A Triassic averostran-line theropod from Switzerland and the early evolution of dinosaurs

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Abstract

Our knowledge of the fossil record of early theropod dinosaurs has greatly improved over the last two decades. Yet still very little is known about European taxa because they are largely incomplete. Here we present an exceptionally well preserved theropod skeleton from the Late Triassic of Europe, pertaining to a new genus and species. The specimen includes a nearly complete skull, two articulated forelimbs, and stomach contents. *Notatesseraeraptor frickensis* gen. et sp. nov. is an early diverging neotheropod with affinities to *Dilophosaurus* + Averostra and displays an interesting mixture of character states typically seen either in coelophysids or in dilophosaurids. Based on our phylogenetic analysis *N. frickensis* gen. et sp. nov. is considered one of the currently oldest and most basal members of the lineage, leading to Averostra. A monophyletic 'traditional Coelophysoidea' including *Dilophosaurus* is not supported.

Since 1961 the Gruhalde clay pit in Frick (Aargau, Switzerland) is well-known for its abundant, articulated *Plateosaurus* material, which is derived from the middle part of the Gruhalde Member of the Klettgau Formation. Within this lithological unit a new dinosaur layer with articulated skeletal material was discovered in 2006. The new layer is located above the classic *Plateosaurus* bone beds. It forms the uppermost part of the Triassic in Frick (latest Norian[1]) and is overlain by marine sediments of the Early Jurassic[1]. Recent excavations in the new layer yielded the excellent preserved theropod *Notatesseraeraptor frickensis* gen. et sp. nov., some large isolated teeth that could be either theropod in origin or provide evidence for pseudosuchians in Frick, and several specimens of a sauropodomorph. The recovered skeletal parts of *N. frickensis* gen. et sp. nov. belong to an immature individual of 2.6 to 3 m length.

The presence of the fairly complete skeleton of the new theropod *N. frickensis* gen. et sp. nov. in the upper Norian[1] beds of Frick increases the scarce knowledge of Late Triassic European neotheropods considerably. The three previously known species are all fragmentary and include: *Liliensternus liliensterni* (Huene, 1934) and *Procompsognathus triassicus* Fraas, 1913 from the middle and late Norian of Germany, and *Lophostropheus airelensis* (Cuny & Galton, 1993) from Rhetian to Hettangian beds of France[2]. With the exception of the skull of the new Swiss theropod and a few incomplete cranial elements of *Liliensternus*, no European Late Triassic neotheropod skulls are known. And even from the Lower Jurassic, there is only the recently reported *Dracoraptor hanigani* (Martill et al., 2016) from Wales with a preserved partial cranium.

Worldwide, however, the fossil record of Late Triassic and Early Jurassic dinosaurs has greatly improved in the last twenty to twenty-five years and the origin and early radiation of Dinosauria has been widely studied e.g.[3–9]. Nonetheless, there are still different hypotheses about early theropod relationships. Most of the taxa that have been assigned to the Coelophysoidea (e.g. *Coelophysis*, "*Syntarsus*", *Dilophosaurus*, *Liliensternus*, *Zupaysaurus*[10–13]) represent the earliest major radiation of Neotheropoda. Within this group, the Coelophysidae (e.g. *Coelophysis*, "*Syntarsus*") is the best supported clade. More recent studies, however, suggest that at least some members of the 'traditional Coelophsoidea' (this term was already used by ref. [14]) (e.g. *Dilophosaurus*) are more closely related to the tetanurans and that the Dilophosauridae may represent a second clade of early non-averostran neotheropods e.g.[15–17]. But the monophyly of both 'traditional Coelophysoidea' and Dilophosauridae is still controversial. Concerning this debate *N. frickensis* gen. et sp. nov. is a critical taxon to help understand the relationships of early theropods because it shares many features with both clades. In addition, due to its good preservation it will promote the phylogenetic assignment of less complete theropods more accurately in the future. In this paper, we describe the new genus and species, *Notatesseraeraptor frickensis* gen. et sp. nov., and discuss its phylogenetic position.

Remarks: For the clade Coelophysoidea, we follow the definition of Sereno *et al.* (2005)[18] (= Coelophysoidea *sensu stricto* of Ezcurra & Brusatte 2011[14]). Hence, it is understood as a monophyletic clade by definition, but with changing taxonomic content, depending of individual phylogenetic analyses. After the present study the clade Dilophosauridae (phylogenetically defined by Hendrickx *et al.* (2015)[19]) may include *Dilophosaurus wetherilli*, *Cryolophosaurus ellioti*, the fragmentary *Dracovenator regenti,* and *Notatesseraeraptor frickensis* gen. et sp. nov. (see Supplementary Information SI for further implications and a suggested diagnosis for Dilophosauridae).

Results

Systematic palaeontology

Dinosauria Owen, 1842

Saurischia Seeley, 1887

Theropoda Marsh, 1881

Neotheropoda Bakker, 1986

Notatesseraeraptor frickensis gen. et sp. nov.

Etymology—*Nota*, feature (Latin); *tesserae*, individually shaped tiles used to create a mosaic (Latin), in reference to the intermixture of features typically known from either dilophosaurid or coelophysoid neotheropods; *raptor*, predator (Latin) and *frickensis*, derived from the village of Frick.

Holotype—Sauriermuseum Frick (SMF) 06-1 and 09-2: cranium (SMF 09-2) and partial postcranial skeleton (SMF 06-1) of a likely juvenile to subadult individual (stages of ontogenetic development *sensu*[12]) consisting of two articulated forelimbs; shoulder and pelvic girdle; 13 dorsal, 4 sacral and 4 proximal caudal vertebrae; cervical, dorsal and sacral ribs; chevrons; and gastralia. Out of the preserved contents of the stomach a well preserved maxilla of the rhynchocephalian *Clevosaurus* could be identified (Fig. 1L)[20–21].

Horizon and locality—New upper dinosaur layer, one meter beneath the Triassic-Jurassic boundary, uppermost Gruhalde Member, Klettgau Formation, latest Norian[1]; clay pit Gruhalde of the Tonwerke Keller AG, Frick, Canton Aargau, Switzerland. Coordinates 2° 642' 960" / 1° 261' 963" (www.strati.ch).

Diagnosis—*Notatesseraeraptor frickensis* gen. et sp. nov. differs from all other theropods by the following unique combination of morphological character states: four exceptionally long but slender premaxillary tooth crowns that are as long as the anterior maxillary teeth but mesio-distally less wide (ratio 3:1 vs. 2.4:1); premaxillary tooth crowns labio-lingually flattened, mesially somewhat broader than distally and with fine serrations along their mesial and distal carinae (5 per 1mm); two recesses in the maxillary antorbital fossa (homologous with the promaxillary foramen, maxillary fossa); supratemporal fossa restricted to the posterior half of the parietal (autapomorphy); shallow basisphenoid recess; exit of vagus nerve through a posterior foramen lateral to the foramina for hypoglossal nerve; three distinct processes of the articular (medial, dorsolateral, and dorsal process); markedly low-rectangular neural spines (ratio 2:1) of the posterior dorsal vertebrae; posteriorly increasing height of dorsal neural spines; flattened ventral surfaces and expanded articular faces of sacral centra; deep fossa on lateral surfaces of 2nd sacral vertebra; anterior caudals with longitudinal fossae on centra and neural arches; prominent antero-proximally located tubercular processes on the first four chevrons; pronounced expansion (=boots) on the distal ends of the pubis and ischium, ischial expansion (boot) larger than pubic expansion.

Description and comparison

The cranial bones are disarticulated, but still closely associated. With the exception of a few elements, each paired bone (facial, palatal, braincase, and lower jaw) was recovered at least from one side (Fig. 1 A-F). Thus over 90% of the skull elements are known which makes SMF 09-2 the most complete theropod skull from the Late Triassic and Early Jurassic of Europe. The reconstructed cranium is proportionally long (about 225 mm from tip of premaxilla to end of quadrate condyle) and low as it is commonly found in 'traditional coelophysoid' grade neotheropods[10–11,23–26]. Based on a 3D-reconstruction of the skull the

preorbital region comprises about two-thirds of the total skull length, which is about 2.5 times the skull's greatest depth in the middle of the orbit when jaws are occluded. With *Dilophosaurus wetherilli*[24], the Coelophysoidea[10–12,23] and *Tawa hallae*[8] it shares a ventral flange on the maxillary process of the premaxilla and a discontinuous upper tooth row (subnarial gap and diastema[27]) at the premaxilla - maxilla transition. Laterally, the premaxilla is perforated by six neurovascular foramina. One particular foramen that is located at the base of the nasal process is slit-shaped and also found in *D. wetherilli*[24], *Dracovenator regenti*[27] and *Dracoraptor hanigani*[28]. Most striking, however, is the mentioned morphology of the premaxillary teeth. In contrast to coelophysids where the mesial premaxillary teeth show only minor curvature, have a nearly circular cross section, and only a few to no serrations[10,29], the premaxillary tooth crowns of *N. frickensis* gen. et sp. nov. are all strongly recurved, laterally compressed, and bear fine serrations (14 per 3mm) along their mesial and distal carinae. Furthermore, like in *Eoraptor*[30(Fig.10,11)], the premaxillary tooth crowns are of similar proportions as the anterior maxillary crowns. In the coelophysid "*Syntarsus*" *kayentakatae* (MNA V2623), where the maxillary dentition looks similar to SMF 09-2, the premaxillary teeth are, on the other hand, conspicuously smaller and much more slender. Such a difference in size is also present in *Coelophysis bauri*[29] (CM P-50530). As in *Dracoraptor*[28] and *Dilophosaurus*[24] the premaxillary crowns are procumbent. The maxilla forms the main border of the large internal antorbital fenestra that constitutes more than 30% of the estimated skull length. A pronounced horizontal ridge is oriented along the ventral rim of the antorbital fossa and, like in *Eoraptor*[30,31], *Zupaysaurus*[25,32], *Monolophosaurus*[33] and abelisaurids[34], the dorsal and ventral margins of the horizontal process are parallel. The antorbital fossa has two relatively large, oval recesses located where the ascending process meets the facial region of the maxilla, here referred to as homologous with the promaxillary foramen[35] and maxillary fossa[16]. While a promaxillary foramen also occurs in "*Syntarsus*" *kayentakatae*[11–12], a maxillary fossa or even a fenestra is absent in coelophysids, *Dilophosaurus*, and ceratosaurians but both recesses are present in *Zupaysaurus*. As in *Zupaysaurus* the maxillary fossa of *N. frickensis* gen. et sp. nov. approaches in size and shape with the maxillary fenestra of basal tetanuran theropods (e.g. *Dubreuillosaurus*[25]), in which the fenestra does not pierce the medial lamina of the maxilla. In SMF 09-2 both the nasal and the lacrimal show no signs of pronounced cranial crests, typically developed in some potential dilophosaurid taxa e.g.[15,24,27,36]. Instead, these bones bear a low marginal ridge projecting dorsolaterally slightly above the maxilla. The preserved left maxilla bears at least 15 alveoli, which is significantly less than in most adult *Coelophysis* specimens[29] with tooth rows bearing usually 22 to 24 alveoli. Anterior to the internal antorbital fenestra *N. frickensis* gen. et sp. nov. has five alveoli in the preserved left maxilla, the juvenile *C. bauri* specimen NMMNH P-42200 on the other hand has already six and adults have seven or even more alveoli (e.g. CM 31374). Laterally, the antorbital fossa of the L-shaped lacrimal is split by an anteriorly extended sinuous lamina. In SMF 09-2, the supratemporal fossa is well developed on the anterior and the posterior process of the postorbital, whereas it is restricted to the posterior half on the parietal. This restriction is most likely an autapomorphic feature of *N. frickensis* gen. et sp. nov., because in closely related taxa, the supratemporal fossa is well developed throughout the parietal and even extends onto the frontal (e.g. CM31374, QG194)[11,15, 25]. Alongside the midline of the unfused parietals, there is a longitudinal shallow trough, resembling the condition found in

"*Syntarsus*" *kayentakatae*[11]. In *N. frickensis* gen. et sp. nov. and *Z. rougieri* the lateral surface of the jugal is quite flat and bears no horizontally running ridge, as it is typically seen in *Herrerasaurus ischigualastensis*[37] and the Coelophysidae[16,26]. Furthermore, the anterior process of the bone is rather long and possibly reached the internal antorbital fenestra in the articulated skulls of both taxa. There is no lacrimal process as seen for example in *Allosaurus* but *N. frickensis* gen. et sp. nov. as well as *Z. rougieri* (PULR 076) possess at least a dorsal bulge in the same anatomical position. The posterior and the dorsal process of the jugal form a nearly right angle in lateral view and the lower temporal bar consists of the jugal and the quadratojugal equally. In SMF 09-2, the quadratojugal and the quadrate are not fused, which could also be related to its ontogenetic age[20–22]. Similar to *D.wetherilli*[24] the lateral quadrate ala of *N. frickensis* gen. et sp. nov. is large, dorsally expanded and fan-shaped. The pterygoid ala on the other hand is double-lobed and looks like the inverted ear of an elephant, resembling strongly the condition seen for example in *Coelophysis rhodesiensis*[38]. The articulated left hemi-mandible of *N. frickensis* gen. et sp. nov. (Fig. 1D-F) is largely comparable to the long but remarkably slender mandibles of the coelophysids. However, compared to *Coelophysis bauri* (AMNH 7240) the teeth in the lower dentition are more widely spaced in the new taxon (2 vs. 3 alveoli per 10 mm)[16]. We estimate a total of 19 to 23 alveoli for each mandibular ramus[22]. The lateral surangular shelf is well developed and merges caudally into the anterior rim of the lateral portion of the glenoid fossa. The retroarticular process of *N. frickensis* gen. et sp. nov. (SMF 09-2; Fig. 1E-F) is long and narrow as in *Eoraptor*[30], the coelophysids and *Dracovenator*[27]. With the coelophysoids it shares also a dorsally orientated attachment area for the musculus depressor mandibulae[16]. Furthermore, *N. frickensis* gen. et sp. nov. possesses three distinct processes arising from the dorsal and the medial rim of the articular, which otherwise are only found in the dilophosaurids and in a reduced number also in averostrans (Fig. 1F). Therefore, the articular shows a mixture of character states that can be seen in *C. rhodesiensis*[23] and *D. regenti*[27].

Overall, the preserved postcranial elements of *N. frickensis* gen. et sp. nov. (SMF 06-1, observations are mainly based on[20–21], Fig.1 G-K) share most of the morphological similarities with "*S.*" *kayentakatae*[20–21]. In SMF 06-1, the length of the vertebrae increases posteriorly, both in the dorsal (31 mm in D2 to 42 mm in D10) and the caudal (28 mm in C1 to 33 mm in C4) series, but is constant in the sacral region. Concerning the length of the dorsal vertebrae, *Dilophosaurus*[24] shows the same relative relation as observed in the Swiss specimen. In *Herrerasaurus*[39], *Coelophysis*[10–11] and *Liliensternus*[40] on the contrary, the centrum length of the dorsal series is rather constant. Most of the preserved vertebrae of *N. frickensis* gen. et sp. nov. bear fossae (longitudinal, cranial and caudal fossa on the centra of anterior dorsals, fossa on centra of sacrals and longitudinal fossae on centra and neural arches of anterior caudals). The transverse processes of the anterior dorsal vertebrae in SMF 06-1 do not have the strongly backswept anterior margin seen in coelophysids and *Ceratosaurus*[41] but are subrectangular and mainly laterally directed in dorsal view. Furthermore, the height of the dorsal neural spines increases posteriorly as seen in *Eoraptor*[30], *Herrerasaurus*[39] and tetanuran theropods (e.g. *Piatnitzkysaurus floresi*[42], *Sinraptor dongi*[43] and *Allosaurus fragilis*[44]). Compared to most other early diverging theropods where the ventral surfaces of the sacral centra are rounded or keeled[45], they are

flattened in SMF 06-1 and *C. rhodesiensis*[23]. The scapula is similar to the corresponding element in coelophysids, *Dilophosaurus*[46] and *Eodromaeus*[7] in possessing a nearly straight posterior margin and a distinctly expanded distal end. As in most basal theropods, *N. frickensis* gen. et sp. nov. has plesiomorphically long forelimbs. The radius (97 mm) is about three quarters of the length of the humerus (128+ mm) and the manus (2nd finger around 127 mm) is of similar length to the two former skeletal elements (Fig. 1G, H). The manus is composed of four digits, whereas the 4th is reduced to a very slim metacarpal (MC), which is only half as wide as MC I to III, and has a single small phalanx. From proximal (I) to distal (IV), the corresponding phalanges of the digits become shorter and the first phalanx of the first digit is the longest non-ungual phalanx of the manus (Fig. 1G, H). Shape and proportions of the ilium are similar to those found in *Coelophysis*[10,23] and other early neotheropods such as *Dilophosaurus*[12:Fig.71C,24]. However, the outline of the bone differs slightly as the dorsal iliac margin is somewhat convex in lateral view, rather than straight (e.g. *Coelophysis*[10,23]) or strongly rounded (e.g. *Sinraptor dongi*[43]). On the caudo-lateral surface of the ilium, there is a distinct rim for the musculus iliofibularis that continues over the whole ventral margin of the posterior blade. The pubis has a slightly downwards curved shaft and is, like the shorter rod shaped ischium, long and slender. As in the Coelophysidae, the ischium has a straight shaft, but compared to the former clade in SMF 06-1 the bone is distally clearly more strongly expanded, since the ischiadic boot is much larger than the pubic one. The pubis is about 1.7 times longer than the ischium and thus shows similar proportions as the pelvic elements of *Dracoraptor*[28]. In the Frick theropod material, *Dilophosaurus*[24] and *Liliensternus*[12], the distal expansion of the ischium is much larger than the corresponding structure of the pubis. In the Coelophysidae these structures are of equal size. As in *Dilophosaurus*[12,24], there is a distinct antero-proximally located tubercular process on each of the four preserved cranially forked chevrons (C1 – C4).

Phylogeny

Our comprehensive phylogenetic analyses, with emphasis on early neotheropods, revealed that *N. frickensis* gen. et sp. nov. is an early averostran-line theropod outside the clade Coelophysoidea (Fig. 2). In correspondence with[8,15,16,19,27,47,48], and regardless of taxa choice, a dichotomy is found at the base of Neotheropoda, which is formed by the two monophyletic clades Coelophysoidea and averostran-line neotheropods. The best supported clade in each of our conducted analyses is the clade that is made up of *Notatesseraeraptor frickensis* gen. et sp. nov., *Dilophosaurus*, *Cryolophosaurus*, (*Dracovenator* if included) and Averostra. *Eoraptor*, *Eodromaeus*, *Herrerasaurus* and *Tawa* are always found to be outside Neotheropoda. One of the trees best reflecting the relationships is shown in figure 2.

Phylogenetic discussion and conclusion

Hypotheses on early neotheropod relationships still agree little. The assignment of several taxa to the Coelophysoidea is uncertain and the monophyly of the clade Dilophosauridae is controversial[8,14,49].

A reduced analysis, where only taxa were included with at least 40% of the available character states ('40%-rule analysis') and which also contained no Averostra, produced a single most parsimonious tree (MPT), where *Notatesseraeraptor* gen. nov. is found as a

member of Dilophosauridae (Supplementary Figure S1, and Supplemetary Information S1 for a suggested diagnosis of the clade). A 'dilophosaur clade' has also been recovered by other authors e.g.[15,17,27] but as it was mostly supported by cranial crest characters, it was thought that the grouping may be artificial[33]. In the '40%-rule analysis' of this study, the monophyly of the Dilophosauridae is supported by three unambiguous synapomorphies and nine additional ones under DELTRAN and ACCTRAN optimization, whereof none is related to cranial crest character states (Supplementary Table S2a). In *D. regenti*, all of the seven synapomorphies pertaining to the articular and the premaxilla are discernible as well. The addition of every further coelophysoid or dilophosaurid taxon to the '40%-dataset' has no influence on the genaral tree topology, but changes at most the position of single neighbouring sister taxa. With the inclusion of any averostran theropod other than *Piatnitzkysaurus* the hypothesis of a monophyletic Diophosauridae is no longer supported. Instead it is suggested that there are several basal neotheropods, more closely related to Averostra than to *Coelophysis*. As shown by the phylogenetic tree in figure 2, which in the main results from the '40%-rule analysis' supplemented by four averostrans, all members of the previously monophyletic Dilophosauridae (inclusive *N. frickensis* gen. et sp. nov.) are recovered as successive basal sister taxa of Averostra. The bootstrap and Bremer support values show that the relationships within the averostran-line neotheropods are very well supported. In contrast the Coelophysoidea as well as the affiliation of *Zupaysaurus* to the non-coelophysoid neotheropods are not supported after only one or two additional steps. In the same analysis, the deletion of *N. frickensis* gen. et sp. nov. leads to an increase from a single MPT to twelve. The strict consensus tree therefore consists of poor resolution with a large polytomy at the base of Neotheropoda. Interestingly, the integration of *Sinraptor* as a fifth averostran theropod, leads to the formation of a clade of *D. wetherilli* and *C. ellioti*. Thus, the dilophosaurids might yet form a monophyletic clade.

As shown by the description and the results of the phylogenetic analysis, *Notatesseraeraptor frickensis* gen. et sp. nov. is an important new taxon with an interesting combination of plesiomorphic and apomorphic features of early theropods. Our study strongly supports a dichotomy at the base of Neotheropoda, formed by the Coelophysoidea (*sensu* ref. 18) on the one hand and the averostran-line theropods, including potential dilophosaurid taxa and Averostra, on the other hand. The question that remains open is whether the potential dilophosaurids are successive sister-taxa to Averostra or form a monophyletic Dilophosauridae. Regardless of whether the Swiss taxon is indeed the possibly oldest dilophosaurid and the first member of this clade known from Europe, it is certainly one of the oldest averostran-line neotheropods and bolsters the origin of this clade in the Triassic. Thus at least two major neotheropod lineages have already diverged in the Late Triassic that both survived the Triassic-Jurassic extinction event.

Methods

Phylogenetic analysis

In order to assess the phylogenetic position of *N. frickensis* gen. et sp. nov., we established a matrix based mainly on those of refs.[15,16,45] and scored 23 taxa for 285 character states (Supplementary Information; 2 (character list) and 3 (character matrix)). Based on this data

set, several phylogenetic analyses with different numbers and combinations of taxa were run in PAUP 4.0b10 (Swofford 2004). The goal of this multiple analyses was to estimate a possible effect of missing data as well as of phylogenetically unstable taxa on the phylogenetic outcome. For the initial analysis we reduced the amount of taxa to 11 (*Eoraptor*, *Herrerasaurus*, *Tawa* and eight Triassic and Jurassic neotheropods) with at least 40% of the available characters scored, both cranial and total (cranial + postcranial) (Supplementary Table S1). This '40%-rule analysis' was the starting point for every further analysis where we added additional coelophysoid and dilophosaurid taxa as well as averostrans where we always used all of the 285 features. Subsequently, all the different tree topologies and synapomorphies of the resulting clades were compared (e.g. Supplementary Table S2). The single most parsimonious tree (MPT) resulting from the '40%-rule analysis' is shown in figure S1.

Dracoraptor hanigani Martill et al., 2016, which is fairly complete is not included in the analyses, since character scoring was nearly finished, when the paper was published. The same is true for the more fragmentary coelophysoid specimens *Camposaurus* Hunt et al., 1998, *Lepidus* Nesbitt & Ezcurra, 2015, *Lucianovenator* Martínez & Appaldetti, 2017 and *Powellvenator* Ezcurra, 2017. Moreover, these taxa are represented mainly by a few elements of the hind legs that are not preserved in the Swiss theropod material.

Nomenclatural acts

This published work and the nomenclatural acts it contains have been registered in ZooBank, the proposed online registration system for the International Code of Zoological Nomenclature (http://zoobank.org/). The LSIDs for this publication is urn:lsid:zoobank.org:act:CD16B061-D440-447E-AD1C-9C11508DF897

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

Acknowledgements

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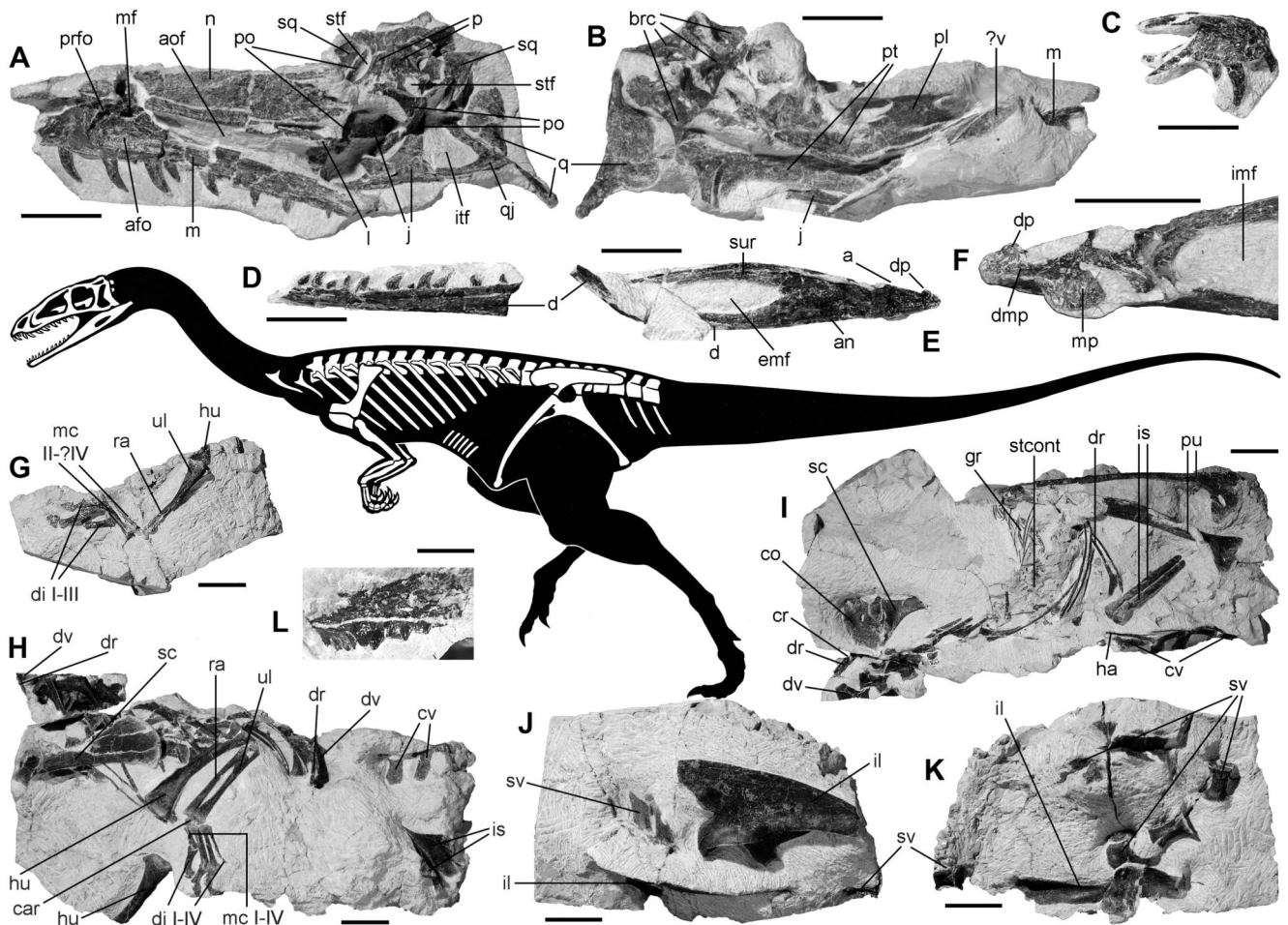
Figure 1. (**A**) to (**K**) skeletal anatomy of *N. frickensis* gen. et sp. nov.
Skull in left lateral (**A**) and palatal (**B**) views. Right premaxilla (**C**) in lateral view. Left ramus of lower jaw: anterior portion (**D**) in lateral view, posterior portion in lateral (**E**) and dorsomedial (**F**) views. (**G**) Right forelimb. Large slab with postcrania from above (**H**) and below (**I**, ventral on top). Small slab with postcrania from above (**J**) and below (**K**). – (**G**) to (**J**) Anterior is left. (**K**) Anterior is right. – (**L**) Maxilla of *Clevosaurus* (stomach content).– Abbreviations: angular (an), articular (a), antorbital fenestra (aof), antorbital fossa (afo), braincase elements (brc), carpals (car), caudal vertebrae (cv), cervical rib (cr), coracoid (co), dentary (d), digit (di), dorsal process of articular (dp), dorsal ribs (dr), dorsomedial process of articular (dmp), dorsal vertebrae (dv), external mandibular fenestra (emf), gastral ribs (gr), haemapophyses (ha), humerus (hu), ilium (il), infratemporal fenestra (itf), internal mandibular fenestra (imf), ischium (is), jugal (j), lacrimal (l), maxilla (m), maxillary fossa (mf), medial process of articular (mp), metacarpals (mc), nasal (n), palatine (pl), parietal (p), postorbital (po), promaxillary foramen (prfo), pterygoid (pt), pubis (pu), quadrate (q), quadratojugal (qj), radius (ra), sacral vertebrae (sv), scapula (sc), stomach contents (stcont), supratemporal fenestra (stf), surangular (sur), squamosal (sq), ulna (ul), vomer (v). – Scale bars: (**A**) to (**E**) 3 cm. (**F**) 2 cm. (**G**) to (**K**) 10 cm. (**L**) 1000 μm.
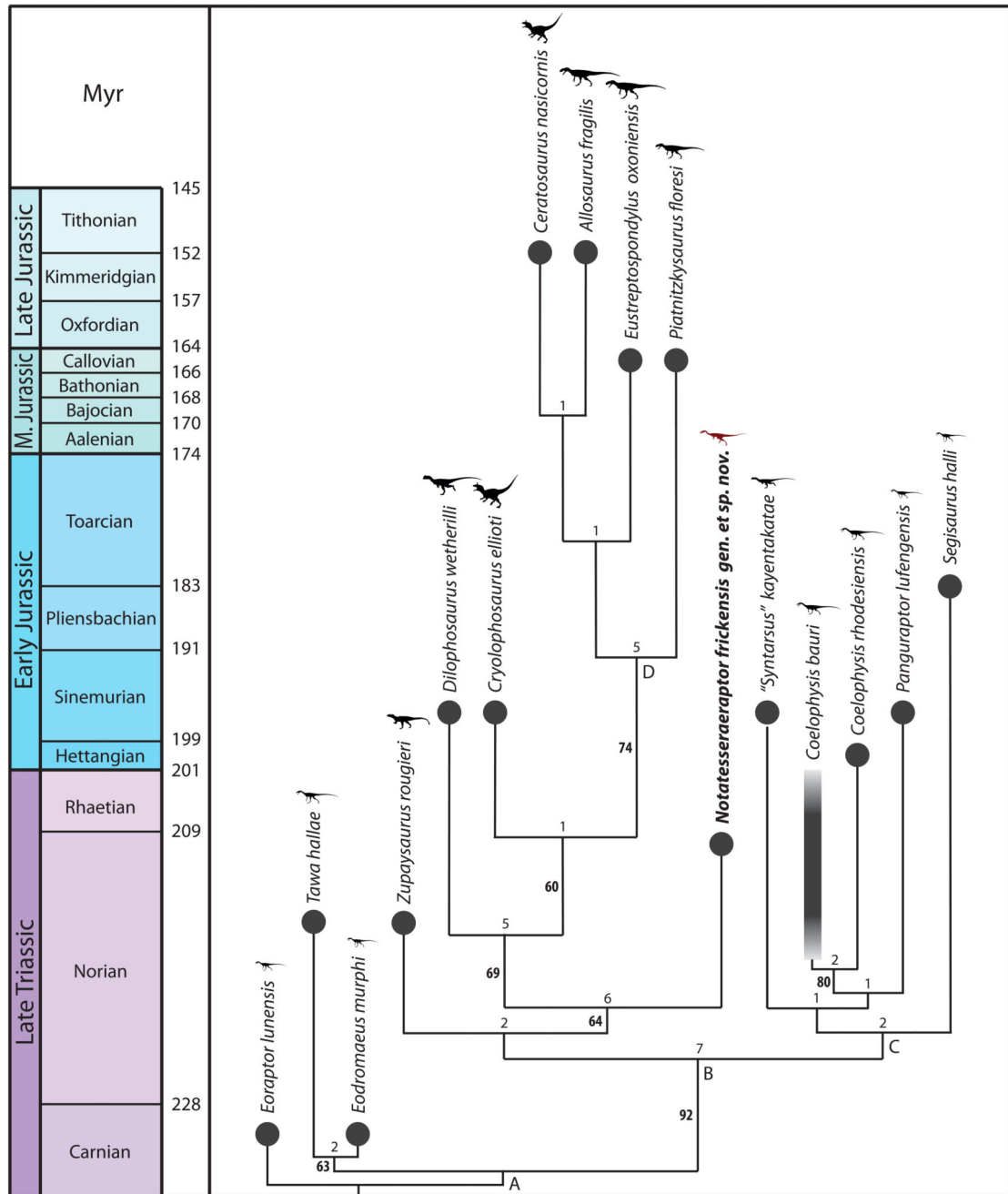
Figure 2. Phylogenetic relationships of *Notatesseraeraptor frickensis* gen. et sp. nov.
Time-scaled single most-parsimonious tree (MPT) resulting from "40%- analysis" (with
Herrerasaurus replaced by *Eodromaeus) + Segisaurus* + 4 Averostra (*Allosaurus*,
Ceratosaurus, *Eustreptospondylus*, *Piatnitzkysaurus*), 155 cranial and 130 postcranial
characters (tree length 547 steps, Consistency Index (CI) = 0.5210, Retention Index (RI) =
0.5379). Bold numbers on the branches indicate bootstrap support when above 50%, regular
numbers show Bremer support indices. **A** Theropoda (*Eoraptor* is not considered a
theropod[30]), **B** Neotheropoda, **C** Coelophysoidea[18], **D** Averostra[50] (is used here for

Piatnitzkysaurus floresi, *Eustreptospondylus oxoniensis*, *Ceratosaurus nasicornis*, *Allosaurus fragilis*, and all the descendants of their last common ancestor). This tree was chosen as an example because it well reflects the main result of our study. Dinosaur silhouettes by Julio Garza (*Dilophosaurus*, "*Syntarsus*"), Scott Hartmann (*Allosaurus, Coelophysis, Dilophosaurus, Eodromaeus, Eoraptor, Eustreptospondylus, Panguraptor, Piatnitzkysaurus, Segisaurus, Tawa*), Brad Mc Feeters (*Ceratosaurus, Cryolophosaurs*), and Iain Raid (*Zupaysaurus*) from Phylopic, used with permission (https://creativecommons.org/licenses/by/3.0/).