NEW MATERIALS OF *DIMETRODON TEUTONIS* (SYNAPSIDA: SPHENACODONTIDAE) FROM THE LOWER PERMIAN OF GERMANY

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ABSTRACT

Additional specimens of the sphenacodontid synapsid *Dimetrodon teutonis*, including a maxilla, dorsal vertebrae, scapulocoracoids, a humerus, and partial, articulated hindlimbs that consist of the epipodials, tarsi, and incomplete digits, not only expand significantly its known anatomy, but also confirm its recognition as a new species of *Dimetrodon*. The new materials, like the holotype, are from the Lower Permian Tambach Formation, lowermost formation of the Upper Rotliegend Group or Series, of the Bromacker quarry locality in the midregion of the Thuringian Forest near Gotha, central Germany, and represent the only record of the genus outside of North America. The original estimated weight of 14 kg for the holotype of *D. teutonis*, calculated on the basis of centra size, is revised to 24 kg for the larger, more fully mature, newly discovered specimens. This is still significantly less than the calculated maximum of nearly 37 kg for the smallest, previously recognized species. *D. nutalis*. Linear measurements of appendicular elements also indicate a substantial size difference between the two species.

KEY WORDS: Sphenacodontidae (Dimetrodon), Lower Permian, Upper Rotliegend, Bromacker locality, Germany

INTRODUCTION

Until recently, occurrences of the best known basal or pelycosaurian-grade synapsids, the dominant predator Dimetrodon, were restricted to the Lower Permian of North America, where remains of its 12 currently recognized species are commonly encountered (Romer and Price, 1940; Reisz, 1986). A much wider distribution of Dimetrodon, however, was realized with the description (Berman et al., 2001) of a new species, D. teutonis, based on a single, adult specimen consisting of a series of 14 thoracic vertebrae from the well-known Bromacker quarry locality, an area of once active commercial sandstone quarries located in the Lower Permian Tambach Formation, lowermost unit of the Upper Rotliegend Group or Series, in the middle region of the Thuringian Forest, near Gotha, central Germany, Undoubtedly, the most notable and easily recognized feature of Dimetrodon is its possession of an extraordinarily high dorsal sail supported by the elongation of the vertebral neural spines. The holotype of D. teutonis was of particular interest in having an estimated total body weight, determined using a methodology based on centrum size that was first formulated and employed by Romer and Price (1940) and Romer (1948), of only 14 kg, which is only half that of the smallest, previously described species, D. natalis. It was reasoned (Berman et al., 2001), on the basis of sphenacodontid phylogeny, that the diminutive size of D. teutonis represents an autapomorphy, which appears to be in accord with an apparent absence of size-dominant, basal synapsid predators at the Bromacker. The diminutive size of D. teutonis was interpreted as a probable adaptation to a truly terrestrial, relatively upland existence like that proposed for the Bromacker locality, which was located near the center of a small, internally drained paleograben (Eberth et al., 2000). Here, D. teutonis is envisioned as having preyed on small vertebrates, as well as possibly large invertebrates, in an assemblage that was dominated in both size and abundance by herbivorous diadectids and where large predators were rarely encountered (Berman et al., 1998; 2003). Newly discovered, slightly larger, more

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fully mature specimens of *D. teutonis* contribute significantly to its known anatomy, provide additional evidence for its generic assignment and recognition as a new species, and allow reassessment of its maximum weight as the smallest of the known species of the genus.

The following acronyms are used to refer to institutional repositories of specimens: MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; MNG, Museum der Natur, Gotha,

Germany: UM, Museum of Paleontology, University of Michigan, Ann Arbor.

Anatomical structures are identified by the following abbreviations: ac, anterior coracoid; as, astragalus; c, lateral centrale; ca, calcaneum; fi, fibula; pc, posterior coracoid; r, rib; sg f, supraglenoid foramen; ti, tibia; tri c, coracoid process for attachment of coracoid head of triceps muscle; v, vertebra; 1–5, distal tarsals one through five

SYSTEMATIC PALEONTOLOGY

Class Amniota
Order Synapsida Osborn 1903
Suborder Eupelycosauria Kemp 1982
Family Sphenacodontidae Williston 1912
Genus Dimetrodon Cope 1878
Dimetrodon teutonis Berman et al. 2001

Revised Diagnosis.—Autapomorphies distinguishing Dimetrodon teutonis from all other members of the genus include: 1) diminutive size, with a calculated maximum weight of 24 kg compared to nearly 37 kg for the otherwise smallest, previously recognized species, D. natalis; 2) relatively smaller height and length of the dorsal centra; 3) free marginal outline of the anterior coracoid formed by an unusually long, straight, dorsal margin that meets the anterodorsally curving ventral margin in a sharply acute angle. Primitive features of the maxilla distinguishing D. teutonis from all other members of the genus except perhaps D. natalis include: 1) marginal tooth formula of two precanines, two canines, and 15 postcanines, as compared to a formula of three, two, and 15, respectively, in D. natalis; 2) ventral margin slightly convex; 3) little or no indication of a dorsally arching, maxillary step at the anterior end of the ventral

Holotype.—MNG 10598 consists of a series of 14 loosely associated vertebrae represented by at least some portion of the centrum and neural spine and considered to approximate serial positions 8–21 of the presacral column and, therefore, possibly all thoracic vertebrae.

Referred Specimens. MNG 10654, partial right scapulocoracoid, greater part of left scapular blade, nearly complete left humerus, and partial, articulated hindlimbs that include epipodials, tarsus, metatarsals, and a few proximal phalanges, with the left also represented by a counterpart impression; MNG 10655, probable posterior dorsal vertebrae that includes three articulated vertebrae and a closely associated fourth with the neural spines either missing or incomplete; MNG 10693, four articulated probable middorsal vertebrae, two of which possess complete neural spines, with three associated left ribs, and several scattered, partial vertebrae and ribs, and the greater part of the left scapulocoracoid with counterpart impression; MNG 13433, right maxilla with dorsal lamina preserved as impression.

Horizon and Locality.—Lower Permian Tambach Formation, lowermost formation of the Upper Rotliegend Group or Series, of the Bromacker quarry locality in the midregion of the Thuringian Forest near the village of Tambach-Dietharz and about 20 km south of the town of Gotha, central Germany. Two superimposed stratigraphic successions that can be characterized by their facies associations are informally referred to as the Lower Beds and Upper Beds (Eberth et al., 2000). All of 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 that are separated by 50 cm in a stratigraphic interval of 1.2 m. The holotype MNG 10598 was collected from the upper sheetflood, whereas the referred specimens MNG 10598, 10654, and 13433 and MNG 10655 and 10693 are from the upper and lower levels, respectively.

DESCRIPTION AND ASSIGNMENT TO DIMETRODON

Included in the new materials referable to *Dimetrodon teutonis* is the first cranial element, an isolated right maxilla (Fig. 1) that conforms exactly to the sphenacodontid pattern. It is exposed in lateral view, and, whereas it is essentially complete along its ventral margin, including most of the dentition, the dorsal lamina is represented by an impression that faithfully preserves its full extent. The slightly convex ventral margin of the maxilla has a maximum length of 82 mm. The dental series includes 19 teeth or their spaces, consisting of two precanines, two canines, and 15 postcanines; it is

possible, however, that an additional tooth may have been present at either end of the series. The precanines decrease serially in size anteriorly from a maximum length of 7 mm. Of the canine pair, only the basal half of the posterior tooth is preserved, but it suggests an approximate length of 10 to 12 mm. The lengths of post-canines increase serially in size posteriorly to about their mid-series from about 4 to 6 mm, then steadily decrease to about 2 mm at the end of the series. In sphenacodontid fashion, all the teeth are slightly to moderately recurved and laterally compressed, particularly the postcanines.

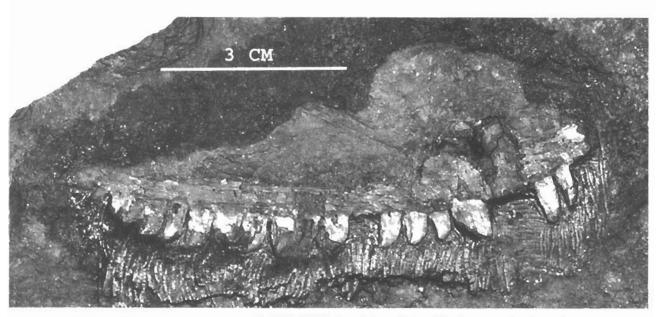


Fig. 1.—Dimetrodon teutonix. Right maxilla MNG 13433 in lateral view with dorsal lamina preserved as impression.

with moderately developed, anterior and posterior cutting edges without serrations, and the postcanines have a slightly bulbous appearance compared to the other teeth. There is a pronounced lateral swelling and increased height of the alveolar shelf to accommodate the roots of the canines. Although the anterior end of the ventral margin may not be complete, there is no indication that it arched dorsally to form a maxillary "step" like that seen in the larger species of *Dimetrodon* (Romer and Price, 1940). The height of the dorsal lamina suggests that, as in all sphenacodontids, it contacted the anterior portion of the lateral or ventral margin of the nasal, shortening the lacrimal anteriorly and preventing it from reaching the external naris.

The vertebrae of MNG 10655 and 10693 (Fig. 2). which appear to be from the posterior and mid-region of the presacral column, respectively, neither deviate in any noticeable way from those in the holotype of *Dimetrodon* teutonis nor provide any distinguishing features about the species (Berman et al., 2001). This, in addition to their exact conformation to the pattern exhibited by the majority of Dimetrodon species, eliminates the need to describe them. What is relevant about the new specimens, however, is that they are slightly larger than those of the holotype, indicating a greater overall body size or weight (see COMPARISONS AND DISCUSSION section below). An overall increase in size also is expressed in the height of the neural spines. Of the four articulated middorsal vertebrae in MNG 10693, only the anteriormost two possess complete neural spines, with the lengths of the first and second being 280 and 326 mm, respectively. However, considering the incompleteness of the preserved presacral column and the marked difference in the lengths of the two complete spines, the longest-spined vertebra(e) may not be represented.

Of the three partially preserved scapulocoracoids, two include the greater portions of the scapula and the anterior and posterior coracoids: a right of MNG 10654 exposed in lateral view (Fig. 3A) and a left of MNG 10693 exposed in medial view (Fig. 3B). In both the missing marginal areas, particularly of the coracoid plate, are partially indicated by a lighter-colored, reduced matrix caused by its contact with the bone. Fortunately, the counterpart block of the scapulocoracoid of MNG 10693 (Fig. 3C) preserves precisely nearly the entire extent of the girdle as impression and in the lighter-colored, reduced matrix caused by contact with the bone. The scapulocoracoid of Dimetrodon teutonis is unmistakably of the pattern for the genus. This is especially evident in the outline of the scapular blade, which is narrow and waisted strongly toward its base. The lateral opening of the supraglenoid foramen is positioned, as in other sphenacodomids, a short distance amerior to the supraglenoid buttress. The sutures between the three elements of the scapulocoracoid are closed and undetectable. Closure of the sutural contacts with the posterior coracoid is particularly suggestive of advanced maturity, inasmuch as this bone typically remains loosely attached until an extremely late stage of development in sphenacodontids (Romer and Price, 1940). The coracoid process for the coracoid head of the triceps muscle is well developed, which also suggests maturity. The counterpart impression of MNG 10693 reveals the outline of the free margins of the anterior coracoid, which is distinctly different from those of other basal synapsids (see COMPARISONS AND DISCUSSION section below) in being formed 2004

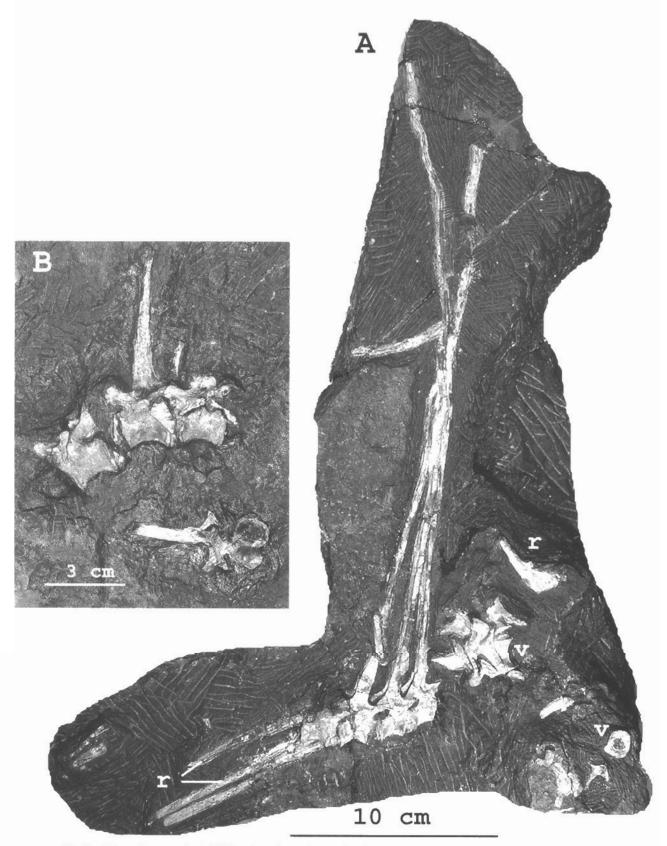


Fig. 2.—Dimetrodon teutonis, A. Middorsal vertebrae and ribs of MNG 10693, B. Probable posterior dorsals of MNG 10655,

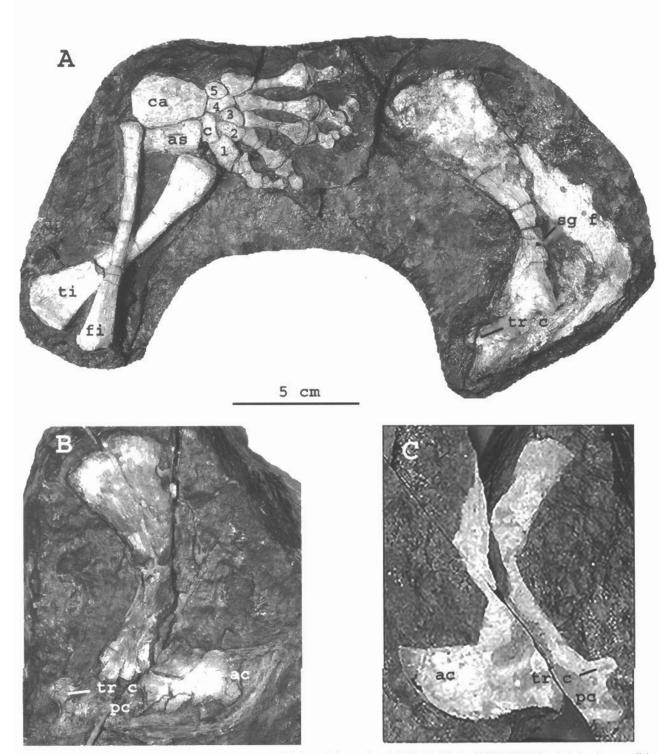


Fig. 3.—Dimetrodon teutonis. A. Partial right scapulocoracoid in lateral view and partial right hindlimb of MNG 10654 that includes the epipodials, tarsus except for probable loss of medial centrale, metatarsals, and a few phalanges in ventral view except for lateral or posterior view of fibula. B. Left scapulocoracoid MNG 10693 in medial view. C. Counterpart block showing nearly its entire extent as impression and by the lighter-colored, reduced matrix caused by contact with the bone of its medial surface.

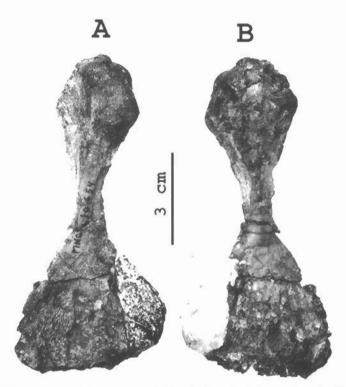


Fig. 4.—Dimetrodon teutonis MNG 10654. A. Dorsal, and B. Ventral views of left humerus (proximal head toward top of page).

by a long, straight, horizontal dorsal margin that meets the anterodorsally curving ventral margin in a sharply acute angle.

The single preserved humerus of *D. teutonis*, a left belonging to MNG 10654 (Fig. 4), is nearly complete, missing mainly the supinator process and the entepicondyle, though the latter portion has been almost entirely restored using its impression in the matrix as a natural mold to cast it in epoxy. Despite some surface bone erosion, it is evident that the processes and articular surfaces were well developed and, therefore, indicative of a fully mature individual. In overall structure the humerus is indistinguishable from those of other species of *Dimetrodon*.

The partial, articulated hindlimbs of MNG 10654 are exposed mainly in ventral view and include the epipodials, tarsi, metatarsals, and a few proximal phalanges. Although the ventrally exposed elements of the left hindlimb are too incompletely preserved and badly weathered to allow description, they are represented by a nearly complete, counterpart impression, whereas those of the right are well preserved (Fig. 3A) and permit the following observations. The well-ossified tibia, exposed in ventral or medial view (flexor surface), and fibula, exposed in lateral or posterior view, offer no basis for challenging a *Dimetrodon* assignment. The ventrally exposed pes is well

ossified, and the tightly fitting tarsal elements are indicative of advanced maturity. The tarsus is complete except for the possible loss of a very small medial centrale that would have been positioned medial to the lateral centrale. The pes of D. teutonis exhibits no features contradictory to a Dimetrodon assignment, and several features are recognized as collectively distinctive of the genus: 1) the horizontal arm of the L-shaped astragalus is extremely short, giving the element a narrowly rectangular outline; 2) the calcaneum is less flared laterally, widening slightly toward its proximal end rather than at its midlength; 3) the large, proximodistally narrow, subrectangular lateral centrale extends across nearly the entire articular face of the distal end of the astragalus; 4) the first distal tarsal is very large, subequal to that of the fourth, and has an exceptionally broad contact with the first metatarsal; 5) the proximal margin of the fourth distal tarsal is limited in contact to the calcaneum and is excluded from contact with the astragalus by the lateral centrale; 6) the distal half of the medial and lateral surfaces of the fourth distal centrale are deeply incised to receive the tightly fitting third and fifth distal tarsals; 7) the proximal head of the first metatarsal is greatly expanded to accommodate its contact with the comparably expanded first distal tarsal; and 8) the metatarsals increase in length serially to the fourth, which is subequal to that of the fifth.

COMPARISONS AND DISCUSSION

In the description of the holotype of Dimetrodon teutonis, based solely on a series of 14 presacral vertebrae believed to be dorsals approximating serial positions 8-21, it was considered remotely possible that the vertebrae might belong to the rare, closely related Early Permian sphenacodontid Secodontosaurus. Although the cranial anatomies of Secodontosaurus and Dimetrodon are easily distinguished from one another (Reisz et al., 1992), their postcrania share some notable similarities, particularly the vertebrae in possessing elongated neural spines that supported a high, dorsal sail (Romer and Price, 1940). However, as was noted (Berman et al., 2001) in the description of the holotype of D. teutonis and is reaffirmed here by the referred specimen MNG 10693, the cross-sectional outline of the distal portion of the dorsal neural spines in D. teutonis conforms within the narrow range of variation described in other members of the genus (except in D. milleri) in being transversely expanded into a distinct figure-eight pattern, whereas in Secodontosaurus it is subcircular, though retaining the fore and aft longitudinal grooves.

Most importantly, the new materials referred to D. teutonis, particularly the maxilla, scapulocoracoids, and pedes, are not only strongly characteristic of Dimetrodon, but the former two are quite distinct from not only those of Secodontosaurus, but other basal or pelycosauriangrade synapsids (Reisz et al., 1992; Romer and Price, 1940). In its overall shape and dentition the maxilla in D. teutonis is typical of the genus and easily distinguished from that in Secodontosaurus: 1) the maxilla in D. teutonis reaches a greatest height at its anterior end of about 33% of the bone's length, which is close to the 40 to 50% values for the other species. The smaller height of the maxilla in D. teutonis is probably a primitive feature (Reisz et al., 1992). In stronger contrast, however, the relatively long, low maxilla in Secodontosaurus reaches a greatest height at its midlength that is only about 16% of its length; 2) the differentiation of the 19 total maxillary teeth in D. teutonis into two precanines, two canines, and 15 postcanines conforms to the range of counts for the genus in which a total of 13 to 20 maxillary teeth includes zero to three precanines, two canines, and 10 to 15 postcanines. This is quite distinct from the range of values for Secodontosaurus in which a total tooth count of 21 to 26 may include as many as six precanines, two canines. and 17 postcanines. In addition, the teeth in Secodontosaurus are in general relatively more slender, sharply pointed, and widely spaced, with frequent gaps that Romer and Price (1940) suggested might indicate a difference in the type of tooth succession. Several features of the scapulocoracoid in Secodontosaurus distinguish it from that in Dimetrodon: 1) the scapular blade is relatively shorter and broadens greatly at its dorsal end; 2) the free margin of the anterior coracoid

forms a broadly expanded, semicircular plate; and 3) the coracoid process for the coracoid head of the triceps muscle is lower, broader, and less pronounced. It is also relevant to point out here that MNG 10654 and 10693 demonstrate the association of the scapulocoracoids and pedes with the *Dimetrodon*-like vertebrae. Taken together, the above observations are considered irrefutable evidence for the correctness of the generic assignment of the holotype and referred specimens of *D. teutonis*. Furthermore, the only other basal synapsids identified, but as yet undescribed, from the Bromacker quarry are a varanopid and caseid (Berman et al., 2003). Both are represented by essentially articulated, postcranial skeletons, one of the former and two of the latter, which are easily distinguished from that of *Dimetrodon*.

It was demonstrated (Berman et al., 2001) that the holotype of Dimetrodon teutonis represents an adult by comparing its vertebrae with the dorsals of a juvenile specimen of an indeterminate species of Dimetrodon (MCZ 2027). Although both specimens are of comparable size, several features easily distinguished the latter as a juvenile: 1) presence of neurocentral sutures or the disarticulation of the centra from the neural arches; 2) much narrower transverse width of the basal portion of the neural spine; and 3) cross-sectional outline of the distal portion of neural spine is oval with an anteroposterior length that slightly exceeds the transverse width, rather than being transversely expanded with a figureeight outline that is typical of *Dimetrodon*, including *D*. teutonis. Not only do the vertebrae, but also the other postcranial elements of the new, slightly larger specimens referred to D. teutonis exhibit features indicative of an adult stage of development: 1) the complete closure and fusion of the sutures of the scapulocoracoid bones, particularly those with the posterior coracoid, and the well-developed coracoid process of the posterior coracoid; 2) the well-developed processes and articular facets of the limb elements; and 3) the fully ossified, tightly articulated elements of the tarsus.

With an estimated weight of 14 kg, it was the diminutive size of the holotype of *Dimetrodon teutonis* that was cited (Berman et al., 2001) as the primary character distinguishing it from the smallest, previously recognized member of the genus, *D. natalis*, having an estimated weight of 28 kg (Romer and Price, 1940). The recognition that the new specimens described here represent individuals larger than the holotype, based on linear measurements of the postcranial elements, allows a recalculation of the adult size and weight of *D. teutonis*. However, as pointed out by Romer and Price (1940) and Romer (1948), comparisons between the 12 closely related, recognized species of *Dimetrodon* on the basis of linear proportions is complicated not only by subtle differences in their proportions, but also by the fact that

they exhibit a general, progressive increase in size with greater upward stratigraphic occurrence. Recognizing the need for a standard unit of measurement in comparing interspecific linear dimensions of primitive synapsids, Romer and Price (1940, p. 8) proposed and employed what they termed the orthometric linear unit (OLU). Simply stated, linear measurements are expressed in values relative to the animal's overall size, in which one orthometric linear unit, $r^{2/3}$, is defined as equal to the radius of an average-sized dorsal centrum to the 2/3 powers. Their derivation of the OLU was based on the following reasoning: 1) if the vertebral column suspended between the shoulder and pelvic girdles is considered to support the greater part of the animal's weight, the roughly circular, cross-sectional area of the dorsal centrum should be directly proportional to the animal's weight as the square of the radius; and 2) if the animal's volume, which is directly related to body weight, is theoretically the cubed totals of all its linear measurements, then the lengths of any given portion of the body should be directly proportional to the cube root of the cross-sectional area of centrum. The utility of the OLU of measurement as an accurate means of comparison between closely related species of similar ontogenetic growth stages has been demonstrated clearly by Currie (1978).

In arriving at the OLU, Romer and Price (1940) based their calculation on the transverse diameter or width at the posterior end of the average-sized dorsal, which for Dimetrodon natalis was 14 mm. Judging from their table of vertebral measurements for numerous museum specimens (Romer and Price, 1940, table 3), however, a maximum of 16 mm was recorded in two specimens of D. natalis (UM 9667 and 16201), which undoubtedly more accurately depicts the maximum size or weight attained by this species. Obviously, if a comparison between the sizes and weights of fully adult specimens of D. natalis and D. teutonis is sought, then the preferred measurements of the dorsal vertebrae of both species would be their maximums. Although vertebral centrum length and transverse width measurements are limited to a few vertebrae in MNG 10655 and 10693, their respective values of 18 and 13 mm are very consistent and greater than the average values of 14.3 and 9.9 mm, respectively, for the dorsal centra in the holotype MNG 10598. Most importantly, the maximum values for D. teutonis are still notably less than those given by Romer and Price (1940) for D. natalis of 27 and 16 mm, respectively. When converted to OLUs the maximum length and width values of 6.75 and 4.00, respectively, for D. natalis exceed substantially those of 5.17 and 3.48, respectively, for D. teutonis. Whether using direct linear measurements or OLUs, the maximum vertebral dimensions of D. teutonis are definitely smaller than those of D. natalis. Using these revised, maximum values for the transverse width of the dorsal centum, a marked difference in the overall body sizes or weights of the two species can also be demonstrated that utilizes the same method employed by Romer and Price (1940) for estimating total weights of Dimetrodon species and other basal synapsids. Initially they used the classical technique of measuring the volume of liquid displaced by a model, which in this instance was based on a nearly complete skeleton of a presumed female of D. limbatus. The weights of other species of Dimetrodon were then calculated on the premise that r² of the OLU is an index of relative weight. On the basis of this reasoning, the revised, maximum weights of D. teutonis and D. natalis are approximately 24 and 38 kg, respectively. Although based on maximum centrum-width values, their estimated weights are still exceeded by the 41 and 47 kg of the otherwise smallest species of Dimetrodon, D. occidentalis and D. milleri (the latter calculated for a presumed smaller female), respectively, which are based on average-sized dorsals (Romer and Price, 1940; Berman, 1977).

Of the series of four articulated middorsal vertebrae of MNG 10693, one possesses a spine length of 326 mm, and, although it may not represent the maximum for that individual, it exceeds substantially the 245 mm for the longest spine in the holotype (Berman et al., 2001). When converted to OLUs the spine length measurement increases from 90 to about 94, possibly suggesting some disproportional increase in sail height with maturity. However, the new OLU value for sail height in D. teutonis duplicates those of 95 and 94 of the slightly larger D. occidentalis and D. milleri (unfortunately sail height is not available for D. natalis, because complete middorsal spines are not known; Romer and Price, 1940), indicating that in the smallest *Dimetrodon* species sail height or size appears to have kept pace with the increase in general body size. On the other hand, Romer (1948) clearly demonstrated that in the much larger and later occurring species, with estimated body weights ranging from 70 to 250 kg, there is a dramatic, disproportional increase in sail size, with OLU values ranging from a little over 100 to 250.

In terms of direct linear measurements, a comparison between the appendicular elements of Dimetrodon teutonis and those recorded for D. natalis by Romer and Price (1940; table 4), clearly indicates that the former is much smaller. The range of measurements given by Romer and Price for the height of six scapulocoracoids of D. natalis, measured from the top of the anterior end of the glenoid to the top of the blade, is 85–114 mm, whereas in D. teutonis this measurement for the right of MNG 10654 is 93 mm. The lengths given by Romer and Price for 51 humeri, 33 tibiae, and 15 fibulae have ranges of 99–133, 72–113, and 85–115 mm, respectively, whereas those for the left humerus and right tibia and fibula of D. teutonis MNG 10654 are 100, 88, and 88 mm, respectively. These differences are even more meaningful considering that the measurements for the elements of D. teutonis probably represent maximums, or near maximums, of fully mature individuals.

A combination of several plesiomorphic features of the maxillae of *D. teutonis* and *D. natalis* distinguish them

from all other members of genus: 1) a greater number of marginal teeth that includes in *D. teutonis* two precanines, two canines, and 15 postcanines, with *D. natalis* differing only in its possession of three precanines, which is not considered specifically significant; 2) ventral margin slightly, rather than strongly, convex; 3) a height-to-length ratio of one third, and 4) little or no indication of a dorsally arching, maxillary step at the anterior end of the ventral margin. Among the new materials of *D. teutonis* is one element, an anterior coracoid, which easily distinguishes it from not only all other sphenacodontids, but also all basal synapsids in which this element is known.

As precisely exemplified by the counterpart impression and the lighter-colored, reduced matrix that contacted the bone of the medial surface of the left scapulocoracoid of MNG 10693 (Fig. 3C), the free, marginal outline of the anterior coracoid is unique in having an unusually long, straight, horizontal dorsal margin that meets the anterodorsally curving ventral margin in a sharply acute angle, rather than being of the standard, basal synapsid shape of a broadly expanded, semicircular plate (Romer and Price, 1940). Unfortunately, neither an illustration nor an adequately preserved example of this element is available for *D. natalis*.

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