1   **Taxonomy, phylogeny and stratigraphic ranges of middle Permian**

2   **pareiasaurs from the Karoo Basin of South Africa**

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13   **Suggested running head:** Middle Permian pareiasaur taxonomy, phylogeny and

14   stratigraphic ranges

15

16   **Abstract**

17

18   Pareiasaurs were relatively abundant, globally distributed, herbivorous parareptiles of the

19   mid to late Permian. The basal-most forms, all members of the Bradysauria, are restricted to

20   the Guadalupian (mid-Permian) of South Africa and went extinct in the late Capitanian near

21   the top of the *Tapinocephalus* Assemblage Zone. Currently four species are recognised in

22 this group: *Bradysaurus seeleyi, B. baini, Embrithosaurus schwarzi* and *Nochelesaurus*

23 *alexanderi*. Those taxa have historically been poorly defined and based on a limited number

24 of specimens, leaving the taxonomic diversity of the group open to doubt and limiting their

25 utility in biostratigraphy. Here we present our fourth and final contribution designed to

26 improve the understanding of this group of pareiasaurs by providing a taxonomic and

27 phylogenetic review, updated stratigraphic ranges and updated diagnoses for each taxon of

28 the Bradysauria. *Bradysaurus seeleyi* is synonymised with *Bradysaurus baini*, resulting in

29 three valid mid-Permian pareiasaur taxa: *Bradysaurus baini, Embrithosaurus schwarzi* and

30 *Nochelesaurus alexanderi*. Our cladistic analysis of cranial and postcranial characters

31 supports the monophyly of Bradysauria with five synapomorphies. *Embrithosaurus schwarzi*

32 is recovered as the sister taxon to a clade containing *Bradysaurus baini* and *Nochelesaurus*

33 *alexanderi*. By identifying 157 pareiasaur specimens in fossil collections we show that the

34 Bradysauria are stratigraphically restricted to the Abrahamskraal Formation of the Beaufort

35 Group and suggest a staggered appearance. *Bradysaurus baini* is first to appear, followed by

36 *Nochelesaurus alexanderi,* and lastly by *Embrithosaurus schwarzi*. All three taxa perished

37 during the Capitanian mass extinction, and have their highest occurrences near the top of

38 the Abrahamskraal Formation.

39 **Keywords:** Bradysauria; Capitanian; Guadalupian; Pareiasauria; *Tapinocephalus* Assemblage

40 Zone.

41

42 **Introduction**

43

44   Pareiasaurs were a group of heavily-built, relatively abundant herbivorous parareptiles that

45   flourished world-wide in the middle to late Permian (Boonstra 1969; Lee 1993, 1994, 1997a,

46   1997b). They are characterised by an expanded 'cheek flange' on the side of the skull,

47   osteoderms, and cranial ornamentation. The South African Beaufort Group records the

48   highest diversity of pareiasaurian species, hosting eleven of the 24 species currently

49   recognised. In South Africa, pareiasaur remains are restricted to two distinct stratigraphic

50   ranges: one cohort of relatively large and lightly armoured genera is found in the

51   Guadalupian (mid-Permian) *Tapinocephalus* Assemblage Zone (AZ), while a second,

52   generally smaller and more heavily armoured cohort is found in the Lopingian (late Permian)

53   *Endothiodon, Cistecephalus* and *Daptocephalus* AZs (Boonstra 1932a; Kitching 1995;

54   Rubidge 1995; Smith & Keyser 1995a, 1995b, 1995c, 1995d; Lee 1997a; Day 2013; Day *et al.*

55   2015; Day & Rubidge 2020; Smith *et al.* 2020). Pareiasaurs were victims of both the late

56   Capitanian (Day *et al.* 2015) and end-Permian mass extinction events (Smith & Botha-Brink

57   2014).

58   The Guadalupian pareiasaurs, from the *Tapinocephalus* AZ, are the most basal genera of the

59   group and are therefore essential to understanding the origin, diversification, and

60   subsequent global dispersal of pareiasaurs (Lee 1997a, 1997b; Jalil & Janvier 2005; Tsuji

61   2010; Tsuji *et al.* 2013; Turner *et al.* 2015; Benton 2016; Liu & Bever 2018; Van den Brandt *et*

62   *al.* 2020). The taxonomy of Guadalupian pareiasaurs was chaotic until the late 20th Century,

63   when an alpha-taxonomic review of all pareiasaurs recognised only four species from the

64   *Tapinocephalus* AZ: *Bradysaurus baini, B. seeleyi, Embrithosaurus schwarzi* and

65   *Nochelesaurus alexanderi* (Lee 1994, 1997a).

66   However, this review considered relatively few specimens and was limited by the nature of

67   the fossils themselves, including poor historic preparation, damage, and deformation of

68   many specimens recovered from the exceptionally hard matrix of the *Tapinocephalus* AZ

69   (see Van den Brandt *et al.* 2020). Broader anatomical distinctions among the taxa and,

70   particularly their stratigraphic ranges, have remained poorly understood. Pareiasaurs were

71   an important component of the tetrapod fauna in the Karoo Basin during the late

72   Guadalupian and knowledge of their ranges and occurrences is necessary to understand

73   both the early evolution of the clade and ecosystem changes before and during the

74   Capitanian mass extinction on land.

75   To better understand the group, we initiated a project in 2015 to study middle Permian

76   pareiasaurs, resulting in an M.Sc, a Ph.D and a series of three descriptive papers (Van den

77   Brandt 2016, 2020; Van den Brandt *et al.* 2020, 2021a*,* 2021b*)*. In our first descriptive paper,

78   we produced an updated cranial description and diagnosis for *Embrithosaurus schwarzi*, and

79   an updated phylogenetic analysis on cranial characters for pareiasaurs in which we

80   established the new clade Bradysauria, comprising the four species from the *Tapinocephalus*

81   AZ (Van den Brandt *et al.* 2020). The second paper produced the first detailed cranial

82   description and updated diagnosis for *Nochelesaurus alexanderi* (Van den Brandt *et al.*

83   2021a). In our third paper we produced the first modern comparative postcranial analysis

84   for the three genera of middle Permian South African pareiasaurs; *Bradysaurus,*

85   *Embrithosaurus,* and *Nochelesaurus* (Van den Brandt *et al.* 2021b).

86   This fourth paper integrates all new anatomical information into an updated taxonomy for

87   the *Tapinocephalus* AZ pareiasaurs, including updated diagnoses, phylogenetic analysis,

88   geographic distribution and biostratigraphic ranges for all three valid species within

89   Bradysauria.

90   **Historical Background**

91   The discovery of large numbers of pareiasaurian specimens in South Africa during the late

92   1800s and early 1900s led to the erection of many new species by early palaeontologists

93   (Owen 1876; Seeley 1888, 1892; Broom 1912, 1913, 1914, 1924). Those early descriptions

94   were often based on fragmentary material and included only short, ambiguous diagnoses,

95   causing much initial taxonomic confusion and disagreement. Some specimens were lost (eg.

96   Owen 1876, NHMUK PV R 4063/R1710/R1710a, holotype skull of *Pareiasaurus serridens*) or

97   mistakenly referred to other taxa (eg. Owen 1856, 1862, NHMUK PV R 4063/R1710/R1710a

98   referred to *Dicynodon tigriceps*).

99   The holotype of *Pareiasaurus bombidens* Owen 1876 (NHMUK PV R 1714/43525), the first

100   described pareiasaur from the *Tapinocephalus* AZ, has been ignored or considered

101   indeterminate by most researchers as it is fragmentary, not well preserved, and lacks

102   diagnostic characters (Watson 1914; Haughton & Boonstra 1929; Boonstra 1934; Lee 1994,

103   1997a; Van den Brandt 2016, 2020). NHMUK PV OR 49426 (holotype of *Bradysaurus seeleyi*)

104   was initially described by Seeley (1888) and referred to Owen's *P. bombidens,* and NHMUK

105   PV R 1971 was described by Seeley (1892) as the holotype of *Pareiasaurus* (=*Bradysaurus)*

106   *baini*. Broom (1903) described SAM-PK-8034 (holotype of *Embrithosaurus schwarzi*) and

107   mistakenly referred it to *Pareiasaurus serridens*.

108   Concerned by the taxonomic confusion existing at the time, Watson (1914) produced the

109   first taxonomic reassessment of pareiasaurs, after he carefully re-examined museum

110　catalogues, reassigned incorrectly referred specimens, and re-evaluated holotypes held at

111　the Natural History Museum, London. Watson's major contribution was to differentiate the

112　South African pareiasaurs into the large, basal, sparsely armoured forms from the

113　*Tapinocephalus* AZ (proposing the new genera *Bradysaurus* and *Embrithosaurus*), and the

114　small- and medium-sized, extensively armoured members of the later *Cistecephalus* AZ

115　(retaining the names of *Pareiasaurus*, *Propappus*, and *Anthodon*). In the process he correctly

116　observed that the genus *Pareiasaurus* occured only in the *Cistecephalus* AZ.

117　Broom (1916) disagreed with Watson's (1914) new generic names for pareiasaurs from the

118　*Tapinocephalus* AZ and continued to create new species of *Pareiasaurus* and *Propappus* for

119　new specimens recovered from the *Tapinocephalus* AZ. Between 1912 and 1924, Broom

120　named and described four such species: *Propappus rogersi* Broom 1912, *Pareiasaurus*

121　*acutirostris* Broom 1913, *Pareiasaurus whaitsi* Broom 1914 and *Pareiasaurus strubeni*

122　Broom 1924.

123　The next major pareiasaurian revision was completed by Haughton and Boonstra between

124　1929 and 1934 in their eleven-part 'Pareiasaurian Studies' series of papers, which included

125　two taxonomic reassessment works based on cranial characteristics (Haughton & Boonstra

126　1929; Boonstra 1934). In their first taxonomic paper, Haughton & Boonstra (1929) noted

127　very brief diagnostic features. They focused primarily on dentition, separating the

128　pareiasaurs into three primary divisions by the number of cusps on their teeth. Secondarily,

129　considering the ratio of the width between the orbits relative to the width between the

130　tabulars, they further subdivided the taxa into three secondary subdivisions. This created,

131　by their own admission, a somewhat compromised classification scheme. For the

132　*Tapinocephalus* AZ they retained the two genera recognised by Watson (*Bradysaurus* and

133 *Embrithosaurus*), added two new species of *Bradysaurus* (*B. seeleyi* and *B. vanderbyli*),

134 named four new species based on new material (*Dolichopareia angusta, Platyoropha*

135 *broomi, Nochelesaurus alexanderi* and *Brachypareia watsoni*) and reassigned the four taxa

136 named by Broom between 1912 and 1924: *Propappus rogersi* to *Brachypareia rogersi,*

137 *Pareiasaurus whaitsi* to *Bradysuchus whaitsi, Pareiasaurus strubeni* to *Nochelesaurus*

138 *strubeni,* and *Pareiasaurus acutirostris* to *Koalemasaurus acutirostris*. Thus Haughton &

139 Boonstra (1929) recognised eight genera and twelve species from the *Tapinocephalus* AZ.

140 Boonstra (1934) later considered *Platyoropha broomi* a junior synonym of *Bradysaurus baini*

141 and so retained seven genera and eleven species recognised by Haughton & Boonstra

142 (1929). He also produced a detailed cranial description for a generalised pareiasaurian skull,

143 including comprehensive accounts of all individual cranial elements. He added more

144 detailed diagnostic cranial features to each species and illustrated comprehensively,

145 although roughly, all individual species in all major cranial views. However, he did not

146 include separate cranial descriptions for individual species and his updated species level

147 diagnoses included many shared features across many taxa (Lee 1994, 1997a; Van den

148 Brandt 2016, 2020).

149 The two landmark contributions of Haughton & Boonstra (1929) and Boonstra (1934)

150 resulted in a plethora of new pareiasaurian taxa with few clearly identifiable features to

151 separate species (Fig. 1).

152 **<<Insert Figure 1>>**

153 Broom (1935) produced a short summary classification in which he briefly discussed the

154 history of the important South African pareiasaur specimens discovered and species

155   described. By now he had accepted the two genera named by Watson (1914) for specimens

156   from the *Tapinocephalus* AZ. He reduced the number of taxa recognised by Haughton &

157   Boonstra (1929) and Boonstra (1934) by recognising only five species of *Bradysaurus* (*B.*

158   *baini, B. acutirostris, B. whaitsi, B. strubeni* and *B. bombidens*) and *Embrithosaurus schwarzi.*

159   Boonstra (1969) lumped all species with fewer than nine cusps on their teeth into

160   *Bradysaurus* (recognising four species: *B. baini, B. seeleyi, B. strubeni* and *B. angusta*) and

161   kept *Embrithosaurus schwarzi* for individuals with nine cusps on their teeth. He removed

162   several species that he had previously considered valid (Boonstra 1934) as they were either

163   based on immature specimens (*Brachypareia*) or on pathological features (*Bradysuchus*).

164   Kuhn (1969) likewise considered all basal South African taxa as either *Bradysaurus* (for those

165   with fewer than nine cusps per tooth) or *Embrithosaurus* (for those with nine cusps per

166   tooth). He considered as valid the full set of twelve species originally diagnosed by

167   Haughton & Boonstra (1929) and resurrected *B. bombidens* which had been rejected by all

168   previous workers except for Broom (1935), resulting in thirteen recognised species. Kuhn

169   (1969) therefore recognised nine species of *Bradysaurus* (*B. baini, B. bombidens, B.*

170   *vanderbyli, B. seeleyi, B. whaitsi, B. acutirostris, B. watsoni, B. rogersi,* and *B. broomi*) and

171   four species of *Embrithosaurus* (*E. schwarzi, E. strubeni, E. alexandri*, and *E. angusta*).

172   Lee (1994, 1997a) performed an alpha taxonomic reassessment of all pareiasaur species

173   around the world. Through a detailed study of all holotypes, he reduced the number of valid

174   species from 49 to 17. In the *Tapinocephalus* AZ, Lee considered only four of the original

175   twelve species recognised by Haughton & Boonstra (1929) to be valid: *Bradysaurus seeleyi,*

176   *B. baini*, *Embrithosaurus schwarzi* and *Nochelesaurus alexanderi.* Amended diagnoses for

177 each valid taxon were produced and he also undertook the first phylogenetic analysis for

178 Pareiasauridae (Lee 1994, 1995, 1996, 1997a, 1997b).

179 Based on crania alone, Van den Brandt (2016) conducted a taxonomic reassessment of the

180 *Tapinocephalus* AZ pareiasaurs and agreed with the four taxa put forward by Lee as valid

181 (1994, 1997a). However, he concluded that *Bradysaurus seeleyi* is the least secure member

182 of the group because of its lack of cranial autapomorphies and distinguishing characters

183 apart from small cheeks. Based on our anatomical study of crania and postcrania, Van den

184 Brandt (2020) and this paper propose synonymising *Bradysaurus seeleyi* with *Bradysaurus*

185 *baini*, resulting in three valid mid-Permian pareiasaur taxa: *Bradysaurus baini,*

186 *Embrithosaurus schwarzi* and *Nochelesaurus alexanderi.*

187

Material and Methods

189 Supplemental material comprises six appendices: Supplemental material, Appendix 1A-C,

190 contains character modifications, character scores and character descriptions; synonym

191 justifications and *Bradysauria indet. s*pecimens; and 240 pareiasaur specimen identifications

192 with justifications. Supplemental material, Appendix 2, contains the updated data matrix

193 (tnt) file; Supplemental material, Appendix 3, cranial and postcranial variability in middle

194 Permian species of Pareiasauria, was used to inform the Diagnoses, which was developed

195 from various sources; Supplemental material, Appendix 4, locality and stratigraphic data for

196 240 pareiasaur specimens; Supplemental material, Appendix 5, a specimen flow chart,

197 showing a summary of previous taxonomic revisions of middle Permian South African

198 pareiasaurs and the changes proposed in this study; and Supplemental material, Appendix

199 6, phylogenetic strict and majority consensus trees with synapomorphies identified for each

200 monophyletic group of pareiasaurians.

Specimen identification methods

202 Many authors have recognised that pareiasaur remains from the *Tapinocephalus* AZ are

203 often distorted, altering cranial proportions and complicating taxonomic assessments. As

204 such our identification criteria focus on the absence or presence of discrete dental, cranial,

205 and post-cranial features.

206 For biostratigraphic purposes, our goal was to identify as many Guadalupian South African

207 pareiasaur specimens as possible to species level. This was not always possible due to

208 deformation, ontogenetic stage of development, distortion, and the degree of preservation

209 of the fossils but we were able to identify sixty-five percent or 157 out of 240 specimens

210 (Supplemental material, Appendix 1C: numbers 1 to 157, Tables 2, 3). Our justifications for

211 every specimen identified are provided in Supplemental material, Appendix 1C: numbers 1

212 to 157.

213 The holotypes of *Bradysaurus baini*, *Embrithosaurus schwarzi* and *Nochelesaurus alexanderi*

214 (Figs. 2, 3) reveal obvious autapomorphies and morphological differences, such as the shape

215 of the pelvis of *Embrithosaurus schwarzi* and the ventromedially oriented (lingually-

216 pointing) upper teeth of *Bradysaurus baini*. However, in accessing a large sample set of over

217 200 pareiasaurs, many comprising relatively complete skeletons, we found that the discrete

218 diagnostic features or combination of features of the holotypes are sometimes not upheld

219 in particular specimens and some specimens may show features of more than one holotype.

220 When a specimen exhibits a combination of characters from more than one species, we

221   have (in some instances) been able to narrow its identification to one of two species

222   (Supplemental material, Appendix 1C: numbers 158 to 180). For example, in specimens

223   FMNH UC 1533 and BP/1/7165, the skull points to a particular species and the postcranium

224   to another. We have also noted specimens as unidentifiable, for example, specimen SAM-

225   PK-9168 has features of *Bradysaurus*, *Nochelesaurus* and *Embrithosaurus* (Supplemental

226   material, Appendix 1C: numbers 181 to 240). It is important to note that most of the 23

227   specimens identified to one of two species and the 60 unidentifiable specimens are poorly

228   preserved, poorly prepared, and as such often have no diagnostic parts preserved.

229   To avoid the scenario whereby a diagnostic model cannot securely identify a specimen, early

230   workers created several species, each with only slightly different features, which led to an

231   inflated number of species (eg. Haughton & Boonstra 1929). To avoid an inflated number of

232   very similar yet slightly different species, we had to:

233   • prioritise diagnostic features that represent major anatomical differences that are

234   less susceptible to deformation: orientation of the upper jaw teeth; shapes of the

235   premaxilla and maxilla, postfrontal, and postparietal; morphology of the posterior

236   cheek bosses and the overall cranial ornamentation; shape of the pelvis; features of

237   the femur; twisting of the humerus; and ornamentation of the osteoderms;

238   • identify the species by the majority of the features represented in a specimen when

239   that specimen exhibits traits of more than one species;

240   • broaden the taxonomic definition of features or measurements within each species

241   by increasing the intraspecific variability (e.g. *Bradysaurus*: cheek size varies from

242   small to large, posterior cheek bosses large or medium-sized; *Embrithosaurus*: tooth

243   cusp numbers seven to nine; *Nochelesaurus*: lateral condyle of the femur extends

244   distally moderately to far beyond the medial condyle).

245 **Phylogenetic methods**

246 The character matrix of Van den Brandt *et al.* (2020) was used for initial cranial character

247 scoring (characters 1-78) and the matrix of Liu & Bever (2018) for the initial postcranial

248 character scoring (characters 79-139).

249 We scored the cranial and postcranial characters for all valid middle Permian South African

250 species based on direct studies of the holotypes and the best-preserved referred specimens.

251 We reworded character statements 14, 31, 49 and 102 to improve clarity (Supplemental

252 material, Appendix 1A). For character 69, state (1) (teeth with 2-7 cusps) was no longer

253 applicable and the character was modified to: state (0) conical, single cusp; state (1) 7-9

254 cusps on each maxillary tooth; state (2) 9-11 cusps; and state (3) more than 11 cusps. The

255 states of all taxa were updated accordingly. For character 74, we swapped the definitions of

256 state (0) and (1), as the previous state definition did not match the data (all known

257 pareiasaurs have teeth on the transverse flange of the pterygoid).

258 Characters 2, 3, 11, 117, and 129 were excluded from the analysis as they are

259 uninformative. *Bradysaurus seeleyi* (because of its synonymy with *B. baini*) was removed

260 from the taxon list resulting in 21 pareiasaurian species and eight non-pareiasaur

261 parareptilian outgroups. All of the modified statements and conditional states for characters

262 44, 48, 50, 51 and 68, introduced by Van den Brandt *et al.* (2020), were retained. A

263 significant number of changes in the scoring were introduced given our redescriptions of the

264 material (see Van den Brandt 2016, 2020; Van den Brandt *et al.* 2020, 2021a, 2021b):

265 changes in scoring for *Embrithosaurus* were introduced in characters 54, 76, 79, 80, 92, 99,

266 113, 115, 124, 136, 139; for *Bradysaurus* in characters 10, 11, 12, 38, 39, 44, 54, 69, 70, 71,

267 79, 80, 92, 98, 102, 107, 111, 113, 115, 125; and for *Nochelesaurus* in characters 3, 4, 5, 10,

268 11, 12, 14, 19, 23, 33, 42, 43, 44, 54, 64, 68, 69, 70, 71, 72, 76, 79, 81, 82, 83, 88, 99, 102,

269 103, 107, 108, 110, 112, 114, 116, 117, 122, 127, 135, and 136 (Supplemental material,

270 Appendix 1A, 2). For character 54, we changed the scores from (1) to (0) for all

271 pareiasaurian taxa, except for *Shihtienfenia*, *Sanchuansaurus*, *Honania* and *Obirkovia* which

272 we left unchanged as ?.

273 The program TNT (Tree Analysis Using New Technology) version 1.5 was used to find the

274 most parsimonious trees (Goloboff *et al.* 2008; Goloboff & Catalano 2016). Considering the

275 relatively large size of the data matrix (29 taxa and 139 characters) the search strategy for

276 the most parsimonious trees (mpt) entailed a heuristic search of 10 random addition

277 sequences with TBR (tree bisection reconnection), saving 10 trees per replication, and an

278 additional search using the trees from RAM as the starting point and implementing TBR on

279 those trees. The default setting for branch collapsing in TNT, rule 1 (minimum length = 0),

280 which collapses branches if the support is ambiguous, was used (Goloboff *et al.* 2008).

281 Millerettidae was selected as the root and all characters were run as unordered and equally

282 weighted.

283 **Stratigraphic methods**

284 Using the updated diagnoses provided below, we examined 240 pareiasaur specimens for

285 re-identification (Tables 2, 3). Where provenance information was available, the

286 stratigraphic position of individual specimens was determined using a dataset of fossil

287 occurrences within the Abrahamskraal Formation and lower Teekloof Formation at the

288   resolution of approximately 50 m bins, first produced by Day (2013) and most recently used

289   by Day *et al.* (2018) (Supplemental material, Appendix 4). The total stratigraphic range for

290   each species was determined from those occurrences. For each valid species, the

291   stratigraphic ranges presented by Day (2013), Van den Brandt (2016), and this study are

292   presented and discussed (Fig. 5). All middle Permian pareiasaur specimens were recovered

293   west of 24° East longitude, where the Abrahamskraal Formation comprises up to six

294   lithostratigraphic members (Day & Rubidge 2014; Cole *et al.* 2016).

295   **Institutional abbreviations**

296   **AM**, Albany Museum, Makhanda (Grahamstown); **AMNH**, American Museum of Natural

297   History, New York; **BP**, Evolutionary Studies Institute, University of the Witwatersrand,

298   Johannesburg (formerly Bernard Price Institute for Palaeontological Research); **CGP**, Council

299   for Geosciences, Pretoria; **FMNH**, Field Museum of Natural History, Chicago; **GPIT**,

300   Paläontologische Sammlung, Eberhard-Karls-Universität Tübingen, Germany; **NHMUK**,

301   Natural History Museum, London, United Kingdom; **NMQR**, National Museum,

302   Bloemfontein; **PIN**, Paleontological Institute, Moscow, Russia; **SAM**, Iziko South African

303   Museum, Cape Town.

304   **Results**

305   **Systematic Palaeontology**

306

307   Superorder **Reptilia** Laurenti, 1768

308   Order **Parareptilia** Olson, 1947

309   Suborder **Pareiasauria** Seeley, 1888

310   **Pareiasauridae** Cope, 1896

311   **Bradysauria** Van den Brandt, Abdala, Rubidge, 2020

312   **Definition**

313   The clade that includes *Bradysaurus baini*, *Embrithosaurus schwarzi*, *Nochelesaurus*

314   *alexanderi*, their common ancestor, and its descendants.

315   **Diagnosis**

316   Clade of large-bodied pareiasaurs diagnosed by five synapomorphies: (1) character 21,

317   presence of regular radiating ridges on the skull roof from the centre of the dermal skull

318   roof bones (also the condition in *Scutosaurus* and *Provelosaurus*); (2) character 39, absence

319   of supernumerary bones on the skull (unambiguous within Pareiasauria, also the condition

320   in *Owenetta*); (3) character 77, medial rows of palatal denticles widely separated,

321   converging anteriorly (unambiguous); (4) character 79, pleurocentrum of the atlas

322   separated from the axial intercentrum (unambiguous); and (5) character 115, notched

323   anterior acetabulum (also the condition in *Pareiasuchus nasicornis* and *P. peringueyi*).

324   The Bradysauria are the only pareiasaurs to exhibit: a basisphenoid body that is wide and

325   strongly constricted, giving it an hourglass shape in ventral view (character 13); width of the

326   humerus ulnar fossa (intercondylar depression) much wider than the olecranon process

327   (character 104); and the absence of a central boss or boss complex on the lateral squamosal

328   (Van den Brandt personal observation, not a listed as a phylogenetic character).

329   The Bradysauria differ from other pareiasaurs by lacking bosses on the ventral margin of the

330   quadratojugal, except for *Parasaurus* (character 48); their cheek ornamentation that

331   consists of low, rounded bosses (except for *Nochelesaurus* which has more distinct, taller,

332   more pointed bosses) (character 50); and their irregularly spaced tooth cusps (character 66)

333   (Haughton & Boonstra 1929, Boonstra 1934, Lee 1997a).

334   Genus ***Bradysaurus*** Watson, 1914

335   Species ***Bradysaurus baini*** Seeley, 1892

336   (Figs 2A, 2B, 3D-F)

337   **Synonyms**

338   1892 *Pareiasaurus baini* Seeley: 311, pls. 17-23

339   1913 *Pareiasaurus acutirostris* Broom: 397.

340   1914: *Bradysaurus baini* Watson: 101.

341   1929 *Bradysaurus vanderbyli* Haughton and Boonstra: 82.

342   1929 *Bradysaurus seeleyi* Haughton and Boonstra: 82.

343   1929 *Koalemasaurus acutirostris* Haughton and Boonstra: 84.

344   1929 *Platyoropha broomi* Haughton and Boonstra: 84.

345   1935 *Bradysaurus bombidens* Broom: 40, figs 2, 4.

346   1935 *Bradysaurus acutirostris* Broom: 43, fig. 3.

347   1969 *Bradysaurus broomi* Kuhn: 75.

Holotype. NHMUK PV R 1971, complete skull and separate lower jaw with very complete postcranium including a complete shoulder girdle and pelvis, nearly complete vertebral column, missing only the end of the caudal vertebrae, complete right fore- and hind-limbs, left humerus, radius, ulna, femur, tibia, and fibula partially preserved, both astragalocalcanea, and a few ribs.

Diagnosis.

Autapomorphies. *Bradysaurus baini* has one cranial autapomorphy (modified from Lee 1994, 1997a): Distal paroccipital process of the opisthotic anteroposteriorly long with a large, dorsomedially elongated, posteriorly projecting, knob-like process on the medial edge of the posterodorsal corner of the distal paroccipital process. *Bradysaurus* has one postcranial autapomorphy: anterior dorsal osteoderms smooth and strongly convex, with an incipient central boss, and very light ornamentation (character 135).

Unique combinations of features. *Bradysaurus* differs from both *Embrithosaurus* and *Nochelesaurus* in having the following combination of characters: maxilla with a large, wide and rugose posterodorsal maxillary boss, lower in juveniles (character 31); mediolaterally wide and curved ventral premaxilla and maxilla (up to 20 mm wider than the tooth row), accommodating horizontally to ventromedially oriented, lingually-pointing upper jaw teeth, that are not visible in lateral view (character 67); posterodorsal maxillary-lacrimal ridge is wide, low, swollen, bulbous and continuous; maxillary teeth with seven to nine marginal cusps; 20 upper jaw teeth (character 68); mandibular teeth with seven to nine marginal cusps; most dorsoventrally elongated and mesiodistally narrow, a minority short and wide, all with a central three-cusped

371   trident, symmetrical or non-symmetrical mesial and distal marginal cusp

372   arrangements, without horizontal cingulum, some mandibular teeth with medial

373   cusps; lingual surface of mandibular teeth bulged or with vertical ridges (character

374   71); relatively small angular boss; frontal central boss large, wide and low, or high

375   and distinct; ventrolateral quadratojugal swollen, bulging and not flat, covered with

376   irregular rugose ridges, and sometimes bulged to form a shelf; corner cheek boss

377   either large, low, wide and bulbous, or medium-sized, round, as wide as high; wide

378   or narrow cheek flanges; cheek flange highly variable, extending between 20° and

379   30° below the tooth row (character 44); smallest cheek flange amongst co-occurring

380   pareiasaurs (extending only 20° below the tooth row); bosses on the posterior

381   margin of the quadratojugal either large, low, bulbous, wider than high or medium-

382   sized, round, as wide as high; epicondyles of the humerus extend distally far beyond

383   the radial and ulnar articulation surfaces, appearing forked (character 98); wider

384   proximal and distal humerus; proximal internal trochanter of the femur high, wide

385   and strongly curved, forming a semi-circular structure, with a perpendicular proximal

386   edge; distal internal trochanter with a short anterior (preaxial) process/projection;

387   parapophysial and diapophysial processes fuse into a single process, creating a single

388   vertical lateral facet from the 4th or 5th vertebra posteriorly; second sacral rib is the

389   largest; posterior dorsal osteoderms flattened, low, thin and disc-like, most with

390   shallow circular central hollow and very light ornamentation.

391   **Differential diagnosis.** *Bradysaurus* differs from *Embrithosaurus* in having: all upper

392   jaw teeth dorsoventrally elongated, mesiodistally narrow, with a three-cusped

393   central trident, and irregularly arranged marginal cusps; postfrontal roughly square,

394 slightly longitudinally elongated, and posteriorly curved medially; low and wide

395 posteroventral process on the clavicle, lacking a distinct notch just medial to the

396 process; humerus with deep intercondylar fossa; delto-pectoral crest large, robust,

397 and 'heart-shaped', with a notch on the ventrodistal corner; short, crescent-shaped,

398 insertion point for muscle attachment on the humeral shaft of the dorsal proximal

399 humerus; presence of a distinct, vertical ridge on the medial radius; pelvis low and

400 wide; posterior iliac blade vertical, oriented parallel to the sagittal plane, and with

401 dorsal margins medially curved and convex a short distance; anterior Iliac blades

402 deeply concave laterally, upwardly bent (everted) 55°-60° (character 111) to present

403 a large surface in dorsal view, strongly curved with the anterior process tip pointing

404 45° off the sagittal plane and extending out far laterally from the main body of the

405 blade; Iliac shaft oriented anterodorsally, approximately 60° off the vertical plane

406 (character 113); puboischiatic plate wide, long, dorsally and ventrally flat; pelvis

407 symphysis dorsoventrally low and anteroposteriorly long (character 118); ventral

408 keel on the puboischiatic plate low and narrow and extends obliquely at a shallow

409 angle; median pubic process small, extending a short distance ventrally, with sharp

410 square edges; major trochanter posterior projection short; small 40° angle between

411 the lateral and medial facets of the proximal articulation surface of the tibia; distal

412 tibia ventromedially expanded and wide; wide tibial shaft; caudal vertebrae with L-

413 shaped lateral projections (character 85).

414 *Bradysaurus* differs from *Nochelesaurus* in having: maxillary teeth with symmetrical

415 mesial and distal marginal cusp arrangement; maxillary teeth lingual surface with a

416 low, smooth bulge; snout wider than high; transversely narrow postparietal; cranial

417   ornamentation comprising low, indistinct bosses (especially on the prefrontal,

418   postfrontal and postorbital); absence of gap (vertical separation) on the posterior

419   edge of the cheek between the dorsal-most quadratojugal boss and the large

420   squamosal boss on most specimens; short scapula blade, mid scapula blade

421   anteroposteriorly wide, distal portion of scapula blade flared; preaxial and postaxial

422   margins of distal portion of scapula blade curved; medial process of scapula blade

423   low and wide; proximal and distal expansions of the humerus twisted 60°-80° apart

424   and almost perpendicular; symmetrical distal and proximal radius; postaxial shaft of

425   femur notable bulged/convex; lateral condyle of the femur extends distally

426   moderately (20-45 mm) beyond the medial condyle; proximal and distal notches of

427   the major trochanter of the femur.

428   **Derivation of name.** *Brady,* slow, heavy (Greek bradys); *saurus*, lizard (Latin); *baini,* after

429   Mr. Thomas Bain (Seeley 1892).

430   **Referred material.** Seventy-four specimens listed in Supplemental material, Appendix 1C:

431   numbers 84 to 157.

432   **Locality, stratigraphy and age.** NHMUK PV R 1971 was collected on 12 August 1889 by

433   Seeley, T. Bain, J.S. Marais, and S. Marais from the farm De Bad in the Beaufort West district

434   of the Western Cape Province (Seeley 1892). *Diictodon – Styracocephalus* Subzone of the

435   *Tapinocephalus* AZ (Day & Rubidge 2020), lower to mid Moordenaars Member of the

436   Abrahamskraal Formation.

437   **Remarks.** Regarding Lee's (1994, 1997a) two other cranial autapomorphies proposed for

438   this taxon: 1) the huge, rounded lump on the maxilla (i.e. a maxillary boss) is shared with

439   *Embrithosaurus*, *Sanchuansaurus*, *Pareiasaurus*, *Scutosaurus*, and *E. mirabilis* (character 31),

440   although it is very large in *Bradysaurus baini*, and; 2) the ventromedially oriented, lingually-

441   pointing, upper jaw teeth (character 67) are shared with *Pareiasuchus nasicornis* and

442   *Sanchuansaurus.* Since a maxillary boss and ventromedially oriented upper jaw teeth occur

443   in more than one pareiasaur species, these two features are removed as autapomorphies of

444   *Bradysaurus baini*, but are included in the comparative diagnosis of the taxon.

445   **<<Insert Figure 2>>**

446   **<<Insert Figure 3>>**

447   Genus ***Embrithosaurus*** Watson, 1914

448   Species ***Embrithosaurus schwarzi*** Watson, 1914

449   (Figs 2C, 2D, 3A-C)

450   **Synonyms**

451   1903 *Pareiasaurus serridens* Broom: 123, pl. 15, figs 1-24, pl. 16.

452   1914 *Pareiasaurus whaitsi* Broom: 138, fig.

453   1914 *Embrithosaurus schwarzi* Watson: 101.

454   1929 *Bradysuchus whaitsi* Haughton & Boonstra: 82.

455   1935 *Bradysaurus whaitsi* Broom: 43, figs 3, 5.

456   **Holotype.** SAM-PK-8034, a distorted skull with occluded lower jaw, vertebrae 1 to 27 with

457   articulated osteoderms, two small articulated caudal vertebrae, partial left scapulocoracoid,

458   cleithrum, both clavicles, and interclavicle, complete right humerus, partial left humerus,

459   complete right radius, partial left radius, both ulnae, both femora, both tibiae, right fibula,

460   partial left fibula, complete pelvis, two digits of the forelimb, two digits of the hindlimb, and

461   several small fragments of vertebrae, ribs and phalanges labeled as "doubtful association".

462   **Diagnosis.**

463   **Autapomorphies.** *Embrithosaurus schwarzi* has three unambiguous pelvic

464   autapomorphies (modified from Lee 1994, 1997a): 1) anterior iliac blade flat and

465   vertical/dorsoventral (not everted or upturned) (character 111); 2) iliac blades

466   diverge anteriorly, oriented 45°-60° off the sagittal plane, and; 3) pelvic symphysis

467   very thick dorsoventrally (character 119).

468   **Unique combinations of features.** *Embrithosaurus* differs from both *Bradysaurus*

469   and *Nochelesaurus* in having all of the following: maxillary teeth with seven or nine

470   marginal cusps; nine-cusped maxillary teeth are dorsoventrally short, mesiodistally

471   wide, lacking an elongated, central, three-cusped trident, and with marginal cusps

472   arranged more regularly around the tooth crown than seven-cusped teeth;

473   mandibular teeth with seven or nine marginal cusps; small, distinct maxillary boss

474   (character 31); posterodorsal maxillary-lacrimal ridge narrow and formed by a small

475   distinct maxillary boss and several small and distinct lacrimal bosses; prefrontal with

476   a central, shallow, wide depression on some specimens; frontal central boss very

477   small and low; postfrontal mediolaterally elongated (internal sutures); largest cheek

478   flange in the group of co-occurring taxa, extending 30°-40° below the tooth row

479   (character 44); large, low, indistinct bulbous bosses, wider than high, on the

480   posterior edge of the quadratojugal; corner cheek boss large, low, wide and bulbous,

481   distal paroccipital process of the opisthotic anteroposteriorly short with a small,

482   dorsomedially elongated, posteriorly projecting, knob-like process on the medial

483   edge of its posterodorsal corner; high and wide posteroventral process on the

484   clavicle and presence of a deep notch medial to the posteroventral process in most

485   specimens; humerus with shallow intercondylar fossa (character 103); delto-pectoral

486   crest small, anteroposteriorly narrow, and with a long, shallow groove on the ventral

487   surface; shaft of the dorsal proximal humerus lacking a short, curved muscular ridge;

488   major trochanter projects far posteriorly (character 122); proximal internal

489   trochanter high, narrow and gently curved, forming a s-shaped structure, with a

490   perpendicular proximal edge; distal internal trochanter with an anterior process;

491   large 60°angle between the medial and lateral facets of the proximal articulation

492   surface of the tibia; narrow tibial shaft; distal tibia narrow and symmetrical; anterior

493   and posterior osteoderms with distinct, rugose, irregular and tab-like (L or E shaped)

494   central boss, and a thin and flat periphery with radial ridges (character 136).

495   **Differential diagnosis.** *Embrithosaurus* differs from *Bradysaurus* in having: vertical

496   and narrow premaxilla and maxilla (< 5 mm wider than the tooth row),

497   accommodating vertically oriented upper jaw teeth, visible in lateral view; 18 upper

498   jaw teeth (character 68); ventrolateral quadratojugal flat and with distinct high,

499   circular, ovoid, bosses arranged posterodorsally; relatively large angular boss;

500   epicondyles of the humerus do not extend distally far beyond the radial and ulnar

501   articulation surfaces; narrower proximal and distal humerus; pelvis high and narrow;

502   Iliac blades straight and laterally flat to very slightly shallowly concave; extreme

503   anteroventral margin of the anterior process of the iliac blade is very slightly curved

504   and bent upwards and laterally outwards; Iliac shaft oriented anterodorsally

505   approximately 30° off the vertical plane (character 113); puboischiatic plate narrow

506   and short; with a strongly and evenly concavely curved (not flat) dorsal surface;

507   pelvic symphysis anteroposteriorly short (character 118); keel on ventral

508   puboischiatic plate high and wide, with steep 50° oblique lateral sides; median pubic

509   process large, tongue shaped with rounded edges, extending far anteroventrally;

510   parapophysial and diapophysial processes fuse into a single process, creating a single

511   vertical lateral facet from the 6th vertebra posteriorly; first sacral rib is the largest;

512   caudal vertebrae with straight lateral projections (character 85).

513   *Embrithosaurus* differs from *Nochelesaurus* in: maxillary teeth with symmetrical

514   mesial and distal marginal cusp arrangement; all mandibular teeth dorsoventrally

515   short and mesiodistally wide, lacking a central three-cusped trident, with

516   symmetrical mesial and distal marginal cusp arrangements, with a bulged lingual

517   surface lacking a cingulum and medial cusps; snout wider than high; transversely

518   narrow postparietal; cranial ornamentation comprising low, indistinct bosses

519   (especially on the prefrontal, postfrontal and postorbital); wide cheek flanges;

520   absence of gap (vertical separation) on the posterior edge of the cheek between the

521   dorsal-most quadratojugal boss and the large squamosal boss; short scapula blade;

522   mid scapula blade anteroposteriorly wide, distal portion of scapula blade flared;

523   preaxial and postaxial margins of distal portion of scapula blade curved; medial

524   process of scapula blade low and wide; proximal and distal expansions of the

525   humerus twisted 60°to 80° apart and almost perpendicular; symmetrical distal and

526   proximal radius; postaxial shaft of femur notably bulged/convex; lateral condyle of

527   the femur extends distally moderately (30-45 mm) beyond the medial condyle;

528   proximal and distal notches of the major trochanter of the femur.

529   **Derivation of name.** *Embritho*, weighty (Greek); *saurus*, lizard (Latin); *schwarzi,* after Mr E.

530   H. L. Schwarz (Broom 1903).

531   **Referred material.** Forty specimens listed in Supplemental material, Appendix 1C: numbers

532   1 to 40.

533   **Locality, stratigraphy and age.** According to Broom (1903), SAM-PK-8034 was collected by

534   Mr A.W. Rogers and Mr E.H.L. Schwarz in 1902 on the farm Hoogeveld Lot A (Hoogeveld

535   270), in the Gouph region, near Knoflock's Fontein, Van der Byl's Kraal, in the Prince Albert

536   district of the Western Cape Province (Broom 1903). *Diictodon – Styracocephalus* Subzone

537   of the *Tapinocephalus* AZ (Day & Rubidge 2020), lower Moordenaars Member of the

538   Abrahamskraal Formation.

539

540   Genus ***Nochelesaurus*** Haughton and Boonstra, 1929

541   Species ***Nochelesaurus alexanderi*** Haughton and Boonstra, 1929

542   (Fig. 2E-F)

543   **Synonyms**

544   1912 *Propappus rogersi* Broom: 323, pl. 19, figs 1-11, pl. 20 , figs 12-21, pl. 21, figs 24-27.

545   1929 *Nochelesaurus alexanderi* Haughton and Boonstra: 83.

546   1929 *Dolichopareia angusta* Haughton and Boonstra: 83.

547   1929 *Brachypareia watsoni* Haughton and Boonstra: 84.

548   1929 *Brachypareia rogersi* Haughton and Boonstra: 84.

549   1969 *Bradysaurus angusta* Boonstra: 30.

550   1969 *Embrithosaurus alexandri* Kuhn: 80, pl. 39, fig. 7d, pl. 41, fig 11, pl. 44, fig. 3.

551   1969 *Embrithosaurus angusta* Kuhn: 80, pl. 38, figs 2, 6-8, pl. 39, figs 2, 6 7f, pl. 44, fig. 5.

552   1969 *Bradysaurus watsoni* Kuhn: 75, pl. 39, fig. 7h, pl. 41, fig. 12

553   1969 *Bradysaurus rogersi* Kuhn: 75, pl. 39, fig. 7g, pl. 40, figs 21-30, pl. 41, fig. 8.

554   **Holotype.** SAM-PK-6239, dorsal and right side of the skull and fragments of the right lower

555   jaw, braincase and palate, a partial right scapulocoracoid, cleithrum and clavicle, partial

556   interclavicle, damaged left humerus, seven articulated osteoderms, complete right femur

557   and tibia, fibula fragment, astragalocalcaneum, and several unnumbered, unidentified

558   fragments.

559   **Diagnosis.**

560   **Autapomorphies.** *Nochelesaurus alexanderi* has one cranial autapomorphy:

561   transversely wide postparietal, twice as wide as long.

562   **Unique combinations of features.** *Nochelesaurus* differs from both *Bradysaurus* and

563   *Embrithosaurus* in having: maxillary teeth with five or seven marginal cusps, creating

564   a symmetrical cusp arrangement or an 8th, low, small, basal cusp on the mesial

565   margin, creating a non-symmetrical cusp arrangement; maxillary teeth with three to

566   five vertical ridges on the lingual surface; up to ten cusps on mandibular teeth;

567   mandibular teeth with non- symmetrical mesial and distal cusp arrangements due to

568   extra, low, very small, mesial marginal cusp on certain teeth; low and narrow

569   maxillary-lacrimal ridge, has a sharp lateral edge on the maxilla and does not reach

570   the small, distinct lacrimal bosses; relatively narrow snout, as high as wide or very

571   slightly wider than high; maxilla without a maxillary boss; cranial ornamentation

572   comprising distinct, high, pointed bosses (especially on the prefrontal, postfrontal

573   and postorbital); central frontal boss large, high and distinct; narrowest cheek

574   flange; corner cheek boss large, elongated, pointed and distinct, with a narrow neck

575   proximally, a raised distal rim, and covered in rugose ridges; posterior edge of the

576   quadratojugal with distinct bosses that vary from horizontally flat, pointed and plate-

577   like to medium-sized, round, as wide as high; flat, vertical separation (gap) on the

578   posterior edge of the cheek, between the dorsal-most quadratojugal boss and the

579   large squamosal boss, through which the horizontal squamosal-quadratojugal suture

580   passes; medial edge of the posterodorsal corner of the distal paroccipital process

581   low and gentle convexly swollen; posteroventral edge of the distal paroccipital

582   process is dorsolaterally elongated and swollen in some specimens; tubercles

583   present on the ventral surface of the basisphenoid/ parabasisphenoid, just behind

584   the basipterygoid processes; most specimens with a long and narrow scapula blade;

585   mid scapula blade anteroposteriorly constricted and very narrow; distal portion of

586   scapula blade narrow with little anteroposterior flaring, preaxial and postaxial

587   margins of distal portion of scapula blade straight and only very slightly curved in

588   most specimens, expanding gradually (character 88); medial process of scapula blade

589   high; proximal and distal expansions of the humerus very flat, only 20°-40° apart and

590   almost on the same plane (character 92); tubercle sometimes present on the

591   postaxial margin of the intercondylar fossa of the humerus; ventrolaterally expanded

592   distal radius; postaxial shaft of femur straight (not notably bulged/convex); lateral

593   condyle of the femur extends distally far (70 mm) beyond the medial condyle in most

594   specimens; major trochanter posterior projection very short; absence of or very

595   shallow proximal and distal notches of the major trochanter of the femur; proximal

596   internal trochanter low and narrow, straight or very slightly curved, with an oblique

597   proximal edge (character 125); distal internal trochanter without an anterior

598   process; osteoderms with a wide central boss covering most of the scute, round or

599   comprising five or six rugose, flattened, radial, tab-like processes, with a high and

600   thick periphery.

601   **Differential diagnosis.** *Nochelesaurus* differs from *Bradysaurus* in having: vertical

602   and narrow premaxilla and maxilla (< 5 mm wider than the tooth row),

603   accommodating vertically oriented upper jaw teeth, visible in lateral view; 18 upper

604   jaw teeth (character 68); large cheek flanges extending approximately 30° below the

605   tooth row; ventrolateral quadratojugal flat and with distinct high, circular to ovoid,

606   bosses arranged posterodorsally; relatively large angular boss; epicondyles of the

607   humerus do not extend distally far beyond the radial and ulnar articulation surfaces

608   in most specimens; narrower proximal and distal humerus; parapophysial and

609   diapophysial processes fuse into a single process, creating a single vertical lateral

610   facet from the 6th vertebra posteriorly.

611   *Nochelesaurus* differs from *Embrithosaurus* in having: postfrontal roughly square,

612   slightly longitudinally elongated, and posteriorly curved medially; all upper jaw teeth

613   dorsoventrally elongated, mesiodistally narrow, with a three-cusped central trident,

614   and irregularly arranged marginal cusps; all mandibular teeth dorsoventrally

615   elongated and mesiodistally narrow, with a central three-cusped trident, with non-

616   symmetrical mesial and distal marginal cusp arrangements, with an incipient

617   horizontal cingulum carrying medially (lingually) placed cusp(s) on the lingual surface

618   of certain mandibular teeth; lingual surface of mandibular teeth with one to three

619   distinct vertical ridges; narrow cheek flanges; low and wide posteroventral process

620   on the clavicle, and lacking a distinct notch just medial to the process; humerus with

621   deep intercondylar fossa; delto-pectoral crest large, robust, and 'heart-shaped', with

622   a notch on the ventrodistal corner; short, crescent-shaped, insertion point for

623   muscle attachment on the humeral shaft of the dorsal proximal humerus; presence

624   of a distinct, vertical ridge on the medial radius; small 40° angle between the lateral

625   and medial facets of the proximal articulation surface of the tibia; distal tibia

626   ventromedially expanded and wide; wide tibial shaft.

627   **Derivation of name.** *Nochele*, sluggish, dull (Ancient Greek νωχελής) (Latinized nocheles);

628   *saurus*, lizard (Latin); *alexanderi,* after Dr. Alexander du Toit (Haughton & Boonstra 1929).

629   **Referred material.** Forty-three specimens listed in Supplemental material, Appendix 1C:

630   numbers 41 to 83.

631   **Locality, stratigraphy and age.** SAM-PK-6239 was collected in 1923 from the farm

632   Boesmanskop (Bushmans Kop 302), Beaufort West district of the Western Cape Province

633   (Haughton & Boonstra 1929). This locality is high in the *Diictodon – Styracocepahlus*

634   Subzone of the *Tapinocephalus* AZ (Day & Rubidge 2020), Karelskraal Member of the

635   Abrahamskraal Formation.

636   **Remarks.** Concerning Lee's (1994, 1997a) three postcranial autapomorphies proposed for

637   *Nochelesaurus alexanderi*: 1) the subscapular fossa is not located close to the anterior

638   margin of the scapula blade and is removed as an autapomorphy; 2) the tubercle on the

639   humerus is manifestly present in only one specimen of *Nochelesaurus*, and it is removed as

640   an autapomorphy and considered an individual variation within the genus, and 3) the flange

641   on the dorsal femur that projects distally far beyond the postaxial tibial facet does not

642   consist of an obvious flange, instead, the distal extension of the lateral condyle of the femur

643   is furthest in most, but not all specimens of *Nochelesaurus*, and is therefore removed as an

644   autapomorphy and considered individual variation within the genus.

645   **Bradysauria indet.**

646   1876 *Pareiasaurus bombidens* Owen: 9, pl. 8, fig. 3, pl. 9.

647   1924 *Pareiasaurus strubeni* Broom: 507, figs 5, 6.

648   1929 *Nochelesaurus strubeni* Haughton and Boonstra: 83.

649   1935 *Bradysaurus strubeni* Broom: 45, fig. 5.

650   1969 *Embrithosaurus strubeni* Kuhn: 80, pl. 39, fig. 7e, pl. 43, fig. 4.

651

652   **Phylogeny**

653   The TNT analyses found 1065 most parsimonious trees (mpt) of length 263 (Retention Index

654   RI = 0.783, Consistency Index CI = 0.615). The strict consensus tree (Fig. 4A) shows

655   Pareiasauria recovered as a monophyletic group, comprising an extended basal polytomy of

656   twelve terminal taxa and three monophyletic groups: *Pareiasuchus nasicornis* and *P.*

657   *peringueyi*, the middle Permian pareiasaurs from the Karoo (*Embrithosaurus* +

658   *Nochelesaurus* + *Bradysaurus*) and the dwarf South African pareisaurs (*Nanopareia* +

659   *Pumiliopareia* + *Anthodon*) with *Provelosaurus*, in which *Nanopareia* and *Provelosaurus* are

660   in a polytomy, and *Pumiliopareia* and *Anthodon* form a clade. Synapomorphies listed for the

661   groups below are after unambiguous optimisation only on the majority rule consensus tree

662   (Fig. 4B). Unambiguous optimization synapomorphies on the strict and majority rule

663   consensus are presented in Supplemental material, Appendix 6.

664   **<<Insert Figure 4>>**

665   In agreement with Van den Brandt *et al.* (2020), South African middle Permian pareiasaurs

666   (*Embrithosaurus* + *Nochelesaurus* + *Bradysaurus*) form a monophyletic Bradysauria

667   supported by five synapomorphies: character 21, presence of regular radiating ridges on the

668   skull roof from the centre of the dermal skull roof bones (also the condition in *Scutosaurus*

669   and *Provelosaurus*); character 39, absence of supernumerary bone on the skull

670   (unambiguous within pareiasaurians, also the condition in *Owenetta*); character 77, medial

671   rows of palatal denticles widely separated, converging anteriorly (unambiguous); character

672   79, pleurocentrum of the atlas separate from the axial intercentrum (unambiguous); and

673   character 115, notched anterior acetabulum (also the condition in in *P. nasicornis* and *P.*

674   *peringueyi*). The condition of character 79 is unknown in most pareiasaurs, but has now

675   been updated for the basal South African forms. The first three synapomorphies (characters

676   21, 39 and 77) were previously presented by Van den Brandt *et al.* (2020).

677   In Bradysauria, *Nochelesaurus* and *Bradysaurus* from a monophyletic group supported by

678   two synapomorphies: character 44, quadratojugal (cheek) flange small, extending 0°-40°

679   below the level of the maxillary tooth row; and character 71, lingual surface of the

680 mandibular teeth with a distinct, triangular ridge, narrowing towards the crown of the

681 tooth. The two elginid taxa also have small cheeks, and several other pareiasaurs have a

682 triangular ridge on the inner surface of the mandibular teeth (i.e. *Shihtienfenia,*

683 *Pareiasuchus peringueyi, Pareiasuchus nasicornis,* and *Scutosaurus*).

684 After the Bradysauria, *Bunostegos* and then *Honania* form an unnamed grade between the

685 basal pareiasaurs and the forms with more derived features (Fig. 4B). *Bunostegos* and all

686 remaining pareiasaurs are united by four synapomorphies: characters 13, 48, 50 and 66,

687 which is the same result found by Van den Brandt *et al.* (2020): character 13, wide, not

688 strongly laterally constricted basisphenoid; character 48, presence of bosses on the ventral

689 margin of the quadratojugal; character 50, cheek ornamentation present on the posterior or

690 ventral margins of the cheek in the form of well-developed, more distinct, taller, more

691 pointed bosses; and character 66, cusps regularly spaced along the tooth crown. In the

692 members of the Bradysauria the basisphenoids are wide and strongly laterally constricted;

693 bosses are not present on the ventral margin of the quadratojugal; cheek ornamentation

694 consists of low, rounded bosses (except for *Nochelesaurus* which has more distinct bosses);

695 and cusps are irregularly spaced along the tooth crown. These basal features of members of

696 the Bradysauria are well established in the literature (Haughton & Boonstra 1929; Boonstra

697 1934; Lee 1997a).

698 The clade formed by *Honania* and all remaining pareiasaurs (Fig. 4B) is united by four

699 synapomorphies: character 69, 9–11 or more cusps on the maxillary teeth; character 90,

700 dorsal edge of the posterior coracoid oriented posteroventrally forming an angle of more

701 than 135° with the posterior border of the scapula; character 91, absence of the cleithrum;

702 and character 92, the torsion of the humerus being less than or equal to 45°. The

703 Bradysauria and *Bunostegos* have fewer cusps (7-9) on the maxillary teeth, the posterior

704 coracoid is more horizontal, meeting the posterior border of the scapula at an angle of less

705 than 135°, the cleithrum is present, and the torsion of the humerus is greater than or equal

706 to 60° (except in *Nochelesaurus*).

707 Crownward to *Honania* there is a polytomy formed by three terminal taxa (*Parasaurus*,

708 *Sanchuansaurus* and *Deltavjatia,* Fig. 4B) and three monophyletic groups, all united by two

709 synapomorphies: characters 122, larger, more distinct major trochanter; and character 124,

710 femur with a narrow postaxial flange at the midpoint of the femur.

711 The Chinese *Shihtienfenia* forms a monophyletic group with *Pareiasuchus* from southern

712 Africa (*P. nasicornis* and *P. peringueyi*, Fig. 4B) all united by four synapomorphies: character

713 71, lingual surface of the mandibular teeth with a distinct, triangular ridge, narrowing

714 towards the crown of the tooth; character 87, length of the scapula blade greater than or

715 equal to three times the glenoid fossa diameter; character 95, narrow and rounded

716 postaxial flange of the entepicondyle; and character 111, strongly everted, almost horizontal

717 anterior margin of the ilium. Character 71 is also a synapomorphy uniting *Nochelesaurus*

718 and *Bradysaurus* (see above). *Pareiasuchus nasicornis* and *P. peringueyi* are united by five

719 synapomorphies: character 72, absence of horizontal cingulum on the lingual surface of the

720 marginal teeth; character 93, narrow and rounded postaxial flange of the ectepicondyle;

721 character 108, strong and sheet-like second and third sacral ribs; character 115, notched

722 anterior acetabulum; and character 120, strong preaxial expansion of the head of the femur.

723 The conditional states of characters 72 and 93 in this group are also present in the three

724 South African dwarf pareiasaurs.

725 The second monophyletic group in the majority rule and the strict consensuses (Fig. 4A, 4B)

726 comprises the three dwarf South African pareiasaurs (*Nanopareia*, *Pumiliopareia*, and

727 *Anthodon*), and the South American *Provelosaurus*. *Pumiliopareia* and *Anthodon* are

728 monophyletic and *Nanopareia* and *Provelosaurus* form a polytomy. The three South African

729 dwarf forms and *Provelosaurus* share ten synapomorphies: character 25, v-shaped anterior

730 interpterygoid vacuity; character 72, absence of a horizontal cingulum on the lingual surface

731 of the marginal teeth; character 92, torsion of the humerus less than or equal to 20°;

732 character 93, narrow and rounded preaxial flange of the ectepicondyle; character 97,

733 entepicondylar foramen exposed in ventral (flexor) view; character 100, radial condyle of

734 the humerus located terminally, encroaching onto the distal end of the humerus; character

735 101, ulnar articulation surface of the humerus forms a groove bordered posteriorly by a

736 prominent tubercle; character 110, no or only slight anterior expansion of the iliac blade;

737 character 113, shaft of the Ilium orientated vertical or posterodorsally; and character 136,

738 osteoderms ornamented with fine, straight, regularly spaced ridges radiating out from a

739 central boss to the edge.

740 Another clade (Fig. 4B) comprises *Scutosaurus*, *Pareiasaurus*, and a monophyletic Elginiidae

741 (*Elginia wuyongae*, *Obirkovia*, *Arganaceras*, and *Elginia mirabilis*) supported by five

742 synapomorphies: character 14, tubercles present on the ventral surface of each

743 basipterygoid process (basisphenoid), immediately posterior to the interpterygoid vacuity

744 and the transverse suture with the pterygoid; character 15, presence of a central boss on

745 the ventral surface of the basioccipital; character 31, prominent boss or horn present on the

746 maxilla immediately posterior to the external naris; character 33, snout as high as wide; and

747 character 111, strongly everted, almost horizontal anterior margin of the ilium.

748   The clade formed by the four elginids is supported by five synapomorphies (Fig. 4B):

749   character 13, basisphenoid narrow with relatively straight margin; character 35, presence of

750   a postfrontal 'horn'; character 41, tabular (supernumerary element), contact, well-

751   developed, making contact posteriorly, excluding the postparietals from the posterior edge

752   of the skull table; character 50, ornamentation present on the posterior or ventral margins

753   of the cheek in the form of prominent, conical horns with sharp, pointed tips; and character

754   58, dermal bosses of cranial bones have a central long, pointed horn.

755   **Resampling and support.** Values of resampling for Pareiasauria varies from 74 with

756   jackknife (with 36 of removal possibility) to 91with symmetric resampling (with 33 of change

757   probability) and can be considered as well supported (Table 1). The situation with

758   Bradysauria is quite different as the support ranges from 54with poissonbootstrapping to

759   77using symmetric resampling. Bradysauria is therefore poorly supported and basically

760   remains with the same degree of support (bootstrapping of 58) previously reported by Van

761   den Brandt *et al.* (2020).

762   **<<Insert Table 1>>**

763   Bremer support for Pareiasauria is 3 and for Bradysauria is 2, as well as for the clades

764   (*Pareiasuchus nasicornis*, *Pareiasuchus peringueyi*)and (*Anthodon*, *Pumiliopareia*). Other

765   pareiasaurian clades recovered in the strict consensus have a Bremer support of 1. The

766   relative Bremer support is 60 for Paraeiasauria and 43 for Bradysauria, suggesting again a

767   poor support of the latter group.

768

769   **Discussion**

770

Biostratigraphic discussion

The stratigraphic ranges of the mid-Permian pareiasaurs of South Africa's Karoo Basin have

never been well established. Initially, when Seeley (1892) briefly described Karoo

stratigraphy as comprising five biozones, he considered that pareiasaurs occurred mostly in

one horizon that cropped out in the Koup Karoo and which he called the Zone of

Pareiasaurians. Though he did not venture to the area around Fort Beaufort, from where

the first known pareiasaurs were collected, Seeley assumed that two of these species

(*Pareiasaurus serridens* and *Propappus omocratus*; but not *Anthodon*) occurred in the same

zone. Later, Watson (1914) realised that the taxa from the Koup belonged to different

genera and that *Pareiasaurus* was only found in younger assemblages, leading him to

rename the *Pareiasaurus* zone as the *Tapinocephalus* zone.

Boonstra (1932a) briefly noted that the large-bodiedpareiasaurs first encountered very near

the base of the *Tapinocephalus* Zone underwent few changes and died out near the top of

the zone. Later, Boonstra (1969) suggested a decreasing abundance of pareiasaurs through

the *Tapinocephalus* Zone, with the majority of specimens (i.e. 189 out of 215) occurring in

his lower subdivision, and only one specimen in the upper (third) subdivision.

In their vertebrate biozonation of the Western Karoo Basin, Keyser & Smith (1979) proposed

renaming Boonstra's lower and middle *Tapinocephalus* AZ together as the Dinocephalian

zone, for which both *Bradysaurus bombidens* and *Embrithosaurus schwarzi* were designated

as characteristic fossil taxa. Both genera were considered to also be present in the overlying

Pristerognathus/Diictodon AZ, though at much lower abundance. This was broadly

reiterated by Smith & Keyser (1995a), who suggested uncertain ranges for the genera

793   *Bradysaurus* and *Embrithosaurus* throughout the *Tapinocephalus* AZ and into the lower part

794   of the overlying renamed *Pristerognathus* AZ.

795   A more refined stratigraphic study of the Guadalupian part of the Beaufort Group by Day

796   (2013) determined the range of the three mid-Permian pareiasaur genera accepted by Lee

797   (1997a) to be mainly restricted to the Moordenaars and Karelskraal members of the upper

798   Abrahamskraal Formation (upper *Tapinocephalus* AZ), with the exception of *Bradysaurus*

799   (Fig. 5: Day 2013). However, this was based on a small number of specimens, mainly those

800   mentioned by Lee (1997a); of the large number of museum specimens, only those identified

801   as *Bradysaurus* were considered by Day (2013), likely contributing to its perceived longer

802   range.

803   More recently, Van den Brandt (2016) re-identified 39 out of 108 pareiasaur specimens from

804   the *Tapinocephalus* AZ (36%), ascribing the low percentage of positive identifications to the

805   study being restricted to crania only and to the poor condition of most of the material.

806   These new identifications nevertheless enabled the reassessment of stratigraphic ranges for

807   pareiasaur taxa in the *Tapinocephalus* AZ (Fig. 5: VdB 2016).

808   **<<Insert Table 2>>**

809   **<<Insert Table 3>>**

810   *Bradysaurus* has historically been a 'waste basket' for most large pareiasaurian specimens

811   collected from the *Tapinocephalus* AZ and so has generally been considered the most

812   abundant genus. We identified 74 specimens that could be reliably assigned to *Bradysaurus*

813   *baini* (Supplemental material, Appendix 1C: numbers 84 to 157). The stratigraphically lowest

814   occurring specimen is BP/1/7886 (from Banksdrif in the Laingsburg district). This locality is

815   well constrained to the mid/upper Koornplaats Member. The highest occurrences are

816   NHMUK PV OR 49426 (Palmietfontein, Beaufort West district) and BP/1/7213 (Witfontein,

817   Sutherland, Namakwa district) both of within the Karelskraal Member (Table 4). The

818   stratigraphic range of *Bradysaurus baini* therefore extends from the upper Koornplaats

819   Member to the Karelskraal Member (Fig. 5: This study), and thus occurs in both subzones of

820   the *Tapinocephalus* AZ (Day & Rubidge 2020).

821   **<<Insert Table 4>>**

822   **<<Insert Figure 5>>**

823   We have identified 40 *Embrithosaurus* specimens, the stratigraphically lowest of which

824   (SAM-PK-9165) was found on Van Der Byls Kraal, Beaufort West district, at the boundary of

825   the Swaerskraal/Moordenaars Members. The highest occurrence is in the Karelskraal

826   Member, represented by specimens BP/1/7241 (from Wolwehoek, Beaufort West district)

827   and SAM-PK-012252 (from Gannakraal, Fraserburg, Namakwa district) (Table 4). The

828   stratigraphic range of *Embrithosaurus* thus corresponds closely with the *Diictodon* –

829   *Styracocephalus* Subzone of the *Tapinocephalus* AZ (Day & Rubidge 2020) (Fig. 5).

830   Forty-three specimens are referable to *Nochelesaurus*. The stratigraphically lowest

831   occurrence is specimen is BP/1/8011 (from De List, Laingsburg district) which was collected

832   from the upper Koornplaats Member. The highest definite occurrence is specimen

833   BP/1/7252 (from Wolwehoek, Hendriks Kraal 298, Beaufort West district), which is within

834   the Karelskraal Member (Table 4). Like *Bradysaurus*, *Nochelesaurus* therefore also occurs in

835   both subzones of the *Tapinocephalus* AZ (Day & Rubidge 2020) (Fig. 5).

836   Pareiasaur occurrences in the mid-Permian are restricted to a relatively small geographic

837   region of the south-western Karoo, and all the species are distributed throughout this

838   region; there is no variation in the distribution of the different species (Fig. 6). The majority

839   of specimens are located in a roughly triangular area between Prince Albert in the south,

840   Sutherland in the west, and Beaufort West in the east. A few specimens are scattered

841   further north, just north of Fraserburg. Towards the north of the basin (eg. Free State

842   Province) exposures of the lower *Tapinocephalus* AZ have not produced any fossils of large

843   animals, including pareiasaurs (Groenewald *et al.* 2019, 2022).

844   No *Tapinocephalus* AZ pareiasaurs are currently known to occur in the southeast of the

845   basin, likely the result of relatively little prospecting in this part of the basin, coupled with

846   less rock outcrop because of vegetation cover.

847   **<<Insert Figure 6>>**

848   Stratigraphic data presented here show *Bradysaurus* and *Nochelesaurus* both occur in the

849   Koornplaats Member, and thus their range begins in the *Eosimops-Glanosuchus* Subzone of

850   the*Tapinocephalus* AZ, whereas *Embrithosaurus* is restricted to the overlying *Diictodon-*

851   *Styracocephalus* Subzone (Day & Rubidge 2020). The fact that *Embrithosaurus* is

852   phylogenetically the most basal genus of the group but stratigraphically the last to appear

853   suggests a ghost lineage for the genus through the lower *Eosimops-Glanosuchus* Subzone

854   (Day & Rubidge 2020). This may simply be the result of inadequate sampling from this lower

855   subzone, particularly below the Koornplaats Member. So far, no bradysaurian fossils have

856   been found in the Teekloof Formation, suggesting they perished (or at least were extirpated

857   from the Karoo Basin) during the Capitanian mass extinction (Day *et al.* 2018).

Anatomical discussion

It has long been known that the large basal South African pareiasaurs, the Bradysauria, possess 'leaf-shaped' tooth crowns compared to the 'fan-shaped' tooth crowns of the younger Lopingian pareiasaurs (Haughton & Boonstra 1929; Boonstra 1934). However, the dental features resulting in 'leaf-shaped' or 'fan-shaped' pareiasaurian teeth are not well explained. Accordingly we compiled a comparative list of characters separating the two tooth types (Table 5). The most important and obvious evolutionary change is the increase in the number of marginal tooth cusps between the members of the Bradysauria and the younger pareiasaurs (characters 69 and 70), probably related to more efficient grasping of plant material.

<<Insert Table 5>>

Horizontal upper teeth of *Bradysaurus baini*. Boonstra (1934) described two contrasting pareiasaurian jaw morphologies relating to the curvature of the maxilla and the orientation of the upper jaw teeth, noting that maxillae with only slight ventral curvature hold vertical teeth, whereas those that are strongly inwardly curved have lingually directed teeth. Most pareiasaurs have a vertical maxilla that is only slightly or gently curved ventrally and the upper jaw teeth point straight down. Lee (1994, 1997a) noted three taxa that show exceptions: the slightly anteriorly or labially-pointing upper teeth of *Scutosaurus* (an autapomorphy for this taxon), and the lingually-pointing or "medially inflected" upper teeth of *Pareiasuchus nasicornis* (Lee *et al.* 1997:307) and *Bradysaurus baini*. He proposed a character to score the orientation of the upper teeth (Lee 1997a, character 27).

882   Jalil & Janvier (2005) reported anteroventrally directed upper jaw teeth in *Arganaceras* to a

883   more exaggerated degree than in *Scutosaurus*. Tsuji (2013, Appendix 3) published a list of

884   autapomorphies per species in which she did not consider the lingually-pointing upper jaw

885   teeth of *Pareiasuchus nasicornis* and *Bradysaurus baini* as autapomorphies (presumably

886   since the condition occurs in more than one taxon). Turner *et al.* (2015, Supplemental data,

887   Appendix 1:8) termed the lingually-pointing condition for these two taxa as "ventromedially"

888   oriented upper teeth for character 67 in their phylogenetic analysis.

889

890   *Scutosaurus* specimens studied by us confirm that, despite the often severely distorted and

891   crushed condition of many skulls, this taxon consistently displays slightly outwardly-oriented

892   upper jaw teeth. This suggests that even severe cranial distortions do not significantly affect

893   the orientation of the teeth. Similarly, the ventromedially oriented (lingually-pointing) upper

894   jaw teeth of *Bradysaurus baini* are probably a true character of the species and not the

895   result of distortion. Moreover, the lingually-pointing upper jaw teeth of *Bradysaurus baini*

896   are always accompanied by a strongly medially curved ventral maxilla, with a large portion

897   curved and directed horizontally just above the tooth row to accommodate the long curved

898   roots of ventromedially oriented, lingually-pointing teeth. In lateral view, these horizontal

899   upper teeth are not visible in specimens of *Bradysaurus baini*, and in ventral view, the

900   inwardly curved maxilla and horizontal upper jaw teeth cover and obscure the anterior and

901   lateral portions of the palate. In *Embrithosaurus* and *Nochelesaurus*, the upper teeth are

902   visible in lateral view and in ventral view, the slightly curved ventral maxilla and vertical

903   teeth do not obscure the palate. We noticed that in all middle Permian pareiasaurs the

904   orientation of teeth in the upper jaw is not consistent along the entire tooth row as the

905   distal most upper teeth point slightly medially. The interspecific differences in tooth

906   orientation discussed here apply to only the premaxillary and anterior maxillary teeth.

907   Speculating on the validity of the horizontal upper teeth of *Bradysaurus* as a diagnostic

908   character we note that all three middle Permian species have lower jaws that are

909   significantly smaller than the upper jaws. When the jaws are occluded, the lower teeth pass

910   well inside the upper teeth, by several centimetres. No tooth wear is evident and no tooth

911   wear patterns have been described for any pareiasaur. The considerable distance between

912   upper and lower jaw teeth and the lack of tooth wear in pareiasaurs led Haughton &

913   Boonstra (1930: 264) to propose that pareiasaurian teeth do not occlude and so did not

914   directly cut or grind vegetation, but merely served as "rugosities to prevent the soft

915   vegetation from slipping out after a mouthful has been taken".

916   Lee *et al.* (1997) explained how the uninterrupted even cutting edge of pareiasaurian

917   dentition, characteristic of herbivores, employs a cropping action which does not require

918   contact between upper and lower teeth but rather the upper and lower teeth move past

919   one another in a scissor-like action. Lee *et al.* (1997) also discussed how the depressed jaw

920   articulation of pareiasaurs (well below the tooth row) produces a posteriorly directed force

921   during mastication. This creates a shearing action that facilitates cropping of tough plant

922   matter, limiting pareiasaurs to cropping off bits of vegetation before swallowing in the

923   absence of propalinal movement. Lee's explanations (no occlusion and posteriorly directed

924   upper forces) may account for the seemingly strange horizontal lingually-pointing upper

925   teeth of *Bradysaurus baini* (and *Pareiasuchus nasicornis*) being functional, and the unusual

926   orientation of the upper dentition is not the result of distortion. Niche partitioning (differing

927   diets) may be related to the unique upper tooth orientation of *Bradysaurus baini* compared

928   to *Embrithosaurus* and *Nochelesaurus* enabling three genera of similar size to coexist

929   without apparently competing for food.

930   **Intraspecific variability among the Bradysauria.** Our study has broadened the taxonomic

931   definition and increased the observed anatomical variability within each species

932   (Supplemental material, Appendix 3).

933   The variability of the number of cusps on the upper and lower teeth rang from seven to nine

934   (*Bradysaurus*), and seven to ten (*Nochelesaurus*). Previously *Embrithosaurus* was considered

935   the only species of the Bradysauria to have more than seven cusps (Boonstra 1934; Lee

936   1994, 1997a; Van den Brandt *et al.* 2020). *Embrithosaurus schwarzi* has either seven-or

937   nine-cusped upper teeth, *Nochelesaurus alexanderi* has seven-or-eight cusped upper teeth

938   (with one outlier, BP/1/7165, having five-and seven-cusped upper teeth) and *Bradysaurus*

939   *baini* seven-, eight- or nine-cusped upper teeth. *Embrithosaurus* may have either

940   dorsoventrally shortened maxillary teeth, lacking a long central trident (nine-cusped teeth)

941   or dorsoventrally elongated maxillary teeth, with a long central trident (seven-cusped

942   teeth). By contrast, *Bradysaurus* and *Nochelesaurus* have only dorsoventrally elongated

943   maxillary teeth with a long central trident.

944   Lower jaw teeth show even more variability in all three species. *Embrithosaurus schwarzi*

945   has the least variability with seven-or nine-cusped, shortened lower teeth which have

946   symmetrical cusp arrangements, no medial cusps, a low lingual bulge, and no lingual

947   cingulum. *Nochelesaurus alexanderi* is highly variable with seven-to ten-cusped lower,

948   elongated teeth, non-symmetrical cusp arrangements, an incipient cingulum ridge on

949   certain teeth, medial cusps sometimes present, and one to three vertical lingual ridges. The

950   lower teeth of *Bradysaurus baini* are also highly variable with elongated or shortened teeth,

951   seven to nine marginal cusps, symmetrical or non- symmetrical cusp arrangements, medial

952   cusps sometimes present, and a bulged lingual surface.

953   Maxillary teeth are vertically oriented in *Embrithosaurus schwarzi* and *Nochelesaurus*

954   *alexanderi*, but vary from ventromedially to horizontally oriented in *Bradysaurus baini.*

955   Both *Bradysaurus baini* and *Embrithosaurus schwarzi* develop a maxillary boss in ontogeny.

956   Juvenile specimens may lack the boss, sub-adults may have a low or small boss, and large

957   adults have the largest maxillary bosses. Individuals of *Nochelesaurus alexanderi* never

958   develop a maxillary boss, even in large adults.

959   For *Bradysaurus baini* the size of the cheek (expressed as degrees below the tooth row that

960   the ventral surface of the quadratojugal creates, Turner *et al.* 2015, character 44) is highly

961   variable, ranging from small (20°) to large (30°) and two specimens have cheeks larger than

962   30°. *Embrithosaurus schwarzi* (30°- 40°) and *Nochelesaurus alexanderi* (~30°) have more

963   consistently larger cheeks. These size differences and patterns are consistent and can

964   reliably be used to identify species. Small cheeks represent *Bradysaurus* specimens and the

965   largest cheeks belong to *Embrithosaurus*.

966   The size and shape of the bosses on the posterior cheek of *Bradysaurus baini* are extremely

967   variable, ranging from small to medium-sized knobs (which are as wide as high), to large,

968   wide and low, indistinct bulbous bosses. The posterior cheek bosses of *Nochelesaurus* are

969   also variable: either horizontally flat and pointed, plate-like bosses, or medium-sized bosses,

970   as wide as high. Only *Embrithosaurus* consistently shows wide, low, bulbous bosses.

971   The size and shape of the angular boss of the lower jaw is highly variable in all species and

972   only one pattern emerges: that most large specimens of *Bradysaurus baini* have relatively

973   small angular bosses compared to *Embrithosaurus schwarzi* and *Nochelesaurus alexanderi*.

974   Accordingly we tentatively include a relatively small angular boss in the diagnosis of

975   *Bradysaurus baini.*

976   Most specimens of *Bradysaurus baini* have a wide, low, irregular frontal central boss, but

977   some specimens have a high, distinct frontal central boss.

978   The three bradysaurian holotypes each have posterolateral and posteromedial nasal tabs

979   (Fig. 2). *Bradysaurus* and *Embrithosaurus* also have anterolateral tabs above the external

980   naris (not present in *Nochelesaurus*). However, when more specimens are studied, it is

981   evident that nasal tabs are highly variable among specimens of the three taxa and no

982   consistent patterns emerge.

983   In the postcranium the development of the olecranon process of the ulna is highly variable

984   (Van den Brandt *et al.* 2021b) and some authors have used the morphology of the olecranon

985   process to distinguish taxa (Watson 1914; Boonstra 1932b). We concur with Lee (1997b)

986   who considered smaller olecranon processes to be the result of early ontogenetic

987   development and should not be used to distinguish species.

988   The morphology of the internal trochanter of the femur differs among the species.

989   Proximally, it is wide, high and curved in both *Bradysaurus* and *Embrithosaurus*, more

990   curved in *Bradysaurus* into a semi-circular shape. In *Nochelesaurus* it is straight or very

991   slightly curved proximally. Distally, the internal trochanters of *Embrithosaurus* and

992   *Bradysaurus* have an anterior process that is absent in *Nochelesaurus*. The distal extension

993   of the lateral condyle of the femur shows great variability in *Nochelesaurus*, being long in

994   most specimens, but not all.

995   Pelvic differences between *Embrithosaurus* and *Bradysaurus* are consistent and are

996   therefore reliable species separators. *Bradysaurus* has a typical pareiasaurian pelvis: wide,

997   long and low, with almost parallel iliac blades and upturned anterior ends. In

998   *Embrithosaurus* the pelvis is narrow, short and high, with three autapomorphies: thick

999   symphysis and flat and straight vertical iliac blades that diverge anteriorly (Van den Brandt

1000   *et al.* 2021b).

1001   Differences in the torsion of the proximal and distal expansions of the humerus fall within a

1002   narrow range within a species and are consistent. They are therefore reliable species

1003   separators. Both *Bradysaurus* and *Embrithosaurus* have high degrees of humeral torsion

1004   within the range 60°-80° and *Nochelesaurus* has flatter expansions and torsion of 20°-40°.

1005   **Are differences due to sexual dimorphism?** Very little has been published on sexual

1006   dimorphism in pareiasaurs. Broom (1935) emphasised that the obvious pelvic differences

1007   between the holotypes of *Bradysaurus baini* and *Embrithosaurus schwarzi* may be the result

1008   of sexual dimorphism. We disagree with Broom, as these pelvic differences, together with

1009   other characters, consistently separate *Bradysaurus* and *Embrithosaurus*. Lee (1994:55-60)

1010   studied several articulated and very complete *Scutosaurus* specimens and showed that two

1011   morphs exist based on size, a smaller and larger morph, which he attributed to sexual

1012   dimorphism.

1013   Our research shows that *Bradysaurus baini* exhibits a large variation in cheek flange size. We

1014   suggest that: 1) small cheeks (extending only 20° below the tooth row) may belong to one

1015   sex and, 2) larger cheeks (30°) to the other. Similarly, the bosses of the posterior cheek of

1016   *Bradysaurus baini* display two morphotypes: 1) small to medium-sized, round, as wide as

1017   high bosses are one condition and, 2) large, low, wider than high, bulbous bosses are the

1018   other. However, we are not able to perfectly correlate those two pairs of morphologies with

1019   each other, and so cannot establish these two conditions as definitive sexual dimorphic

1020   characters in *Bradysaurus baini*.

1021   **Effects of distortion.** Several authors have recognised that pareiasaur remains from the

1022   *Tapinocephalus* AZ are often distorted and deformed, complicating taxonomic assessments.

1023   Despite acknowledging this, after the use of dental factors as their primary divisions,

1024   Haughton & Boonstra's (1929) pareiasaurian classification scheme relied on cranial

1025   proportional differences (interorbital width compared to tabular width) for their sub-

1026   divisions. Lee (1994, 1997a) and Van den Brandt (2016, 2020) later determined that this

1027   particular cranial proportion does not vary among pareiasaur species, and pointed out that

1028   it is more reliable to focus on the absence or presence of discrete dental and cranial

1029   features. Van den Brandt (2016) briefly discussed his observation of two typical cranial

1030   morphotypes: 1) wide, broad, dorsoventrally flattened skulls with splayed out lateral

1031   cheeks, and 2) narrow, high, mediolaterally compressed skulls with tall, thin external nares.

1032   Whilst it is often possible to identify clear signs of distortion (e.g. buckled or displaced

1033   cranial bones), it is also true that in many cases the wider or the narrower skulls appear to

1034   be genuine morphological characters which are not affected by distortion. Interpreting the

1035   true skull shape is therefore often challenging. In general, most pareiasaur skulls from the

1036   *Tapinocephalus* AZ are dorsoventrally flat and wider than high (Turner *et al.* 2015, character

1037   33, snout dimensions) apart from *Nochelesaurus*, which appears to be taller, more square

1038   and almost as high as wide. It is tempting to classify the pareiasaurs from the

1039   *Tapinocephalus* AZ in two broad categories based on skull shape (wide vs. narrow), but this

1040   approach would group many specimens based on deformation and distortion, and not on

1041   cranial features.

1042   **Implications of bilateral asymmetry for species identification.** Van den Brandt (2016) and

1043   Van den Brandt *et al.* (2020) were the first to identify two different arrangement patterns of

1044   the posterior cheek bosses on the quadratojugal in basal South African pareiasaurs: a

1045   pattern with one small boss above the large corner boss and a pattern with two small

1046   bosses above the large corner boss. Van den Brandt (2016) found both arrangement

1047   patterns to be present for specimens of *Bradysaurus baini*, *Bradysaurus seeleyi* and

1048   *Nochelesaurus alexanderi*, but not for specimens of *Embrithosaurus schwarzi*, where the

1049   pattern of one small boss above the corner boss is always present. Our final study now has

1050   revealed specimens of *Bradysaurus baini* (SAM-PK-5624) and *Embrithosaurus schwarzi* (CGP

1051   CBT 112) in which both patterns are present on an individual skull, one on either cheek,

1052   indicating bilateral asymmetry. Therefore, posterior cheek boss arrangement patterns are

1053   not diagnostic of any particular species since one individual can have two different

1054   arrangement patterns.

1055   This brings into question the diagnostic validity of using the arrangement patterns of the

1056   posterior cheek bosses in closely related pareiasaurian species, such as the members of the

1057   Bradysauria. Van den Brandt *et al.* (2021a) discussed the validity of cranial ornamentation in

1058   pareiasaurian species identification, especially the size and shape of the posterior cheek

1059   bosses, and found that size and shape (but not arrangement pattern) to be a reliable species

1060   separator, even though there is overlap in that both *Bradysaurus* (holotype: wide, low

1061   bosses) and *Nochelesaurus* (holotype: high, pointed bosses) specimens may present

1062   medium-sized, as wide as high, posterior cheek bosses.

1063 There is also large variation and asymmetry within a single individual: the ulnae of the

1064 holotype of *Bradysaurus baini*, show extreme size differences of the olecranon process

1065 between the left (which is short , at 15 mm dorsoventrally high) and the right (which is three

1066 times as high, at 45 mm dorsoventrally high) (Van den Brandt *et al.* 2021b). If not found as

1067 part of an articulated skeleton (Seeley 1892) these two ulnae would be sufficiently different

1068 to be assigned to two different individuals and maybe two different species. Similarly, the

1069 femora of *Nochelesaurus alexanderi* specimen SAM-PK-9137 shows asymmetry with an

1070 internal trochanter that is straight on the left femur, but slightly curved on the right femur.

1071 These examples of bilateral asymmetry in cranial and postcranial features in middle Permian

1072 pareiasaur specimens, which might well identify individual elements as belonging to

1073 different species, should caution against the use of minor morphological differences to

1074 separate species.

1075 **Phylogenetic discussion**

1076 Lee (1997b) produced the first cladistic phylogenetic analysis of the relationships among

1077 pareiasaur taxa, using knowledge gained from his earlier work on the relationships among

1078 parareptiles (Lee 1993, 1994, 1997a). His first cladistic analysis of pareiasaurs found

1079 numerous most parsimonious trees (MPTs) in which the consensus tree showed

1080 *Bradysaurus seeleyi* as the most basal pareiasaur, followed by a polytomy including *B. baini*,

1081 *Nochelesaurus alexanderi* and a clade including *Embrithosaurus schwarzi* and all remaining

1082 pareiasaurs (Lee 1997b). *Embrithosaurus schwarzi* was recovered as the species with the

1083 most derived features of the four taxa from the middle Permian of South Africa and Lee

1084 (1997b) did not recover a monophyletic *Bradysaurus*.

1085   The initial character scores assigned to the four basal South African taxa by Lee (1997b)

1086   have received little revision, especially from direct study of the material. As a result, the

1087   phylogenetic position of the four *Tapinocephalus* AZ pareiasaurs has been virtually

1088   unchanged across all subsequent analyses (Lee 1997b; Jalil & Janvier 2005; Tsuji & Muller

1089   2008; Tsuji 2013; Tsuji *et al.* 2013; Turner *et al.* 2015; Xu *et al.* 2015; Benton 2016, Liu &

1090   Bever 2018). In the most recent phylogenetic analysis (before our work), Liu & Bever (2018)

1091   recovered *B. seeleyi* as the most basal pareiasaur, followed by a polytomy including *B. baini*

1092   and *Nochelesaurus* and a clade including *Embrithosaurus* and all remaining pareiasaurs. In

1093   all these previous analyses, *Embrithosaurus* is recovered as the taxon with the most derived

1094   features among the basal group of the four taxa from the middle Permian of South Africa.

1095   In our first phylogenetic analysis, Van den Brandt *et al.* (2020) described the cranium of

1096   *Embrithosaurus schwarzi* and rescored the cranial characters (characters 1-78) using the

1097   matrix of Liu & Bever (2018) excluding postcranial characters (characters 79-139). All 30 taxa

1098   used by Liu & Bever (2018) were retained and the phylogenetic analysis for the first time

1099   recovered Bradysauria (supported by three synapomorphies) as a monophyletic group

1100   comprising the four basal middle Permian South African pareiasaurs (Van den Brandt *et al.*

1101   2020). *Nochelesaurus alexanderi* and *B. seeleyi* formed a polytomy, and *Embrithosaurus*

1102   *schwarzi* and *Bradysaurus baini* formed a monophyletic group.

1103   Here, in our updated phylogenetic analysis, we have recovered a monophyletic Bradysauria

1104   supported by five synapomorphies. *Nochelesaurus alexanderi* and *Bradysaurus baini* form a

1105   monophyletic group and, in contrast to all previous analyses, *Embrithosaurus* is recovered as

1106   the most basal member. Derived phylogenetic features of *Embrithosaurus schwarzi* (Lee

1107   1997b) included a greater number of marginal cusps on the teeth (seven to nine); straight

1108   lateral projections on the caudal vertebrae; a shorter and thicker pubic symphysis; a large

1109   major trochanter on the femur; postaxial flange of the femur that narrows in the middle; a

1110   proximally curved internal trochanter; and a central boss on the osteoderms. Our research

1111   shows that a higher number of marginal cusps are found in all middle Permian South African

1112   pareiasaurian taxa, the postaxial flange of the femur of *Embrithosaurus* does not narrow in

1113   the middle, and a proximally curved internal trochanter also applies to *Bradysaurus baini*. In

1114   addition, we have made significant character score updates to all members of Bradysauria.

1115   This new phylogenetic result contradicts the stratigraphic ranges which show

1116   *Embrithosaurus* to be the last genus of South African middle Permian pareiasaurs to appear

1117   in the stratigraphic succession, suggesting a ghost lineage for the genus.

1118   **Taxonomic discussion**

1119   **How many species: one or many?** Figure 1 provides a summary of previous taxonomic

1120   schemes relating to middle Permian South African pareiasaurs, including the changes

1121   proposed in this study (see also Supplemental material, Appendix 5).

1122   A robust taxonomy with reliable distinguishing diagnostic characters to differentiate the

1123   pareiasaur species from the *Tapinocephalus* AZ of the Karoo remains challenging (Lee 1994,

1124   1997a; Van den Brandt 2016, 2020; Van den Brandt *et al.* 2020, 2021a, 2021b).

1125   Due to the high degree of intraspecific variability within each species and some overlapping

1126   features among all three species now evident from our study, it is tempting to argue that

1127   only one, extremely variable, pareiasaurian genus existed in the Karoo Basin in the

1128   Guadalupian, and that the differences are the result of extreme variability, ontogenetic

1129   development, sexual dimorphism, and/or distortion. This idea is supported by the fact that

1130 23 specimens with intermediate morphology exist, which cannot be confidently assigned to

1131 any taxon and whose identification we narrowed down to one of two species (Supplemental

1132 material, Appendix 1C: numbers 158 to 180).

1133 Here we have synonymised *Bradysaurus seeleyi* with *Bradysaurus baini* based on the

1134 observation that the holotype of *B. seeleyi* possesses no autapomorphies and otherwise

1135 appears to be a sub-adult *Bradysaurus baini.* The holotype of *B. seeleyi* is smaller and more

1136 gracile, cranially and postcranially, than any of the other bradysaurian holotypes, and we

1137 interpret the lack of a distinct maxillary boss as the result of incomplete ontogenetic

1138 development. This decreases the number of recognised pareiasaur species from the

1139 *Tapinocephalus* AZ to three. We chose to recognise these three genera on the basis that the

1140 three holotypes are clearly different from each other, and each shows unambiguous

1141 autapomorphies. The most important morphological differences among the three species

1142 are the orientation of the upper jaw teeth; the shapes of the postfrontal, postparietal, and

1143 the posterior cheek bosses; the shape and dimensions of the pelvis; the morphology of the

1144 internal trochanter of the femur; the degree of twisting of the humerus and the

1145 ornamentation style of the osteoderms. Moreover, the first appearances of all three taxa

1146 show clearly separate stratigraphic ranges (Fig. 5), which further supports the notion that

1147 they should not be synonymised. As such, we believe it is more cautious, given the current

1148 state of knowledge, to maintain the validity of these three genera and species.

Conclusion

1150 This study has reviewed the pareiasaurs from the *Tapinocephalus* AZ of the Karoo Basin and

1151 differs from previous attempts in that it has considered almost all relevant pareiasaur

1152   material from multiple museums around the world (240 specimens). Having done so we

1153   recognise three monospecific pareiasaur genera from the *Tapinocephalus* AZ.

1154   *Embrithosaurus schwarzi* has the largest cheek flange of all middle Permian pareiasaurs, the

1155   only genus to reach and marginally exceed a 40° angle below the tooth row; distinctive wide

1156   dentition; and a combination of other cranial features (eg. narrow postparietal and a

1157   mediolaterally elongated postfrontal). In the dentition, there is a wider range in the number

1158   of cusps (seven to nine cusps) than the nine we previously proposed (Van den Brandt *et al.*

1159   2020). *Embrithosaurus schwarzi* is most easily separated from the co-occurring species

1160   through features of the pelvis and osteoderms: pelvis high, narrow, and short, with a deeply

1161   concave dorsal puboischiatic plate, and a large and long median pubic process; iliac blades

1162   oriented obliquely from the longitudinal midline, vertical; the thickest midline pelvic

1163   symphysis; anterior dorsal osteoderms with distinct and high, small central bosses, with thin

1164   and flat peripheries.

1165   *Nochelesaurus alexanderi* is cranially recognised by its autapomorphic wide postparietal and

1166   more distinctive cranial ornamentation, especially the larger and more pointed bosses on

1167   the posterior margins of the cheeks; features of the dentition (non-symmetrical marginal

1168   cusp arrangements, incipient horizontal cingulum with medially (lingually) placed cusp(s))

1169   and a combination of other cranial features (e.g. square postfrontal, large cheeks, vertical

1170   upper jaw teeth, lack of a maxillary boss, more gracile distal paroccipital process of the

1171   opisthotic). *Nochelesaurus alexanderi* is most easily separated from the co-occurring species

1172   by: straight internal and small external trochanters of the femur; longer and narrower

1173   scapula blade; less twisting of the humerus; and relatively rugose osteoderms.

1174 *Bradysaurus baini* is diagnosed by maxillary teeth ventromedially or medially (horizontally)

1175 oriented; low cranial ornamentation; large maxillary boss, and autapomorphic distal

1176 paraoccipital process of the opisthotic. Variability in the sizes of the cheeks and in the sizes

1177 of the bosses on the posterior margin of the cheeks is large in this species. Specimens may

1178 have smaller (20°) to larger (30°) cheek flanges, which may have either large and wide,

1179 bulbous bosses on the posterior margins or medium-sized bosses, as high as wide. New

1180 dental features and increased dental variability have been found in *B. baini,* such as bulged

1181 or ridged lingual surfaces of lower jaw teeth and a higher number of marginal cusps, seven

1182 to nine, on upper and lower teeth. *Bradysaurus baini* is easily separated from the other

1183 middle Permian South African pareiasaurs through: twisted humerus; wide, low and long

1184 pelvis with posterior iliac blades parasagittal and anterior blades lateral and horizontally

1185 bent; unornamented osteoderms; short and distally flared scapula blade; large femur with a

1186 distinctive, curved and projecting internal trochanter and lack of a large external trochanter,

1187 and second sacral rib the largest.

1188 *Bradysaurus baini*, *Embrithosaurus schwarzi* and *Nochelesaurus alexanderi* are the only valid

1189 species of South African middle Permian pareiasaurs. *Bradysaurus seeleyi* is synonymised

1190 with *Bradysaurus baini*. The list of distinguishing features among the three species has been

1191 updated and we have documented intraspecific variability. Despite rigorous re-description

1192 and analysis of both cranial and postcranial characters which lead to the recognition of only

1193 three valid taxa, there are a few specimens that exhibit characters of more than one taxon,

1194 or characters intermediate to the condition present in two taxa. This suggests either greater

1195 intraspecific variability, or a greater diversity of taxa. This problem can be addressed only by

1196 the discovery of more well-preserved, well-prepared, and stratigraphically well-

1197 provenanced specimens.

1198 Our phylogenetic analysis recovered the clade Bradysauria (Van den Brandt *et al.* 2020) and

1199 suggests that it represents the early pulse of pareiasaurian diversification which is restricted

1200 to the middle Permian of the South African Karoo. *Nochelesaurus* and *Bradysaurus* are sister

1201 taxa and *Embrithosaurus* is the most basal member of the group. This new phylogenetic

1202 result contradicts the stratigraphic ranges, which shows *Embrithosaurus* as the last genus of

1203 South African middle Permian pareiasaurs to appear in the stratigraphic succession,

1204 suggesting a ghost lineage for the genus.

1205 The stratigraphic provenance of 142 of the 240 pareiasaur specimens from the

1206 *Tapinocephalus* AZ were determined to enable an accurate illustration of the range of each

1207 species (Supplemental material, Appendix 4; Fig. 5: This study). *Bradysaurus baini* is the

1208 oldest pareiasaurian and has the stratigraphically lowest first occurence in the Koornplaats

1209 Member of the Abrahamskraal Formation. *Nochelesaurus* has its first occurrence in the

1210 uppermost part of the Koornplaats Member and so, along with *Bradysaurus,* is a constituent

1211 part of the *Eosimops-Glanosuchus* Subzone of the *Tapinocephalus* AZ (Day & Rubidge 2020).

1212 All three genera are found throughout most of the *Diictodon-Styracocephalus* Subzone and

1213 have their highest occurrence within the Karelskraal Member near the top of the

1214 *Tapinocephalus* AZ, where they fell victim to the Capitanian mass extinction.

References

1250 **Benton, M. J.** 2016. The Chinese pareiasaurs. *Zoological Journal of the Linnean Society*, **177**,

1251 813–853, doi.org/10.1111/zoj.12389.

1252 **Boonstra, L. D.** 1932a. The phylogenesis of the Pareiasauridae: a study in evolution. *South*

1253 *African Journal of Science,* **29**, 480–486.

1254 **Boonstra, L. D.** 1932b. Pareiasaurian studies. Part 8. The osteology and myology of the

1255 locomotor apparatus. B – fore limb. *Annals of the South African Museum,* **28**, 437–503.

1256 **Boonstra, L. D.** 1934. Pareiasaurian studies. Part 9. The cranial osteology. *Annals of the*

1257 *South African Museum*, **31**, 1–38.

1258 **Boonstra, L. D.** 1969. The fauna of the *Tapinocephalus* zone (Beaufort beds of the Karoo).

1259 *Annals of the South African Museum,* **56**, 1–73.

1260 **Broom, R.** 1903. On an almost perfect skeleton of *Pareiasaurus serridens* Owen. *Annals of*

1261 *the South African Museum*, **4**, 123–138.

Broom, R. 1912. On a new species of *Propappus*, and on the pose of the pareiasaurian limbs. *Annals of the South African Museum,* **7**, 323–331.

Broom, R. 1913. On four new fossil reptiles from the Beaufort Series, South Africa. *Records of the Albany Museum,* **2**, 397–401.

Broom, R. 1914. Further observations on the South African fossil reptiles. *The American Museum Journal,* **14**, 139–143.

Broom, R. 1916. Pareiasaurian nomenclature. *Annals and Magazine of Natural History,* **17,** 347–348.

Broom, R. 1924. On some points in the structure of the pareiasaurian skull. *Proceedings of the Zoological Society of London,* **1924**, 499–508.

Broom, R. 1935. Notes on some species of pareiasarian reptiles. *Annals of the Transvaal Museum,* **18,** 37–51.

Cole, D. I., Johnson, M. R. & Day, M. O. 2016. Lithostratigraphy of the Abrahamskraal Formation (Karoo Supergroup), South Africa. *South African Journal of Geology,* **119**, 415–424.

Cope, E. D. 1896. The reptilian order Cotylosauria. – Proceedings of the American Philosophical Society, **34**, 436–456.

Day, M. O. 2013. Middle Permian continental biodiversity changes as reflected in the Beaufort Group of South Africa: a bio-and lithostratigraphic review of the *Eodicynodon, Tapinocephalus,* and *Pristerognathus* Assemblage Zones. Unpublished Ph.D thesis, University of the Witwatersrand, Johannesburg, 1–387.

1283 **Day, M. O. & Rubidge, B. S.** 2014. A brief lithostratigraphic review of the Abrahamskraal and

1284 Koonap formations of the Beaufort Group, South Africa: towards a basin-wide stratigraphic

1285 scheme for the Middle Permian Karoo. *Journal of African Earth Sciences*, **100**, 227–242,

1286 doi.org/10.1016/j.jafrearsci.2014.07.001.

1287 **Day, M. O., & Rubidge, B. S.** 2020. Biostratigraphy of the *Tapinocephalus* Assemblage Zone

1288 (Beaufort Group, Karoo Supergroup), South Africa. *South African Journal of Geology* 2020,

1289 **123(2)**, 149–164, doi.org/10.25131/sajg.123.0012.

1290 **Day, M. O., Ramezani, J., Bowring, S. A., Sadler, P. M., Erwin, D. H., Abdala, F. & Rubidge,**

1291 **B.S. 2015.** When and how did the terrestrial mid-Permian mass extinction occur? Evidence

1292 from the tetrapod record of the Karoo Basin, South Africa. *Proceedings of the Royal Society*

1293 *of London B,* **282**, doi.org/10.1098/rspb.2015.0834.

1294 **Day, M. O., Benson, R. B., Kammerer, C. F., & Rubidge, B. S.** 2018. Evolutionary rates of

1295 mid-Permian tetrapods from South Africa and the role of temporal resolution in turnover

1296 reconstruction. *Paleobiology*, **44(3)**, 347–367, doi.org/10.1017/pab.2018.17.

1297 **Geological Survey.** 1979: 3222 Beaufort West 1:250 000 Geological Map Series. *Compiled*

1298 *by*: Marsh, A., Leaman, P.W., and Johnson, M.R., 1978. Government Printer, Pretoria, South

1299 Africa.

1300 **Geological Survey.** 1983: 3220 Sutherland 1:250 000 Geological Map Series. *Compiled by*:

1301 Wickens, H. de V., and Siegfried H.P., 1978. Government Printer, Pretoria, South Africa.

1302 **Geological Survey.** 1989a: 3122 Victoria West 1:250 000 Geological Map Series. *Compiled*

1303 *by*: Leroux, F.G. and de Beer, C.H., 1987. Government Printer, Pretoria, South Africa.

1304 **Geological Survey.** 1989b: 3120 Williston 1:250 000 Geological Map Series. *Compiled by*:

1305 Viljoen, J.H.A., 1985. Government Printer, Pretoria, South Africa.

1306 **Goloboff, P., Farris, J. & Nixon, K.** 2008. TNT, a free program for phylogenetic analysis,

1307 *Cladistics*, **24**, 774–786.

1308 **Goloboff, P. & Catalano, S. A.** 2016. TNT version 1.5, including a full implementation of

1309 phylogenetic morphometrics, *Cladistics*, **32**, 221–238, doi:10.1111/cla.12160.

1310 **Groenewald, D. P., Day, M. O. & Rubidge, B. S.** 2019. Vertebrate assemblages from the

1311 north-central Main Karoo Basin, South Africa, and their implications for mid-Permian

1312 biogeography, *Lethaia*, **52**, 486–501, doi.org/10.1111/let.12326.

1313 **Groenewald, D. P., Day, M. O., Penn-Clarke, C. R. & Rubidge, B. S.** 2022. Stepping out

1314 across the Karoo retro-foreland basin: Improving constraints on the Ecca-Beaufort shoreline

1315 along the northern margin. *Journal of African Earth Sciences*, **185**, 104389.

1316 **Haughton, S. H. & Boonstra, L. D.** 1929. Pareiasaurian studies. Part I. An attempt at a

1317 classification of the pareiasauria based on skull features. *Annals of the South African*

1318 *Museum*, **28**, 79–87.

1319 **Haughton, S. H. & Boonstra, L. D.** 1930. Pareiasaurian studies. Part 5. On the pareiasaurian

1320 mandible. *Annals of the South African Museum,* **28**, 261–288.

1321 **ICZN** (International Commission on Zoological Nomenclature). 1999. International Code of

1322 Zoological Nomenclature, fourth edition. *International Trust for Zoological Nomenclature*,

1323 London, **xxix**, 1–306.

1324 **Jalil, N.-E. & Janvier, P.** 2005. Les pareiasaures (Amniota, Parareptilia) du Permien superieur

1325 du Bassin d'Argana, Maroc. *Geodiversitas*, **27(1)**, 35–132.

1326 **Keyser, A. W. & Smith, R. H. M**. 1979. Vertebrate biozonation of the Beaufort Group with

1327 special reference to the Western Karoo Basin. *Annals Geological Survey South Africa*, **12**, 1–

1328 36.

1329 **Kitching, J.W.** 1995. Biostratigraphy of the *Dicynodon* Assemblage Zone. In: Rubidge, B.S.

1330 (ed.). Biostratigraphy of the Beaufort Group (Karoo Supergroup), Biostratigraphic Series 1.

1331 *South African Committee for Stratigraphy*, Pretoria, 29–34.

1332 **Kuhn, O.** 1969. *Cotylosaria. Handbuch der Palaoherpetologie, Teil 6.* Stuttgart: Gustav

1333 Fischer Verlag.

1334 **Laurenti, J. N.** 1768. Classis Reptilium. Specimen medicum, exhibens synopsis Reptilium

1335 emendatum, cum experimentis circa venena et antidote Reptilium Austriacorum. *J. Thom.,*

1336 *Nob. et Trattnern*, Vienna.

1337 **Lee, M. S. Y.** 1993. The origin of the turtle body plan: bridging a famous morphological gap,

1338 *Science*, **261**, 1716–1720.

1339 **Lee, M. S. Y.** 1994. Evolutionary morphology of pareisaurs. Unpublished Ph.D thesis,

1340 University of Cambridge, Cambridge, 1–392.

1341 **Lee, M. S. Y.** 1995. Historical burden in systematics and the interrelationships of

1342 'parareptiles'. *Biological Reviews*, **70**, 459–547.

1343 **Lee, M. S. Y.** 1996. Correlated progression and the origin of turtles. *Nature*, **379**, 812–815.

1344   **Lee, M. S. Y.** 1997a. A taxonomic revision of pareiasaurian reptiles: implications for Permian

1345   terrestrial palaeoecology. *Modern Geology*, **21**, 231–298.

1346   **Lee, M. S. Y.** 1997b. Pareiasaur phylogeny and the origin of turtles. *Zoological Journal of the*

1347   *Linnean Society*, **120**, 197–280.

1348   **Lee, M. S. Y., Gow, C. E. & Kitching, J. W.** 1997. Anatomy and the relationships of the

1349   pareiasaur P*areiasuchus nasicornis* from the upper Permian of Zambia. *Palaeontology*,

1350   **40(2)**, 307–335.

1351   **Liu, J & Bever, G. S.** 2018. The Tetrapod Fauna of the Upper Permian Naobaogou Formation

1352   of China: a new species of *Elginia* (Parareptilia, Pareiasauria). *Papers in Palaeontology*, **4(2)**,

1353   197209. doi.org/10.1002/spp2.1105.

1354   **Olson, E. C.** 1947. The Family Diadectidae and its bearing on the classification of reptiles.

1355   *Fieldiana Geology*, **11**, 1–53.

1356   **Owen, R. 1856.** Report on the reptilian fossils of South Africa. Part 3. On parts of the

1357   skeleton of the trunk of the *Dicynodon tigriceps. Transactions of the Geological Society of*

1358   *London, Series 2,* **7**, 241–247.

1359   **Owen, R. 1862.** On the dicynodont Reptilia, with a description of some fossil remains

1360   brought by H.R.H. Prince Alfred from South Africa, November 1860. *Philosophical*

1361   *Transactions of the Royal Society of London B,* **152**, 455–467.

1362   **Owen, R. 1876.** Descriptive and Illustrated Catalogue of the Fossil Reptilia of South Africa in

1363   the Collection of the British Museum. London, British Museum (Natural History).

1364   **Rubidge, B. S.** (ed.), 1995. *Biostratigraphy of the Beaufort Group (Karoo Supergroup).*

1365   Pretoria, South African Committee for Stratigraphy, Biostratigraphic Series 1, 46p.

1366   **Seeley, H.G.** 1888. Researches on the structure, organisation, and classification of the fossil

1367   Reptilia. II. On *Pareiasaurus bombidens* (Owen), and the significance of its affinities to

1368   amphibians, reptiles and mammals*. Philosophical Transactions of the Royal Society of*

1369   *London B,* **179**, 59–109.

1370   **Seeley, H.G.** 1892. Researches on the structure, organisation, and classification of the fossil

1371   Reptilia. VII. Further observations on *Pareiasaurus. Philosophical Transactions of the Royal*

1372   *Society of London B,* **183**, 311–370.

1373   **Smith, R. M. H. & Botha-Brink, J.** 2014. Anatomy of a mass extinction: Sedimentological and

1374   taphonomic: evidence for drought-induced die-offs at the Permo-Triassic boundary in the

1375   main Karoo Basin, South Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **396**,

1376   99–118, doi.org/10.1016/j.palaeo.2014.01.002.

1377   **Smith, R. M. H. & Keyser, A. W.** 1995a. Biostratigraphy of the *Tapinocephalus* Assemblage

1378   Zone. In: Rubidge, B.S. (ed.). Biostratigraphy of the Beaufort Group (Karoo Supergroup),

1379   Biostratigraphic Series 1. *South African Committee for Stratigraphy*, Pretoria, 8–12.

1380   **Smith, R. M. H. & Keyser, A. W.** 1995b. Biostratigraphy of the *Pristerognathus* Assemblage

1381   Zone. In: Rubidge, B.S. (ed.). Biostratigraphy of the Beaufort Group (Karoo Supergroup),

1382   Biostratigraphic Series 1. *South African Committee for Stratigraphy*, Pretoria, 13–17.

1383   **Smith, R. M. H. & Keyser, A. W.** 1995c. Biostratigraphy of the *Tropidostoma* Assemblage

1384   Zone. In: Rubidge, B.S. (ed.). Biostratigraphy of the Beaufort Group (Karoo Supergroup),

1385   Biostratigraphic Series 1. *South African Committee for Stratigraphy*, Pretoria, 18–22.

1386   **Smith, R. M. H. & Keyser, A. W.** 1995d. Biostratigraphy of the *Cistecephalus* Assemblage

1387   Zone. In: Rubidge, B.S. (ed.). Biostratigraphy of the Beaufort Group (Karoo Supergroup),

1388   Biostratigraphic Series 1. *South African Committee for Stratigraphy*, Pretoria, 23–28.

1389   **Smith, R.M.H., Rubidge, B.S., Day, M.O. & Botha, J**. 2020. Introduction to the tetrapod

1390   biozonation of the Karoo Supergroup. *South African Journal of Geology,* **123**, 131–140.

1391   https://doi.org/10.25131/sajg.123.0009

1392   **Tsuji, L. A. & Muller, J.** 2008. A re-evaluation of *Parasaurus geinitzi*, the first named

1393   pareiasaur (Amniota, Parareptilia). *Canadian Journal of Earth Sciences.* **45(10)**, 1111–1121,

1394   doi.org/10.1139/E08-060.

1395   **Tsuji, L. A. 2010.** Evolution, Morphology and Paleobiology of the Pareiasauria and their

1396   Relatives (Amniota: Parareptilia). Unpublished Ph.D thesis, Humboldt-University of Berlin,

1397   Berlin, 1–188.

1398   **Tsuji, L. A**. 2013. Anatomy, cranial ontogeny and phylogenetic relationships of the

1399   pareiasaur *Deltavjatia rossicus* from the Late Permian of central Russia. *Earth and*

1400   *Environmental Science Transactions of the Royal Society of Edinburgh*, **104**, 1–42.

1401   **Tsuji, L. A., Sidor, C. A., Steyer, S. J., Smith, R. M. H., Tabor, N. J. & Ide. O.** 2013. The

1402   vertebrate fauna of the Upper Permian of Niger –VII. Cranial anatomy and relationships of

1403   *Bunostegos akokanenis* (Pareiasauria). *Journal of Vertebrate Palaeontology*, **33(4)**, 747–763,

1404   doi.org/10.1080/02724634.2013.739537.

1405   **Turner, M. L., Tsuji, L. A., Ide, O. & Sidor, C. A.** 2015. The vertebrate fauna of the Upper

1406   Permian of Niger –IX. The appendicular skeleton of *Bunostegos akokanenis* (Parareptilia:

1407   Pareiasauria). *Journal of Vertebrate Palaeontology*, **35(6)**,

1408   doi.org/10.1080/02724634.2014.994746.

1409   **Van den Brandt, M. J**. 2016. Cranial morphology of *Embrithosuarus schwarzi* (Parareptilia,

1410   Pareiasauria) and a taxonomic and stratigraphic reassessment of the South African middle

1411   Permian pareiasaurs. Unpublished MSc thesis, University of the Witwatersrand,

1412   Johannesburg, 1–214.

1413   **Van den Brandt, M. J.** 2020. Morphology, taxonomy, phylogeny and stratigraphic ranges of

1414   South African middle Permian pareiasaurs. Unpublished Ph.D thesis, University of the

1415   Witwatersrand, Johannesburg, 1–565.

1416   **Van den Brandt, M. J., Abdala, F. & Rubidge, B. S.** 2020. Cranial morphology and

1417   phylogenetic relationships of the Middle Permian pareiasaur *Embrithosaurus schwarzi* from

1418   the Karoo Basin of South Africa. *Zoological Journal of the Linnean society*. **188**, 202–241,

1419   doi.org/10.1093/zoolinnean/zlz064.

1420   **Van den Brandt, M. J., Rubidge, B. S., Benoit, J. & Abdala, F.** 2021a. Cranial morphology of

1421   the middle Permian pareiasaur *Nochelesaurus alexanderi* from the Karoo Basin of South

1422   Africa. *Earth and Environmental Science Transactions of the Royal Society of Edinburg,* **112**,

1423   29-49, doi:10.1017/S1755691021000049.

1424   **Van den Brandt, M. J., Benoit, J., Abdala, F. & Rubidge, B. S.** 2021b. Postcranial morphology

1425   of the South African middle Permian pareiasaurs from the Karoo Basin of South Africa.

1426   *Palaeontologia africana*, **55**, 1–91, https://hdl.handle.net/10539/31290.

1427   **Watson, D. M. S.** 1914. On the nomenclature of pareiasaurs. *Annals of the Magazine of*

1428   *Natural History,* **14**, 98–102.

1429 **Xu, L., Li, X. W., Jia, S. H. & Liu, J.** 2015. The Jiyuan Tetrapod Fauna of the Upper Permian of

1430 China: New Pareiasaur Material and the Reestablishment of *Honania complicidentata. Acta*

1431 *Palaeontologica Polonica*, **60(3),** 689–700, https://doi.org/10.4202/app.00035.2013.

1432 **Figure Captions**

1433 **Figure 1:** Species flow chart, showing a summary of previous taxonomic revisions of

1434 Guadalupian South African pareiasaurs and the changes proposed in this study. Rows

1435 represent species. Columns indicate author recognition of species: dotted lines indicate

1436 where a species was not recognized by an author, solid lines indicate the species assigned,

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1438 (1929) and Kuhn (1969) consider *Platyoropha broomi* (SAM-PK-5002) a synonym of

1439 *Bradysaurus baini*. Lee (1997a) lumped several taxa into only four species, which were

1440 retained by Van den Brandt (2016, *et al.* 2020). This study proposes synonymising

1441 *Bradysaurus seeleyi*, *Bradysaurus vanderbyli* and *Bradysaurus acutirostris* with *Bradysaurus*

1442 *baini*, *Bradysaurus whaitsi* with *Embrithosaurus schwarzi,* and *Dolichopareia angusta*,

1443 *Brachypareia rogersi* and *Brachypareia watsoni* with *Nochelesaurus alexanderi.*

1444 **Figure 2:** Interpretive drawings of the skull of the holotype of *Bradysaurus baini* (NHMUK PV

1445 R 1971), in A, dorsal, and B, left lateral views; the skull of the holotype of *Embrithosaurus*

1446 *schwarzi* (SAM-PK-8034) in C, dorsal, and D, left lateral views; the skull of the holotype of

1447 *Nochelesaurus alexanderi* (SAM-PK-6239), in E, dorsal, and F, left lateral views. A, B from Lee

1448 (1994, 1997a) reproduced with permission. Abbreviations: **ang**, angular; **den**, dentary; **fr**,

1449 frontal; **ju**, jugal; **la**, lacrimal; **mf**, maxillary foramen**; max**, maxilla; **na**, nasal; **par**, parietal;

1450 **pob**, postorbital; **pm**, premaxilla; **po**, postorbital; **pof**, postfrontal; **pp**, postparietal; **prf**,

1451 prefrontal; **qj**, quadratojugal; **spl**, splenial; **sq**, squamosal; **st**, supratemporal; **sur**,

1452 surangular. Numbers indicate marginal cheek bosses. Cranial bosses are in bold, rugose

1453 ridges are in regular line thickness. Sutures drawn in solid lines have been positively

1454 identified; those in dotted lines are perpendicular extrapolations from internal surface

1455 sutures; light grey indicates sides of bones or bone breaks, dark grey indicates foramen or

1456 fenestra, black indicates deep cavities such as orbits.

1457 **Figure 3:** Interpretive drawings of the pelvis of the holotype of *Embrithosaurus schwarzi*

1458 (SAM-PK-8034) in A, anterior, B, dorsal, and C, right lateral views; the pelvis of the holotype

1459 of *Bradysaurus baini* (NHMUK PV R 1971), in D, anterior, E, dorsal, and F, right lateral views.

1460 Dorsal to the top of the page in A, D, C and F. Anterior to the top of the page in B, E.

1461 Abbreviations: **ace,** acetabulum**; ib**, ischial buttress; **lpp**, lateral pubic process; **mpp,** median

1462 pubic process; **pb**, pubic buttress**; pf**, pubic/obturator foramen; **sb**, supra-acetabular

1463 buttress.

1464 **Figure 4:** Cladistic relationships of the Bradysauria within Pareiasauria, A, strict consensus

1465 tree, B, 50% majority-rule consensus tree of 1065 most parsimonious trees. Numbers at

1466 each node indicate the frequency of clades in the fundamental trees.

1467 **Figure 5:** Composite minimum stratigraphic ranges of pareiasaur genera in the Guadalupian

1468 Beaufort Group based on positively identified specimens of each species, Day (2013), Van

1469 den Brandt (2016) and this study. Biostratigraphy after Day & Rubidge (2020). WUC =

1470 Wuchiapingian.

1471 **Figure 6:** Geographic distribution of localities for 142 identified pareiasaur specimens in the

1472 middle Permian Beaufort Group, superimposed on geological data. Almost all specimens

1473 occur between 33° and 32° South latitude. Figure created using the software Global Mapper

1474   version 15. Geology is based on the 1:250 000 Geological map sheets 3122 Victoria West

1475   (Geological Survey 1989a); 3120 Williston (Geological Survey 1989b); 3220 Sutherland

1476   (Geological Survey 1983); 3222 Beaufort West (Geological Survey 1979). M = Member, Fm =
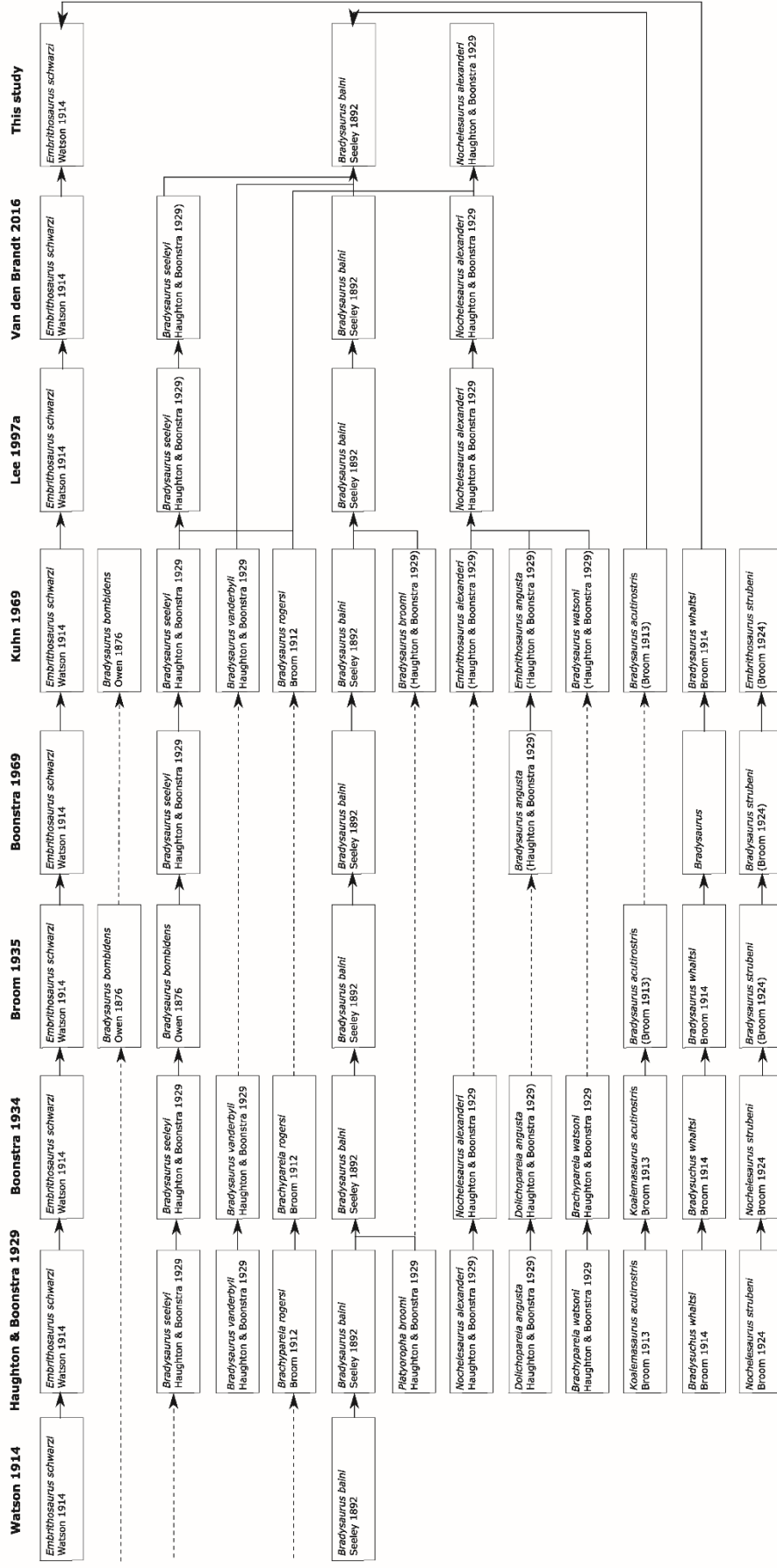
1477   Formation.

1478

Figure 1 Species flow chart, showing a summary of previous taxonomic revisions of Guadalupian South African pareiasaurs and the changes proposed in this study. Rows represent species. Columns indicate author recognition of species: dotted lines indicate author recognition of species; dotted lines indicate where a species was not recognized by an author, solid lines indicate the species assigned, including synonymising with other species. All authors apart from Haughton and Boonstra (1929) and Kuhn (1969) consider *Platyoropha broomi* (SAM-PK-5002) a synonym of *Bradysaurus baini*. Lee (1997a) lumped several taxa into only four species, which were retained by Van den Brandt (2016, *et al.* 2020). This study proposes synonymising *Bradysaurus seeleyi*, *Bradysaurus vanderbyli* and *Bradysaurus acutirostris* with *Bradysaurus baini*, *Bradysaurus vanderbyli* and *Bradysaurus acutirostris* with *Bradysaurus baini*, *Bradysaurus whaitsi* with *Embrithosaurus schwarzi*, and *Dolichopareia angusta*, *Brachypareia rogersi* and *Brachypareia watsoni* with *Nochelesaurus alexanderi*.
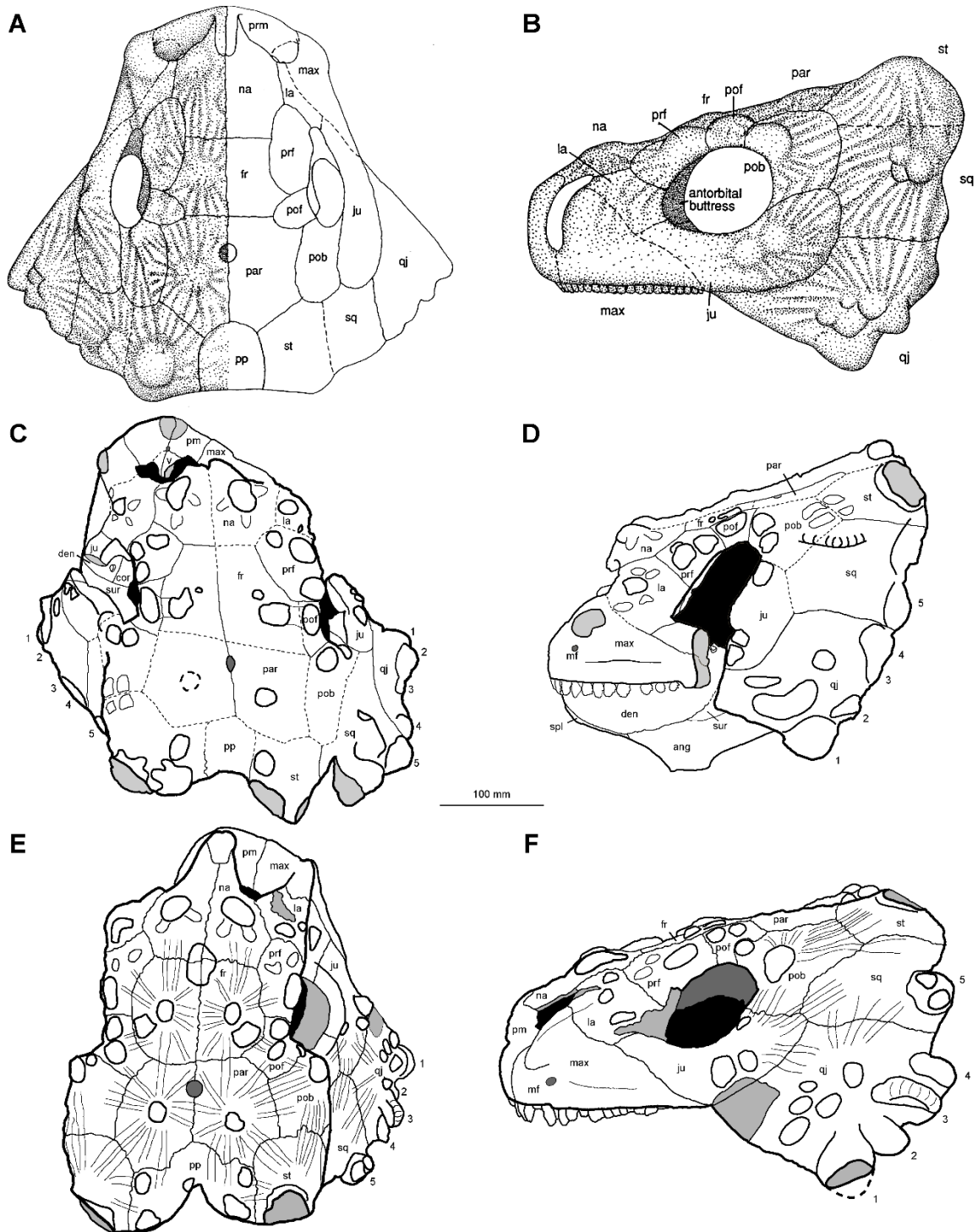
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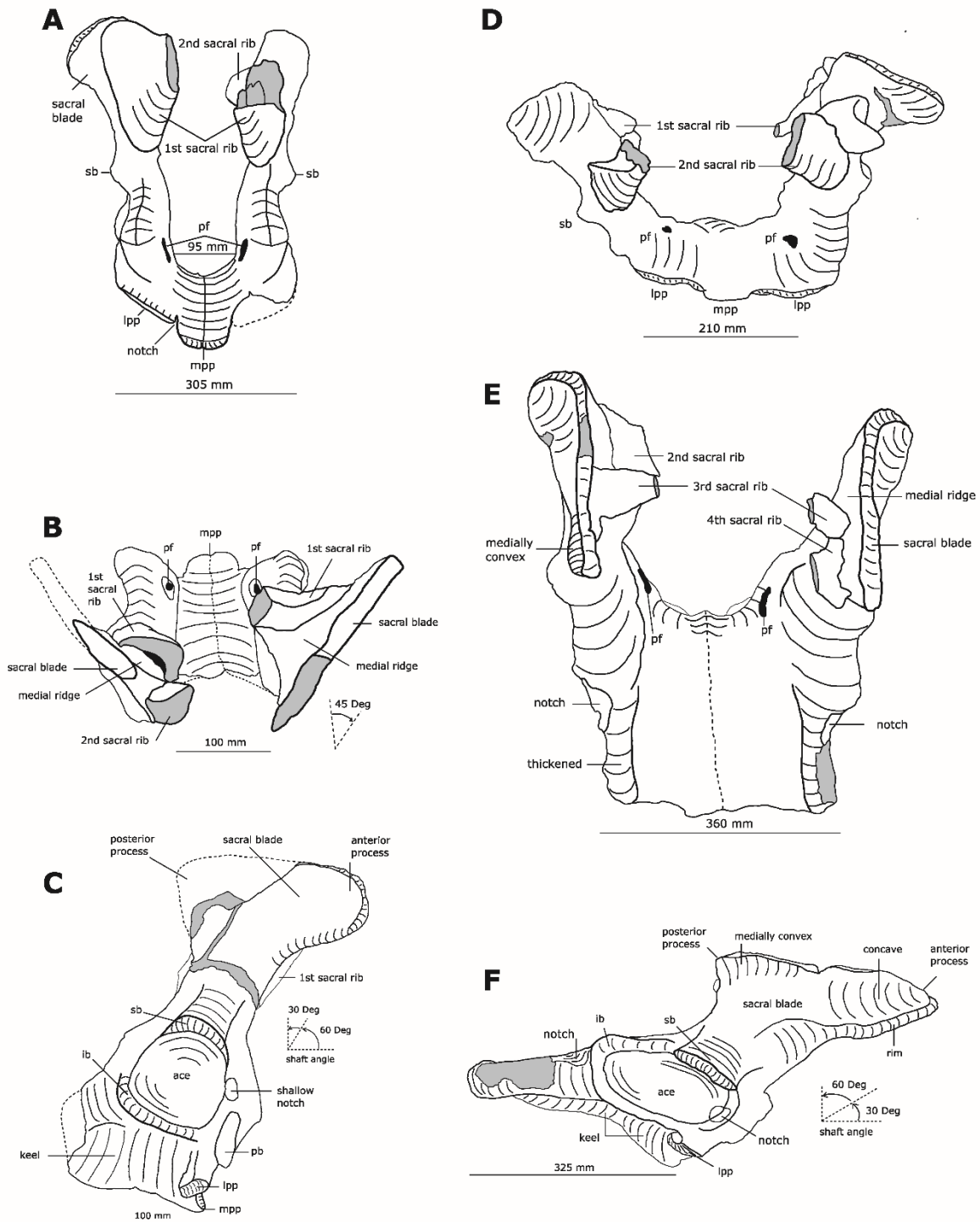
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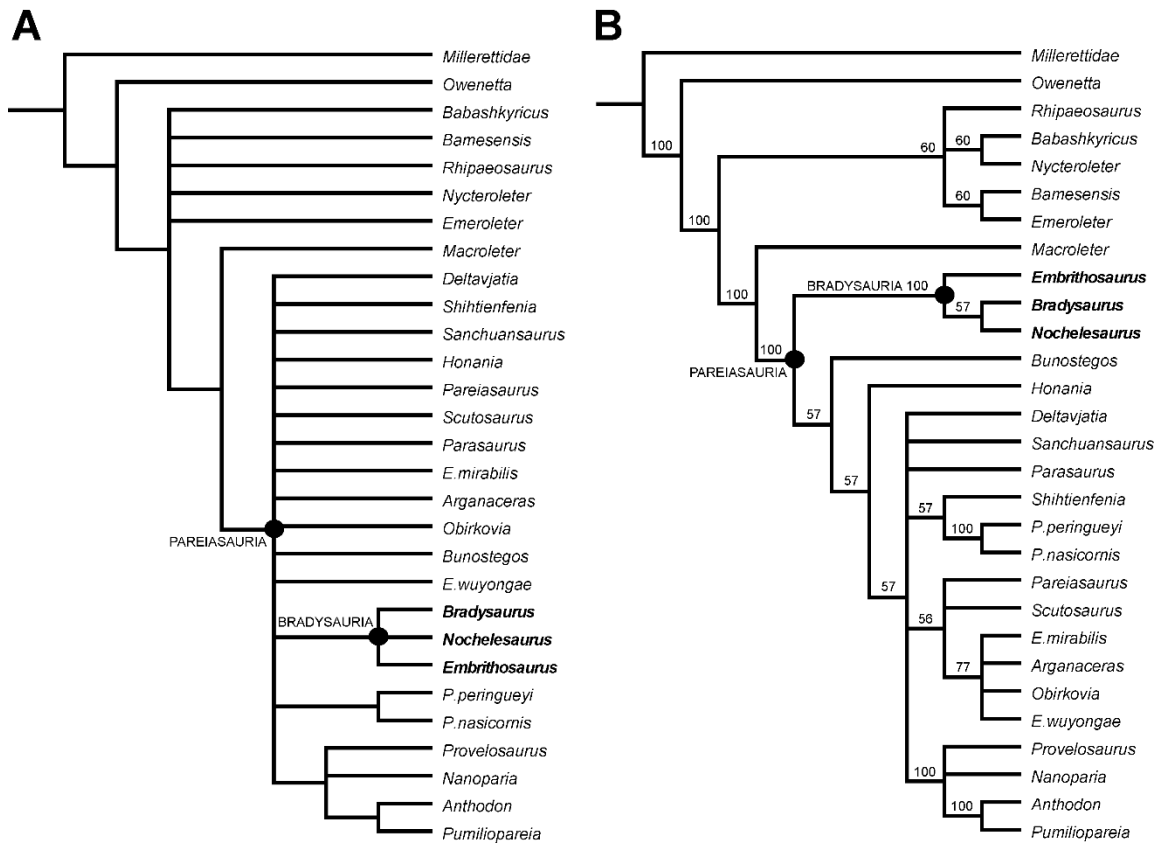
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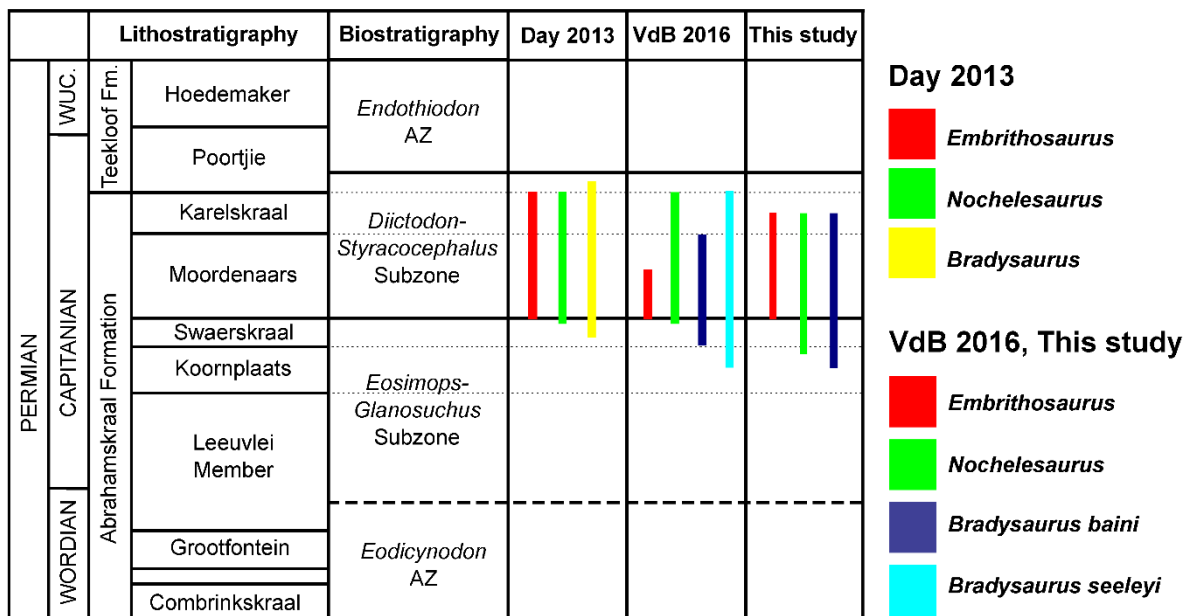

Figure 4 Composite minimum stratigraphic ranges of pareiasaur genera in the Guadalupian Beaufort Group based on positively identified specimens of each species, Day (2013), Van den Brandt (2016) and this study. Biostratigraphy after Day & Rubidge (2020). WUC = Wuchiapingian.
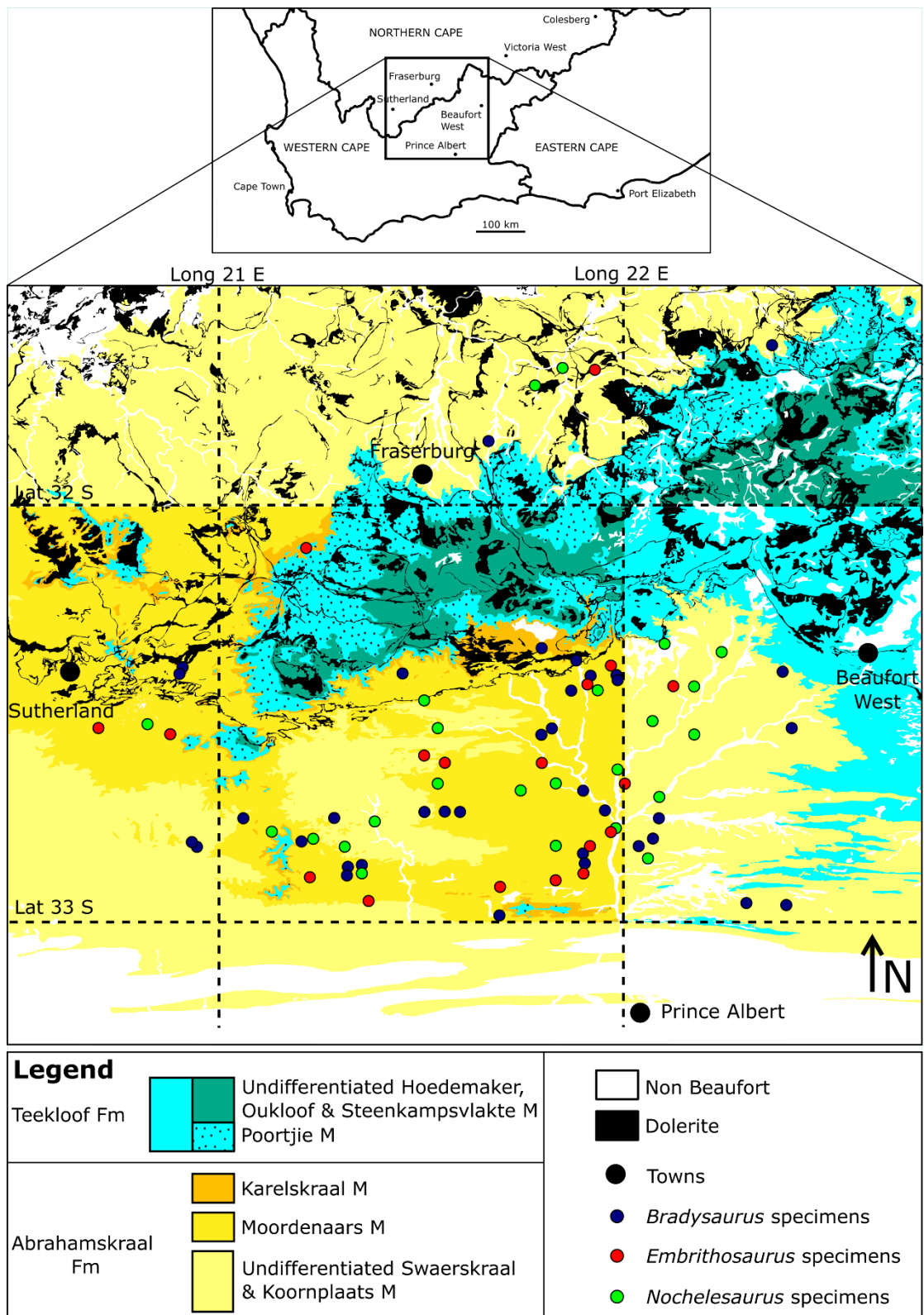
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Resampling	Van den Brandt et al. (2020)		This study	
Standard Bootstrapping	Par 69	Bra 58	Par 85	Bra 62
Poisson Bootstrapping	Par 68	Bra 56	Par 84	Bra 54
Jackknife	Par 62	Bra 60	Par 74	Bra 76
Symmetric Resampling	Par 76	Bra 69	Par 91	Bra 77

Table 1: Values of resampling obtained using different methods, after data of Van den Brandt *et al.* (2020) and this study. Jackknife and symmetric resampling used default values in TNT. Par, Pareiasauria; Bra, Bradysauria.

Institution	Identified	Unidentified/ Identifications to one of two species	Total
GPIT	1	0	1
CGP	16	10	26
SAM	84	25	109
BPI/ESI	24	27	51
NHMUK	5	1	6
AM	1	2	3
AMNH	7	13	20
FMNH	19	5	24
Total	**157**	**83**	**240**

Table 2: Numbers and identification of pareiasaur specimens from the *Tapinocephalus* Assemblage Zone considered in this study.

Taxa	Specimens
Bradysaurus baini	74
Embrithosaurus schwarzi	40
Nochelesaurus alexanderi	43
Bradysaurus or *Embrithosaurus*	6
Bradysaurus or *Nochelesaurus*	7
Embrithosaurus or *Nochelesaurus*	10
Unidentified	60
TOTAL	**240**

Table 3: Numbers of pareiasaur specimens from the *Tapinocephalus* Assemblage Zone identified by taxa.

Genus	Species	Lowest specimen	Level	Lowest biostrat
Bradysaurus	*baini*	BP/1/7886	Koornplaats Member	*Eosimops-Glanosuchus* subzone
Nochelesaurus	*alexanderi*	BP/1/8011	upper Koornplaats Member	*Eosimops-Glanosuchus* subzone
Embrithosaurus	*schwarzi*	SAM-PK-9165	Swaerskraal/ Moordenaars Member boundary	Boundary of *Eosimops-Glanosuchus* & *Diictodon-Styracocephalus* subzones
Genus	**Species**	**Highest specimen**	**Level**	**Lowest biostrat**
Bradysaurus	*baini*	NHMUK PV OR 49426 or BP/1/7213 or several from north of the Nuweveldberge.	Karelskraal Member	*Diictodon-Styracocephalus* subzone
Nochelesaurus	*alexanderi*	BP/1/7252	Karelskraal Member	*Diictodon-Styracocephalus* subzone
Embrithosaurus	*schwarzi*	BP/1/7241 or SAM-PK-12252	Karelskraal Member	*Diictodon-Styracocephalus* subzone

Table 4: Stratigraphically lowermost and uppermost occurring specimens of each valid genus *Bradysaurus*, *Embrithosaurus* and *Nochelesaurus*, from which their stratigraphic range is determined.

Bradysauria: 'leaf-shaped' tooth morphology	Lopingian pareiasaurs: 'fan-shaped' tooth morphology
Presence of elongated, central, three-cusped tridents on upper and/or lower teeth	Absence of central, three-cusped tridents
Tooth crowns elongated	Tooth crowns shorter
Teeth narrower, less mesio-distally expanded	Teeth wider, more mesio-distally expanded
Fewer marginal cusps per tooth (7-9)	More marginal cusps per tooth (9+)
Cusps irregularly arranged around the crown (spaces between cusps variable)	Cusps regularly arranged around the crown (consistent spaces between cusps)
Larger spaces between the cusps	Smaller spaces between cusps
Symmetrical or non-symmetrical mesial and distal cusp arrangements	Symmetrical mesial and distally cusp arrangements
Longer individual marginal cusps that project far out from the crown	Shorter individual marginal cusps that do not project far out from the crown

Table 5: Difference in tooth morphology between South African Guadalupian pareiasaurs (Bradysauria) and Lopingian pareiasaurs.