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RESEARCH PAPER

Edaphosauridae (Synapsida, Eupelycosauria) from Europe and their relationship to North American representatives

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Abstract

A recent discovery from the Carboniferous–Permian transition of the southwest German Saar–Nahe Basin has revealed a medium-sized edaphosaurid skeleton. It is described as *Remigiomontanus robustus* gen. et sp. nov. Apart from a largely complete dorsal column, showing the typical hyper-elongated spines with lateral tuberculation, few other elements are preserved. Although lacking certain autapomorphies, the unique character combination of this new form strongly suggests an intermediate position between *Ianthasaurus* and *Edaphosaurus*. This study presents a revision of the complete European material of Edaphosauridae, counting the newly named genus *Bohemiclavulus* (type species *Naosaurus mirabilis* Fritsch, 1895), and a confirmation that *Edaphosaurus credneri* is an indeterminate juvenile of this most derived genus. Further fragments include a second young juvenile from the Döhlen Basin, east Germany, the lost spine set of *Ramodondron* from Boskovice Basin, Czech Republic, and a poorly preserved specimen from Autun, France, for which its hitherto parareptilian classification is debated. A renewed dataset is used to carry out a phylogenetic analysis. Exhaustive comparisons allow for a deeper understanding of back sail characters, which on the other hand hamper a phylogenetic resolution for both European and North American taxa. Previously reconstructed faunal provinces of edaphosaurid distribution are not evident from the present knowledge.

Keywords Sphenacomorpha · Herbivory · Back sail · Tuberculation · Paleobiogeography

Introduction

Edaphosauridae form a clade of Pennsylvanian to Cisuralian early synapsid tetrapods that spark interest for at least three reasons: (1) they are phylogenetically close to the origin of therapsids as the stem-group of mammals (Reisz 1986; Benson 2012, Spindler 2015); (2) they developed, independently from the related sphenacodontid eupelycosaurs, a back sail of hyper-elongated dorsal spines (Romer and Price 1940); and (3) they are supposed to be among the earliest herbivorous amniotes (Sues and Reisz 1998; Reisz and Fröbisch 2014). To date, edaphosaurids are perceived as an essentially North American group of early tetrapods. This is surprising as a Late Paleozoic exchange of terrestrial tetrapods between today's North America and Europe has long been known and is approved even at low taxonomic levels (Fröbisch et al. 2011; Berman et al. 2014; Spindler et al. 2016).

Remains of edaphosaurid eupelycosaurs from Europe are rare and fragmentary (Reisz 1986). Most of the material was discovered by chance in the course of subsurface mining of limestones or coal more than a century ago. The sparse record of European edaphosaurids is substantially increased by an almost complete trunk that was found in Pennsylvanian–Permian strata of the SW German Saar–Nahe–Basin in autumn 2013 (Voigt et al. 2014). This specimen comes from near-surface strata of an active

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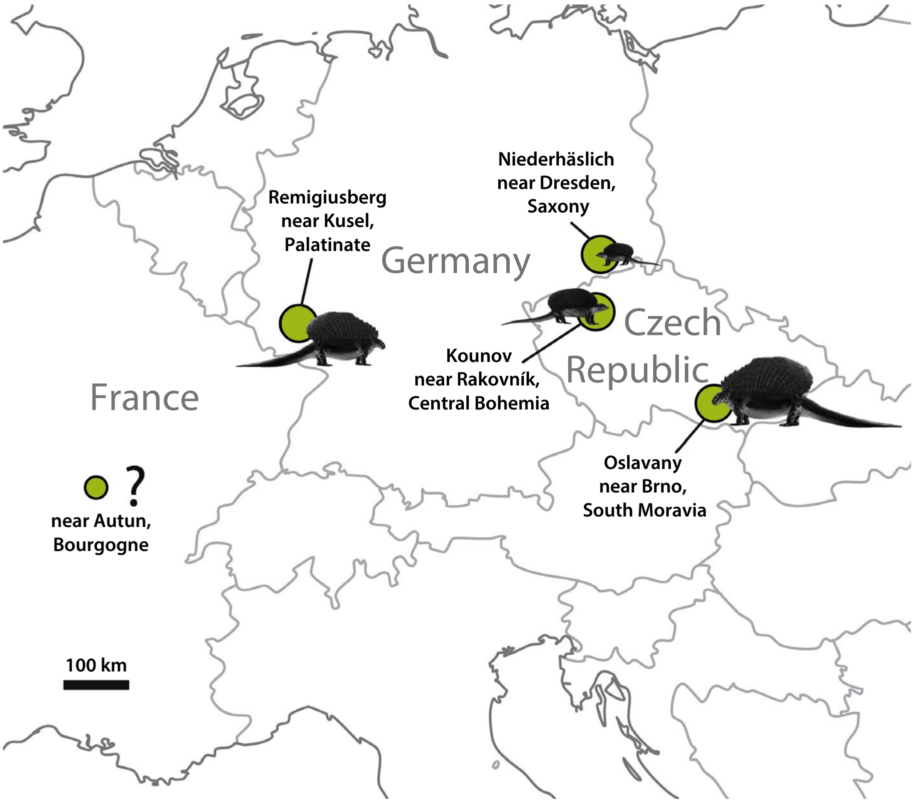


Fig. 1 Map showing localities of European edaphosaurid discoveries

quarry producing crushed subvolcanic rock for road and railroad construction and is by far the most completely preserved edaphosaurid from outside North America.

We have taken the description and phylogenetic analysis of the most recent edaphosaurid find from Germany as a reason to review the entire European record of this specific group of sail-backed eupelycosaurs. Beyond introducing additional bone material, the purpose of this paper is an increased understanding of the evolutionary history and paleobiogeography of Edaphosauridae.

Materials and methods

There are five definite and two ambiguous specimens of edaphosaurids from Europe (Fig. 1) that will be described more or less in order of their discovery and publication. Original fossil work was carried out for three specimens from Germany. In the case of the Czech specimen, we received generous assistance with high resolution photographs and computer tomography scanning (CT) by courtesy of Boris Ekrt from Czech National Museum Prague. Comparison with North American material is mainly based on personal observation of original specimens. For cladistic method see below.

Institutional abbreviations. AMNH—American Museum of Natural History, New York, USA; CM—Carnegie Museum, Pittsburgh, USA; "FO"—University of Toronto Mississauga Fossil (field number); KUVP—University of Kansas Museum of Natural History, Lawrence, USA; LfULG RS/SS—Landesamt für Umwelt, Landwirtschaft und Geologie, Freiberg, Germany (Regionalsammlung/Saurier Sachsen); MCZ—Museum of Comparative Zoology, Harvard University, Cambridge, USA; MNHN.F.AUT—Muséum National d'Histoire Naturelle, Paris, France (Autun Collection); NM—National Museum, Prague, Czech Republic; NMMNH—New Mexico Museum of Natural History, Albuquerque, New Mexico, USA; OMNH—Oklahoma Museum of Natural History, Norman, USA; ROM—Royal Ontario Museum, Toronto, Canada; SNSD SaP—Senckenberg Naturhistorische Sammlungen Dresden, Germany (Collection Sachsen Perm); UGKU—Urweltmuseum GEOSKOP, Burg Lichtenberg (Pfalz), Germany, POLLICHIA Geoscience Collection.

Edaphosaurid record and research history

The first edaphosaurid fossils have been found in the American Southwest, followed by discoveries in Pennsylvania, during the second half of the nineteenth century (Cope 1882; Case 1907, 1908). A few remains became known from Europe, namely the Czech Republic (*Naosaurus mirabilis*

Fritsch, 1895) and Germany (*N. credneri* Jaekel, 1910). From the earliest discoveries, there was some confusion about *Naosaurus* and *Dimetrodon*, as edaphosaurids have been mixed up with sail-bearing sphenacodontids (Osborn 1903; Williston 1912; the latter argued for the identity of *Naosaurus* and *Edaphosaurus*). The comprehensive revision of "pelycosaurs" by Romer and Price (1940) counted the lupeosaurid or edaphosaurid *Lupeosaurus kayi* (postcranium only) as well as seven valid species of *Edaphosaurus*: *E. raymondi*, *mirabilis*, *credneri*, *novomexicanus*, *boanerges*, *cruciger*, and *pogonias*. This revision had solved the "embarrassing taxonomic snarls" (Romer and Price 1940: 388) and assigned *E. microdus* (Case 1907: pl. 29, fig. 2) to *E. cruciger*, and likewise *E. claviger* to *E. pogonias*. These synonymy is maintained in the present study.

Material from European Russia, originally described as *Naosaurus uralensis*, is now assigned to a captorhinid reptile, *Riabininus uralensis* (Romer and Price 1940; Ivakhnenko 2008). Prantl (1943) mentioned edaphosaurids from Asia, which is apparently a mistake, or erroneously refers to the Russian material.

Subsequent studies have described *Ramodendron obvispinosum* (Švestka 1943; disregarded in the international literature), *E. ecordi* (Peabody 1957; validly re-described as *Xyrospondylus ecordi* by Reisz et al. 1982), *E. minuta* (Tasch 1963; identified as xenacanth shark teeth by Simpson 1978), and the currently valid Carboniferous species *E. colohistion* (Berman 1979) of similar size as *E. boanerges*. The standard work by Reisz (1986) debated *E. mirabilis*, *credneri* and *raymondi* as questionable taxa. *Lupeosaurus*, *Xyrospondylus*, and the enigmatic skull of *Glaucosaurus megalops* (formerly assumed to be in vague proximity to edaphosaurids, Romer and Price 1940) were listed as Pelycosauria incertae sedis by Reisz (1980, 1986).

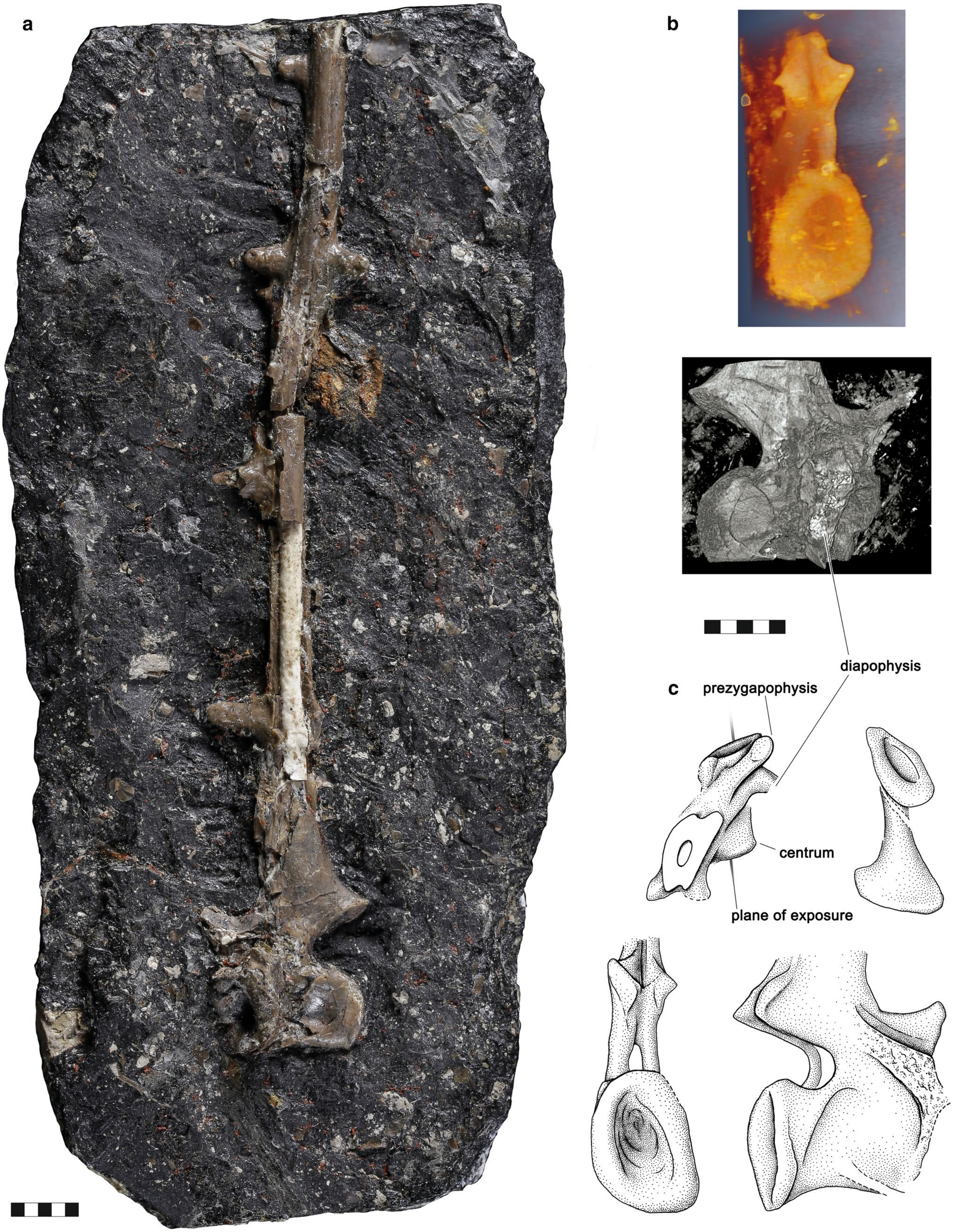
A putative juvenile edaphosaurid has been collected by A.S. Romer and L.W. Price in 1939. It was originally referred to *Glaucosaurus* (MCZ 1746), but later determined as cf. *Bayloria* (handwritten note by Modesto and Reisz 1992), after Reisz and Heaton (1982) had assigned *Bayloria morei* to the eureptilian *Captorhinus aguti*. The supposed cross connection to the invalid *Edaphosaurus minuta* (Reisz 1986: 86) is incomprehensible. Additional confusion with reptilian remains affects a large tooth plate from Texas, which Olson (1956) identified as a new, but indeterminate edaphosaurid genus. Recently, it was recognized to represent a moradisaurine captorhinid (Modesto et al. 2016).

Remains of a small edaphosaurid from the Pennsylvanian Garnett assemblage of Kansas have been distinguished from *Xyrospondylus* and tentatively assigned to *Edaphosaurus* (Reisz et al. 1982). The new taxon *Ianthasaurus hardestii* was introduced for this material by Reisz and Berman (1986; epithet revised as *hardestiorum* by Kissel and Reisz 2004). The validity of *Ianthasaurus hardestiorum* was confirmed by additional findings (Modesto and Reisz 1990a; Mazierski and Reisz 2010). The tentative assignation of the *Ianthasaurus* type material to *Edaphosaurus* was based on the presence of laterally arranged tubercles on the hyper-elongated dorsal spines. This character is recorded in all species of *Edaphosaurus*, but not present in *Lupeosaurus*. Reisz and Berman (1986) demonstrated that tubercles are common throughout the edaphosaurid lineage. This raised doubt on the classification of *Lupeosaurus*, enhanced by the almost contemporaneous separation of Caseidae and "Edaphosauria" that formerly included Caseidae and Edaphosauridae (Reisz 1980, 1986; Brinkman and Eberth 1983).

Sumida (1989a) provided more arguments for the edaphosaurid nature of *Lupeosaurus* and re-assigned this taxon to Edaphosauridae. At the same time, *Edaphosaurus raymondi*, based on a single spine fragment from Pennsylvania, was rejected as a valid taxon (nomen vanum according to Modesto and Reisz 1990b). *E. novomexicanus* was re-evaluated and supposed to represent the oldest herbivorous amniote (Modesto and Reisz 1992). Eberth and Berman (1993) as well as Harris et al. (2004) yielded further evidence for a Virgilian (~ Gzhelian) first occurrence date of the genus *Edaphosaurus*.

A few small edaphosaurid remains from the Pennsylvanian of Colorado were referred to *Edaphosaurus* aff. *raymondi* (Vaughn 1969; Edaphosauridae incertae sedis according to Modesto and Reisz 1990a). This occurrence is probably of similar age as the type locality of *Ianthasaurus* (Kissel and Reisz 2004: fig. 10), which somewhat conflicts with a supposedly derived form such as *E. raymondi*. Vaughn (1969) also compared the remains from Colorado with the smaller central European taxa *Edaphosaurus mirabilis* and *E. credneri*. Finally, Sumida and Berman (1993) recognized the Colorado fossils to belong to *Ianthasaurus* sp., suggesting an assignation that might be reasonable for the type material of *E. raymondi* as well (Spindler 2015). Another supposed edaphosaurid specimen from Colorado is represented by an isolated dorsal spine tip (CM 47699, Sumida and Berman 1993: fig. 6; formerly attributed to what is now *Xyrospondlyus* by Vaughn 1972; rejected as undeterminable by R. Reisz, pers. comm. 2013).

The first cladistic analysis of the inner systematics of Edaphosauridae was carried out by Modesto (1994), who found *Glaucosaurus* to plot between the unquestionable edaphosaurids *Ianthasaurus* and *Edaphosaurus*. By a detailed re-description of the skull of *E. boanerges*, Modesto (1995) resolved several species of *Edaphosaurus*. This analysis was extended by Mazierski and Reisz (2010), who included *Lupeosaurus* for the first time and found it unresolved at one level with *Glaucosaurus* and the monophyly of *Edaphosaurus* spp. The latest progress is the discovery and analysis of *Gordodon* from New Mexico (Lucas et al. 2018).


a
b
c
diapophysis
prezygapophysis
centrum
plane of exposure

◂**Fig. 2** NM 633, holotype of *Bohemiclavulus mirabilis* (Fritsch, 1895). **a** Photograph of specimen, exposing the left lateral aspect of damaged dorsal vertebra; **b** CT scan images, from posterior and right lateral (perspectives not fully orthogonal); **c** reconstruction from several CT images in dorsal view with cut off spine, in ventral, posterior, and right lateral view with eroded diapophysis. a and b by courtesy of B. Ekrt, Prague. Scale bar in mm

The only tetrapod tracks that have been explicitly referred to edaphosaurid trackmakers are from the Middle to Late Permian of Tunisia (Newell et al. 1976). A recent detailed description of the material, however, argues for non-mammalian therapsids as likely track producers (Contessi et al. 2018). Edaphosaurids and sphenacodontids are considered to be potential trackmakers of the ichnotaxon *Dimetropus* (Romer and Price 1940; Haubold 2000; Voigt 2005; Lucas et al. 2016). So far, both groups cannot be distinguished solely based on fossil footprints. *Dimetropus* tracks are well-known from Pennsylvanian to Early Permian deposits of North America and Europe (Voigt and Lucas 2018). More recent discoveries of *Dimetropus* in Pennsylvanian–Permian strata of Morocco extend the potential distribution of early sphenacomorphs to NW Africa (Voigt et al. 2011a, b; Lagnaoui et al. 2018).

Systematic Paleontology

(unranked) **Synapsida** Osborn, 1903
(unranked) **Sphenacomorpha** Ivakhnenko, 2003 sensu Spindler et al. 2015
Family **Edaphosauridae** Cope, 1882

Genus ***Bohemiclavulus*** nov.

Type species. *Naosaurus mirabilis* Fritsch, 1895.

Etymology. New Latin genus designation means “little nail from Bohemia” and refers to the delicate nature of the spine tuberculi.

Diagnosis. Very small edaphosaurid with lateral tuberculation on hyper-elongated spine, dorsal centrum not elongated, ventral side not ridged, prezygapophyses meet in narrow V-shape.

Bohemiclavulus mirabilis (Fritsch, 1895)
Figure 2; Online Resource 1

Material. Holotype—NM 633, isolated dorsal vertebra.

Locality and horizon. Kounov, Kladno-Ravovník Basin, Czech Republic; Kounova coal beds, Slaný Formation, middle Gzhelian, Late Pennsylvanian (Štamberg and Zajíc 2008; Opluštil et al. 2016).

Diagnosis. As for genus.

Description. In the isolated dorsal vertebra, the centrum is at least 0.8 times as high as long. No keel or ridge is present on the ventral side. The neural arches are slightly excavated laterally. Both prezygapophyses form a sharp *V* shaped wedge, contrasting with the shallow *U* shaped trough typical of *Edaphosaurus*. Although being very close to each other, the postzygapophyses do not contact medially, nor do they form a hyposphene.

A CT scan of the delicate specimen (Fig. 2b) revealed that the diapophyses are placed rather anterior, as is typical for all edaphosaurids. Their lateral expansion is unknown due to crushing. At the basis of the dorsal spine, low and confluent shoulders are present. Distal to this portion, the spine is round in cross section. The hollow cavity is surrounded by a delicate cortex. Both the anterior and the posterior side exhibit vertical grooves. Of the delicate lateral tubercles, some pieces are broken off, compared to the historical drawing (Fritsch 1895a: fig. 309, 1895b: fig. 1).

The absence of the neurocentral suture is a true anatomical observation, confirmed by the isolated position of the vertebra without disarticulation. Along with the overall slender proportions this suggests that the bone belonged to an adult individual.

Discussion. NM 633 represents the first find of an edaphosaurid in Europe. The specimen was primarily thought to be a fish remain (Fritsch 1883: 29, no. 52), but has been correctly identified shortly thereafter (Fritsch 1901). Additional information and last original fossil work date back to Fritsch (1895b). The original name *Naosaurus mirabilis* Fritsch, 1895 was changed to *Edaphosaurus mirabilis* by Prantl (1943), and later proposed to be a nomen dubium (Reisz 1986; Reisz and Berman 1986). Full chresonymy is provided by Štamberg and Zajíc (2008: 189).

Modesto and Reisz (1990a, b) suggested assignment to *Ianthasaurus* by inferred individual size and stratigraphic age of the specimen. Various phylogenetic tests (Sect. 5) support a basal edaphosaurid that is close to *Ianthasaurus*, but apparently distinct. The differential diagnosis is based on three characters (39, 40, 56, Online Resource 4): First, elongated dorsal centra are typical of edaphosaurids, except for *Xyrospondylus* and *Edaphosaurus cruciger*. In the latter, the condition might represent a reversal, whereas the same is an expected plesiomorphy of edaphosaurids more basal than *Ianthasaurus*. Furthermore, ventrally ridged centra are found only in Garnett specimens of *Ianthasaurus* and outgroup taxa, but are missing in the well-ossified Badger Creek material. Either, this is caused by an autapomorphic reversal, or due to ontogenetic patterns in *Ianthasaurus*. However, since the holotypic vertebra of *Bohemiclavulus* represents a grown individual, this

Fig. 3 Photograph of *Edaphosaurus credneri*, holotype counter slabs: **a** LfULG RS 14758, where minor losses can be observed in comparison with the plate of Jaekel (1910); circles in the upper left mark the position of drilling samples from 2013 that failed to rediscover long-bone tissue; **b** RS 14759. Bright components represent numerous tiny bone fragments as a unique sedimentological observation in the Niederhäslich limestone, suggesting a reworked and transported bone bed. Scale bar equals 5 cm

character yields distinction from *Ianthasaurus*. At last, the plesiomorphic condition of the prezygapophysis differs from the initial apomorphic state in *Ianthasaurus*. Therefore, the Badger Creek material must remain open in taxic assignment, whereas *Bohemiclavulus* is clearly distinct from *Ianthasaurus*.

Naming of such fragmentary material is questionable. However, the phylogenetic results exhibit clears trends in the testable character conditions, instead of mosaic patterns. There is no grouping with *Ianthasaurus*. Therefore, naming this material is more profound than declaring a holotype invalid.

Edaphosaurus credneri (Jaekel, 1910)
Figures 3, 4

Material. Holotype—LfULG RS 14758 and 14759, part and counterpart of an articulated trunk portion.

Locality and horizon. Freital-Niederhäslich near Dresden, Döhlen Basin, Saxony, Germany; Limestone member of the upper Niederhäslich Formation, Artinskian, Early Permian (Schneider and Gebhardt 1992; Gebhardt and Schneider 1993; Schneider 1993).

Diagnosis. Derived edaphosaurid with reduced rib tuberculi, posterior spine sail exhibiting a reduced tuberculation, with a low number of spike rows restricted to the proximal dorsal spine. This diagnosis is affected by the juvenile stage of the material, and thus expected to lack additional synontomorphies.

Fig. 4 Interpretative drawing of *Edaphosaurus credneri*, holotype counter slabs: **a** LfULG RS 14759; **b** RS 14758. A fault disturbs the area of neural arch bases. Scale bar equals 5 cm

Description. The only known skeleton is preserved within a layer of abundant allochthonous bone fragments, which is untypical of this limestone member. Where the centra are placed, a fault hampers clear observations, such that the neurocentral suture is hidden. The juvenile condition is indicated by overall proportions and less ossified appendicular elements. This contrasts earlier descriptions, which assumed a dwarf edaphosaurid similar to "*E.*" *mirabilis* (Jaekel 1910; Romer and Price 1940).

As in most edaphosaurids, there are longitudinally broadened bases of the spines, herein designated as confluent shoulders. No distal terminus of any dorsal spine is preserved with certainty, except of the posterior positions, in which the possible terminus suggests a relatively low sail (Fig. 4; Online Resource 4: character 43). Since the distal regions of the spines lack lateral tubercles, which is similar to the condition in *Ianthasaurus*, the sail might not have been much taller than indicated by the preserved portion.

In the five anterior-most spines of the preserved set, the lateral spikes of the right side are often placed at a slightly higher position than on the left. This is estimated from a graphical match of the two counter slabs, in which the most proximal spikes are at the same vertical position on both sides. Distinction from "*E.*" *mirabilis* was recognized by Jaekel (1910) and Romer and Price (1940), regarding spike shape and distribution. The second of the preserved spines contains a position in which one tubercle opposes two on the other side. In the sixth and seventh of the preserved spines, no indication of tubercle positions is visible. Whereas the right side of the "lumbar" spines is badly preserved, the left shows that the posterior sail is poor in lateral spikes, somewhat resembling *Ianthasaurus* (Online Resource 3). The second last spine preserved two spikes, or one, if the proximal one is a prezygapophysis.

Both sets of dorsal ribs are arranged in place and articulated to the vertebral column. Their stout shape and large head support the low ontogenetic age of this individual. In all ribs, the tuberculum is clearly reduced in a way not seen in other juvenile basal synapsids (Spindler 2015). Therefore, this structure is confidently interpreted as an age-independent anatomical feature that in its present strength is diagnostic for *Edaphosaurus*.

A large field of gastralia is present in RS 14759, with two smaller patches on RS 14758. No deviation from early synapsid gastral patterns was recognized.

Pelvic and long bone fragments are present, but only as indistinctly preserved impressions in the host rock. The simple and narrow terminal regions confirm the interpretation as of juvenile condition. Histological sampling could not find long bone fragments in the mould of the limestone matrix.

Discussion. Originally named as *Naosaurus credneri* Jaekel, 1910, the species was redefined as belonging to *Edaphosaurus* by Prantl (1943) and Romer and Price (1940) on the basis of a single-genus concept of Edaphosauridae, which has not been questioned until the diagnosis of *Ianthasaurus* (Reisz 1986). The assignment to *Edaphosaurus* is not fully testable, though some derived characters including the rib morphology suggest such a classification. Because spine tubercles grow rapidly in *Edaphosaurus*, which is in contrast to their incremental proliferation in *Ianthasaurus* (Huttenlocker et al. 2011), the sail tuberculation of *E. credneri* could be determined as a juvenile stage of certain species of *Edaphosaurus*. In phylogenetic tests, *E. credneri* groups with derived edaphosaurids. Because of the lack of specific diagnostics, the epithet is declared as a nomen dubium.

Edaphosauridae indet.

[?*Edaphosaurus credneri* (Jaekel, 1910) or ?*E.* aff. *pogonias* Cope, 1882]
Figure 5

Material. SNSD SaP 344, disarticulated cranial and postcranial elements.

Locality and horizon. Same as for the type material of *E. credneri* (see above).

Description. This partial skeleton is interpreted to be an edaphosaurid for the first time. It refers to an individual tinier than any known specimen of *Palaeohatteria longicaudata* and is apparently much smaller (ca. 40% of total length) than the type of *E. credneri* (Online Resource 9). Its differential determination is based on the interclavicular shape, which precludes SaP 344 from *Palaeohatteria*, and the proportionally stout limb elements, distinguishing it from the contemporary basal diapsid *Kadaliosaurus*. Taking into consideration that all long bones and pectoral elements are markedly unfinished, SaP 344 most likely preserves an early juvenile individual.

In the area of the crushed and incompletely recovered skull, only the pair of slightly dislocated parietals deserves clear identification. Each parietal is about as wide as long. The large pineal foramen is located at the mid-length of the interparietal suture. On the anterior margin, coarse striation indicates the frontal overlap. The postfrontal articulation is preserved as a simple round embayment. There is an expanded process reaching towards the postorbital contact, which is somewhat resembling the parietal of *Edaphosaurus pogonias*, in which this process contributes to the brow shield (Case 1907: fig. 66, pl. 34; Romer and Price 1940: pl. 17), but unlike *E. boanerges* (Modesto 1995: fig. 7) and *Gordodon kraineri* (Lucas et al. 2018). In order to avoid bias from ontogenetic allometry, the potential affinity to *E. pogonias* is not indicated in the phylogenetic coding of this study.

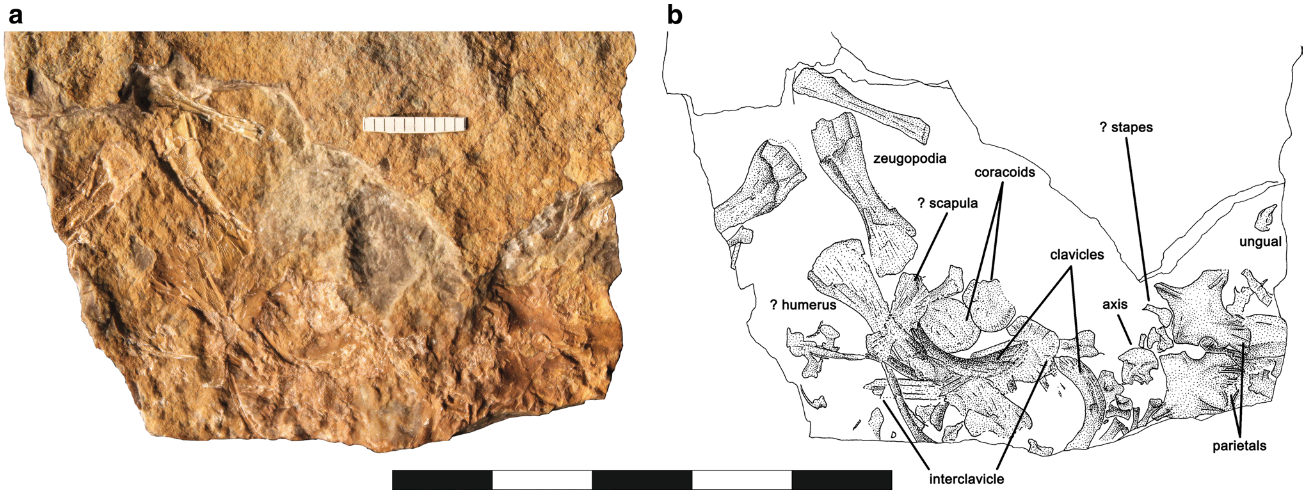


Fig. 5 Partial skeleton of the smallest known edaphosaurid SNSD SaP 344, referable to *Edaphosaurus*, juvenile. **a** Photograph of slab; **b** interpretative drawing using microscopy. Scale bar equals 5 cm

The posterior wing of the parietal is apparently short. Between this the supratemporal contact and the laterally expanded postorbital process, the lateral outline of the parietal is concave. This pattern indicates a synapsid or diapsid condition of the temporal fenestration. The presence of an antero-lateral process in the parietal resembles basal diapsids, e.g. *Petrolacosaurus* (Reisz 1977), whereas the shoulder and limb proportions of SaP 344 clearly support the assignment to early synapsids. Among those, such parietals are found only in Edaphosauridae (Romer and Price 1940: pl. 17). Moreover, although unknown, it is likely that this constriction of the posterior skull roof caused a loss of the postorbital-squamosal contact, as typical for derived edaphosaurids (*Gordodon*, *Edaphosaurus*).

A putative single stapes is located at the straight posterior margin of the left parietal. If correctly identified, a long quadrate process can be stated.

Unfortunately, no long spines are present to verify the edaphosaurid status of SaP 344. Right posterior to the parietals, an axis neural arch is preserved. It is proportionally large, compared to that of *Palaeohatteria* (Currie 1979; Spindler 2016). The dorsal spine is short and round, which could result from the low ontogentic age. Edaphosaurids must have gained their sail-backed condition early after hatchling. However, in this case it could also reflect the morphology of grown individuals. The axis bears an elongated spine in *Ianthasaurus* (Modesto and Reisz 1990a), but not in *Gordodon* (Lucas et al. 2018) and *Edaphosaurus* (Romer and Price 1940: 36A, figs. 66, 68), which SaP 344 resembles the most.

In the shoulder girdle, the anterior coracoids, both clavicles, and some uncertain elements like a possible scapula are preserved. Beyond the orthogonal orientation of the clavicular ventral and dorsal processes, no valuable anatomical observation can be made. All shoulder elements are poorly ossified and support the early juvenile stage of this specimen.

The long bones are stout, with broadened terminal regions. By this, the proportions of SaP 344 resemble *Palaeohatteria* juveniles or captorhinid eureptilians. Of the latter, only vague fragments have been identified in the Niederhäslich assemblage (Spindler et al. in prep.). Since the temporal fenestration is unquestionable, the long bones support the synapsid interpretation. At least one humerus and one zeugopodial can be labelled. The strongly juvenile stage hampers further anatomical observations, such as of a probably preserved femur.

A single ungual is exposed near the cranium. It is short and tall, with a strong flexor tubercle. This morphology resembles other early synapsids, especially since it is the same as in *Palaeohatteria* juveniles.

Discussion. A recent revision of the basal sphenacodontian *Palaeohatteria* from the Early Permian Niederhäslich assemblage (Spindler 2013, 2016) allowed the identification of another edaphosaurid specimen from this site that may be conspecific with *Edaphosaurus credneri*. The specimen SaP 344 was originally labelled as "*Haptodus baylei*" (sensu Currie 1979) = *Palaeohatteria longicaudata* (revalidated by Laurin 1993). For fragmentary specimens, a single inclusion to cladistic tests is recommended. When including SaP 344 among better known taxa, it shows that this potential second specimen of *E. credneri* is drawn to the derived portion of edaphosaurids.

?Edaphosauridae indet.

Material. LfULG SS 13531, fragmentary slab with complete pes and pelvic remains.

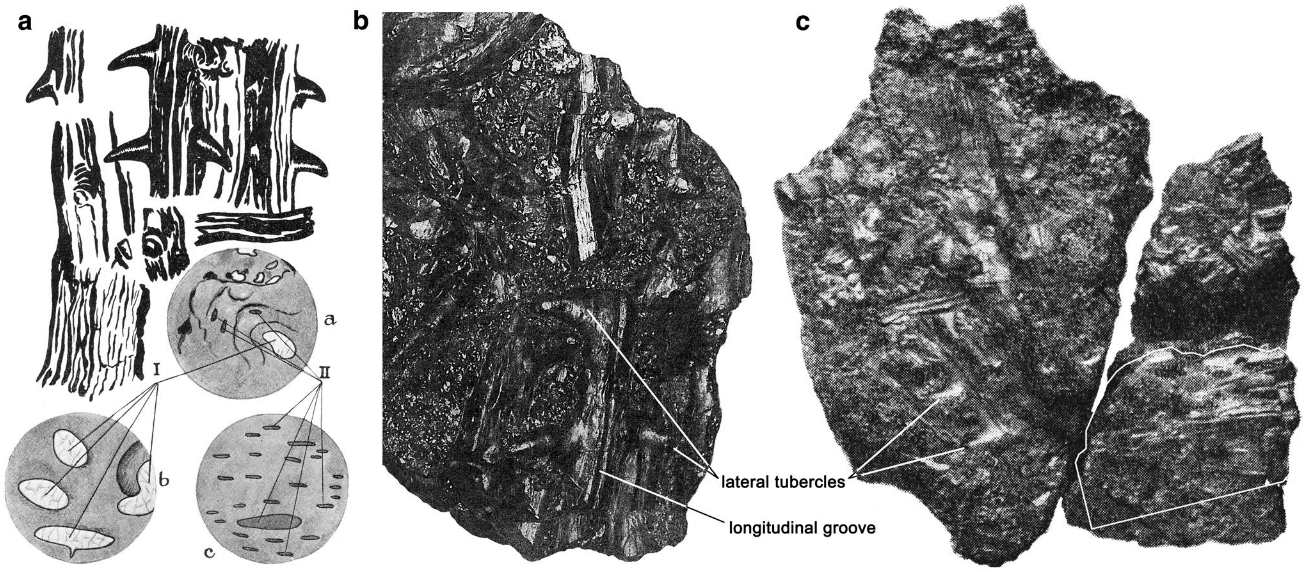


Fig. 6 *Ramodendron obvispinosum*, only available documentation of a lost and indeterminate edaphosaurid specimen. **a** Interpretative drawing as plant remains, with histological sketches not explained in the original description, from Švestka (1943); **b** photography of slab, from Prantl (1943); **c** photography, apparently showing the entire material, from Švestka (1944), with white outline indicating the position of b, whereas the larger slab exposes the original to a (rotated about 140°). No absolute scaling was provided in the cited figures

Locality and horizon. Same as for the type material of *E. credneri* (see above).

Description. This apparently half-grown sphenacomorph is described as the most mature individual known of *Palaeohatteria longicaudata* (Credner 1893; Romer and Price 1940; Spindler 2016: fig. 24).

Discussion. The weathered fragment of the iliac blade shows a slightly concave dorsal margin and probably projecting anterior process. This pattern is typical of *Edaphosaurus*, but also of certain Sphenacodontidae. The specimen in question also preserved some broader and apparently shortened phalanges, along with ungual elements. Regarding their ungual morphology, the difference between *Edaphosaurus* and *Dimetrodon* is not significant (Maddin and Reisz 2007: fig. 4), although more bluntly shaped in mounted skeletons of *Edaphosaurus*. Both the metacarpals and phalanges of SS 13531 are moderately broadened and in the spectrum of Sphenacodontidae (Henrici et al. 2005: fig. 2; pers. obs. MCZ 1365). However, little is known about *Edaphosaurus* autopodia. Although SS 13531 most likely represents *Palaeohatteria* and, therefore, a basal sphenacodontian, its edaphosaurid determination is not fully precluded.

Ramodendron obvispinosum Švestka, 1943
Figure 6

Material. Unknown catalogue number (specimen lost), portion of dorsal spine set.

Locality and horizon. Oslavany, Boskovice Basin, Czech Republic; Rosice-Oslavany Formation, Gzhelian–Asselian, Pennsylvanian–Permian boundary (Štamberg and Zajíc 2008: fig. 5; Opluštil et al. 2017).

Diagnosis. No generic distinction possible due to limited morphological data.

Description. Since the original specimen got lost (Štamberg and Zajíc 2008), the limited morphological observations are based on the description by Prantl (1943), who recognized its edaphosaurid nature, with additional support of published images (Fig. 6). There are seven longer spine fragments reported, with additional elements from the counter slab (Prantl 1943: 95). The longest piece is 65 mm long. In cross section, the spines are circular to transversely oval, measuring 12 mm in maximal diameter. A longitudinal groove is present on the midline of the anterior or posterior surfaces. Lateral tuberculation occurs on all doubtless spines. These spikes are 10 to 12 mm long and curved ventrally, which was used to distinguish this form from "*E.*" *mirabilis* (Prantl 1943). Although slightly different in vertical position, they form pairs of apparently consistent intervals, used as a distinction from both *mirabilis* and *credneri*.

Discussion. The genus name refers to the fact that broken spine fragments of this partial skeleton were first considered to represent plant remains, as has been assumed also from some American specimens of *Edaphosaurus* (Fritsch 1901). The first description introduced *Ramodendron obvispinosum* as a new plant species (Švestka 1943). As we could not find any database entry for the generic designation, this might also be the authorship for *Ramodendron* Švestka, 1943 (as also stated by Prantl 1943). However, all subsequent workers assigned it to *Edaphosaurus* (for chresonymy see Štamberg and Zajíc 2008: 189; to be completed by their reference to Petrbok 1944), mostly with doubt on the validity of the species.

This specimen, though doubtlessly a derived edaphosaurid, is not included to the phylogenetic analysis due to a lack of indicative conditions. Almost no codings were possible for *Ramodondron*. With respect to spine robustness, tubercle shape and density, it appears intermediary between *Edaphosaurus boanerges* and the new edaphosaurid from Germany described below, to none of which it can be assigned, nor distinguished from. With *E. boanerges*, it shares absolute spine dimensions, making *Ramodondron* the largest edaphosaurid ever found in Europe. However, no diagnostics can be raised, making this genus, along with its only ascribed species, a nomen nudum,

"Belebey" augustodunensis Falconnet, 2012
Figure 7a

Material. Holotype—MNHN.F.AUT 891, fragmentary maxilla and rib remain, probably a humerus.

Locality and horizon. Autunois, Autun Basin, France; Millery Formation, Artinskian (Schneider et al. 2014), Early Permian.

Diagnosis. No diagnostic combination found for generic or specific identification. This fragmentary fossil represents a small amniote, only little larger than *Ianthasaurus* ROM 59933. The bulbous marginal teeth lack serration, but exhibit cutting edges. A dorsal rib appears robust and less curved.

Description. A fragmentary, low maxilla is preserved, bearing six teeth. Their shape is intermediary between basal sphenacodontians and derived edaphosaurids, with blunt tips and cutting edges. As seen also in *Edaphosaurus* (Modesto 1995: fig. 9; Davis 2012: 125), offset tooth tips co-occur with bulbous crowns (see Online Resource 4, character 6). The vertical bar, labelled with "?" by Falconnet (2012: fig. 1) might belong to the lacrimal.

A partially preserved dorsal rib associated to the cranial remains is robust and less curved. The tentatively assigned humerus (Falconnet 2012: fig. 3) is stout, much like the long bones of juvenile sphenacomorphs such as *Haptodus baylei* (Spindler 2015) or *Palaeohatteria longicaudata* (Spindler 2016). This does not match with early reptilian proportions, including those of bolosaurs (Watson 1954: fig. 6; Berman et al. 2000; Modesto et al. 2015).

Discussion. The new species erected for the otherwise well-known bolosaurid parareptile *Belebey* is based on crushed remains that were originally assigned to the early sphenacodontian *Haptodus baylei* (Thévenin 1910). With respect to the former bolosaurid classification (Falconnet 2012), this assignment was based on the observation of bulbous teeth. Designing a phylogenetic test that includes basal parareptiles only, combined with the few codings possible for MNHN.F.AUT 891, this taxonomic unit would of course plot among bolosaurids. Likewise, the present revision yields no final evidence that the specimen in question is an edaphosaurid. However, the lack of alternative interpretations is a serious point about the previous study.

What has been coded for "*Belebey*" *augustodunensis* is largely not informative. The greatest point of critique originates from the fact that the characteristic heel of bolosaurid teeth is not present in MNHN.F.AUT 891. The bulbous tooth shape is shared with numerous herbivorous or durophagous amniotes. In fact, what is demonstrated for "*Belebey*" *augustodunensis* (Falconnet 2012: fig. 2) does in no way justify scoring the presence of an offset heel. For comparison (Fig. 7), the typical bolosaurid tooth shape is well documented (Watson 1954; Lucas et al. 2005; Müller et al. 2008).

Although the current re-assignment to Edaphosauridae is vague, it bases on some positive arguments, confirmed by serious doubts on the bolosaurid classification (R. Reisz, pers. comm.). After all, even a captorhinid classification is not fully rejected. From the phylogenetic tests, a position more basal than *Edaphosaurus* can be concluded. Any constant pattern, such as a frequent plotting among either basal or derived forms, is missing. Because of this lack of determination and diagnosis, we suggest treating *"Belebey"augustodunensis* as a nomen dubium.

Genus ***Remigiomontanus*** nov.

Type species. Remigiomontanus robustus gen. et sp. nov.

Etymology. The name *Remigiomontanus* is the latinized form of the type locality Remigiusberg.

Diagnosis. Edaphosaurid of intermediate size, without discernable autapomorphies, but a distinctly unique combination of character conditions; clear plesiomorphies comprise the lack of a hyposphene, *V* shaped prezygapophysial angle, shorter "lumbar" ribs than in *Edaphosaurus*, as well as slender phalanges; clear apomorphies within the Edaphosauridae are the shortened cervicals, elongated dorsals, elongated

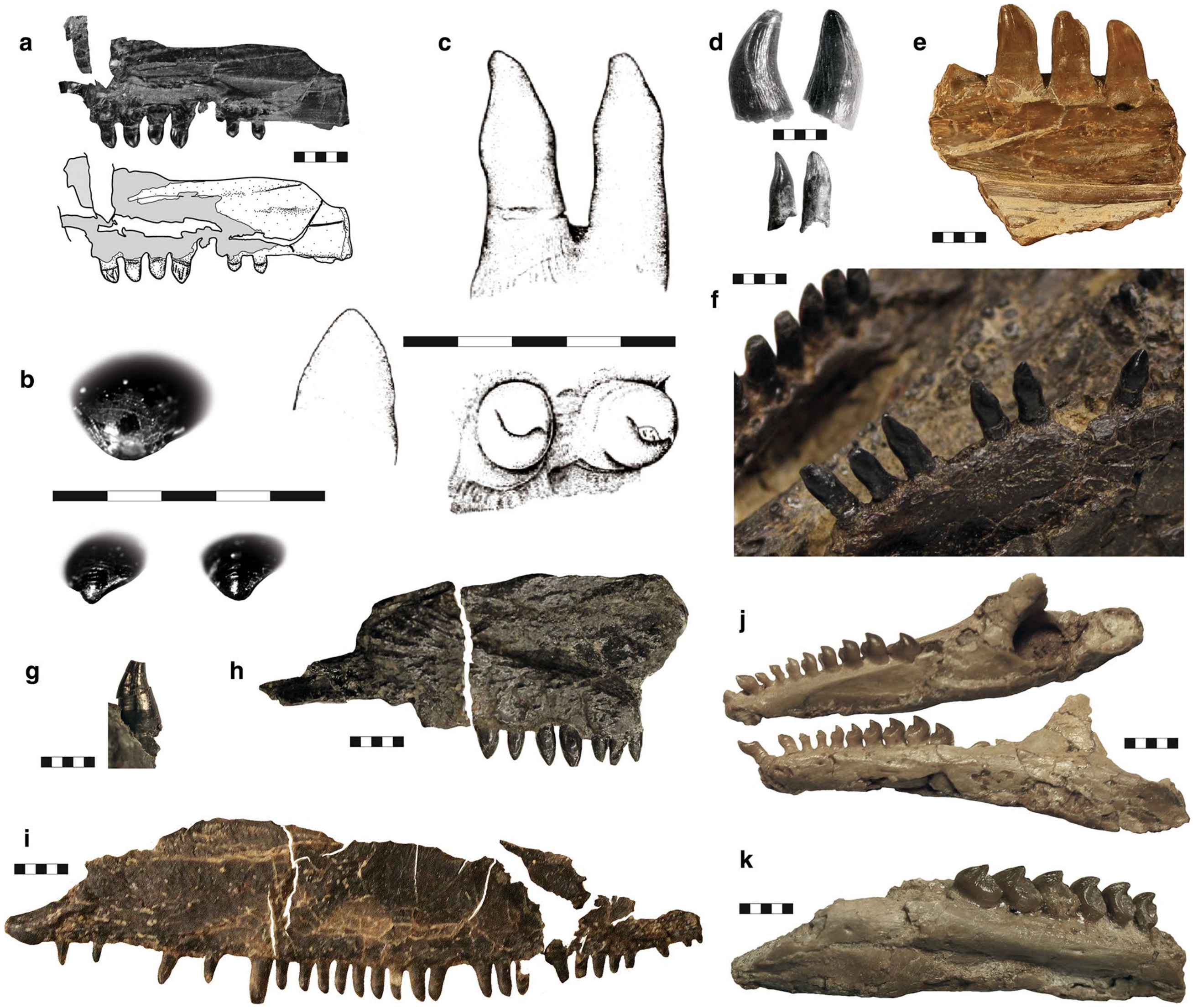


Fig. 7 Marginal teeth and tooth rows of Edaphosauridae for comparison with Bolosauridae. **a** "*Belebey*" *augustodunensis*, jaw fragment of supposed bolosaurid and herein interpreted as an edaphosaurid, taken from Falconnet (2012: fig. 1); **b** tooth tips of the latter in vertical perspective (Falconnet 2012: fig. 2); **c** *Edaphosaurus boanerges* MCZ 1762 (Modesto 1995: fig. 9); **d** *Edaphosaurus* cf. *boanerges* (Davis 2012: 124, 125); **e** cf. *Edaphosaurus* (Vamoosa Formation, Virgilian of Seminole County, Oklahoma), OMNH 73688, pers. obs.; **f** *Edaphosaurus boanerges* MCZ 1762, right maxilla in foreground; **g** cf. *Ianthasaurus* CM 47700, possible premaxillary tooth; **h** cf. *Ianthasaurus* CM 34449, maxilla; **i** *Ianthasaurus hardestiorum* ROM 59933, maxilla of largest known specimen; **j** *Belebey vegrandis* PIN 104B/2021, mandible with typical heel-bearing teeth; **k** *Belebey vegrandis* PIN 104B/2022, partial dentary. Scale bar measuring 5 mm each

and ventrally notched diapophyses, and heightened caudal spines; intermediate combinations affect the distinctly present, but reduced rib tubercules (resembling *Lupeosaurus*) and a moderate curvature throughout the rib length (resembling *Ianthasaurus* and *E. colohistion*); back sail tall (spine robustness and relative height resembling *Edaphosaurus*) with full tuberculation, counting nine spike rows of even intervals, simple tubercles that are rather constant in size, including relatively short basal spikes.

Remigiomontanus robustus gen. et sp. nov.
Figures 8, 9, 10, 11, 12; Online Resource 2

Material. Holotype—UGKU 1997, largely complete trunk skeleton, caudal fragments, and a few phalanges, associated with freshwater shark coprolites and teeth. Referred specimens (same horizon as holotype, but some 150 m away from it)—UGKU 2546 and 2551, dorsal spine fragments; UGKU

Fig. 8 Complete image of UGKU 1997, holotype of *Remigiomontanus robustus* gen. et sp. nov. For a larger photography see Online Resource 2. Scale bar measures 10 cm

2552, dorsal rib. The assignment of isolated marginal teeth requires further anatomical overlap.

Locality and horizon. Type locality—UGKU L-71, Remigiusberg-Rammelskopf quarry at the northeastern rim of the Remigiusberg (387631 E, 5487527 N, UTM 32U, WGS 84), about 1 km northeast of Haschbach, Kusel county, western Rhineland–Palatinate, Saar–Nahe Basin, Germany (Voigt et al. 2014: fig. 1). Type horizon—topmost limestone of the lower Theisbergstegen lake level, middle part of the Remigiusberg Formation, local base of Rotliegend, Gzhelian–Asselian boundary, latest Pennsylvanian or earliest Permian. A volcanic ash bed about 30 km to the west of the type locality, correlated with the middle to upper part of the Remigiusberg Formation, was radioisotopically dated to 300 ± 2.4 Ma (Burger et al. 1997; Boy et al. 2012; von Seckendorff 2012).

Etymology. The species name refers to Latin *robustus*, since dorsal spines are proportionally more robust than in other members of its family.

Diagnosis. As for genus.

Description. The robust skeleton is disarticulated, though some of the presacral vertebrae are preserved in natural sequence. What is preserved of the axial skeleton implies a grown individual: Despite disarticulation, none of the presacral to mid-caudal centra or neural arches occur isolated. In a few cases, the neurocentral sutures appear gaping. Some centra are exposed with their ventral sides, implying some degree of vertebral disassociation either due to post mortem decay or diagenetic deformation. In total, the individual represents a subadult stage of ossification.

All vertebral centra are amphicoelous, low and elongated. The articular ends are expanded, giving the entire centrum a spool-shaped profile. The heavy deformation hampers a decisive observation of whether the central side is keeled or rounded. A distinct, but stout keel occurs in cervical centra. A blunt ridge that is enclosed by deep lateral excavations seems present in a "lumbar" vertebra, whereas a supposed proximal caudal is rounded ventrally. The cervical centra are shortened in comparison with the dorsals. There is one unquestionable intercentrum, appearing as a slender and shallow element, as typical for *Edaphosaurus* (Romer and Price 1940; Berman 1979).

Fig. 9 Close-up of dorsal spine concentration in UGKU 1997, holotype of *Remigiomontanus robustus* gen. et sp. nov. Scale bar measures 10 cm

In the skeletal reconstruction (Fig. 13), the position of cervical, anterior dorsal and "lumbar" vertebrae could be reconstructed from the comparison with *Edaphosaurus*, whereas mid-dorsals are tentatively arranged with respect to their estimated order in the original fossil.

Two definite cervical neural arches are known. Their elongated spines indicate that the unknown axial spine was most likely low, as is in all basal synapsids, except for *Ianthasaurus* (Modesto and Reisz 1990a) and certain sphenacodontids. The spines are pointed and not more robust than in the dorsal region. On the sixth or seventh spine, two pairs of lateral tubercles occur with a wider interval than in the thoracic spine tuberculation.

In the dorsal sequence, several well-preserved neural arches allow for a reconstruction of vertebral characters. There is no trace of a lateral excavation. The prezygapophyses bear planar articulation facets that contact on midline (Fig. 10b). Several degrees of obtuse angles are present, resulting from deformation, but altogether a clear *V* shape is formed by the prezygapophyses. From the postzygapophyses, an angle of about 120° can be given as a general estimation. Careful, specific preparation revealed that no hyposphene is present in *Remigiomontanus*. Few anterior to mid-dorsal vertebrae expose a moderately elongated diapophysis. The diapophysial lamina is incised ventrally, causing a gap medial to the articulated collum costae. The diapophysis is placed well anterior on the neural arch and bears a broad, rounded articular surface for the rib capitulum.

As characteristic of edaphosaurids, hyper-elongated dorsal spines form a back sail that is only slightly lower than in *Edaphosaurus boanerges* (Fig. 13), being proportionally higher than in *E. pogonias* and *E. cruciger* (Romer and Price 1940: figs. 66–68). In the basal part of the spine, an anteroposteriorly expanded shoulder is clearly visible. This character has usually been noticed in sphenacodontids (Reisz et al. 1992; Brink and Reisz 2014). In edaphosaurids, these blades are more confluent to the lower part of the neural arch and, therefore, overlooked as a morphological detail. The dorsal extend of shoulders marks the level of soft tissue cover of the back lateral to the characteristic sail.

Dorsal to the shoulders, the spines are circular to transversally oval in cross section, with a thick cortex similar to the internal structure in *Edaphosaurus* (Fig. 12). In comparison to *E. boanerges*, the spines are more robust. Although tilting forward and backward in the front and rear ends of the sail, respectively, they are less curved than in *E. boanerges*. A vertical groove runs along the posterior surface of

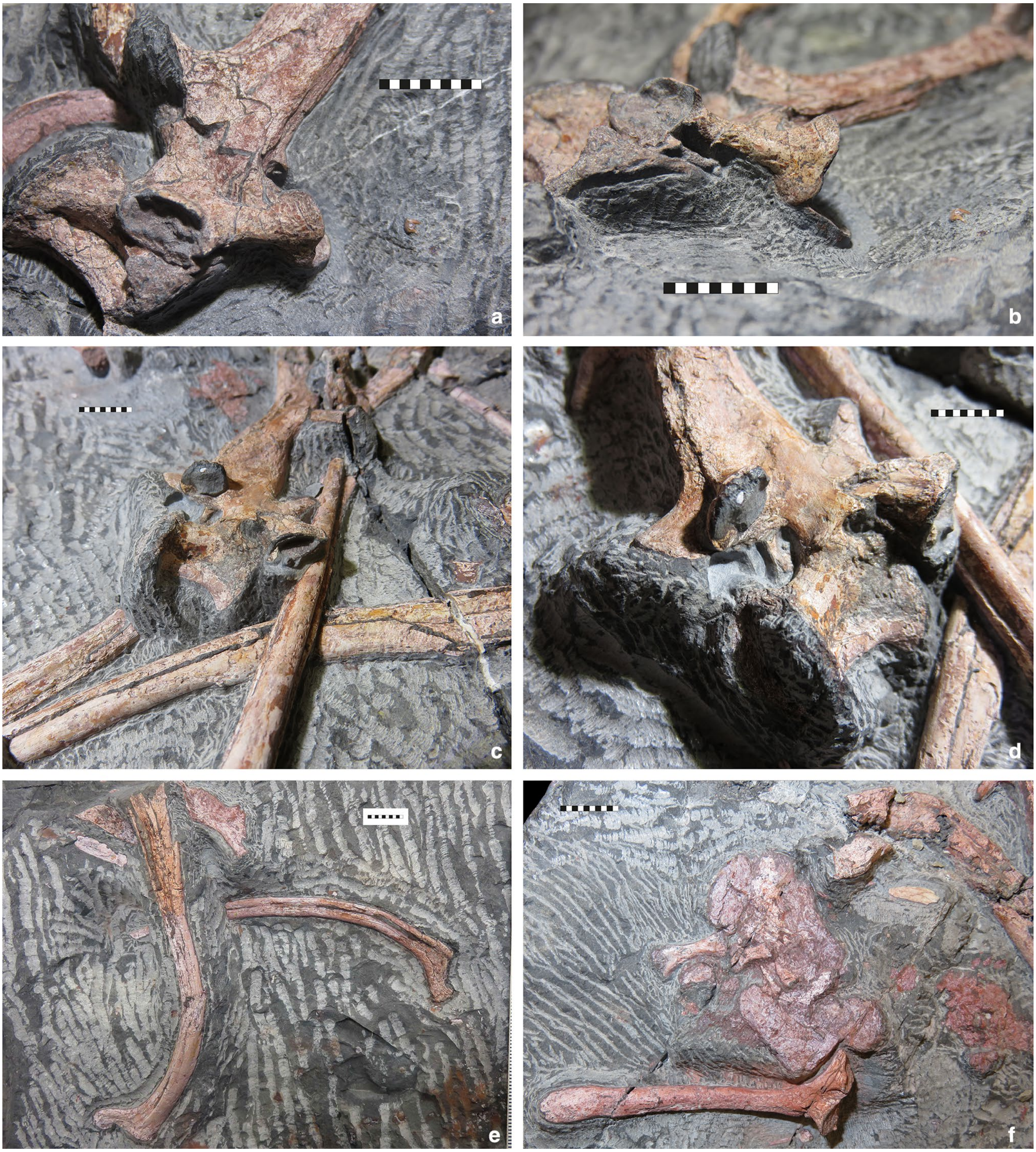
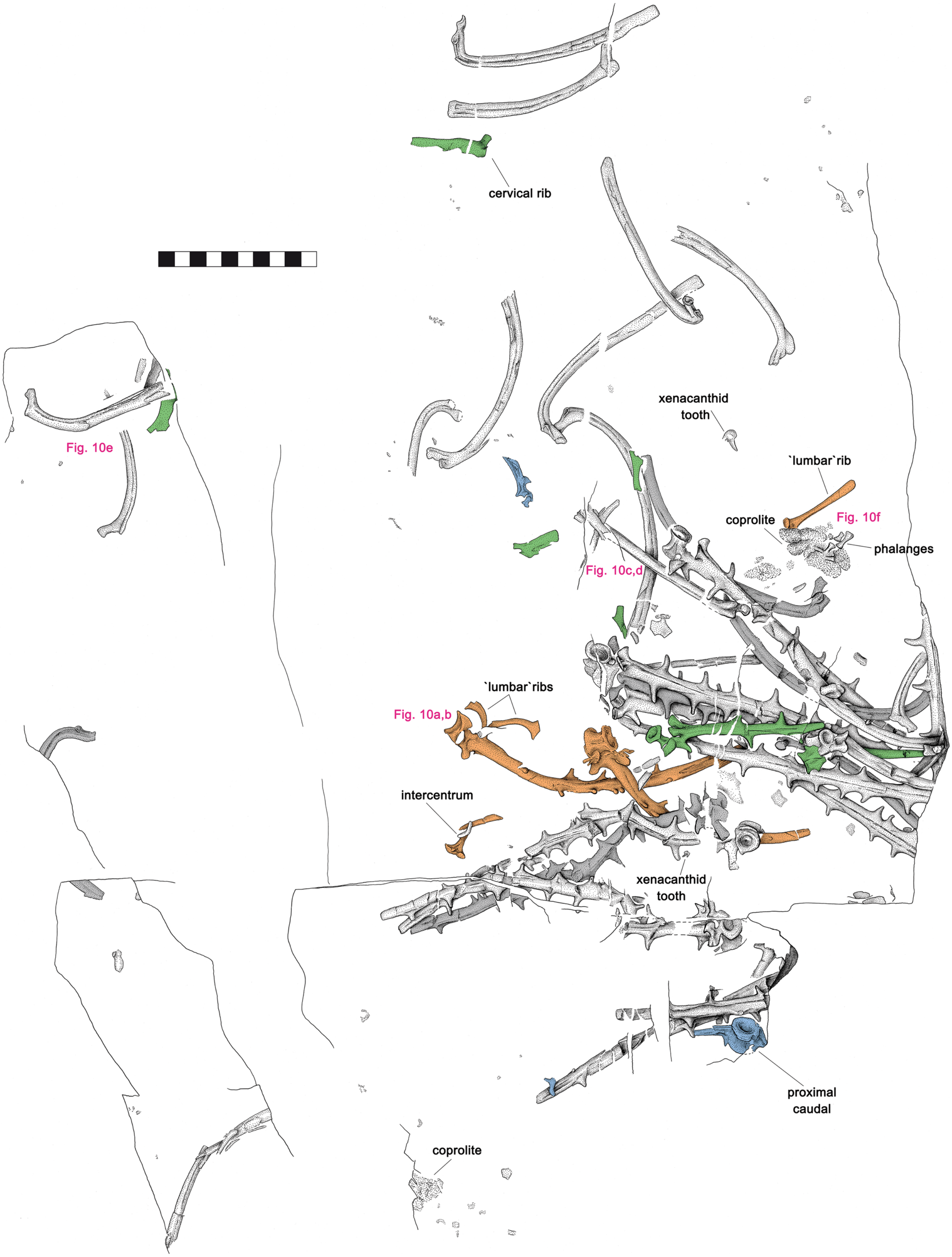


Fig. 10 Close-ups of vertebrae (**a**–**d**), ribs (**e**, **f**) and autopodial elements (**f**, on coprolite) of UGKU 1997, holotype of *Remigiomontanus robustus* gen. et sp. nov. Additional preparation has been carried out for these details. Positions of **a**–**f** are mapped out in Fig. 11. Scale bars measuring 10 mm each

the spine. Since almost every spine fragments bears such a thin trough, it is likely that this feature applied also to the anterior side, although not unambiguously preserved in the holotype. UGKU 2546 (Fig. 12) exhibits shallow furrows on both the frontal and the rear side. The spine tuberculation shows the same irregularities as described from *Edaphosaurus* (Romer and Price 1940). There are nine vertical positions of lateral tubercles in the anterior dorsal region,


cervical rib
Fig. 10e
xenacanthid tooth
`lumbar`rib
coprolite
Fig. 10f
phalanges
Fig. 10c,d
`lumbar`ribs
Fig. 10a,b
intercentrum
xenacanthid tooth
proximal caudal
coprolite

◂**Fig. 11** Interpretative drawing of UGKU 1997, holotype of *Remigiomontanus robustus* gen. et sp. nov. Positions of Fig. 10a–f are indicated. Green elements are from the cervix, orange marks a "lumbar" position, blue elements are caudal ones, the remaining dorsal elements are white and grey for distinction. Scale bar measures 10 cm

mostly performed by paired tubercles, but also frequently showing alternating positions, unpaired spines or doubled on one body side. Most tubercles are short, pointed and curved ventrally. Many of them show a vertical webbing, making it confluent with the lateral spine. The tuberculation does not show a vertical trend in terms of density or irregularity. As far as visible, even the distal regions of spines can bear tuberculation, regardless of their longitudinal position in the vertebral column.

Of the caudal sequence, two distal elements are present. One persists of a distal neural arch that is probably disarticulated from its centrum. The other is a well exposed midcaudal, displaying the short and tall appearance as typical for derived edaphosaurids. The spine is elongated and constricted at its base, most closely resembling *Edaphosaurus* (Romer and Price 1940: pl. 37C).

Five cervical ribs were found, with smooth succession in both size and shape. The shaft is stout and anteroposteriorly dilated. There is a well-developed anterior process. The cervical ribs are of typical edaphosaurid morphology (Romer 1952: fig. 13a; Mazierski and Reisz 2010: fig. 4b).

Numerous dorsal ribs are preserved. Whereas their shape is heavily affected by microtectonically induced deformation, some appear to retain the original curvature. In most cases, the curvature is less developed than in *Edaphosaurus* (pers. obs. OMNH 35186; Case 1907: fig. 65; Williston and Case 1913: fig. 48). Nonetheless, the robustness of the ribs and the occurrence of curvature along the entire shaft is shared with *Edaphosaurus*. In the head, the collum is elongated. The capitulum has a concave articular facet. The tuberculum is reduced, although to a lesser degree than in *Edaphosaurus* (Romer and Price 1940: pl. 37B), with many tubercles developed as a prominent bulge.

In the "lumbar" region, the ribs are relatively shorter than in *Edaphosaurus*. The head is typically dichocephalous, with a large, protruding tubercular facet (Case 1907: fig. 64). In contrast to the curved last and second last rib, the third and fourth last rib shafts appear almost straight, with slightly expanding distal ends. Additional preparation was carried out on the fourth last rib, since its articular region is covered by the largest coprolite. The anterior rim of the tubercular facet bears some coarse indentation. This might imply an initial stage of the stiff articulation seen in *E. boanerges* (Romer and Price 1940: pl. 36D).

At one end of the slab, a large centrum is exposed with its ventral surface. A long and slender process emerges from the same region where a short zygapophysis is visible. On the broken opposite side of the centrum, a similar process seems present. Most likely, this is a proximal caudal with fused caudal ribs. Such a co-ossification is shared with *Lupeosaurus* (see Online Resource 4, comment on excluded character).

Of the appendicular skeleton, nothing is preserved but a set of phalanges, somewhat blurred by the largest coprolite. At first sight, these appear very small for the robust skeleton. Estimated from the reconstruction (Fig. 13), there is no striking discrepancy in relative size. Therefore, the autopodial remains can be assigned to the remainder of the skeleton. Their shape indicates a slender condition, unlike the broadened phalanges in *Edaphosaurus* (Online Resource 4, character 82). This observation reflects the general appearance of the new form.

Discussion. Prior to the phylogenetic analysis, it can be concluded that *Remigiomontanus* is intermediary between *Ianthasaurus* and *Edaphosaurus* in many aspects.

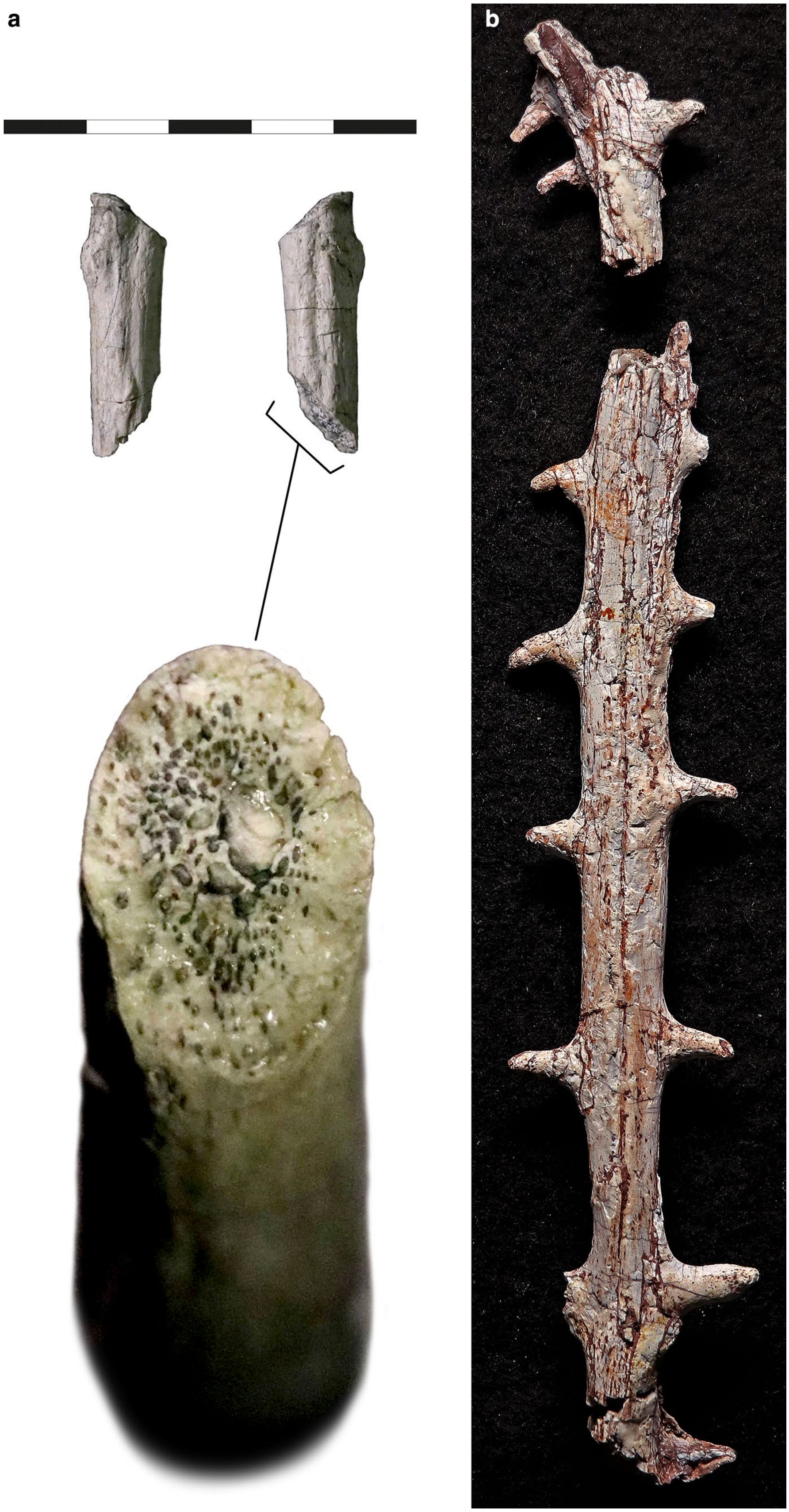
Phylogenetic analysis

Patterns of spine morphology

Several potential characters could be extracted from the comparative morphology of edaphosaurid back sails. Since interdependencies and evolutionary trends are poorly understood, a more comprehensive discussion is needed to define distinct conditions. Fundamental insights regarding the sail morphology of Edaphosauridae were described by Berman (1979). On this basis, some species assignments of fragmentary remains (Romer 1952) are rejected. For example, the large-sized edaphosaurid CM 8540 cannot be determined as *Edaphosaurus cruciger* anymore. In general, the tuberculation patterns of all known edaphosaurids seem highly variable. Along with the fragmentary nature of much of the material, the phylogenetic value of many related characters is questionable.

Before phrasing the renewed character list for the cladistic analysis, an overview of spine tuberculation features was created (Online Resource 3). Only eight out of 14 characters were used in the final coding (Online Resource 4, with important additional remarks). No general trends that affect several of these characters can be reconstructed. Therefore, similarities such as club-shaped anterior spine tips, gall-like tuberculi, or number of spike pairs might support relationships between certain taxonomic units. However, several conditions can re-occur throughout the spectrum of edaphosaurid material. It shows that variability is even intraspecific, as seen in *Ianthasaurus*. Partially irregularly arranged lateral tubercles represent a common feature even in derived taxa, especially concerning the anterior sail and distal spine portions. Nonetheless, *Remigiomontanus* and

Fig. 12 Dorsal spine fragments referred to *Remigiomontanus robustus* gen. et sp. nov. **a** UGKU 2546 in anterior and posterior aspect, as well as oblique section (enlarged); **b** UGKU 2551 in anterior or posterior aspect (opposite damaged). Scale bar measures 5 cm for a and b; image plane of detail in a not strictly oblique



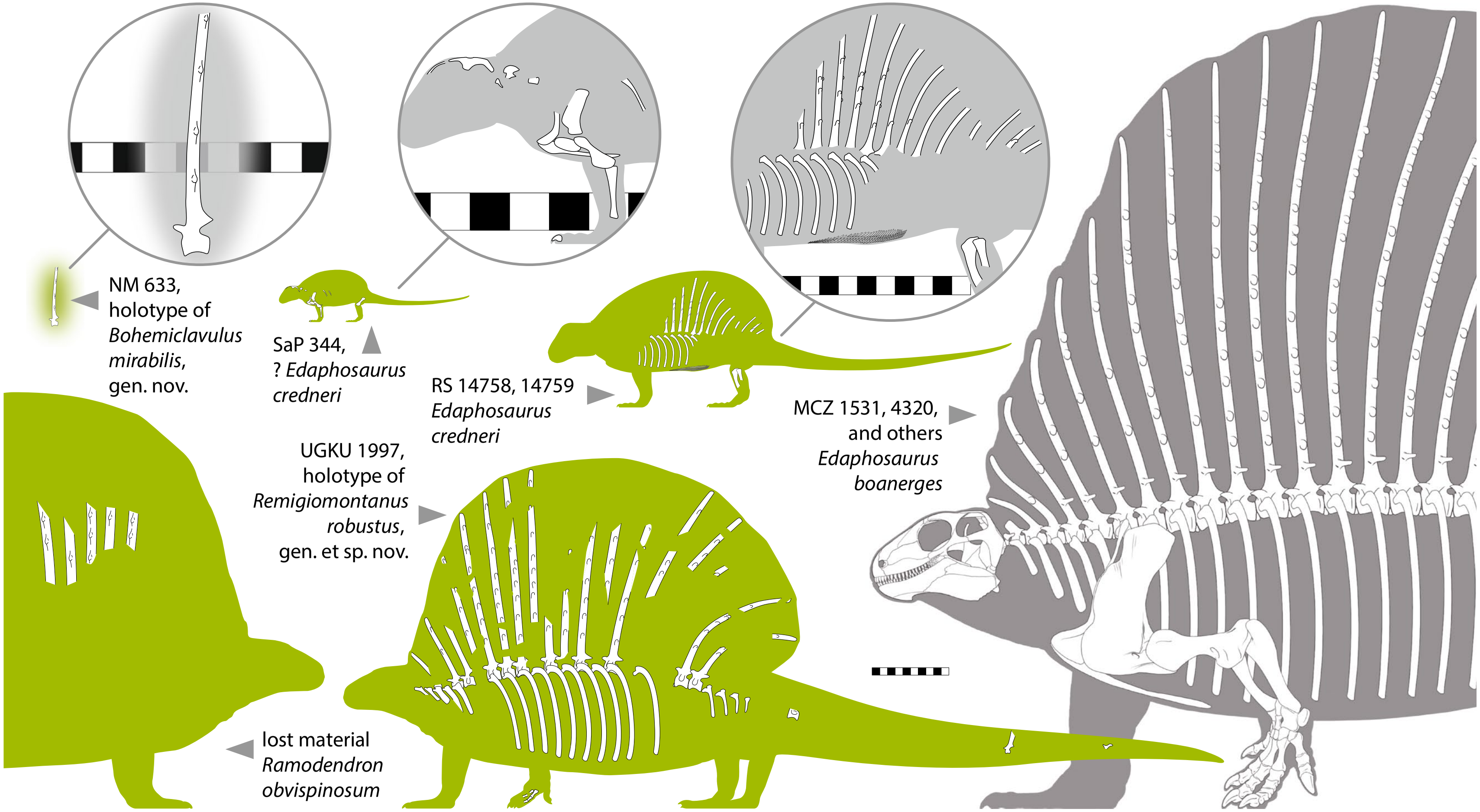


Fig. 13 Skeletal reconstructions of edaphosaurids from Europe (green) compared to *Edaphosaurus boanerges* (Romer and Price 1940: fig. 66, combined with own documentations of MCZ 1531 and 4320, referring to casts in OMNH 74084; skull enlarged and taken from Modesto 1995: fig. 2). Scale bars in cm (sizing of *Ramodendron* estimated from measurements in the descriptions, see text for citation)

Ramodendron share the same degree of regularity in tuberculation as observed in certain species of *Edaphosaurus*.

Berman (1979) recognized that edaphosaurids from the "Tri-state area" (northeastern USA) do not reflect the clear trends stated for the supposed chronospecies ("species phylum" according to Romer and Price 1940) from Texas, to which *Edaphosaurus novomexicanus* appears to be antecedent. In conclusion, the southwestern edaphosaurids were supposed to represent a province distinct from the northeastern one. Now, based on the revision of European remains, no certain rules could be found to either erect or debate the concept of edaphosaurid faunal provinces. It should be noted that Berman (1979) still based on the monogeneric concept of the family Edaphosauridae, as further genera were not described until *Xyrospondylus* (Reisz et al. 1982) and *Ianthasaurus* (Reisz and Berman 1986), with *Lupeosaurus* still doubted (Romer and Price 1940; Sumida 1989a). Therefore, after increased generic diversity, none of the fragments from the northeastern province can be assigned to *Edaphosaurus* at all. Single comparisons with basal edaphosaurids are mentioned in the following.

The proximal pair of tubercles is the only one placed at a fixed position to form a continuous longitudinal row right above the edge where the sail and the trunk periphery might have met in life. At about this level, the spine turns from its laterally compressed base into a round cross-section, which defines confluent shoulders. The lowermost spikes are elongated in *Ianthasaurus* and *Edaphosaurus*, generally reduced in *E. novomexicanus*, strongly pronounced in *E. cruciger* (Case 1907: pl. 29, fig. 2), elongated even far up the spine in *E. pogonias* (Reisz 1986), but rather short in *Remigiomontanus*.

It has early been recognized that the remaining lateral spikes form loose longitudinal rows (Romer and Price 1940). There are up to eight positions in *Ianthasaurus* (ROM 59933, 29942), nine in *Remigiomontanus*, and more than twelve in *Edaphosaurus*, except for the reduced condition in *novomexicanus*. From proximal to distal, lateral spikes decrease in size in *Edaphosaurus* (Berman 1979), contrasting the more constant shape in *Remigiomontanus*.

The lowermost tubercles are not only strengthened in most edaphosaurids, but also perform the only strictly paired ones. Since much variation is possible in terms of asymmetric tuberculation, this ornamentation should not be designated as "cross-bars" (Romer and Price 1940; Peabody 1957; Reisz 1986), implying a frequently occurring alternation. Instead, other terms offered by Romer and Price (1940) like lateral spikes, lateral tubercles, tuberculation, or lateral processes are more accurate. Admittedly, *Edaphosaurus* tends to show bilaterally symmetrical pairs with fairly regular intervals, but there are frequent exceptions such that longitudinal rows on the sail can set in (Romer and Price 1940; Berman 1979). The more distal a spine is observed, the more irregularities can occur. The simplest and most abundant type of irregularity exhibits shifted vertical positions of two opposing tubercles or entire sets. Since the descriptions of *Ianthasaurus*, isolated spikes on only one side or triple positions with one spike opposing two on the other side are documented. Maybe representing special cases, even webbings with multiple tubercles on the same side (ROM 37751, Modesto and Reisz 1990a) or bifid positions (CM 8540, Berman 1979: fig. 3c; CM 34576, Sumida and Berman 1993: fig. 5c) have been found. It appears that these strong asymmetries a more abundant in moderately derived edaphosaurids, as also the single vertebra of *Bohemiclavulus* exposes a triple position. In *Remigiomontanus*, abundant triple positions occur in markedly lower areas of dorsal spines. That in *Edaphosaurus credneri* only unpaired single spikes seem to be present could be counted as additional indication for its derived status. Although triple positions are documented also for *E. boanerges* (Romer and Price 1940: fig. 66), Modesto and Reisz (1990a) report "accessory processes" or "multiple tubercles" as restricted to *Ianthasaurus* and the supposed "*Edaphosaurus cruciger*" CM 8540 (according to Romer 1952). Doubtless triples are present in the spine clubs of *E. pogonias* (Case 1907: pl. 28, fig. 1) and the enigmatic second Badger Creek form CM 47699 (Sumida and Berman 1993).

Additional variation originates from vertical intervals of tubercle rows. Valuable observations were collected by Romer and Price (1940) and Berman (1979). These intervals are also affected by increasing irregularity towards distal spine tips of *Edaphosaurus* and *Remigiomontanus*. Probably, this vertical effect is related to ontogeny and growth, as spike formation differs between *Edaphosaurus* and *Ianthasaurus*. The spine histology (Huttenlocker et al. 2011; Davis 2012: 132f.) suggests that tubercles in *Edaphosaurus* were defined by sudden, rapid growth over a few seasons, but incremental growth in *Ianthasaurus*. In conclusion, regardless of the uncertainly known function of spine tuberculation, the morphological and/or ontogenetic differences of certain genera are not only the result of variability.

Several edaphosaurids exhibit zones of reduced tuberculation. The anterior sail is rather smooth in *E. novomexicanus* and *colohistion*, in the completely spike-less sail of *Lupeosaurus*, and probably in *Xyrospondylus*, thus reflecting an abundant feature in edaphosaurids of different evolutionary height. The opposite is seen in *Ianthasaurus*. The large specimens ROM 22941 and 59933 imply that tubercles are reduced in the upper and posterior sail, as is also clearly visible in smaller specimens. Probably, this arrangement is age-independent in *Ianthasaurus*, whereas in *credneri* this condition might reflect a juvenile pattern of an *Edaphosaurus*-like edaphosaurid. In ROM 59933, two mid-dorsal spines are flared in the smooth distal portion, implying an unknown functional reason for reduced tubercles.

At last, even the presence of robust spines and club-shaped distal ends reveal a modular principle that dominates the evolution of edaphosaurid spine modifications. Originally, a straight trend was stated for *Edaphosaurus boanerges* over *cruciger* to *pogonias* (Romer and Price 1940). That club-bearing forms like the second Badger Creek edaphosaurid (Sumida and Berman 1993) and even the basal-most representative *Xyrospondylus* have been doubted to be edaphosaurids (Reisz et al. 1982 and pers. comm.) was triggered by this clear trend in *Edaphosaurus* species. Since even *Ianthasaurus* and *Edaphosaurus boanerges* yield evidence for strengthened anterior spines, general functional requirements for a reinforced cervical portion of the sail can be concluded.

In general, the phylogenetic value of sail tuberculation is questionable. It can be expected that certain characters would hamper cladistic resolution.

Data set and iterative tests

Few cladistic analyses of edaphosaurids have been published so far, and none have included basal forms in greater detail. Particularly for Edaphosauridae, the complete analysis of early synapsids presented by Benson (2012) included only chosen representatives. The same is true for the characters used to resolve this clade. Therefore, this overview study added nothing to the tree topology of edaphosaurids beyond Modesto (1994, 1995) and Mazierski and Reisz (2010).

For the phylogenetic analysis, the matrix of Mazierski and Reisz (2010; basing on Modesto 1995) was used. Additional data were taken from Benson (2012) and further references, along with a few new characters. In Online Resource 4, references to Benson (2012) do not automatically indicate that the characters were originally introduced by him. Comments and modifications on characters are given in this attached character list, comprising 83 characters in total.

The list of operational taxonomic units (OTU) comprises all known edaphosaurids, except for few that code uninformatively (“*Edaphosaurus*” *raymondi*; *Ramodondron*; CM 47699 of the second Badger Creek form; CM 8540) and one that is not documented in detail (Whipple and Case 1930). The specific references used for character scoring are listed in Online Resource 3, with support of additional observations by Benson (2012), new information on *E. colohistion* (courtesy of D. Berman, pers. comm.) and from own fossil work. *Lupeosaurus* is scored based on Romer and Price (1940) and Sumida (1989a). The scoring for *Glaucosaurus* was taken from Modesto (1994). *Ianthasaurus hardestiorum*, for which the conspecifity of published specimens has been doubted because of conflicting conditions (Spindler 2015), is resolved to single individuals in order to test them for hidden diversity. Isolated remains from Badger Creek, described as *Ianthasaurus* sp. (Sumida and Berman 1993) are bundled to a locality synopsis, as they would appear uninformative when separated. In total, there are 14 edaphosaurid OTU plus *Ianthasaurus* with eight single specimens and three synoptic lines. One of these synopses is bundling all assigned specimens, another one counting Garnett remains only. In a third line only Garnett specimens with tipped teeth were merged. A sequence of six dorsal neural spines (CM 70291, pers. obs.) adds nothing to the characters as coded for the *Ianthasaurus* holotype.

The enigmatic *Xyrospondylus* and all European fossils are included to a cladistic analysis for the first time. The outgroup taxa are coded from given descriptions of *Archaeothyris* (Reisz 1972), *Varanosaurus* (Romer and Price 1940; Sumida 1989b; Berman et al. 1995), *Ophiacodon* (Romer and Price 1940; Harris et al. 2010); *Ianthodon* (Spindler et al. 2015), “*Haptodus*” *garnettensis* (Spindler 2015), and Palaeohatteriidae (*Palaeohatteria* plus *Pantelosaurus*, Spindler 2016).

There are two major issues that dominate the analysis of edaphosaurids. One originates from immense matrix gaps that concern different osteological portions in several taxa, causing little overlap of knowledge between some OTU, most strikingly *Glaucosaurus* (skull only) and *Lupeosaurus* (postcrania only). Furthermore, several modular characters hamper the reconstruction of parsimonious trees. In order not to overestimate the impact of single characters, many OTU combinations were used in iterative tests. These are listed in Online Resource 7, also presenting the investigation of *Ianthasaurus* single specimens and synopses.

All tests were carried out using PAUP* 4.0b10 (Swofford 2001) under the Branch-and-Bound mode, with multistate entries treated as polymorphism. Fragmentary OTU are best analyzed when isolated within a context of better-known taxa. No outgroup taxa were pre-defined.

Few characters were eliminated in certain taxa combinations, addressing sail features (characters 43, 45, 48–52). Mostly, these deletions could not trigger a better resolution. However, the deletion of characters 51 and 52, addressing interpretative issues, helped to tremendously increase the tree resolution.

Resulting phylo-taxonomy

Resolvability of edaphosaurid phylogeny is low. Including the taxa known prior to this analysis required an observation of frequent patterns to conclude for their evolutionary height (Fig. 14a shows a generalized tree), but there was no single convincing hypothesis. As a general result, a strict separation is seen between early forms, such as *Ianthasaurus* and related finds and derived ones, namely *Lupeosaurus*, *Remigiomontanus*, and *Edaphosaurus* including *E. credneri*. The state-of-the-art phylogeny (Mazierski and Reisz 2010) appears weakened when including more fragmentary

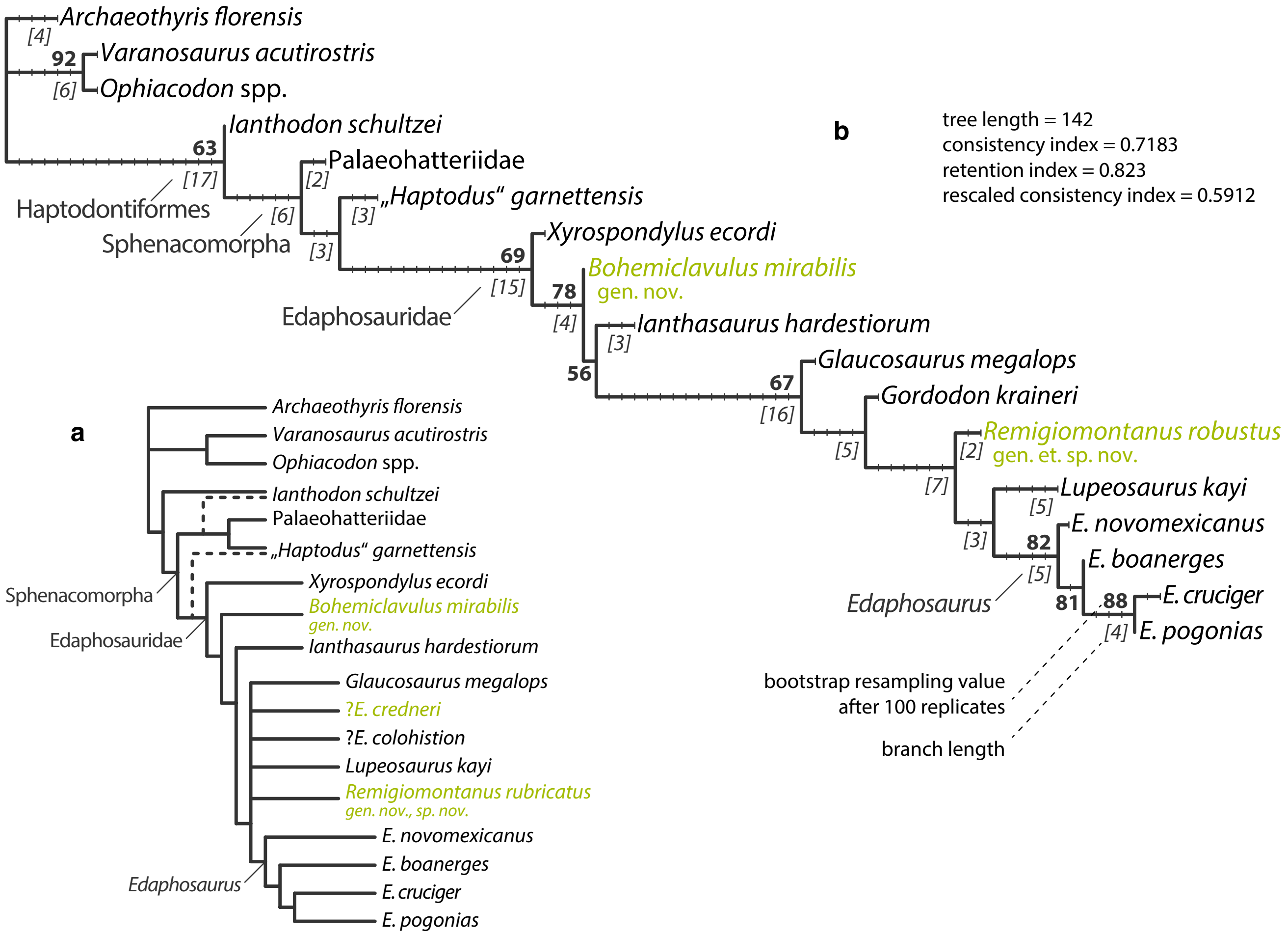


Fig. 14 Phylogenetic hypothesis of Edaphosauridae. European representatives are marked in green. **a** Synopsis sketched from multiple tree combinations (Online Resource 7). A lack of osteological overlap between certain taxa and a general variability of sail characters hamper a better resolution. Fragmentary taxa were investigated each by separate tests; **b** single tree hypothesis resulting from chosen taxa list, mainly stabilized by *Gordodon kraineri*, NMMNH P-70796, with tree statistics

specimens, instead of gaining a better resolution. Additional character discussion is offered in Online Resource 7. Insights addressing North American material and outgroup relationships are presented in Online Resource 8.

Contemporaneous to the research for this study, a well-preserved New Mexican edaphosaurid has been investigated (Lucas et al. 2018). *Gordodon kraineri* exhibits very gracile centra and neural spines with almost random tuberculation. The authors point out that this new taxon is intermediary in its shortening of both the entire skull and the antorbital portion, as well as in its mandible height, regarding known trends in Edaphosauridae. *Gordodon* helps to solve the issue of uncomparability between *Lupeosaurus* and *Glaucosaurus*, as the latter OTU is clearly less derived than *Gordodon*, which itself is considered the sister to *Lupeosaurus* + *Edaphosaurus*. The analysis of Lucas et al. (2018), based on Mazierski and Reisz (2010), also found that the inclusion of *E. colohistion* hampers to resolve derived edaphosaurids. Increased resolution is expected because of the following remarkable observations: *Gordodon* shares slender phalanges and a tall back sail with *Remigiomontanus*; on the other hand, it exhibits a higher amount of spine tubercles; it is less derived than *Remigiomontanus* in having short diapophyses and long cervical centra; *Gordodon* is comparable with *Glaucosaurus*, regarding their mandibel symphysis, splenial exposure, tooth plates, and brow shield; the frontal lateral lappet is similar to the condition in *E. novomexicanus*; furthermore, the new taxon has a slight precanine step, as seen in *Ianthasaurus*, but combined with a large, autapomorphic diastema.

Iterative tests including *Gordodon* are much clearer, although not highly robust. Various combinations are commented on in Online Resource 7. The branch-and-bound tests resulted in few trees, some only in a single one (Fig. 14b). Interestingly, all of these tests produced the same constellation in the basal tree section ranging from the outgroup to *Ianthasaurus*. This offers further support to a position of *Ianthodon* outside Sphenacomorpha as well as the possibility that "*Haptodus*" *garnettensis* is closer to Edaphosauridae than to Sphenacodontia (Laurin 1993; Spindler 2015; Online Resources 7, 8). Likewise, the constellation of *Edaphosaurus* species excluding *E. colohistion* was the same in all test combinations. The main question left open due to the impact of fragmentary OTUs is whether *Lupeosaurus* or *Remigiomontanus* is closer to *Edaphosaurus*, with a clear preference of the first.

Branch lengths given in Fig. 14b imply significant distances (1) between the outgroup and Haptodontiformes, (2) towards Edaphosauridae, (3) dividing early and derived Edaphosauridae. When deleting *Glaucosaurus*, the latter branch measures 19 steps, instead of 16. This implies that *Glaucosaurus*, although possibly holding a minimum position due to its juvenile status, is indeed a rather derived edaphosaurid. The same is true for *Gordodon*, in which the diastema is not directly related to that occurring in a supposedly haptodontine-grade sphenacodontian (Spindler 2015).

The inclusion of *Bohemiclavulus*, the new name for "*Naosaurus*" *mirabilis*, never interfered with *Ianthasaurus* in specimen-based tests. Along with the above diagnosis, this supports a distinct genus. That the centrum is not yet elongated, although being a doubtless edaphosaurid, reveals this evolutionary step to have occurred immediately antecedent to *Ianthasaurus*, which in return supports the classification of *Xyrospondlyus* with likewise plesiomorphic centrum proportions. *Bohemiclavulus* shares a round spine section with all edaphosaurids but *Xyrospondylus*.

Reisz and Berman (1986) assumed that the phylogenetic position of *Edaphosaurus credneri* might be resolved, whereas Huttenlocker et al. (2011) counted it as Edaphosauridae incertae sedis. As expected from the above description, the supposed position of this potentially valid species is rather high within the derived edpahosaurids. Although based on very few scored characters, it shows a strong affinity to *Edaphosaurus*, to which it most likely belongs regardless its specific status. The tiny SaP 344 reveals no certain behavior during the tests, except that it is apparently more derived than *Ianthasaurus*. Taking its obvious juvenile condition into account, an assignment to *Edaphosaurus* is possible. The parietal morphology of SaP 344 tempts connection to *E. pogonias*, but there is little comparability to other edaphosaurids. The faunal overlap with *E. credneri* is counted as additional indication for the tentative assignment to *Edaphosaurus*.

Remigiomontanus, *Lupeosaurus*, *Glaucosaurus*, and "*Edaphosaurus*" *colohistion* were difficult to resolve until the inclusion of *Gordodon*. The low number of tubercle rows suggests a position of *Remigiomontanus* more basal than any species of *Edaphosaurus*, possibly including *E. colohistion*. A position of *Remigiomontanus* more basal than *Edaphosaurus* + *Lupeosaurus* is supported by the low neural arch (excluded character, listed by Huttenlocker et al. 2011), the absence of a hyposphene (apparently shared with *E. colohistion*), and slender phalanges. Regarding spine robustness, *Remigiomontanus* resembles the Texas species of *Edaphosaurus* and *E. colohistion*, whereas *Lupeosaurus* resembles *E. novomexicanus*. The latter also share a reduced tuberculation, which could yield additional support for a sister-group relationship of *Lupeosaurus* and *Edaphosaurus*, suggesting a secondary evolution of full tuberculation. However, any scenario of the history of tuberculation, spine height, etc. contains discontinuities. In the light of new insights to the variation of dorsal vertebrae characters "*Edaphosaurus*" *colohistion* needs revision.

Discussion

Evolutionary history of Edaphosauridae

During the late Pennsylvanian, the major clades of basal synapsids diverged, including the therapsid lineage (Spindler 2014, 2015). The presence of large edaphosaurids in the Carboniferous (Berman 1979) parallels the evolution of other families, such that genera such as *Ophiacodon*, *Sphenacodon* and *Dimetrodon* persisted throughout much of the Cisuralian. Although raising doubt on the generic assignment of *E. colohistion*, this seems likely for *Edaphosaurus* in general. A derived *Edaphosaurus*-like form has also been yielded by the Virgilian Vamoosa Formation (OMNH 73688). Taking into account that the rich assemblages from Garnett and Badger Creek reflect a sphenacomorph diversity shortly after or during the late phase of a radiation event (Spindler 2015), edaphosaurid origins can be estimated as of Kasimovian age. With KUVP 1425 from Garnett being even a derived representative, the same pattern seen in ophiacodontids and sphenacodontians can be stated, recognizing a wide diversification within short time. *Remigiomontanus*, along with other European members, provides further evidence for a high diversity until the Carboniferous-Permian boundary. Subsequently, in the Cisuralian, *Lupeosaurus* and *Edaphosaurus* indicate surviving lineages in overall decreased edaphosaurid diversity. Even beyond the chronospecies of *Edaphosaurus* from Texas (Romer and Price 1940: 387; Berman 1979), size increase can be assumed as a superior mode of evolution, whereas some highly variable traits hamper to apply certain trends to the majority of edaphosaurid material.

Functional implications for edaphosaurid back sails

All certain edaphosaurids bear a back "fin" built up of elongated neural spines that had evolved convergently to certain sphenacodontid synapsids, most commonly regarding *Dimetrodon*. Mostly, edaphosaurids can be recognized due to characteristic lateral spikes. In case the functional aspects of both herbivory-induced trunk modifications and spine morphology reflect rather constant trends, axial characters should yield valuable phylogenetic signals.

It remains enigmatic when and how the iconic fin back of edaphosaurids evolved, although the Garnett assemblage contains hyper-elongated spines with the apomorphic rounded cross section (*Ianthasaurus*), the plesiomorphic blade-like section (*Xyrospondylus*), and the low blades in sister taxa ("*Haptodus*" *garnettensis*, *Ianthodon*). From the current knowledge, this evolution might have taken place rather quickly, with lateral tubercles being present since the very beginning. Various interpretations have been suggested for primary and secondary functions of the back sail, such as the support of specialized soft tissues, thermo-regulation, individual recognition or defense (Romer and Price 1940; Bailey 1997; Modesto and Reisz 1990a; Huttenlocker et al. 2011). Although a lateral rotation of spines (Jaekel 1910: fig. 1, 1911: fig. 158) is impossible due to vertebral interlocking, a defensive structure seems possible, especially since this herbivorous branch is distinguished from carnivorous, sail-backed sphenacodontids by the presence of lateral spikes. This protection of edaphosaurids as potential prey of contemporary synapsids gains further support by the development of clubs and robust areas in the anterior sail. Probably, the more robust spines in the anterior sail of *Ianthasaurus* exist for the same reason. In the holotype, a possible callus in the 21st to 23rd spine is documented (Reisz and Berman 1986: fig. 2), which would confirm a source of destruction that does not affect neighboring spines, as would be expected from a bite. Recent investigations also found indication that the characteristic lateral tubercles have worn keratinous caps in life (courtesy of C. Shelton, pers. comm. 2016). However, since the increased skin surface of the back sail would inevitably result in thermo-regulatory effects, a multi-function nature of edaphosaurid spines seems likely. *Remigiomontanus* demonstrates the continuous component of sail evolution at a stage to which *Edaphosaurus* species could add only restricted variation due to considerable functional conservatism.

Trophic adaptation

Along with derived anamniotes of the clade Diadectidae, the synapsid Edaphosauridae represent the oldest known terrestrial vertebrate herbivores (Reisz and Fröbisch 2014: fig. 4). It remains unknown how large the herbivorous component was in the diet of their earliest representative *Ianthasaurus*, since variable dental characters (Mazierski and Reisz 2010; Spindler 2015) require a closer look at this potentially oldest herbivorous tetrapod. However, the late Pennsylvanian to Cisuralian genus *Edaphosaurus* is as strongly adapted to a high fiber herbivorous lifestyle as ever gained until its time. With respect to this ecological guild, Edaphosauridae precede any other synapsid herbivores, such as Caseidae and certain Therapsida. In the early evolution of herbivorous lineages (Sues and Reisz 1998; Reisz and Sues 2000; Hotton et al. 1997; Pearson et al. 2013; Reisz and Fröbisch 2014; Spindler et al. 2016), the clade Edaphosauridae holds a key position. As is typical for large plant-eaters, not only the skulls are highly apomorphic. Additionally, their trunks have evolved a typical ton-shape, involving modifications in the zygapophysial, diapophysial, and costal morphology (Mazierski and Reisz 2010; Table 1).

Ianthasaurus has been recognized to be faunivorous in juvenile stages (Mazierski and Reisz 2010). This interpretation is confirmed by our specimen-based cladistic tests, in which juvenile stages purport a more basal phylogenetic position. If a protective structure is assumed for the ornamented back sail to indicate a prey and primary consumer, adult herbivory can be assumed as nearly ancient to the known spectrum of edaphosaurids. Herbivory in the large ROM 59933 is indicated by straight and bulbous teeth, saddle-shaped quadrate condyles (Mazierski and Reisz 2010), the anteriorly shortened pterygoid, probably with initial formation of a chewing plate, and proportionally longer dorsal ribs to include a larger digestive tract. In the Badger Creek specimens, the tooth shape is closer to that seen in *Edaphosaurus*. Subsequent to the stage of *Ianthasaurus*, further adaptations concern the smaller skull with shortened snout, loss of the prefrontal lateral recess (probably related to an adaptation for carnivore vision), gonys-like deepened dentary tip, corresponding chewing apparatus in palate and mandible, and the barrel-shaped trunk due to longer and incised diapophyses and a gradual loss of the tuberculum in stronger curved, robust ribs. After all, edaphosaurid osteology shows step-wise increasing adaptation to herbivorous lifestyle.

Edaphosaurid teeth can be serrated and bear cutting edges (Modesto 1995). A bizarre, broad-based tooth type documented for *E. pogonias* (Case 1907: pl. 34; Davis 2012: 125) would represent an early case of distinct heterodonty in the postcanine region. However, neither Romer and Price (1940) nor Reisz (1986) commented on this structure.

Modesto and Reisz (1990a) as well as Mazierski and Reisz (2010; Table 1) listed insectivorous versus herbivorous adaptations, of which the elongated trunk of 29 presacral vertebrae is considered a striking autapomorphy of *Ianthasaurus* (Reisz and Berman 1986). This is debated herein, because the underlying assumption that hyper-elongated spines do not include sacral vertebrae was based solely on Texas species of *Edaphosaurus*. Since a back sail reaching to the proximal tail is possible in *Dimetrodon*, there is no anatomical necessity to estimate the presacral number from the 30 elongated spines of *Ianthasaurus*. A detailed comment is made in Online Resource 4 (excluded character).

Probably, *Glaucosaurus* (Modesto 1994) indicates that juveniles of derived forms might still have exhibited the modifications from faunivorous to herbivorous lifestyle in their ontogeny, as a rough reflection of their early evolution. Nonetheless, the marginal teeth of *Glaucosaurus* are not as pointed as in the smallest *Ianthasaurus*.

After all, *Remigiomontanus* is found to be a grown individual of a fully herbivorous form, although the zygapophysial angle and dorsal rib morphology are not as derived as in Texas species of *Edaphosaurus*. With shortened cervical centra and the observation that anterior cervical ribs significantly increase in size towards the trunk, the unknown skull can be reconstructed as proportionally small in *Remigiomontanus* and *Lupeosaurus*.

Paleobiogeography and environments

Several localities are confirmed as having produced *Ianthasaurus*, rejecting a preliminary hypothesis that this genus and the early sphenacomorph radiation are endemic in Garnett (Spindler 2015). *Ianthasaurus* and at this time indistinguishable close relatives occurred in nowadays Colorado (Badger Creek form) and Pennsylvania (“*Edaphosaurus raymondi*”). In Badger Creek, a “haptodontine” has been identified by Sumida and Berman (1993), which closely resembles *Ianthodon* (pers. obs.) and, therefore, yields further support for the non-endemic nature of the Garnett assemblage. The European counterparts to Garnett synapsids are not identical, but remarkably close, comprising the haptodontine-grade sphenacodontian *Haptodus baylei*, and the edaphosaurid *Bohemiclavulus mirabilis*.

Concerning more derived edaphosaurids, no faunal provinces (previously stated by Berman 1979) can be reconstructed from the increased variability and diversity. The total picture of edaphosaurid evolution is a compound of North American and European material, without regional or stratigraphic specifics recognizable so far. Revised edaphosaurid diversity includes basal, moderately derived, *Edaphosaurus*-like, and large-sized forms from both continents.

As for most early synapsid localities, the Permian edaphosaurid record is largely restricted to non-juvenile specimens. After the rejection of *Edaphosaurus minuta* and *Bayloria morei*, the Niederhäslich assemblage is the only one that contains early juvenile material. As contributing to a multitaxon nursery (Spindler 2013), this record is not random. Like in Palaeohatteriidae (Spindler 2013, 2016), a significant ontogenetic habitat shift might have applied to Edaphosauridae. Regardless of ontogenetic stages, the co-occurrence of edaphosaurids with eryopids, diadectids and sphenacodontians is evident for North American and European assemblages (e.g., Remigiusberg, Kounov, Niederhäslich, Autun, Garnett, Badger Creek, Waurika, Dunkard Group, Wichita and Clear Fork Group).

Many edaphosaurid remains are associated with coaly sediments, suggesting hygrophilous vegetation as preferred habitat. Such an environment is documented for “*Edaphosaurus raymondi*”, *Ramodondron*, *Bohemiclavulus*, partially the Badger Creek *Ianthasaurus*, associated with limestones for “*Edaphosaurus*” *colohistion*, and probably for the Niederhäslich specimens (limestone member underlying a coal seam). The type of *Remigiomontanus* is embedded in a lacustrine limestone (Fig. 15). This general swamp-dwelling habitat preference is intensively discussed by Berman (1979). There might be exceptions, as for the xerophytic flora associated with *E. novomexicanus* (Romer and Price 1940) and the Garnett forms (Reisz et al. 1982: 748; Moore et al. 1936; Peabody 1952). However, there are intensively sampled localities that still lack edaphosaurid remains, with a noticeable absence in the Bromacker locality, Thuringia, and Richards Spur, Oklahoma. These proximal or probably upland environments could indicate a general tolerance limit for edaphosaurids, concerning aridity or seasonality, connected to resulting vegetation.

If “*Belebey*” *augustodunensis* is correctly identified, this Autun edaphosaurid would be the only known edaphosaurid that co-occurred with a caseid, being the admittedly basal caseid *Callibrachion* (Spindler et al. 2016; Brocklehurst et al. 2016). In general, the decline of edaphosaurids in the Artinskian apparently correlates with the spreading of large-bodied caseids (Reisz and Fröbisch 2014: fig. 4).

Conclusions

The revision and new description of European edaphosaurid material increases the known diversity, whereas disparity of this lineage remains limited, suggesting a more or less straight trend of herbivorous adaptation. Valid determinations include: (1) *Bohemiclavulus mirabilis* (Fritsch, 1895) [*Bohemiclavulus* gen. nov.]; (2) juvenile specimens tentatively referred to *Edaphosaurus*, including *E. credneri* Jaekel, 1910 [nomen dubium]; (3) *Ramodendron obvispinosum* Švestka, 1943 [nomen nudum], as the largest edaphosaurid from Europe; and (4) *Remigiomontanus robustus* gen. et sp. nov.

Remigiomontanus was recently discovered in latest Pennsylvanian to earliest Permian shallow lacustrine deposits of the SW German Saar–Nahe Basin. Its type material exhibits a unique character combination filling the morphological gap between *Ianthasaurus* and *Edaphosaurus*. *“Belebey” augustodunensis* from the French Autun Basin, introduced as a bolosaurid parareptile by Falconnet (2012), is possibly another European edaphosaurid.

Fig. 15 Artist's impression of *Remigiomontanus* carcass from a lacustrine deposit, as a potential food source of xenacanthids that are abundant in this assemblage

Full resolution in phylogenetic hypotheses is hampered by immense variation in sail characters, as well as substantial matrix gaps. Convincing resolution was gained by the description of *Gordodon* (Lucas et al. 2018).

During the late Pennsylvanian, a broad radiation of Edaphosauridae took place. From the early forms on, no faunal provinces, endemism or evolutionary centers could be identified. Between North America and Europe, the spectrum of Edaphosauridae is largely comparable. The same is true for the evolution of back sails, implying strong functional constraints. Variation in this structure might be explainable by multi-function. In general, Edaphosauridae represent a case of size selection (with different rates, see Brocklehurst and Brink 2017: fig. 3) that parallels adaptive traits required to perform herbivory. The latter is initially present in adult *Ianthasaurus* and to some degree in *Remigiomontanus*. An overall preference of Edaphosauridae for hygrophilous habitats can be confirmed.

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