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

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Although our knowledge of the fossil record of early theropod dinosaurs has greatly improved over the last two decades, 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 Dilophosauridae and 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) has been 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) and is overlain by marine sediments of the Early Jurassic. Recent excavations in the new layer yielded the excellent preserved theropod N. 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 length 2.6–3.0 m.

The presence of the fairly complete skeleton of the new theropod N. frickensis gen. et sp. nov. in the upper Norian1 beds of Frick increases the scarce knowledge of Late Triassic European neotheropods considerably. The three previously known species are all fragmentary, and include Liliensternus lifiensterni (von Huene2) and Procompsognathus triassicus Fraas, 1913 from the Middle and Late Norian of Germany, and Lophostropheus aulensis (Cuny & Galton, 1993) from the Rhetian to Hettangian Beds of France3. 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 Dracoreptor hanigani (Martill et al.4) from Wales with a preserved partial cranium.

Worldwide, however, the fossil record of Late Triassic and Early Jurassic dinosaurs has greatly improved in the past 20–25 years, and the origin and early radiation of Dinosauria has been widely studied, for example5–11. Nonetheless, there are different hypotheses about early theropod relationships. Most of the taxa that have been assigned to the Coelophysoidea (for example, Coelophysis, ‘Syntarsus’, Dilophosaurus, Liliensternus and Zupaysaurus12–15) represent the earliest major radiation of Neotheropoda. Within this group, the Coelophysidae (for example, Coelophysis and Syntarsus) is the best-supported clade. More recent studies, however, suggest that at least some members of the ‘traditional Coelophysoidea’ (for example, Dilophosaurus; this term was previously used in ref. 16) are more closely related to the tetanurans and that the Dilophosauridae may represent a second clade of early non-averostran neotheropods, for example17–19. Nevertheless, the monophyly of both traditional Coelophysoidea and Dilophosauridae is still controversial. Concerning this debate, N. frickensis gen. et sp. nov. is a taxon that is key to understanding 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.

For the clade Coelophysoidea, we follow the definition of ref. 20 (Coelphysoidea sensu stricto of Ezcurra & Brusatte). Hence, it is understood as a monophyletic clade by definition but with changing taxonomic content, depending on individual phylogenetic analyses. Following the present study, the clade Dilophosauridae (phylogenetically defined in ref. 21) may include Dilophosaurus wetherilli, Cryolophosaurus ellioti, the fragmentary Dracoreptor regenti and N. frickensis gen. et sp. nov. (see Supplementary information for further implications and a suggested diagnosis for Dilophosauridae).

Results

Systematic palaeontology.

Dinosauria Owen, 1842
Saurischia Seeley, 1887
Theropoda Marsh, 1881
Neotheropoda Bakker, 1986
N. frickensis gen. et sp. nov.

Etyymology. 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 sensu14) consisting of two articulated forelimbs; shoulder and...
pelvic girdle; 13 dorsal, four sacral and four proximal caudal vertebrae; cervical, dorsal and sacral ribs; chevrons; and gastralia. From the preserved contents of the stomach, a well-preserved maxilla of the rhynchocephalian *Clevosaurus* could be identified (Fig. 1l)\(^2,\)\(^3\).

**Horizon and locality.** New upper dinosaur layer, 1 m 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.** *Notatesseraeptor frickensis* gen. et sp. nov. differs from all other theropods in 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 versus 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 1 mm); two recesses in the maxillary antorbital fossa (homologous with the promaxillary foramen and maxillary fossa); supratemporal fossa restricted to the posterior half of the parietal (autopomorph); 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 second 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 from at least one side (Fig. 1a–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 is commonly found in traditional coelophysoid-grade neotheropods21,24–27. Based on a three-dimensional 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 the jaws are occluded. With Dilophosaurus wetherilli24, the Coelophysoidea24,25,28 and Tawa hallae29) 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. wetherilli30, Dracovenator regenti31 and Dracoraptor hanigani32. Most striking, however, is the above-mentioned morphology of the premaxillary teeth. Most specimens29 with tooth rows bearing usually 22–24 alveoli. Anterior teeth show only minor curvature, have a nearly circular cross-section and are, on the other hand, conspicuously smaller and much more slender than the posterior ones. Such a difference in size is also present in Coelophysus bauri33 (CM P-50530). As in Dracoraptor and Dilophosaurus24, the premaxillary crowns are very broad. 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, as in Eoraptor13, Zupaysaurus24–26, Monolophosaurus14 and abelisaurids24, 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 premaxillary foramen24 and maxillary fossa34. While a promaxillary foramen also occurs in S. kayentakatae13,14, 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. possesses three distinct processes arising from the dorsal and medial rims of the articular, which otherwise are found only in the dilophosaurids and, in reduced numbers, also in avostraostes (Fig. 1l). Therefore, the articular shows a mixture of character states that can be seen in C. rhodesiensis24, D. regenti, L. splendidus and Eoraptor35. Overall, the preserved postcranial elements of N. frickensis gen. et sp. nov. (SMF 06-1, observations based mainly on refs. 23,24; Fig. 1g–k) share most of their morphological similarities with S. kayentakatae22,23. In SMF 06-1, the length of the vertebrae increases posteriorly in both the dorsal (31 mm in D2 to 42 mm in D10) and caudal (28 mm in C1 to 33 mm in C4) series, but is constant in the sacral region. In regard to the length of the dorsal vertebrae, Dilophosaurus shows the same relative relation as observed in the Swiss specimen. In Herrerasaurus, Coelophysis21,27 and Liliisterapus 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, but are subrectangular and mainly laterally directed in dorsal view. Furthermore, the height of the dorsal neural spines increases posteriorly as seen in Eoraptor28, Herrerasaurus and tetanuran theropods (for example, Piatnitzkysaurus floresi42, Sinaraptor dongi31 and Allosaurus fragilis43). Compared to most other early-diverging theropods where the ventral surfaces of the sacral centra are rounded or keeled44, they are flattened in SMF 06-1 and C. rhodesiensis24. The scapula is similar to the corresponding element in coelophysids, Dilophosaurus and Eudromaeus 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.
Fig. 2 | Phylogenetic relationships of *N. frickensis* gen. et sp. nov. Time-scaled single MPT resulting from 40% analysis (with *Herrerasaurus* replaced by *Eodromaeus*) and *Segisaurus* and 4 Averostra (*Allosaurus*, *Ceratosaurus*, *Eustreptospondylus*, *Piatnitzkysaurus*), 155 cranial and 130 postcranial characters (tree length, 547 steps, consistency index = 0.5210, retention index = 0.5379). Bold numbers on the branches indicate >50% bootstrap support, regular numerals show Bremer support indices. A, Theropoda (*Eoraptor* is not considered a theropod); B, Neotheropoda; C, Coelophysoidea; D, Averostra (used here for *Piatnitzkysaurus floresi*, *Eustreptospondylus oxoniensis*, *Ceratosaurus nasicornis*, *Allosaurus fragilis* and all descendants of their last common ancestor). This tree was chosen as an example because it well reflects the main result of our study. MYR, million years. Dinosaur silhouettes by Julio Garza (*Dilophosaurus*, ‘Syntarsus’); Scott Hartman (*Allosaurus*, *Coelophysis*, *Dilophosaurus*, *Eodromaeus*, *Eoraptor*, *Eustreptospondylus*, *Panguraptor*, *Piatnitzkysaurus*, *Segisaurus*, *Tawa*); Brad McFeeters (*Ceratosaurus*, *Cryolophosaurus*); and Iain Reid (*Zupaysaurus*) from Phylopic, used with permission (https://creativecommons.org/licenses/by/3.0/).
The radius (97 mm) is about three-quarters of the length of the humerus (≥128 mm) and the manus (second finger, ~127 mm) is of a length similar to the two former skeletal elements (Fig. 1f,h). The manus is composed of four digits, whereas the fourth is reduced to a very slim metacarpal, which is only half as wide as metacarpals I–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 Coelophysidae and other early neotheropods such as Dilophosaurus. However, the outline of the bone differs slightly as the dorsal iliac margin is somewhat convex in lateral view, rather than straight (for example, Coelophysis or strongly rounded (for example, S. dongi)). On the caudo-lateral surface of the ilium, there is a distinct rim for the musculus iliobifurcatus that continues over the whole ventral margin of the posterior blade. The pubis has a relatively downward-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 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 proportions similar to the pelvic elements of Dracoraptor. In the Frick theropod material, Dilophosaurus and Liliensternus, 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, 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 averosorhn-line theropod outside the clade Coelophysoidae (Fig. 2). In concord with refs. 4, 18, 52, 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 comprises N. 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 Fig. 2.

Phylogenetic discussion and conclusion. Hypotheses on early neotheropod relationships still attract little general agreement. The assignment of several taxa to the Coelophysoidae is uncertain, and the monophyly of the clade Dilophosauroidae is controversial 11,12,49. A reduced analysis, with the inclusion of only taxa with at least 40% of the available character states (‘40%-rule analysis’) and which also contained no Averostron, produced a single most parsimonious tree (MPT) where N. frickensis gen. nov. is found as a member of Dilophosauroidae (see Supplementary Fig. 1 and Supplementary information for a suggested diagnosis of the clade). A ‘dilophosaur cladet has also been recovered by other authors, for example 18, 19, 29, but as it was mostly supported by cranial crest characters it was thought that the grouping may be artificial. In the 40%-rule analysis of this study, the monophyly of the Dilophosauroidae is supported by three unambiguous synapomorphies and nine additional ones under DELTRAN and ACCTRAN optimization, where none is related to cranial crest character states (Supplementary Table 2a). In D. regenti, all of the seven synapomorphies pertaining to the articulare and the premaxilla are also discernible. The addition of every further coelophysoid or dilophosaurid taxon to the 40%-dataset has 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 proportions similar to the pelvic elements of Dracoraptor. In the Frick theropod material, Dilophosaurus and Liliensternus, 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, there is a distinct antero-proximally located tubercular process on each of the four preserved cranially forked chevrons (C1–C4).
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Author contributions
M.Z. and W.B. established the character matrix, scored the taxa for character states and wrote the manuscript. M.Z. carried out the descriptive and comparative work, conducted the phylogenetic analyses, discussed the results and wrote the suplement. W.B. made the Figures.

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Competing interests
The authors declare no competing interests.

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Study description
The study includes the morphological description, comparison and the phylogenetic analysis of the holotype specimen of the first theropod dinosaur skeleton from Switzerland. The phylogenetic analyses bases on a character matrix of 285 characters for which 23 taxa were scored.

Research sample
Holotype of Notatesseraeraptor frickensis gen. et sp. nov. Partial skull (SMF 09-2) and postcranial skeleton (SMF 06-1) of an early averostran –line neotheropod dinosaur.

Sampling strategy
Does not apply.

Data collection
The fossil was collected in the Gruhalde clay pit in Frick by a team of volunteers on behalf of the dinosaur commission of the local community of Frick. The data for the phylogenetic analysis was collected by literature research, collection visits and personal communication to corresponding authors.

Timing and spatial scale
First digging in the uppermost dinosaur layer: spring 2006 (postcranial skeleton (SMF 06-1))
Second digging in the uppermost dinosaur layer: corresponding skull (SMF 09-1)

Data exclusions
For the phylogenetic analysis we excluded Dracoraptor hanigani, since character scoring was already finished, when the paper was published. The same is true for the more fragmentary coelophysoid specimens Camposaurus, Lepidus, Lucianovenator and Powellvenator. Moreover the latter taxa are represented mainly by elements that are not preserved in the Swiss theropod material.

Reproducibility
The phylogenetic analyses are reproducible. The character list and character scoring for all included taxa are given in the supplement of this study.

Randomization
Does not apply.

Blinding
Does not apply.

Did the study involve field work? Yes No

Reporting for specific materials, systems and methods
We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems
n/a Involved in the study
☐ Antibodies
☐ Eukaryotic cell lines
☐ Palaeontology
☐ Animals and other organisms
☐ Human research participants
☐ Clinical data

Methods
n/a Involved in the study
☐ ChIP-seq
☐ Flow cytometry
☐ MRI-based neuroimaging

Palaeontology
Specimen provenance
Gruhalde clay pit, Frick, Aargau, Switzerland. The specimen was collected by order of the dinosaur commission of the municipality of Frick and the permission of the Keller AG, owner of the clay pit.

Specimen deposition
Sauriermuseum, Frick, Aargau, Switzerland

Dating methods
no new dates are provided

☐ Tick this box to confirm that the raw and calibrated dates are available in the paper or in Supplementary Information.