FURTHER CONSIDERATION OF THE CAPITOSAURIDS FROM THE UPPER LUANGWA VALLEY, ZAMBIA

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Recently Chernin (1974) described the capitosaurid material collected from the Upper Horizon of the N’tawere Formation by Drysdall and Kitching in 1961, and tentatively assigned the two most complete specimens to Parotosaurus prorus (Howie, 1970). This taxon was founded for material collected from the Middle Triassic Manda Formation in the Ruhuhu Valley, Tanzania. The material from the N’tawere Formation is probably of Early Middle Triassic age, perhaps somewhat older than the Manda Formation specimens (Chernin and Cruickshank, 1970).

Welles and Cosgriff (1965) reviewed the Superfamily Capitosauridea, relegating a large number of specific taxa to the nomen vanum category and reducing the taxonomic content to 3 families, 6 genera and 18 species. The families retained are Benthosuchidae, Mastodonsauridae and Capitosauridae. The first two hold one genus each and the remaining 4 genera are grouped in the Capitosauridae. The Benthosuchidae comprises only the one species Benthosuchus sushkini (Efremov) 1928, and two species of Mastodonsaurus, M. cappelen­sus Wepfer (1923) and M. jaegeri Meyer (1864) constitute the Mastodonsauridae. Within the Capitosauridae, Parotosaurus has 8 species, P. nasutus (Meyer) 1858, P. helgolandicus (Schroeder) 1913, P. haughtoni (Brolli and Schroeder) 1937, P. semiclausus (Swinton) 1927, P. angustifrons (Ribbinn) 1930, P. brookealesnis (Watson) 1958, P. birdi (Brown) 1933 and P. peabodyi Welles and Cosgriff, 1965. Cyclotosaurus has 4 species, C. robustus (Quenstedt) 1850, C. stantonensis (Woodward) 1904, C. ebrachensis Kuhn, 1932 and C. hemprichii Kuhn, 1942. Kestrosaurus has one species, K. dreyeri Haughton, 1925 and ParacycLotosaurus has one species, P. davidi Watson, 1958.

Since the time of the Welles and Cosgriff revision the contents of the superfamily have been enlarged and many changes in its structure have been proposed. Subsequent literature has included taxonomic alterations within the superfamily as it was constituted at that time and, in addition, a number of new taxa have been added. These alterations and additions have greatly added to the knowledge of the morphology, diversity and geographic distribution of the group and have raised numerous and provocative questions regarding its evolutionary radiation. As a result of this expansion, however, the capitosaurid taxonomy is currently in a confused and unreconciled state. A complete new revision of the superfamily is called for but this is beyond the scope of the present paper which is confined to justifying a new specific designation for the Luangwa Valley capitosaur. Clearly, however, the present uncertainty in the classification must affect this effort. The revised diagnosis for the species (see below) is necessarily incomplete and its allocation to genus and family provisional pending a new review and integrated new structuring of the group. Also, it is possible that subfamilies will have to be inter­jected in the new classification. Such a review should preferably be conducted through direct inspection and comparison of all or most of the specimens currently assigned to the superfamily. A brief summary in rough chronologic order is presented here without comment merely to indicate the problems involved.

Welles and Cosgriff (1965) overlooked the following new taxa that were described in the years just previous to the publication of their review: Cyclotosaurus mechnichenensis Jux and Pflug (1958) from the Muschelkalk of West Germany; Promastodonsaurus bellmani Bonaparte (1963) from the Ischigualasto Formation of Argentina; and Parotosaurus orenburgensis (Konzhukova, 1965) from zone VI of the Cis-Uralian sequence of the Soviet Union. All three of these were placed in the family Capitosauridae by the authors describing them. A new species of Mastodonsaurus, M. torvus, was added by Konzhukova (1955) but also overlooked by Welles and Cosgriff.

Ootschev (1966) contributed an extensive consideration and revision of capitosaurid systematics and phylogeny, summarized in detail (pages 157–160) in a classification that is at considerable variance with that provided by Welles
and Cosgriff (1965, pages 5 and 97). Otschev conducted his research contemporaneously with that conducted by Welles and Cosgriff but each party was, at the time, unaware of the work of the other. The points of difference are best summarized by beginning with genera and proceeding up through the subfamilies (not employed by Welles and Cosgriff) to the families. The variance in treatment of species is omitted here as none of it is presently relevant to determining a provisional taxonomic position for the Luangwa Valley capitosaur. The reader is referred to the two reviews for a comparison of the listings of species regarded as valid. Otschev’s list is more extensive than that of Welles and Cosgriff as he retains a number of species that the latter place either as junior synonyms of other species or relegate to the *nomen vanum* category and a few species that the latter overlooked or considered as non-capitosaurid. The Welles and Cosgriff review places a number of other species in *nomen vanum* status or in synonymy that are not mentioned in Otschev’s review.

Regarding capitosaurid genera, Otschev recognised a number that were disposed of in various ways by Welles and Cosgriff. These, in chronologic order and with the dispositions of Welles and Cosgriff parenthetically following each, are:

*Capitosaurus* Münster, 1856 (*nomen vanum*);
*Mentosaurus* Roepke, 1930 (not mentioned);
*Wetlugasaurus* Riabinin, 1930 (synonym of *Parotosaurus*);
*Stenocephalosaurus* Brown, 1933 (synonym of *Parotosaurus*);
*Heptasaurus* Säve-Söderbergh, 1935 (synonym of *Mastodonsaurus*);
*Austropelor* Longman, 1941 (not mentioned);
*Sassenisaurus* Nilsson, 1942 (*nomen vanum*);
*Stenotosaurus* Romer, 1947 (synonym of *Parotosaurus*);
*Procyclotosaurus* Watson, 1958 (synonym of *Cyclotosaurus*);
*Subcyclotosaurus* Watson, 1958 (synonym of *Parotosaurus*); and
*Jarengia* Shishkin, 1960 (*nomen vanum*).

In addition, Otschev proposed the new generic designations: *Karosuchus* for *Parotosaurus haughtoni*, Broili and Schroeder 1937; *Watsonisuchus* for *Wetlugasaurus magnus* Watson, 1962 (regarded as *nomen vanum* by Welles and Cosgriff); and *Meyerosuchus* for *Labyrinthodon färstenbergianus* Meyer, 1855 (regarded as a synonym of *Parotosaurus semidactylus* by Welles and Cosgriff). Also, he included *Mastodonsaurus silesiacus* Kunisch, 1885 with question in his new genus *Erysuchus* founded for material from the U.S.S.R. (Welles and Cosgriff regarded *M. silesiacus* as a *nomen vanum*).

New species erected by Otschev (1966) for material from the Cis-Uralian sequence include *Wetlugasaurus kizlasajensis*, *Wetlugasaurus ? lehmani*, *Parotosaurus orientalis*, *Parotosaurus panteleevi*, *Bukobaja enigmatica*, *Erysuchus antiquus*, *Erysuchus tovrochlebovi*, and *Erysuchus garpainowi*. *Benthosuchus uralensis* Otschev, 1958 is also listed. Most of these were described in more detail by Otschev (1972).

The classification of the Capitosauridae of Otschev (1966) down through the category genus is as follows:

**Superfamily Capitosauroida**
- Family Rhinesuchidae Watson, 1919
  - *Rhinesuchus* Broom, 1908
  - *Rhinesuchoides* Broom and Olson, 1937
- Family Uranocentrodontidae Romer, 1947
  - *Uranocentrodon* van Hoepen, 1917
- *Laccacophalus* Watson, 1919
- ? *Gondwanosaurus* Lydekker, 1885
- ? *Pachygonia* Huxley, 1865
- Family Rhinecepidae Otschev, 1966
  - *Rhineceps* Watson, 1962
- Family Lydekkerinidae Watson, 1919
  - *Lydekkerina* Broom, 1915
- Family Sclerothoracidae von Huene, 1931
  - *Sclerothorax* von Huene, 1931
- Family Capitosauridae, Watson, 1919

**Subfamily Wettugasaurinae Otschev, 1958**
- *Wettugasaurus* Riabinin, 1930
- *Sassenisaurus* Nilsson, 1942
- *Parotosaurus* Jackel, 1922
- *Karoosuchus* Otschev, 1966
- *Watsonisuchus* Otschev, 1966
- *Stenotosaurus* Romer, 1947
- *Erysuchus* Otschev, 1966
- *Mentosaurus* Roepke, 1930
- *Capitosaurus* Münster, 1836

**Subfamily Cyclotosaurinae Otschev, 1966**
- *Procyclotosaurus* Watson, 1958
- *Cyclotosaurus* Fraas, 1889
- *Paracyclotosaurus* Watson, 1948
- *Austropelor* Longman, 1941
- *Stanocephalosaurus* Brown, 1933
- *Moenkopiisaurus* Shishkin, 1960
- *Rhadolagnathus* Welles, 1947
- Family Mastodontosauridae Lydekker, 1885
  - *Heptasaurus* Säve-Söderbergh, 1935
  - *Mastodonsaurus* Jaeger, 1828
  - *Promastodontaurus* Bonaparte, 1963
- Family Bukobajidae Otschev, 1966
  - *Bukobaja* Otschev, 1966
  - *Kestrosaurus* Haughton, 1925
  - *Meyerosuchus* Otschev, 1966
- Family Benthosuchidae Efremov, 1931
  - *Benthosuchus* Efremov, 1929
  - *Jarengia* Shishkin, 1960

In comparing this classification with that of Welles and Cosgriff (1965) many differences will be noted. Among these are the much greater number of
previously described genera recognised by Otschew, the addition of new genera and families, the inclusion of the families Rhinesuchidae, Uranocentrodontidae, Lydekkerinidae and Sclerothoracidae in the superfamily and the division of the Capitosauridae into subfamilies.

New genera and species have been added to the superfamly since the revisions of Welles and Cosgriff (1965) and Otschew (1966). These are, by stratigraphic unit and region: from the Triassic portion of the Cis-Uralian region of the U.S.S.R. — Benthosuchus bashkiricus Otschew (1972); from the Lower Triassic of Sinkiang — Parotosaurus turfanensis Young (1965); from the Upper Bunter of West Germany — Eocyclotosaurus worschmidtii Ortlam (1970); from the Lower Triassic of the Vosges, France — Stenotosaurus lehmani Heyler (1969); from the Lower Triassic Zarattine Series of Algeria — Parotosaurus lapparenti Lehman (1971) and Wellesaurus bussoni Lehman (1971); from the Yerrapalli Formation of India — Parotosaurus rajaredy Chowdhury (1970); from the Middle Triassic Manda Formation of Tanzania — Parotosaurus pronus Howie (1970); and from the Lower Triassic Gosford Formation of New South Wales — Parotosaurus wadei Cosgriff (1972).

Further alterations in generic assignments and familial grouping have also appeared in the recent literature. Jux (1962) changed the generic designation of the form described by Jux and Pflug (1958) from Cyclotosaurus mechernichensis to Parotosaurus mechernichensis and, later, Jux (1966) to Parotosaurus mechernichensis; Heyler (1969) removed Stenotosaurus from the Capitosauridae, placing it in its own family, Stenotosauridae; Lehman (1970) changed Parotosaurus peabodyi to Wellesaurus peabodyi; Paton (1974) revalidated the three species Labyrinthodon leptognathus Owen (1842), Labyrinthodon pachygnathus Owen (1842) and Labyrinthodon lavisi Seeley (1876), placing the first two in Cyclotosaurus and the last in Mastodontosaurus. Paton placed Cyclotosaurus stantoniensis (Woodward, 1904) as referred specimen of C. leptognathus and supported Heyler's segregation of Stenotosaurus in its own family, Stenotosauridae, adding to this family Kestrosaurus dreyeri Haughton (1925).

A recent inspection of the capitosaurids from the Karroo by both authors suggests that recon siderations of this complex will be necessary. Parotosaurus africanus Broom (1909) was considered nomen vanum by Welles and Cosgriff, 1965 as they believed the holotype of this form was too incomplete for meaningful comparisons. The specimen, however, consists of most of the postorbital portions of the skull which are well prepared and capable of being compared directly with these portions on other taxa. It may well prove to be a distinct and definable species. Kestrosaurus dreyer i Haughton (1925) is obviously close to other parotosaurs and it is doubtful if it should be retained in a separate genus. It seems distinct, however, from Parotosaurus africanus and its status as a separate species is probably firm. Parotosaurus haughtoni Broom and Schroeder (1937) will probably also retain its species status but should be compared again with both Parotosaurus africanus and Kestrosaurus dreyer i. A reappraisal of Parotosaurus sp. Welles and Cosgriff (1965) (Wellolagasaurus magnus Watson, 1962) is also desirable.

Reliable comparisons within the genus Parotosaurus are presently limited to those species for which extensive sets of measurements of the skull roof have been provided. These include, first, the species recognised by Welles and Cosgriff (1965): P. nasutus, P. helgolandicus, P. haughtoni, P. semelaius, P. angustifrons, P. brookvalensis, P. birdi and P. peabodyi. Comparisons of this nature are also possible with P. mechernichensis, P. pronus, P. rajaredy and P. wadei. In Table 2 the computed indices are listed. The eight species considered by Welles and Cosgriff (1965) are given in one column as a range for each index. All but one of these are taken directly from Table 1 of that work. The exception is the range for the O:C index which is computed directly from the illustrations in Welles and Cosgriff. The range shown for this index (57–68) actually falls within the range for the species population of P. peabodyi as computed from Welles and Cosgriff (1965, Table II). For P. mechernichensis, P. pronus, P. rajaredy and P. wadei the indices cited are those listed in the respective descriptions of these species (Jux, 1966, Howie, 1970, Chowdhury, 1970 and Cosgriff, 1972) or are taken from measurements of the published illustrations.

The Luangwa Valley capitosaurs were assigned with question to P. pronus primarily because of the marked resemblance in the construction of their otic notches to that form and because of general morphologic similarities. In spite of the correspondence of the otic notches the senior author has always entertained misgivings regarding even a tentative assignment to P. pronus and, therefore, in conjunction with the junior author, has undertaken a new reconstruction (Fig. 1) of the outlines of the best preserved specimen, B.P.I. No. 414 (specimen B of Chernin, 1974) which has led us to create a new species, based on this specimen, which we propose to call Parotosaurus megahrinus Chernin and Cosgriff, 1975. This new reconstruction of the dorsal surface was accomplished by making separate drawings of the distorted parts of the skull, reassembling them and checking their accuracy by direct measurements from the skull. The measurements that form the basis for the reconstruction were taken with allowances for distortion and are listed in Table I. It will be noted that some of these are at appreciable variance with those listed in Table I of Chernin (1974) which were taken not directly from the specimen, but from a reconstruction based on
photographs. These new measurements, in turn, have produced a new set of indices that are listed in the first column of Table 2. It must be noted that the new method of reconstruction was only attempted in the case of specimen B. Specimen A (B.P.I. No. 424) proved to be too distorted and incomplete for line drawing restoration and is referred with question to the new species for which

![Image of a fossil skull with measurements]

**FIG. 1** 10 CMS.

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<td>60–85</td>
<td>84</td>
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<tr>
<td>S:L</td>
<td>47</td>
<td>32</td>
<td>28–48</td>
<td>38</td>
<td>47</td>
<td>27</td>
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<tr>
<td>A:L</td>
<td>11</td>
<td>(1)* 13</td>
<td>14–17</td>
<td>16</td>
<td>15</td>
<td>42</td>
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<td>C:L</td>
<td>24</td>
<td>(1)* 50</td>
<td>31–38</td>
<td>36</td>
<td>42</td>
<td>42</td>
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<td>A:C</td>
<td>45</td>
<td>(1)* 45</td>
<td>41–49</td>
<td>45</td>
<td>36</td>
<td>42</td>
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<tr>
<td>N:C</td>
<td>45</td>
<td>(1)* 48</td>
<td>42–63</td>
<td>46</td>
<td>46</td>
<td>68,5</td>
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<tr>
<td>P:C</td>
<td>9</td>
<td>(1)* 8</td>
<td>6,1–13,7</td>
<td>6,3</td>
<td>(1)* 0</td>
<td>27</td>
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<tr>
<td>T:C</td>
<td>28</td>
<td>(1)* 28</td>
<td>25–38</td>
<td>31</td>
<td>(1)* 41</td>
<td>31</td>
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<tr>
<td>K:C</td>
<td>24</td>
<td>(1)* 50</td>
<td>17–58</td>
<td>20,1</td>
<td>(1)* 25</td>
<td>24</td>
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<tr>
<td>O:L</td>
<td>78</td>
<td>(1)* 70</td>
<td>(2)* 57–68</td>
<td>(1)* 65</td>
<td>(1)* 56</td>
<td>70</td>
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(1)* These indices were obtained by taking measurements from the plates of the dorsal view of the skull that were available in the respective descriptions of these species.

(2)* Taken only from paratypes of *P. peabodyi.*
specimen B is designated holotype. As a result of the new interpretations, specimen B is somewhat different in gross outline and in the shapes of the tabular horns and external nares from conditions shown in Fig. 7 of Chernin, 1974.

As compared in Table 2, the type of the new species differs from Parotosaurus promus, P. rajareddyi, P. wadei and the eight parotosaur species of Welles and Cosgroff (1965) by having a very broad snout (S:L index), a very long preorbital region (O:L index), orbits and otic notches closely spaced on the skull roof relative to skull length (A:L and C:L indices). P. wadei is identical to our new type in breadth of snout but differs from it in the other proportions. The species considered by Welles and Cosgroff (1965) and also P. rajareddyi differ from P. megarhinus in all respects. They have shorter preorbital regions, narrower snouts and more widely spaced orbits and otic notches. P. promus shows the nearest approach to the new species in the relative length of the preorbital region but differs from it in having a very narrow snout and more widely spaced orbits and otic notches.

Skull roof indices of Parotosaurus mechernichensis are available only for the postorbital region (Jux, 1966). In this species the measurements (a) least distance between orbit and otic notch (N) and (b) orbits to parietal foramen (P) are much greater relative to least interotic distance (C) than in P. megarhinus or the other species of the genus.

Comparisons of P. megarhinus with the remainder of capitosaurid species that have been described in recent years are less reliable than the foregoing comparisons, as the literature concerning them does not cite the measurements and indices that serve as the base for our comparative work. Many of the described species are based either on postcranial or evolutionary relationship to open otic notches are certain to bear fairly close reference to published illustrations cited in parenthesis, includes Parotosaurus orenburgensis (Konzhukova, 1965, fig. 1), Parotosaurus orientalis (Otschev, 1972, pl. VIII), Parotosaurus lapparenti (Lehman, 1971, figs. 4 and 6), Eryosuchus tsverdachensoi (Otschev, 1972, pl. XVI), Eryosuchus garjainoi (Otschev, 1972, pl. XXV and XXVI), Promastodonsaurus bellmanni (Bonaparte, 1963, fig. 1) and Wellesaurus bussoni (Lehman, 1971, fig. 3). Rough comparisons by eye suggest that P. megarhinus is distinguishable for the most part from these recently described species through the same indices (S:L, O:L, A:L and C:L) used in distinguishing it from the more familiar species. Generally, P. megarhinus appears to have a longer and broader snout (O:L and S:L indices) and more closely spaced orbits and otic notches (A:L and C:L indices) than any of the forms in this list of newly described species. However, Parotosaurus lapparenti and Parotosaurus orientalis may approach P. megarhinus in relative length of snout and P. orientalis may have orbits proportionately as close together.

B.P.I. No. 414 (Specimen B), therefore, represents a distinct species of Parotosaurus. B.P.I. No. 424 (Specimen A) is referred with question to this species but possibly represents still another species. Its orbits seem farther apart and the texture of its surface sculpture is decidedly coarser.

Parotosaurus megarhinus sp. nov.

Holotype: B.P.I. No. 414 (Specimen B).
? Referred specimen: B.P.I. No. 424 (Specimen A).

Locality and Horizon: Locality 15 of the N'tawere Formation in the Upper Luangwa Valley, Zambia. Probably Middle Triassic.

Diagnosis: Skull broad posteriorly (B:L index 73), tapering slightly to a broad snout (S:L index 47). Orbits close together (A:L index 11) and otic notches close together (C:L index 24). Snout relatively very long (O:L index 78). Parietal foramen rectangular, just posterior to rear borders of orbits.

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