

AETOSAUR PES FROM THE UPPER TRIASSIC OF KRASIEJÓW (POLAND), WITH REMARKS ON TAXONOMY OF ISOLATED BONES

Szymon GÓRNICKI^{1*}, Mateusz ANTCZAK² & Adam BODZIOCH²

¹European Centre of Palaeontology of the University of Opole, ul. Oleska 48, 45-052 Opole, Poland
e-mail: szgornicki@gmail.com

²University of Opole, Institute of Biology, ul. Oleska 22, 45-052 Opole, Poland
e-mails: abodzioch@uni.opole.pl; mateusz.antczak@uni.opole.pl

* Corresponding author

Górnicki, S., Antczak, M. & Bodzioch, A., 2021. Aetosaur pes from the Upper Triassic of Krasiejów (Poland), with remarks on taxonomy of isolated bones. *Annales Societatis Geologorum Poloniae*, 91: 389–396.

Abstract: The incomplete, articulated, right pes of an aetosaur, extracted from the lower bone-bearing horizon of the Krasiejów Late Triassic site, is larger than any other, known from among the Aetosauria. Its individual bones resemble those of at least three genera: *Desmatosuchus* (astragalus), *Typhorax* (ungual phalanges), and *Stagonolepis* (metatarsals). This underscores the highly speculative nature of the taxonomical classification of isolated postcranial bones and makes it impossible to assign the limb to any particular genus. The phalangeal formula is 2-3-4-5-?; for the fifth finger: 2/3/4 is possible. The anatomy of the pes indicates adaptation for digging.

Key words: Aetosauria, postcranial bones, pes, Late Triassic.

Manuscript received 4 August 2020, accepted 15 October 2021

INTRODUCTION

Aetosaurs (Aetosauria, Marsh, 1884) were quadrupedal, armoured reptiles, similar to the Cretaceous ankylosaurid dinosaurs or crocodiles. They were typical representatives of Late Triassic terrestrial faunas with a body length ranging from 1 m (*Coahomasuchus*; Heckert and Lucas, 1999) to over 5–6 m (*Desmatosuchus*; Parker, 2008; Desojo *et al.*, 2013). The name of the group comes from the Greek, meaning eagle-lizards, as their light skull with many openings is similar to the skulls of birds. However, the dermal armour consisted of numerous rectangular osteoderms and this is their most characteristic and best-known feature. They previously were considered to have been herbivorous animals (Walker, 1961; Parrish, 1994) but more recent analysis revealed that they probably were omnivorous (e.g., Small, 2002). Aetosaurs were discovered in the Late Triassic deposits of North America (Chinle Group, e.g., Heckert *et al.*, 1999), Greenland (Fleming Formation, e.g., Jenkins *et al.*, 1994), South America (Ischigualasto Formation, e.g., Desojo and Ezcurra, 2011; Los Colorados Formation, e.g., Desojo and Báez, 2005), Africa (Zarzitine Series, e.g., Heckert and Lucas, 1999), India (Maleri Formation; e.g., Heckert *et al.*, 2007) and Europe (Calcare di Zorzino Formation, e.g., Heckert and Lucas, 2000; Lossiemouth Sandstone, e.g., Walker, 1961; Löwenstein Formation, e.g., Schoch and Desojo, 2016), including at Krasiejów in southern Poland

(e.g., Dzik *et al.*, 2000; Dzik and Sulej, 2007). On the basis of cranial material collected by the Polish Academy of Sciences, a new species was described from the Krasiejów locality (*Stagonolepis olenkae* Sulej, 2010). However, its synonymy with *S. robertsoni* Agassiz, 1844 and wide, individual variation also was considered on the grounds of other cranial material, collected by the University of Opole (Antczak, 2016). Postcranial material reveals no distinct differences (Lucas *et al.*, 2007) from the Scottish material (Lossiemouth Sandstone, Elgin area). The recent phylogenetic analysis does not give any certain answers (Parker, 2016, 2018). Later, a forelimb also was assigned to the new species *S. olenkae* (Drózdź, 2018).

Therefore, the taxonomy of aetosaurs from the Krasiejów site is still unclear. The debate about cranial features makes assigning postcranial material to a new species controversial. The description of an aetosaurian pes below is a contribution to the general discussion about the validity of the taxonomical classification of isolated, postcranial bones of fossil animals.

MATERIALS AND METHODS

The material analyzed was discovered at the Late Triassic site at Krasiejów, Poland. Fine-grained sedimentary rocks

(mudstones and claystones with sandstone and limestone intercalations) are exposed there in a post-mining outcrop (Fig. 1). At the Krasiejów site, two bone-bearing horizons occur (Dzik *et al.*, 2000; Dzik and Sulej, 2007; Gruszka and Zieliński, 2008; Bodzioch and Kowal-Linka, 2012; Szulc *et al.*, 2015a, b). The age of the deposits, previously regarded Carnian on the grounds of the occurrence and evolution of vertebrates (e.g., Dzik and Sulej, 2007), which is supported by vertebrate biostratigraphy (Lucas, 2015), is now considered to be Norian (Szulc *et al.*, 2015a, b), on the basis of the complex litho-, bio-, chemo- and climatostratigraphy.

The specimen has some elements of the right pes (autopodium) of an aetosaur, which is deposited in the collection of the University of Opole (Tab. 1; Appendix 1). Specimens were recognized as representing aetosaurs on the basis of general morphology and from comparison with other skeletal elements from Krasiejów that were found in association with osteoderms or long bones, like the specimens of forelimbs presented by Drózdź (2018) and the hindlimb presented by Walker (1961). The material was found articulated, therefore it belongs to one individual. The articulated bones were found in the lower bone-bearing horizon of the Krasiejów site, like most of the other aetosaur remains at that locality. The hindlimb analyzed lacks the femur, tibia and fibula (Fig. 2). The tarsus, metatarsus and phalanges are incomplete

(Appendix 2), lacking several bones; this justifies comparison with known appendicular remains of aetosaurs from other sites.

The bones after excavation were still partially covered by sediment. They were prepared using sculptural chisels and a hand grinder.

DESCRIPTION

In the tarsus, only the astragalus is complete (Fig. 2B). The calcaneus is preserved in eight very poorly preserved fragments; the other distal tarsals were not found. The astragalus is massive, which indicates that the animal was sexually mature and large (Heckert *et al.*, 2003). The bone possesses a very large, round, convex, distal roller and a much smaller, anterior hollow. The medial tibia articulation surface is also large. The posterior groove is relatively small. Between the groove and the medial tibia articulation surface, a relatively small, shallow, astragalar fossa is located.

In the foot, four of the five metatarsals are preserved (metatarsals I, II, III and IV; Fig. 2). All bones are proportionally wide and robust; the proximal end is wider than the distal end, differing in the length and twist of the shaft. Metatarsal I is the shortest bone, with the widest distal and proximal ends. Metatarsal II is the longest foot bone, and

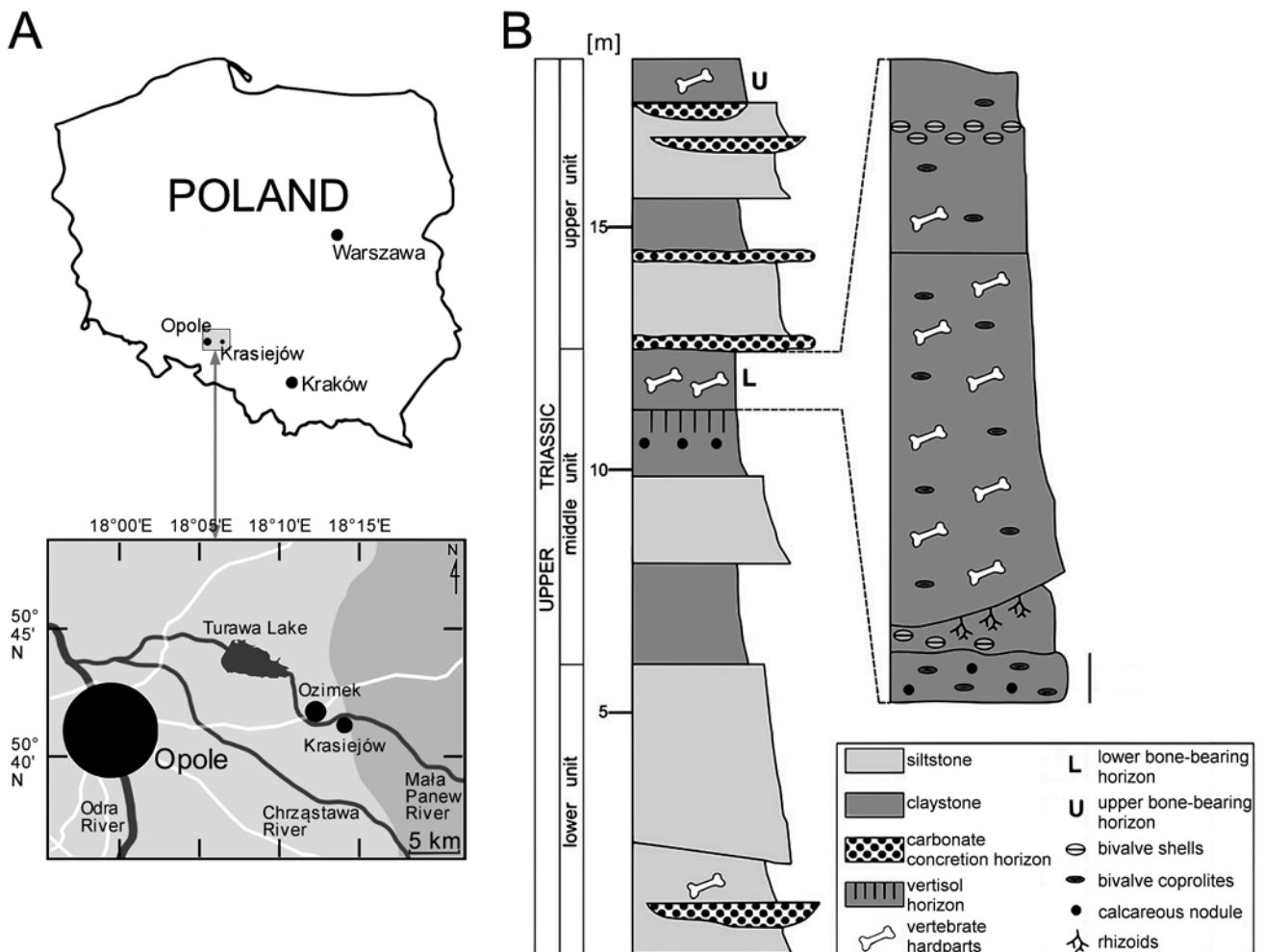


Fig. 1. Setting of the aetosaurian hindlimb described. **A.** Geographical. **B.** Geological (after Bodzioch and Kowal-Linka, 2012).

Table 1

Measurements in millimetres (mm) of the hind limb (all comprising the maximum preserved measurement). * incomplete

Bone	Anteroposterior length	Transverse width	Dorsoventral height	Length	Proximal width	Distal width	Maximal transverse height
Astragalus	33	76	73				
Metatarsal I				80	54	33	19
Metatarsal II				105	46	28	20
Metatarsal III				104	44	22	17
Metatarsal IV				93	44	30	24
Pedal phalanx I-1				34	29	22	19
Pedal phalanx I-2				50	15		20
Pedal phalanx II-1				43	29	27	22
Pedal phalanx II-2				32	26	22	17
Pedal phalanx II-3				33	14		15
Pedal phalanx III-1				28	22	19	20
Pedal phalanx III-2				19	20	17	13
Pedal phalanx III-4				*27	17		19
Pedal phalanx IV-1				36	28	23	23
Pedal phalanx IV-2				24	21	21	17
Pedal phalanx IV-3				19	18	17	14
Pedal phalanx IV-4				12	11	11	8

together with the slightly shorter metatarsal III does not have a collateral fossa at the distal end. Metatarsal IV is the most massive of the metatarsals. It has the thickest shaft and one collateral fossa on the left side of the distal end.

The specimen contains twelve phalanges (Fig. 2B), including three ungual phalanges. Only one ungual phalanx is incomplete. The phalanges, except for the ungual phalanges, are wide, fairly massive, relatively flat and much shorter than any metatarsal. Some of them show twisting of the axis. The unguals are curved, large and laterally compressed, reminiscent of those found in predators. All have grooves for blood vessels, analogical to those described by Martz (2002). The complete ungual phalanges have sharp tips.

The phalangeal formula, including the ungual phalanges, is 2-3-4-5-?; for the fifth finger, the values 2/3/4 are possible.

DISCUSSION

The pes described may be discussed in the terms of its taxonomical position, size, adaptations, and general concepts of the taxonomy of isolated, postcranial bones.

Taxonomy

There are large gaps in the fossil material of other aetosaur taxa available for comparison, which makes it impossible to compare each bone with every taxon (Tab. 2). In general, the pes described is similar to many genera of aetosaurs, described by Walker (1961), Casamiquela (1967), Martz (2002), Heckert *et al.* (2003, 2010), Desojo and Baéz (2005), Schoch (2007), Desojo *et al.* (2012), and

Roberto-da-Silva *et al.* (2014). Because of the poor state of preservation of the calcaneus, it is not possible to identify its basic differences and similarities with respect to other taxa. The astragalus, metatarsals and phalanges can be compared to material known from other sites.

The astragalus is a very massive and fairly typical pseudosuchian crocodile-normal bone, in that the peg articulates with the calcaneum (Fig. 2), for example, as in the case of *Typosuchus* (Martz, 2002), *Gracilisuchus* (Lecuna and Desojo, 2011) and *Postosuchus* (Weinbaum, 2013). The overall shape of the bone slightly differs from those of all known aetosaurian genera, being more rounded than in *Aetosaurus*, *Polesinesuchus*, and *Typosuchus* (Martz, 2002; Lucas *et al.*, 2002; Schoch, 2007; Roberto-da-Silva *et al.*, 2014).

In the material described here, the peg is upturned towards the fibular facet in the posterior view, whereas in *Typosuchus*, *Polesinesuchus*, and *Desmotosuchus*, the astragalus peg is parallel to this structure. The distal roller is relatively large and its shape is more semicircular, as in *Desmotosuchus*, in contrast to *Aetosaurus*, *Polesinesuchus* and *Typosuchus* (Lucas *et al.*, 2002; Martz, 2002; Heckert *et al.*, 2003; Schoch, 2007; Roberto-da-Silva *et al.*, 2014). The anterior hollow has a proportionally smaller area than in *Aetosaurus*, *Typosuchus* and *Desmotosuchus* (Lucas *et al.*, 2002; Martz, 2002; Heckert *et al.*, 2003; Schoch, 2007). The astragal fossa in *Desmotosuchus* and *Typosuchus* is deeper and located relatively higher in the posterior view (Martz, 2002; Heckert *et al.*, 2003).

The metatarsal bones, in terms of proportions and morphology, more closely resemble *Stagonolepis robertsoni*

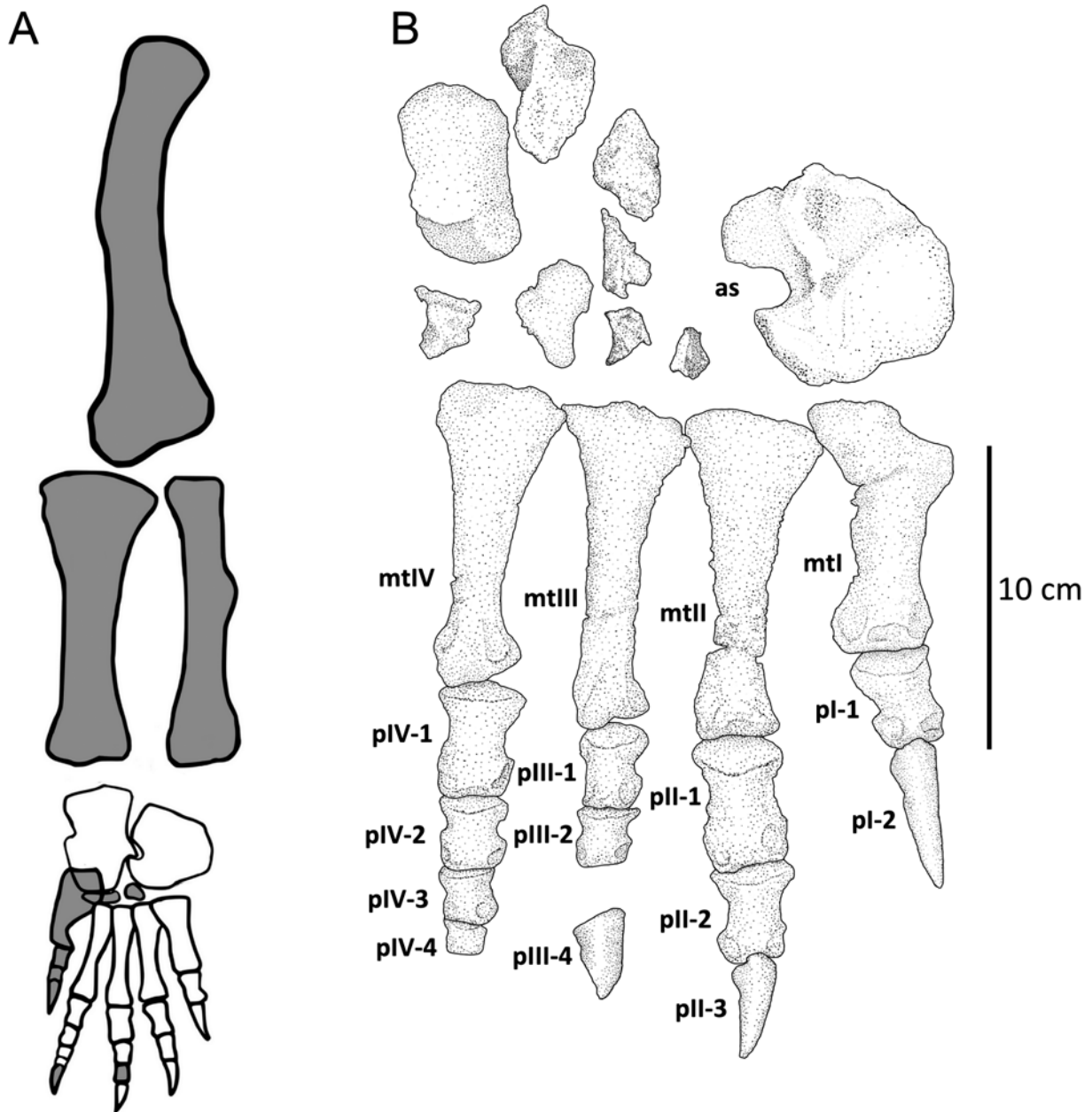


Fig. 2. The aetosaurian hindlimb described. **A.** Schematic drawing of the whole hindlimb (missing bones marked in grey; after Desojo and Baez, 2005; Schoch, 2007, modified). **B.** Illustration of the analyzed specimen in dorsal view. Abbreviations: as – astragalus; mt – metatarsal; p – pedal phalanx.

bones (Walker, 1961) than other aetosaur species. However metatarsals II, III and IV of *Stagonolepis* are progressively more slender, while in the material described they are not. As in *S. robertsoni* (Walker, 1961), the metatarsal bones are massive. The bones have relatively wider proximal ends than those of *Aetosauroides* (Casamiquela, 1967), *Aetosaurus* and *Aetobarkinoides* (Desojo *et al.*, 2012). The distal ends are wider than in *Polesinesuchus*, yet narrower than in *Typothorax* (Martz, 2002). Metatarsals II and III in the material described are similar in size, although metatarsal IV is shorter (Tab. 1); in *Aetosaurus ferratus* (Schoch, 2007) and *Aetosauroides scagliai* (Casamiquela, 1967); metatarsals III and IV are almost the same length. Metatarsal III of *Aetosaurus*, *Aetobarkinoides* (Desojo *et al.*,

2012), *Aetosauroides* (Casamiquela, 1967; Schoch, 2007) and *Neoaetosauroides* (Desojo *et al.*, 2012) is longer and slimmer than metatarsal II, while in the material described, it is not. In *Typothorax*, metatarsal III is explicitly the longest one (Heckert *et al.*, 2010; Lucas and Heckert, 2011).

There are only two complete digits (I and II) in the material described. As in other known genera, digit II is longer and has more phalanges than digit I (e.g., Walker, 1961; Desojo and Baez, 2005; Schoch, 2007; Heckert *et al.*, 2010). All the phalanges are shorter than the metatarsals, each more distant phalanx is shorter and narrower than the more proximal, except for the unguals (Fig. 2). Digits I and II have the most massive phalanges. The unguals are proportionally large, curved and sharp, as in *Typothorax* (Martz, 2002;

Table 2

Similarities (v) and differences (x) between the UOPB specimen described and known aetosaur genera

Element	<i>Stagonolepis</i>	<i>Desmotosuchus</i>	<i>Aetosauroides</i>	<i>Neoaetosauroides</i>	<i>Aetosaurus</i>	<i>Typothorax</i>	<i>Paratyphothorax</i>	<i>Polesinesuchus</i>	<i>Aetobarbakinoides</i>
Astragalus peg		x				v/x		x	
Astragalus distal roler		v			x	x		x	
Astragalus fossa		x				x			
Metatarsals	v		x	x	x	x		x	x
Digits						v			
phalangeal formula	v			v	v	v			

Heckert *et al.*, 2010). The probable phalangeal formula of the specimen is greater than the minimum proposed for *Typothorax* (2-3-3?-4?-3?; Heckert *et al.*, 2010). It could be 2-3-4-5-2 as in *Neoaetosauroides* (Desojo and Baez, 2005), 2-3-4-5-3 like the probable formula of *Aetosaurus ferratus* (Schoch, 2007), or 2-3-4-5-4 like the formula of *Stagonolepis* (Walker, 1961).

For the pes presented, it is difficult to identify the species (or even the genus), owing to the similarities of these bones to those of various genera, e.g., astragalus is similar to *Desmotosuchus*, *Stagonolepis*, and *Typothorax*. The lack of any osteoderms associated with the specimen increases the difficulty of identification of taxa. The bones of the specimen show most similarities to *Stagonolepis robertsoni* (Walker, 1961) and *Typothorax coccinarum* (Martz, 2002; Heckert *et al.*, 2003, 2010; Lucas and Heckert, 2011).

Pes size

The pes described is larger than the pedes of *Aetosaurus ferratus*, *Stagonolepis robertsoni* (Walker, 1961), *Aetosauroides scagliai* (Casamiquela, 1967), *Typothorax coccinarum* (Martz, 2002; Heckert *et al.*, 2010; Lucas and Heckert, 2011), *Aetobarbakinoides brasiliensis* (Desojo *et al.*, 2012) and *Polesinesuchus aurelioi* (Roberto-da-Silva *et al.*, 2014).

The length of *Polesinesuchus aurelioi* metatarsal III (Roberto-da-Silva *et al.*, 2014) is only 31% that of the specimen presented here. Furthermore, the length of the metatarsals of *Aetobarbakinoides brasiliensis* (Desojo *et al.*, 2012) is consecutively smaller (metatarsal I) 35%, (m. II) 42%, (m. III) 48% and (m. IV) 39% of the lengths of the specimen bones. In the *Typothorax coccinarum*, described by Martz (2002), the only complete metatarsal (probably II, III, or IV) is about two times shorter than the metatarsals of the specimen examined. The length of MCZ 1488 bones (left pes of *Typothorax coccinarum*; Lucas and Heckert, 2011) is between 50% and 83% of the length of the new pes material from Krasiejów. The metatarsals of the specimen presented here are on average 37% longer than those of *T. coccinarum*, described by Heckert *et al.* (2010), and the phalanges

are on average 34% longer. The length of the metatarsals of *Aetosauroides scagliai* (Casamiquela, 1967), represents 52–62% of the length of analogous bones in the specimen discussed. Metatarsal III of the pes described is 31% longer than in the large individual of *Stagonolepis robertsoni* described by Walker (1961).

Adaptation of the pes

Like Heckert *et al.* (2010) earlier, the authors examined the specimen in the context of adaptation for digging. Unfortunately, most of the features previously related to this subject (e.g., Hildebrand 1974, 1983; Benton 1983; Coombs 1983), mentioned as a characteristic of digging animals, cannot be examined in the specimen described here. Some of the adaptations for digging are seen in the morphology of unguals (see earlier descriptions; Fig. 1), and proximal phalanges, which are relatively short and wide. All the toes, especially the second one, are relatively large. Furthermore, the metatarsals are massive and strong, and the bones are stocky. This is somewhat less typical of digging animals in comparison to *Typothorax coccinarum*. However, this comparison is incomplete, because *T. coccinarum* is known from a nearly complete skeleton (Heckert *et al.*, 2010). Also, no biomechanical studies were made. The assumptions were made on the basis of morphology.

Remarks on taxonomy of isolated postcranial bones in palaeontology

From the beginning of the history of palaeontology, the incompleteness of remains caused many scientific errors. For example, the first description of the genus *Iguanodon* (Mantell, 1825) was made on the basis of a few teeth (Paul, 2007). It was reconstructed as a huge, crawling lizard (Górnicki, 2017). Taxonomic designations of individual, postcranial, skeletal bones may be very far from the truth, as with the discovery of the claws of the theropod dinosaur *Therizinosaurus*, which was first considered to be a huge turtle (Maleev, 1954). Even when more complete skeletons were found, represented by elements that did not overlap,

the wrong taxonomic conclusions were made, as in the case of a Triassic archosaur skull of *Shuvosaurus inexpectatus* Chatterjee, 1993 and the postcranial bones of the same taxon, named *Chatterjeea elegans* Long and Murry, 1995 (Lucas *et al.*, 2007), or *Opisthocoelicaudia* known mostly from postcrania and *Nemegtosaurus* mainly known from cranial material, which is the reason for discussing sauropod taxonomy in the Upper Cretaceous Nemegt Formation of Mongolia today (Averianov and Lopatin, 2019).

Unfortunately, the vast majority of fossil vertebrates are not known from 100% complete skeletons. Thus, the possibility of comparing and correctly classifying single bones or incomplete skeletal fragments is significantly reduced. Moreover, most of fossil vertebrate systematics are based on many diagnostic characters of craniodental fossils (Davis and McHorse, 2013). This contributes to the fact that different phylogenetic trees are formed, when craniodental and postcranial characters are considered singly (Mounce *et al.*, 2016). Going further, the hominid fossil record showed that the cranial and postcranial skeleton can evolve in different steps through time (McHenry and Brown, 2008). It should not be overlooked that convergence in the body plans of animals from different groups may occur. Therefore, it is not surprising that even in the case of modern animals, there are difficulties in distinguishing postcranial bones. An example of such challenges in zooarchaeology is the bones of sheep and goats (Salvagno and Albarella, 2017). In palaeontology, this problem is much larger.

The present authors argue here that, in cases of incomplete finds, similar to the pes aetosaur specimen, one should make the most accurate palaeontological documentation, however cautious and limited the classification. A fine example illustrating this problem is *Maraapunisaurus fragillimus* Cope, 1878 (Carpenter, 2018). The specimen was a single, incomplete, sauropod vertebra (Carpenter, 2018). Unfortunately, sauropods were animals that had many vertebrae and their skeletons often are incomplete (Sander *et al.*, 2011). In addition, the various types of vertebrae (cervical, dorsal, sacral or caudal) differ from each other. There are also ontogenetic and intraspecific varieties. Therefore, the authors think that in such a case, a description of the species, the whole taxonomy, and phylogeny, etc., should not be created immediately. Such works create confusion in taxonomy and a large and unnecessary amount of invalid taxa. On the other hand, assigning postcranial bones to an already known species may indirectly create a chimera. If we attribute every such aetosaur specimen from the Krasiejów “Trias” site to the species *Stagonolepis robertsoni* or *S. olenkae*, indirectly we create a chimera and related taxonomic problems. Such an approach also causes some taxa to become a “taxonomic grab-bag”, e.g., the genus *Iguanodon* (Paul, 2007). For these reasons, before creating a new species, it is necessary to consider sexual dimorphism, ontogeny and individual variation, taking into account such examples as the pachycephalosaurids (Stokstad, 2007). On the other hand, attributing *a priori* the taxonomical affiliation of postcranial material to species known only from cranial material may also be valid and should be left without specifying a genus and a species, until there is a more nearly complete specimen for comparison.

CONCLUSIONS

On the basis of the current state of the quantity and completeness of aetosaur specimens, the authors leave the pes unclassified to any genus and species of aetosaur. The pes possesses some unique features, similar to those of *Desmotosuchus* (distal roller of astragalus), and *Typhothorax* (unguals). Accordingly, it cannot be described as *Stagonolepis*, the remains of which are undoubtedly abundant at the site. However, the specimen also possesses some features similar to those of *Stagonolepis* (metatarsal bones). It is also uncertain that the specimen could be described as a different species or genus.

The specimen is interesting in terms of its size. The bones are larger than the corresponding bones of other aetosaurs, known from the literature. The entire animal could have measured more than three metres in length.

No new, ecological adaptations of the hindlimb were found. The limb anatomy indicates adaptation for digging.

Acknowledgments

We would like to thank Andrew B. Heckert (Appalachian State University) for sharing his materials with us and for his helpful comments. We also thank Julia B. Desojo (Universidad Nacional de La Plata) and Spencer G. Lucas (New Mexico Museum of Natural History) for their helpful reviews, Dariusz Kasztelan and Delfin Łakatosz for help with photographing the specimen, and Janet Trythall (Elgin Museum) for photographs of specimens.

REFERENCES

- Agassiz, L., 1844. *Monographie des poissons fossiles du Vieux Grès Rouge ou Système Dévonien (Old Red Sandstone) des îles Britanniques et de Russie*. Jent et Gassmann, Neuchâtel, 171 pp.
- Antczak, M., 2016. Late Triassic aetosaur (Archosauria) from Krasiejów (SW Poland): new species or an example of individual variation? *Geological Journal*, 51: 779–788.
- Averianov, A. O. & Lopatin, A. V., 2019. Sauropod diversity in the Upper Cretaceous Nemegt Formation of Mongolia – a possible new specimen of *Nemegtosaurus*. *Acta Palaeontologica Polonica*, 64: 313–321.
- Benton, M. J., 1983. The Triassic reptile Hyperodapedon from Elgin: functional morphology and relationships. *Philosophical Transactions of the Royal Society of London, Series B*, 302: 605–718.
- Bodzioch, A. & Kowal-Linka, M., 2012. Unravelling the origin of the Late Triassic multitaxic bone accumulation at Krasiejów (S Poland) by diagenetic analysis. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 346–347: 25–36.
- Carpenter, K., 2018. *Maraapunisaurus fragillimus*, n.g. (formerly *Amphicoelias fragillimus*), a basal rebbachisaurid from the Morrison Formation (Upper Jurassic) of Colorado. *Geology of the Intermountain West*, 5: 227–244.
- Casamiquela, R., 1967. Materiales adicionales y reinterpretación de *Aetosauroides scagliai* (de Ischigualasto, San Juan). *Revista del Museo de La Plata*, 5: 173–196.
- Chatterjee, S., 1993. *Shuvosaurus*, a new theropod. *Research and Exploration*, 9: 274–285.

- Coombs, M. C., 1983. Large mammalian clawed herbivores: a comparative study. *Transactions of the American Philosophical Society*, 73: 1–96.
- Cope, E. D., 1878. A new species of *Amphicoelias*. *American Naturalist*, 12: 563–565.
- Davis, E. B. & McHorse, B. K., 2013. A method for improved identification of postcrania from mammalian fossil assemblages: multivariate discriminant function analysis of camelid astragali. *Palaeontologia Electronica*, 16: 1–15.
- Desojo, J. B. & Báez, A. M., 2005. The postcranial skeleton of *Neoaetosauroides* (Archosauria: Aetosauria) from the Upper Triassic of west central Argentina. *Ameghiniana*, 41: 115–126.
- Desojo, J. B. & 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: 596–609.
- Desojo, J. B., Ezcurra, M. D. & Kischlat, E. E., 2012. A new aetosaur genus (Archosauria: Pseudosuchia) from the early Late Triassic of southern Brazil. *Zootaxa*, 3166: 1–33.
- Desojo, J. B., Heckert, A. B., Martz, J. W., Parker, W. G., Schoch, R. R., Small, B. J. & Sulej, T., 2013. Aetosauria: a clade of armoured pseudosuchians from the Upper Triassic continental beds. In: Nesbitt, S. J., Desojo, J. B. & Irmis, R. B. (eds), *Anatomy, Phylogeny, and Palaeobiology of Early Archosaurs and Their Kin*. Geological Society, London, *Special Publications*, 379: 203–239.
- Drózdź, 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*, 6: e5595.
- Dzik, J. & Sulej, T., 2007. A review of the early Late Triassic Krasiejów biota from Silesia, Poland. *Palaeontologica Polonica*, 64: 3–27.
- Dzik, J., Sulej, T., Kaim, A. & Niedźwiedzki, R., 2000. A late Triassic tetrapod graveyard in the Opole Silesia (SW Poland). *Przegląd Geologiczny*, 48: 226–235. [In Polish, with English summary.]
- Górnicki, S., 2017. Education and Outreach: The history of dinosaur palaeoart. *Palaeontology Online*, 7: 1–9.
- Gruszka, B. & 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 Quarterly*, 52: 239–252.
- Heckert, A. B. & 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: 50–68.
- Heckert, A. B. & Lucas, S. G., 2000. Taxonomy, phylogeny, biostratigraphy, biochronology, paleo-bio-geography, and evolution of the Late Triassic Aetosauria (Archosauria: Crurotarsi). *Zentralblatt für Geologie und Paläontologie, Teil I*, 1998: 1539–1587.
- Heckert, A. B., Lucas, S. G. & Harris, J. D., 1999. An aetosaur (Reptilia: Archosauria) from the Upper Triassic Chinle Group, Canyonlands National Park, Utah. *National Park Service Paleontological Research Technical Report*, v. NPS/NRGRD/GRDTR-99/03: 23–26.
- Heckert, A. B., Lucas, S. G., Hunt, A. P. & Spielmann, J. A., 2007. Late Triassic aetosaur biochronology revisited. *New Mexico Museum of Natural History & Science Bulletin*, 41: 49–50.
- Heckert, A. B., Lucas, S. G., Rinehart, L. F., Celeskey, M. D., Spielmann, J. A. & 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: 619–642.
- Heckert, A. B., Zeigler, K. E. & 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: 115–126.
- Hildebrand, M., 1974. *Analysis of Vertebrate Structure*. John Wiley & Sons, New York, 710 pp.
- Hildebrand, M., 1983. Digging of quadrupeds. In: Hildebrand, M., Bramble, D. M., Liem, K. F. & Wake, D. B. (eds), *Functional Vertebrate Morphology*. Harvard University Press, Cambridge, Massachusetts, pp. 89–109.
- Jenkins, F. A., Shubin, N. H., Amaral, W. W., Gatesy, S. M., Schaff, C. R., Clemmensen, L. B., Downs, W. R., Davidson, A. R., Bonde, N. & Osbaeck, F. F., 1994. Late Triassic continental vertebrates and depositional environments of the Fleming Fjord Formation, Jameson Land, East Greenland. *Meddelelser om Grønland, Geoscience*, 32: 1–25.
- Lecuona, A. & Desojo, J. B., 2011. Hind limb osteology of *Gracilisuchus stipanicorum* (Archosauria: Pseudosuchia). *Earth and Environmental Science Transactions of the Royal Society of Edinburgh*, 102: 105–128.
- Long, R. A. & 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, 254 pp.
- Lucas, S. G., 2015. Age and correlation of Late Triassic tetrapods from southern Poland. *Annales Societatis Geologorum Poloniae*, 85: 627–635.
- Lucas, S. G. & Heckert, A. B., 2011. Late Triassic aetosaurs as the trackmaker of the tetrapod footprint ichnotaxon *Brachychirotherium*. *Ichnos*, 18: 197–208.
- Lucas, S. G., Heckert, A. B. & Hunt, A. P., 2002. A new species of the aetosaur *Typothorax* (Archosauria: Stagonolepididae) from the Upper Triassic of east-central New Mexico. *New Mexico Museum of Natural History and Science Bulletin*, 21: 221–233.
- Lucas, S. G., Spielmann, J. A. & Hunt, A. P., 2007. Taxonomy of *Shuvosaurus*, a Late Triassic archosaur from the Chinle Group, American Southwest. *New Mexico Museum of Natural History and Science Bulletin*, 41: 259–261.
- Maleev, E. A., 1954. Noviy cherepachobrazhniy yashcher v Mongolii. *Priroda*, 43: 106–108. [In Russian.]
- Mantell, G. A., 1825. Notice on the Iguanodon, a newly discovered fossil reptile, from the sandstone of Tilgate forest, in Sussex. *Philosophical Transactions of the Royal Society*, 115: 179–186.
- 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*. Unpublished PhD. Thesis, Texas Tech University, 279 pp.
- McHenry, H. M. & Brown, C. C., 2008. Side steps: the erratic pattern of hominin postcranial change through time. *Journal of Human Evolution*, 55: 639–651.
- Mounce, R. C. P., Sansom, R. & Wills, M. A., 2016. Sampling diverse characters improves phylogenies: craniodental and postcranial characters of vertebrates often imply different trees. *Evolution*, 70: 666–686.
- Parker, W. G., 2008. Description of new material of the aetosaur *Desmatosuchus spurensis* (Archosauria: Suchia) from the Chinle Formation of Arizona and a revision of the genus *Desmatosuchus*. *PaleoBios*, 28: 281–40.
- Parker, W. G., 2016. Revised phylogenetic analysis of the Aetosauria (Archosauria: Pseudosuchia); assessing the effects of incongruent morphological character sets. *PeerJ*, 4:e1583, DOI: 10.7717/peerj.1583
- Parker, W. G., 2018. Anatomical notes and discussion of the first described aetosaur *Stagonolepis robertsoni* (Archosauria: Suchia) from the Upper Triassic of Europe, and the use of pleiomorphies in aetosaur biochronology. *PeerJ*, 6:e5455, DOI: 10.7717/peerj.5455
- Parrish, J. M., 1994. Cranial osteology of *Longosuchus meadei* and the phylogeny and distribution of the Aetosauria. *Journal of Vertebrate Paleontology*, 14: 196–209.
- Paul, G. S., 2007. Turning the old into the new: a separate genus for the gracile iguanodont from the Wealden of England. In: Carpenter, K. (ed.), *Horns and Beaks: Ceratopsian and Ornithomimid Dinosaurs*. Indiana University Press, Bloomington, pp. 69–77.
- Roberto-da-Silva, L. C., Desojo, J. B., Cabreira, S. R. F., Aires, A. S. S., Müller, R. T., Pacheco, C. P. & Dias-Da-Silva, S. R., 2014. A new aetosaur from the Upper Triassic of the Santana Maria Formation southern Brazil. *Zootaxa*, 3764: 240–278.
- Salvagno, L. & Albarella, U., 2017. A morphometric system to distinguish sheep and goat postcranial bones. *PLoS ONE*, 12: e0178543.
- Sander, P. M., Christian, A., Clauss, M., Fechner, R., Gee, C. T., Griebeler, E. M., Gunga, H. C., Hummel, J., Mallison, H., Perry, S. F., Preuschoft, H., Rauhut, O. W., Remes, K., Tütken, T., Wings, O. & Witzel, U., 2011. Biology of the sauropod dinosaurs: the evolution of gigantism. *Biological Reviews of the Cambridge Philosophical Society*, 86: 117–155.
- Schoch, R. R., 2007. Osteology of the small archosaur *Aetosaurus* from the Upper Triassic of Germany. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 246: 1–35.
- Schoch, R. R. & 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 für Geologie und Paläontologie, Abhandlungen*, 279: 73–95.
- Small, B. J., 2002. Cranial anatomy of *Desmatosuchus haplocerus* (Reptilia: Archosauria: Stagonolepididae). *Zoological Journal of the Linnean Society*, 136: 97–111.
- Stokstad, E., 2007. Did horny young dinosaurs cause illusion of separate species? *Science*, 318: 1236.
- 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: 860–881.
- Szulc, J., Racki, G. & Jewuła, K., 2015a. Key aspects of the stratigraphy of the Upper Silesian middle Keuper, southern Poland. *Annales Societatis Geologorum Poloniae*, 85: 557–586.
- Szulc, J., Racki, G., Jewuła, K. & Środoń, J., 2015b. How many Upper Triassic bone-bearing levels are there in Upper Silesia (southern Poland)? A critical overview of stratigraphy and facies. *Annales Societatis Geologorum Poloniae*, 85: 587–626.
- Walker, A. D., 1961. Triassic reptiles from the Elgin area: *Stagonolepis*, *Dasygnathus* and their allies. *Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences*, 244: 103–204.
- Weinbaum, J. C., 2013. Postcranial skeleton of *Postosuchus kirkpatricki* (Archosauria: Paracrocodylomorpha), from the upper Triassic of the United States. In: Nesbitt, S. J., Desojo, J. B. & Irmis, R. B. (eds), *Anatomy, Phylogeny, and Palaeobiology of Early Archosaurs and Their Kin*. *Geological Society, London, Special Publications*, 379: 203–239.

Appendix 1

Referred material collection numbers

Hindlimb fragment	Collection number
astragalus	UOPB-01140
calcaneus	UOPB-01141--01148
metatarsal (mt) I	UOPB-01137
mt II	UOPB-01139
mt III	UOPB-01138
mt IV	UOPB-01136
pedal phalanx (p) I-1	UOPB-01134
p I-2	UOPB-01129
p II-1	UOPB-01132

Hindlimb fragment	Collection number
p II-2	UOPB-01128
p II-3	UOPB-01124
p III-1	UOPB-01131
p III-2	UOPB-01127
p III-4	UOPB-01135
p IV-1	UOPB-01133
p IV-2	UOPB-01126
p IV-3	UOPB-01130
p IV-4	UOPB-01125