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Callibrachion and *Datheosaurus*, two historical and previously mistaken basal caseasaurian synapsids from Europe

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This study represents a re-investigation of two historical fossil discoveries, *Callibrachion gaudryi* (Artinskian of France) and *Datheosaurus macrourus* (Gzhelian of Poland), that were originally classified as haptodontine-grade sphenacodontians and have been lately treated as nomina dubia. Both taxa are here identified as basal caseasaurs based on their overall proportions as well as dental and osteological characteristics that differentiate them from any other major synapsid subclade. As a result of poor preservation, no distinct autapomorphies can be recognized. However, our detailed investigations of the virtually complete skeletons in the light of recent progress in basal synapsid research allow a novel interpretation of their phylogenetic positions. *Datheosaurus* might represent an eothyridid or basal caseid. *Callibrachion* shares some similarities with the more derived North American genus *Casea*. These new observations on *Datheosaurus* and *Callibrachion* provide new insights into the early diversification of caseasaurs, reflecting an evolutionary stage that lacks spatulate teeth and broadened phalanges that are typical for other caseid species. Along with *Eocasea*, the former ghost lineage to the Late Pennsylvanian origin of Caseasauria is further closed. For the first time, the presence of basal caseasaurs in Europe is documented.

Key words: Synapsida, Caseasauria, Carboniferous, Permian, Autun Basin, France, Intra-Sudetic Basin, Poland.

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Introduction

During the late 19th and early 20th century, the knowledge about the taxic diversity and phylogenetic relationships of early amniotes was quite limited (Brocklehurst and Fröbisch 2014). During that time, many fossils, including poorly preserved specimens, were described and compared to members of the reptilian (sauropsid) lineage of amniotes by using features later recognized as representing symplesiomorphic characters. Almost every new discovery from Europe and North America once has been discussed as related either to the parareptile *Mesosaurus* ("Proganosauria") or the archosauromorph diapsid *Protorosaurus*, each of which has undergone major changes in taxonomic assignment through the decades (compiled by Case 1907; Romer and Price 1940; see also Osborn 1903; Huene 1908; Williston 1912). A great impact was achieved by the description of the sphenacodontian synapsid *Palaeohatteria longicaudata* (Credner 1888), originally named after the extant tuatara (*Hatteria*, today *Sphenodon*, with which it only shares symplesiomorphies). At that time, the term of a "*Palaeohatteria*-group" was coined to supposedly contrast with synapsid groups (Huene 1908), likely triggered by the myth of a diapsid skull condition in *Palaeohatteria*. This skull morphology was first an assumption coherent with the rhynchocephalian classification of *Palaeohatteria* by Credner (1888), but later erroneously reconstructed and described more confidently (e.g., Osborn 1903). The actual presence of a synapsid skull condition in *Palaeohatteria* was first correctly recognized by Williston (1914; confirmed by Nopcsa 1928).

Among the early amniotes discussed to belong to one of those ancient "reptile" branches, two single and poorly pre-

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served, but almost complete skeletons are missing in modern revisions: *Callibrachion gaudryi* Boule and Glangeaud, 1893b from the Autunian series, Autun Basin (France), and *Datheosaurus macrourus* Schroeder, 1904 from red beds of the Intra-Sudetic Basin (Poland). In the influential monographic treatment of "Pelycosauria" by Romer and Price (1940), both taxa were correctly recognized as belonging to basal synapsids. However therein, alongside *Palaeohatteria* and *Pantelosaurus*, both *Callibrachion* and *Datheosaurus* were synonymized with the basal sphenacodontian genus *Haptodus*. From that time on, no re-evaluation has been attempted, either accepting this classification (Romer 1956; Huene 1956; Devillers 1961; Kuhn 1961; Currie 1977, 1979; Reisz 1986) or treating them as nomina dubia (thus excluded by Laurin 1993, 1994). Laurin (1994) personally examined the type of *Callibrachion* and subsequently doubted its synapsid condition. After all of this work, a re-study of *Callibrachion* and *Datheosaurus* has not been carried out since then, leaving these two taxa as tentative nomina dubia. During the recent revision of basal sphenacodontians (Spindler 2015), a re-evaluation of the complete material pertaining to *Callibrachion* and *Datheosaurus* was possible and leads now to their re-validation and revised identification as members of the clade Caseasauria.

Caseasaurs are generally considered to represent the sister taxon to Eupelycosauria (Reisz 1980, 1986; Reisz and Fröbisch 2014). However, Benson (2012) recently discussed an alternative hypothesis with caseasaurs being the sister taxon of Edaphosauridae + Sphenacodontia (forming the clade Sphenacomorpha), with varanopids and ophiacodontids representing more basal branches. In any case, caseasaurs played an important role in the early evolution of terrestrial ecosystems as they include some of the first pioneer taxa to evolve an herbivorous lifestyle, next to Diadectidae, Captorhinidae, and Edaphosauridae, later followed by parareptilian examples (Sues and Reisz 1998; Pearson et al. 2013; Reisz and Fröbisch 2014). Moreover, in addition to varanopids, caseasaurs include some of the geologically youngest pelycosaur-grade synapsids (e.g., Maddin et al. 2008; Modesto et al. 2011; Silva et al. 2012; Brocklehurst et al. 2013). Caseasauria consists of Caseidae (Williston 1912) as well as *Eothyris parkeyi* (Romer 1937) and *Oedaleops campi* (Langston 1965), which either form a monophylum, the Eothyrididae (Reisz 1986; Reisz et al. 2009; Reisz and Fröbisch 2014), or a stem paraphylum (Sumida et al. 2014). Research on caseasaurs, specifically caseids, reached its climax with the publication of Olson's (1968) monograph "The family Caseidae", which was thereafter followed by a drought of almost four decades with very few exceptions (e.g., Sigogneau-Russell and Russell 1974). However, increased research interest in recent years generated a number of publications, including the description of new taxa and new material as well as the re-description of already known caseasaur fossils (Reisz 2005; Maddin et al. 2008; Reisz et al. 2009, 2011; Ronchi et al. 2011; Reisz and Fröbisch 2014; Romano and Nicosia 2014, 2015; Sumida et al. 2014; LeBlanc and Reisz 2014) as well as an undescribed large caseid from the Lodève Basin, France (Schneider et al. 2006). While the knowledge in particular on advanced members of the clade increased much in recent years, our understanding of their early evolutionary history and diversification is still limited.

Here, we re-describe *Callibrachion gaudryi* and *Datheosaurus macrourus* for the first time in detail. The specimens are too poorly preserved to allow their inclusion in a phylogenetic analysis. Nonetheless, their assignment to Caseasauria is robust, therefore we attempt to discuss the historical findings as well as caseasaurian phylogenetic and evolutionary trends.

Institutional abbreviations.—CM, Carnegie Museum, Pittsburgh, USA; MB, Museum für Naturkunde, Berlin, Germany; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, USA; MNHN, Muséum National d'Histoire Naturelle, Paris, France; NHMS, Naturhistorisches Museum Schleusingen, Thuringia, Germany; OMNH, Oklahoma Museum of Natural History, Norman, USA; RM, Redpath Museum, McGill University, Montréal, Canada; SNSD, Senckenberg Naturhistorische Sammlungen Dresden, Germany; UC, University of Chicago (today collection of Field Museum), Chicago, USA.

Historical background

Taxonomic history of *Callibrachion*.—The first paleontologists having named and described *Callibrachion* (Boule and Glangeaud 1893a–c; repeated by Mazion 1959) noted major similarities with *Palaeohatteria*, which are now known to be mostly plesiomorphic (e.g., the unfused jaw symphysis) or the result of their juvenile ontogenetic stage (e.g., unfused centra and neural arches). *Callibrachion* was first assigned to the "Pelycosauria" by Baur and Case (1899), and then by Case (1907) to the supposedly primitive "Poliosauridae" (today considered a polyphyletic assemblage of mainly ophiacodontid taxa). Huene (1908) again classified *Callibrachion* as a member of the "*Palaeohatteria*-group" (including the sphenacodontian synapsid *Haptodus baylei*, and the diapsid reptiles *Aphelosaurus* and *Protorosaurus*), initially thought to oppose the "pelycosaur" status. Although Thévenin (1910) followed Huene's (1908) opinion, he also noted that the differences in the ossification of *Callibrachion*, *Haptodus* and *Palaeohatteria* may in fact originate in their ontogeny. Williston (1912) stated that *Callibrachion* showed no discrepancy from his "Theromorpha", that is, Pelycosauria, Proterosauria (including "Paleohatteridae"), Caseasauria, Kadaliosauridae. Later, Williston (1914) transferred provisionally *Callibrachion* and *Haptodus baylei* to the "Protorosauria" alongside the diapsids *Araeoscelis*, *Kadaliosaurus*, and *Protorosaurus*. In a list of European "pelycosaurs", Huene (1925) followed Case (1907) by assigning *Callibrachion* to "Poliosauridae". Williston (1925) regrouped *Palaeohatteria*, *Haptodus*, and *Callibrachion* into the Palaeohatteriidae, characterized in part by their weak ossification, but was unable to assign this family to one of his "theromorph" suborders in particular. The taxonomy adopted by Nopcsa (1928) was very different. He proposed indeed to move *Callibrachion* to the "Theropleurinae" with "*Oxyodon*" and *Theropleura*, currently known as the sphenacodontid *Sphenacodon britannicus* and the ophiacodontid *Ophiacodon uniformis*.

Romer and Price (1940) recognized the subadult osteology of *Callibrachion*, with the humerus and ilium resembling sphenacodontids (today sphenacodontians, sensu Reisz et al. 1992). These authors did not study the European material first hand, thus the assignments of *Callibrachion* and *Datheosaurus* (see below) was vague and lacked diagnostic characters, although considered to match the stratigraphy, geography and morphology of *Haptodus*. It was this doubtful decision to rename them *Haptodus gaudryi* and *H. macrourus* that led later workers to follow this "haptodontine" classification. As an exception, Heyler (1969) recognized that *Haptodus* and *Callibrachion* differ little in size but much in the ossification stages of the humeri, thus questioning the lumped taxonomy. In contrast, Currie (1979) went even further by synonymizing almost all Permian "haptodonts" within the type species *Haptodus baylei*, including *Callibrachion* and *Datheosaurus* without personally restudying the specimens, and explaining any differences globally by ontogeny and diagenesis.

Taxonomic history of *Datheosaurus*.—Schroeder (1904) cited Dathe (1900; including personal communication of Ernst Dathe with Eberhard Fraas) that *Datheosaurus* possibly belongs to the "*Palaeohatteria*-group", reflecting the classification among Proganosauria (Baur 1889), antecedent to the "*Palaeohatteria*-group" of Huene (1908) that also included *Haptodus*. Without recognizing the juvenile condition of *Palaeohatteria*, Schroeder (1904) compared *Datheosaurus* to the latter as being more advanced. Huene (1910), based on plesiomorphic characters, later suggested close relationships to *Kadaliosaurus* (a basal diapsid), *Labidosaurus* (a captorhinid), and Cotylosauria. Jaekel (1911) ranked *Datheosaurus* with *Labidosaurus* and *Isodectes* (in fact a temnospondyl) within the supposed cotylosaurian group "Datheosauri". Despite the poor preservation, Williston (1912) argued that the vertebral morphology excludes *Datheosaurus* from Cotylosauria and preferred a position close to *Palaeohatteria*, *Kadaliosaurus*, and *Araeoscelis*. Nopcsa (1923) assumed that *Datheosaurus* is extremely primitive, closely related to *Seymouria*, and established the Datheosauridae to contain also "*Eosauravus*" (which is now the "microsaur" *Tuditanus*). Furthermore, he considered *Datheosaurus* to be a potential trackmaker of lacertoid ichnia, such as *Dromopus*.

In a monograph on Permian reptiles from Madagascar, Piveteau (1926: pl. 12: 2) tentatively referred a specimen, currently numbered as MNHN.F.MAP360, to *Datheosaurus* based on its humeral shape, its short forelimb, and its so-called "prehensile" tail. This specimen has since been described as the holotype of the neodiapsid *Thadeosaurus colcanapi* (Carroll 1981). Other figured and measured specimens ascribed to the same species were listed as "*Datheosaurus*" by Currie (1982).

Romer and Price (1940) stated that *Datheosaurus* could not be distinguished from other "haptodonts" by any clear feature. Its identification as a "haptodontine" was supported by Currie (1977, 1979, see above). It is unknown how the sphenacodontian status was established. Maybe it is a relic from its original grouping with *Palaeohatteria* and the reptilian taxa *Kadaliosaurus*, *Protorosaurus*, and *Mesosaurus*. In fact, several questionable taxa were still considered to be closely related to *Palaeohatteria* after most of the others have otherwise been reclassified with increasing knowledge of basal amniote relationships and diversity.

Systematic paleontology

Synapsida Osborn, 1903

Caseasauria Williston, 1912

Emended definition.—*Casea broilii* Williston, 1910, and synapsids related more closely to it than to either *Varanops brevirostris* Williston, 1914, *Ophiacodon mirus* Marsh, 1878, or *Edaphosaurus pogonias* Cope, 1882.

Diagnosis.—As provided by Reisz et al. (2009).

Remarks.—The classification of *Callibrachion* and *Datheosaurus* matches the diagnosis for Caseasauria given by Reisz et al. (2009). In both taxa, the skull is relatively short, including a short facial region. This crucial observation excludes them from other basal synapsid families. Further caseasaurian characters are the reduced marginal dentition (*Callibrachion*), the unusually large pineal foramen (*Datheosaurus*) and the low and broad skull, as reconstructed for both genera in question. The large dorsal blade in the ilium of *Callibrachion* suggests a possible caseid classification, whereas the maxillary contour of *Datheosaurus* might indicate an eothyridid affinity. More support of the differential diagnosis is given by the following descriptions.

?Caseidae Williston, 1911

Genus *Callibrachion* Boule and Glangeaud, 1893b

Type species: *Callibrachion gaudryi* Boule and Glangeaud, 1893b; Margenne (France); Artinskian (Cisuralian).

Callibrachion gaudryi Boule and Glangeaud, 1893b

Figs. 1, 2.

1893 *Callibrachion Gaudryi* (gen. nov., sp. nov.); Boule and Glangeau [sic!] 1893b: 646–647.
1893 *Callibrachion Gaudryi* (gen. nov., sp. nov.); Boule and Glangeaud 1893a: 1–17, text-figs. 1–4, pl. 3.
1893 *Callibrachion Gaudryi*; Boule and Glangeaud 1893c: 218. [cop. Boule and Glangeaud 1893a: 1–2, 16–17].
1910 *Callibrachion Gaudryi* Boule et Glangeaud; Thévenin 1910: 50, fig. 28. [cop. Boule and Glangeaud 1893a: fig. 1].
1928 [nec] *Kallibrachion*; Nopcsa 1928: 171.

1940 *Haptodus gaudryi* (Boule and Glangeaud 1893); Romer and Price 1940: 307–308.

1959 *Callibrachion Gaudryi*; Mazion 1959: 7–10, figs. 1, 2, 4, 5. [cop. Boule and Glangeaud 1893a: 1–2, 16–17, figs. 1–4].

1979 *Haptodus baylei* Gaudry, 1886 [sensu novo]; Currie 1979: 138–160, table 2.

Holotype: MNHN.F.AUT490, single slab with a three-dimensionally preserved partial skull and almost complete skeleton, but missing part of the vertebral column, part of the pectoral and pelvic girdles as well as the left hind limb (Figs. 1, 2). This specimen was previously cited correctly by Currie (1979: 134) under its entry number MNHN 1891-23 (1979: 138) and incorrectly as MNHN 1893-23.

Two spiral heteropolar coprolites have been added to the plaster jacket, artificially arranged to fit into a wooden frame. This practice was common at the end of the 19th century for specimens intended for exhibition in the new "Galerie de Paléontologie" of the MNHN, including other Autunian tetrapods from the Autun Basin.

Two thin sections have been sampled (Boule and Glangeaud 1893c: fig. 2), one from the maxillary canines and one containing two of the dorsal vertebrae. The current location of these thin sections is unfortunately unknown.

Type locality: Black shales of Autun, near Margenne, Saône-et-Loire Department, Bourgogne Region, France.

Type horizon: According to modern stratigraphy (Werneburg and Schneider 2006), the sites that revealed *Callibrachion* as well as the type and only specimen of *Haptodus baylei* (Gaudry 1886) are part of the Upper Millery Formation (Autunian, Rotliegend, Cisuralian), which has recently been shifted from Sakmarian to Artinskian age (Schneider et al. 2014). The dark grayish bituminous shale represents a lacustrine depositional environment (Marteau and Feys 1989) where rare amniote skeletons are allochthonous.

Material.— Holotype only.

Diagnosis.—A small to mid-sized caseasaur with slender and straight conical teeth, moderately thickened ribs, possibly an enclosed ectepicondylar foramen, an ilium with the typical caseid high dorsal blade, and robust but not expanded phalanges that show no reduction in phalangeal count.

Description.—The bones in MNHN.F.AUT490 often show questionable outlines, due to the crude original preparation and dispersed pyrite remodeling the shapes and blurring the contrast to the rock matrix. The slab exposes the skeleton on its ventral side, indicated by the visible interclavicular shaft, the inclination of the manual unguals, the rib cage, missing exposure of neural spines, and the relative position of the femur and the ilium with exposed acetabulum.

The type and only specimen of *Callibrachion gaudryi* is represented by a robustly built skeleton. To estimate its ontogenetic stage, it can be noted that the notochordal canal is well visible, as illustrated by Boule and Glangeaud (1893a: fig. 3). The authors also remark unfused neurocentral sutures, although these were not visible during the current review. As rarely reported in early amniotes, the scapulocoracoid is disarticulated, which underlines the juvenility of the specimen in question. No trace of a scapulocoracoid suture is seen in any known caseasaur shoulder girdle, except for that in the immature holotype of *Ruthenosaurus* (Reisz et al. 2011). In the ilium, the bone vascularization is visible, which together with the disarticulation of this element supports an early ontogenetic stage. The humerus has a broad distal end and a well ossified proximal head. In general, the limb bones show rather undifferentiated heads that correspond to the stages I and III of Brinkman (1988). The metapodials are ossified. Consequently, MNHN.F.AUT490 does not represent a very juvenile but still immature individual.

Cranial skeleton: The skull is possibly not only represented by the region originally interpreted as such, but also by a number of very uncertain elements between the jaw fragments and the left manus. This is supported by the mostly articulated postcranium of which all elements are known or at least identifiable, and thus can be excluded as a source for these additional elements.

Several certain skull bones have been identified in the original description (Boule and Glangeaud 1893a, c). Among these, the pterygoid and a dorsal coronoid process could not be confirmed in the current study, and the supposed quadrate is tentatively accepted.

The maxilla (and probable continuation to the premaxilla) is the only unquestionably identifiable element in the skull, characterized by its marginal tooth row. The ventral rim is slightly convex, with a canine region at the anterior end indicated by the broad tooth bases in contrast to the smaller ones preserved posteriorly to the latter. It is not possible to provide a definite tooth count or a length estimate for the maxilla, since the outline of the element is somewhat questionable. However, the maxilla seems to bear a steep dorsal process, as it has been reported for Varanopidae (e.g., Langston and Reisz 1981: fig. 5) and Caseasauria (e.g., Sigogneau-Russell and Russell 1974: fig. 2), even though both groups show differing sutural patterns. If not partly belonging to the lacrimal, the element designated as the maxilla is relatively high compared to eothyridids (see Reisz et al. 2009). According to its proportions, a contribution of the maxilla to the rim of the orbit is possible, but not certain. The most diagnostic and striking feature of the maxilla of *Callibrachion* is in fact the marginal dentition. The preserved teeth have a slender, conical crown with a smooth surface, lacking any significant curvature except in the anterior part of the preserved tooth row. Some teeth are partly broken and expose the internal pulp cavity. Among basal synapsids, a similar tooth type is found only in ophiacodontids, the basal sphenacodontian *Pantelosaurus* (FS personal observation), eothyridids, and the undescribed basal caseid from the German Bromacker locality (Reisz and Fröbisch 2014; Martens et al. 2014; Thomas Martens, personal communication 2014). Reconstructing the maxillary tooth row of *Callibrachion* with the canines in an anterior position, a second region of enlarged teeth posterior to the caniniform positions is reflecting the eothyridid pattern. Considering the combined information regarding the overall skull dimensions, the maxillary outline and the dentition, the limited data available for *Callibrachion* only matches the condition in Caseasauria.

With the same preservation as in the posterior part of the maxilla, some bluish-white fractures of tooth bases indicate that part of the palatal dentition may have been preserved

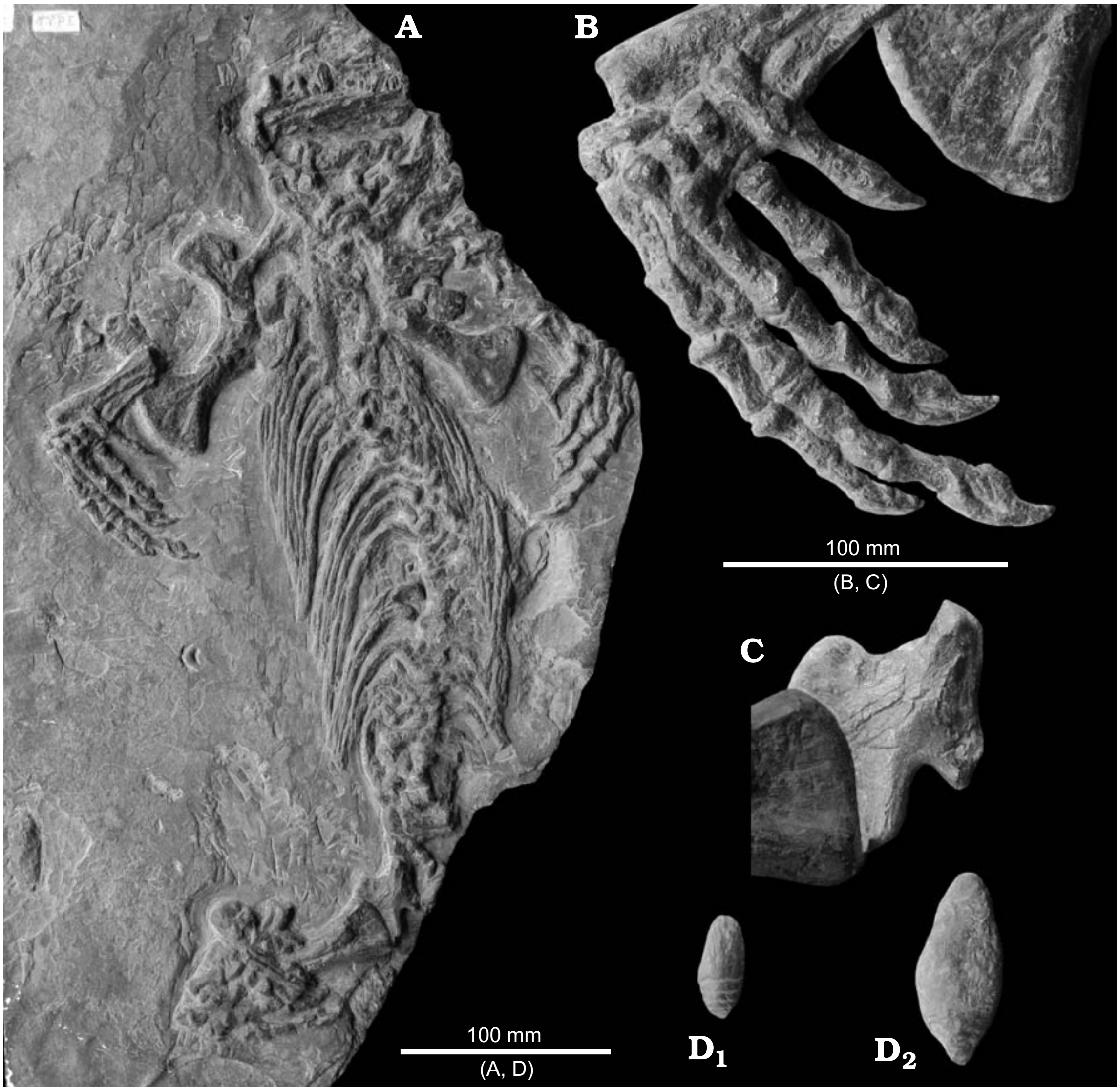

Fig. 1. Holotype of caseasaurian synapsid *Callibrachion gaudryi* Boule and Glangeaud, 1893 from Cisuralian of Autun, France (MNHN.F.AUT490). **A**. General view. **B**. Close-up of right manus. **C**. Right ilium, dorsally covered by proximal femur. **D**. Isolated shark coprolithes from the holotypic slab (Jörg W. Schneider, personal communication 2015).

in the region ventral to the mandible. They seem large compared to the smallest marginal teeth, strongly resembling the coarse denticles in the anterior part of the palate of *Cotylorhynchus romeri* (OMNH 04327; FS personal observation). Unfortunately, the poor preservation precludes a certain identification of the dentigerous element, but considering its size, it possibly includes a pterygoid.

The mandible is represented by a straight, slender, and rather shallow right jaw ramus. Its preserved length of about 70 mm could be close to its original length, since large and slightly curved teeth are found in what is most likely the dentary tip, lacking a deepened symphysis. The identification of individual elements is difficult, given its preservation, but the configuration suggests nevertheless that the ventral element is in fact a downturned splenial. Another element contacting the dorsal margin of the mandible was tentatively described by Boule and Glangeaud (1893a) as a "coronoid process" in a lepidosaur fashion. Such a structure would not resemble the more confluent process present in caseids, such as in *Euromycter* (Sigogneau-Russell and Russell 1974). As for now, there is no evidence for the presence of a coronoid process in *Callibrachion*, given the poor definition of this area in the holotype.

Axial skeleton: Although mostly articulated, the vertebrae provide only limited information. The vertebral column of *Callibrachion* is only represented by about twelve centra of the dorsal region, as well as uncertain remains of the cervical series and neural arches. Two barely outlined cervical centra appear to be located between the skull and the pectoral girdle. Some of the vertebrae have been damaged by preparation, while some others are overlapped by the pectoral girdle. Nonetheless, as a result of the articulation of the skeleton, it is possible to provide an estimate of the presacral count. In particular the uninterrupted series of about 21 dorsal ribs indicates a minimal presacral count of 23 vertebrae, in agreement with previous interpretations (Huene 1908).

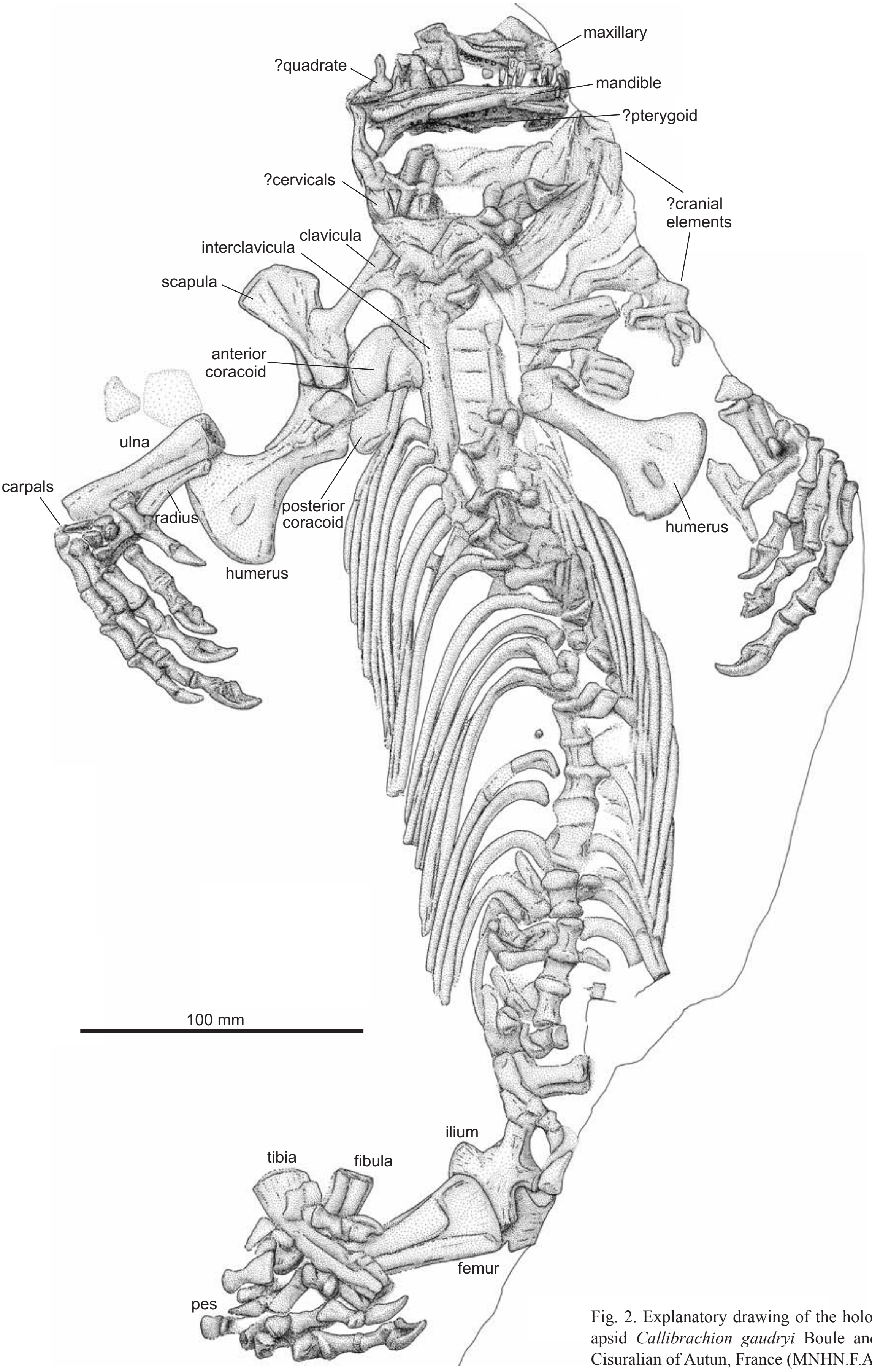

Fig. 2. Explanatory drawing of the holotype of caseasaurian synapsid *Callibrachion gaudryi* Boule and Glangeaud, 1893 from Cisuralian of Autun, France (MNHN.F.AUT490).

As this number is close to the plesiomorphic dorsal count reconstructed for synapsids (Müller et al. 2010), it is likely that only a few vertebrae are missing or still in the matrix.

As shown by a thin section, the dorsal centra are amphicoelous, notochordal, and rather elongated (Boule and Glangeaud 1893a: fig. 3). In average, the dorsal centra measure about 11 mm in width, and 15 mm in length. Given this ratio of about three-quarters, *Callibrachion* differs from basal sphenacodontians (Currie 1979: table 4). Although their articular facets are rounded, the lateral surfaces of the dorsal centra are slightly compressed. The resulting subtriangular cross-section ends in a weak ventral ridge.

The dorsal neural arches mentioned by Boule and Glangeaud (1893a) could not be identified with confidence. According to them, only two are well preserved enough for description, which they considered to be separated from the centra, showing a strong prezygapophysis, a smaller postzygapophysis, no transverse process, and a well-developed neural spine with a slight transverse dilatation.

The dorsal ribs are strongly built. The heads are difficult to reconstruct. Some appear to be elongated, but do not compare to the enormous length related to the expanded transverse processes in the neural arches of derived caseids. In the posterior dorsal region the ribs decrease in length, but not in width. The ribs have a distinct inflexion zone in their proximal region, which contrasts with all known members of Caseasauria including *Datheosaurus* (see below), but this morphology is very similar to a pattern seen in other pelycosaur-grade synapsids (e.g., *Archaeothyris*, *Ianthodon*, *Ianthasaurus*, and basal Sphenacodontia).

Pectoral girdle: The pectoral girdle of *Callibrachion* is well preserved and nearly complete, retaining its articulation on the anatomical right side of the skeleton. Boule and Glangeaud (1893a) already recognized the unfused condition of the scapulocoracoid. The clavicle has a relatively straight, rod-like shaft and overlaps the scapula with its wide ventral plate. Medially it meets the interclavicle, which displays a long, straight, parallel-sided and relatively slender shaft, whereas the head shape and proportions are not known with certainty. This is very much unlike the condition in *Oedaleops* (Sumida et al. 2014: fig. 2.5a), which has an interclavicular shaft that is broad proximally and narrows continuously distally and its head is very short but projects far laterally on either side.

With a height of about 50 mm, the right scapula of *Callibrachion* is much shorter than its humerus. It has a flaring dorsal edge and a strongly developed supraglenoid buttress. No diagnostic feature can be identified, but it does not seem to resemble the stout and broadly rounded shape of the scapula of *Oedaleops* (Sumida et al. 2014: fig. 2.5b), which may be the result of a low level of ossification in *Callibrachion*. The coracoids show little of their anatomy. Their outlines indicate nevertheless that the larger anterior coracoid has a strongly convex anterior margin and that the posterior coracoid has a weak triceps tubercle. Neither a supraglenoid foramen in the scapula nor a coracoid foramen are observable, but this may also be an artifact of poor preservation.

Forelimb: Both humeri are well exposed, each measuring about 70 mm in length and 40 mm in width distally. The proximal end is rather well ossified, with a short but robust deltopectoral crest and a well-developed process for the Musculus latissimus dorsi. Currie (1977, 1979) interpreted this shape to be less ossified than that of "*Haptodus*" *garnettensis* (holotype RM 14,156). Personal examination of the latter (Spindler 2015) in fact indicates a progressed ossification in *Callibrachion*, with the two distal foramina being enclosed within the epiphysis. In contrast to the description by Romer and Price (1940), who reported a ventrally pointing supinator process in *Callibrachion*, the distal epiphysis is almost flat and shows diffuse outlines of both an entepicondylar and ectepicondylar foramen. Though not fully ossified in distal outline, the ectepicondylar groove is clearly closed, which represents a condition seen in *Edaphosaurus* (Reisz 1986), *Heleosaurus* (Botha-Brink and Modesto 2009), and Caseidae (Olson 1968: fig. 16).

The right ulna is well preserved and exposed on the right side of the specimen, measuring 58 mm in length. Its concave proximal articulation lacks a distinct olecranon. The radius is only partially exposed on both sides and little can be said about its anatomy except that it was certainly a more slender element compared to the ulna.

Both manus are well preserved and mostly articulated. Although present, the proximal carpals cannot be identified with certainty, including the ulnare mentioned by Boule and Glangeaud (1893a). The individual elements of the manus are robust and well developed. In digit IV, which is the longest, the metacarpal measures 22 mm. The metacarpals and phalanges are of plesiomorphic amniote morphology, contrasting the stout and broadened shape of all known caseids except *Eocasea martini*, *Casea broilii*, and the intermediate "*Casea*" *nicholsi*. Due to its poor preservation, some of the interphalangeal joints are not easy to identify, but the specimen seems to display the plesiomorphic phalangeal formula (2-3-4-5-3) of amniotes (Figs. 1A, 2). The middle phalanx of digit IV is shortened, measuring about 70% the lengths of the neighboring elements. With this feature *Callibrachion* resembles *Datheosaurus* (see below). The terminal phalanges are strongly curved, with a strong flexor tubercle and a broadened flat dorsal roof.

Pelvic girdle: In the pelvic girdle, only the right ilium is exposed measuring 33 mm in length and 30 mm in height. The iliac blade has a simple plate-like morphology, showing no feature except a distinct anterodorsal expansion, resembling the ilium of Sphenacomorpha as well as Caseidae (and even *Oedaleops*, see Langston 1965: fig. 4; contradicting Sumida et al. 2014: figs. 2.5, 2.9). This is the only region of the entire postcranial skeleton preserving the original bone texture. Radiating from the neck of the ilium, the surface of the blade is unfinished, displaying long osteons. None of the surrounding fragments can be identified as a pubis or ischium with certainty.

Hind limb: Despite its poor preservation and partial disarticulation, the hind limb appears to have equivalent di-

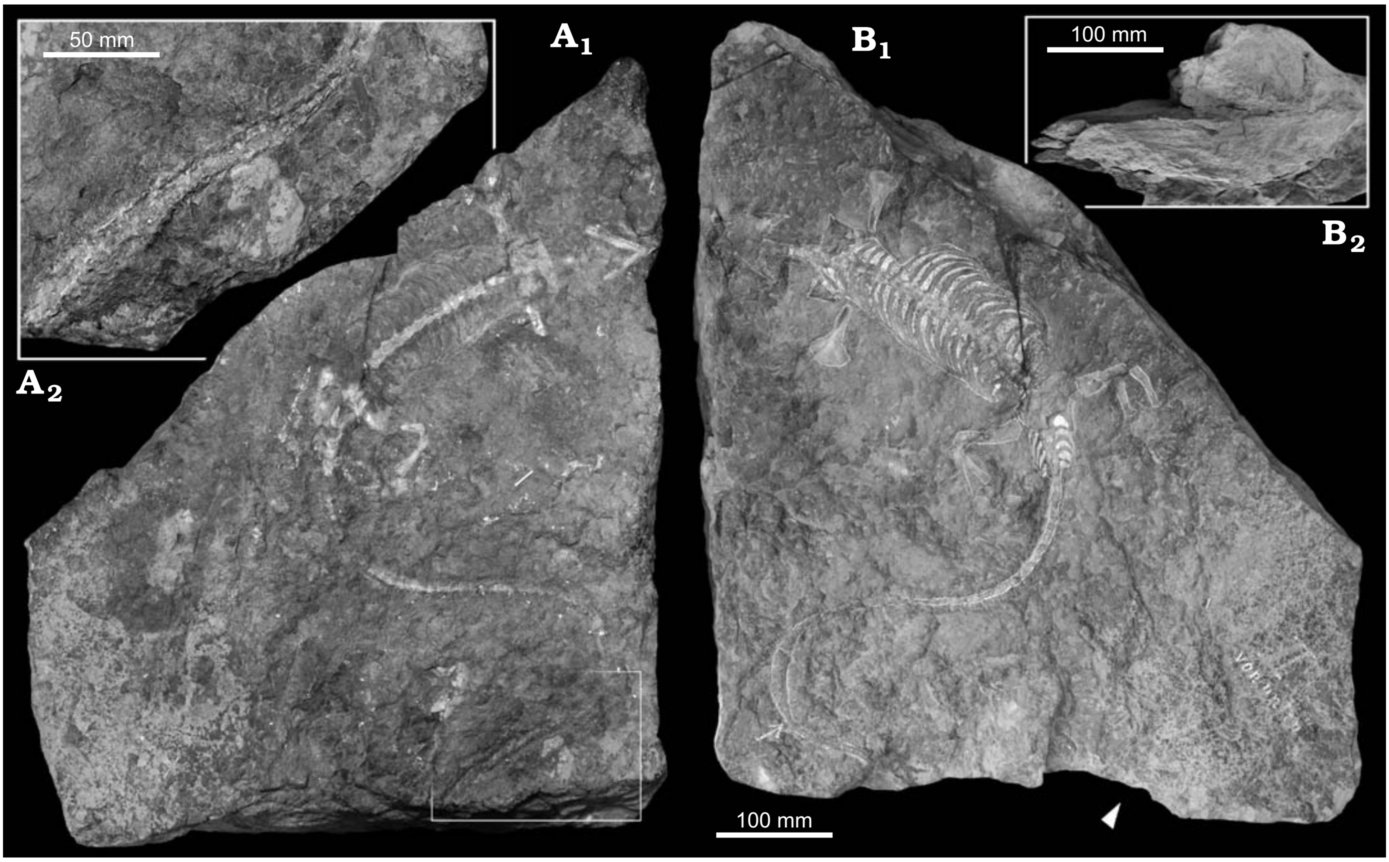

Fig. 3. Holotype of caseasaurian synapsid *Datheosaurus macrourus* Schroeder, 1904 from Upper Pennsylvanian of Nowa Ruda, Poland. **A**. MB.R. 1015.1 (laying slab), exposing an internal view onto ventral elements (A_1), with close-up of distal-most tail portion (A_2). **B**. MB.R. 1015.2 (hanging slab), exposing an internal view onto dorsal elements (B_1), detail (B_2), trough stratification of the area indicated by the arrowhead in B_1.

mensions to the forelimb, but exact measurements of the individual elements are not available as they overlap in part with other bones. Only the proximal half of the right femur is exposed, clearly showing a relatively shallow intertrochanteric fossa delimited by the posterior ridge and a deep, distinct internal trochanter. As a side note, the presence of a fracture parallel to the femoral long axis shows that the orientation of this trochanter is artifactual. Now resting along the shaft of the femur, the internal trochanter was likely projecting ventrally originally. The femoral shaft is straight. The proximal articulation of the femur is convex, but its simplicity suggests it is not fully ossified.

The zeugopodials are disarticulated. The element that most likely represents the tibia is positioned across the distal end of the femur. It is robust and slightly curved with a broad proximal end. Another, more slender element is only partially exposed and possibly represents the fibula.

The pedal elements are mostly disarticulated. It is not possible to make any definite statement about the phalangeal formula or potential phalanx shortening, but the individual elements seem to be equally robust and strongly developed as those of the manus.

Scales: Several small, shiny scales with a rhomboidal outline and fine surface fluting have been associated with *Callibrachion* (Boule and Glangeaud 1893a, who remarked that these scales have been extracted from the slab). As already pointed out by Romer and Price (1940), this description indicates they actually belong to a palaeoniscoid actinopterygian, very common in the Millery Formation.

Stratigraphic and geographic range.—Known only from type locality and horizon; Margenne (France), Artinskian (Cisuralian).

Genus *Datheosaurus* Schroeder, 1904

Type species: *Datheosaurus macrourus* Schroeder, 1904 (not 1907; see Currie 1979 and others); Nowa Ruda (Poland); Gzhelian (Pennsylvanian).

Datheosaurus macrourus Schroeder, 1904

Figs. 3, 4.

1904 *Datheosaurus macrourus* (gen. nov., sp. nov.); Schroeder 1904: 282–294, pl. 12, 13.

1926 non? *Datheosaurus* sp.; Piveteau 1926: 171–172, pl. 17: 2 [MNHN.F.MAP360, holotype of *Thadeosaurus colcanapi* Carroll, 1981].

1940 *Haptodus macrourus* (Schroeder, 1904); Romer and Price 1940: 308–309.

1979 *Haptodus baylei* Gaudry, 1886 [sensu novo]; Currie 1979: 138–160, table 2.

1982 non "*Datheosaurus*"; Currie 1982: 248–259, table 1, figs. 3C, 5, 6 [MNHN.F.MAP360, holotype of *Thadeosaurus colcanapi* Carroll, 1981, and referred specimens MNHN.F.MAP318, 331, 334, 349, 350, 613].

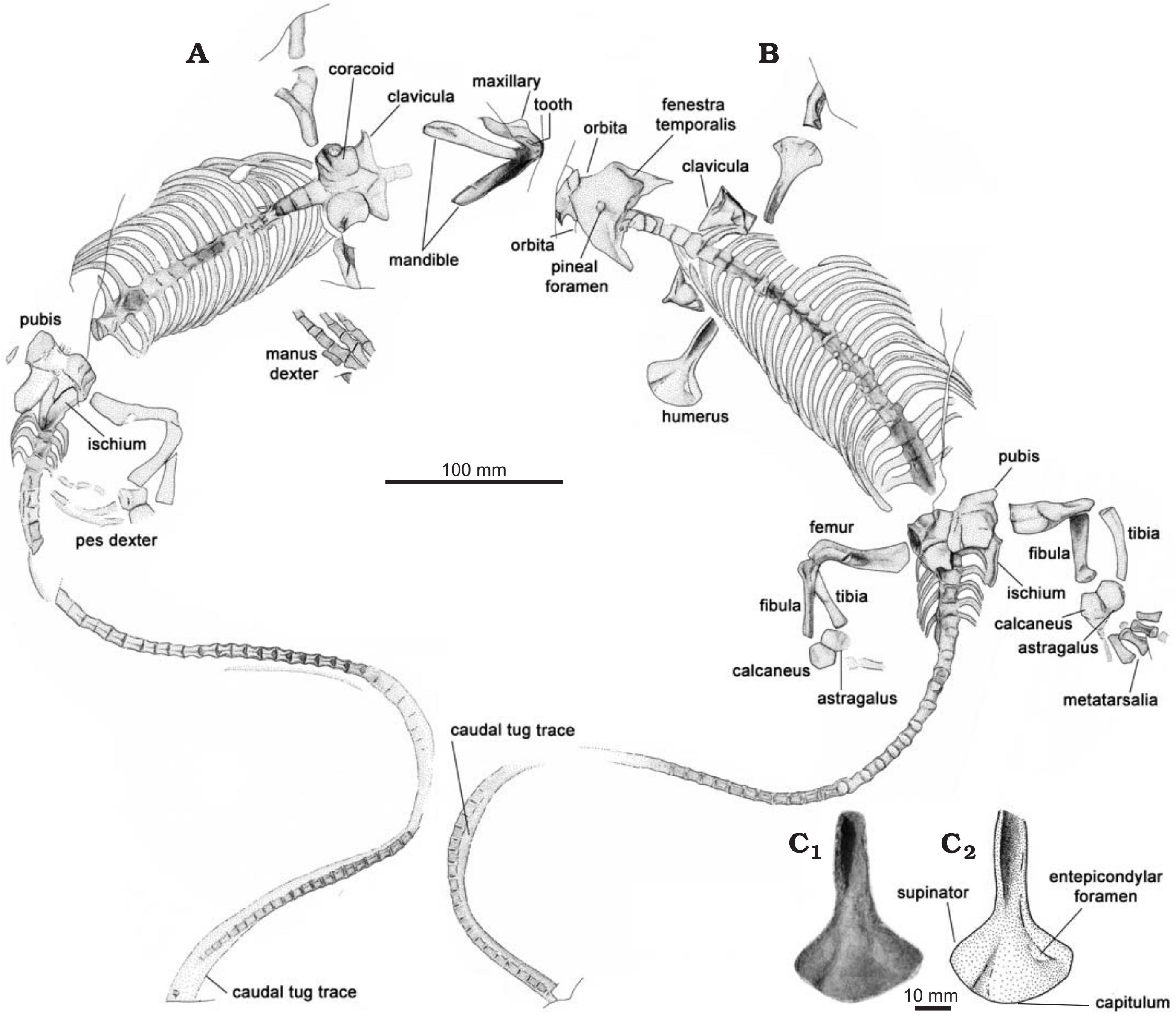

Fig. 4. Explanatory drawing of the holotype of caseasaurian synapsid *Datheosaurus macrourus* Schroeder, 1904 from Upper Pennsylvanian of Nowa Ruda, Poland. MB.R. 1015.1 (**A**) and MB.R. 1015.2 (**B**). **C**. Right humerus of MB.R. 1015.2 in ventral aspect, photograph (C_1), drawing (C_2).

Holotype: MB.R. 1015.1–2, an almost complete and fully articulated, but poorly preserved skeleton, split in half and preserved on two blocks, slab and counter slab. MB.R. 1015.1, laying slab, displays ventral elements in internal view (Schroeder 1904: pl. 12), shown in Figs. 3A and 4A. MB.R. 1015.2, hanging slab, displays dorsal elements in internal view (Schroeder 1904: pl. 13), shown in Figs. 3B and 4B. The fossil was originally housed in the Königlich-Preußische Geologische Landesanstalt (Schroeder 1904). It was later considered as having been lost during WWII (Currie 1979) and documented only by a plaster cast of the specimen in Nowa Ruda (Haubold 1982), but the original was re-discovered and catalogued at the Museum für Naturkunde Berlin by Johannes Müller in 2008.

Type locality: A quarry 1.5 km east to the town of Nowa Ruda, Lower Silesian Voivodship, Poland (Dathe 1900). This city was known as Neurode, when the region of Silesia was held by the German Empire until WWII. The fossil was brought to Berlin before or in 1900.

Type horizon: According to Schroeder (1904), the specimen was excavated from the lowermost unit of the Untere Kuseler Schichten (correlation to the Lower Kusel beds from the Saar-Nahe Basin in Germany), Lower Rotliegend (Lower Autunian) from Neurode (today Nowa Ruda), Intra-Sudetic Basin, Poland. The specimen is labeled as of higher Lower Rotliegend. Huene (1956) dated it back to the lowermost Permian. According to modern stratigraphy it corresponds to the Pennsylvanian Ludwikowice Formation (Niedźwiedzki and Bojanowski 2012: fig. 1). The age can be stated as Stephanian C, corresponding to Gzhelian (Nowak 1998; Awdankiewicz et al. 2003; Werneburg and Schneider 2006; Schneider and Werneburg 2012; Schneider et al. 2014). The holotype and only specimen of *Datheosaurus* is preserved in reddish brown sandstone, interbedded with rhyolitic conglomerate. It originates from the so-called Upper Sandstone bank (Schroeder 1904), a unit of ca. 0.5 m thickness, with high clay content. The holotypic block consists of fine to middle-coarse sandstone with siltic layers and claystone pebbles. The hanging slab MB.R. 1015.2 shows channel fill structures, several decimeters wide (Fig. 3B). The lower slab MB.R. 1015.1 is horizontally layered.

Material.—Holotype only.

Diagnosis.—A small, long-tailed caseasaur with indication of a closed ectepicondylar groove and unreduced phalangeal formula. The cranium and manus are proportionally less pronounced than in *Callibrachion* (see reconstruction; Fig. 5).

Description.—The total length of the specimen from the snout to the last preserved vertebra is approximately 0.9 m. The actual bone substance of the specimen is barely preserved, probably due to early diagenetic alteration of the bone tissue. Hence, little can be said about the actual anatomy of the specimen. In addition, some of the original outlines of the bones are obscured by white paint and scratching, younger than 1904, but even Schroeder (1904) identified some elements as bone only based on their greenish-gray appearance.

The ontogenetic stage of MB.R. 1015 is difficult to estimate. Romer and Price (1940) considered it to be a half-grown individual, based on unfinished long bone epiphyses, a separate anterior coracoid (procoracoid), and a presumably unossified posterior coracoid. However, the present re-study of the specimen indicates a much older ontogenetic stage, based on the differentiated coracoid, the complete closure of the thyroid fenestra in the pelvis, the blunt posterior tip of the ischium, and the polygonal shape of the articulating proximal tarsals. In fact, the long bone ossification is not in a young juvenile stage, but rather that of a still growing subadult according to the growth stages established by Brinkman (1988; confirmed by Shelton et al. 2013).

Cranial skeleton: The skull of *Datheosaurus* measures 56 mm in width. In dorsal view it is short and sub-triangular. In general, the skull of *Datheosaurus* resembles that of *Eothyris* in all observable details, including the overall proportions and the size and position of the pineal foramen. Schroeder (1904) reported potential palatal elements on the hanging slab, but it seems instead that this slab only reveals the broad exposure of the skull roof in ventral view. As a result of the poor preservation, no sutures can be identified with certainty. The snout and left antorbital region are preserved on the lower slab.

Due to the complete preservation in full articulation the jaws are in a natural anatomical position. The upper jaw projects beyond the anterior margin of the lower jaw, forming a distinct overbite and possibly resulting in protruding nostrils. Although close to the block margin, the anterior outline of the premaxilla is completely preserved. The only definite statement that can be made about the premaxillary morphology is that it was short and probably tall below the naris. The exact location of the suture between the premaxilla-maxilla is uncertain.

In the laying slab (Fig. 4A), the skull remains are preserved in a depression of the matrix rock. Therefore, the left maxillary is lingually exposed. It is the only skull bone that seems to preserve its actual and complete outline. Although as badly preserved as the remainder of the specimen, it provides key information for the identification of MB.R. 1015. The body of the maxilla has a low, rounded dorsal process on its anterior half, as in *Eothyris* (Reisz et al. 2009: fig. 2). This process may indicate the position of a caniniform region in *Datheosaurus*, as already suggested by Romer and Price (1940), even if their opinion was possibly influenced by their interpretation of this taxon as sphenacodontian. However, given that such a dorsal process is present in all adequately known caseids (e.g., Olson 1968; Sigogneau-Russell and Russell 1974; Reisz 2005), it cannot be considered as evidence for the presence of caniniforms. The maxilla of *Datheosaurus* seems to have been taller than that of *Eothyris* and especially than that of *Oedaleops* (Reisz et al. 2009), but lower and more rounded than that of caseids (Olson 1968; Sigogneau-Russell and Russell 1974; Reisz 2005). The presence of a broad, rounded embayment between the dorsal and anterior maxillary processes show also that *Datheosaurus* had probably large, rounded external nares. Posteriorly, the maxilla forms a stout ramus with a slightly concave dorsal margin which most likely marks the ventral rim of the orbit, resembling more *Eothyris* than *Oedaleops* (Reisz et al. 2009). The maxilla contributes widely to the orbital margin in *Eothyris* but not in *Oedaleops* and in caseids in which it is excluded from it by a short lacrimal-jugal contact (Sigogneau-Russell and Russell 1974; Laurin and Reisz 1995: fig. 6C; Reisz 2005; Maddin et al. 2008; Reisz et al. 2009). For *Datheosaurus*, this is supported when both slabs are graphically superimposed over each other to compare the preserved portions of the skull. When superimposed, the supposed position of the orbit relative to the maxilla matches that on the counter slab. The skull table is a broad, flat surface that is widely emarginated by the orbits. Overhung by a lateral expansion of the prefrontals and postfrontals, the orbits were therefore facing dorsolaterally at mid-length of the skull of *Datheosaurus*.

Most conspicuous in the skull table, the parietals are wide and enclose a large pineal foramen, as already recognized by Schroeder (1904). It is located along the middle to anterior part of the interparietal suture, at least a certain distance from their posterior edge. This condition matches the pattern seen in all members of Caseasauria, in contrast to the smaller pineal foramen of Edaphosauridae (Modesto 1995) and a more posterior position seen in basal Sphenacodontia (Laurin 1993). The posterior edge of the parietals is well visible, outlining the dorsal margin of the occiput.

The posterolateral margin of the skull table, which was probably made up by part of the squamosal, supratemporal and parietal wings, projects far posteriorly. Even considering diagenetic deformations, the jaw joint seems to have been set far behind the posterior margin of the skull roof, around 20% of the total skull length. On the hanging slab, the anatomically left cheek exhibits a longitudinal step that tentatively marks the position of the temporal opening (Fig. 4B).

The lower jaws are preserved in articulation on the lower slab and only slightly flattened due to compaction. Regarding the straightness of each jaw ramus, the mandible is acutely triangular with a pointed tip, as typical for caseasaurs. The symphyseal region appears to be higher than in *Eothyris*. Both hemi-mandibles are exposing their lingual

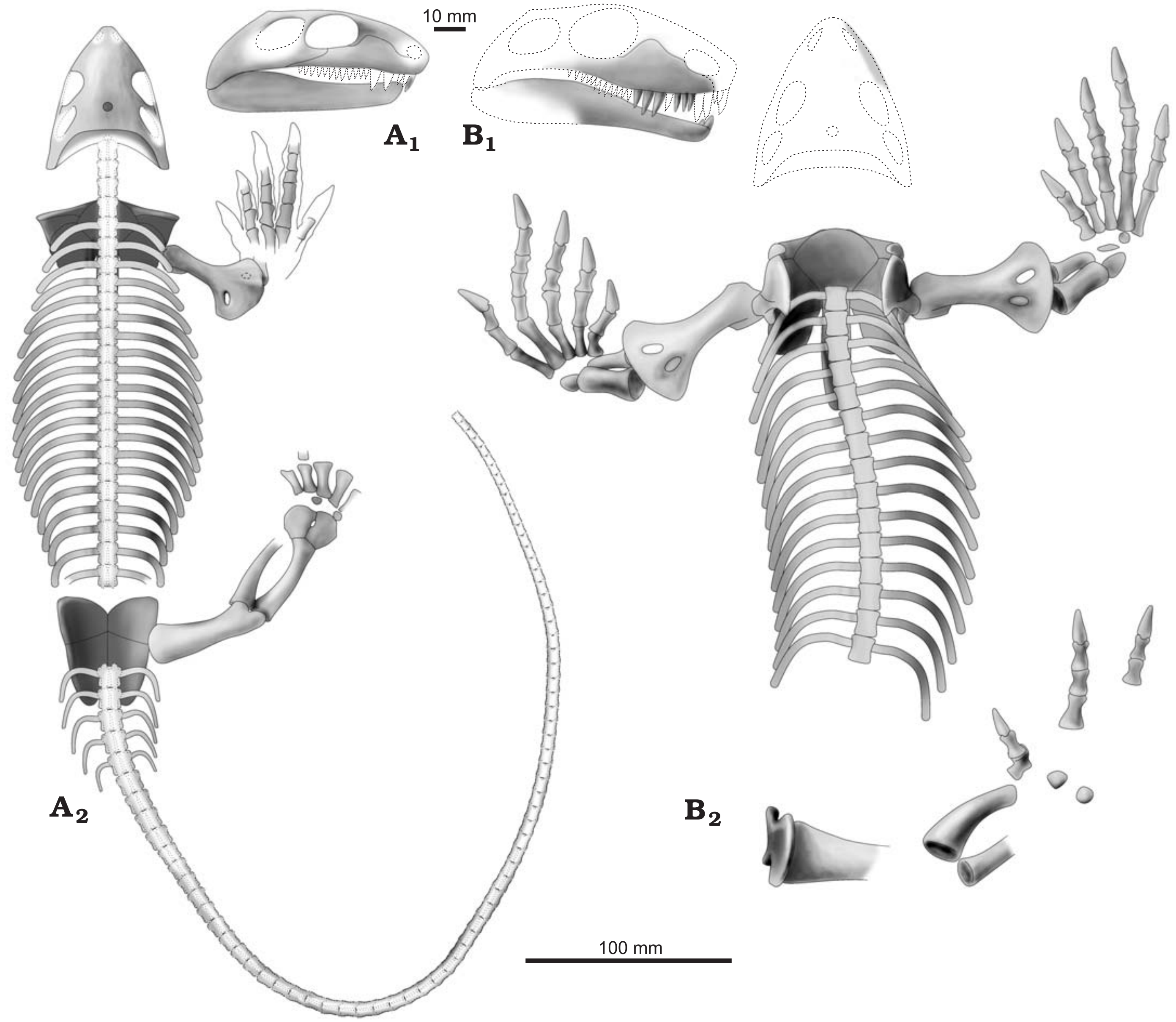

Fig. 5. Reconstructions of caseasaurian synapsid skeletons in dorsal views (A_2, B_2) and lateral aspects of skulls (A_1, B_1). **A**. *Datheosaurus macrourus* Schroeder, 1904 (Upper Pennsylvanian, Poland). **B**. *Callibrachion gaudryi* Boule and Glangeaud, 1893 (Cisuralian, France).

sides. The left jaw ramus is mostly complete and measures 60 mm in length. It shows a slight dorsal eminence in the posterior third. There is no convincing indication of the adductoral fossa or sutural contacts.

A singular element, distinguished by its smooth surface, might represent the only preserved tooth of MB.R. 1015. It is located left to the mandibular symphysis, possibly arising from the upper jaw. If correctly identified, it reveals a slender, rod-like morphology, but lacks information about the tip of the tooth.

Axial skeleton: The holotype of *Datheosaurus* displays an almost complete and fully articulated vertebral column, but its preservation is extremely poor. Only few anatomical details of the vertebrae themselves can be observed. The widths of the vertebrae appear to be subequal to their lengths from the cervical to the proximal caudal region. The cervical and posterior dorsal vertebrae are slightly longer than the mid-dorsals, whereas a certain count of a cervical or possible 'lumbar' region is hampered by indistinct preservation. The exceptionally complete articulation of the specimen provides a presacral vertebral count of 26 including an unpreserved atlas, which has been reconstructed to represent the plesiomorphic condition for synapsids and all amniotes (Müller et al. 2010). Except for *Cotylorhynchus* with a presacral count of 26, caseids have a reduced number of presacrals (24–25) (Olson 1968). Among caseasaurs, only the recently described *Eocasea martini* with a count of 27 has a higher number of presacrals (Reisz and Fröbisch 2014).

The size of the pelvic girdle suggests a number of two or three sacral vertebrae, but a certain assessment is not possible as the iliac blade is not preserved. Based on the position of the first caudal rib, the sacrum most likely consisted of two segments only, which is consistent with other basal synapsids, including *Eocasea* (Reisz and Fröbisch 2014), but contrasts a higher number of three to four sacrals in more derived caseids.

The caudal vertebrae are more slender than the presacrals and continuously decrease in size posteriorly. It is likely that most of the tail is preserved, with a number of at least 75 caudals. In parts of the series, a segmented midline structure can be seen (Fig. 4A), which resembles the notochordal canal, whereas a section of the neural canal would scarcely produce a trail this constant in thinness. The posteriormost portion of the tail shows preservation of actual vertebrae, contradicting Schroeder (1904) who assumed this part to only represent a tug-trace. Nonetheless, the surrounding area of the tail does indeed have a modified texture compared to the matrix rock, thus potentially supporting an interpretation of this structure as traces from the last movements of the suddenly buried and possibly suffocating animal. The reconstructed biotratonomy implies that the animal might bave been surprised by a mass flow event, embedded while resting or walking. Its exaggerated walking posture suggests that it tried to excape until sudden death. The specimen in question may represent one of the rare cases where an ichnofossil is preserved with its producer.

The presacral ribs of *Datheosaurus* are rather broad and interestingly show a constant thickness. The majority bends along their complete length, whereas more posteriorly the ribs display a bending zone just proximal to their mid-length. The posterior cervical ribs and anterior dorsal ribs are the shortest, while from around the 10th to the 21st presacral rib they are of approximately the same length. Towards the posterior dorsal series, the ribs are incomplete, but retain a broad shape, as typical for Caseidae and especially contrasting the slender posterior dorsal ribs in sphenacodontians. Since *Eocasea* recently revealed slender ribs (Reisz and Fröbisch 2014), *Datheosaurus* is either more derived or independently developed broad ribs.

Five proximal caudal rib pairs are preserved. They strongly decrease in size posteriorly, but share the same strong, hook-like shape. However, the two body sides are slightly asymmetrical, which can be explained by tectonic shear in the clayish embedding and largely altered bone tissue, distorting the sacral region.

Pectoral girdle: The holotype of *Datheosaurus* only exposes the ventral elements of the pectoral girdle, all articulated, indicating that the vertical elements such as the scapula have not been affected by compaction. The outlines of the ventral plate of the clavicles, the anterior half of the interclavicle, and the anterior coracoids are visible on MB.R. 1015.1. This is not the case for the posterior extension of the interclavicle, which is still covered by vertebral remains in the laying slab (contra Williston 1912, who interpreted the matrix gap as the space for the interclavicular shaft). The clavicles have a rather broad, triangular ventral plate, which is only half the size of the anterior coracoid. From what can be seen, the interclavicle has a rhomboidal head. It shows otherwise no apparent features. The anterior coracoids are subcircular in outline. A shallow dorsal concavity marks the sutural contact for the scapula, meaning that the anterior coracoids were nevertheless largely ossified. On both sides the location of the glenoid is indicated by a diagonal bar, the coracoid ridge, pointing towards the proximal head of the humerus. A posterior coracoid is not exposed (contra Huene 1910, who suggested both coracoids were co-ossified). The position of the anterior-most ribs suggests that the actual posterior coracoids may still be located below the first dorsal vertebrae and ribs, as is the posterior portion of the interclavicle. As a whole, the pectoral girdle is massively built, even though not co-ossified. It does not provide any diagnostic features beyond representing a typical ‘pelycosaur’ condition. The strengthened anterior rim supported by the clavicles resembles that of large skeletons, e.g., in derived caseids (FS personal observation).

Forelimb: Both humeri are exposed, but their proximal ends are poorly preserved and a distinct deltopectoral crest is not visible. On the hanging slab, the right humerus appears as a robust bone with a straight shaft (Fig. 4C). It has a minimal length of 54 mm and a distal width of 35 mm. Exposing the actual ventral surface, the anatomically right humerus of the hanging slab is the better preserved of the two and serves therefore as a basis for the following description. The entepicondylar foramen is located rather proximally and close to the posterior margin. A shallow trough in the anterior portion is definitely anatomical, separating a very large supinator process from the shallow swelling that represents the capitulum. Thus the radius articulated close to the middle of the distal head of the humerus. The trough most certainly represents the closed ectepicondylar groove, producing a unified semicircular contour in the distal humerus.

Currie (1977: 938) interpreted the humerus of *Datheosaurus* as representing a younger ontogenetic stage than that of the holotype of “*Haptodus*” *garnettensis* (RM 14,156; see Spindler 2015). Later, Currie (1979: 160; based on Schroeder 1904) mentioned the same features of the humerus stated here. He interpreted the humerus of *Datheosaurus* as indicating a juvenile, at the beginning of the ossification of the supinator and epicondyles, but ontogenetically older than in the juvenile series of *Palaeohatteria longicaudata* (*Haptodus baylei* sensu Currie 1979). However, in contrast to the condition in *Datheosaurus*, the entepicondylar foramen is placed more distally in juvenile individuals of *Palaeohatteria*, whereas the supinator process is already separated from the capitulum by a step, even in some very small individuals (e.g., SNSD SaP 342, former “D 2223” in Currie 1979, see Spindler 2015: fig. 5.17). Therefore, the absence of a stepped supinator process in *Datheosaurus* does not indicate an early ontogenetic stage under a supposed sphenacodontian classification. The holotype of *Datheosaurus* is here considered subadult with respect to its ossification, with the closed ectepicondylar foramen representing a phylogenetic signal comparing to adult caseids, rather than representing an early juvenile stage. The outline of the foramen itself is blurred by the poor preservation, as it is also the case for the entepicondylar foramen.

In the forelimb only one partial zeugopodial element is preserved, which most likely represents a radius, judging from its overall shape and the concave proximal articulation surface for the humerus.

In the laying slab, a partial right manus is preserved in ventral view. Given the size of the skeleton, it documents a heavily built forefoot. Only the distal ends of metacarpals II to V are exposed and nothing can be said about their relative lengths. The respective digits show the phalangeal formula? -3-3+-5-1+, with digits II and IV including their terminal phalanges. This indicates the likely presence of an unreduced, plesiomorphic phalangeal formula of 2-3-4-5-3. All non-terminal phalanges are moderately expanded, with only the middle phalanx of digit IV being significantly shortened.

Pelvic girdle: Of the pelvic girdle of *Datheosaurus*, only the ventral plates are clearly identifiable. A long fragment located on the left lateral side of the caudal ribs in the hanging slab corresponds to the left ischium on the lower slab, and thus does not represent an ilium (Fig. 4). The ventral elements are largely ossified, with a fully developed shape, including a complete symphyseal rim. Hence, the only immature features are the lack of a co-ossified pelvic symphysis and a visible puboischiadic suture. The pubis is shorter than the ischium, with a strong anterior ridge running toward the acetabulum. Likewise, the ischium has a thickened dorsal edge posterior to its acetabular contribution. The ventral plates of the ischia are sutured to each other along their anterior half but are separate and rounded in their posterior ends. No diagnostic features are observable in the pelvis. The length ratio of pubis and ischium, with the pubis being shorter than the ischium, seems to be plesiomorphic in synapsids (Romer and Price 1940: figs. 25–28) and contrasts the inverse condition in some caseids (Olson 1968: fig. 19).

Hind limb: The two hind limbs are in a flexed position, with the femora perpendicular to the pelvic girdle and the zeugopodia and pedes directed posteriorly. Both femora are present but poorly preserved, with a minimum length of 59 mm. The right femur exhibits a distinct sigmoid curvature, with the proximal head weakly bent dorsally and the distal head strongly bent ventrally. There is also a distinct strong fourth trochanter, at about one-third of the femur, which continues apparently in a high adductor ridge. Although this might be purported by the plane of splitting between the two blocks, there is some resemblance with caseid femora (Olson 1968: fig. 20). The femoral curvature was erroneously interpreted as typically sphenacodontid by Currie (1979). In fact, this feature is not consistently present within Sphenacodontidae (see Romer and Price 1940: figs. 36, 37).

All posterior zeugopodials are preserved, with both tibiae measuring 41 mm in length. They are only slightly bent and have well-developed terminal articulations. The fibulae are slightly more slender and more strongly bent. The left fibula from the hanging slab reveals a finished ossification of the distal articulation facets, indicating a mature state of ossification in this area.

On the lower slab, only traces of the right pes are preserved, as a barely visible altered bone fan, including the astragalus, calcaneum and possibly three digits pointing towards the base of the tail. The left pes is better and slightly more completely preserved on the hanging slab and includes the proximal tarsals that are large and approximately of equal size. Their polygonal shape and straight midline contact indicate full ossification. The foramen for the perforating artery is placed directly distal to the center of the articulation between the two elements. The low neck of the astragalus in *Datheosaurus* is a pattern seen also in most varanopids and caseids. Additional tarsals cannot be identified with certainty, but a single distal tarsal is preserved at the base of the third metatarsal in the same pes. This foot also displays the complete metatarsus, of which the fifth metatarsus is only faintly preserved. The metatarsals differ only slightly in length.

Stratigraphic and geographic range.—Known only from type locality and horizon; Upper Pennsylvanian of Nowa Ruda, Poland.

Discussion

Classification of *Callibrachion* and *Datheosaurus* as Caseasauria.—As a result of the incompleteness and generally poor preservation of the holotypic and only specimens of *Callibrachion* and *Datheosaurus*, no definite autapomorphic characters can be identified. Instead, it is rather a combination of characters that supports or excludes their identification, which ultimately only leaves a basal position within Caseasauria as possible identification.

For both *Callibrachion* and *Datheosaurus* the overall skeletal proportions along with the skull shape and dimensions restrict their classification to Caseasauria or Edaphosauridae, when compared to all better-known pelycosaur-grade synapsids. A rather shallow, short, triangular skull is seen in all caseasaurs and advanced edaphosaurids, which possibly correlates with their specialized diet or feeding behavior, but not necessarily a strict herbivorous lifestyle (compare *Oedaleops*; Sumida et al. 2014). The dentition of *Callibrachion* and *Datheosaurus* re-described herein is of an apomorphic, "eothyridid" type, comprising remarkably slender, conical teeth of less recurvature, with higher size variation than in ophiacodontids and a reduced precanine region. This combination is quiet unique among basal synapsids, matching the tooth types seen in *Eothyris* and *Oedaleops* (Reisz et al. 2009) as well as the Bromacker caseid (mentioned in Reisz and Fröbisch 2014). Such a dentition appears to be most suitable for a predominantly faunivorous diet. The first skull reconstruction presented here (Fig. 5) is based on the maxilla only, with a tentatively identified lower jaw ramus that fits the proportions of basal, non-caseid caseasaurs (Fig. 6).

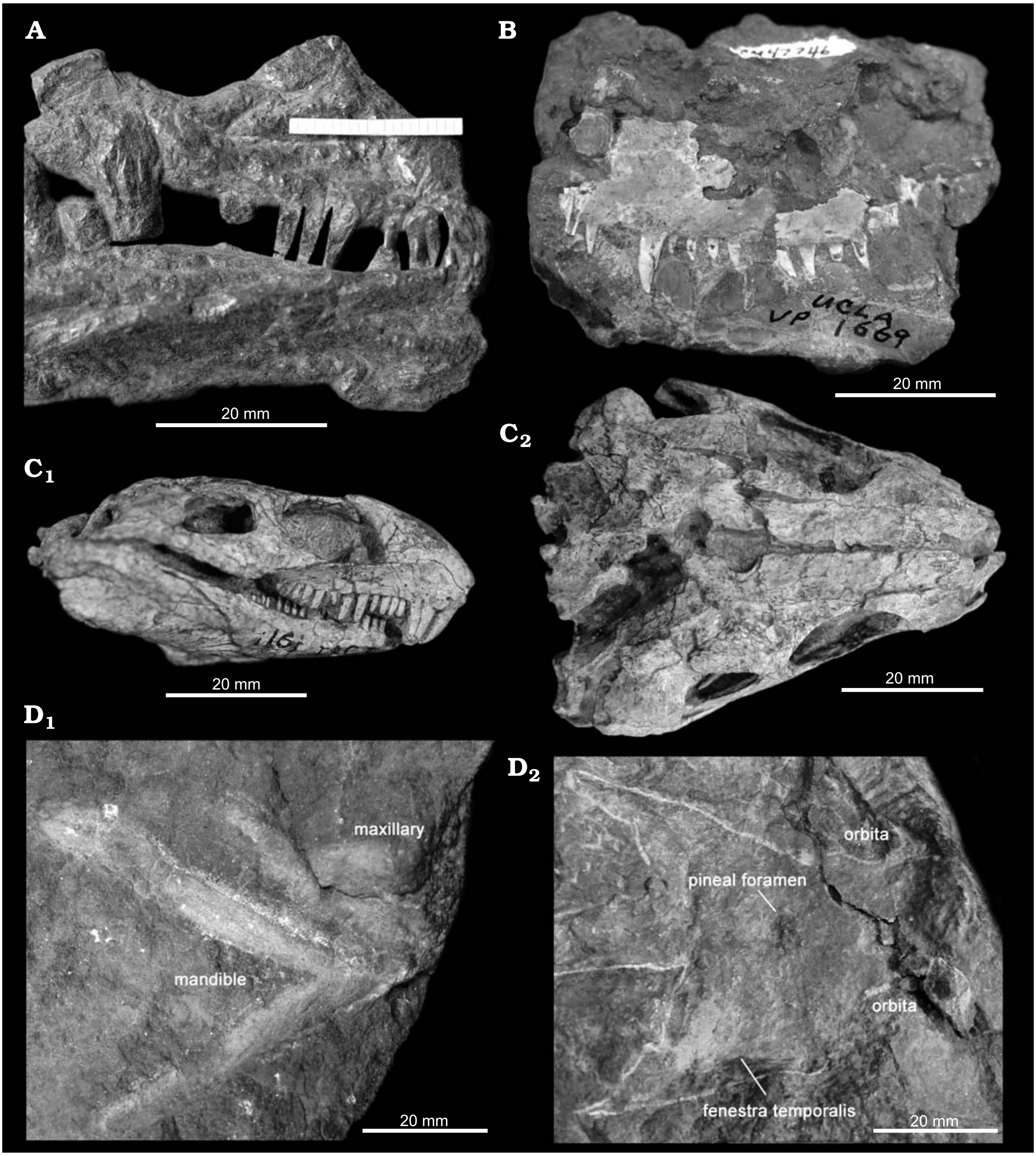

Fig. 6. Skull remains of (putative) basal Caseasauria. **A**. *Callibrachion gaudryi* Boule and Glangeaud, 1893, holotype MNHN.F.AUT490 from Margenne (France), Artinskian (Cisuralian). **B**. ?Eothyrididae indet., CM 47746 from Lisbon Valley (Arizona, USA), Cutler Group (Cisuralian). **C**. *Eothyris parkeyi* Romer, 1937, holotype MCZ 1161 from Archer County (Texas, USA), Kungurian (Cisuralian), in lateral (C_1) and dorsal (C_2) views. **D**. *Datheosaurus macrourus* Schroeder, 1904, holotype MB.R. 1015 from Nowa Ruda (Poland), Gzhelian (Pennsylvanian), in ventral (D_1) and dorsal (D_2) views.

The available cranial data for *Callibrachion* and *Datheosaurus* fit the basal caseasaurian pattern. Especially the shape of the maxillae of both genera and the size and position of the pineal foramen in *Datheosaurus* strongly support this classification and exclude all others. Moreover, the mandibular morphology of both taxa excludes them from an identification as derived members of both Edaphosauridae and Caseidae. The jaw hinge is positioned at a lower level than the coronoid eminence, as also seen in *Ianthasaurus* (Reisz and Berman 1986), indicating that this pattern is not restricted to taxa with a strictly herbivorous diet.

The postcranial features further support a classification within Caseasauria. The thick posterior dorsal ribs are remarkable in *Callibrachion* and *Datheosaurus* and argue against their previous assignment to Sphenacodontia.

The complete skeleton of the holotype of *Datheosaurus* reveals the first insights into the general body proportions of a basal, non-caseid caseasaur. Its long tail with a number of at least 75 caudals resembles that of the well-known varanopid *Aerosaurus*, which had at least 80 caudals (Pelletier 2014). This indicates that this condition is possibly a plesiomorphic feature of basal synapsids or at least more common than in more derived pelycosaur-grade and therapsid taxa (e.g., Fröbisch and Reisz 2011: table 1). For Caseasauria, a complete caudal count was previously unknown. Stovall et al. (1966) and Olson (1968) estimated 55 caudals for *Cotylorhynchus romeri* and 60 for *Angelosaurus romeri*. According to Romer and Price (1940), *Dimetrodon milleri* had 64 caudals. Complete tails are not known in other pelycosaur-grade synapsids; partial counts are: *Casea* (~50), *Varanops* (> 47), *Varanosaurus acutirostris* (> 32), *Ophiacodon retroversus* (> 40) (Romer and Price 1940). The count of 75 in *Datheosaurus* remains therefore very high. It is even higher than in reptilian amniotes: e.g., the mesosaurids *Brazilosaurus* 66 (Sedor and Ferigolo 2001) and *Mesosaurus* 60–65 (Modesto 2010), the bolosaurid *Eudibamus* ~55 (Berman et al. 2000), and the diapsid *Petrolacosaurus* 60–63 (Reisz 1981).

Neural spines of the dorsal series of the axial skeleton, although not exposed, are most likely not elongate, judging from the orientation of both specimens in the rock, which excludes Edaphosauridae as an identification.

The scapula of *Callibrachion* is much shorter than its humerus, with a scapula/humerus length ratio of 0.71. For comparison, the ratio is approximately 0.70 in *Oedaleops* (based on Sumida et al. 2014: fig. 2.5; depicting different individuals that are comparable considering the glenoid size), 0.84 in *Casea broilii* and 0.85 in “*Casea*” *nicholsi* (Olson 1968: table 3a), and approximately 1.0 in “haptodontine”-grade Sphenacodontia (FS personal observation). The distal epiphyses of the humeri in both *Callibrachion* and *Datheosaurus* indicate a subadult ontogenetic stage, respectively, and the humeri of both taxa seem to bear a closed ectepicondylar groove. This is a crucial observation, in that the closed ectepicondylar groove in the re-studied genera matches the condition otherwise only seen in the edaphosaurid *Edaphosaurus*, the varanopid *Heleosaurus* (Botha-Brink and Modesto 2009), and Caseidae (Romer and Price 1940: fig. 32; Olson 1968: fig. 16; Reisz 1986: fig. 24). Nonetheless, the appendicular elements can be distinguished from other caseasaurs (Fig. 7).

The ilium of *Callibrachion* clearly shows the development of a dorsal blade, a feature seen only in Sphenacomorpha (Edaphosauridae + Sphenacodontia) and Caseasauria (for *Oedaleops* compare Langston 1965: fig. 4; contrary to Sumida et al. 2014: fig. 2.5g). Thus, it is not diagnostic for distinguishing between those clades.

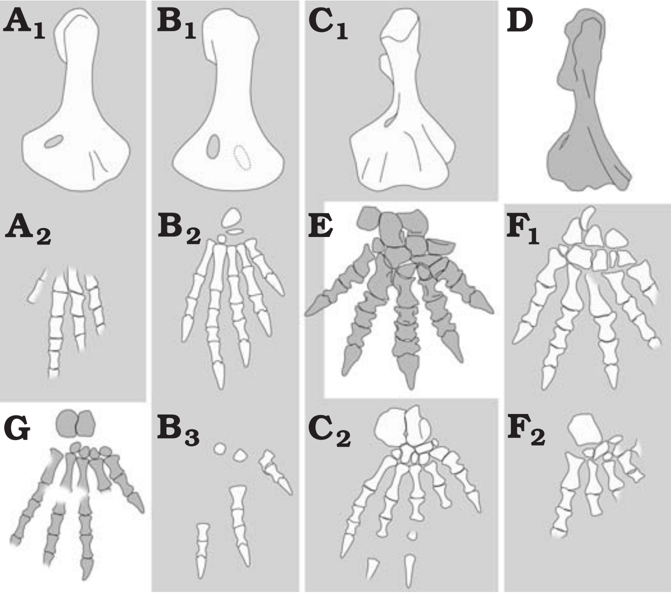

Fig. 7. Drawings of appendicular elements of selected Caseasauria: humeri (A_1–C_1, D), manus (A_2, B_2, E, F_1), and pedes (B_3, C_2, F_2, G). **A**. *Datheosaurus*. **B**. *Callibrachion*. **C**. *Casea*, refers to *C. broilii*. **D**. *Oedaleops*. **E**. *Euromycter*. **F**. “*Casea*” *nicholsi* (from Olson 1968: fig. 18G, H). **G**. *Eocasea*. Compiled from: C, UC 657 (FS personal observation) and UC 656 (after Romer and Price 1940: fig. 41H); D, Sumida et al. (2014); E, Sigogneau-Russell and Russell (1974); F, Olson (1954, 1968); G, Reisz and Fröbisch (2014). Not to scale.

In *Eocasea*, the ilium seems to be the least derived in all caseids with a tall dorsal blade bearing a well-developed posterior but a less pronounced anterior process (Reisz and Fröbisch 2014). This condition matches the fact that *Eocasea* has only two sacral vertebrae, although there is no unambiguous correlation between these two features. Nonetheless, the more pronounced and well-developed ilium in *Callibrachion* could indicate that the increased number of three sacrals seen in more derived caseasaurs than *Eocasea* (LeBlanc and Reisz 2014) was already present in *Callibrachion*.

Both *Callibrachion* and *Datheosaurus* show a plesiomorphic manual phalangeal formula and only slightly broadened phalanges. This combination is also known in varanopids (e.g., *Watongia*; see Reisz and Laurin 2004), *Ophiacodon* (Romer and Price 1940: fig. 40), *Edaphosaurus* (OMNH 74084, MCZ 4320), and *Eocasea* (Reisz and Fröbisch 2014), but not in derived caseids.

Since broad phalanges also appear in the small and basal caseid *Oromycter* (Reisz 2005; Benson 2012), but not in *Casea* (Fig. 7), this feature is likely related to function rather than body size. While the phalangeal shape may vary more widely due to functional disparity, the phalangeal formula, in the light of well-documented Caseidae, seems to represent a more common and straight evolutionary trend and allows a rough classification of *Datheosaurus* and *Callibrachion* as among the basal-most caseids or within their ("eothyridid") stem-group.

"*Casea*" *nicholsi* (Olson 1954) has a reduced phalangeal formula (2-3-3-4-3) in its manus, with slightly broadened phalanges (Fig. 7). Reisz et al. (2011) noted that this poorly known species is the only and therefore questionable source to reconstruct the manus of *Casea*. Regarding the unbroadened phalanges in *C. broilii* (Romer and Price 1940: fig. 41H) and the fact that fore- and hindfeet usually share similar patterns, we recognize a remarkable difference between these two species. In the pes of *Casea broilii* (Fig. 7), the phalanges are slender, and no reduction of the phalangeal formula can be stated. The autopodium of *Casea broilii*, as described by Williston (1911), is usually accepted as showing no reduction in the phalangeal formula. In fact, it is incompletely known and has been reconstructed before a reduced formula was recognized in caseids (Romer and Price 1940). Therefore, from the material validly assigned to *Casea*, no certain determination of the phalangeal formula can be concluded. It appears that "*Casea*" *nicholsi* represents a more derived genus distinct from *Casea*, which, however, is too fragmentary to be renamed. This is additionally supported by the proportional reconstruction (Fig. 8), showing that a compilation of the material described by Olson (1954) results in a large head, most closely resembling composite mounted skeleton of the Russian genus *Ennatosaurus* (FS personal observation at the Paleontological Institute, Russian Academy of Sciences, Moscow). The polyphyletic nature of *Casea broilii* and "*Casea*" *nicholsi* has recently been demonstrated by the cladistic analysis of Romano and Nicosia (2015), discovered independently from the current study (see Spindler 2015).

A cladistic analysis was not included in the current study, for the following reasons: (i) the early caseasaur *Eocasea* is known only from a juvenile individual, hampering its comparability to related taxa; (ii) *Eothyris* and *Oedaleops* are very incompletely known from elements that lack detailed preservation in *Datheosaurus* and *Callibrachion*; (iii) the well-preserved Bromacker caseid skeletons are still undescribed, but will provide reliable comparisons, for example, due to autopodial similarities to the genera described here. This will hopefully substantially stabilize the phylogenetic reconstruction of early Caseasauria.

Relation of *Datheosaurus* to tracks.—So far only very few remains of pelycosaur-grade synapsids are known from the Intra-Sudetic Basin. The exact type locality of *Datheosaurus* is unknown, but nevertheless this taxon is a possible producer of a track reported by Niedźwiedzki and Bojanowski (2012). These tracks, consisting of imprints of the ventral body side along with footprints, were assigned to a member of the Eupelycosauria, with large caseids being excluded based on their advanced foot type. However, regardless of their phylogenetic position, early caseasaurian tracks are expected to resemble those of eupelycosaurs. Therefore the mentioned tracks are not restricted to a certain basal synapsid subclade, but rather represent a plesiomorphic type. Variations from this pattern of digital proportions appear only in very large taxa (e.g., *Ophiacodon*, Robert Reisz, personal communication 2013) or as a result of functional specializations, such as in Caseidae or the extreme span of digit lengths in Varanopidae.

At this point, we note with respect to the tracks described by Niedźwiedzki and Bojanowski (2012: figs. 2, 4) that the epidermal scutes are questionable. Though matching the expected skin condition, the particular ichnological structures could alternatively represent a lift-off pattern produced by the body when getting up from a muddy substrate.

Questionable basal caseasaur material.—A so far undescribed "eothyridid" maxilla from the Cutler Group of Arizona (CM 47746; see Fig. 6B) bears the same dental features seen in basal caseasaurs, but the teeth are slightly more recurved. Nonetheless, the classification of this specimen remains questionable since its well-developed precanine region conflicts with the eothyridid pattern described by Reisz et al. (2009). CM 47746 also shows some similarity with *Baldwinonus*, which has been considered to represent an eothyridid by Romer and Price (1940). However, their assumption of a close relationship of Eothyrididae and Ophiacodontidae might have influenced their interpretation of the Cutler specimen. Later, after the introduction of the modern concept of Caseasauria (Reisz 1980), *Baldwinonus* was re-evaluated as an ophiacodontid (Brinkman and Eberth 1986; see also Lucas 2013).

A dorsal blade of the ilium, such as in *Callibrachion* and all certain caseids, is also known in *Mycterosaurus* and *Nitosaurus* (Romer and Price 1940: fig. 28), but the phylogenetic positions of these genera have to be re-evaluated. For *Mycterosaurus*, the pelvis originally ascribed to this taxon has later been considered to represent temnospondyl material assigned by mistake (Berman and Reisz 1982). The conspecifity of *Nitosaurus* material is questionable and may partly include postcrania of the contemporary varanopid *Aerosaurus* (Reisz 1986), although the pelvis (Romer and Price 1940: fig. 28) is clearly distinguished from varanopids like *Aerosaurus* (Langston and Reisz 1981: fig. 14D). At least for the cranial remains assigned to *Nitosaurus jacksonorum*, a position close to *Oedaleops* is likely based on similarities in the dentary (Romer and Price 1940: fig. 70; Sumida et al. 2014: fig. 2.2), whereas the anatomy of the maxilla is not decisive.

An isolated humerus from the lower Permian of Thuringia (NHMS-WP 2195) was compared to *Datheosaurus* and identified as ?*Haptodus* sp. by Werneburg (1999). However, this specimen does not have a closed ectepicondylar contour. Its revision (Spindler 2015) does not confirm a certain determination, leaving several possibilities such as a varanopid, early caseasaur, or an undetermined basal sphenacodontian.

Evolutionary history.—The re-identification of *Callibrachion* and *Datheosaurus* as basal caseasaurs expands our knowledge of the clade (Fig. 8). Previous findings of eothyri-

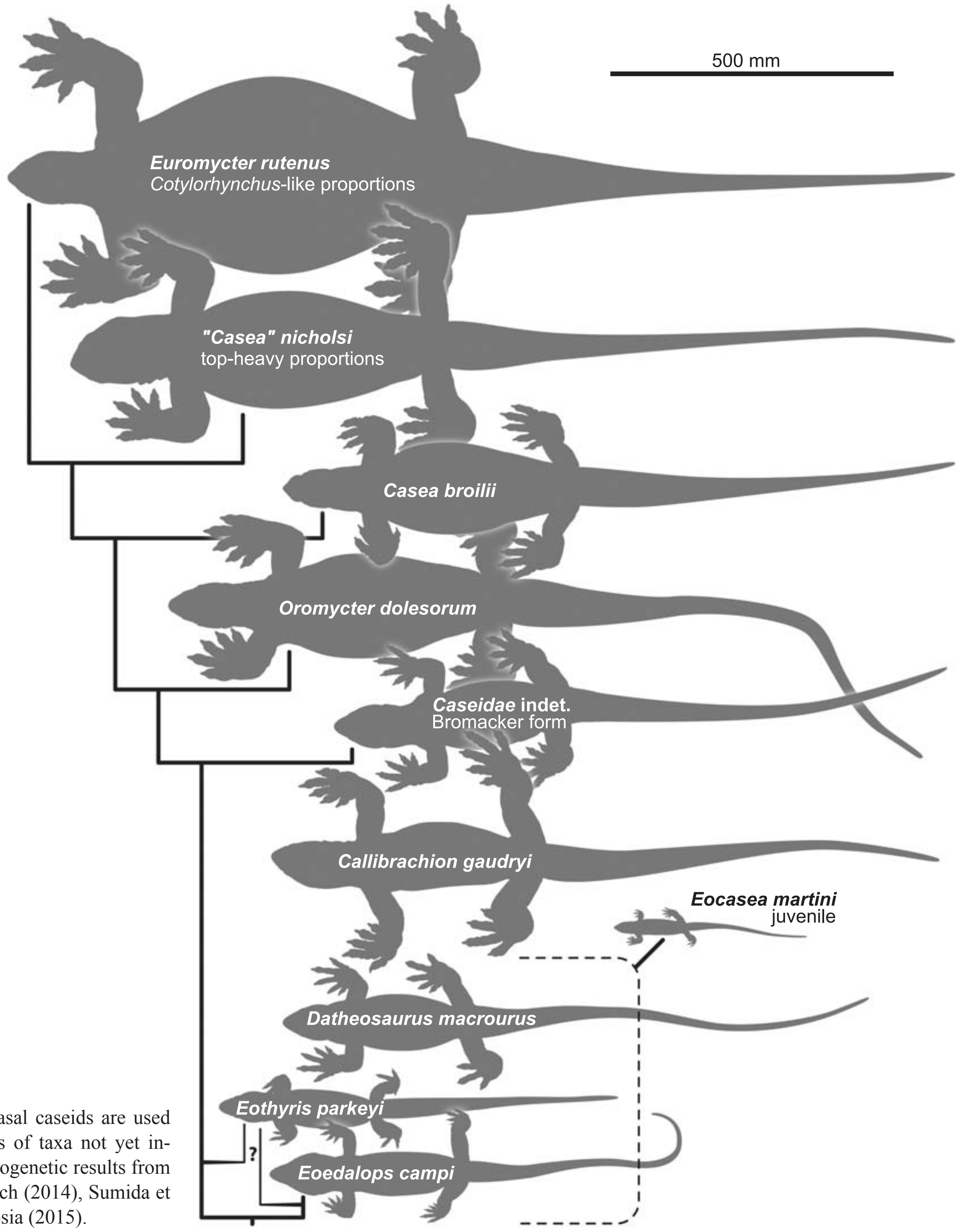

Fig. 8. Evolutionary trends in basal caseids are used to suggest hypothetical positions of taxa not yet included to cladistic analyses. Phylogenetic results from Benson (2012), Reisz and Fröbisch (2014), Sumida et al. (2014), and Romano and Nicosia (2015).

dids date back to the early Permian (Reisz et al. 2009). Reisz and Fröbisch (2014) recently described the oldest known caseid, *Eocasea martini,* from the late Pennsylvanian of Kansas, filling a significant gap in the fossil record of caseasaurs, which were otherwise only known from the Permian. An exhaustive analysis of caseid interrelationships (Romano and Nicosia 2015) found *Eocasea* to plot alternatively as a basal caseid, an eothyridid, or the basal-most caseasaur according to the amended definition applied herein. The description of *Callibrachion* and *Datheosaurus* as early caseasaurs from the Carboniferous and early Permian provides additional evidence for the early diversification of the Caseasauria. This is particularly significant, because caseasaurs also represent one of the long-lived clades of early synapsids. The geologically youngest caseids survived into the middle Permian (e.g., *Ennatosaurus*; Maddin et al. 2008) and possibly late Permian (Silva et al. 2012) in typically therapsid-bearing faunas, only paralleled by Varanopidae (*Mesenosaurus*, *Pyozia*, *Heleosaurus*, and *Elliotsmithia*; see Anderson and Reisz 2004; Botha-Brink and Modesto 2007; Modesto et al. 2011).

Nevertheless, with respect to caseids it is unclear when exactly the specialized herbivores with their spatulate tooth type appeared first in the evolutionary history of caseasaurs. A single tooth reported by Harris et al. (2004) of Virgilian age was recently questioned by Reisz and Fröbisch (2014). Instead, our study supports the previously documented pattern that the large herbivorous caseids from the Permian evolved from small non-herbivorous caseids that appear already in the Pennsylvanian (Reisz and Fröbisch 2014). *Datheosaurus* and *Eocasea* reflect that the basal radiation of caseasaurs not only took place in the Late Pennsylvanian, but also achieved a wide paleobiogeographic distribution.

Callibrachion represents the oldest known Permian caseid, as questionable caseid tracks of Sakmarian age (Hunt et al. 1993) more likely represent undertracks of *Dimetropus* (Sebastian Voigt, personal communication 2015). *Oromycter* and the yet undescribed Bromacker caseid are of Artinskian to Kungurian age (Reisz 2005; Woodhead et al. 2010; Lucas 2006; Lützner et al. 2012). It is thus possible that the European part of equatorial Pangaea was the area where basal caseasaurs flourished before evolving the specialized spatulate tooth type of fully herbivorous Caseidae.

Conclusions

The new classification of *Callibrachion* and *Datheosaurus* as basal caseasaurs is well supported, although the outstanding completeness of the specimens is in great contrast to their poor preservation. As a result of the limited data a phylogenetic analysis was not conducted. However, we are able to confidently identify both taxa as members of Caseasauria, possibly within Eothyrididae or as members of the Caseidae, but more basal than *Oromycter*. This is mainly based on a list of features, including (i) a small, low and broad skull, (ii) a short facial region, (iii) a large pineal foramen (*Datheosaurus*), (iv) maxillae with low, rounded dorsal process and rounded anteroventral embayment, (v) a reduced marginal dentition (*Callibrachion*), (vi) slender, slightly recurved and otherwise simple conical teeth, (vii) broad posterior dorsal ribs, and (viii) a closed entepicondylar groove. The maxillary outline and the putatively plesiomorphic condition of two sacrals allows *Datheosaurus* to be either classified as eothyridid or early caseid. The ilium of *Callibrachion* suggests it is more derived than the questionable oldest caseid *Eocasea*.

Late Paleozoic European basins are often smaller and less exposed than those from North America, potentially biasing the fossil record of early synapsids and contemporaneous terrestrial tetrapods. However, the true diversity in these regions may not have differed much, which is supported by the here presented identification of early caseasaurs in Europe. *Datheosaurus* and *Callibrachion* document a previously unrecognized early diversification of this clade and help to resolve the evolution of the specialized caseid body plan. Specifically, the body proportions began to approach the caseid condition even before the evolution of an herbivorous lifestyle, as evidenced by their advanced dentition. A modified feeding or locomotory pattern led to a body shape no longer resembling the plesiomorphic proportions seen in other early pelycosaur-grade synapsids.

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