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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 pronus* (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 Capitosauroidea, relegating a large number of generic and specific names 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. cappelensis* Wepfer (1923) and *M. jaegeri* Meyer (1844) constitute the Mastodonsauridae. Within the Capitosauridae, *Parotosaurus* has 8 species, *P. nasutus* (Meyer) 1858, *P. helgolandicus* (Schroeder) 1913, *P. haughtoni* (Broili and Schroeder) 1937, *P. semiclausus* (Swinton) 1927, *P. angustifrons* (Riabinin) 1930, *P. brookvalensis* (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. hemprichi* 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 capitosauroid 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 mechernichensis* 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.

Otschev (1966) contributed an extensive consideration and revision of capitosauroid systematics and phylogeny, summarized in detail (pages 157—160) in a classification that is at considerable variance with that provided by Welles

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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-capitosauroid. 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 capitosauroid 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, 1836 (*nomen vanum*);
Mentosaurus Roepke, 1930 (not mentioned);
Wetlugasaurus Riabinin, 1930 (synonym of *Parotosaurus*);
Stanocephalosaurus 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: *Karoosuchus* 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 fürstenbergianus* Meyer, 1855 (regarded as a synonym for *Parotosaurus semiclausus* by Welles and Cosgriff). Also, he included *Mastodonsaurus silesiacus* Kunisch, 1885 with question in his new genus *Eryosuchus* 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 kzilsajensis*, *Wetlugasaurus ? lehmani*, *Parotosaurus orientalis*, *Parotosaurus panteleevi*, *Bukobaja enigmatica*, *Eryosuchus antiquus*, *Eryosuchus tverdochlebovi*, and *Eryosuchus garjainovi*. *Benthosuchus uralensis* Otschev, 1958 is also listed. Most of these were described in more detail by Otschev (1972).

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

Superfamily Capitosauroidea
- Family Rhinesuchidae Watson, 1919
  - *Rhinesuchus* Broom, 1908
  - *Rhinesuchoides* Broom and Olson, 1937
  - *? Jugosaurus* Riabinin, 1962
- Family Uranocentrodontidae Romer, 1947
  - *Uranocentrodon* van Hoepen, 1917
  - *Laccocephalus* Watson, 1919
  - *? Muchocephalus* Watson, 1962
  - *? 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 Wetlugasaurinae Otschev, 1958
    - *Wetlugasaurus* Riabinin, 1930
    - *Sassenisaurus* Nilsson, 1942
    - *Parotosaurus* Jaekel, 1922
    - *Karoosuchus* Otschev, 1966
    - *Watsonisuchus* Otschev, 1966
    - *Stenotosaurus* Romer, 1947
    - *Eryosuchus* Otschev, 1966
    - *Mentosaurus* Roepke, 1930
    - *Capitosaurus* Münster, 1836
  - Subfamily Cyclotosaurinae Otschev, 1966
    - *Procyclotosaurus* Watson, 1958
    - *Cyclotosaurus* Fraas, 1889
  - Subfamily Paracyclotosaurinae Otschev, 1966
    - *Subcyclotosaurus* Watson, 1958
    - *Paracyclotosaurus* Watson, 1948
    - *Austropelor* Longman, 1941
    - *Stanocephalosaurus* Brown, 1933
    - *Moenkopisaurus* Shishkin, 1960
    - *Rhadalognathus* Welles, 1947
- Family Mastodonsauridae Lydekker, 1885
  - *Heptasaurus* Säve-Söderbergh, 1935
  - *Mastodonsaurus* Jaeger, 1828
  - *Promastodonsaurus* Bonaparte, 1963
- Family Bukobajidae Otschev, 1966
  - *Bukobaja* Otschev, 1966
  - *Kestrosaurus* Haughton, 1925
  - *Meyerosuchus* Otschev, 1966
- Family Benthosuchidae Efremov, 1931
  - *Benthosuchus* Efremov, 1929
  - *Yarengia* 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 Otschev, 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 superfamily since the revisions of Welles and Cosgriff (1965) and Otschev (1966). These are, by stratigraphic unit and region: from the Triassic portion of the Cis-Uralian region of the U.S.S.R. — *Benthosuchus bashkirikus* Otschev (1972); from the Lower Triassic of Sinkiang — *Parotosaurus turfanensis* Young (1965); from the Upper Bunter of West Germany — *Eocyclotosaurus woschmidti* Ortlam (1970); from the Lower Triassic of the Vosges, France — *Stenotosaurus lehmani* Heyler (1969); from the Lower Triassic Zarzaitine Series of Algeria — *Parotosaurus lapparenti* Lehman (1971) and *Wellesaurus bussoni* Lehman (1971); from the Yerrapalli Formation of India — *Parotosaurus rajareddyi* 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 *Procyclotosaurus 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 *Mastodonsaurus*. Paton placed *Cyclotosaurus stantonensis* (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 reconsiderations 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 dreyeri* 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* Broili and Schroeder (1937) will probably also retain its species status but should be compared again with both *Parotosaurus africanus* and *Kestrosaurus dreyeri*. A reappraisal of *Parotosaurus* sp. Welles and Cosgriff (1965) (*Wetlugasaurus 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. semiclausus*, *P. angustifrons*, *P. brookvalensis*, *P. birdi* and *P. peabodyi*. Comparisons of this nature are also possible with *P. mechernichensis*, *P. pronus*, *P. rajareddyi* 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 I 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. rajareddyi* 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 megarhinus* 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

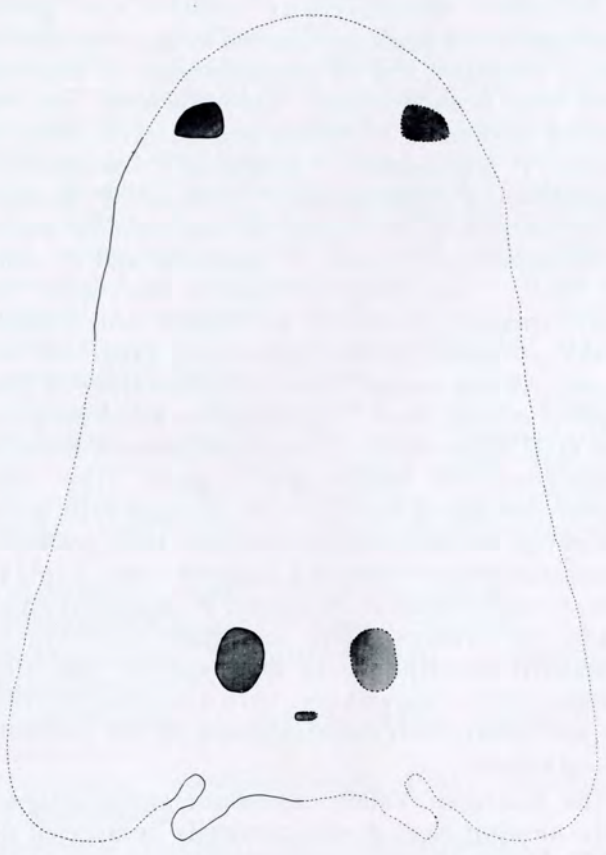

FIG. 1 **10 CMS**

Table 1
Measurements of skull roof of B.P.I. No. 414 (in millimetres)

1. Breadth of skull across quadrates (B)	575
2. Length of skull (L)	787
3. Interorbital distance taken at mid-length of orbit (A)	87
4. Distance from tip of snout to level of anterior edge of orbit (O)	613
5. Distance from level of posterior limit of orbit to level of centre limit of skull (D)	110
6. Distance from postero-lateral corner of eye to otic notch (N)	87
7. Midline distance from centre posterior limit of skull to level of posterior limit of tabular horn (K)	46
8. Inter-otic distance (least) (C)	192
9. Distance from mid-length of orbit to lateral edge of same side (I)	190
10. Distance from posterior mid-point of nares to anterior mid-point of orbit (F)	491
11. Internarial distance taken at mid-length of nares (J)	165
12. Distance from level of anterior limit of nares to edge of snout (M)	90
Breadth of snout 1/5th of skull length from tip (S)	370
14. Distance from level of posterior limit of orbit to parietal foramen taken at centre of skull (P)	18
15. Midline distance from level of anterior limit of otic notch to parietal foramen (T)	53
16. Orbit length	64

Table 2
Comparison of some indices with some specimens of Parotosaurs

Indices (Welles and Cosgriff, 1965)	Specimen B B.P.I. No. 414	*Parotosaurus pronus* (Howie, 1969)	Welles and Cosgriff, 1965 Tables I and II	*Parotosaurus rajareddyi* (Chowdhury, 1970)	*Parotosaurus wadei* (Cosgriff, 1972)	*Parotosaurus mechernichensis* (Jux, 1966)
B:L	73	75	60—85	84	91	
S:L	47	32	28—43	38	47	
A:L	11	(1)* 13	14—17	16	15	
C:L	24	(1)* 30	31—38	36	42	
A:C	45	(1)* 45	41—49	45	36	42
N:C	45	(1)* 43	42—63	46	46	68,5
P:C	9	(1)* 8	6,1—13,7	6,3	(1)* 0	27
T:C	28	(1)* 28	25—38	31	(1)* 41	31
K:C	24	(1)* 30	17—38	20,1	(1)* 25	24
O:L	78	(1)* 70	(2)* 57—68	(1)* 65	(1)* 56	

(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 pronus*, *P. rajareddyi*, *P. wadei* and the eight parotosaur species of Welles and Cosgriff (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 Cosgriff (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. pronus* 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 capitosauroid 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 jaw material or on skull material that is complete enough for quantitative analysis. Among those species founded on adequate skulls, those possessing open otic notches are certain to bear fairly close evolutionary relationship to *P. megarhinus*. Some of these have been assigned to *Parotosaurus* and some placed in other genera. The list of these, with reference to published illustrations cited parenthetically, includes *Parotosaurus orenburgensis* (Konzhukova, 1965, fig. 1), *Parotosaurus orientalis* (Otschev, 1972, pl. VIII), *Parotosaurus lapparenti* (Lehman, 1971, figs. 4 and 6), *Eryosuchus tverdochlebovi* (Otschev, 1972, pl. XVI), *Eryosuchus garjainovi* (Otschev, 1972, pla. 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.

Parotosaurus cf. *pronus* Chernin and Cruickshank (1970); Chernin (1974).

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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