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REEVALUATION OF THE CRETACEOUS MARINE LIZARD *ACTEOSAURUS CRASSICOSTATUS* CALLIGARIS, 1993

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ACTEOSAURUS CRASSICOSTATUS Calligaris, 1993 was erected based on a partial skeleton of a small lizard found in marine carbonate rocks from the Cretaceous (Upper Cenomanian-Lower Turonian) of Comen, Slovenia. Here, we show that the holotype and only known specimen cannot be assigned to the genus *Acteosaurus* (Calligaris, 1993), but instead is referable to and indistinguishable from *Adriosaurus suessi* Seeley, 1881. *Acteosaurus crassicostatus* is therefore a junior objective synonym of *Adriosaurus suessi*.

The holotype of *Acteosaurus crassicostatus* is in a small block of rock that is split horizontally into part and counterpart (MCSNT 9400a & b). The material consists of an articulated portion of the anterior postcranial skeleton. Photographs of both part and counterpart have been published (Calligaris, 1993), however, these photographs were small and not easily interpreted. We illustrate the ''part'' (MCSNT 9400a) of the specimen using drawings and a photograph (Fig. 1.1–1.3) as the part contains the skeletal remains while the counterpart is a natural mold.

A series of 13 anterior dorsal vertebrae is preserved on MCSNT 9400a, with further portions of two extra vertebrae at both ends (Fig. 1.1, 1.2). All are exposed only in dorsal view. The neural arches are wide, with the anterior and posterior zygapophyses projecting laterally giving them a ''butterfly'' shape in dorsal view. They are all pachyostotic, with the neural arches swollen and heavily ossified. Adjacent neural spines interlock, indicating the presence of zygosphene-zygantral articulations, but the precise morphology of these joints cannot be determined as no one vertebra is isolated. The neural spines are all broken off (embedded in the counterpart) and their height cannot be determined. However, they were wide transversely as a correlate of pachyostosis and extended anteroposteriorly along the entire length of the neural arch. Ribs are associated with all vertebrae but are only exposed proximally, with the distal ends projecting posteroventrally into the rock; these have not been prepared free of the matrix. Like the vertebrae, the ribs are pachyostotic, being greatly thickened and heavily ossified. They project only a short distance laterally before curving ventrally, thus indicating a narrow (laterally compressed) body shape. The vertebrae and ribs all increase in size gradually along the length of the preserved column.

Parts of both forelimbs are also preserved and are small relative to the axial elements. Each forelimb is represented by the distal portion of the humerus and a rather complete radius, ulna, and manus. The shaft of the humerus is narrow and the distal end is only slightly expanded. The radius and ulna are both narrow rods, expanded proximally and distally. They are very close together proximally (at the articulation with the humerus) but diverge distally (at the articulation with the manus). The manus is wide and completely exposed on the left and is the basis for the following description of the meso- and metapodium.

All carpal elements appear to be preserved in natural position and are represented by tiny, rounded ossifications. The proximal row consists of a radiale, intermedium, and ulnare (Fig. 1.3). Five distal carpals are present, with the first and fifth being smaller than the central three. All five metacarpals are preserved. All are elongate, rodlike elements expanded proximally and distally with the exception of the first metacarpal; this element is much broader and thicker than metacarpals two through five. The third is the longest, followed by the second and fourth, with the shortest being the first and fifth. Ossified epiphyses are visible on the proximal ends of the second, fourth, and fifth metacarpals. All phalanges are well preserved and the phalangeal formula is 2-3-4-5-3. The longest digit is the fourth, followed by the third, then the second and fifth, and finally the first. The unguals are curved and taper to a sharp point, indicating that the digits terminated in distinct claws.

The specimen was originally described as a new species of *Acteosaurus*. It was interpreted as congeneric with, and presumably related to, *Acteosaurus tommasinii* (von Meyer, 1860), a small marine lizard also found at Comen. Calligaris (1993) presumably based his assignment on the anatomy and proportions of the forelimb elements and the length of the anterior dorsal vertebrae. Although similar in these respects to *Acteosaurus tommasinii*, Calligaris (1993) considered the specimen a distinct species from *A. tommasinii* because of its pachyostotic vertebrae (not present in *A. tommasinii*).

However, the present specimen is clearly very distinct from *Acteosaurus tommasinii*. As noted by Calligaris (1993), vertebrae of MCNST 9400 are much wider and exhibit pachyostosis. Further differences are as follows. The ribs of MCNST 9400 are twice as thick and also pachyostotic. The forelimb is larger than in *A. tommasinii*, with the epipodials (radius and ulna) being slightly longer than the length of an anterior dorsal vertebra, rather than slightly shorter. Also, the epipodials of both left and right limbs are preserved sharply diverging distally in the current specimen, while in both limbs of *A. tommasinii* they are preserved approximately parallel, suggesting that the limb was wider distally (as well as longer) in MCSNT 9400. Accordingly, the manus in MCNST 9400 is wider than in *A. tommasinii*. Thus, the current specimen is very distinct from *Acteosaurus*. Although the limits of ''genera'' (and indeed all higher taxa) are highly subjective (Ereshevsky, 2001), most would interpret these differences (which occur in almost all elements preserved in both taxa) as at least ''generic.''

Apart from the current specimen, the only small Mesozoic reptiles with pachyostotic vertebrae and ribs and a laterally compressed body are the limbed marine snakes (pachyophiids) and the dolichosaurs, *Adriosaurus* Seeley, 1881 and *Pontosaurus* (Kornhuber, 1873). All adequately known pachyophiids [*Pachyrhachis* Haas, 1979; *Pachyophis* Nopcsa, 1923; *Eupodophis* (Rage and Escuillié, 2000); *Haasiophis* Tchernov, Rieppel, Zaher, Polcyn, and Jacobs, 2000; and *Mesophis* Bolkay, 1925] lack all traces of forelimbs (e.g., Lee and Scanlon, 2002); thus, the current specimen is very distinct from pachyophiids. In contrast, it is indistinguishable from *Adriosaurus* (Seeley, 1881; Nopcsa, 1908, 1923; Lee and Caldwell, 2000). *Adriosaurus* is currently known from two specimens, the type in the Naturhistorisches Museum, Vienna (a posterior postcranial skeleton), and a second specimen in the Natural History Museum, London (a fully articulated, complete skeleton). The two specimens can be unambiguously associated via shared derived features (Lee and Caldwell, 2000),

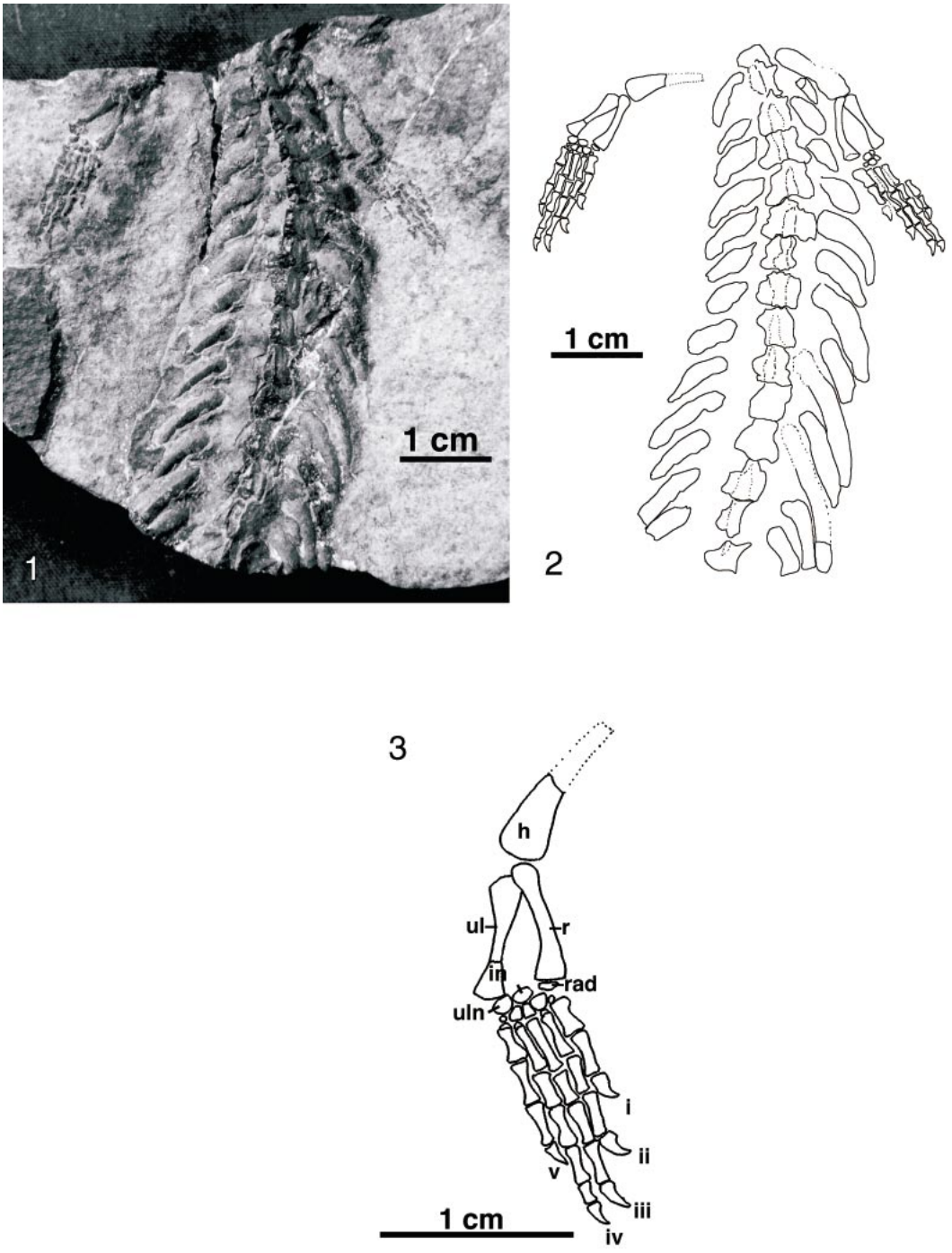

FIGURE *1—1–3, Acteosaurus crassicostatus* Calligaris, 1993 (MCSNT 9400a—part); *1,* photograph of the holotype; *2,* line drawing of the holotype; *3,* line drawing of left forelimb. Abbreviations: h, humerus; in, intermedium; r, radius; rad, radiale; ul, ulna; uln, ulnare; i–v, digits one through five.

though only the London specimen (NHM R2867) preserves the region comparable to the current specimen. Fortuitously, the London *Adriosaurus* is also exposed dorsally, with the same elements visible in the same aspect as the current specimen. The vertebrae of the London *Adriosaurus* are identical in morphology to the current specimen, being pachyostotic, with wide, ''butterfly-shaped'' neural arches, zygosphene-zygantral articulations, and wide neural spines that extend the length of the neural arch. The ribs are also pachyostotic and thick, and curve ventrally to give a laterally compressed body. The vertebrae gradually increase in size posteriorly along the anterior dorsal region. The forelimb is of similar size to the current specimen, with the epipodials being slightly longer than an anteriormost dorsal. The humerus, radius, and ulna of *Adriosaurus* appear to be slightly wider than those of the current specimen, but this is probably a result of crushing. Finally, the Vienna *Adriosaurus* is from the same locality and horizon as the current specimen, while the London *Adriosaurus* comes from the same horizon in nearby Lesina, Slovenia.

Thus, the current specimen (holotype of *Acteosaurus crassicostatus*), although rather incomplete, can be excluded from the genus *Acteosaurus*, but can be referred to and is indistinguishable from *Adriosaurus suessi*. On this basis, *Acteosaurus crassicostatus* is here made an objective junior synonym of *Adriosaurus suessi*.

An important future consideration will be a comparison of *Adriosaurus* and *Pontosaurus*. Pontosaurine dolichosaurs have been described from Cenomanian rocks outcropping on the island of Hvar, Croatia (Kornhuber, 1873; Pierce and Caldwell, in press), and from Nammoura, Lebanon (Dal Sasso and Renesto, 1999). There are a number of similarities in the postcranial skeleton of both *Adriosaurus* and *Pontosaurus* that suggest close relationship if not synonomy (see Kornhuber, 1873; Lee and Caldwell, 2000; Pierce and Caldwell, in press). The separation of these two taxa is currently justified by reference to the cranial skeleton. However, as noted by Lee and Caldwell (2000) the skull of *Adriosaurus* is not well preserved and is difficult to interpret. New specimens of *Adriosaurus* are required if this problem, the possible synonomy of *Adriosaurus* and *Pontosaurus*, is to be solved.

The referral of the current specimen to *Adriosaurus suessi*, a conservative approach to the *Adriosaurus-Pontosaurus* problem, sheds some new light on the morphology of *A. suessi*. Most elements preserved in the current specimen are already well known in *Adriosaurus*, based on the very complete London specimen (Nopsca, 1908, 1923; Lee and Caldwell, 2000). However, the manus is poorly preserved in the latter specimen, with the carpals being crushed into an indistinguishable mass and the phalangeal formula being impossible to ascertain. Fortuitously, the current specimen, despite its incompleteness, includes a very well-preserved left forelimb. It thus reveals new information about the manus of *Adriosaurus*: it possessed a full complement of carpals, a phalangeal formula of 2-3-4-5-3 (typical and primitive for squamates: Greer, 1991), and well-developed terminal claws.

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