with gradual switching to a more highly energetic diet. In the case of aetosaurs, that would possibly mean underground protein-reach parts of tropical plants, that would require digging them out from the ground.

CONCLUSIONS

1. Limbs and pelvic girdle of *Stagonolepis olenkae* are the most similar to large and middle sized aetosaurs form the Northern Pangea (Scotland, USA).
2. *Stagonolepis olenkae* was a digitigrade animal with erect hind limbs and at least semi-erect forelimbs, which contrasts with the previous descriptions that presented it as a sprawling animal.
3. Morphology of the limbs and pelvic girdle in *Stagonolepis olenkae* is nearly identical as in *Stagonolepis robertsoni*. Those two forms are very close in the terms of osteology and visible differences in postcranial skeleton can be explained either by taphonomic effects or ontogeny.
4. Morphology of the limbs and pelvic girdle in aetosaurs is conservative with little intra-specific variation. However, better development of features associated with a more erect posture or increased strength of the movements are observed in advanced forms.
5. The most different are the smallest aetosaurs species, postulated by some authors to be juvenile individuals, however, even in those aetosaurs the general architecture of the limbs is the same.
6. Aetosaur limbs and pelvic girdle share the general body plan typical for all pseudosuchians, but are evolutionary modified to support the high weight of the body and perform strong movements with the limbs, at the cost of mobility, in contrast to other contemporary pseudosuchians that possessed cursorial adaptations.
7. *Stagonolepis olenkae* has many characters suggesting that it could perform scratch-digging with both the forelimbs and hind limbs.
8. Similar features can be found in other aetosaurs, regardless their size, but are more prominent in larger species.
9. It was detected that elements of the sacrum and pelvis grew in thickness and fused during the ontogeny in *Stagonolepis olenkae*. The fusions occurred between the scapula and coracoid in the pectoral girdle.
10. The suture obliteration process in the sacrum seems uniform and could be used as an indicator of the ontogenetic stage if other methods would not be available. The fusions in the pelvis do not seem to have a clear pattern.

11. Articular surfaces of the long bones in *Stagonolepis olenkae* express a clear pattern of tuberosities that can be correlated with growth and therefore used for age approximation if other methods are not available.
12. The aetosaur specimen from Woźniki is probably the first certain record of a juvenile aetosaur.
13. Its morphology is most similar to other small aetosaur species postulated to be juveniles by some authors, which have more lightly built skeletons and longer zeugopodia compared with larger species.
14. It is probable that youngling aetosaurs were more mobile and agile than the adults, that allowed them to easier escape from predators or hunt for fast prey.
15. The adults most likely relied on the armor for protection against predators, and development of the dermal armor induced the increase of the thickness of bones as well as enlargement of muscle attachments to compensate for the high mass of the armor.
16. Probably, it was also related with the change of the diet, which in the case of the aetosaurs would require a scratch-digging ability.

BIBLIOGRAPHY

Agassiz, L. 1844. *Monographie des Poissons fossiles du vieux grès rouge ou Système Dévonien (Old Red Sandstone) des Isles Britanniques et de Russie.* Jent et Gassman, Neuchâtel, .

Allen, V., Molnar, J., Parker, W., Pollard, A., Nolan, G. and Hutchinson, J.R. 2014. Comparative architectural properties of limb muscles in Crocodylidae and Alligatoridae and their relevance to divergent use of asymmetrical gaits in extant Crocodylia. *Journal of Anatomy* 225 (6): 569–582.

Antczak, M. 2016. Late Triassic aetosaur (Archosauria) from Krasiejów (SW Poland): new species or an example of individual variation? *Geological Journal* 51 (5): 779–788.

Avanzini, M., Dalla Vecchia, F.M., Mietto, P., Piubelli, D., Preto, N., Rigo, M. and Roghi, G. 2007. A vertebrate nesting site in northeastern Italy reveals unexpectedly complex behavior for Late Carnian reptiles. *Palaios* 22 (5): 465–475.

Benton, M.J. 1983. The Triassic reptile *Hyperodapedon* from Elgin: functional morphology and relationships. *Philosophical Transactions of the Royal Society of London B* 302: 605–717.

Benton, M.J. and Clark, J.M. 1988. Archosaur phylogeny and the relationships of the Crocodylia. *In*: Benton, M.J. (ed.), *The Phylogeny and Classification of the Tetrapods, Volume 1: Amphibians, Reptiles, Birds*, 298–338. Oxford University Press, Oxford.

Biacchi Brust, A.C., Desojo, J.B., Schultz, C.L., Paes-Neto, V.D. and Da-Rosa, Á.A.S. 2018. Osteology of the first skull of *Aetosauroides scagliai* Casamiquela 1960 (Archosauria: Aetosauria) from the upper Triassic of Southern Brazil (Hyperodapedon Assemblage Zone) and its phylogenetic importance. *PLoS ONE* 13 (8).

Bodzioch, A. and Kowal-Linka, M. 2012. Unraveling the origin of the Late Triassic multitaxic bone accumulation at Krasiejów (S Poland) by diagenetic analysis. *Palaeogeography, Palaeoclimatology, Palaeoecology* 346–347: 25–36.

Bonaparte, J.F. 1971. Los tetrapods del sector superior de la formation Los Colorados, La Rioja, Argentina. *Opera Liloana* 22.

Bonaparte, J.F. 1984. Locomotion in Rauisuchid Thecodonts. *Journal of Vertebrate Paleontology* 3 (4): 210–218.

Brochu, C.A. 1996. Closure of neurocentral sutures during crocodilian ontogeny: Implications for maturity assessment in fossil archosaurs. *Journal of Vertebrate Paleontology* 16 (1): 49–62.

Bronowicz, R. 2017. Morfologia i osteohistologia fitozaurów z górnego triasu Krasiejowa.University of Warsaw, 298pp.

Brusatte, S.L., Butler, R.J., Sulej, T. and Niedźwiedzki, G. 2009. The taxonomy and anatomy of rauisuchian archosaurs from the Late Triassic of Germany and Poland. *Acta Palaeontologica Polonica* 54 (2): 221–230.

Brusatte, S.L., Benton, M.J., Desojo, J.B. and Langer, M.C. 2010a. The higher-level phylogeny of Archosauria (Tetrapoda: Diapsida). *Journal of Systematic Palaeontology* 8 (1): 3–47.

Brusatte, S.L., Benton, M.J., Lloyd, G.T., Ruta, M. and Wang, S.C. 2010b. Macroevolutionary patterns in the evolutionary radiation of archosaurs (Tetrapoda: Diapsida). *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* 101 (3–4): 367–382.

Buckley, L.G. and Currie, P.J. 2014. Analysis of intraspecific and ontogenetic variation in the dentition of *Coelophysis bauri* (Late Triassic), and implications for the systematics of isolated theropod teeth. *New Mexico Museum of Natural History & Science Bulletin* 63: 1–73.

Budziszewska-Karwówska, E., Bujok, A. and Sadlok, G. 2010. Bite marks on an upper triassic dicynodontid tibia from Zawiercie, Kraków- Częstochowa Upland, Southern Poland. *Palaios* 25 (6): 415–421.

Bullock, S.H. and Solis-Magallanes, J.A. 1990. Phenology of Canopy Trees of a Tropical Deciduous Forest in Mexico. *Biotropica* 22 (1): 22.

Carrier, D.R. and Farmer, C.G. 2000. The evolution of pelvic aspiration in archosaurs. *Paleobiology* 26 (2): 271–293.

Casamiquela, R.M. 1960. Noticia preliminar sobre dos nuevos estagonolepoideos argentinos. *Ameghiniana* 2 (1): 3–9.

Casamiquela, R.M. 1961. Dos nuevos estagonolepoideos Argentinos (de Ischigualasto, San Juan). *Revista de la Asociacion Geologica Argentina* 16: 143–203.

Casamiquela, R.M. 1967. Materiales adicionales y reinterpretacion de *Aetosauroides scagliai* (de Ischigualasto, San Juan). *Revista del Museo de La Plata* 5 (33): 173–196.

Case, E.C. 1922. *New reptiles and stegocephalians from the Upper Triassic of western Texas.* Carnegie Institution of Washington, Washington.

Cerda, I.A. and Desojo, J.B. 2011. Dermal armour histology of aetosaurs (Archosauria: Pseudosuchia), from the Upper Triassic of Argentina and Brazil. *Lethaia* 44 (4): 417–428.

Cerda, I.A., Desojo, J.B. and Scheyer, T.M. 2018. Novel data on aetosaur (Archosauria, Pseudosuchia) osteoderm microanatomy and histology: palaeobiological implications. *Palaeontology* 61 (5): 721–745.

Charig, A.J. 1972. The evolution of the archosaur pelvis and hind limb: an explanation in functional terms. *In*: Joysey, K.A. and Kemp, T.S. (eds.), *Studies in Vertebrate Evolution*, 121–155. Oliver and Boyd, Edinburgh.

Chatterjee, S. 1978. A primitive parasuchid (phytosaur) reptile from the Upper Triasic Maleri fromation of India. *Palaeontology* 21 (1): 83–127.

Chatterjee, S. 1985. *Postosuchus*, a new Thecodontian reptile from the Triassic of Texas and the origin of Tyrannosaurs. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences* 309 (1139): 395–460.

Cignoni, P., Callieri, M., Corsini, M., Dellepiane, M., Ganovelli, F. and Ranzuglia, G. 2008. MeshLab: An open-source mesh processing tool. *6th Eurographics Italian Chapter Conference 2008 - Proceedings* (January): 129–136.

Coombs, W.P. 1978. Theoretical Aspects of Cursorial Adaptations in Dinosaurs. *The Quarterly Review of Biology* 53 (4): 393–418.

Coombs, M.C. 1983. *Large Clawed Mammalian Herbivores: Comparative Study*. Vol. 73.

Czepiński, Ł., Dróżdż, D., Szczygielski, T., Tałanda, M., Pawlak, W., Lewczuk, A., Rytel, A. and Sulej, T. 2021. An Upper Triassic Terrestrial Vertebrate Assemblage from the Forgotten Kocury Locality (Poland) with a New Aetosaur Taxon. *Journal of Vertebrate Paleontology*.

D'Amore, D.C. 2015. Illustrating ontogenetic change in the dentition of the Nile monitor lizard, *Varanus niloticus*: A case study in the application of geometric morphometric methods for the quantification of shape-size heterodonty. *Journal of Anatomy* 226 (5): 403–419.

Deligne, J., Quennedey, A. and Blum, M.S. 1981. The enemies and defense mechanisms of termites. *In*: Herman, H.R. (ed.), *Social Insects. Volume II*, 1–76. Academic Press, New York, London, Toronto, Sidney, San Francisco.

Demuth, O.E., Rayfield, E.J. and Hutchinson, J.R. 2020. 3D hindlimb joint mobility of the stem-archosaur *Euparkeria capensis* with implications for postural evolution within Archosauria. *Scientific Reports* 10 (1): 1–14.

Desojo, J.B. and Báez, A.M. 2005. The postcranial skeleton of *Neoaetosauroides* (Archosauria: Aetosauria) from the Upper Triassic of west-central Argentina. *Ameghiniana* 42 (1): 115–126.

Desojo, J.B. and Vizcaíno, S.F. 2009. Jaw biomechanics in the South American aetosaur *Neoaetosauroides engaeus*. *Palaontologische Zeitschrift* 83 (4): 499–510.

Desojo, J.B. and Ezcurra, M.D. 2011. A reappraisal of the taxonomic status of *Aetosauroides* (Archosauria, Aetosauria) specimens from the Late Triassic of South America and their proposed synonymy with *Stagonolepis*. *Journal of Vertebrate Paleontology* 31 (3): 596–609.

Desojo, J.B., Ezcurra, M.D. and Kischlat, E.E. 2012. A new aetosaur genus (Archosauria: Pseudosuchia) from the early Late Triassic of southern Brazil. *Zootaxa* 33 (3166): 1–33.

Desojo, J.B., Heckert, A.B., Martz, J.W., Parker, W.G., Schoch, R.R., Small, B.J. and Sulej, T. 2013. Aetosauria: A clade of armoured pseudosuchians from the upper Triassic continental beds. 1. *In*: Nesbitt, S.J., Desojo, J.B. and Irmis, R.B. (eds.), *Anatomy, Phylogeny, and Palaeobiology of Early Archosaurs and Their Kin*, Vol. 379, 203–239. The Geological Society Publishing House, Bath.

Diedrich, C.G. 2012. The Middle Triassic marine reptile biodiversity in the Germanic Basin, in the centre of the Pangaean world. *Central European Journal of Geosciences* 4 (1): 9–46.

Diedrich, C.G. 2013. Shallow Marine Sauropterygian Reptile Biodiversity and Change in the Bad Sulza Formation (Illyrian, Middle Triassic) of Central Germany, and a Contribution To the Evolution of Nothosaurus in the Germanic Basin. *New Mexico Museum of Natural History Bulletins* 61 (February): 132–158.

Dróżdż, D. 2018. Osteology of a forelimb of an aetosaur *Stagonolepis olenkae* (Archosauria:

Pseudosuchia: Aetosauria) from the Krasiejów locality in Poland and its probable adaptations for a scratch-digging behavior. *PeerJ* 2018 (10).

Drymala, S.M. and Bader, K. 2012. Assessing predator–prey interactions through the identification of bite marks on an aetosaur (Ppseudosuchia) osteoderm from the Upper Triassic (Norian) Chinle Formation in Petrified Forest National Park (Arizona, USA). *Journal of Vertebrate Paleontology* 32 (sup 1): Abstract 89.

Dubiel, R.F. and Survey, U.S.G. 1987. Sedimentology of the Upper Triassic Chinle Formation, Southeastern Utah : Paleoclimatic Implications. *Journal of the Arizona-Nevada Academy of Sciences* 22: 35–45.

Dzik, J. 2001. A new Paleorhinus fauna in the Early Late Triassic of Poland. *Journal of Vertebrate Paleontology* 21 (3): 625–627.

Dzik, J. 2003a. A beaked herbivorous archosaur with dinosaur affinities from the early late triassic of Poland. *Journal of Vertebrate Paleontology* 23 (3): 556–574.

Dzik, J. 2003b. Krasiejów u zarania ery dinozaurów. *Ewolucja* 1: 40.

Dzik, J. 2008. Gill structure and relationships of the triassic cycloid crustaceans. *Journal of Morphology* 269 (12): 1501–1519.

Dzik, J. and Sulej, T. 2007. A review of the early Late Triassic Krasiejów biota from Silesia, Poland. *Palaeontologia Polonica* (64): 3–27.

Dzik, J. and Sulej, T. 2016. An Early Late Triassic Long-Necked Reptile with a Bony Pectoral Shield and Gracile Appendages. *Acta Palaeontologica Polonica* 61 (4): 805–823.

Dzik, J., Niedźwiedzki, G. and Sulej, T. 2008. Zaskakujące uwieńczenie ery gadów ssakokształtnych. *Ewolucja* 3: 2–21.

Dzik, J., Sulej, T., Kaim, A. and Niedźwiedzki, R. 2000. Późnotriasowe cmentarzysko kręgowców lądowych w Krasiejowie na Śląsku Opolskim. *Przegląd Geologiczny* 48 (3): 226–235.

Estes, R. and Williams, E.E. 1984. Ontogenetic variation in the molariform teeth of lizards. *Journal of Vertebrate Paleontology* 4 (1): 96–107.

Ezcurra, M.D. 2016. The phylogenetic relationships of basal archosauromorphs, with an emphasis on the systematics of proterosuchian archosauriforms. *PeerJ* 2016 (4).

Ezcurra, M.D., Butler, R.J. and Gower, D.J. 2013. ‘Proterosuchia’: The origin and early history of archosauriformes. *Geological Society Special Publication* 379 (1): 9–33.

Farlow, J.O., Hayashi, S. and Tattersall, G.J. 2010. Internal vascularity of the dermal plates of *Stegosaurus* (Ornithischia, Thyreophora). *Swiss Journal of Geosciences* 103 (2): 173–185.

Farlow, J.O., Schachner, E.R., Sarrazin, J.C., Klein, H. and Currie, P.J. 2014. Pedal Proportions of *Poposaurus gracilis*: Convergence and Divergence in the Feet of Archosaurs. *Anatomical Record* 297 (6): 1022–1046.

Frass, O. 1877. *Aetosaurus ferratus*, die gepanzerte Vogelechse aus dem Stubensandstein bei Stuttgart. *Jahreshefte des Vereins für vaterländische Naturkunde in Württemberg* 33: 1–21.

Gąsiorowski, S.M. and Piekarska, E. 1976. Woźniki Limestone (? Lower Jurassic, Upper Silesia). *Bulletin de l’Academie Polonaise des Sciences.* 24 (3): 177–182.

Gaudin, T.J., Emry, R.J. and Morris, J. 2016. Skeletal Anatomy of the North American Pangolin *Patriomanis americana* (Mammalia, Pholidota) from the Latest Eocene of Wyoming (USA). *Smithsonian Contributions to Paleobiology* (98): vii–102.

Gauthier, J.A., Nesbitt, S.J., Schachner, E.R., Bever, G.S. and Joyce, W.G. 2011. The bipedal stem crocodilian *Poposaurus gracilis*: Inferring function in fossils and innovation in archosaur locomotion. *Bulletin of the Peabody Museum of Natural History* 52 (1): 107–126.

Gignac, P.M. and Erickson, G.M. 2014. Ontogenetic changes in dental form and tooth pressures facilitate developmental niche shifts in American alligators. *Journal of Zoology* 295 (2): 132–142.

Górnicki, S. 2015. Morphology of the hind limb of an aetosaur from the Upper Triassic of Krasiejów. *13th Annual Meeting of the European Association of Vertebrate Palaeontologists*: 146.

Górnicki, S., Antczak, M. and Bodzioch, A. 2021. Aetosaur pes from the Upper Triassic of Krasiejów (Poland), with remarks on taxonomy of isolated bones. 91.

Gruszka, B. and Zieliński, T. 2008. Evidence for a very low-energy fluvial system: a case study from the dinosaur-bearing Upper Triassic rocks of Southern Poland. *Geological Quarterlyly* 52 (3): 239–252.

Heckert, A.B. and Lucas, S.G. 1999. A new aetosaur (Reptilia: Archosauria) from the Upper Triassic of Texas and the phylogeny of aetosaurs. *Journal of Vertebrate Paleontology* 19 (1): 50–68.

Heckert, A.B. and Lucas, S.G. 2000. Taxonomy, phylogeny, biostratigraphy, biochronology, paleobiogeography, and evolution of the Late Triassic Aetosauria (Archosauria: Crurotarsi). *Zentralblatt für Geologie und Paläontologie, Teil I, 1998* 11–12: 1539–1587.

Heckert, A.B. and Lucas, S.G. 2002. South american occurences of the Adamanian (Late Triassic: latest carnian) index taxon *Stagonolepis* (Archosauria: Aetosauria) and their biochronological significance. *Journal of Paleontology* 76 (5): 852–863.

Heckert, A.B., Zeigler, K.E. and Lucas, S.G. 2003. Aetosaurs (Archosauria: Stagonolepididae) from the Upper Triassic (Revueltian) Snyder quarry, New Mexico. *New Mexico Museum of Natural History and Science Bulletin* 24 (24): 115–126.

Heckert, A.B., Fraser, N.C. and Schneider, V.P. 2017. A new species of *Coahomasuchus* (Archosauria, Aetosauria) from the Upper Triassic Pekin Formation, Deep River Basin, North Carolina. *Journal of Paleontology* 91 (1): 162–178.

Heckert, A.B., Lucas, S.G., Rinehart, L.F., Celeskey, M.D., Spielmann, J.A. and Hunt, A.P. 2010. Articulated skeletons of the aetosaur *Typothorax coccinarum* Cope (Archosauria: Stagonolepididae) from the upper triassic bull canyon formation (Revueltian: Early-Mid Norian), Eastern New Mexico, USA. *Journal of Vertebrate Paleontology* 30 (3): 619–642.

Heptner, V.G., Nasimovich, A.A., Bannikov, A.G. and Hoffman, R.S. 1989. *Mammals ofthe Soviet Union, Volume 1, Artiodactyla and Perissodactyla.* Smithsonian Institution Libraries and The National Science Foundation, Washington, D.C..

Hildebrand, M. 1983. Digging of Quadrupeds. *In*: Hildebrand, M., Bramble, D.M., Liem, K.F. and Wake, D.B. (eds.), *Functional Vertebrate Morphology*, 89–109. Harvard University Press, Cambridge.

Hildebrand, M. 1988. *Analysis of vertebrate structure.* John Wiley & Sons, Inc., New York, .

Hoffman, D.K., Heckert, A.B. and Zanno, L.E. 2019. Disparate Growth Strategies within Aetosauria: Novel Histologic Data from the Aetosaur *Coahomasuchus chathamensis*. *Anatomical Record* 302 (9): 1504–1515.

Holliday, C.M., Ridgely, R.C., Sedlmayr, J.C. and Witmer, L.M. 2010. Cartilaginous epiphyses in extant archosaurs and their implications for reconstructing limb function in dinosaurs. *PLoS ONE* 5 (9): 1–16.

Hutchinson, J.R. 2006. The evolution of locomotion in archosaurs. *Comptes Rendus - Palevol* 5 (3–4): 519–530.

Hutchinson, J.R. and Gatesy, S.M. 2000. Adductors, abductors, and the evolution of archosaur locomotion. *Paleobiology* 26 (4): 734–751.

Huxley, T.H. 1875. On *Stagonolepis robertsoni*, and on the evolution of the Crocodilia. *Quarterly Journal of the Geological Society of London* 31 (1–4): 423–438.

Irmis, R.B. 2007. Axial skeleton ontogeny in the Parasuchia (Archosauria: Pseudosuchia) and its implications for ontogenetic determination in Archosaurs. *Journal of Vertebrate Paleontology* 27 (2): 350–361.

Jackson, D.C., Andrade, D. V. and Abe, A.S. 2003. Lactate sequestration by osteoderms of the broad-nose caiman, *Caiman latirostris*, following capture and forced submergence. *Journal of Experimental Biology* 206 (20): 3601–3606.

Jewuła, K., Matysik, M., Paszkowski, M. and Szulc, J. 2019. The late Triassic development of playa, gilgai floodplain, and fluvial environments from Upper Silesia, southern Poland. *Sedimentary Geology* 379: 25–45.

Klein, H. and Lucas, S.G. 2021. The Triassic tetrapod footprint record. *New Mexico Museum of Natural History and Science Bulletin* 83: 1–194.

Klinkhamer, A.J., Wilhite, D.R., White, M.A. and Wroe, S. 2017. Digital dissection and three-dimensional interactive models of limb musculature in the Australian estuarine crocodile (*Crocodylus porosus*). *PLoS ONE* 12 (4): 17–22.

Kosch, J.C.D. and Zanno, L.E. 2020. Sampling impacts the assessment of tooth growth and replacement rates in archosaurs: implications for paleontological studies. *PeerJ* 8.

Kowalski, J., Bodzioch, A., Janecki, P.A., Ruciński, M.R. and Antczak, M. 2019. Preliminary report on the microvertebrate faunal remains from the late triassic locality at Krasiejów, SW Poland. *Annales Societatis Geologorum Poloniae* 89 (3): 291–305.

Kozur, H.W. and Weems, R.E. 2010. The biostratigraphic importance of conchostracans in the continental Triassic of the northern hemisphere. *Geological Society Special Publication*

334: 315–417.

Książkiewicz, K. 2014. Morfo-funkcjonalna analiza szkieletu postkranialnego opancerzonego archozaura rodzaju *Stagonolepis* z późnego triasu Polski.Uniwersytet Wrocławski, 147pp.

Kubo, T. and Benton, M.J. 2007. Evolution of hindlimb posture in archosaurs: limb stresses in extinct vertebrates. *Palaeontology* 50 (6): 1519–1529.

Kubo, T. and Kubo, M.O. 2012. Associated evolution of bipedality and cursoriality among Triassic archosaurs: a phylogenetically controlled evaluation. *Paleobiology* 38 (3): 474–485.

Long, R.A. and Ballew, K.L. 1985. Aetosaur dermal armor from the Late Triassic of Southwestern North America, with special reference to material from Chinle Formation of Petrified Forest National Park. *Museum of Northern Arizona Bulletin* 54: 45–68.

Long, R.A. and Murry, P.A. 1995. Late Triassic (Carnian and Norian) tetrapods from the Southwestern United States. *New Mexico Museum of Natural History and Science Bulletin* 4: 1–254.

Lucas, S.G. and Heckert, A.B. 2011. Late Triassic aetosaurs as the Trackmaker of the Tetrapod Footprint ichnotaxon *Brachychirotherium*. *Ichnos:an International Journal of Plant and Animal* 18 (4): 197–208.

Lucas, S.G., Heckert, A.B. and Hunt, A.P. 2002. A new species of the aetosaur *Typothorax* (Archosauria: Stagonolepididae) from the Upper Triassic of east-central New Mexico. *Bulletin of the New Mexico Museum of Natural History and Science* 21 (21): 221–233.

Lucas, S.G., Heckert, A.B. and Rinehart, L.F. 2006. The Late Triassic aetosaur *Paratypothorax*. *Natural History* (1992): 575–580.

Lucas, S.G., Spielmann, J.A. and Hunt, A.P. 2007. Biochronological significance of Late Triassic tetrapods from Krasiejów, Poland. *New Mexico Museum of Natural History and Science Bulletin* (41): 248–258.

Lydekker, R. 1887. The fossil Vertebrata of India. *Records of the Geological Survey of India* 20: 51–80.

Mallison, H. 2010a. The digital *Plateosaurus* I: Body mass, mass distribution and posture assessed using cad and cae on a digitally mounted complete skeleton. *Palaeontologia*

Electronica 13 (2): 1–26.

Mallison, H. 2010b. The digital *Plateosaurus* II: An assessment of the range of motion of the limbs and vertebral column and of previous reconstructions using a digital skeletal mount. *Acta Palaeontologica Polonica* 55 (3): 433–458.

Marsh, O.C. 1884. The classification and affinities of dinosaurian reptiles. *Nature* (31): 68–69.

Martz, J.W. 2002. The morphology and ontogeny of *Typothorax coccinarum* (Archosauria: Stagonolepididae) from the Upper Triassic of the American Southwest.Texas Tech University, 279pp.

Mccoy, V.E., Young, R.T. and Briggs, D.E.G. 2015. Factors controlling exceptional preservation in concretions. *Palaios* 30 (4): 272–280.

Müller, R.T., Langer, M.C. and Dias-da-Silva, S. 2018. An exceptionally preserved association of complete dinosaur skeletons reveals the oldest long-necked sauropodomorphs. *Biology Letters* 14 (11).

Nau, D., Lallensack, J.N., Bachmann, U. and Sander, P.M. 2020. Postcranial osteology of the first early-stage juvenile skeleton of *Plateosaurus trossingensis* from the Norian of Frick, Switzerland. *Acta Palaeontologica Polonica* 65 (4): 679–708.

Nesbitt, S.J. 2003. *Arizonasaurus* and its implications for archosaur divergence. *Proceedings of the Royal Society B: Biological Sciences* 270 (SUPPL. 2).

Nesbitt, S.J. 2011. The Early Evolution of Archosaurs: Relationships and the Origin of Major Clades. *Bulletin of the American Museum of Natural History* 352 (352): 1–292.

Nesbitt, S.J., Butler, R.J., Ezcurra, M.D., Barrett, P.M., Stocker, M.R., Angielczyk, K.D., Smith, R.M.H., Sidor, C.A., Niedźwiedzki, G., Sennikov, A.G. and Charig, A.J. 2017. The earliest bird-line archosaurs and the assembly of the dinosaur body plan. *Nature* 544 (7651): 484–487.

Niedźwiedzki, G., Sulej, T. and Dzik, J. 2012. A large predatory archosaur from the Late Triassic of Poland. *Acta Palaeontologica Polonica* 57 (2): 267–276.

Novas, F.E., Agnolin, F.L., Ezcurra, M.D., Temp Müller, R., Martinelli, A.G. and Langer, M.C. 2021. Review of the fossil record of early dinosaurs from South America, and its phylogenetic implications. *Journal of South American Earth Sciences* 110 (April):

103341.

Pacyna, G. 2014. Plant remains from the Polish Triassic. Present knowledge and future prospects. *Acta Palaeobotanica* 54 (1): 3–33.

Padian, K., Li, C. and Pchelnikova, J. 2010. The trackmaker of *Apatopus* (Late Triassic, North America): Implications for the evolution of archosaur stance and gait. *Palaeontology* 53 (1): 175–189.

Paes-Neto, V.D., Desojo, J.B., Brust, A.C.B., Schultz, C.L., Da-Rosa, A.A.S. and Soares, M.B. 2021. Intraspecific variation in the axial skeleton of *Aetosauroides scagliai* (Archosauria: Aetosauria) and its implications for the Aetosaur diversity of the late Triassic of Brazil. *Anais da Academia Brasileira de Ciencias* 93: 1–36.

Parker, W.G. 2006. The stratigraphic distribution of major fossil localities in Petrified Forest National Park, Arizona. *2. A century of research at Petrified Forest National Park 1906-2006, Geology and Paleontology* 62 (62): 46–61.

Parker, W.G. 2008. Description of new material of the aetosaur *Desmatosuchus spurensis* (Aetosauria: Suchia) from the Chinle Formation of Arizona and a revison of the genus *Desmatosuchus*. *PaleoBios* 28 (1): 1–40.

Parker, W.G. 2016a. Revised phylogenetic analysis of the Aetosauria (Archosauria: Pseudosuchia); assessing the effects of incongruent morphological character sets. *PeerJ* 2016 (1).

Parker, W.G. 2016b. Osteology of the Late Triassic aetosaur *Scutarx deltatylus* (Archosauria: Pseudosuchia). *PeerJ* 2016 (8): 1–58.

Parker, W.G. 2018a. Redescription of *Calyptosuchus* (*Stagonolepis*) *wellesi* (Archosauria: Pseudosuchia: Aetosauria) from the Late Triassic of the Southwestern United States with a discussion of genera in vertebrate paleontology. *PeerJ* 2018 (2).

Parker, W.G. 2018b. Anatomical notes and discussion of the first described aetosaur *Stagonolepis robertsoni* (Archosauria: Suchia) from the Upper Triassic of Europe, and the use of plesiomorphies in aetosaur biochronology. *PeerJ* 2018 (8).

Parker, W.G. and Martz, J.W. 2010. The Late Triassic (Norian) Adamanian-Revueltian tetrapod faunal transition in the Chinle Formation of Petrified Forest National Park, Arizona. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* 101 (3–4):

231–260.

Parrish, M.J. 1986. Locomotor adaptations in the hindlimb and pelvis of the Thecodontia. *Hunteria* 1 (2): 1–35.

Parrish, M.J. 1987. The origin of crocodilian locomotion. *Paleobiology* 13 (4): 396–414.

Parrish, M.J. 1994. Cranial osteology of *Longosuchus meadei* and the phylogeny and distribution of the Aetosauria. *Journal of Vertebrate Paleontology* 14 (2): 196–209.

Peyer, K., Carter, J.G., Sues, H.-D., Novak, S.E. and Olsen, P.E. 2008. A new suchian archosaur from the Upper Triassic of North Carolina. *Journal of Vertebrate Paleontology* 28 (2): 363–381.

Piechowski, R. and Dzik, J. 2010. The axial skeleton of *Silesaurus opolensis*. *Journal of Vertebrate Paleontology* 30 (4): 1127–1141.

Piechowski, R. and Tałanda, M. 2020. The locomotor musculature and posture of the early dinosauriform *Silesaurus opolensis* provides a new look into the evolution of Dinosauromorpha. *Journal of Anatomy* 236 (6): 1044–1100.

de Ricqlès, A.J., Padian, K. and Horner, J.R. 2003. L'histologie osseuse de quelques archosauriens pseudosuchiens triasiques et formes apparentées. *Annales de Paleontologie* 89 (2): 67–101.

Roberto-Da-Silva, L., Desojo, J.B., Cabreira, S.F., Aires, A.S.S., Müller, R.T., Pacheco, C.P. and Dias-Da-Silva, S. 2014. A new aetosaur from the Upper Triassic of the Santa Maria Formation, southern Brazil. *Zootaxa* 3764 (3): 240.

Romer, A.S. 1923. Crocodilian pelvic muscles and their avian and reptilian homologues. *Bulletin of the American Museum of Natural History* 48 (15): 533–552.

Romer, A.S. 1956. *Osteology of the Reptiles*. The University of Chicago Press, Chicago, .

Rowe, T. 1986. Homology and evolution of the deep dorsal thigh musculature in birds and other reptilia. *Journal of Morphology* 189 (3): 327–346.

Sawin, H.J. 1947. The pseudosuchian reptile *Typothorax meadei*. *Journal of Paleontology* 21 (3): 201–238.

Schachner, E.R., Manning, P.L. and Dodson, P. 2011. Pelvic and hindlimb myology of the basal archosaur *Poposaurus gracilis* (archosauria: Poposauroidea). *Journal of Morphology* 272

(12): 1464–1491.

Schachner, E.R., Irmis, R.B., Huttenlocker, A.K., Sanders, K., Cieri, R.L. and Nesbitt, S.J. 2020. Osteology of the Late Triassic Bipedal Archosaur *Poposaurus gracilis* (Archosauria: Pseudosuchia) from Western North America. *Anatomical Record* 303 (4): 874–917.

Schoch, R.R. 2007. Osteology of the small archosaur Aetosaurus from the Upper Triassic of Germany. *Neues Jahrbuch für Geologie und Paläontologie - Abhandlungen* 246 (1): 1–35.

Schoch, R.R. 2012. A dicynodont mandible from the Triassic of Germany forms the first evidence of large herbivores in the Central European Carnian. *Neues Jahrbuch fur Geologie und Palaontologie - Abhandlungen* 263 (2): 119–123.

Schoch, R.R. and Desojo, J.B. 2016. Cranial anatomy of the aetosaur *Paratypothorax andressorum* Long & Ballew, 1985, from the Upper Triassic of Germany and its bearing on aetosaur phylogeny. *Neues Jahrbuch fur Geologie und Palaontologie - Abhandlungen* 279 (1): 73–95.

Sereno, P.C. 1991. Basal Archosaurs: phylogentic relationships and functional implications. *Journal of Vertebrate Paleontology* 11: 1–53.

Simms, M.J. and Ruffell, A.H. 1990. Climatic and biotic change in the late Triassic. *Journal - Geological Society (London)* 147 (2): 321–327.

Skrzycki, P. 2015. New species of lungfish (Sarcopterygii, Dipnoi) from the Late Triassic Krasiejow site in Poland, with remarks on the ontogeny of Triassic dipnoan tooth plates. *Journal of Vertebrate Paleontology* 35 (5).

Small, B.J. 1985. The Triassic thecodontian reptile *Desmatosuchus*: osteology and relationships.Texas Tech University, 83pp.

Small, B.J. 1998. The occurrence of *Aetosaurus* in the Chinle Formation and its biostratigraphic significance. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 1998: 289–300.

Small, B.J. 2002. Cranial anatomy of *Desmatosuchus haplocerus* (Reptilia: Archosauria: Stagonolepididae). *Zoological Journal of the Linnean Society* 136 (1): 97–111.

Small, B.J. and Martz, J.W. 2013. A new aetosaur from the upper Triassic chinle formation of the Eagle Basin, Colorado, USA. 1. *In*: Nesbitt, S.J., Desojo, J.B. and Irmis, R.B. (eds.), *Anatomy, Phylogeny, and Palaeobiology of Early Archosaurs and Their Kin,* Vol. 379, 393–412. The Geological Society Publishing House, Bath.

Sookias, R.B. 2016. The relationships of the Euparkeriidae and the rise of Archosauria. *Royal Society Open Science* 3 (3).

Sookias, R.B. and Butler, R.J. 2013. Euparkeriidae. *Geological Society Special Publication* 379 (1): 35–48.

Sookias, R.B., Sullivan, C., Liu, J. and Butler, R.J. 2014. Systematics of putative euparkeriids (Diapsida: Archosauriformes) from the Triassic of China. *PeerJ* 2014 (2): 1–44.

Sulej, T. 2002. Species discrimination of the Late Triassic temnospondyl amphibian *Metoposaurus diagnosticus. Acta Palaeontologica Polonica* 47 (3): 535–546.

Sulej, T. 2005. A new rauisuchian reptile (diapsida: Archosauria) from the Late Triassic of Poland. *Journal of Vertebrate Paleontology* 25 (1): 78–86.

Sulej, T. 2007. Osteology, variability, and evolution of *Metoposaurus,* a temnospondyl from the Late Triassic of Poland. *Palaeontologia Polonica* 64 (January 2007): 29–139.

Sulej, T. 2010. The skull of an early Late Triassic aetosaur and the evolution of the stagonolepidid archosaurian reptiles. *Zoological Journal of the Linnean Society* 158 (4): 860–881.

Sulej, T. and Majer, D. 2005. The temnospondyl amphibian *Cyclotosaurus* from the upper Triassic of Poland. *Palaeontology* 48 (1): 157–170.

Sulej, T., Niedwiedzki, G. and Bronowicz, R. 2012. A new Late Triassic vertebrate fauna from Poland with turtles, aetosaurs, and coelophysoid dinosaurs. *Journal of Vertebrate Paleontology* 32 (5): 1033–1041.

Sulej, T., Bronowicz, R., Tałanda, M. and Niedźwiedzki, G. 2011. A new dicynodont-archosaur assemblage from the Late Triassic (Carnian) of Poland. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* 101 (3–4): 261–269.

Sulej, T., Kowalski, J., Bodzioch, A. and Hara, E. 2021. Eucynodont teeth from the Late Triassic of Krasiejów, Southern Poland. *Historical Biology* 33 (12): 3633–3640.

Sulej, T., Niedźwiedzki, G., Tałanda, M., Dróżdż, D. and Hara, E. 2020. A new early Late Triassic non-mammaliaform eucynodont from Poland. *Historical Biology* 32 (1).

Syme, C.E. and Salisbury, S.W. 2014. Patterns of aquatic decay and disarticulation in juvenile Indo-Pacific crocodiles (*Crocodylus porosus*), and implications for the taphonomic interpretation of fossil crocodyliform material. *Palaeogeography, Palaeoclimatology, Palaeoecology* 412: 108–123.

Szczygielski, T. 2017. Homeotic shift at the dawn of the turtle evolution. *Royal Society Open Science* 4 (4).

Szczygielski, T. and Sulej, T. 2016. Revision of the Triassic European turtles *Proterochersis* and *Murrhardtia* (Reptilia, Testudinata, Proterochersidae), with the description of new taxa from Poland and Germany. *Zoological Journal of the Linnean Society* 177(2):395–427.

Szczygielski, T. and Sulej, T. In press. *Woznikella triradiata* – a new kannemeyeriiform dicynodont from the Late Triassic of northern Pangea and the global distribution of Triassic dicynodonts. *Comptes Rendus Palevol*.

Szulc, J. 2005. Sedimentary environments of the vertebrate-bearing Norian deposits from Krasiejow, Upper Silesia (Poland). *Hallesches Jahrbuch für Geowissenschaften. Reihe B, Geologie, Paläontologie, Mineralogie* 19: 2005.

Szulc, J. 2007. Krasiejów – inactive clay pit and tetrapod exposition. *In*: Szulc, J. and Becker, A. (eds.), *International Workshop on the Triassic of Southern Poland. Pan-European Correlation of the Epicontinental Triassic 4th Meeting.*, 53–55. Polish Geological Society, Polish Geological Institute, Jagiellonian University, Institute of Geological Sciences, Cracow.

Szulc, J., Racki, G. and Jewuła, K. 2015. Key aspects of the stratigraphy of the Upper Silesian middle Keuper, Southern Poland. *Annales Societatis Geologorum Poloniae* 85 (4): 557–586.

Taborda, J.R.A., Cerda, I.A. and Desojo, J.B. 2013. Growth curve of *Aetosauroides scagliai* Casamiquela 1960 (Pseudosuchia: Aetosauria) inferred from osteoderm histology. *Geological Society Special Publication* 379 (1): 413–423.

Talmage, R. V. and Buchanan, G.D. 1954. The Armadillo: A Review of its Natural History, Ecology, Anatomy and Reproductive Physiology. *Rice Institute Pamphlet - Rice*

University Studies 41 (2): 1–134.

Tsai, H.P. and Holliday, C.M. 2015. Articular soft tissue anatomy of the archosaur hip joint: Structural homology and functional implications. *Journal of Morphology* 276 (6): 601–630.

Tucker, A.D. 1997. Validation of skeletochronology to determine age of freshwater crocodiles (*Crocodylus johnstoni*). *Marine Freshwater Research* 48: 343–351.

Walker, A.B. 1961. Triassic reptiles from the Elgin area: *Stagonolepis*, *Dasygnathus* and thier allies. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 244 (709): 103–204.

Wang, B., Yang, W., Sherman, V.R. and Meyers, M.A. 2016. Pangolin armor: Overlapping, structure, and mechanical properties of the keratinous scales. *Acta Biomaterialia* 41: 60–74.

Weinbaum, J.C. 2013. Postcranial skeleton of *Postosuchus kirkpatricki* (Archosauria: Paracrocodylomorpha), from the upper Triassic of the United States. *Geological Society Special Publication* 379 (1): 525–553.

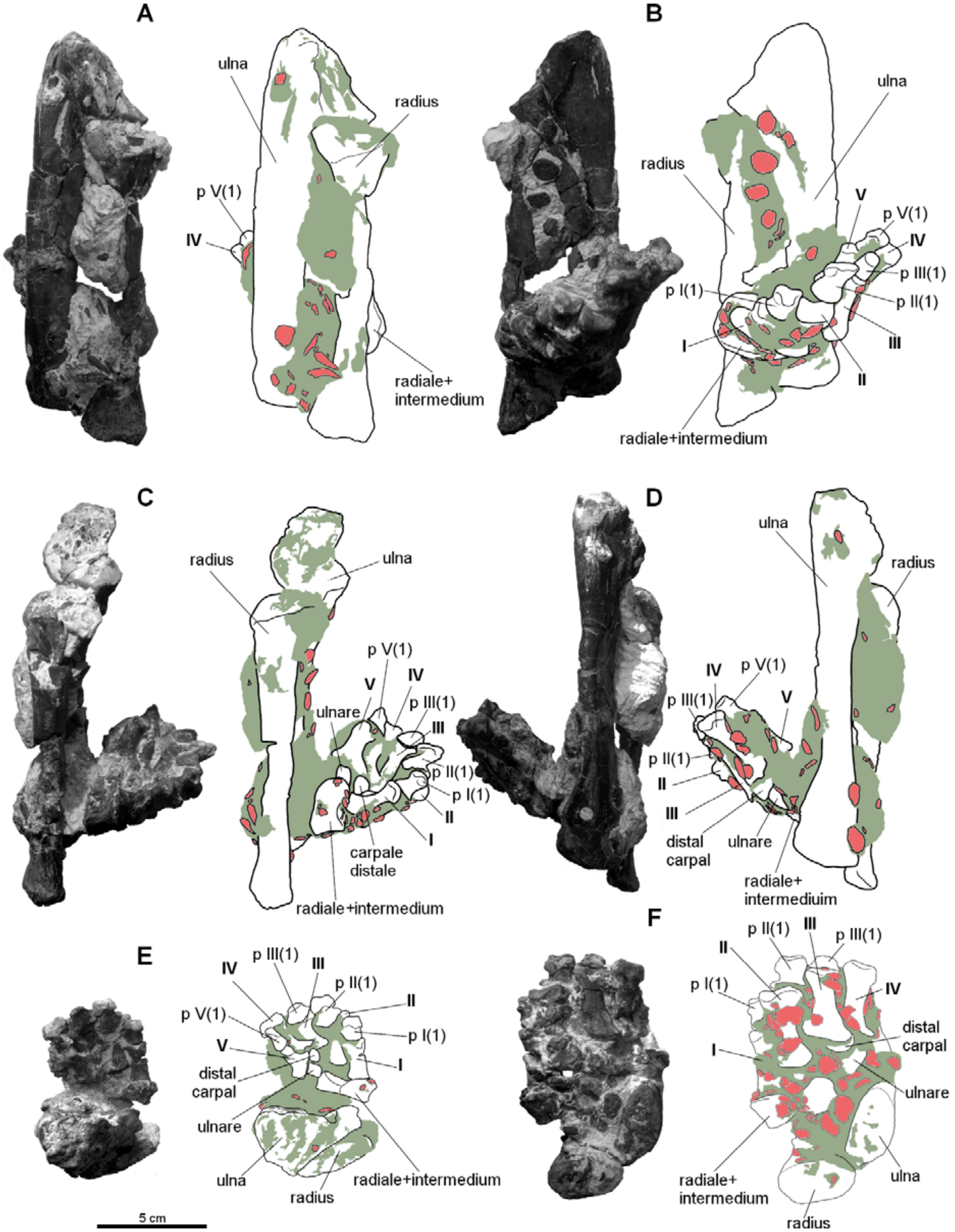
Woodward, H.N., Horner, J.R. and Farlow, J.O. 2011. Osteohistological evidence for determinate growth in the American alligator. *Journal of Herpetology* 45 (3): 339–342.

Yang, W., Chen, I.H., McKittrick, J. and Meyers, M.A. 2012. Flexible dermal armor in nature. *Jom* 64 (4): 475–485.

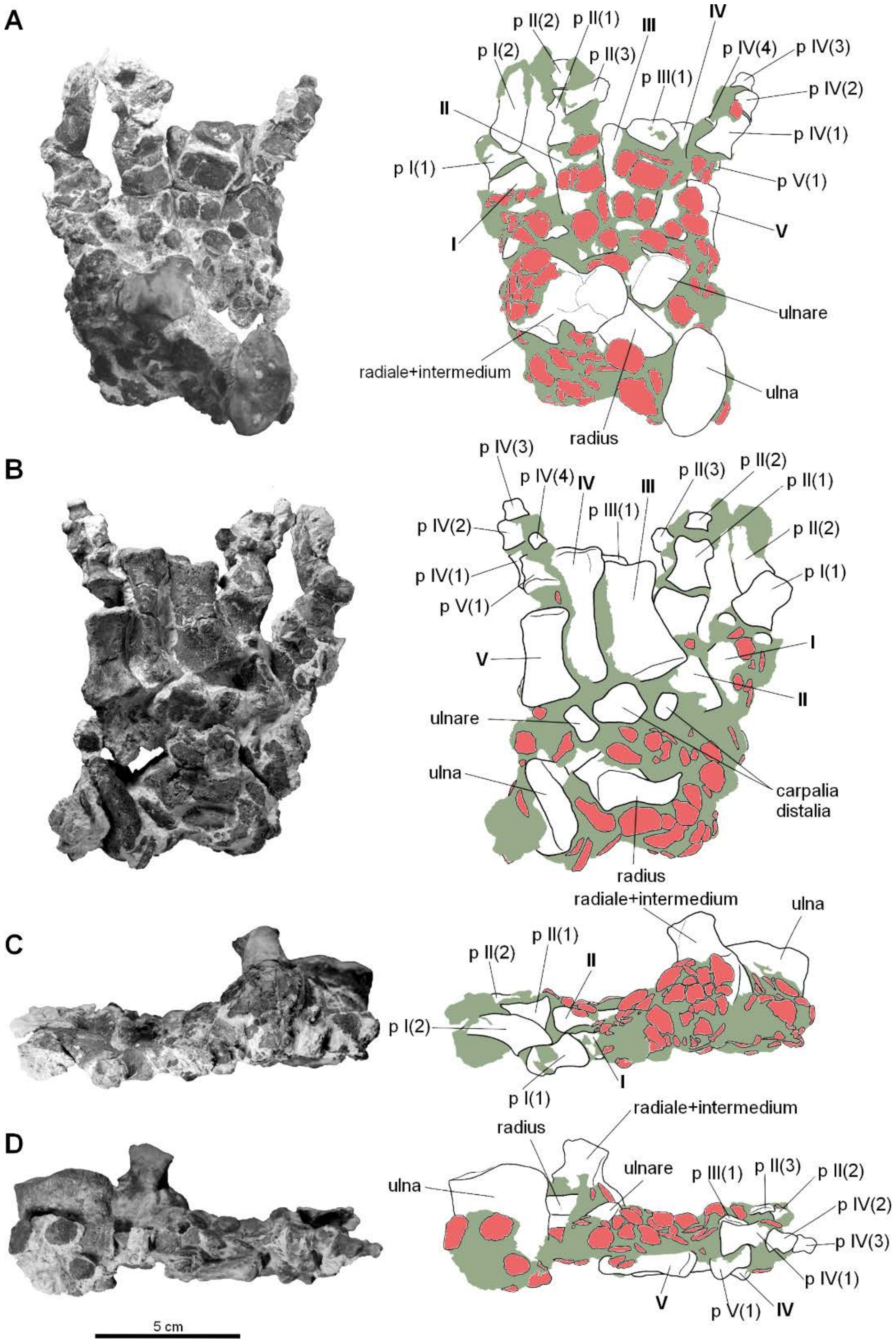
Zatoń, M., Piechota, A. and Sienkiewicz, E. 2005. Late Triassic charophytes around the bone-bearing bed at Krasiejów (SW Poland) - Palaeoecological and environmental remarks. *Acta Geologica Polonica* 55 (3): 283–293.

Zittel, K.A. 1887. *Abteilung: Palozoologie, Band 3, Vertebrata (Pisces, Amphibia, Reptilia, Aves).* Druck and Verlag von R. Oldenbourg, München und Leipzig, .

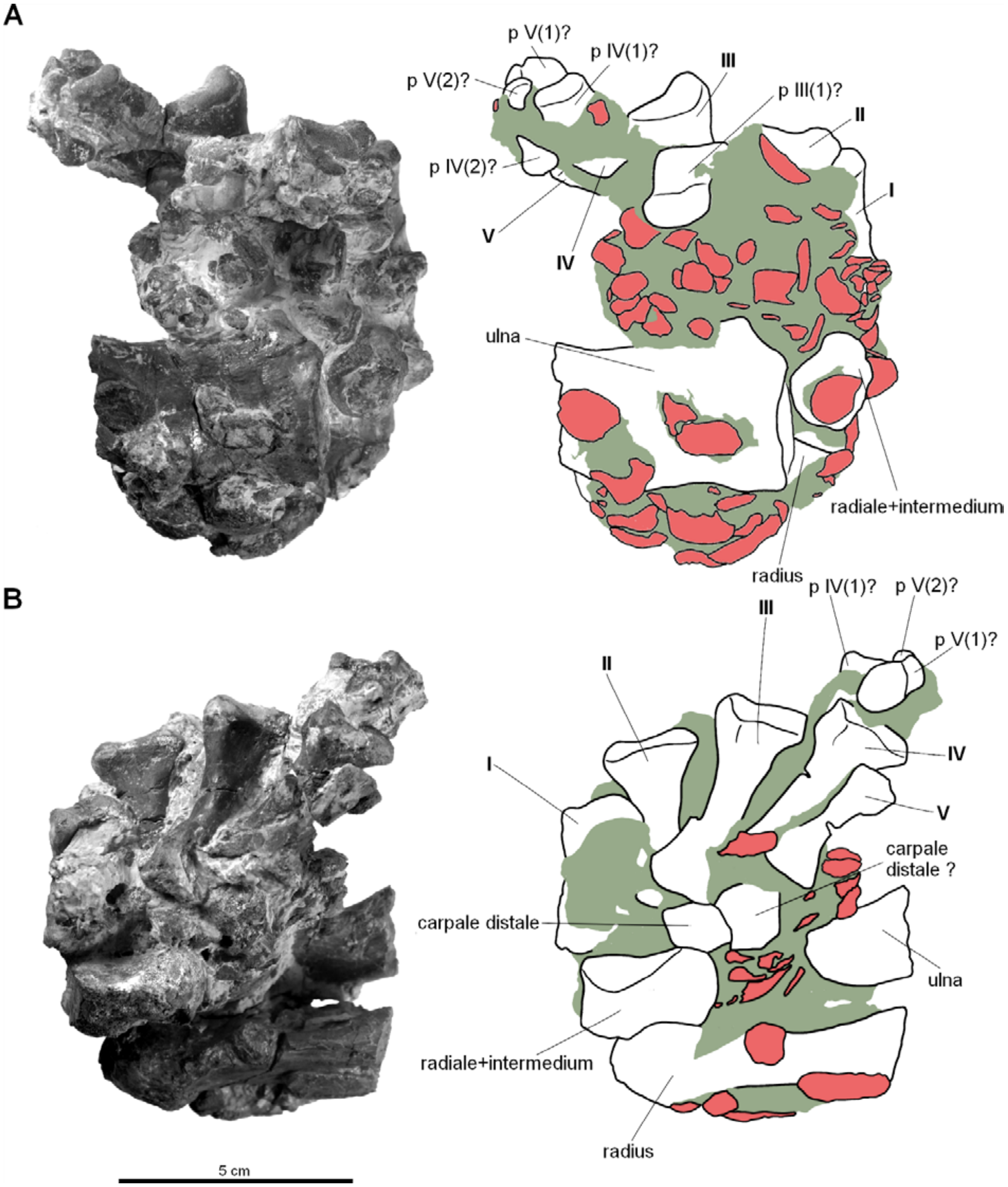
APPENDIX



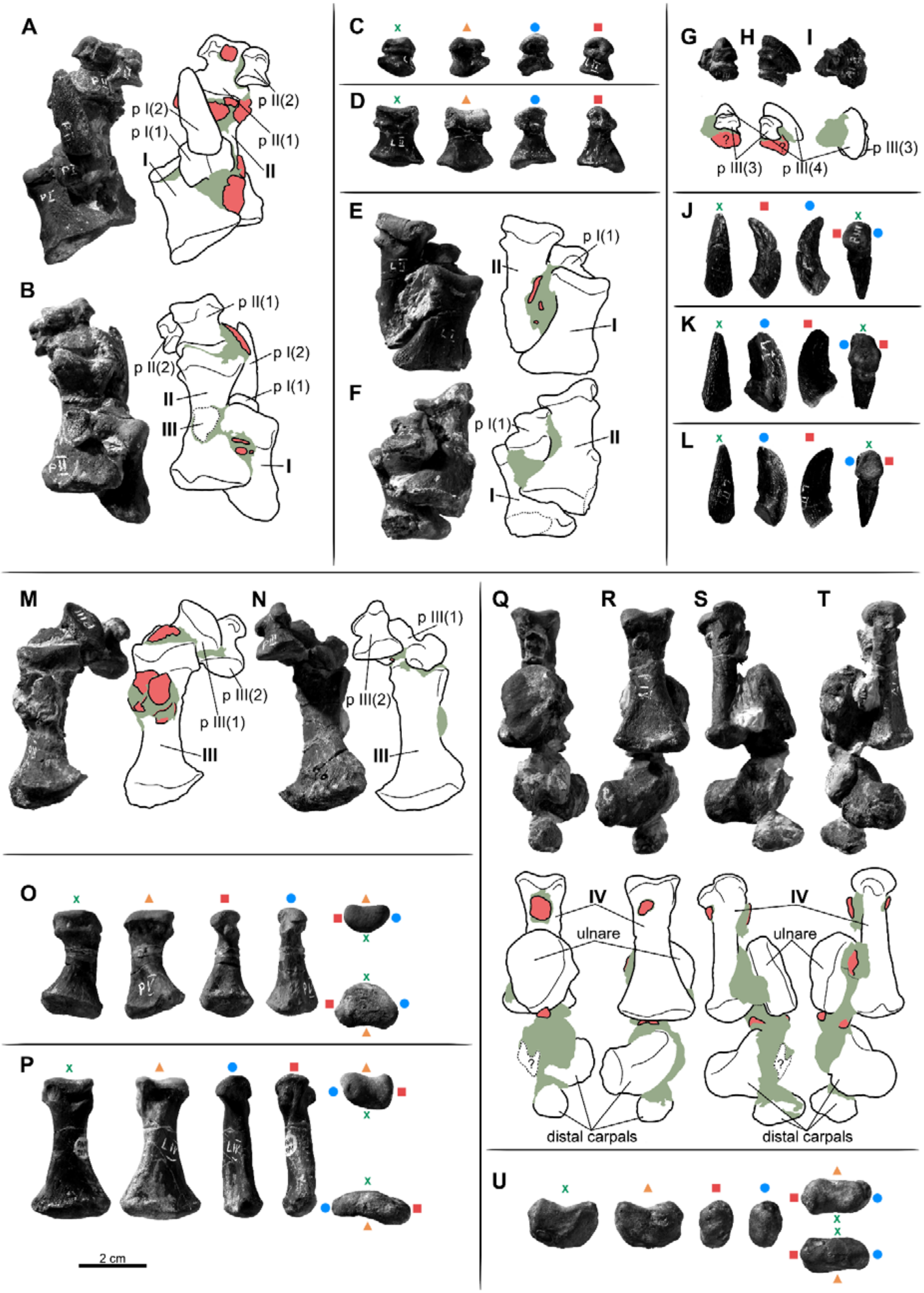
Supplementary Figure 1. The right manus and forearm of the aetosaur *Stagonolepis olenkae* ZPAL AbIII/2407. Photograph and schematic drawing of the specimen with the forearm in dorsal (A), ventral (B), medial (C), and lateral (D) view. Photograph and schematic drawing of the specimen with hand bones exposed in ventral (E) and dorsal (F) view. In the schematic drawings osteoderms are marked red and the sediment is marked grey.



Supplementary Figure 2. The right manus and part of the forearm of the aetosaur *Stagonolepis olenkae*, ZPAL AbIII/3349/1. Photograph and schematic drawing of the specimen with the metacarpals and phalanges exposed in dorsal (A), ventral (B), medial (C) and lateral (D) view. In the schematic drawings osteoderms are marked red and the sediment is marked grey.



Supplementary Figure 3. The left manus and part of the forearm of the aetosaur *Stagonolepis olenkae*, ZPAL AbIII/3349/2. Photograph and schematic drawing of the specimen with the metacarpals exposed in dorsal (A) and ventral (B) view. In the schematic drawings osteoderms are marked red and the sediment is marked grey.


A
p I(2)
p I(1)
I
p II(2)
p II(1)
II
B
p II(1)
p II(2)
p I(2)
p I(1)
II
III
I
C
D
E
p I(1)
II
I
F
p I(1)
II
I
G
H
I
p III(3)
p III(4)
p III(3)
J
K
L
M
p III(2)
p III(1)
III
N
p III(1)
p III(2)
III
O
P
Q
R
S
T
IV
ulnare
IV
ulnare
distal carpals
distal carpals
U
2 cm

Supplementary Figure 4. Elements of the right and the left manus of the aetosaur *Stagonolepis olenkae,* ZPAL AbIII/2071. Schematic drawings and/or photographs of (A) metacarpals and phalanges of the first and second digit of the right manus in dorsal and (B) ventral view; (C) the second phalanx of the second digit of the left manus; (D) the first phalanx of the second digit of the left manus; (E) metacarpals and phalanx of the first and second digit of the left manus in dorsal and (F) ventral view; (G) the third phalanx and ungual of the third digit of the right manus, with the phalanx in dorsal, (H) lateral, and (I) medial view; (J) the ungual of the second digit of the right manus; (K) the ungual of the first digit of the left manus; (L) the ungual of the second digit of the left manus; (M) the metacarpal and phalanges of the third digit of the right manus in dorsal and (N) ventral view; (O) the metacarpal of the fifth digit of the right manus; (P) the metacarpal of the fourth digit of the left manus; (Q) the metacarpal of the fourth digit and carpals of the right manus, with the metacarpal in dorsal, (R) ventral, (S) medial, and (T) lateral view; (U) lunar-shaped carpal bone of the left manus. Symbols attached to some pictures show which surface is exposed in the photograph, with (X) for the dorsal, (▲) for the ventral, (■) for the medial, and (●) for the lateral, and how the surfaces are oriented in proximal and distal view. In (U) the anatomical directions are not determined.