Cranial morphology and phylogenetic analysis of Cynosaurus suppostus (Therapsida, Cynodontia) from the upper Permian of the Karoo Basin, South Africa

Marc J. Van den Brandt* & Fernando Abdala1,2
1Evolutionary Studies Institute and School of Geosciences, University of the Witwatersrand, Johannesburg, WITS 2050, South Africa
2Unidad Ejecutora Lillo, CONICET-Fundación Miguel Lillo, Miguel Lillo 251, Tucumán, Argentina

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INTRODUCTION

Non-mammaliaform cynodonts are an important fossil lineage which include the ancestors of mammals and which illustrate the gradual evolution of mammalian characteristics. The earliest cynodonts (‘basal cynodonts’) are known from the late Permian. Cynosaurus is the second most abundant basal cynodont from the late Permian of the Karoo Basin of South Africa, but is poorly studied, with the most recent description of this taxon being 50 years old. Since then, several important new specimens of this species have been collected, meriting a thorough description of its cranial anatomy and exploration of its interspecific variation. Here we present a comprehensive description of the cranial morphology of Cynosaurus suppostus, producing an updated diagnosis for the species and comparisons amongst basal cynodonts. Cynosaurus is identified by three autapomorphies amongst basal cynodonts: a subvertical mentum on the anterior lower jaw; a robust mandible with a relatively high horizontal ramus; and the broadest snout across the canine region, representing up to 31.74% of basal skull length. One of the new specimens described here preserves orbital scleral ossicles, structures rarely preserved in non-mammaliaform cynodonts. Cynosaurus is now only the third cynodont in which scleral ossicles have been reported. An updated phylogenetic analysis of basal cynodont interrelationships recovered Cynosaurus suppostus as a member of the Galesauridae in only two of 16 most parsimonious trees, providing poor support for its inclusion in that family. The majority of known Cynosaurus specimens were collected in a geographically restricted area approximately 150 kilometres in diameter. Most specimens have been recovered from the latest Permian Daptocephalus Assemblage Zone, with only two specimens known from the older Cistecephalus Assemblage Zone.

Keywords: Cynodontia, late Permian, Karoo Basin, South Africa.

Non-mammaliaform cynodonts are an important fossil lineage which include the ancestors of mammals and which illustrate the gradual evolution of mammalian characteristics. Thus, they are essential for understanding the origins and evolution of typical mammalian morphology (Kemp 2005; Liu & Olsen 2010). The earliest or most basal cynodonts (non-eucynodonts) are known from the late Permian and Early Triassic, and consist mostly of small- to medium-sized carnivores and insectivores (Brink 1965; Kemp 1979, 2005, 2012; Botha et al. 2007; Botha-Brink & Abdala 2008; Kammerer 2016). They demonstrate early phases in the attainment of typical mammalian characteristics, such as complex multi-cusped postcanine teeth, double occipital condyles, and the initial development of a bony secondary palate (Sidor & Smith 2004).

Historically species-poor, the number of basal cynodonts known from the late Permian of South Africa has recently expanded, with the discovery of the oldest known cynodonts Charassognathus and Abdalodon from the Tropidostoma Assemblage Zone (AZ) (Botha et al. 2007; Kammerer 2016). In addition to these earliest forms, Permian cynodonts in the Karoo are represented by the abundant taxa Procynosuchus and Cynosaurus (Abdala & Ribeiro 2010, Viglietti et al. 2015: supplementary file) and the rare, derived taxon Nanictosaurus (Van Heerden 1976, Van Heerden & Rubidge 1990). Finally, a new, currently unnamed taxon was recently recovered from levels close to the Permo-Triassic boundary (Abdala & Smith 2011).

None of the late Permian species of cynodonts are known to have crossed the Permo-Triassic boundary (Botha-Brink & Abdala 2008), but the clade as a whole survived the extinction and radiated extensively in the Triassic. Early Triassic cynodonts from South Africa are represented by four basal taxa, Progalesaurus, Galesaurus, Thrinaxodon and Platycraniellus (Abdala 2007; Jasinoski et al. 2015; Jasinoski & Abdala 2017; Sidor & Smith 2004). Later Triassic cynodonts consist almost exclusively of the major clade Euycodontia, with the exception of the relictual Middle Triassic basal cynodont Bolotridon (Abdala et al. 2005).
Cynosaurus suppostus was initially described by Owen (1876; Fig.1A–B) as Cynosuchus suppostus, and a second species, Cynosuchus whaitsi, was established by Haughton (1918; Fig. 1C–D). Schmidt (1927) proposed the replacement name Cynosaurus for this genus, because the name Cynosuchus was preoccupied by a crocodilian (Cynosuchus Gray 1862). Broom (1931) reassigned C. whaitsi to a new genus (Cynosuchoides) and Brink (1965) described a second specimen (BP/1/3926) referred to Cynosuchoides whaitsi.

In their revised classification of cynodonts, Hopson & Kitching (1972) considered Cynosuchoides whaitsi to be synonymous with Cynosuchus suppostus. They also considered the type specimens of the nominal Permian cynodont taxa Nanictosaurus kitchingi, Mygalesuchus peggyae and Baurocynodon gracilis to be juvenile specimens of Cynosaurus suppostus, leaving it as the only valid species of Cynosaurus. However, Van Heerden (1976) and Van Heerden & Rubidge (1990) later argued against synonymization of Nanictosaurus with Cynosaurus, upholding Nanictosaurus as a valid, more derived taxon.

With the most recent anatomical description of Cynosaurus being over 50 years old (Brink 1965), this taxon is due for reevaluation. Even though Cynosaurus is the second most abundant late Permian cynodont, the cranial morphology of the species is still inadequately known, as recognized by Van Heerden (1976) and Van Heerden & Rubidge (1990). Furthermore, several informative, undescribed specimens of Cynosaurus are present in South African collections (AM4947, BP/1/1563, BP/1/4469, SAM-PK-K5211 and SAM-PK-K10694) (Fig. 2). Although too fragmentary to assign to Cynosaurus with certainty, additional potential specimens are also known which may bear on the distribution of this taxon (see Geographic and geological provenance and stratigraphic range).

The aim of this paper is to address the current lack of knowledge of Cynosaurus suppostus with a comprehensive description of its cranial morphology, incorporating all available specimens of the taxon. This new information is used to rescore character data for Cynosaurus in a recently published data matrix of basal cynodonts (Kammerer 2016) and to test the phylogenetic placement of this taxon in light of different proposals that include it inside (Sidor & Smith 2004) or outside (Abdala 2007; Kammerer 2016) of the otherwise-Triassic family Galesauridae.

Figure 1. Holotypes of Cynosaurus. A–B, NHMUK PV R1718 Cynosuchus suppostus (Owen 1876) in (A) right lateral and (B) dorsal view; C–D, SAM-PK-4333 Cynosaurus whaitsi, (Haughton 1918) in (C) dorsal and (D) ventral view. Scale bar equals 20 mm.
MATERIAL AND METHODS

The following nine specimens of Cynosaurus and comparative specimens of other basal cynodonts were examined for this study:

Holotypes

NHMUK PV R1718, the holotype of Cynosuchus suppostus Owen (1876), poorly-preserved snout up to the orbits and partial mandible in occlusion (Fig. 1A–B).

SAM-PK-4333, the holotype of Cynosuchus whaitsi Haughton (1918), well-preserved cranium lacking lower jaw (Fig. 1C–D).

Referred material

AM4947, damaged partial cranium and mandible (Fig. 2D).

BP/1/1563, partial well-preserved small cranium, lacking lower jaw (Fig. 2A).

BP/1/3926, the second specimen of C. whaitsi described by Brink (1965), well-preserved cranium lacking lower jaw (Fig. 2E).

BP/1/4469, virtually complete and well-preserved small cranium including lower jaw (Fig. 2B).

Comparative material

Procynosuchus delaharpeae (BP/1/226, BP/1/591, BP/1/2600, BP/1/3748, NHMUK PV R 37054, RC 5, RC 12, RC 72, RC 87, RC 92, RC 130), Galesaurus planiceps (AMNH FAR 2223, AMNH FARB 2227, BP/1/5064, NMQR 860, NMQR 1451, NMQR 3340, NMQR 3542, SAM-PK-K9956), Thrinaxodon liorhinus (BP/1/1375, BPI/1/2513a, BP/1/4263, BP/1/4280, BP/1/4714, BP/1/5208, BP/1/5372, BSPG 1934 VIII 506, MMK 4283, NHMUK R511, NHMUK R3731, NHMUK R5480, NMQR 24, NMQR 812, NMQR 810, SAM-PK-K379, SAM-PK-K1467, SAM-PK-K1498, SAM-PK-K1499, TM 81, TM 180, UCMP 42865, UCMP 42866, UCMP 42877, UCMP 42878), Progalesaurus lootsbergenisi (SAM-PK-K9954) and Platycraniellus elegans (TM 25) were consulted.

Specimens of Cynosaurus were CT-scanned at the Evolutionary Studies Institute (University of the Witwatersrand, Johannesburg, South Africa) using a Nikon Metrology XTH 225/320 LC dual source CT system. We
used these data to present a virtual reconstruction of the specimen BP/1/1563 (Fig. 9A–D). As this contribution is centred on the anatomical description of gross external morphology in *Cynosaurus*, we have not used the CT data to reconstruct endocranial morphology. Studies of internal cranial structure as well as of morphological changes in the snout of *Cynosaurus* over ontogeny will be addressed in future studies. However, CT data were used to reveal features hidden under matrix or occluded by bone (e.g. incisor number in the occluded lower jaw of BP/1/4469).

**Key to interpretative drawings**

Sutures in solid lines have been positively identified; those in dotted lines are extrapolated. Light grey indicates matrix, dark grey indicates plaster, sides of bones or bone breaks, black indicates foramen or fenestra.

**SYSTEMATIC PALAEONTOLOGY**

THERAPSIDA Broom, 1905

CYNODONTIA Owen, 1861

EPICYNODONTIA Hopson and Kitching, 2001

CYNOSAURUS Schmidt, 1927

*Cynosaurus suppostus* (Owen, 1876)

**Synonyms**

*Cynosuchus suppostus* Owen 1876; *Cynosuchus whaitsi* Haughton 1918 (= *Cynosuchoides whaitsi* Broom 1931).

**Emended diagnosis**

Medium-sized basal cynodont with three autapomorphies: subvertical mentum on the anterior lower jaw; a robust mandible with a relatively high horizontal ramus; broad snout (measured across the upper canines) representing up to 31.74% of basal skull length; adult lacking pineal foramen. Adult dental formula of I_4/i_3, C_1/c_1, P_2/p_2, M_5/m_5.

**Geographic and geological provenance and stratigraphic range**

Most *Cynosaurus* specimens were found within an area approximately 150 kilometres in diameter. Seven of the nine specimens were found within a restricted region between the towns of Graaff-Reinet, Murraysburg and Nieu Bethesda in the Eastern Cape and Western Cape provinces of South Africa (Table 1, Fig. 3). A similarly-restricted geographic distribution has also been reported in some other *Cistecephalus-Daptocephalus AZ* therapsids, such as the dicynodont *Pelanomodon* and the gorgonopsian *Clelandina* (Kammerer et al. 2015, Kammerer 2017). This region also includes areas known for producing Lower Triassic specimens of *Galesaurus*, *Progalesaurus* and *Thrinaxodon*, namely Loostenberg (Tweefontein, Loostenberg Pass and Old Wapadsberg Pass) and Nieu Bethesda (Ripplemead) (Sidor & Smith 2004; Jasinoski & Abdala 2017). The Permo-Triassic boundary is also exposed in this region (Smith & Botha-Brink 2014).

All known *Cynosaurus* specimens have been found in sedimentary beds corresponding to the *Cistecephalus* and *Daptocephalus AZs*, Balfour Formation, Beaumont Group, Karoo Supergroup, South Africa (upper Permian) (Table 1, Fig. 3). Vignetti et al. (2015: supplementary file) reported 11 specimens of *Cynosaurus*, three from the *Cistecephalus AZ*, five from the Lower *Daptocephalus AZ* and three from the Upper *Daptocephalus AZ*. Five of these 11 specimens cannot be confirmed as members of *Cynosaurus*. BP/1/47 (holotype of *Baurocynodon gracilis*, synonymized with *C. suppostus* by Hopson & Kitching 1972), BP/1/863 and BP/1/5741 are too fragmentary for confident identification as *Cynosaurus*. BP/1/4259 repre-

**Table 1. *Cynosaurus suppostus* specimen location table showing the geographic distribution of the specimens. ECP = Eastern Cape Province, WCP = Western Cape Province.**

<table>
<thead>
<tr>
<th>Specimen</th>
<th>Specimen no.</th>
<th>District</th>
<th>Farm</th>
<th>Assemblage Zone</th>
</tr>
</thead>
<tbody>
<tr>
<td>a</td>
<td>BP/1/1563</td>
<td>Murraysburg (WCP)</td>
<td>Ringsfontein</td>
<td>Daptocephalus</td>
</tr>
<tr>
<td>b</td>
<td>BP/1/4469</td>
<td>Graaff-Reinet (ECP)</td>
<td>Zwagershoek</td>
<td>Daptocephalus</td>
</tr>
<tr>
<td>c</td>
<td>SAM-PK-4333</td>
<td>Graaff-Reinet (ECP)</td>
<td>Weltevrede</td>
<td>Daptocephalus</td>
</tr>
<tr>
<td>d</td>
<td>BP/1/3926</td>
<td>New Bethesda (ECP)</td>
<td>Tweefontein</td>
<td>Daptocephalus</td>
</tr>
<tr>
<td>e</td>
<td>SAM-PK-10694</td>
<td>Graaff-Reinet (ECP)</td>
<td>Krugerskraal</td>
<td>Daptocephalus</td>
</tr>
<tr>
<td>f</td>
<td>SAM-PK-5211</td>
<td>Graaff-Reinet (ECP)</td>
<td>Graaff-Reinet Allotment Area</td>
<td>Cistecephalus</td>
</tr>
<tr>
<td>g</td>
<td>SAM-PK-5819</td>
<td>Graaff-Reinet (ECP)</td>
<td>Doornplaats (Rust 126)</td>
<td>Cistecephalus</td>
</tr>
<tr>
<td>AM4947</td>
<td></td>
<td>Unknown</td>
<td>Unknown</td>
<td>Daptocephalus*</td>
</tr>
</tbody>
</table>

*Sneeuwberg mountain range, Graaff-Reinet, Eastern Cape. Original locality unreliable. Suggested by Kitching (1977) as probably coming from levels corresponding to the Daptocephalus Assemblage Zone, as in most other known skulls of the genus *Cynosaurus.*
sents a forelimb of the similarly-named gorgonopsian *Cyonosaurus*, not *Cynosaurus*. BPI/1/4281 exhibits morphology of the intertemporal region, internal choana and basicranium that does not match that of *Cynosaurus*, and appears to represent a different cynodont taxon. Three specimens included in the current description (AM4947, NHMUK PV R1718 and SAM-PK-K10694) were not considered in the study of Viglietti et al. (2015). This leaves a total of nine confidently-identified specimens of *Cynosaurus* (Table 1, Fig. 3), five of which were previously unpublished (AM4947, BP/1/1563, BP/1/4469, SAM-PK-K5211 and SAM-PK-K10694). The geologically oldest specimen is represented by the fragmentary specimen SAM-PK-K5211 from the *Cistecephalus* AZ (Viglietti et al. 2015). Most representatives of *Cynosaurus* are known from the geologically younger *Daptocephalus* AZ. BP/1/5741, identified as the last appearance datum for *Cynosaurus* in the upper *Daptocepalus* AZ (Viglietti et al. 2015), is poorly preserved and its lower jaw does not appear to show the typical high chin of *Cynosaurus*, so we cannot endorse its identity as *Cynosaurus*. The species appears to be better represented in the Lower *Daptocepalus* Zone (where it makes up 1% of 477 tetrapod specimens), than in the Upper *Daptocepalus* Zone (2% of 151 tetrapod specimens) (Viglietti et al., 2015: figure 4).

**DESCRIPTION**

**Preservation**

NHMUK PV R1718 comprises a snout with lower jaw, broken just anterior to the orbits. The postcanine crowns are broken off on both right and left sides (Fig. 1A–B).

SAM-PK-4333 comprises a dorso-ventrally and diagonally crushed skull lacking the lower jaw and with incomplete zygomas (Fig. 1C–D). The majority of the postcanines are broken off approximately halfway down the crown.

BP/1/1563 is a very small skull (basal skull length of 50.29 mm, Table 2) lacking the lower jaw (Fig. 2A). The majority of both zygomatic arches are not preserved, including the ventral and posterior margins of both orbits. The anteroventral portion of the premaxilla is damaged, lacking the incisors. The upper canines are not preserved, having only the upper canine alveoli. Postcanine tooth crowns are not preserved – the majority of the teeth are broken off at or shortly above the alveolar margin (Fig. 2A).

BP/1/4469 comprises a well-preserved skull with lower jaw, but has some damage to the left jugal, at the ventral orbital margin (Fig. 2B). Although the skull is covered by cracks, sutures are identifiable. The dentition is well preserved. Additional preparation of the palate and the temporal region was performed for this study.

SAM-PK-K10694 comprises a snout with lower jaw and has the upper and lower postcanines very well preserved (Fig. 2C). The lower incisors are not preserved, but their alveoli are. A vertebra is visible below the jaw. Additional preparation of the orbits was performed for this study.

AM4947 comprises a poorly-preserved and damaged cranial specimen, but with well-preserved upper postcanines (Fig. 2D). There is some damage to the left postcanine series. Additional preparation of the left suborbital region was performed for this study.

BP/1/3926 is damaged, with parts of the cranium having been infilled with plaster, notably the right anterior portion of the nasal and the orbital edge of the left jugal (Fig. 2E). The anterior sides of the right premaxilla below the naris and the left premaxilla above the naris are damaged, with the right incisors partially exposed and the left incisors broken off at their emergence. A large portion of the left posterior squamosal is missing. The right zygoma is not preserved. Tooth crowns are not preserved, with the majority of the teeth broken off at or shortly above the alveolar margin. Additional preparation of the basicranial
region of this specimen was performed for this study.
SAM-PK-K5211 comprises a fragmentary skull lacking the anterior portion of the snout and lower jaw.
SAM-PK-K5819 comprises a partial snout exposing broken upper postcanines.

Cranial measurements and proportions
Basal skull length (BSL) varies between 50.29 mm to 121.69 mm (Table 2). The snout length (SL) is comparatively longer than the temporal length (TL) in both small and large specimens.

The snout length (SL) varies between 32.25% to 38.80% of the BSL (Table 2: row 25) with most of the large specimens close to the higher value.

The cranial width (W) is 76.31% to 78.80% of the BSL (Table 2: row 26) indicating a relatively wide skull for a basal cynodont, second only to *Platycraniellus* at 88% (Abdala 2007).

The snout width (SW) (measured above the upper canines) is very broad, at up to 31.74% of basal skull length (BSL) for the large and undistorted specimen BP/1/3926. All large *Cynosaurus* specimens are over 30% for this measure (Table 2: row 26).

The orbital length (OL) varies between 17% to 19% of the BSL (Table 2: row 27) whereas the temporal length (TL) varies between 32% (for the large specimen BP/1/3926) to 23% of the BSL (Table 2: row 29).

Table 2. Cranial measurements of *Cynosaurus suppostus* specimens, in mm.

<table>
<thead>
<tr>
<th>No.</th>
<th>Measurement</th>
<th>SAM-PK-4333</th>
<th>SAM-PK-K10694</th>
<th>BP/1/3926</th>
<th>AM4947</th>
<th>BP/1/4469</th>
<th>BP/1/1563</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Basal skull length (BSL)</td>
<td>121.69</td>
<td>115.26</td>
<td>56.31</td>
<td>50.29</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>Middle dorsal length</td>
<td>99.03</td>
<td>102.31</td>
<td>45.46</td>
<td>41.65</td>
<td></td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>Snout length (SL)</td>
<td>45.93</td>
<td>33.56</td>
<td>44.42</td>
<td>35.13</td>
<td>21.85</td>
<td>16.22</td>
</tr>
<tr>
<td>4</td>
<td>Orbital length (OL)</td>
<td>22.88 (b)</td>
<td>16.45 (b)</td>
<td>20.51</td>
<td>21.05</td>
<td>10.15</td>
<td>9.68 (b)</td>
</tr>
<tr>
<td>5</td>
<td>Temporal length (TL)</td>
<td>27.77</td>
<td>28.33</td>
<td>31.21</td>
<td>26.42</td>
<td>14.19</td>
<td>10.79</td>
</tr>
<tr>
<td>6</td>
<td>Minimum interorbital width/distance</td>
<td>17.88 (b)</td>
<td>14.84 (b)</td>
<td>21.44</td>
<td>18.90</td>
<td>8.44</td>
<td>9.40 (b)</td>
</tr>
<tr>
<td>7</td>
<td>Orbital diameter</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>8</td>
<td>Secondary palate length</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>9</td>
<td>Width of snout at anterior margin of orbits</td>
<td>49.89</td>
<td>41.9</td>
<td>51.28</td>
<td>44.69</td>
<td>27.38</td>
<td>22.24</td>
</tr>
<tr>
<td>10</td>
<td>Upper canine width</td>
<td>28.06</td>
<td>28.74</td>
<td>35.08</td>
<td>27.84</td>
<td>16.07</td>
<td>14.98</td>
</tr>
<tr>
<td>11</td>
<td>Maximum width of snout over upper canines (SW)</td>
<td>29.29 (c)</td>
<td>30.42</td>
<td>36.58</td>
<td>29.28</td>
<td>17.41</td>
<td>14.98</td>
</tr>
<tr>
<td>12</td>
<td>Lower canine width</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>13</td>
<td>Max width of snout under canines</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>14</td>
<td>Lower postcanine series length</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>15</td>
<td>Upper postcanine series length</td>
<td>24.19</td>
<td>21.72</td>
<td>27.25</td>
<td>23.72</td>
<td>11.66</td>
<td>14.03</td>
</tr>
<tr>
<td>16</td>
<td>Anterior upper post canine distance</td>
<td>18.19</td>
<td>18.04</td>
<td>20.67</td>
<td>20.02</td>
<td>10.55</td>
<td>8.70</td>
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<tr>
<td>17</td>
<td>Posterior upper post canine distance</td>
<td>26.25</td>
<td>35.68</td>
<td>33.94</td>
<td>30.47</td>
<td>15.99</td>
<td>16.66</td>
</tr>
<tr>
<td>18</td>
<td>Maximum width of skull (W)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>19</td>
<td>Maximum height of zygomatic arch</td>
<td>11.43</td>
<td>12.57</td>
<td>8.5</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>20</td>
<td>Occipital plate height</td>
<td>39.1</td>
<td>40.15</td>
<td>17.02</td>
<td>14.20</td>
<td></td>
<td></td>
</tr>
<tr>
<td>21</td>
<td>Occipital plate base width</td>
<td>52.97</td>
<td>41.84</td>
<td>19.6</td>
<td>15.29</td>
<td></td>
<td></td>
</tr>
<tr>
<td>22</td>
<td>Basilarial girder width</td>
<td>11.24</td>
<td>8.01</td>
<td>6.7</td>
<td>6.14</td>
<td></td>
<td></td>
</tr>
<tr>
<td>23</td>
<td>Transverse process width</td>
<td>43.64</td>
<td>36.35</td>
<td>33.59</td>
<td>17.27</td>
<td></td>
<td></td>
</tr>
<tr>
<td>24</td>
<td>Occipital condyle width</td>
<td>16.36</td>
<td></td>
<td></td>
<td>9.81</td>
<td>8.34</td>
<td></td>
</tr>
<tr>
<td>25</td>
<td>Proportion: SL/BSL</td>
<td>37.74%</td>
<td>38.54%</td>
<td>38.80%</td>
<td>32.52%</td>
<td></td>
<td></td>
</tr>
<tr>
<td>26</td>
<td>Proportion: W/BSL</td>
<td>76.31%</td>
<td>78.80%</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>27</td>
<td>Proportion: SW/BSL</td>
<td>24.07%</td>
<td>31.74%</td>
<td>30.92%</td>
<td>29.79%</td>
<td></td>
<td></td>
</tr>
<tr>
<td>28</td>
<td>Proportion: OL/BSL</td>
<td>18.80%</td>
<td>17.79%</td>
<td>18.03%</td>
<td>19.25%</td>
<td></td>
<td></td>
</tr>
<tr>
<td>29</td>
<td>Proportion: TL/BSL</td>
<td>32.43%</td>
<td>23.90%</td>
<td>31.32%</td>
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Notes:
(a) Estimate, as anterior border of snout is damaged/missing.
(b) Estimate, posterior half of orbit is missing/broken off.
(c) Estimate, as cranium is distorted and crushed flat.
(d) Estimate, right zygomatic arch missing, so doubled left zygomatic arch measurement.
(e) Estimate, as anterior border of snout is damaged/missing.

Snout

**Premaxilla**

The premaxilla is a small, elongated bone, located at the anterior margin of the snout, forming the anteromedial and ventral margins of the external nares. In SAM-PK-K10694 and BP/1/4469, the premaxilla is well preserved and includes the dorsal ascending process that extends dorsally onto the anterior nasal edge, then continues posteriorly 3–4 mm beyond the level of the posterior margin of the nares (Figs 4A, 4B, 8A). The dorsal ascending process of the premaxilla extends proportionally further posteriorly in the smaller specimen BP/1/4469 than the larger SAM-PK-K10694. In BP/1/3926, the premaxilla houses a small anterior premaxillary foramen above the first incisor. This foramen is also observed on the right side of BP/1/4469.

**Septomaxilla**

The septomaxilla is small and elongated and is well preserved in SAM-PK-K10694 and BP/1/4469. The septomaxilla in cynodonts can be divided into the body and the facial process (Sidor & Smith 2004). The body forms the inside border of each nasal passage, covering the floor of the external nares. In SAM-PK-K10694, the body of the septomaxilla preserves the horizontal, intranarial process, forming a flat bridge or shelf that divides each nasal
passage into two approximately equal upper and lower halves (Fig. 4A).

In SAM-PK-K10694 and BP/1/4469, the septomaxillary facial process covers the posterior margin of the external naris before forming a very short, thin laterally-located process between the maxilla and nasal (Figs 4A, 8A). There is no discernible septomaxillary foramen visible on the lateral surface of the snout.

Maxilla

The maxilla is a large bone that forms most of the lateral side of the snout. This bone is bounded by its anterior contact with the premaxilla and septomaxilla, its long dorsal contact with the nasal, its posterior contact with the lacrimal and the jugal, and its ventral alveolar border.

The lateral surface of the maxilla contains numerous small nutritive foramina, extending posteriorly from a region above the last incisor to the level of the fifth or sixth postcanine (Figs 4A, 6A, 8A, 9C). These foramina are laid out in two roughly horizontal parallel lines. The foramina in the ventral row are generally larger than those in the dorsal one. The ventral foramina row of SAM-PK-K10694 has a single, noticeably larger foramen in the anterior portion of the maxilla, anterior to the level of the canine (Fig. 4A).

In dorsal view, the maxilla is convex anteriorly, with a
ridge or swelling above each canine, whereas posteriorly the maxilla becomes concave just before contacting the lacrimal, and flares outwardly where it contacts the jugal below the orbit (Figs 1, 2, 5). In SAM-PK-K10694, the maxilla carries a raised rounded projection, near the dorsal contact with the nasal bones, probably related to the presence of the upper canine root (Fig. 4).

Nasal

The nasal is a large bone that covers the majority of the dorsal surface of the snout. Anteriorly, the nasal forms the dorsal edge of the external naris, between the septo-maxilla and the ascending process of the premaxilla. The nasal bone is broader posteriorly than anteriorly, showing the greatest breadth where the bone contacts the lacrimal.

The external surface of the nasal in SAM-PK-K10694 contains numerous small nutritive foramina, arranged in an anteroposteriorly-oriented line or row, extending from near the anterior margin of the nasal to a point just beyond its narrowest concave region (Fig. 4B). The smaller specimens BP/1/4469 and BP/1/1563 also display these nasal nutritive foramen rows, but they are formed by fewer foramina than in the larger specimen (Fig. 9A). The naso-frontal suture is an inverted V-shape in most specimens (Fig. 4B), but is straighter in the large specimen BP/1/3926 (Fig. 5A).

Posteromedially, the nasal presents a slightly raised ridge near the contact with the frontal, as seen in BP/1/3926 and SAM-PK-K10694.

Orbito-temporal region

Frontal

The frontal bone is elongated anteroposteriorly and contacts the nasals anteriorly, the prefrontals anterolaterally and the postorbitals posterolaterally. The frontal does not form part of the dorsal margin of the orbits but reaches close to the orbital margin in the smaller specimen BP/1/4469.

In dorsal view, the frontal initially widens posteriorly, along the lateral contact with the prefrontal, and tapers posteriorly along the lateral contact with the postorbital and parietal (Figs 5A, 9A). The frontal contacts the parietal at the narrowest posterior point on the sagittal crest. In BP/1/3926, the frontal is slightly depressed compared to the level of the surrounding postorbital bone.

In lateral view, a small portion of the frontal appears below the prefrontal and postorbital as an elongated segment forming part of the dorsal margin of the orbital vacuity (Figs 4A, 6A).

Lacrimal

The lacrimal is a small bone forming the anterior edge of the orbit and contacts the prefrontal and the nasal dorsally, the maxilla anteriorly, and the jugal posteros-ventrally. On the anterior margin of the orbit of SAM-PK-K10694 and AM4947 there is a protuberance at the level of the lacrimal foramina. In SAM-PK-K10694 and BP/1/1563, two foramina are observed inside the anterior margin of the orbit, which are positioned vertically, approximately 3 mm apart. The ventral foramen is the larger. Although these two foramina appear to be present in BP/1/3926, damage and poor preservation makes confirmation difficult.

Prefrontal

The prefrontal is a small bone forming the anterodorsal edge of the orbit, contacting the frontal medially, the nasal anteriorly, the lacrimal anterodorsally and the postorbital posteriorly. The contact of the prefrontal with the frontal shows a longitudinal suture, directed slightly towards the lateral side posteriorly (Figs 4B, 5A, 9A). In SAM-PK-K10694 and BP/1/3926 the level of the postorbital is higher than the level of the prefrontal at the contact whereas in the smaller specimens these bones are at the same level.

Postorbital

The postorbital contacts the prefrontal anteriorly, the frontal dorsally, and the jugal ventrally. The postorbital forms: a) the dorsal margin of the orbit, contacting the prefrontal anteriorly, b) the posterodorsal portion of the postorbital bar, and c) the posterior temporal ramus of the postorbital, which covers the lateral surface of the parietal, ventral to the sagittal crest (Fig. 5A). In lateral view, the temporal ramus extends posteriorly in two directions, dorsally and ventrally, creating a forked shape, with the dorsal extension reaching below the orbito-temporal groove to contact the epipterygoid (Fig. 6A).

In BP/1/4469, the contact of the postorbital and the jugal in the postorbital bar displays a wedge shape (Fig. 8A), with the jugal overlapping the postorbital and creating an inverted V-shape at the contact. The jugal-postorbital contact occurs approximately midway along the postorbital bar.

Orbital scleral ossicles are preserved in the matrix of the left orbit of AM4947 (Fig. 7). These elements are located out of place in two parallel diagonal rows. Seven small scleral ossicles are visible in these rows, the upper row containing three and the lower row four bones. They are very delicate, laminar, and rectangular.

Jugal

The jugal forms the suborbital bar anteriorly, the ventral portion of the zygomatic arch posteriorly, and the ventral portion of the postorbital bar dorsally. This bone contacts the maxilla anteriorly, the lacrimal anterodorsally, the squamosal posteriorly and the postorbital dorsally.

In SAM-PK-K10694, the jugal extends anteriorly, as part of the suborbital bar, contacting the maxilla ventrally, and extending up to the level of the anterior margin of the orbit, where the bone contacts the lacrimal anteriorly (Fig. 4A). Within the left orbit, the jugal shows a single foramen (Fig. 4B). The suborbital bar does not show any process or angulation between the maxilla and the jugal.

Only BP/1/4469 preserves complete zygomatic arches, which are wide, robust and laterally flared (Fig. 8). The jugal makes up a large portion of the zygomatic arch, and extends posterolaterally outwards in a convex shape, accommodating the squamosal dorsally.

The inferior margin of the jugal in the zygomatic arch is longitudinally well developed and low. The temporal
Figure 5. Photograph and interpretive drawing of *Cynosaurus suppostus*, specimen BP/1/3926, **A**, in ventral view, and **B**, in right lateral view. Abbreviations: bo, basisciptal; bs, basisphenoid; c, canine; ect, ectopterygoid; ept, epippterygoid; exo, exoccipital; f, frontal; fm, foramen magnum; i, incisor; j, jugal; jf, jugular foramen; l, lacrimal; mx, maxilla; n, nasal; op, opisthotic; pal, palatine; par, parietal; pcf, paracanine fossa; pmx, premaxilla; po, postorbital; pre, prefrontal; pro, prootic; pt, pterygoid; ptf, post-temporal fenestra; ptp, pterygoid process; so, supraoccipital; sq, squamosal; tf, trigeminal foramen; v, vomer. Scale bar equals 20 mm.
Figure 6. Photograph and interpretive drawing of *Cynosaurus suppostus*, specimen BP/1/3926, **A**, in right lateral view and **B**, in occipital view. Abbreviations: *c*, canine; *dep*, depression; *ept*, epipterygoid; *f*, frontal; *fm*, foramen magnum; *i*, incisor; *j*, jugal; *jf*, jugular foramen; *l*, lacrimal; *mri*, median ridge; *mx*, maxilla; *n*, nasal; *op*, opisthotic; *otg*, orbitotemporal groove; *pa*, proatlas; *par*, parietal; *pmx*, premaxilla; *po*, postorbital; *pre*, prefrontal; *pro*, prootic; *pt*, pterygoid; *ptf*, post-temporal fenestra; *ptp*, pterygoid process; *so*, supraoccipital; *sq*, squamosal; *t*, tabular; *tf*, trigeminal foramen; *v*, vomer. Scale bar equals 20 mm.
fenestra is wide, being of equal width throughout its anteroposterior length.

Squamosal

The squamosal is a large bone forming the postero-dorsal portion of the zygomatic arch anteriorly, the posterolateral portion of the occipital crest posteriorly and the squamosal portion of the posterolateral occipital region. This bone contacts the jugal anteriorly and anteroventrally, the parietal posteromedially, and the tabular posteriorly.

In BP/1/4469, the squamosal makes up the smaller portion of the zygomatic arch and extends postero-laterally outwards in a convex shape. The dorsal margin of the squamosal portion of the zygomatic arch continues dorso-medially to form the dorsal margin of the occipital crest. The squamosal overlaps the parietal on the proximal surface of the occipital crest.

Parietal

The parietal is a large bone and is located on the medial surface of the temporal fenestra. The parietal contacts the frontal anteriorly, the postorbital anterolaterally, the occipital crest of the squamosal posterolaterally and post-parietal posteriorly.

In BP/1/4469, the squamosal makes up the smaller portion of the zygomatic arch and extends postero-laterally outwards in a convex shape. The dorsal margin of the squamosal portion of the zygomatic arch continues dorso-medially to form the dorsal margin of the occipital crest. The squamosal overlaps the parietal on the proximal surface of the occipital crest.

Palate

Premaxilla

A large paracanine fossa is located anteromedially to each upper canine. The anterior margin of the paracanine fossa is formed by the premaxilla, and the posterior by the maxilla (Fig. 5B). There is a gap along the midline between the premaxillary palatal processes (Figs 5B, 9B).

Vomer

The vomer is unpaired and forms a medially-located vertical septum that extends anteroposteriorly. This bone contacts the premaxilla anteriorly and the palatines posteriorly. The vomer is observed in the gap between the palatal processes of the premaxillae (Figs 5B, 9B) and continues posteriorly in the gap formed between the palatal processes of the maxillae and palatines, emerging posteriorly beyond the palatal processes of the palatines. Posterior to the palatal processes, the vomer tapers until reaching a sharp point on the palatine, at a point roughly in line with the last postcanine. The vomer does not reach the pterygoid posteriorly (Fig. 5B).

In the small specimen BP/1/1563, the vertical septum of the vomer is exposed between the palatal processes of the maxilla and the palate and shows a well-developed, distinct, deep channel on its ventral surface.

Maxilla

The maxilla forms the anterior portion of the incomplete secondary palate, contacting the premaxilla anteriorly and the palatine posteriorly. The palatal processes of each maxilla do not meet in the midline (Figs 5B, 9B). The incisive foramina are not closed by the palatal processes of

Figure 7. Scleral ossicles in the left orbit of *Cynosaurus suppostus*, specimen AM4947, photograph and interpretive drawing. Abbreviations: sb, scleral ossicles. Scale bar equals 1 cm.
the maxilla. The narrowest point of the incisive foramen is posterior to the level of the paracanine fossa. In smaller specimens, the gap between the edges of the incomplete secondary palate is proportionally wider than in larger specimens (Figs 5B, 9B). A large posterior palatal foramen is located anterolaterally to the maxillary-palatine suture (Fig. 9B).

**Palatine**

The palatine forms a large portion of the palate. This bone contacts the maxilla anteriorly and the pterygoid posteriorly. The anterior contact between the maxilla and palatine occurs on the secondary palate, whereas the posterior contact between the palatine and the pterygoids occurs immediately posterior to the posterior edge of the vomer. Posterolateral to the vomer, a posteromedially-oriented palato-pterygoid crest rises from the palatine, tapering dorsally to a thin sharp edge. The dorsal, thin, sharp edge of this crest is contributed by the palatine, whereas the more ventral underlying body of the crest is formed by the pterygoid. The sutures between the palatine and pterygoid occur along the rising medial surface of the crest (Fig. 5B).

The palatal plates of the palatine do not meet in the midline but contribute to the posterior portion of the incomplete secondary palate (Figs 5B, 9B). The palatal processes of the palatine are short in relation to the overall secondary palate length, as the maxilla contributes the greatest length. The posterior edge of the bony secondary palate on the palatine forms a curved, arch-shaped margin and extends laterally to reach a point just anterior to the last upper postcanine (Fig. 5B).

**Ectopterygoid**

The small ectopterygoid is located anterolaterally to the pterygoid process, contacting the flange posteriorly (Fig. 5B). The ectopterygoid contacts the palatine anteriorly. A single large foramen is identifiable on the right ectopterygoid process of AM4947, where the ectopterygoid-pterygoid suture is clear.

**Pterygoid**

The pterygoid is a large bone forming the posterior portion of the primary palate region, contacting the palatines anteriorly and extending posteriorly towards the basicranium to contact the basisphenoid posteriorly and the quadrate via the quadrate ramus of the pterygoid, posterolaterally (Fig. 5B).

Anteriorly, the pterygoids form the transverse flange or pterygoid process, located posterolaterally to the palatine crests (Fig. 5B). In ventral view, the pterygoid processes thin laterally and taper medially. The posterior margins of the pterygoid processes are vertically oriented.

The interpterygoid vacuity is present in the small specimen BP/1/1563 (Fig. 9A), but is not present in the larger specimens. This ontogenetic loss of the paired interpterygoid vacuities has also been reported in *Thrinoaxodon* (Jasinoski et al. 2015), whereas vacuities are absent altogether in *Galesaurus* (Jasinoski & Abdala 2017).

The posterior part of the pterygoid and the rostrum of the parasphenoid form the basicranial girder. This portion of the pterygoid tapers initially medially to reach its narrowest width, after which it expands laterally to contact the basisphenoid (Fig. 5B).

**Basicranium**

The basicranium is a triangular structure relatively longer than wide (Figs 5B, 9B).

**Basisphenoid**

The basisphenoid forms the anterior portion of the basicranium and is roughly triangular with the apex pointing anteriorly. The surface of this bone is generally flat, but it has a shallow fossa covering the majority of the central portion of the bone. This depression has a faint median ridge running through the centre, which is most visible in the small specimen BP/1/1563 (Fig. 9B). In this specimen, the outer circular edges of the fossa are slightly raised above the level of the surrounding bone.

**Basioccipital**

The basioccipital is roughly circular in shape, having an anterior contact with the basisphenoid in the form of an inverted U-shape medially. The basioccipital tapers anteriorly and broadens posteriorly. A deep parasagittal depression covers the majority of the bone (Fig. 5B). This depression has a strong central ridge running through the centre of the bone. The outer circular edges of the parasagittal depression are slightly raised above the level of the surrounding bone. This parasagittal depression is much deeper in the larger specimen BP/1/3926 (Fig. 5B).

**Quadrate and quadratojugal**

The quadrate and quadratojugal are only observable in the small specimen BP/1/4469 and are best observed on the occiput (Fig. 8B), although the quadrate is still mostly obscured by matrix. The quadratojugal is represented by the ascending process: a thin splint of bone, oriented vertically, located on the lateroventral edge of the occiput. Medial to this bone, the squamosal forms the quadrate notch medially and the quadratojugal notch laterally. The quadratojugal contacts the articular ventrally at the same height as the postcanine tooth row.

**Prootic**

The prootic forms the anterior part of the wall of the fenestra ovalis, whereas the episthotic forms the posterior margin of this opening. The lateral flange of the prootic is present in BP/1/3926 (Fig. 5B).

In BP/1/1563, the basisphenoid wing or parasphenoid ala is long, extending posteriorly, but does not contribute to form the margin of the fenestra ovalis. The cavum epipetricum is open ventrally (Fig. 9B). The fenestra ovalis is located anterolaterally to the jugular foramen (Fig. 9B). Anterior to the fenestra ovalis, a small primary facial foramen is observed on the prootic, along with a small, anteroposteriorly-oriented crest separating the fenestra ovalis from the cavum epipetricum. The primary facial foramen is proportionally much larger in the small specimen BP/1/1563.
Opisthotic
The opisthotic forms the anterolateral rim and the exoccipital forms the posterior rim of the jugular foramen in BP/1/3926 (Fig. 5B). In ventral view on BP/1/4469, the paroccipital process appears as a rectangular projection. This process is latero-medially elongated and widens laterally. The paroccipital process appears to contact the quadrate on the left side in BP/1/4469.

Lateral wall of the braincase

Prootic
In lateral view, the prootic is located on the posterior part of the lateral wall of the braincase, ventral to the parietal, and contributes to the posterior margin of the very large trigeminal foramen, with the epipterygoid forming the anterior margin (Figs 6A, 9C).

Epipterygoid
The epipterygoid is an anteroposteriorly elongate, thin bone, situated dorsal to the quadrate ramus of the pterygoid. The epipterygoid bears a long anterior extension or ascending process dorsally.

In BP/1/3926, the orbito-temporal groove forms a well-defined, long, horizontal channel between the parietal dorsally and the prootic and epipterygoid ventrally. This forms a shallow furrow on the parietal, and extends from its anterior contact with the postorbital to the level of the trigeminal foramen posteriorly (Fig. 6).

Occiput
The occiput of the large specimens is relatively wide, broad, flat, and oriented vertically, whereas in the small specimens the occiput slopes anteriorly. The sutures of the occipital plate are difficult to identify in the large specimen BP/1/3926 (Fig. 6B) and are best exposed in the small specimen BP/1/4469 (Fig. 8B).

Postparietal
The postparietal is a vertically-oriented bone located on the dorsal medial portion of the occiput, which contacts the tabulars laterally and the supraoccipital ventrally. Dorsally, the postparietal forms a small pentagonally-shaped wedge of bone, reaching the parietal on the sagittal crest, just posterior to the pineal foramen in the small specimens (Fig. 8B). The postparietal features a shallow parasagittal depression, separated by a faint vertically-oriented median ridge. In BP/1/3926, this depression is much deeper and the median ridge is much more sharply raised and pronounced (Fig. 6B).

Supraoccipital
The supraoccipital is a relatively wide bone, forming the dorsal margin of the foramen magnum (Figs 8B, 9E), and broadens ventrally, reaching its widest point ventrolaterally at the ventromost contacts with the tabulars. The vertically-oriented median ridge running through the centre of the postparietal extends ventrally onto the surface of the supraoccipital (Fig. 6B). As is the case on the postparietal, the ridge size and extension onto the supraoccipital is more pronounced in the large specimen BP/1/3926.

Tabulars
The tabulars are located on the dorsolateral portion of the occiput, contributing to the occipital crests. The tabular makes a small contact with the paroccipital process of the opisthotic ventrally, between the squamosal and the

Figure 8. Photograph and interpretive drawing of *Cynosaurus suppostus*, specimen BP/1/4469, A, in left lateral view and B, in occipital view. Abbreviations: ang, angular; bo, basioccipital; c, canine; d, dentary; fm, foramen magnum; i, incisor; j, jugal; l, lacrimal; mx, maxilla; n, nasal; nf, nutritive foramina; pa, proatlas; par, parietal; parp, paroccipital process; pmx, premaxilla; po, postorbital; pp, postparietal; pre, prefrontal; ptf, post-temporal fenestra; qi, quadratojugal; smx, septomaxilla; sq, squamosal; ss, squamosal sulcus; sur, surangular; t, tabular. Scale bar equals 10 mm.
exoccipital (Fig. 8B). The tabular is in contact with the squamosal via the squamosal sulcus ridge (Fig. 8B). The tabulars form the lateral and dorsal borders of the post-temporal fenestra (Fig. 9E) and the paroccipital process appears to form the base. However, there is a thin horizontal piece of bone also at the base of the fenestra, which could be part of the tabular (Figs 6A, 8B). The post-temporal fenestra is much smaller than the foramen magnum (Figs 6B, 8B, 9E).

**Squamosal**

The squamosal is positioned laterally in the occiput and contacts the tabulars medially, at the junction of the zygoma and occipital crests (Figs 8B, 9E). In occipital view, a shallow V-shaped notch is formed by the dorsal surface of the medial tabular part of the occipital crest and the dorsal surface of the lateral squamosal part of the zygoma. The squamosal sulcus is a vertically-oriented ridge running along the squamosal-tabular contact that forms a moderately deep vertical groove, ending behind the quadrate (Fig. 8B). There is no posterior horizontal projection of the squamosal dorsal to the squamosal sulcus.

**Basioccipital**

The basioccipital forms the ventral rim of the foramen magnum, medial to the double occipital condyles of the exoccipitals (Fig. 8B). The exoccipital contacts the tabulars dorsally and ventrally forms the occipital condyles. The exoccipitals also make up the lateral margins of the foramen magnum.

**Proatlas**

A right partial proatlas is preserved in BP/1/3926 (Fig. 6B) and is located on the right dorsal margin of the foramen magnum. In specimen BP/1/4469, both proatlantes are preserved, the left being better preserved (Fig. 8B). In dorsal view, the proatlas is rectangular in shape, wider proximally, and the distal lateral margin is curved 90° compared to the rest of the bone.

**Lower jaw**

The mandible is robust in *Cynosaurus*, with the horizontal ramus very high and the mentum subvertical.

**Dentary**

The left and right dentaries are unfused at the symphysis in both large (e.g. SAM-PK-K10694) and small (e.g. BP/1/4469) specimens. In lateral view, the symphysis is anteriorly convex in specimen BP/1/4469 (Fig. 8A). The lateral surface of the horizontal ramus of the dentary is generally smooth and almost flat, but the anterior portion posterior to the level of the canines is slightly concave. The ramus maintains a relatively equal height over most of its extension and bends sharply upwards posterior to the last postcanine, at the level of the anterior margin of the orbits, producing the coronoid process. The anterior margin of this process is mediolaterally thickened. The coronoid process slopes posterodorsally and presents a shallow depression, the masseteric or adductor fossa, on its lateral surface. In BP/1/4469, the fossa is present as a wide depression separated by a posterodorsally-oriented lateral crest or sharp ridge that runs through the middle of the coronoid process. This well-developed ridge extends onto the angle of the dentary, dividing the fossa into distinct dorsal and ventral portions. The ventral portion extends ventrally onto the angle of the dentary. The situation is similar in the mandible of AM4947, but the lateral crest is broad and slightly raised (Fig. 7).

The articular process of the dentary is poorly developed. In BP/1/4469 (Fig. 8A), the angular process of the dentary is poorly developed.
not completely preserved on the left and is better preserved and more complete on the right side. On both sides it forms a relatively distinct and sharply angled keel/heel upwards at approximately 30° from the horizontal (Fig. 8A). The angular process of the dentary is located at the level of the postorbital bar.

Angular
The angular is only preserved in BP/1/4469 (Fig. 8A). This bone forms the ventral posterolateral portion of the mandible and is located ventrally to the coronoid process of the dentary, forming a concave lamina. The angular contacts the base of the coronoid process of the dentary dorsally and the articular posteriorly. The reflected lamina of the angular is not preserved in any specimen. Part of the surangular is exposed posteriorly in BP/1/4469, but it is not possible to see the suture between the surangular and angular.

Articular-prearticular
In ventral view, the articular-prearticular bar is an anteroposteriorly raised bar, running along the medial margin of the angular. Posteriorly, the bone widens to stretch between the lateral and medial surfaces of the ventral mandible margin, forming a triangular shape. In ventral view, in BP/1/4469, the articulars are observed as smooth flattened areas of bone with slightly concave surfaces for articulation to the quadratojugal of the cranium.

Splenial
The splenial is a thin, elongated vertical lamina located medial to the dentary. In AM4947, the splenial continues posteriorly, well beyond the level of the pterygoid processes, as a shallow, thin bone limited to the medial surface of the mandible.

Dentition
Dental formula and preservation
The dental formula of Cynosaurus is I4/c3, C1/c1, PC6-9/pc6-9 and the adult formula is I4/c3, C1/c1, PC8-9/pc8-9 (Table 3). The upper tooth row extends posteriorly to just beyond the level of the anterior margin of the orbits. There is no evidence for occlusion, as the surfaces of the upper and lower teeth lack wear facets.

Incisors
Upper incisors number four on both sides in almost all specimens where they are preserved (Table 3). The number of incisors is peculiar in SAM-PK-K10694, a large specimen, which preserves five right and four left upper incisors (Fig. 10C). The additional right incisor may represent the retention of a replacement tooth. There are three lower incisors in the small specimen BP/1/4469, as revealed by CT-scanning. However, based on alveolar count, there are only two lower incisors on either side in the large specimen SAM-PK-K10694.

The upper incisors are pointed and conical, without serrations. In the larger specimens, all incisors are of similar width and length, with no marked differences between them. The small specimen BP/1/4469 shows variation in size and length, with the left second tooth being very small, possibly due to it being newly erupted (Fig. 10F). In SAM-PK-4333 (Fig. 1D), each incisor shows several deep, ridged, longitudinal grooves or striations. These longitudinal grooves also occur over the entire length of the crown in SAM-PK-K10694 (Fig. 10C) and BP/1/4469 (Fig. 10F).

The incisors are vertically oriented and point slightly backwards in the small specimen BP/1/4469 (Fig. 10F).

In BP/1/3926 (Fig. 5B), the incisor crowns are not preserved, but the cross-section reveals variation from spherical to oval and the damaged left upper incisors in SAM-PK-K10694 are oval in cross-section.

A diastema of approximately 4mm between the last incisor and the canine is observed on both sides of the larger specimens SAM-PK-4333 (Fig. 1D) and BP/1/3926 (Fig. 5B). In SAM-PK-K10694, the diastema is also approximately 4–5 mm, but a portion of the diastema is occupied by small canine replacement teeth, located immediately anteriorly to each upper canine (Figs 4A, 10C).

Canines
There are single upper and lower canines, oval in cross-section, which are anteroposteriorly elongated and unserrated. They have a convex anterior and a concave posterior edge, and have several longitudinal grooves or striations occurring over the entire length of the crown, most clearly seen in SAM-PK-K10694 (Fig. 10A–C) and BP/1/4469 (Fig. 10D–F). The upper canines show a distinct posterior ridge in SAM-PK-K10694.

In SAM-PK-K10694, small canine replacement teeth are located immediately anteriorly to each upper canine (Fig. 10A–C), whereas in the small specimen BP/1/1563, canine replacement teeth are located immediately posterior to each canine.

Postcanines
Upper and lower postcanines number seven to eight in most specimens (Table 3). However, there are only six upper postcanines in the small specimen BP/1/4469 (Fig. 10D, E) and the first, fifth, and sixth postcanines are smaller than the second, third and fourth. The large specimen BP/1/3926 has nine upper postcanines (Fig. 5B), with...
the same pattern of tooth sizes as the first and last two postcanines as the smallest.

The postcanine morphology consists of a slightly curved main cusp per tooth, with a variety of anterior and posterior accessory cusps which differ in their number and placement. The external surfaces are smooth, with no cingula or cingular cusps present. In general, the postcanine teeth exhibit one of two morphological conditions: 1) the first and second postcanines have a main recurved cusp with a convex anterior edge and with a single posterior accessory cusp, or 2) from the third postcanine backwards, the postcanines have a main recurved cusp, with a single anterior and a single posterior accessory cusp.

The large specimen SAM-PK-K10694 provides the best preserved and most complete postcanine dentition of all specimens. In this specimen (Fig. 10A–C), the first upper postcanine (PC) is small, simple and pointed and bent slightly backwards. The PC2 has a straight main cusp, with a slight posterior ledge, but no true cusp (on the right side), or a small posterior accessory cusp (on the left side). The PC3 on the left side is an erupting postcanine tooth deeply set in the maxilla, with a recurved main cusp and a small posterior accessory cusp. The PCs 4 and 5 show recurved main cusps with small single posterior accessory cusps, whereas PCs 6 and 7 show recurved main cusps with equally-sized small single anterior and posterior accessory cusps. The PC8 is broken off on the left, and the right side is very small and shows a recurved main cusp with a small posterior accessory cusp. The first lower postcanines (pc) of SAM-PK-K10694 are separated from the canines by a diastema of 4mm (Fig. 10A–B). On the left side, pcs 1 to 3 show a recurved main cusp with single posterior accessory cusp each. The pcs 4 to 6 show a recurved main cusp with single anterior and posterior accessory cusps, the anterior being more developed than the posterior. The pc7 shows a recurved main cusp, a single posterior accessory cusp and two anterior accessory cusps. On the right side, the pcs 1 and 2 consists of a single recurved main cusp, with a single posterior accessory cusp. The pcs 3 to 6 show single recurved main cusps, with single anterior and posterior accessory cusps, the anterior being more developed than the posterior.

In AM4947, the upper left postcanines are damaged, but PCs 4 to 6 show a recurved main cusp with single posterior accessory cusps. In addition, the fourth postcanine also exhibits a single anterior accessory cusp. The upper right postcanines consist of a recurved main cusp only, with PCs 5 to 8 also showing single posterior accessory cusps. In the small specimen BP/1/4469 (Fig. 10D, E), the first PC on both sides displays a single recurved main cusp with a small posterior accessory cusp. The PCs 2 to 6 have recurved main cusps, with single anterior and posterior accessory cusps, with the anterior accessory cusps being better developed than the posterior ones.

DISCUSSION

Comparisons with other basal cynodonts

When compared with other basal (non-eucynodont) cynodonts, the most important diagnostic characters in Cynosaurus are represented in the snout. Cynosaurus’s snout length (obtained from the average of the two large specimens BP/1/3926 and SAM-PK-4333) is approximately 38% of the basal skull length (Table 4). This is the second shortest snout among basal cynodonts, very close to Progalesaurus at 37% and also to the 39% of Platycraniellus. Other basal cynodonts have proportionally longer snouts: Procynosuchus at 45%, Galesaurus at 43% and Thrinaxodon at 44% (Table 4). As well as being short, Cynosaurus has the proportionally broadest snout, at approximately 32% of basal skull length, for the large complete and undistorted specimen BP/1/3926 (with the closest other taxon being Platycraniellus at 30%) (Table 4). The Cynosaurus specimen
Table 4. Measurements (in cm) of the basal skull length (BSL), snout width (SW), snout length (SL) and the percentages of the ratio between snout width and the basal skull length (SW/BSL) and snout length and basal skull length (SL/BSL). Measurements by Fernando Abdala.

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SAM-PK-4333 is crushed and distorted, so the estimated ratio of snout width to basal skull length in this individual (24.07%) is not reliable (Table 2). All other taxa compared have narrower snouts: Procyonosuchus, Progalesaurus and Galesaurus at 26% and Thrinaxodon at 25% (Table 4).

In the orbital region of Cynosaurus, Progalesaurus and a few specimens of Galesaurus, the frontal forms a flat or slightly depressed region, below the level of the surrounding postorbital (Jasinoski & Abdala 2017), whereas in Procyonosuchus and Thrinaxodon the frontal bears a medially raised ridge, which originates in the posterior part of the nasals and continues through to the frontals. In Cynosaurus and Progalesaurus, the posterior projection of the postorbital on the parietal forms a sharply forked shape with well-differentiated dorsal and ventral processes (Fig. 6). In the small specimen of Cynosaurus BP/I/4469 the ventral process is well preserved and longer than the dorsal process, although the dorsal process is somewhat eroded. In the large specimen BP/I/3926 these processes are more equal. Juveniles of Thrinaxodon and Galesaurus present a long ventral process and a short incipient dorsal process, whereas subadults and adults exhibit dorsal and ventral processes that produce a C-shaped bifurcated posterior projection (Jasinoski et al. 2015; Jasinoski & Abdala 2017).

In Cynosaurus and Galesaurus, the pineal foramen is large in juveniles. Cynosaurus closes the pineal foramen in adulthood (Benoit et al. 2015), an atypical condition amongst basal cynodonts, otherwise occurring only in eucynodonts (e.g. Massetognathus). Galesaurus specimens retain a very small pineal foramen into adulthood (Jasinoski & Abdala 2017) whereas the foramen remains large in adult Thrinaxodon, Procyonosuchus and Progalesaurus. In Cynosaurus, Platycraniellus, Procyonosuchus and Thrinaxodon, the sagittal crest is also developed in front of the pineal foramen. In Thrinaxodon, this anterior portion of the crest develops late in ontogeny and is only present in adult specimens (Jasinoski et al. 2015). In Galesaurus and Progalesaurus there is no sagittal crest formed in front of the pineal foramen, with the exception of one large Galesaurus skull (Jasinoski & Abdala 2017).

Interestingly, the Cynosaurus specimen AM4947 shows the presence of orbital scleral ossicles. These elements are more commonly recorded in basal therapsids (e.g. biarmosuchians, gorgonopsians and therocephalians). This is only the third record of scleral elements in non-mammaliaform cynodonts, the others being in a juvenile late Permian Procyonosuchus and in a specimen of the Early Jurassic Tritylodon (Angelczyk & Schmitz 2014). The long phylogenetic and temporal ranges represented between species preserving scleral ossicles suggests that these elements are quite likely present in other non-mammaliaform cynodonts but not recovered in the fossil record. Unfortunately, only a few scleral ossicles are preserved out of place in the centre of the orbit in AM4947 (Fig. 7), so it is not possible to determine the type of visual activity in Cynosaurus.

The paired secondary palatal processes of the maxillae and palatine bones show a relatively narrow separation from one another in the midline posteriorly, which is
similar in Cynosaurus and Galesaurus. In Procyonosuchus, the secondary palate is also incomplete, but the gap between the palatal processes of the maxillae and palatine bones is wider than the condition found in Cynosaurus or Galesaurus. In Thrinaxodon and Platycteniellus, the secondary palate is almost completely closed. Jasinowski et al. (2015) report the palatal shelves of Thrinaxodon as not tightly articulated along the midline and therefore not truly closed. The anteroven tral margin of the vomer is broader than the open secondary palate cleft in Cynosaurus and Galesaurus.

The mandible of Cynosaurus is very robust and relatively high in relation to the length of the horizontal ramus, with a high, subvertical mentum. Galesaurus has a more gracile mandible, whereas those of Procyonosuchus and Thrinaxodon are much more gracile and slender. In all of these taxa the mentum is shallower than in Cynosaurus.

In Cynosaurus, the masseteric fossa on the lateral surface of the dentary is made of dorsal and ventral portions separated by a coronoid eminence. In Progalesaurus and Galesaurus, this fossa is not well defined, but is also composed of dorsal and ventral portions, separated by a well-developed coronoid eminence. In Procyonosuchus, Deinia and Abdalodon the masseteric fossa is positioned on the dorsal portion of the coronoid eminence.

In the dentition, the canines of Cynosaurus and Progalesaurus present strong longitudinal grooves or striations that are also present but fainter in Platycraniellus, Procyonosuchus and Galesaurus. These grooves are absent in the strongly-faceted canine of Thrinaxodon. The postcanines of Cynosaurus, Platycraniellus, Progalesaurus and Galesaurus lack lingual cingula, whereas postcanines in Thrinaxodon and Procyonosuchus display definite lingual cingula and are therefore considered more complex elements.

Phylogeny of basal cynodonts

Updated character scores for Cynosaurus supportus were included in the data matrix provided by Kammerer (2016), who analysed basal cynodont interrelationships. Kammerer (2016) used the matrix provided by Botha et al. (2007) as the basis for his revised analysis. This originally included 59 craniodental characters scored for one gorgonopsian, six therapsidans and 10 non-mammaliform cynodonts, but Kammerer (2016) eliminated five therapsidans taxa from the analysis. We retained the gorgonopsian Cynosaurus and the basal therapsid Lycosuchus as outgroups and added Platycraniellus to the ingroup. The taxon reduction in the data matrix as presented by Kammerer (2016) resulted in the deletion of some characters, as they showed no variation in the taxa represented in the revised matrix. Therefore characters 10 (boss/crest anterior to the interpterygoid vacuity), 11 (suborbital vacuity in the palate), 16 (postorbital bar), 18 (temporal fossa), 23 (occipital crests), 34 (stapes), 36 (mastoid and quadrates processes of the paroccipital process), 41 (longitudinal depression on the lateral side of the dentary), 53 (lower canine) and 57 (postcanine occlusion) were deleted (see Supplementary information 1).

We also introduced other changes in the data matrix. For character 4, incisive foramen; absent (0), present and closed posteriorly (1), we added a new character state: present, not closed posteriorly (2) and rescored all taxa. The following changes were made to the scores of Cynosaurus (scoring of characters of the lower jaw should be considered with caution as we could only check the condition in the juvenile BP/1/4469): character 14, pineal foramen we changed from present (0) to absent in adults (1), based on Benoit et al. (2015); character 25, paroccipital process in the base of the posttemporal fossa, was rescored from ‘?’ to present (0); character 40, angular region of the dentary, was rescored to anterior to the postorbital bar (0) (but the angle of the dentary is not totally preserved in BP/1/4469); character 43, foramen on external surface of the lower jaw between dentary and angular, changed from ‘?’ to present (0); character 46, position of the dentary/ surangular dorsal contact, changed from closer to postorbital bar (0) to midway (1); character 49, lower incisor number, changed from ‘?’ to three (1); character 53, lower canine, changed from ‘?’ to large (0), based on AM4947; character 40, angular region of the dentary, changed from at the same level or posterior (1) to anterior to the postorbital bar (0); character 30, pterygo-par occipital foramen, changed from present (1) to ‘?’.

Some changes were also made to character scores for other taxa. For Abdalodon: character 9, interpterygoid vacuity in adults, changed from ‘?’ to present (0) as originally stated by Botha-Brink and Abdala (2008) after further preparation of the specimen (F.A., pers. obs.); character 47, upper postcanine morphology, changed from ‘?’ to sectorial with lingual cingulum (3), as this morphology is visible on the right side of Abdalodon (Botha-Brink & Abdala 2008). For Deinia, character 28, epitypegid ascending process, changed from ‘?’ to greatly expanded (2), after Ivakhnenko (2013).

We reinstated the character state for character 45: masseteric fossa in the dentary, notch in the base of the coronoid process (1) and scored it in Charassognathus. Considering its placement on the dentary, our primary homology hypothesis is that the notch represents a precursor of the masseteric fossa. Masseteric or masseteric-like fossae have been described at least in two theropods, the akidnognathid Olivierosuchus and the bauriid Microgomphodon (Botha-Brink & Modesto 2011; Abdala et al. 2014) and also seems to be present in Promoschorhynchus (F.A., pers. obs.). However, there is no evidence in therapsidans of the presence of a notch as in the dentary of Charassognathus. We assume this notch is correlated with occlusal muscles based on its position high in the coronoid process, coincident with the placement of the masseter process in three late Permian cynodonts: Procyonosuchus, Deinia and Abdalodon. We rescored this character in Galesaurus and Progalesaurus from absent (0) to fossa extends to the angle of the dentary (2). Kammerer interpreted the fossa as present only if there is a ridge clearly delimiting this structure anteriorly (C. Kammerer pers. comm.). Here, we reworded this character based on homology of the attachment area of the masseter muscle (which would be located on the angle of the dentary even if the ridge limiting the fossa is not
The interpretation of the presence of this muscle in Galesaurus and Progalesaurus implies its insertion on the area of the angle of the dentary (see Jasinoski & Abdala 2017 and Lautenschlager et al. 2016).

For Charassognathus we changed character 60, diastema between maxillary canine and postcanine, from present (1) to absent (0), as the gap between the teeth is small, unlike the large diastema observed (and diagnostic) in Abdalodon. Multistate characters 1, 4, 6, 8, 15, 18, 23, 32, and 36–38 were treated as additive considering adjacency of character states (Lipscomb 1992).

The program TNT (Tree Analysis Using New Technology) version 1.5 was used for searching for most parsimonious trees (Goloboff et al. 2008; Goloboff & Catalano 2016). Considering the size of the data matrix (52 characters and 14 taxa) an implicit enumeration was used for the search of shortest trees. We also present Bremer support and bootstrapping (Fig. 11).

The analyses resulted in 16 most parsimonious trees (mpt) of 108 steps, with the majority rule consensus depicted in Fig. 11. Bremer support values higher than 1 are recovered for Cynodontia, Epicynodontia, Galeosauridae and Eucynodontia (Fig. 11).

We recovered a successive series of polytomies, the basal one recovering the monophyletic groups Charassognathidae, including Charassognathus and Abdalodon, as proposed by Kammerer (2016); Procyonosuchida, formed by Galesauridae (originally proposed by Kemp 1982), but also included Cynosaurus and Charassognathus gnathidae, including one recovering the monophyletic groups Charassognathidae and Eucynodontia (Fig. 11). Bremer support values higher than 1 (mpt) of 108 steps, with the majority rule consensus and bootstrapping (Fig. 11).

The analyses resulted in 16 most parsimonious trees. The program TNT (Tree Analysis Using New Technology) version 1.5 was used for searching for most parsimonious trees (Goloboff et al. 2008; Goloboff & Catalano 2016). Considering the size of the data matrix (52 characters and 14 taxa) an implicit enumeration was used for the search of shortest trees. We also present Bremer support and bootstrapping (Fig. 11).

The analyses resulted in 16 most parsimonious trees (mpt) of 108 steps, with the majority rule consensus depicted in Fig. 11. Bremer support values higher than 1 are recovered for Cynodontia, Epicynodontia, Galeosauridae and Eucynodontia (Fig. 11).

We recovered a successive series of polytomies, the basal one recovering the monophyletic groups Charassognathidae, including Charassognathus and Abdalodon, as proposed by Kammerer (2016); Procyonosuchida, formed by the cosmopolitan Procyonosuchus and the Russian Dvinia; and Cynosaurus + Epicynodontia. Procyonosuchia was originally proposed by Kemp (1982), but also included galesaurids (Galesaurus was later employed by Hopson & Kitching (2001) to define Epicynodontia and thus excluded from the ‘procyonosuchian’ grade). More recently, Kemp (2005) used Procyonosuchia to include the same taxa included here, but he considered the group paraphyletic. Resampling and Bremer support for Charassognathidae are poor (Bootstrap value of 45 and Bremer support of 1) and extremely poor in the case of Procyonosuchia, as the group is only recovered in the majority consensus tree (Bootstrap value of 3). Kammerer (2016) considered Charassognathidae as well supported, citing the bootstrap value of 84. However the Bremer support for the group was 1 (Kammerer 2016: fig, 6), indicating poor support for this clade.

The second polytomy in our analysis corresponds to Epicynodontia, including Cynosaurus, Galesauridae (formed by Progalesaurus and Galesaurus) and a group including remaining cynodonts (Fig. 11). Six synapomorphies support Epicynodontia: character 1, short septomaxillary facial process (1); character 14, moderately deep zygomatic arch dorsoventral height (1); character 31, incipient lateral crest of the dentary (1); character 36, masseteric attachment area on dentary, extends to angle (3); character 37, dentary-surangular dorsal contact, midway between the postorbital bar and the cranio-mandibular joint (1); and character 46, sectorial upper postcanines (1).

Hopson & Kitching (1972) included Cynosaurus, Galesaurus, Thrinaxodon, Platycraniellus and Bolotridon in Galesauridae (see also Kemp 1982), but this family was later restricted to Cynosaurus and Galesaurus (Battail 1991) based on the similar palatal morphology of these two taxa. Sidor & Smith (2004) later described a new genus, Progalesaurus, which they included in Galesauridae. Our result fails to find unequivocal evidence of Cynosaurus as member of Galesauridae (Fig. 11), as the genus is recovered inside the family in only two of the 16 mpt. This is in agreement with phylogenies by Abdala (2007), Botha et al. (2007) and Kammerer (2016). Galesauridae in our analysis is supported by two synapomorphies: character 15, presence of a suborbital angulation between maxilla and jugal (1), and character 49, strongly curved main cusp in posterior postcanines (1).

CONCLUSION

Cynosaurus suppostus is a medium-sized late Permian basal cynodont, known from only nine confidently-identified specimens recovered in the Karoo Basin, five of them previously unpublished. Specimens of Cynosaurus for which the provenance is known suggest a very restricted geographic distribution of the taxon, within a diameter of approximately 150 kilometres. There are two specimens known from layers of the Cistecephalus AZ and six specimens from levels of the Daptocephalus AZ.

Figure 11. Majority rule consensus of the 16 most parsimonious trees recovered in the phylogenetic analysis of basal cynodonts. Asterisk indicates position of Cynosaurus. Numbers below the branch indicate frequency of clades in the fundamental trees. Numbers above the branch represent bootstrapping value/Bremer support (presented only for groups with Bremer support higher than one).
From The postcanine morphology is a slightly curved main and from Progalesaurus but both with poor support. A monophyletic Gale-sauridae comprises only Galesaurus and Progalesaurus. The incomplete secondary palate in Progalesaurus is only recovered as a member of this family in one of the new specimens described, representing only the third instance of a non-mammaliaform cynodont taxon possessing these bones.

An updated phylogeny of basal cynodonts recovered monophyletic Charassognathidae and Probainognathia, but both with poor support. A monophyletic Gale-sauridae comprises only Galesaurus and Progalesaurus. Cynosaurs is only recovered as a member of this family in two of the 16 mpt, and therefore its identity as a galesaurid cannot be confirmed at present.

ABBREVIATIONS

Institutional
AM Albany Museum, Grahamstown, South Africa.
MMK McGregor Museum, Kimberley, South Africa.
AMNH FARBB American Museum of Natural History, Fossil Amphibian, Reptile, and Bird Collection, New York, U.S.A.
BP Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg, South Africa (formerly the Bernard Price Institute for Palaeontological Research).
BSPG Bayerische Staatsammlung fur Paläontologie und Geologie, Munich, Germany.
NMQR National Museum, Bloemfontein, South Africa.
NHMUK The Natural History Museum, London, United Kingdom.
RC Rubidge Collection, Wellwood, Graaff-Reinet, South Africa.
SAM Iziko South African Museum, Cape Town, South Africa.
TM Ditsong National Museum of Natural History (formerly Transvaal Museum, Northern Flagship Institution), Pretoria, South Africa.
UCMP University of California Museum of Paleontology, Berkeley, U.S.A.

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