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Source: Acta Palaeontologica Polonica, 60(1) : 169-182

Published By: Institute of Paleobiology, Polish Academy of Sciences

URL: <https://doi.org/10.4202/app.2012.0105>

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The sphenacodontid synapsid *Neosaurus cynodus*, and related material, from the Permo-Carboniferous of France

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Falconnet, J. 2015. The sphenacodontid synapsid *Neosaurus cynodus*, and related material, from the Permo-Carboniferous of France. *Acta Palaeontologica Polonica* 60 (1): 169–182.

Sphenacodontid synapsids were major components of early Permian ecosystems. Despite their abundance in the North American part of Pangaea, they are much rarer in Europe. Among the few described European taxa is *Neosaurus cynodus*, from the La Serre Horst, Eastern France. This species is represented by a single specimen, and its validity has been questioned. A detailed revision of its anatomy shows that sphenacodontids were also present in the Lodève Basin, Southern France. The presence of several synapomorphies of sphenacodontids—including the teardrop-shaped teeth—supports the assignment of the French material to the Sphenacodontidae, but it is too fragmentary for more precise identification. The discovery of sphenacodontids in the Viala Formation of the Lodève Basin provides additional information about their ecological preferences and environment, supporting the supposed semi-arid climate and floodplain setting of this formation. The Viala vertebrate assemblage includes aquatic branchiosaurs and xenacanthids, amphibious eryopoids, and terrestrial diadectids and sphenacodontids. This composition is very close to that of the contemporaneous assemblages of Texas and Oklahoma, once thought to be typical of North American lowland deposits, and thus supports the biogeographic affinities of North American and European continental early Permian ecosystems.

Key words: Synapsida, Sphenacodontidae, anatomy, taxonomy, ecology, Carboniferous, Permian, France.

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Received 13 September 2012, accepted 17 June 2013, available online 10 July 2013.

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Introduction

Sphenacodontidae represented a major component of early Permian terrestrial ecosystems as apex predators (Olson 1961, 1966, 1977). These synapsids were widely distributed in North America and Western Europe, though their remains are most common in the United States (Eberth 1985; Olson 1962; Reisz 1986; Romer and Price 1940). Sphenacodontids are also well known for being the closest relatives of therapsids, so their study is crucial to understand the early evolution of synapsids (Amson and Laurin 2011; Fröbisch et al. 2011; Hopson 1991; Kemp 1982; Reisz et al. 1992; Sidor and Hopson 1998). Six sphenacodontid genera are currently recognized: *Sphenacodon* Marsh, 1878, *Dimetrodon* Cope, 1878a, *Ctenospondylus* Romer, 1936, *Secodontosaurus* Romer, 1936, *Ctenorhachis* Hook and Hotton, 1991, and *Cryptovenator* Fröbisch, Schoch, Müller, Schindler, and Schweiss, 2011 (Berman 1977, 1978; Berman et al. 2001, 2004b; Eberth 1985; Evans et al. 2009; Fröbisch et al. 2011; Hook and Hotton 1991; Olson 1962; Reisz et al. 1992; Romer and Price 1940; Sidor and Hopson 1995). All these taxa were

discovered in the United States except for two recently described German forms: *Dimetrodon teutonis* Berman, Reisz, Martens, and Henrici, 2001 from the Lower Rotliegend of Thuringia (Berman et al. 2001, 2004b) and *Cryptovenator hirschbergeri* Fröbisch, Schoch, Müller, Schindler, and Schweiss, 2011 from the Gzhelian of the Saar-Nahe Basin (Fröbisch et al. 2011). Additional taxa were named on fragmentary material: the Late Carboniferous *Macromerion schwarzenbergii* (Frič, 1875), from the Czech Republic (Romer 1945); the latest Carboniferous–earliest Permian *Neosaurus cynodus* (Gervais, 1869), from France (Romer and Price 1940) and the early Permian *Bathygnathus borealis* Leidy, 1854 from Canada (Case 1905) and “*Sphenacodon*” *britannicus* from the United Kingdom (Paton 1974). Even if these taxa are sphenacodontids, their validity has been questioned (Eberth 1985). Other potential sphenacodontids are *Steppesaurus gurleyi* Olson and Beerbower, 1953, *Eosyodon hudsoni* Olson, 1962, and *Gorgodon minutus* Olson, 1962, all from the early Permian of the USA. The three of them were originally described as early representatives of the therapsids (Olson 1962; Olson and Beerbower 1953), but they have since been reinterpreted as badly deformed

sphenacodontid specimens (Sidor and Hopson 1995). Given the absence of anatomical evidence supporting these claims, a detailed redescription of this material is necessary. For now, none of these taxa will be considered in this study.

The only French sphenacodontid known to date is the so-called *Neosaurus cynodus* represented by a single partial maxilla and its impression, HN004 2009-00-1, collected in “Autunian” red beds of the La Serre Massif area, Eastern France. This specimen has a complex taxonomic history. It was originally described by Coquand (1857, 1858) as pertaining to the German diapsid *Protorosaurus speneri* on the basis of its thecodont dentition. After re-examining this specimen, however, Gervais (1869) rejected Coquand’s identification, because *Protorosaurus* differs in having equally separated teeth (i.e., no diastema) and no caniniform teeth. Gervais then erected a new species for HN004 2009-00-1 that he included tentatively in the genus *Geosaurus*, a Jurassic thalattosuchian, as ?*Geosaurus cynodus*.

Following the discovery of new sphenacodontid material in the United States, Baur and Case (1899) pointed out that “*Geosaurus*” *cynodus* is definitely not a crocodylomorph, but more likely an early synapsid (“pelycosaur”). They also noted that it is seemingly distinct from the ophiacodontid *Stereorachis dominans*, from the nearby Autun Basin. Case (1907) was more skeptical about its assignment, but recognized “*Geosaurus*” *cynodus* as similar to his “poliosaurids”, a group interpreted now as a mix of ophiacodontids and sphenacodontids (Romer and Price 1940).

On the basis of a restudy of HN004 2009-00-1, Thévenin (1910) provisionally assigned *Geosaurus cynodus* to *Stereorachis*, but conceded nevertheless its closer affinities with the small *Dimetrodon nalis*, rather than *Stereorachis dominans*, based on its compressed cutting teeth. Similarly, later authors compared ?*Geosaurus cynodus* to both ophiacodontids and sphenacodontids (e.g., Huene 1925; Nopcsa 1923; Watson 1917), as several members of Ophiacodontidae were indeed placed in Sphenacodontidae and vice versa at this time.

In a discussion of *Dimetrodon* and its relatives, Nopcsa (1923) erected a new genus, *Neosaurus*, to accommodate Gervais’ (1869) species. Though Nopcsa gave no justification, this was later accepted by Romer and Price (1940). They regarded *Neosaurus* as a primitive sphenacodontid, but unusual in retaining a high number of precaniniforms and a low number of postcaniniforms, but comparable to *Dimetrodon nalis* in size and in having a weak maxillary step. They suggested the species *Neosaurus cynodus* might actually pertain to one of the better-known sphenacodontids, *Sphenacodon* or *Dimetrodon*—at that time, no skull material was referred to *Ctenospondylus*. Romer and Price (1940) also proposed an alternative hypothesis in which *Neosaurus* would have arisen independently from European “haptodontines”, because of their similar reduced number of postcaniniforms.

Neosaurus has not been restudied since then, although frequently mentioned in the literature (e.g., Berman et al. 2000b; Devillers 1961; Eberth 1985; Heyler 1969, 1987;

Langston 1963; Watson 1954; Reisz 1986). Most followed Romer and Price’s (1940) statements, except Heyler (1969, 1987) and Campy et al. (1983), who did not even cite their work, and Eberth (1985) who more thoroughly discussed the validity of *Neosaurus* (see below). So far, the name *Neosaurus* appeared only once in the French literature, in a review based on Romer and Price’s (1940) monograph (Devillers 1961). It was otherwise mentioned as *Protosorus speneri* [sic!] by Campy et al. (1983) and Farjanel (1989) and as ?*Stereorachis* by Heyler (1969, 1987).

Finally, the validity of *Neosaurus cynodus* was discussed by Eberth (1985) in the light of new data regarding major ontogenetic changes of the maxilla shape and tooth count within the genus *Sphenacodon*. Eberth (1985) stated that the diagnostic features listed by Romer and Price (1940) might be explained if the holotype of *N. cynodus* is a juvenile of one of the better known, deep-snouted sphenacodontids, *Sphenacodon*, *Ctenospondylus*, or *Dimetrodon* (as already suspected by the latter authors). However, Eberth (1985: 38) also stated that “[w]hile it may be argued that generic assignment of these forms is impossible on the basis of the present material, and that the names are invalid, retaining the generic names as paleogeographical convenience terms is desirable”.

Because it is the second ever described sphenacodontid species (after *Bathygnathus borealis*), *Neosaurus cynodus* requires an accurate redescription of its holotype and a re-evaluation of its taxonomic status in order to clarify sphenacodontid nomenclature. Furthermore, the examination of newly prepared, overlooked cranial material from the early Permian Viala Formation suggests sphenacodontids occurred also in the Lodève Basin. A left dentary (MNHN.F.LOD213) collected by Jacques Garric was first mentioned by Heyler (1969) as an indeterminate tetrapod, and by Heyler (2008) as a possible caseid, following the discovery of caseids in the Rodez (Sigogneau-Russell and Russell 1974) and Lodève (Werneburg et al. 2007) basins. Heyler (2008) claimed to have been unable to locate this specimen when he reorganized the MNHN collections from the Lodève Basin between 1996 and 2004. Fortunately, Daniel Heyler had given it before to Jean-Sébastien Steyer (CNRS-MNHN) who entrusted it to Renaud Vacant (MNHN) for preparation. Two undescribed dentaries (UM 5902, 5903) collected by Paul Ellenberger in 1986 were also found in the collections of the Université Montpellier 2 with the help of Suzanne Jicquel (UM), which were prepared in great part by Renaud Vacant and in part by the author.

Institutional abbreviations.—AMNH, American Museum of Natural History, New York, USA; ANSP, Academy of Natural Sciences of Drexel University, Philadelphia, USA; CNRS, Centre National de la Recherche Scientifique, Paris, France; HN, Muséum d’Histoire Naturelle de Besançon, Besançon, France; MCZ, Museum of Comparative Zoology, Harvard, USA; MNHN, Muséum National d’Histoire Naturelle, Paris, France; UM, Université Montpellier 2, Hérault, France; YPM, Yale Peabody Museum, New Haven, USA.

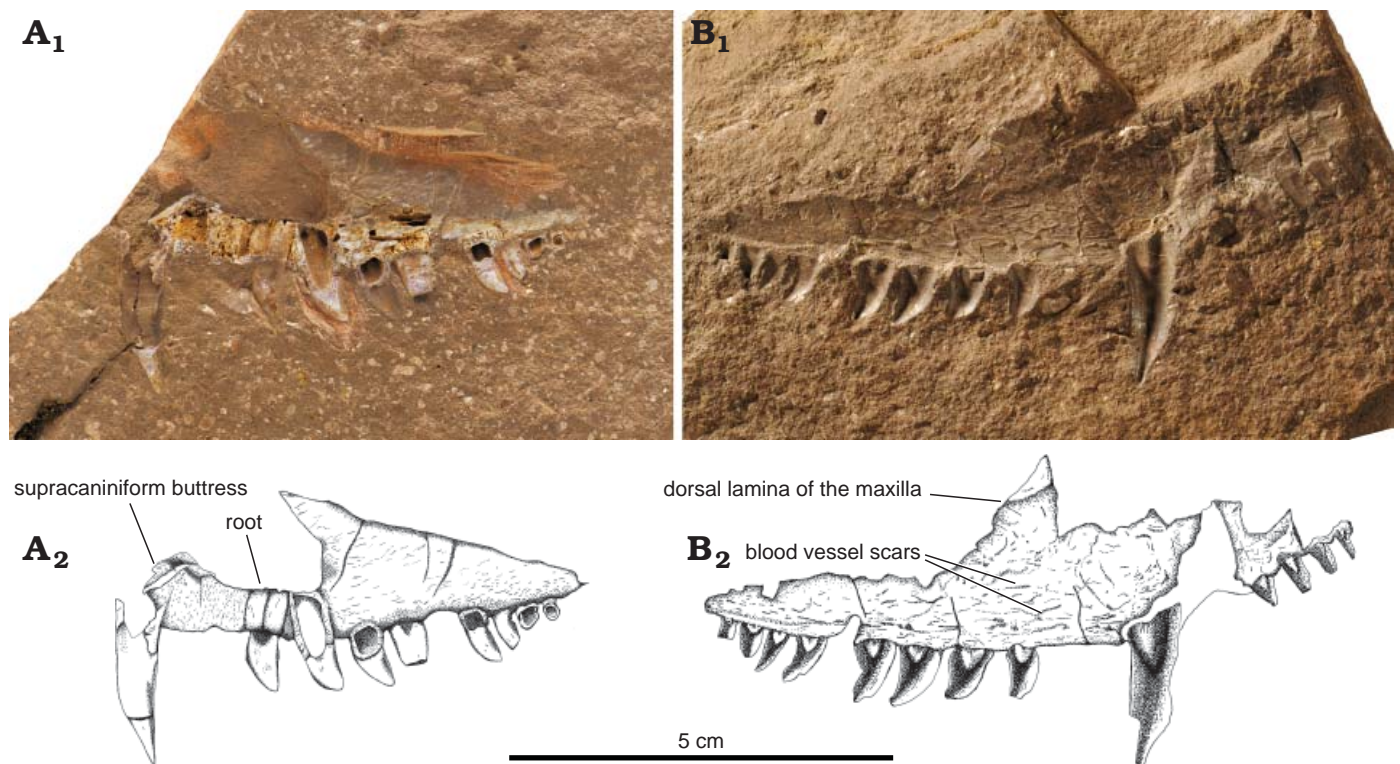


Fig. 1. Sphenacodontid synapsid *Neosaurus cynodus* (Gervais, 1869), holotype, from Moisse, Late Gzhelian–Asselian. **A.** Left maxilla (HN004 2009-00-1A) in lateral view. **B.** Corresponding impression (HN004 2009-00-1B) in lateral view. Drawings by Peggy Vincent.

Systematic palaeontology

Remarks.—The terminology used in the descriptions found below follows the standardized nomenclature proposed by Smith and Dodson (2003) for vertebrate dentition.

Sphenacodontia Romer and Price, 1940 sensu Amson and Laurin, 2011

Diagnosis.—Branch-based clade including all taxa that are more closely related to *Haptodus baylei* Gaudry, 1886, *Haptodus garnettensis* Currie, 1977, and *Sphenacodon ferox* Marsh, 1878 than to *Edaphosaurus pogonias* Cope, 1882.

Sphenacodontidae Marsh, 1878 sensu Benson, 2012

Definition.—Branch-based clade including all taxa that are more closely related to *Sphenacodon ferox* Marsh, 1878 than to *Casea broili* Williston, 1910, *Eothyris parkeyi* Romer, 1937, *Edaphosaurus cruciger* (Cope, 1878b), *Ophiacodon mirus* Marsh, 1878, *Varanops brevirostris* (Williston, 1911), or *Mus musculus* Linnaeus, 1758.

Genus *Neosaurus* Nopcsa, 1923

Type species: *Geosaurus cynodus* Gervais, 1869; see below.

1923 *Neosaurus* Nopcsa, 1923: 5

non *Neosaurus* Gilmore and Stewart, 1945 (= *Parrosaurus* Gilmore, 1945, nomen novum)

Neosaurus cynodus (Gervais, 1869)

Figs. 1, 2.

1858 *Protorosaurus Speneri*; Coquand 1858: pl. 1: 1, 2.

1869 ?*Geosaurus cynodus* Gervais: 222, figs. 29, 30.

1907 ?*Geosaurus cynodus*; Case 1907: 67, fig. 20 [copied from Gervais 1869: fig. 30].

1910 ?*Stereorachis cynodus*; Thévenin 1910: 57, pl. 8: 5 [counterpart of HN004 2009-00-1B].

1923 *Neosaurus cynodus*; Nopcsa 1923: 5.

1969 *Stereorachis*; Heyler 1969: pl. 52: 6 [counterpart of HN004 2009-00-1B].

Holotype: HN004 2009-00-1, partial tooth-bearing left maxilla and counter-part impression in a red, micaceous sandstone, here respectively referred to informally as HN004 2009-00-1A and HN004 2009-00-1B for convenience. Collected by Henri Coquand (accompanied by Charles Grenier) between 1854 and 1856. It was housed in the collections of the Faculté des sciences de Besançon, where he was teaching at the time. It was then successively loaned to Gervais (1869) and Thévenin (1910). The holotype was re-discovered in 2007 by Jocelyn Falconnet in the MNHN collections, where it is still housed today.

Type locality: Les Gorges, Moisse Commune, Jura Department, Franche-Comté Region, Eastern France. The type locality was misspelled “Moissy” on p. 31 but correctly on p. 320 by Romer and Price (1940). Eberth (1985: 37) and Berman et al. (1997: 129) each indicated an incorrect locality for *Neosaurus* (“near Paris” and “Besançon”, respectively).

Type horizon: Red, micaceous sandstones, unnamed stratigraphic unit (Campy et al. 1983); late Gzhelian–Asselian. The macroflora recovered in the Moisse area indicates a late Autunian age (Corsin and Devaux 1959). Although the validity of the Autunian regional stage has been challenged, a typical Autunian floral assemblage found in the Donets Basin was correlated to the Late Gzhelian–Asselian interval using biostratigraphic markers present in marine intercalations (Broutin et al. 1999; Izart et al. 1998a, b; see details in Falconnet 2014).

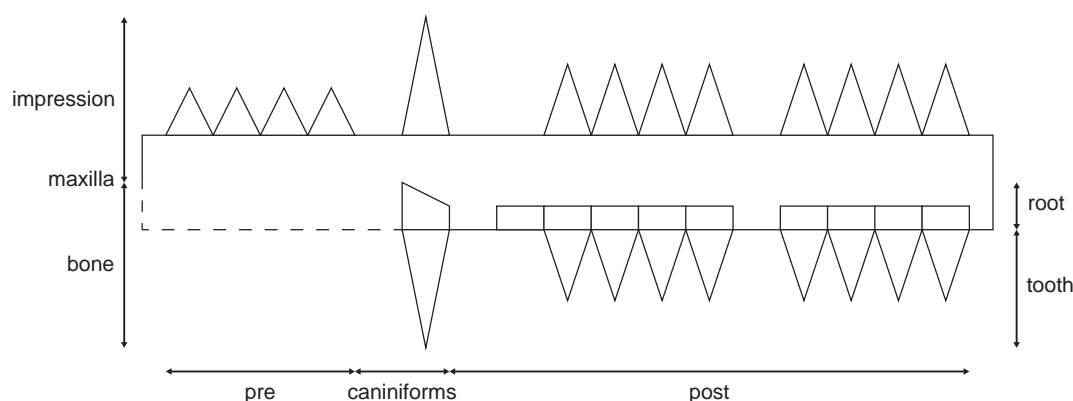


Fig. 2. Sphenacodontid synapsid *Neosaurus cynodus* (Gervais, 1869), holotype (HN004 2009-00-1), from Moisssey, Late Gzhelian–Asselian. Schematic comparison between the structure preserved in bone and impression.

Description

Preservation.—The holotype of *Neosaurus cynodus* is preserved in two small blocks. HN004 2009-00-1A comprises a left tooth-bearing maxilla exposed in lateral view (Fig. 1A, B). The area anterior to the level of the caniniform is missing and the anterior half of the preserved portion is damaged. The tooth row is still present, but the overlying dorsal lamina is incomplete. Most of the teeth are broken, but some of them are preserved in the counterpart impression. Several roots are visible laterally, revealing fine details about their inner structures. Fortunately, further data can be gathered from HN004 2009-00-1B on the lateral impression of the maxilla and its teeth—including the anterior area, which is missing in HN004 2009-00-1A (Figs. 1C, D, 2). The dorsal lamina margin is nevertheless missing. Its upper half is preserved only as an impression at the level of the first postcaniniforms, whereas its lower half is partly missing above the precaniniforms only. In addition, the impression of the dorsal lamina is concealed between the level of the caniniform and the precaniniforms by a small detached piece of the maxilla.

Maxilla.—The maxilla consists of a thick tooth-bearing alveolar ridge, convex ventrally and with a low step anterior to the single caniniform tooth. Dorsally the maxilla extends into a thin vertical lamina. On HN004 2009-00-1B, the surface shows a number of vessel scars parallel to the tooth row that narrows posteriorly. The position of the caniniform root is indicated laterally by a slight swelling of the dorsal lamina of the maxilla and medially by the thickening and deepening of the alveolar ridge just posterior to the caniniform (Fig. 1A, B). These features indicate the presence of a supracaniniform buttress, the development and extent of which is unknown.

Dentition.—There are 13 tooth impressions on HN004 2009-00-1B: four precaniniforms, one caniniform, and eight postcaniniforms. In addition, HN004 2009-00-1A displays also an empty space mesial to the caniniform and a root without a crown and two empty spaces distal to the caniniform. This suggests there were nine to 11 postcaniniforms (Fig. 2; see also Discussion).

All the teeth are roughly triangular in outline and labiolingually compressed, with moderately developed but un-

serrated mesiodistal cutting edges. Their surface shows a slight longitudinal fluting on the apical two-thirds. The base, squarish in cross section, displays a low V-shaped median longitudinal groove, on both the labial and lingual surfaces. This groove results from the labiolingual constriction of the roots, giving them an hourglass-like cross section. The respective crowns acquired consequently an almost similar shape, as displayed by the broken postcaniniforms, though with some variations. The labiolingual groove narrows as it extends apically from the base, extending up to the two-thirds of the length of most teeth, but only to the first third on the caniniform. This groove is not observable on the last postcaniniform, but this is probably because of its small size.

The size of the single preserved caniniform tooth is a little more than twice that of the largest postcaniniform tooth. As far as preserved, the precaniniforms are of subequal size, whereas postcaniniforms increase slightly in size from the caniniform tooth to the midlength of the maxilla, then diminish rapidly posteriorly. The non-caniniform teeth are much stouter than the narrow, sharply pointed caniniform. A pronounced recurvature is exhibited by the caniniform and most postcaniniforms, whereas it is nearly absent in the precaniniforms and the two last postcaniniforms.

Sphenacodontidae indet. 1

Fig. 3A.

- 1969 “Mâchoire provenant de Lodève”; Heyler 1969: pl. LII: 7.
- 2002 “Mâchoire provenant de Lodève”; Garric 2002: pl. I: 7 [cop. Heyler 1969: pl. LII: 7].
- 2008 “mâchoire de Reptile”, “Mâchoire d’un reptile [...] probablement d’un Caséidé”; Heyler 2008: 36, fig. 7.

Material.—MNHN.F.LOD213, partial left tooth-bearing dentary preserved mostly as an impression transferred on resin. Collected in 1963 by Jacques Garric (Garric 2002) from Locality G9, Saint-Julien, Le Bosc Commune, Hérault Department, Languedoc Region, southern France; β bone breccia, lower Viala Formation, Autunian Group, Lodève Basin; Sakmarian, early Permian. The Viala Formation was dated of 289.3 ± 6.7 Ma using U-Pb radiometric dating (Schneider et al. 2006), a long interval ranging from the late Asselian to the early Kungurian (International Commission on Stratigraphy

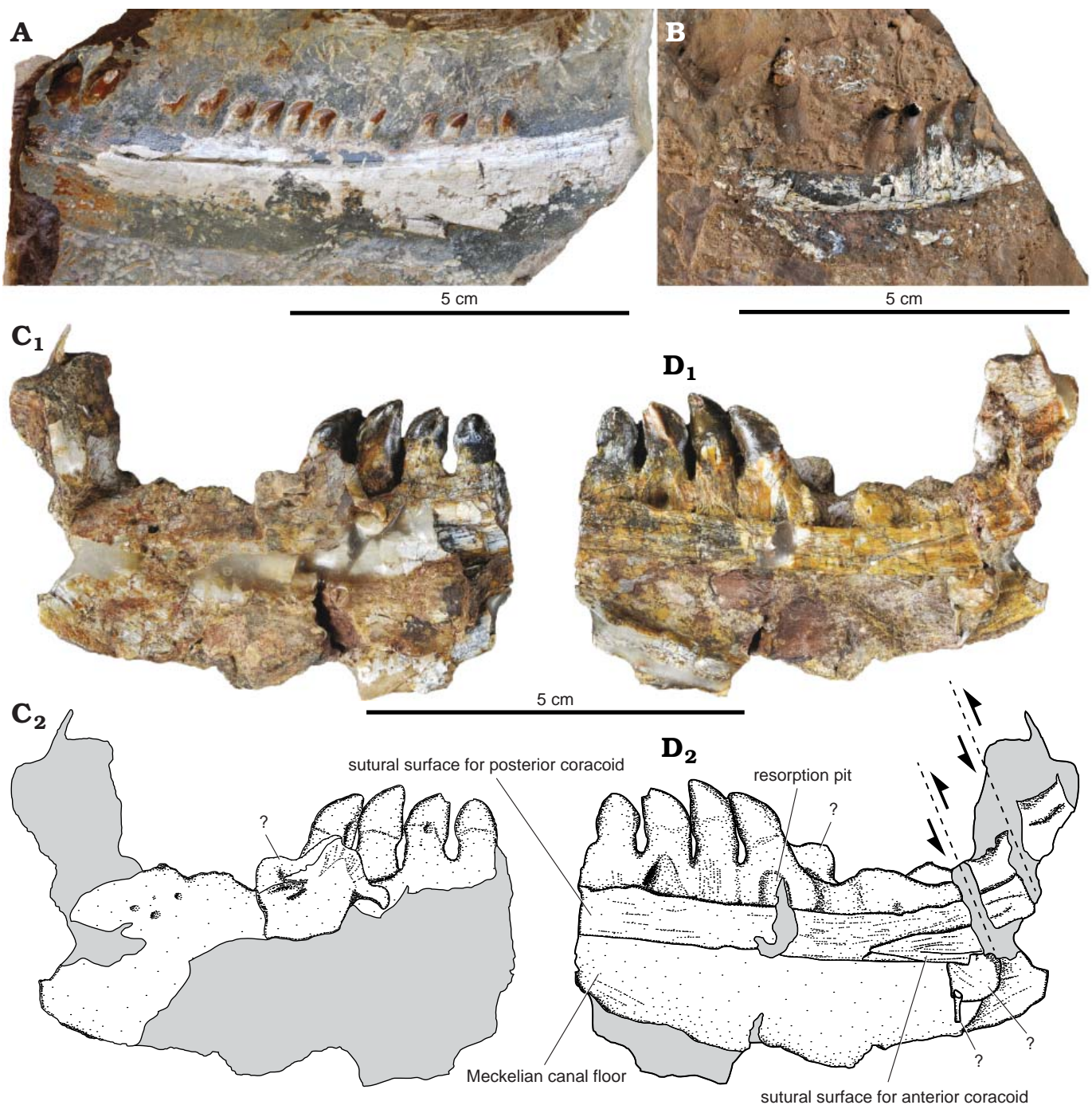


Fig. 3. Unidentified sphenacodontids. **A.** Sphenacodontidae indet. 1, left dentary (MNHN.F.LOD213), from Saint-Julien, Sakmarian, in lateral view. **B.** Sphenacodontidae indet. 2, right dentary (UM 5902), from Le Capitoul, Sakmarian, in medial view. **C, D.** Sphenacodontidae indet. 3, right dentary (UM 5903), from Saint-Julien, Sakmarian, in lateral (**C**) and medial (**D**) views. Photographs (**C**₁, **D**₁), explanatory drawings (**C**₂, **D**₂).

2013). The abundant typical Autunian macro- and microflora (Broutin et al. 1992) suggest a Late Gzhelian to Asselian age for the underlying Usclas-Saint-Privat and Tuilières-Loiras formations, by comparison with the Autun (Broutin et al. 1999) and Donets (Izart et al. 1998a) basins. These datings are in agreement with the Asselian–Sakmarian age assigned by Gand and Durand (2006) to the Tuilières-Loiras and Viala formations on the presence of their footprint associations I and II.

Description

Dentary.—The dentary is a long, shallow bone, measuring about 9 cm in length, that is exposed in lateral view (Fig. 3A). Both extremities are missing, anterior to the level of the first preserved tooth and posterior to the tooth row. The dorsal margin of the dentary is gently curved ventrally, but rises dorsally more abruptly at the level of the first preserved mesial teeth. On its anterior half the ventrolateral margin of the dentary exhibits a weak (though distinct) medial inflec-

tion. The entire preserved surface is smooth, with no sutures or sutural scars.

Dentition.—Fourteen teeth are preserved and gaps indicate at least two more. Most teeth are damaged, but those located in the middle of the tooth row are fairly well preserved. The teeth decrease steadily in size distally. The teeth have a rather triangular outline with somewhat bulbous, pointed crowns, but lacking evidence of labial or apical wear. In most teeth, the root is slanted and the crown recurved, so that the apex is mesial to the level of the base. On several teeth the mesial and distal margins are strongly compressed labiolingually, forming sharp, apparently unserrated cutting edges that run from the base to the apex of the crown. These features—slanting, recurvature, compression—are less marked distally. The two distalmost teeth are indeed not slanted but vertical, with a symmetrical crown in which the apex is located at the level of the midline of the tooth. They present faint, unserrated, mesiodistal cutting edges, but there is otherwise no sign of labiolingual compression.

Sphenacodontidae indet. 2

Fig. 3B.

Material.—UM 5902, partial right tooth-bearing dentary preserved mostly as an impression and exposed in medial view. Collected the 4th and 8th of March 1986 by Paul Ellenberger from east of Le Capitoul, Lodève Commune, Hérault Department, Languedoc Region, southern France; α or β bone breccia, lower Viala Formation, Autunian Group, Lodève; Sakmarian, early Permian (see above).

Description

Dentary.—The dentary is a long, ventrally bowed, tooth-bearing bone (Fig. 3B). Its medial surface is ornamented with low ridges radiating at the level of the caniniform but becoming parallel to the tooth row posteriorly. This sculpturing likely preserved traces of blood vessels supplying this area.

Dentition.—At least six teeth are present: five are preserved as impressions and a sixth one is represented distally by a fragmentary root. The most mesial tooth is identified as a probable caniniform. It is approximately twice the length of the preserved postcaniniforms. There is room for two additional teeth between the caniniform and postcaniniforms, and possibly two more mesial ones. The postcaniniforms decrease gradually in size distally. The teeth are conical, recurved distally, and end in a sharply pointed apex. The development of mesiodistal sharp edges gives the crown a bulbous aspect in lateral view. There are no visible serrations along these edges, but this might be due to the poor preservation.

Sphenacodontidae indet. 3

Figs. 3C, D.

Material.—UM 5903, partial right tooth-bearing dentary. Two flat and a rod-like unidentified bones of unknown affinity (“?” in Fig. 3C₂, D₂) and a tiny xenacanthid tooth were found during the preparation of UM 5903. Collected the 9th of Sep-

tember 1986, by Paul Ellenberger from Saint-Julien, Le Bosc Commune, Hérault Department, Languedoc Region, southern France; α or β bone breccia, lower Viala Formation, Autunian Group, Lodève Basin; Sakmarian, early Permian (see above).

Description

Dentary.—UM 5903 consists of an incomplete dentigerous posterior portion of a dentary (Fig. 3C, D). Its anterior end has been displaced dorsally along two vertical fractures. The deep ventral lamina displays a slight medial curvature that forms the medial wall of the Meckelian canal (Fig. 3C₂, D₂). Dorsally the dentary thickens abruptly to form a slightly ventrally bowed alveolar ridge with a squarish cross section. Its medial surface is covered with numerous, parallel antero-posterior striations of a sutural scar for the coronoids. The anterodorsally oriented line of contact between the anterior and posterior coronoids is preserved on the medial surface of the alveolar ridge. The lateral surface of the dentary is smooth where it is well preserved (Fig. 3C₁, D₂).

Dentition.—A series of four teeth are preserved as well as three empty alveoli mesial to them, indicating a minimal count of seven teeth. The dentition is subthecodont. Resorption pits are visible at the bases of the first and third preserved teeth and at the mesial, unoccupied position. The teeth show a basal neck constriction below a bulbous, distally recurved crown. The mesiodistal expansion of the crown results in sharp and apparently unserrated edges. The crowns are asymmetrical, with a more bulbous aspect labially than lingually. Distally there is a steady serial decrease in tooth size, which is paralleled by a decrease in recurvature and labiolingual compression of the crowns. Consequently, the most distal tooth has a more conical, bulbous aspect than the others.

Discussion

Phylogenetic position

Although fragmentary, these specimens display synapomorphies of sphenacodonts, more specifically of sphenacodontids. Yet, several of these characters are homoplastic within Synapsida, whereas some others are based on incorrect interpretations. It is therefore necessary to discuss their significance. The presence of a supracaniniform buttress in HN004 2009-00-1, for instance, is a synapomorphy of both Sphenacodontia (Laurin 1993) and Ophiacodontidae (Berman et al. 1995). The shape of the buttress differs nevertheless in these taxa. In the former the buttress consists of a low, rounded medial swelling that expands dorsal to the caniniform. In the latter a slender process with a triangular cross section arises dorsally from this buttress. Unfortunately, this area is mostly lacking in HN004 2009-00-1. According to Romer and Price (1940), the dentary in sphenacodontids typically has a concave tooth row (MNHN.F.LOD213, UM 5902, UM 5903) and a swollen anterior tip (MNHN.F.LOD213), and the first mesial teeth it bears are larger than the remainder of

its dentition (MNHN.F.LOD213, UM 5902). These features, however, are not unique to sphenacodontids. They are even frequently associated in supposedly predaceous eupelycosaurs, such as “*Stereorachis*” *blanziacensis* (personal observations of holotype, Desbrosses Collection without number), *Stereorachis dominans* (personal observations of holotype, MNHN.F.AUT489), *Haptodus garnettensis* (Laurin 1993), or *Cutleria* (Laurin 1994). This morphology should not be mistaken for that seen in therapsids, where the dentary dentition is differentiated in size and shape into incisiforms, caniniforms, and postcaniniforms (Sidor and Hopson 1998). Such a distinct heterodonty is not present in the French material.

Fortunately, the dentition provides crucial information allowing the confident assignment of the studied material to Sphenacodontidae. The marginal dentition of HN004 2009-00-1, MNHN.F.LOD213, UM 5902, and UM 5903 exhibits mesiodistal sharp edges, a synapomorphy of the sphenacodontian clade that includes *Cutleria*, sphenacodontids, and therapsids (Laurin 1993). Teeth with cutting edges are fairly common in synapsids, and they have also been reported in the varanopid clade, including mycterosaurines and varanodontines (Anderson and Reisz 2004), ophiacodontids (Brinkman and Eberth 1986; personal observations on MNHN.F.AUT489 and Desbrosses Collection without number), and even in edaphosaurids (Modesto 1995; Mazierski and Reisz 2010). *Neosaurus* bears also a distinct caniniform (the other one having been lost), as in eothyridids, ophiacodontids, the edaphosaurid *Ianthasaurus*, and sphenacodonts (Brinkman and Eberth 1986; Laurin 1993; Mazierski et al. 2010; Reisz et al. 2009). The combination of the aforementioned characters is in agreement with the sphenacodontian assignment of *Neosaurus*. The most interesting feature of the specimens described here is the unusual shape of their postcaniniform teeth. They indeed exhibit a basal neck overhanged by a robust crown with mesiodistal cutting edges, a morphology typical of sphenacodontids (e.g., Berman 1977, 1978; Evans et al. 2009; Fröbisch et al. 2011; Romer and Price 1940; Williston 1911; ANSP 9524, holotype of *Bathynathus borealis*; AMNH FR 4116, holotype of *Dimetrodon incisivus*; AMNH FR 4001, holotype of *D. semiradicatus*). In fact, it was recently identified as a synapomorphy of a clade including all sphenacodontids except *Secodontosaurus* (Fröbisch et al. 2011; Benson 2012). This condition has been specifically termed as “lachryform” or “teardrop-shaped” by Evans et al. (2009). It is unlike the dentition of *Cutleria* (Laurin 1994) or therapsids, which display a wide range of dental features, such as serrated to macroserrated mesiodistal cutting edges, as well as wear facets, heels or cusps (e.g., Ivakhnenko 2008). In addition to the features listed above, the teeth of HN004 2009-00-1 exhibit a distinct labiolateral constriction of the crown at the base resulting in a longitudinal V-shaped groove. This has been described as a figure-eight section by Case (1907) and is not unusual in sphenacodontids. It had already been observed in the holotype of *D. semiradicatus* AMNH FR 4001 by Cope (1881) who even used it to diagnose and name his new species. It appears to be common in *Dimetro-*

don (Romer and Price 1940) but it is also clearly present in *Ctenospondylus ninevehensis* (holotype MCZ 3386; Berman 1978: fig. 1B) and in *Sphenacodon ferox* (holotype YPM 806; Spielmann et al. 2010: fig. 2; UCMP 34226; Spielmann et al. 2010: fig. 3). Even if this figure-eight section may have been an interesting character for taxonomy and phylogeny, the study of sphenacodontid jaw material suggests that this feature is in fact artefactual. A careful examination of AMNH FR 4001 led indeed Case (1907) to interpret this figure-eight section as the result of post-mortem breaking and crushing. Sphenacodontid teeth having a subrectangular basal section, post-mortem labiolingual compression would thus result in the collapse of the labial and lingual walls of the pulp cavity. First-hand examination of AMNH FR 4001 and many other sphenacodontid remains in the AMNH and MCZ collections showed that such a feature is not uncommon in these synapsids, and that it is usually associated with other damage resulting from taphonomic or diagenetic processes, therefore supporting Case’s (1907) conclusions.

The precaniniform and postcaniniform tooth counts are frequently used as characters in phylogenetic analyses of early synapsid relationships, especially for sphenacodonts according to Reisz et al. (1992), Laurin (1993), Sidor and Hopson (1998), Fröbisch et al. (2011), and Benson (2012). The character states they use vary greatly, but all agree in that there is a general tendency toward a reduction of the number of precaniniforms in sphenacodonts, with therapsids having none. Consequently, *Neosaurus* retained the plesiomorphic condition in having four precaniniforms. The reduction of the postcaniniform tooth count is also a therapsid synapomorphy, according to Laurin (1993), Sidor and Hopson (1998), and Benson (2012), although they viewed this evolutionary trend differently. Nine postcaniniforms are preserved on *Neosaurus*. Two additional gaps indicate that there were possibly two more postcaniniforms, one in the middle of the series and the other one just distal to the caniniform (Fig. 2). The latter gap was interpreted by Romer and Price (1940) as the alveolus of the second caniniform, so that *Neosaurus* would have had up to 10 postcaniniforms. Two fully erupted caniniforms are indeed present sometimes in sphenacodontids (Eberth 1985; Romer and Price 1940), but the two teeth usually alternate in development, so that a single caniniform was functional while the other was being replaced (Edmund 1960). This is also the case in *Tetraceratops*, currently the sister-taxon of all other therapsids (Amson and Laurin 2011; Laurin and Reisz 1996). Whereas *Raranimus* retained two functional caniniforms, there is only a single functional at a time in other therapsids (Liu et al. 2009). In HN004 2009-00-1B, the caniniform is located immediately ventral to the posterior level of the supracaniniform buttress (Figs. 1A₁, A₂, 2). This suggests that two caniniforms were present and that the preserved caniniform was the second distal one of the pair, where the so-called “edentulous” step occurs. Finally, the maxilla of *Neosaurus* had a maximum total count of 17 teeth, including 11 postcaniniforms, thus exhibiting what is a therapsid synapomorphy according to Laurin (1993) and Sidor

and Hopson (1998). The relevance of characters relying on tooth count was questioned by Eberth (1985), who suggested an inverse relationship between the precaniniform and postcaniniform tooth counts during ontogeny. In this case, the plesiomorphic high precaniniform count of *Neosaurus* could have risen because the individual was a juvenile. This relation is seemingly more complex than what Eberth (1985) suggested (pers. obs.), but it allows one to question the significance of tooth count in taxonomy—and thus phylogeny—in early sphenacodonts. Regardless of ontogenetic variations, the deduced postcaniniform tooth count of *Neosaurus* agrees well with that of sphenacodontids and of the therapsid *Biarmosuchus tener* (Table 1). The precaniniform and postcaniniform counts of *Neosaurus* should, therefore, be used with caution in a taxonomic or phylogenetic perspective.

The tooth morphology alone is nevertheless sufficient to assign confidently HN004 2009-00-1, MNHN.F.LOD213, UM 5902, and UM 5903 to Sphenacodontidae. This conclusion is in agreement with other features of the dentition, maxilla, and dentary (see above).

Taxonomy

Taxonomic status of *Neosaurus cynodus*.—Romer and Price (1940) provided a diagnosis for *Neosaurus cynodus* with the following characters: (i) low maxillary step, (ii) four precaniniform teeth, and (iii) ten postcaniniform teeth. The combination of primitive and derived sphenacodontian features led them to emphasize its probable intermediate position between their “*Haptodus*” (now paraphyletic; see Laurin 1993) and other sphenacodontids, a view followed by subsequent authors (Berman 1978; Currie 1979; Reisz 1986). Their diagnosis was, however, justifiably questioned by Eberth (1985: 37) in his re-study of the cranial anatomy of *Sphenacodon ferocior*. Indeed, he noted that diagnostic characters of the dentition and maxilla, on which Romer and Price (1940) relied, vary considerably during ontogeny in both *S. ferocior* and *S. ferox*. The maxilla, for instance, expands ventrally at the level of the caniniforms but narrows more anteriorly in such a way that the tooth row forms a kind of step anterior to the caniniforms and becomes increasingly concave posteroventrally. In the youngest individuals of *S. ferox* and *S. ferocior*, the step and concavity of the tooth row are therefore barely present, whereas they become prominent features in the largest individuals according to Eberth (1985: 33, fig. 36). He concluded that the three diagnostic characters offered by Romer and Price (1940) should be discarded, arguing that they may reflect the juvenile stage of the holotype of *N. cynodus*.

The lack of serrations on the marginal dentition of HN004 2009-00-1, despite its fairly good preservation, shows that *Neosaurus cynodus* is distinct from at least *Bathygnathus borealis* (ASNP 9524), *Dimetrodon incisivus* (AMNH FR 4116), and *D. semiradicatus* (AMNH FR 4001).

In conclusion, there are no features to distinguish *Neosaurus* from all other sphenacodontids because a juvenile

Table 1. Precaniniform (prec.) and postcaniniform (postc.) counts in sphenacodonts. A plus sign indicates minimum values for taxa in which the complete tooth count is unknown.

Taxon	Prec.	Postc.	Reference
<i>Haptodus garnettensis</i>	4–6	22–24	Laurin (1993: 209)
Sphenacodontidae			
<i>Bathygnathus borealis</i>	1–2?	9+	this study
<i>Ctenospondylus ninevehensis</i>	3	16	Berman (1978: 4 98)
<i>Dimetrodon natalis</i>	3	15	Romer and Price (1940: tab. 2)
<i>Dimetrodon grandis</i>	1	10–13	Romer and Price (1940: tab. 2)
<i>Dimetrodon limbatus</i>	0–2	11–13	Romer and Price (1940: tab. 2)
<i>Dimetrodon loomisi</i>	1–3	12–13	Romer and Price (1940: tab. 2)
<i>Dimetrodon teutonis</i>	2	15–16?	Berman et al. (2004a: 49)
<i>Neosaurus cynodus</i>	4	11	this study
<i>Secodontosaurus obtusidens</i>	6–7	13–17	Reisz et al. (1992: 156)
<i>Sphenacodon ferocior</i>	0–4	12–15	Eberth (1985: tab. 1)
<i>Sphenacodon ferox</i>	2	11–12	Romer and Price (1940: tab. 2)
Therapsida			
<i>Biarmosuchus tener</i>	0	9–13	Ivakhnenko (1999: 292)
<i>Eotitanosuchus olsoni</i>	0	9	Olson (1962: 51)
<i>Raranimus danshankouensis</i>	1	3+	Liu et al. (2009: 396)
<i>Tetraceratops insignis</i>	1	8	Laurin and Reisz (1996: 96)

stage of development of the holotype cannot be ruled out, and because the lack of axial material precludes an assignment to one or another of the better known genera of the family (i.e., *Sphenacodon*, *Ctenospondylus*, *Dimetrodon*, and *Secodontosaurus*). Therefore, despite minor disagreements with previous comparisons, this work supports the conclusion of Eberth (1985) in considering the species *Neosaurus cynodus* as a nomen dubium and its holotype HN004 2009-00-1 as a Sphenacodontidae indeterminate.

Identification of MNHN.F.LOD213, UM 5902, and UM 5903.—Examination of these specimens offers no support for assignment to any of the previously described sphenacodontid taxa. This is mainly because many features of the feeding apparatus (jaws and dentition) of sphenacodontids are not only related with each other, but are also dependent on size and ontogeny (Eberth 1985; Reisz et al. 1992; Romer and Price 1940) and are therefore of little help in taxonomy (contra Fröbisch et al. 2011). In addition, poor preservation precludes the detection of serrations on their teeth. MNHN.F.LOD213, UM 5902, and UM 5903 are, therefore, considered as Sphenacodontidae indeterminate.

Paleoecology and paleoenvironments

Sphenacodontids are a major component of North American early Permian tetrapod faunas (Olson 1958, 1961, 1977; Romer and Price 1940; Vaughn 1966, 1970), but they remain

exceedingly rare in Europe. The restriction of *Sphenacodon* to New Mexico and *Dimetrodon* and *Ctenospondylus* to northern Texas had long been explained by the presence of a geographical barrier precluding faunal exchanges (Romer and Price 1940). Subsequent discoveries in the Four Corners area (where Arizona, Colorado, New Mexico, and Utah meet) but also in Ohio have indicated that the biogeography of these genera is more complex and cannot be merely explained by the presence of a fluctuating seaway. *Ctenospondylus* and *Dimetrodon* material have indeed been collected from lower Permian deposits of the Four Corners (Sumida et al. 1999; Vaughn 1964, 1966). *Dimetrodon* has been also found in earlier strata from New Mexico that may be Pennsylvanian (Berman 1977, 1993; Vaughn 1970). In addition, *Sphenacodon* is not restricted to New Mexico as a result of finds from Arizona (Vaughn 1966) and Utah (Sumida et al. 1999), although this genus is still unknown in Texas. Vertebrate assemblages that were previously considered as typical of northern Texas have been found in many areas of the Four Corners (Vaughn 1966, 1970). Similar assemblages have been recognized in the uppermost Pennsylvanian to lower Permian Dunkard Group of the Tri-State area (where Ohio, West Virginia, and Pennsylvania meet), which has yielded specimens referred to a distinct species of *Ctenospondylus*, *C. ninevehensis*, and to *Dimetrodon* cf. *limbatus* (Berman 1978; Olson 1970, 1975). Several hypotheses have been proposed to explain the biogeographical evolution of the Tri-State and Midcontinent vertebrate fauna, such as the presence of a faunal corridor or some kind of selective geographical barrier, but none of them could be directly tested because Upper Pennsylvanian to lower Permian outcrops are lacking in the Central United States (Berman 1978).

Regardless, these discoveries led Vaughn (1966, 1970) to suggest that the Midcontinental Seaway separating the Four Corners and Texas acted at most as a filter and instead proposed that these differences in relative abundances are the result of different paleoecological preferences. *Dimetrodon* was for instance labeled as a “truly deltaic marker” (Vaughn 1970) that would have preferred lowland coastal areas in contrast to the more upland *Sphenacodon* (Vaughn 1966), a hypothesis confirmed by Olson (1958, 1977). Indeed, Olson (1958) discovered that *Dimetrodon* also occurs in channel deposits, but that it is especially common among lacustrine vertebrate assemblages where it is represented by isolated, complete bones and partly articulated skeletons on the margins, but only by isolated, fragmentary remains in offshore deposits. *Dimetrodon* was a common inhabitant of early Permian flood plains (Olson 1958, 1977; Sander 1987, 1989). It was the largest and one of the most abundant predators at that time, preying upon other large vertebrates living in lakes or in their vicinities, including xenacanthids or *Diplocaulus* (Olson 1961, 1977). The limited data regarding the taphonomy of *Ctenospondylus* indicates that it was a rare component of an amphibious to aquatic pond or lake fauna and that its remains had been transported a relatively short

distance before being deposited (Berman 1978). These data suggest that *Ctenospondylus* had a similar ecology.

Regarding the ecology of sphenacodontids, two localities are informative: the lower Permian Richards Spur (or Fort Sill) locality, Oklahoma, and the Bromacker Quarry, Germany, in which sphenacodontid remains are rare in comparison with other tetrapods (Berman et al. 2001, 2004b; Evans et al. 2009). Both localities have yielded an abundant and diverse tetrapod fauna, including dissorophoid temnospondyls, “microsaur” lepospondyls, *Seymouria*, diadectids, bolosaurid parareptiles, captorhinid eureptiles, and caseid, varanopid, and sphenacodontid synapsids (e.g., Heaton 1979; Boy and Martens 1991; Modesto 1996; Berman et al. 1998, 2000a, b, 2001, 2004a, b, 2011; Sumida et al. 1998; Sullivan and Reisz 1999; Eberth et al. 2000; Sullivan et al. 2000; Reisz and Sutherland 2001; Kissel et al. 2002; Reisz et al. 2002; Reisz 2005; Maddin et al. 2006; Müller et al. 2006; Anderson et al. 2008, 2009; Evans et al. 2009; Henrici et al. 2011; Fröbisch and Reisz 2012; Anderson and Bolt 2013). These terrestrial assemblages indicate an “upland” paleoenvironment for both the Richards Spur and Bromacker localities in contrast with the contemporaneous more lowland faunas of North America (Eberth et al. 2000). Stratigraphic and sedimentological data suggest a depositional environment in which sheet flooding alternated seasonally with the sedimentation of suspended fines in temporary lakes and ponds, in association with a hot, semi-arid climate, for the Tambach Formation at Bromacker (Eberth et al. 2000). There is little information regarding the depositional environment of the fissure-fill deposits of Richards Spur, but streams or standing bodies of water were apparently rare in this area (Olson 1991; Sullivan and Reisz 1999). Even if these two localities share many taxa, the Bromacker tetrapod assemblage was recognized as an original, early stage in the development of a modern terrestrial trophic ecosystem dominated by plantivorous tetrapods (Eberth et al. 2000). This is not the case of the Richards Spur tetrapod assemblage. It is easy to distinguish these two assemblages using the relative abundance of tetrapods. Diadectids are the most frequent tetrapods in Bromacker (Eberth et al. 2000) whereas captorhinids overwhelmingly dominate in Richards Spur (Sullivan and Reisz 1999). Sphenacodontids are the most common synapsids in Bromacker, with one species represented by five specimens, whereas only a single varanopid specimen has been recovered (Berman et al. 2001, 2004b). Conversely, varanopids are not uncommon in Richards Spur (Evans et al. 2009; Maddin et al. 2006), whereas sphenacodontids are scarce (Evans et al. 2009).

The abundance of sphenacodontids appears therefore to be strongly environmentally controlled, a suggestion that may account in large part for their rarity in Europe (Table 2). Though the Gorges de Moisey locality has yielded an interesting macroflora, the only animal remains it has produced consist of indeterminate bivalve internal casts and the holotype of *Neosaurus cynodus* (Coquand 1857, 1858; Corsin and Devaux 1959; Ogérien 1867; Pidancet 1863).

Table 2. Distribution of Late Carboniferous–Early Permian spheonacodonts in Europe. Taxa for which column “S” is checked are spheonacodontids. Note that *Datheosaurus* might not be a spheonacodont at all (Frederik Spindler, personal communication 2012).

Country	Area	Taxon	S	Reference
Czech Republic	Kladno-Rakovník Basin	<i>Macromerion schwanzenbergii</i>	×	Frič (1875)
France	Autun Basin	<i>Callibrachion gaudryi</i>		Boule and Glangeaud (1893)
		<i>Haptodus baylei</i>		Gaudry (1886)
	La Serre Horst	Sphenacodontidae indet.	×	this study
	Lodève Basin	Sphenacodontidae indet.	×	this study
Germany	Döhlen Basin	<i>Palaeohatteria longicaudata</i>		Credner (1888)
		<i>Pantelosaurus saxonicus</i>		Huene (1925)
	Saar-Nahe Basin	<i>Cryptovenator hirscherbergeri</i>	×	Fröbisch et al. (2011)
	Thüringer Wald Basin	<i>Dimetrodon teutonis</i>	×	Berman et al. (2001)
		? <i>Haptodus</i> sp.		Werneburg (1999)
Poland	Intra-Sudetic Basin	<i>Datheosaurus macrourus</i>		Schroeder (1905)
United Kingdom	Warwickshire Coalfield	<i>Haptodus grandis</i>		Paton (1974)
		“ <i>Sphenacodon</i> ” <i>britannicus</i>	×	Huene (1908)

The lower Viala Formation, which has yielded the Lodève spheonacodontids, offers much greater palaeoecological information. These specimens were collected from the α and β bone breccias in which disarticulated bones are mixed together and embedded in a red silty matrix. These breccias resulted, according to Garric (2002), from marked water level fluctuations, causing the death en masse of the aquatic fauna, notably branchiosaurids, during droughts. Larger, more resistant bones would have been deposited with reworked bones as water levels rose. The proximity of channels to the breccias is underlined by the dominance of aquatic and amphibious vertebrate remains in the lower Viala Formation. Their remains may have been transported by strong currents that resulted in their complete disarticulation and breakage. The Viala fauna, therefore, lived in a proximal floodplain environment, very close to stream channels. Although uncommon in Europe, the association of spheonacodontids with xenacanthids, branchiosaurids, and eryopoids (Heyler 1997; personal observations) in the Viala Formation also occurs in the Late Stephanian Kounov Member, Western Bohemia (Štamberg and Zajíc 2008) and in the Gzhelian–Asselian Remigiusberg Formation, Saar-Nahe Basin (Fröbisch et al. 2011). If the Viala Formation is Sakmarian, then this association persisted during the early Permian. Xenacanthids, eryopoids, and spheonacodontids are commonly associated in the early Permian of Texas and Oklahoma, where they played a major role in the local floodplain to lacustrine ecosystems (Olson 1958, 1961, 1977).

The Bromacker vertebrate assemblage differs in the absence of an aquatic component (Eberth et al. 2000). This more terrestrial assemblage comprises dozens of partial to subcomplete articulated skeletons that indicates that these tetrapods lived instead in a distal floodplain, far from potential sources of transport. Although streams and standing bodies of water were present according to sedimentary and palaeontological data, the good drainage and the semi-arid climate of the region would have prevented the establishment of aquatic (or even amphibious) vertebrate populations

(Eberth et al. 2000). During floods, individuals that were not able to escape would have been buried or trapped in mud before dying from exhaustion—similar but rarer examples are known from contemporaneous deposits from Texas (Sander 1989). In this case, there would have been little or no transport.

Despite the proximity of fluvial channels, the tetrapod footprint assemblages in the lower part of the Viala Formation suggest that more upland taxa were also present. These tracks have been attributed to branchiosaurids, eryopoids, eupelycosaurids, and “edaphosaurs” (Gand 1987, 1989). These putative “edaphosaurs” (a taxon formerly considered to include Caseidae and Edaphosauridae), although not confirmed by a body fossil record, are represented by a few tracks referred to the ichnospecies *Ichniotherium cottaie*. Recently, however, Voigt et al. (2007) have been able to identify the diadectid *Diadectes absitus* as the trackmaker of *Ichniotherium cottaie* through a detailed comparison of limb remains and tracks from Bromacker. Though diadectids are relatively abundant in upland areas (Eberth et al. 2000), they are much rarer in lowlands (Olson 1958, 1977; Sander 1987, 1989).

The Viala vertebrate assemblage is therefore definitely typical of lowlands, with xenacanthids, branchiosaurids, and eryopoids living in shallow lakes and ponds subjected to drought and spheonacodontids living in marginal areas, preying upon other vertebrates (Fig. 4). They probably fed also upon diadectids that would have ventured into this area. Spheonacodontids, eryopoids, and xenacanthids were at the apex of the food chain, feeding potentially upon all other vertebrates.

Conclusions

Although not common, spheonacodontids were represented only by *Neosaurus cynodus* from the La Serre Horst area, which was thought to represent a distinct species. Re-examination of its holotype shows that it cannot be diagnosed

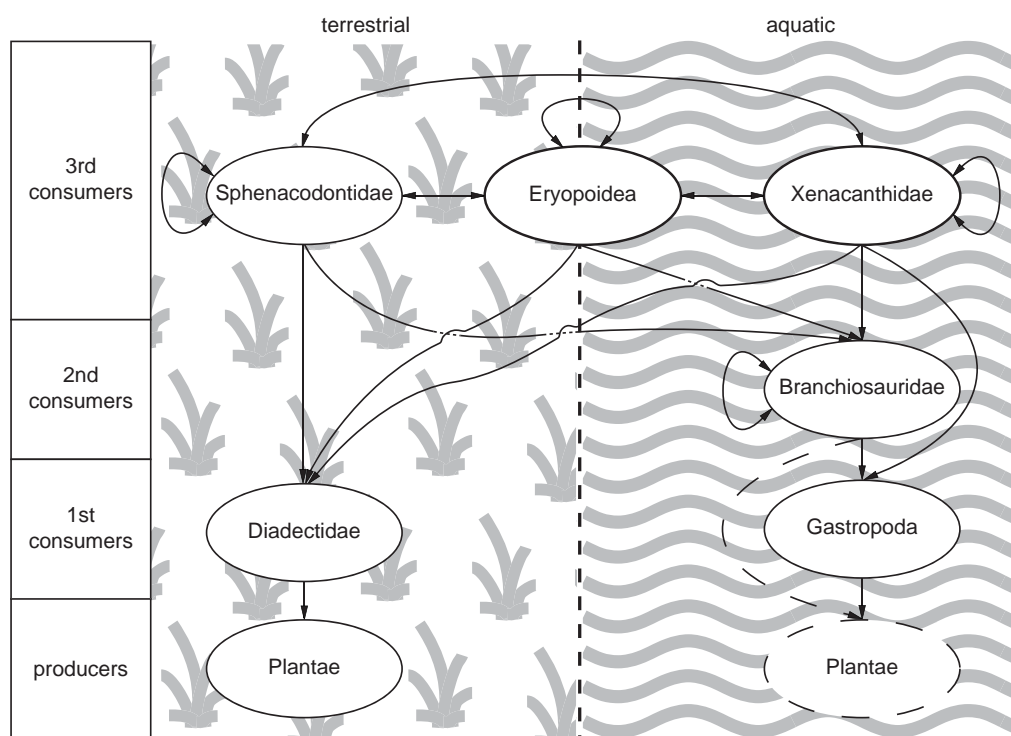


Fig. 4. Hypothetical trophic web for the lower Viala Formation based on relative size and functional morphology. Primary producers are poorly known, but a callipterid has been recently described from the Viala Formation (Galtier and Broutin 2008).

below the family level, as an indeterminate sphenacodontid. Three additional specimens from the Lodève Basin are also described as indeterminate members of this family. Their association with xenacanthids and eryopoids confirms the close biogeographic affinities of Europe and North America during the early Permian.

Acknowledgements

I thank my Ph.D. supervisors, Jean-Claude Rage and Jean-Sébastien Steyer (both CNRS-MNHN) for their precious help and advice. Many thanks to Peggy Vincent (CNRS-MNHN) for the excellent drawings of HN004 2009-00-1 (Fig. 1) and to Christian Lemzaouda (MNHN) for the photographs (Figs. 1, 3). I am also very grateful to Renaud Vacant (MNHN) for bringing to my attention the existence of MNHN.F.LOD213 and for helping me prepare UM 5903, and to Suzanne Jiquel (UM) who gave me full access to the collections of the Université Montpellier 2, helped me to find the relevant specimens (UM 5902 and 5903), and allowed me to borrow them for study. Thanks also to Lionel François (HN) for providing a collection number for the holotype of *Neosaurus cynodus* and for allowing its transfer to the MNHN, in Paris. This work profited from discussions with Frederik Spindler (Bergakademie Freiberg, Freiberg, Germany) about the identity of *Datheosaurus*. I would have been unable to complete this work without the help of the curators Carl Mehling (AMNH), Daniel Brinkman (YPM), and Jessica Cundiff (MCZ) during my visit in USA, and to Jorge Mondéjar Fernández (MNHN) who was kind enough to take photographs with the authorization of the curator Edward Daeschler (ANSP). Finally, the thorough scientific and linguistic reviews of David Berman (Carnegie Museum of Natural History, Pittsburgh, USA), Robert Reisz (University of Toronto Mississauga, Mississauga, Canada), and Michel Laurin (CNRS-MNHN) and the editing of Michael Benton (University of Bristol, United Kingdom) greatly improved the quality of this manuscript. May they be warmly thanked.

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