

A new species of *Dimetrodon* (Synapsida: Sphenacodontidae) from the Lower Permian of Germany records first occurrence of genus outside of North America

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Abstract: A new species of the sphenacodontid synapsid *Dimetrodon*, *D. teutonis*, is described on the basis of a single, adult specimen consisting of a large portion of the presacral vertebral column. The holotype was collected from the Lower Permian Tambach Formation, lowermost formational unit of the Upper Rotliegend, of the Bromacker quarry locality in the midregion of the Thuringian Forest near Gotha, central Germany. This is the first record of the genus outside of North America and, therefore, provides not only additional biological evidence of a continuous Euramerican landmass during the Early Permian, but also the absence of any major physical or biological barrier to faunal interchange of terrestrial vertebrates. An estimated weight of 14 kg for *D. teutonis* is half that of the smallest, previously recognized species, *D. natalis*. Sphenacodontid phylogeny indicates that the diminutive size of *D. teutonis* represents an autapomorphy and is in general accord with the absence of large-sized, basal synapsid predators at this truly terrestrial upland locality. It is speculated that the diminutive size of *D. teutonis* was probably an adaptation to a truly terrestrial, relatively uplands existence like that represented by the Bromacker locality. Here it subsisted on small vertebrates (and possibly large invertebrates) of the Bromacker assemblage, in which the dominant members in both size and abundance were herbivorous diadectids, and it was unlikely to encounter large predators.

Résumé : Une nouvelle espèce du genre synapside sphenacodontidé *Dimetrodon*, *Dimetrodon teutonis* est décrite sur la base d'un seul spécimen adulte consistant en une grande partie de la colonne vertébrale antéro-sacrée. L'holotype provient de l'unité basale de la Formation Tambach du Rotliegend supérieur (Permien inférieur), à la carrière de Bromacker au centre de la Forêt Thuringienne, près de Gotha, Allemagne centrale. Il s'agit de la première trouvaille de cette l'espèce en dehors de l'Amérique du Nord ce qui fournit non seulement des preuves biologiques additionnelles de l'existence d'une masse continentale Europe-Amérique durant le Permien précoce, mais aussi de l'absence de toute barrière physique ou biologique majeure aux échanges de vertébrés terrestres sur cette masse. Le poids de *D. teutonis*, estimé à 14 kg, est la moitié de celui de *Dimetrodon natalis*, l'espèce la plus petite reconnue antérieurement. La phylogénie des sphenacodontidés suggère que la petite taille de *D. teutonis* est une autapomorphie, ce qui pourrait être aussi en accord avec l'absence de prédateurs synapsides de grande taille dans cette localité montagneuse. La petite taille suggère que *D. teutonis* était adapté à une existence terrestre, dans des zones relativement arides comme celle du site de Bromacker. De petits et peut-être aussi de gros invertébrés qui étaient présents dans l'association faunistique de Bromacker, y vivaient également. Les membres plus dominants par leur taille et abondance étaient les diadectidés herbivores. Il était peu probable qu'il y avait aussi de grands prédateurs.

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Introduction

The Early Permian synapsid amniotes, the so-called pelycosaurs, are of special interest as the basal members of a major evolutionary radiation that culminated in mammals. Among the basal synapsids the genus *Dimetrodon* is proba-

bly the best known, most commonly encountered, and most speciose. Along with a few other members of the group, *Dimetrodon* is particularly notable for its possession of an extraordinarily high, dorsal sail supported by extensions of the vertebral neural spines. Collectively, the approximately dozen recognized species span the entire Early Permian, dur-

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ing which time they were the dominant predators, ranging in length and weight from about 1.7 m and 28 kg to about 4.6 m and 250 kg (Romer and Price 1940; Reisz 1986). Until the relatively recent discoveries of *Dimetrodon* in Utah (Vaughn 1966), Arizona (Vaughn 1969), Ohio (Olson 1975), and New Mexico (Berman 1977), its known distribution was limited to Texas and Oklahoma, where the overwhelming number of the specimens still originates. Mainly in view of this distribution record the new species of *Dimetrodon* described here from the Lower Permian of Germany is of particular interest as representing the first reported occurrence of the genus outside of North America. Primitive Early Permian synapsids from western and central Europe, however, are quite rare, and consist typically of poorly preserved, often scrappy materials. They include, most notably, the carnivores *Ophiacodon* from England (Paton 1974); *Haptodus* from Germany, Poland, France, and England (Paton 1974; Currie 1979); *Sphenacodon* from England (Paton 1974); and *Neosaurus* from France (Romer and Price 1940; Reisz 1986), and the herbivores *Edaphosaurus* from Germany (Romer and Price 1940; Reisz 1986) and *Casea* from France (Sigogneau-Russell and Russell 1974). Also noteworthy, the single specimen on which the German *Dimetrodon* species is based, the greater portion of an adult presacral vertebral column that includes a well-developed dorsal sail, is unique in representing the smallest member of the genus.

The German *Dimetrodon* is part of a growing, diverse assemblage of terrestrial vertebrates from the well-known Bromacker quarry locality, an intermittently active, commercial sandstone quarry that lies in the Lower Permian Tambach Formation, lowermost unit of the Upper Rotliegend, in the middle part of the Thuringian Forest, near Gotha, central Germany (Sumida et al. 1996; Eberth et al. 2000). The Bromacker locality is unique among European localities in yielding vertebrates that are known elsewhere only from the Upper Pennsylvanian and Lower Permian of the United States (Berman and Martens 1993; Sumida et al. 1998; Berman et al. 1998; Berman et al. 2000). This assemblage has been the basis for (1) assigning an earliest Permian Wolfcampian age for the Tambach Formation; and (2) suggesting the absence of any strong physical or biological barriers to tetrapod dispersal across Euramerica during the Early Permian.

Systematic paleontology

Amniota
 Synapsida Osborn 1903
 Eupelycosauria Kemp 1982
 Family Sphenacodontidae Williston 1912
 Genus *Dimetrodon* Cope 1878
Dimetrodon teutonius sp. nov.

Holotype

Museum of Natur Gotha specimen MNG 10598 consists of 14 vertebrae represented by at least some portion of the centrum and neural spine. Although loosely associated, they are for the most part arranged linearly and probably retain their correct sequential relationships. For convenience, they are numbered 1 to 14 from the anteriormost. Five complete

neural spines are represented by vertebrae 5–7, 13, and 14. Intercentra are associated with several of the centra, and one, exposed in end view, lies anterior to the spine of the anteriormost vertebra. Although described as thoracics, a posteriormost cervical or an anteriormost lumbar may be included. The head of a rib lies adjacent to the centrum of vertebrae 13. In addition, vertebral fragments are preserved on isolated blocks and counter-block pieces of the principal slab, and as loose pieces.

Horizon and locality

Lower Permian Tambach Formation, Upper Rotliegend, in the Bromacker quarry locality of the middle part of the Thuringian Forest near the village of Tambach-Dietharz and about 20 km south of the town of Gotha, central Germany. At the Bromacker quarry site are two superimposed stratigraphic successions that can be characterized by their facies associations and are referred to as the Lower Beds and Upper Beds (Eberth et al. 2000). All the vertebrates from the Bromacker quarry come from the Upper Beds, which consist of alluvial paleochannel and sheetflood facies and lacustrine suspension deposits. The vertebrates are almost exclusively restricted to two massive, red-brown, very fine-grained sandstone and siltstone sheetflood facies, which are separated by 50 cm in a stratigraphic interval of 1.2 m. *Dimetrodon teutonius* MNG 10598 was collected from the upper sheetflood deposit at the far eastern margin of the quarry (Eberth et al. 2000).

Diagnosis

This species differs from all known *Dimetrodon* species by its extremely small size, having an estimated weight of about 14 kg, which is half that of the smallest, previously recognized species, *D. natalis* (Romer and Price 1940). Relatively smaller height and length of the dorsal centra, measured in orthometric linear units (Romer and Price 1940), are autapomorphic features, distinguishing *D. teutonius* from all other members of the genus. Dorsal vertebrae of the small to moderate-sized species *D. natalis*, *D. milleri*, and *D. occidentalis* can be distinguished from those of not only *D. teutonius*, but also from the larger species of *Dimetrodon* by a combination of primitive and derived characters. Primitive characters include a weakly developed ventral keel of centrum in *D. natalis*, a marked narrowing of distal portion of neural spines anterior to about the middorsal region in *D. occidentalis*, and the subcircular cross-sectional outline of the distal portion of neural spines in *D. milleri*. The square or nearly square cross-sectional outline of the proximal portion of the dorsal spines in *D. natalis*, rather than being strongly compressed laterally and bladelike, is considered an autapomorphy of that species. The relatively smaller sail sizes of *D. teutonius*, *D. milleri*, and *D. occidentalis*, determined by the longest neural spine measured in orthometric linear units, distinguish them from all other members of the genus in which this structure is known. The figure-eight cross-sectional outline of the distal portion of the thoracic neural spines of *D. teutonius* distinguishes it, as well as all species of the genus except *D. milleri*, from the closely related genus *Secodontosaurus*, in which the cross-sectional outline is subcircular, but retains the fore and aft longitudinal grooves.

Etymology

Latin, *teutonis*, meaning an individual of a German tribe, refers to the geographic origin of the holotype.

Description

The holotype of *Dimetrodon teutonis*, MNG 10598, consists of 14 vertebrae represented by at least some portion of the centrum and neural spine (Fig. 1). Although loosely associated, they are arranged for the most part linearly, so as to retain their probable correct sequential order. For convenience of description, the elements of the series have been numbered consecutively 1 (anteriormost) through 14 in Fig. 2 to reflect this sequence. Thirteen vertebrae are complete enough to provide some meaningful description, including reliable measurements (Table 1). Large portions of the neural spines are represented by impressions, and, although the centrum and base of the neural arch in vertebra 1 are represented by a natural mold exposed in cross section, important features are accurately portrayed. Assuming a standard sphenacodontid number of 27 presacral vertebrae that includes seven cervicals (ribs do not reach sternum), 15 or more thoracics, and five or fewer lumbar (ribs fused to centra) (Romer and Price 1940), the series is believed to include probably only thoracics, although the last cervical or the first lumbar may also be included. Judging from Romer and Price's (1940) reconstructions of the sails of various *Dimetrodon* species, the spine of vertebra 1, even though it is not complete distally, appears to be much too long relative to those of vertebrae 4–7 to be a posterior cervical. At the other end of the series, the centra exhibit no signs of fused ribs, but rather a discrete rib head lies adjacent to centrum 13. The short neural spines of these vertebrae relative to those of the midthoracics also indicate a far posterior position in the presacral column. On this basis, the 14 vertebrae of MNG 10598 are considered to approximate serial positions 8–21 of the complete column, and therefore they may all represent thoracics. In no way do the vertebrae deviate from the known range of variation of the characteristic features seen in *Dimetrodon* (Romer and Price 1940; Reisz 1986).

Where feasible, length and horizontal width of the centra and length of the neural spines are given in Table 1. Width and height dimensions appear to have been slightly distorted during preservation. In those centra with the long axis oriented perpendicular to the bedding plane the centrum rims are subcircular, whereas in those with the long axis oriented parallel to the bedding plane the rims are slightly compressed, narrowing the horizontal width while exaggerating the vertical height. In most instances, the width was probably equal to or only slightly exceeded by the height. In lateral view, the ventral halves of the centrum rims are seen to be beveled slightly, so as to accommodate the intercentrum. The lateral surfaces of the centra are deeply concave, flaring outward to meet the rim. A midventral ridge or keel extends downward at either end of the centrum to merge with the ventral margin of the centrum rims. The latter may be expanded ventrally as lip-like structures for the articulation of the intercentra. As expected, in the anterior thoracics, best exemplified by vertebra 1, the ventral keel is sharply V-shaped in cross section, whereas farther posteriorly in the series (vertebrae 10–14) the keel, though remaining narrow, becomes bluntly rounded. Prominent centrosphenes are pre-

served on the dorsal margin of the anterior centrum rim of vertebra 6, but are poorly preserved or developed elsewhere. The general features of the well-developed transverse processes of the anterior thoracics of vertebrae 1, 2, and 6 are well exhibited. Extending about 10 mm laterally out from the anterodorsal margin of the pedicel, but curving slightly downward and backward, the process is roughly triangular in cross section, with the apex directed downward. The process ends in a facet that is egg-shaped in outline and faces ventrolaterally and slightly posteriorly. The transverse process of vertebra 12 (exposed in lateral view), the only other one that is well-preserved, extends about 2 mm directly laterally from the center of the pedicel and is subcircular in cross section and in the outline of its laterally facing facet. In vertebra 1, as is typical in sphenacodontids, the lateral surface of the neural arch is deeply excavated just above the transverse process. This feature is only partially preserved in vertebra 2, and poor preservation makes its presence difficult to detect in any of the other vertebrae.

Details of the anatomy of the elongated neural spines conform within the narrow range of variation described in other species of *Dimetrodon* generally. For a very short distance of about 12 mm above the level of the zygapophyses, the spines of the anterior thoracics are laterally compressed blades with an anteroposterior length of about 7 or 8 mm and a transverse width of about 4 mm. Within a few millimetres, there is an abrupt change in morphology of the spines from the proximal portion to the much longer distal portion. Distally, the spines narrow in anteroposterior length to about 3 mm, while expanding in transverse width to about 6 mm. In the posterior thoracics, although these dimensions are slightly reduced, the proportions remain essentially the same. Poor preservation makes it difficult to determine the presence of fore and aft grooves and ridges on the proximal portion of the neural spines. However, fore and aft grooves are particularly evident on the distal portions of the spines, giving them the typical *Dimetrodon* figure-eight cross-sectional outline, and in the preserved middle portions of the anterior thoracics the anterior groove is divided by an extremely thin ridge. Spine lengths are available only for vertebrae 5–7, 13, and 14 (see Table 1). The spine of vertebra 5, however, does not represent the maximum sail height, as the distal end of the 245 mm long spine of vertebra 4 is missing.

Several intercentra are represented, most of which are closely associated with their respective centra. One considerably displaced intercentrum, lying anterior to the spine of vertebra 1, is exposed in end view and exhibits the typical crescentic outline, in which the apices are directed dorsally from the ends of a ventrally flattened base. The only rib included in the holotype is the proximal end of a double-headed rib lying adjacent to vertebra 13.

Paramount to recognizing that the Bromacker specimen of *Dimetrodon* represents a new species (see in following text) is demonstrating that its extremely small size (Table 2) is an adult feature. This was established principally by comparing MNG 10598 with partial, juvenile skeletons of an indeterminate species of *Dimetrodon* in the collections of the Museum of Comparative Zoology at Harvard University. One of these (MCZ 2027), consisting of parts of 17 dorsal and 12 caudal vertebrae from the Lower Permian Petrolia Formation (ex Belle Plains Formation) of the Wichita Group of Texas (as

Fig. 1. Photograph of *Dimetrodon teutonius* n. sp., holotype, MNG 10598, as preserved on principal block.

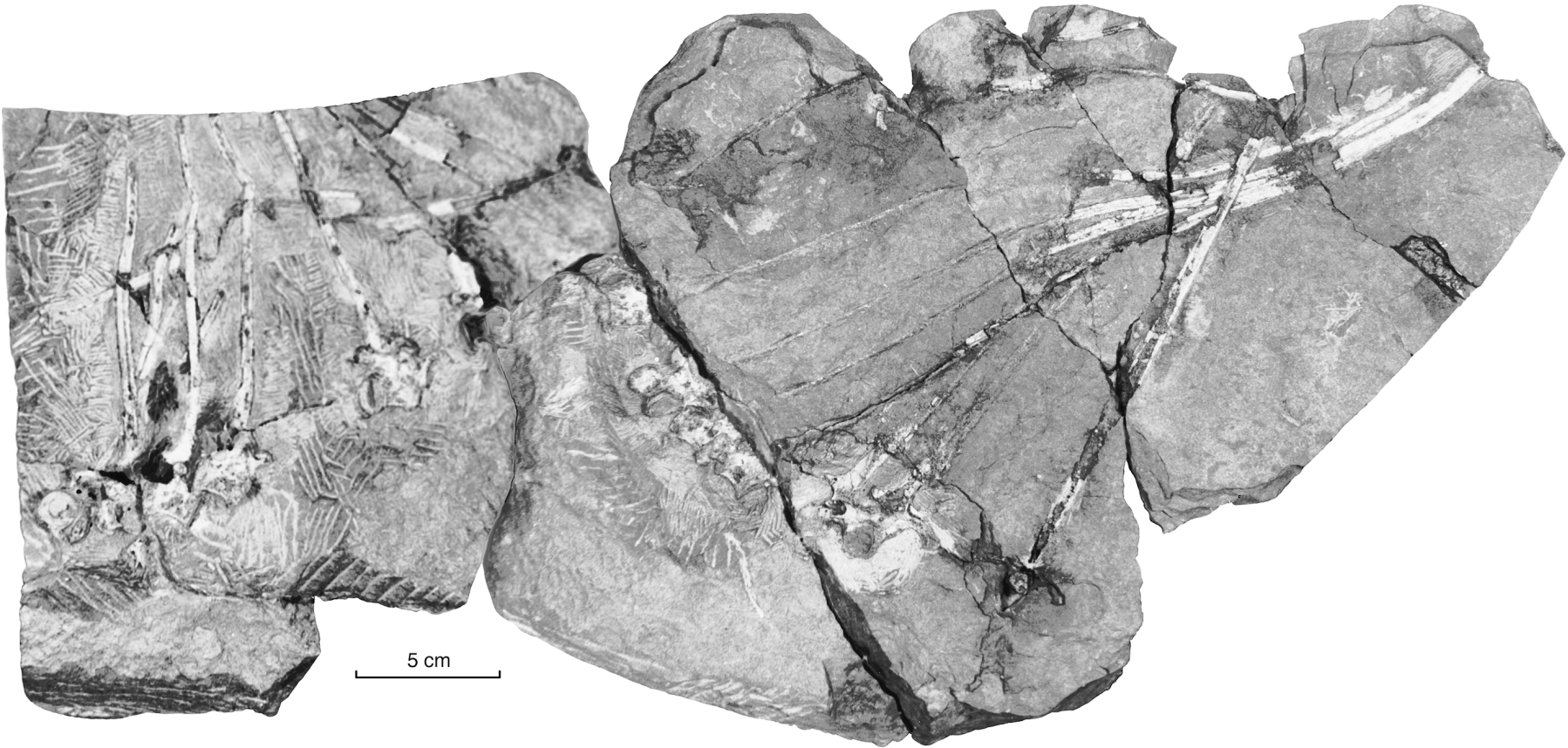


Fig. 2. Drawing of *Dimetrodon teutonius* n. sp., holotype, MNG 10598, as seen in Fig. 1. Vertebrae numbered according to their presumed sequential relationships, 1 being anteriormost, and not according to probable serial position in column. ic, intercentrum; r, rib.

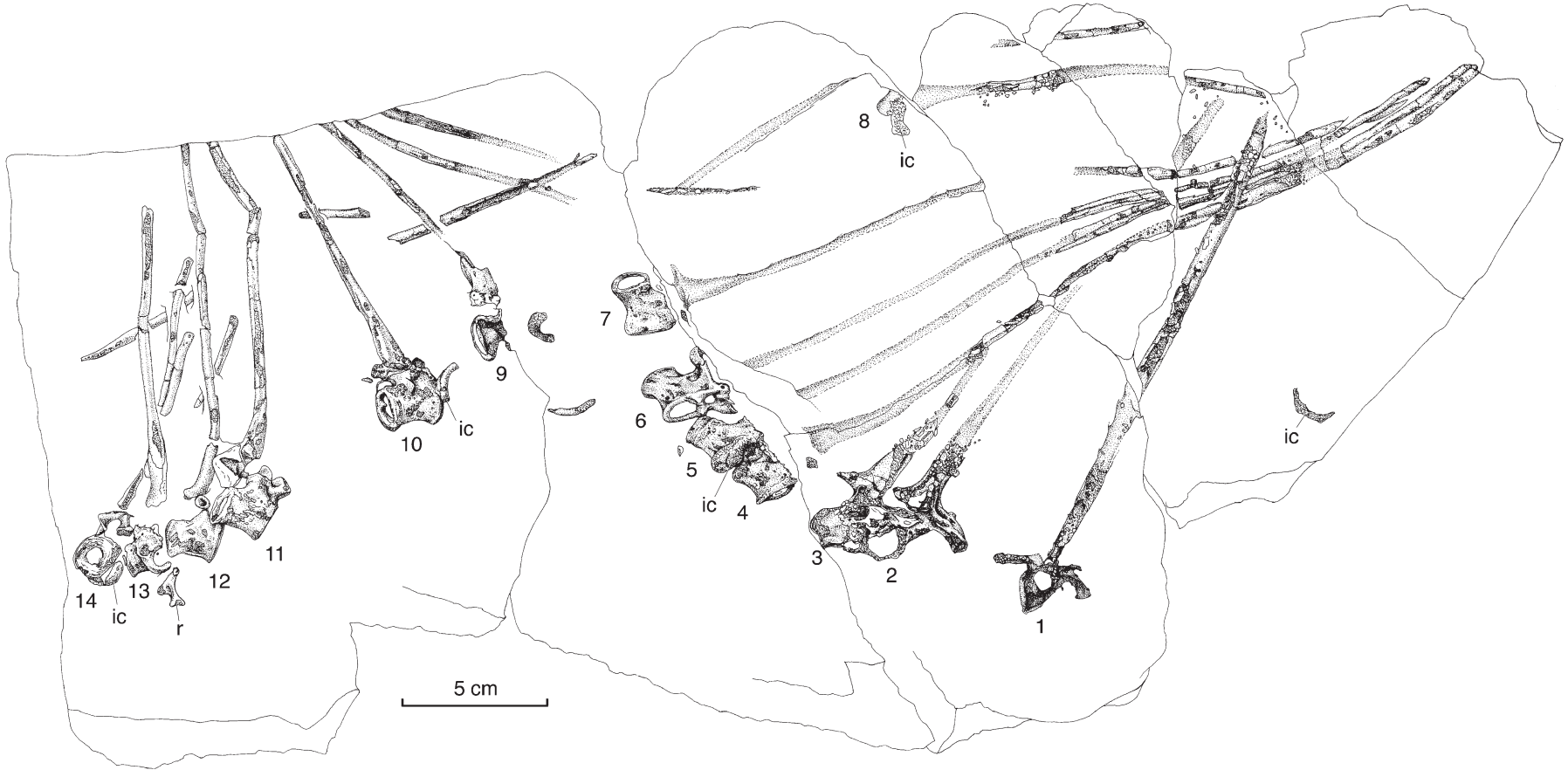


Table 1. Measurements (in mm) of vertebrae in *Dimetrodon teutonius* MNG 10598.

Vertebral number	CL	CW	CH	SH
1	—	—	—	—
2	—	11	12.7	—
3	—	—	12.4	—
4	14	9a	12.3	—
5	13	—	11.2	245
6	14	8a	11.5	231
7	15	9	10.6	222
8	—	—	—	—
9	—	—	11.5	—
10	16	9	11.2	—
11	17	10a	11.2	—
12	16	11a	11.4	—
13	13	11a	11.4	91
14	11	11	11.7	80

Note: CL, length of centrum; CW, width of centrum; CH, height of centrum; SH, height of complete neural spines measured from above level of zygapophyses. CW and CH measurements made at posterior end of centrum unless denoted by an "a" to indicate anterior end. Vertebral number follows that indicated in Fig. 2.

revised by Hentz 1988), is particularly illustrative. It is of comparable size to the holotype of *D. teutonius*, but can be distinguished by several juvenile features of its presacral vertebrae.

- (1) Only one of the presacral vertebrae, a posterior dorsal, includes a centrum, which is loosely attached to the neural arch. The other neural arches, although complete, lack attached centra, which presumably separated post-mortem. In none of the vertebrae of MNG 10598 is there any sign of a suture or a roughened ridge marking the union of the centrum with the neural arch.
- (2) The basal portion of the presacral neural spines, although expanded anteroposteriorly 6–7.0 mm into a blade-like structure, has a very narrow transverse width of only 1.5 mm. In MNG 10598, the comparable region has a width of 4 mm.
- (3) The distal portion of the presacral neural spines is oval in cross-sectional outline, with an anteroposterior length slightly exceeding the transverse width, but, most significantly, lacking any sign of the fore and aft grooves, which produce the typical figure-eight cross-sectional outline. Such grooves are present in MNG 10598.

Comparisons

Diagnoses of the approximately 12 *Dimetrodon* species have been based primarily on vertebral structure and proportions, overall body size, and to some extent, stratigraphic level, but rarely on cranial features (Romer and Price 1940; Reisz 1986). Because of its extremely small size, *D. teutonius* need only be compared in detail with the small to the moderate-sized species. Interestingly, *Dimetrodon* species exhibit not only subtle differences in proportions, but also a progressive increase in overall size with greater upward stratigraphic occurrence. However, this presents a common problem in distinguishing among closely related species on the basis of

differences in linear proportions without having a standard unit of measurement. As a resolution, the most commonly employed method in comparing interspecific linear dimensions of primitive synapsids has been the orthometric linear unit, first proposed and used by Romer and Price (1940, p. 8). Here, linear measurements are expressed in values relative to the animal's overall size, in which one linear unit is defined as equal to the radius of an average-sized dorsal centrum to the 2/3 power. Currie (1978) has demonstrated that this unit of measurement provides an accurate means of comparison among closely related species of similar ontogenetic growth stage. Because the holotype of *D. teutonius* is unquestionably an adult, the application of the orthometric linear unit in this study is appropriate.

In terms not only of its direct linear measurements, but also in orthometric linear units, vertebral dimensions of *D. teutonius* are considerably smaller than those of the otherwise smallest known species, *D. natalis* (Table 2). A marked difference in overall body size can also be demonstrated utilizing the same method of estimating total weights of *Dimetrodon* species utilized by Romer and Price (1940). Initially, in calculating the total weights of species of *Dimetrodon* and other primitive synapsids, they used the standard technique of measuring volume displacement of a clay-model that was based on the nearly complete skeleton of a presumed female of *D. limbatus*. The volume displacement was then multiplied by the average of the available estimates of the specific gravity of reptiles. From this, the weights of other *Dimetrodon* species were computed on the assumption that r^2 of the orthometric linear unit is an index of relative weight. In Table 2, the weight of *D. teutonius*, as well as that of *D. occidentalis* (Berman 1977), is calculated using r^2 as an index of comparison with those weights given by Romer and Price (1940) for other species. The result indicates a very diminutive *D. teutonius*, weighing only 14 kg compared to the 28 kg for *D. natalis*. Furthermore, conversion of the estimated longest spine of *D. teutonius* to orthometric linear units yields a value very close to those for *D. occidentalis* and *D. milleri* (Table 3). Unfortunately, sail size is not available for *D. natalis*, as complete spines of its thoracic vertebrae are not known (Romer and Price 1940). Whereas the height or size of the dorsal sail appears to keep pace with a marked increase in the general body size in the smaller species *D. teutonius*, *D. milleri* and *D. occidentalis*, this is not the case in the larger and later occurring species (Table 3), in which there is a progressive and dramatic disproportional increase in sail size (Romer 1948). Case (1907, pl. 5) restored the sail of *D. natalis* as relatively very low, but Romer and Price (1940) cautioned that his restoration was without foundation, as complete neural spines are preserved only in the lumbar vertebrae.

Several, presumably primitive, features of the thoracic vertebrae can be noted that distinguish the small to moderate-sized *Dimetrodon natalis*, *D. occidentalis*, and *D. milleri* not only from *D. teutonius*, but also from the large species. According to Romer and Price (1940), in *D. natalis* the ventral keel of the thoracic vertebrae is little developed and in the lumbar becomes rounded ventrally. They also described the neural spines in *D. milleri* as being nearly circular in cross section, whereas Berman (1977) described in *D. occidentalis* a sharp decrease in the cross-sectional area of

Table 2. Average measurements of dorsal vertebrae and estimates of body weights of *Dimetrodon* (*D.*) *teutonius* and small to moderate-sized species of *Dimetrodon* from U.S.A.^a

Species	CL (mm)	CW (mm)	CH (mm)	OLU value	CL (OLU)	CH (OLU)	Weight (kg)
<i>D. teutonius</i>	14.3	9.9	10.0	2.88	4.97	3.47	14
<i>D. natalis</i>	20.0	14.0	14.0	3.66	5.50	3.80	28
<i>D. occipitalis</i>	23.0	17.0	19.5	3.78	6.10	5.20	41
<i>D. milleri</i> ♀	22.0	17.0	19.0	4.33	5.10	4.40	47
<i>D. milleri</i> ♂	27.0	22.0	25.0	4.95	5.50	4.50	70
<i>D. boonerorum</i>	25.0	21.0	22.0	4.80	5.20	4.60	63
<i>D. limbatus</i> ♀	30.0	26.0	31.0	5.53	5.40	5.60	97
<i>D. limbatus</i> ♂	36.0	30.0	35.0	6.08	5.90	5.80	129
<i>D. loomisi</i>	34.0	26.0	26.0	5.53	6.10	4.70	97

Note: OLU refers to orthometric linear unit (radius of centrum to the 2/3 power) of Romer and Price (1940). CL, centrum length; CH, centrum height; CW, centrum width.
^aRomer and Price 1940, tables 5, 7; Berman 1977.

Table 3. Length of longest neural spines in *Dimetrodon* (*D.*) *teutonius* and various species of *Dimetrodon*.

Species	Longest spine (mm)	OLU value	Longest spine (OLU)
<i>D. teutonius</i>	245	2.73	90
<i>D. occidentalis</i>	360	3.78	95
<i>D. milleri</i>	390	4.16	94
<i>D. limbatus</i> ♀	630	5.53	114
<i>D. limbatus</i> ♂	675	6.08	111
<i>D. loomisi</i>	678	5.53	123
<i>D. gigashomogenes</i>	920	6.61	139
<i>D. grandis</i>	1190	7.61	156

Note: OLU refers to orthometric linear unit of Romer and Price (1940). Measurements for U.S. species from Romer (1948) and Berman (1977).

the distal portions of the neural spines anterior to approximately the midthoracic region. On the other hand, whereas the distal portions of the thoracic spines in *D. natalis* exhibit the typical cross-sectional figure-eight outline, the square or nearly square cross-sectional outline of the proximal portions described by Romer and Price (1940) must be judged as an autapomorphic character, inasmuch as in all sphenacodontids the basal portion of the neural spine is a laterally compressed, blade-like structure.

Not considered here is *D. kempae*, a very small, questionable species of *Dimetrodon* from the Lower Permian of Texas. It is very poorly known, and Romer and Price (1940) described it as approximately the size of *D. natalis*. (no linear measurements of its vertebrae were given except for a centrum height-to-width ratio of 1.53), but cautioned that it may pertain to a sphenacodontid of some other genus. Reisz (1986) considered it as Sphenacodontidae *incertae sedis*.

In terms of orthometric linear units, the thoracic centra of *D. teutonius* differ from those of all other species of *Dimetrodon* in being relatively smaller in length and vertical diameter. Inasmuch as these measurements exhibit a general increase in value in larger and later occurring species (Romer 1948), the lower values in *D. teutonius* might reasonably be judged as strictly primitive features. However, the intrafamilial relationships of Sphenacodontidae indicate that

the extraordinary small size of this species is more likely an autapomorphy. As determined by Reisz et al. (1992), phylogenetic analysis of the four well-documented sphenacodontid genera reveals a pattern of relationships, in which *Dimetrodon* and *Secodontosaurus* share a more recent ancestor with one another than does either with *Ctenospondylus* and *Sphenacodon*, which in turn represent progressively more distant sister taxa. Given the relatively large adult size of the earliest known representatives of the non-*Dimetrodon* sphenacodontids (Romer and Price 1940; Berman 1978; Reisz et al. 1992), parsimony dictates that *Dimetrodon* was also primitively large, certainly much larger than *D. teutonius*. Consequently, optimization of size as a character in sphenacodontid phylogeny indicates that *D. teutonius* is autapomorphic for being smaller than any other member of the sphenacodontid clade. That is, the diminutive size of *D. teutonius* represents a secondary reduction, rather than a plesiomorphic feature, of this species.

It is conceivable, but very unlikely, that the vertebrae of *Dimetrodon teutonius* could belong to the closely related, Early Permian sphenacodontid *Secodontosaurus*. Whereas the cranial anatomy of *Secodontosaurus* is very distinctive (Reisz et al. 1992), the postcranium could be confused for *Dimetrodon*, particularly the vertebrae, in which the neural spines are also elongated to support a high, dorsal sail (Romer and Price 1940). There are, however, several arguments against such a misidentification. In *Secodontosaurus*, the cross-sectional outline of the distal portion of the thoracic neural spines is subcircular, though retaining the fore and aft longitudinal grooves, whereas in *Dimetrodon*, with the exception of *D. milleri*, it is transversely expanded into a distinct figure-eight pattern. Furthermore, documented occurrences of *Secodontosaurus* are very rare and have a greatly restricted geographic distribution that includes only Texas (Romer and Price 1940; Reisz et al. 1992).

Discussion

The *Dimetrodon* from the Bromacker quarry is part of a

growing vertebrate assemblage that is unique from those of all other Early Permian European localities in its taxonomic composition and in its paleoenvironmental source. Described (Eberth et al. 2000) as representing a truly upland, terrestrial deposit that accumulated in a small (250 km²), internally drained basin, the Tambach Formation at the Bromacker quarry site is unusual in not including aquatic or semi-aquatic taxa. Fish and obligatory aquatic amphibians found in deposits of roughly comparable age elsewhere in Europe are absent at the Bromacker quarry. Instead, highly terrestrial tetrapods characterize the assemblage, the most significant of which, in addition to *Dimetrodon*, include (1) a new genus and species of trematopid amphibian, *Tambachia trogallas* (Sumida et al. 1998); (2) the seymouriamorph amphibian *Seymouria sanjuanensis* (Berman and Martens 1993; Berman et al. 2000); (3) a new species of the diadectid diadectomorph *Diadectes*, *D. absitus* (Berman et al. 1998); (4) a new, undescribed genus of diadectid closely related to *Diadectes* (Berman et al. 2000); (5) a new genus and species of protorothyridid captorhinomorph reptile, *Thuringothyris mahlendorffae* (Boy and Martens 1991); and (6) a new, undescribed genus of bolosaurid reptile (Sumida and Berman 1997; Eberth et al. 2000; Berman et al. 2000).

Among the vertebrates from the Bromacker, the trematopid, *Seymouria*, *Diadectes*, *Dimetrodon*, and the protorothyridid record first occurrences outside of North America. Occurrences of bolosaurids are restricted to *Bolosaurus* from the Lower Permian of Texas (Watson 1954) and *Belebey* from the Late Permian of Russia (Ivachnenko and Tvredokhlebova 1987). Despite this strong commonality, however, three unusual features of the Bromacker assemblage have been recognized (Eberth et al. 2000; Berman et al. 2000), which contrast it significantly from the well-known, contemporary, mixed terrestrial-aquatic assemblages of southwestern United States (Olson and Vaughn 1970; DiMichele and Hook 1992; Berman 1993). Firstly, it was argued (Eberth et al. 2000) that the apparent absence of aquatic and semi-aquatic vertebrates at the Bromacker reflects the lack of a suitable, perennial environment. The small Tambach Basin was envisioned as internally drained, isolated from regional drainage systems, and subjected to subseasonal to seasonal drying, and therefore not allowing, or severely limiting, the establishment of aquatic or semi-aquatic vertebrates. Secondly, the Bromacker assemblage is unique from all other Early Permian terrestrial vertebrate assemblages in being apparently dominated numerically by herbivores. *Diadectes* and the closely related, undescribed diadectid, both of which probably subsisted on a diet consisting mainly of high-fiber, terrestrial plants (Hotton et al. 1997), not only account for over half the articulated skeletons recovered to date, but are the largest members of the Bromacker assemblage, attaining a snout-vent length of about 60 cm. If, as proposed by Hotton et al. (1997), *Bolosaurus* also subsisted primarily on a high-fiber diet, then the same can be assumed about the Bromacker bolosaurid, as their unusual cranial anatomies and dentitions are essentially identical (Berman et al. 2000).

The third, unusual feature of the Bromacker assemblage is the rarity of pelycosaurian-grade, carnivorous synapsids. A quarter century of collecting vertebrates at the Bromacker quarry (Martens 1980) has resulted in the discoveries of only

three specimens, representing two taxa of basal or pelycosaurian-grade synapsids. The greater portions of two, very closely associated, articulated skeletons, MNG 10595 and 10596, almost certainly represent a single taxon. On the basis of general features of the vertebrae and limbs and a maximum, estimated snout-vent length of about 50–60 cm, they have been tentatively identified as adults of a varanopseid or as juveniles of a sphenacodontid (Eberth et al. 2000). Both of these taxa were among the dominant terrestrial predators of the Early Permian. The second taxon is represented by the *Dimetrodon* specimen described here. In dramatic contrast, well-documented Early Permian, mixed terrestrial-aquatic vertebrate assemblages from localities in the southwestern United States typically include abundant carnivorous synapsids (Olson and Vaughn 1970; DiMichele and Hook 1992; Berman 1993; Eberth and Berman 1993). Eberth et al. (2000) and Berman et al. (2000) recognized a possible ecological link between the rarity of carnivorous synapsids and the absence of aquatic and semi-aquatic forms at the Bromacker, citing Olson's (1961, 1966, 1971, 1984) explanation for why large carnivorous "pelycosaurs" of the Lower Permian deposits in the southwestern United States are typically found associated with aquatic environments. Olson argued, on the basis of morphology, coprolite content, and disassociation with large herbivores, that, whereas the "pelycosaurs" were well-suited structurally to an exclusively terrestrial existence, they were limited in ecological distribution to aquatic environments because of their dependence on aquatic and semi-aquatic vertebrates as their principal food source. The rare appearances of primitive synapsids at the Bromacker, however, may not represent contradictions to this hypothesis.

The probable carnivorous synapsids MNG 10595 and 10596 were discovered in 1994 in a large, highly concentrated bone pocket, which included numerous other vertebrates in greatly varying stages of completeness and articulation (Eberth et al. 2000). This prompted the speculation that the bone-pocket synapsids may represent an "erratic" occurrence, having been transported or introduced into the Bromacker assemblage from another faunal complex (Berman et al. 2000). Olson (1968, 1971, 1975) used the term "erratic" to explain the presence of an uncharacteristic fossil in the collection of a well-known faunal complex. *Dimetrodon* is typically viewed as occupying the ecological role of dominant carnivore in Early Permian assemblages, at the end of an aquatic-based food chain (Olson 1952, 1976; DiMichele and Hook 1992). It is evident, however, that the extremely small size of *D. teutonius* would have restricted it to predation on very small forms. Furthermore, *D. teutonius* was certainly large enough to have preyed on the numerous, small aquatic fish and amphibians that have been discovered in the lacustrine grey sediments and black shales of the ubiquitous limnic or aquatic, basinal coal-swamp environments of Rotliegend localities represented most notably by Niederhaesslich, Friedrichroda, and various Saar-Nahe sites, such as Lebach. However, also present in these habitats were much larger predaceous amphibians such as *Eryops* (Werneburg, 1993b) and synapsids, such as the ophiacodontids and sphenacodontids (Romer and Price 1940; Reisz 1986), that were clearly capable of reversing the role of *D. teutonius* to that of prey. Therefore, it is most likely that *D. teutonius*

was not an erratic, but was adapted to a truly terrestrial, relatively uplands existence, like that represented by the Bromacker locality. Here it subsisted on small vertebrates (and perhaps large invertebrates) of an assemblage in which herbivorous diadectids were the dominant forms in both size and abundance, and it was unlikely to encounter larger predators. The diminutive size of *D. teutonis*, therefore, may represent an adaptation to this truly terrestrial, upland environment.

In overall size, excluding the development of the dorsal sail, *D. teutonis* is most comparable to *D. natalis* from the Lower Permian Nocona Formation (ex Admiral Formation) of the Wichita Group of Texas (as revised by Hentz 1988), which is regarded as a primitive member of the genus (Romer and Price 1940; Reisz 1986). Inasmuch as a Wolfcampian age is assigned to this level of the Texas section (Hentz 1988) and *Dimetrodon* exhibits a general trend toward overall increase in size in increasing higher stratigraphic levels, this resemblance is consistent with the similar age estimation of the Bromacker locality based on other faunal similarities (Berman and Martens 1993; Sumida et al. 1996, 1998; Berman et al. 1998).

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