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# **New dicynodonts (Therapsida, Anomodontia) from near the Permo-Triassic boundary of Laos: implications for dicynodont survivorship across the Permo-Triassic mass extinction and the paleobiogeography of Southeast Asian blocks**

Chloe Olivier, Bernard Battail, Sylvie Bourquin, Camille Rossignol, J.-Sébastien Steyer, Nour-Eddine Jalil

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**New dicynodonts (Therapsida, Anomodontia) from near the Permo–Triassic boundary of Laos: implications for dicynodont survivorship across the Permo–Triassic mass extinction and the paleobiogeography of Southeast Asian Blocks**

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3 New dicynodonts (Therapsida, Anomodontia) from near the  
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6 Permo–Triassic boundary of Laos: implications for dicynodont  
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9 survivorship across the Permo–Triassic mass extinction and the  
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12 paleobiogeography of Southeast Asian Blocks  
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14 CHLOE OLIVIER, \*,<sup>1</sup> BERNARD BATAIL, <sup>1</sup> SYLVIE BOURQUIN, <sup>2</sup> CAMILLE

15 ROSSIGNOL, <sup>3</sup> J. -SEBASTIEN STEYER, <sup>1</sup> and NOUR-EDDINE JALIL<sup>1,4</sup>

16 <sup>1</sup> CR2P -Centre de Recherche en Paléontologie –Paris, MNHN –Sorbonne Université

17 –CNRS, 57 rue Cuvier, CP 38, F-75005, Paris, France, chloe.olivier@mnhn.fr,

18 bernard.battail@mnhn.fr, jean-sebastien.steyer@mnhn.fr, nour-eddine.jalil@mnhn.fr;

19 <sup>2</sup> Univ Rennes, CNRS, Géosciences Rennes, UMR 6118, 35000 Rennes, France,

20 sylvie.bourquin@univ-rennes1.fr;

21 <sup>3</sup> Universidade de São Paulo, Departamento de Geofísica, Instituto de Astronomia,

22 Geofísica e Ciências Atmosféricas – Rua do Matão, 1226 - Cidade Universitária,

23 Butantã – 05508-090 São Paulo – SP, Brazil

24 camil.rossignol@gmail.com;

25 <sup>4</sup> Université Cadi Ayyad, Faculté des Sciences Semlalia, Laboratoire Biodiversité et

26 Dynamique des Ecosystèmes, Boulevard Prince My Abdellah, 40000 Marrakech,

27 Maroc.

28 \*Corresponding author

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31 OLIVIER ET AL.–NEW DICYNODONTS FROM NEAR THE PERMO-TRIASSIC  
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33 BOUNDARY OF LAOS  
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3 ABSTRACT—The dicynodonts are an emblematic group of herbivorous therapsids,  
4  
5 which survived the Permo–Triassic (P–Tr) crisis. Laotian dicynodonts from  
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7 stratigraphically constrained beds, recently dated using the U–Pb zircon method,  
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9 yield new insights into terrestrial faunas of Southeast Asia during latest Permian and  
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11 the earliest Triassic. Summarily described, they were attributed to the genus  
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13 *Dicynodon*. We provide a new phylogenetic analysis for Laotian dicynodonts, based  
14  
15 on three well-preserved skulls indicating that they belong to two new species:  
16  
17 *Counillonia superoculis* gen. et sp. nov. and *Repelinosaurus robustus* gen. et sp.  
18  
19 nov. Our phylogenetic analysis within Dicynodontia indicate that 1) *Counillonia* is  
20  
21 closely related to some “*Dicynodon*”-grade taxa; and 2) *Repelinosaurus* is a  
22  
23 kannemeyeriiform. The phylogenetic affinities of these new Laotian dicynodonts allow  
24  
25 discussing the survivorship of multiple lineages (Kannemeyeriiformes and  
26  
27 “*Dicynodon*”-grade dicynodontoids) across the P–Tr crisis. The Laotian dicynodonts  
28  
29 also shed new light on the paleobiogeography of the Southeast Asia from the late  
30  
31 Paleozoic to the early Mesozoic, particularly about the timing of collisions between  
32  
33 the Indochina, the South China and the North China blocks. The presence of  
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35 dicynodonts in Laos most likely in the Early Triassic thus implies that the connection  
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37 between the Indochina Block and South China Block occurred no later than the latest  
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39 Permian or earliest Triassic (i.e., when the dicynodonts provide direct evidence for a  
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41 connection).  
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## INTRODUCTION

The dicynodonts are emblematic Permian and Triassic (P–Tr) therapsids. They constitute an important component of the terrestrial P–Tr fauna and were the dominant herbivores in their ecosystems (Cluver and King, 1983). As such, dicynodonts represent a key group for understanding the impact of the P–Tr crisis on terrestrial environments. Known Early Triassic dicynodont genera include the cosmopolitan speciose *Lystrosaurus*, the small-bodied emydopoids *Myosaurus* from South Africa/Antarctica and *Kombuisia* from Antarctica, and the Chinese kannemeyeriiform *Sungeodon* (Fröbisch et al., 2010; Maisch and Matzke, 2014).

In North China, Liu et al. (2013) used U–Pb zircon method (based on zircon U–Pb sensitive high-resolution ion microprobe [SHRIMP] dating) within the Ermaying and Tongchuan dicynodont-bearing formations (with the kannemeyeriiform genera *Shansiodon* and *Sinokannemeyeria*) and dated them to Early to Middle Triassic. More recently, the higher-resolution chemical abrasion-thermal ionization mass spectrometry (CA–TIMS) dated these formations as Middle Triassic (Anisian–Ladinian) (Liu et al., 2018). Thus, the main kannemeyeriiform radiation seems to have occurred after the beginning of the Triassic, with roughly 40 species known by the Middle Triassic (Fröbisch, 2008).

The first record of dicynodonts in Laos (Southeast Asia) dates back to the 19th century: Counillon (1896) mentioned a poorly-preserved and incomplete skull found in the Purple Claystone Formation (Fm) of the Luang Prabang Basin, northern Laos (Fig. 1A). This specimen was first studied by Repelin (1923), who assigned it to a new species of *Dicynodon*, *D. incisivum*, which he considered to be closely related to *Dicynodon orientalis* from the Panchet Fm of India. Later, Das Gupta (1922)

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2  
3 transferred *D. orientalis* to the genus *Lystrosaurus* and Woodward (1932), followed  
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5 by Yuan and Young (1934), attributed Counillon's specimen to *Lystrosaurus*.  
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7 Piveteau (1938) redescribed the specimen and brought the specimen back to  
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9 *Dicynodon*. Based on this study, Battail (2009) and Kammerer et al. (2011) also  
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11 favored this taxonomic attribution. Nevertheless this specimen continued to be  
12  
13 mentioned as *Lystrosaurus* without further comment (Keyser and Cruickshank, 1979;  
14  
15 King, 1988). The Counillon's specimen has unfortunately been lost, preventing  
16  
17 further investigations. The illustrations accompanying the original description cannot  
18  
19 be interpreted with confidence (Colbert, 1982; Kammerer et al., 2011). The taxon  
20  
21 "*Dicynodon incisivum*" should then be considered a nomen dubium (as pointed out by  
22  
23 many authors, e.g., Battail, 2009; Fröbisch, 2009; Kammerer et al., 2011).  
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28 Between 1993 and 2003, Franco-Laotian expeditions led by P. Taquet (MNHN,  
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30 Paris, France) collected an abundant dicynodont remains from the Purple Claystone  
31  
32 Fm of the Luang Prabang Basin. Among these fossils, three dicynodont skulls (LPB  
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34 1993-2, LPB 1993-3, and LPB 1995-9) were tentatively ascribed to the genus  
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36 *Dicynodon* by Battail (2009). However, no phylogenetic analysis has been performed  
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38 on these specimens and their relationships with other dicynodonts remain equivocal.  
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42 The age of these specimens, collected in the Purple Claystone Fm, has long been  
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44 a subject of debate. Indeed, this formation was first been attributed to the Early  
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46 Triassic (Counillon, 1896; Repelin, 1923; Piveteau, 1938), but was later considered to  
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48 be Late Triassic to Middle Jurassic in age (Saurin, 1962). Based on the dicynodont  
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50 skulls and their supposed attribution to the genus *Dicynodon* (Battail, 2009), this  
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52 formation was considered to be late Permian in age (Battail, 2009). Recent  
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54 geochronological analyses (based on U–Pb detrital zircons dated by Laser Ablation  
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56 Induction Coupled Plasma Mass Spectroscopy [LA ICPMS]) performed on  
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3 volcaniclastic rocks from the Purple Claystone Fm suggest a maximum depositional  
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5 age of  $251.0 \pm 1.4$  Ma (Table 1) (Rossignol et al., 2016).  
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8 This temporal framework thus allows us to document dicynodont survivorship and  
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10 post-extinction recovery in a P–Tr basin located outside the classic extensively  
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12 studied Russian (e.g., Benton et al., 2004) and South African ones (e.g., Ward et al.,  
13  
14 2005; Smith and Botha-Brink, 2014; Viglietti et al., 2018). The fauna preserved in the  
15  
16 Luang Prabang Basin also offers new evidence concerning the paleobiogeography of  
17  
18 dicynodonts.  
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21 Here, we provide detailed description of the three Laotian skulls (LPB 1993-2, LPB  
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23 1993-3, and LPB 1995-9), which represent two new taxa. Phylogenetic analysis is  
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25 then performed to test the relationships of these new taxa within Dicynodontia.  
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28 **Institutional Abbreviations**—**BP**, Evolutionary Studies Institute (formerly known  
29  
30 as the Bernard Price Institute for Palaeontological Research and the Institute for  
31  
32 Human Evolution), Johannesburg, South Africa; **LPB**, Laotian specimens found in the  
33  
34 Luang Prabang Basin currently in the Savannakhet Dinosaur Museum, Savannakhet,  
35  
36 Laos; **MCZ**, Museum of Comparative Zoology, Harvard University, Cambridge,  
37  
38 Massachusetts, USA; **NHMUK**, Natural History Museum, London, UK.  
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42 **Anatomical Abbreviations**—**aPt**, anterior ramus of the pterygoid; **Bo**,  
43  
44 basioccipital; **Ch**, choana; **EcPt**, ectopterygoid; **Eo**, exoccipital; **EpiPt**, epipterygoid;  
45  
46 **Fm**, foramen magnum; **Fr**, frontal; **Ip**, interparietal; **Ipv**, interpterygoid vacuity; **Ju**,  
47  
48 jugal; **La**, lacrimal; **Laf**, lacrimal foramen; **Lbf**, labial fossa; **mPt**, median plate of the  
49  
50 pterygoid; **Mx**, maxilla; **Na**, nasal; **Oct**, occipital tuber; **Opt**, opisthotic; **Pa**, parietal;  
51  
52 **Pal**, palatine; **Pant**, pila antotica; **Pbs**, parabasisphenoid; **Pi**, pineal foramen; **Pm**,  
53  
54 premaxilla; **Po**, postorbital; **Pp**, preparietal; **PrF**, prefrontal; **Q**, quadrate; **Qj**,  
55  
56 quadratojugal; **qPt**, quadrate ramus of the pterygoid; **Smx**, septomaxillae; **So**,  
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3 supraoccipital; **Sq**, squamosal; **T**, tusk; **Tpf**, posttemporal fenestra; **Vo**, vomer; **Va**,  
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5 vagus nerve aperture.  
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## 10 GEOLOGICAL SETTING

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14 The Luang Prabang Basin, located in the Indochina Block (Fig. 1A), was originally  
15 studied by Counillon (1896) and consists of an asymmetric NE–SW (Northeast–  
16 Southwest) syncline with NE–SW thrusts separating the Purple Claystone Fm and  
17 the Limestone and Sandstone Fm to the North from younger formations to the South  
18 (Fig. 1B; Blanchard et al., 2013).  
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25 The Limestone and Sandstone Fm is made up of shallow marine deposits, dated  
26 to the late Changhsingian on the basis of its ammonoid remains (Blanchard et al.,  
27 2013). These marine deposits are overlain by black claystone layers, containing a  
28 typical Cathaysian flora (Bercovici et al., 2012).  
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35 The Limestone and Sandstone Fm is overlain by the Purple Claystone Fm, from  
36 which various fossil remains have been excavated (dicynodonts and a  
37 chroniosuchian; Steyer, 2009; Arbez et al., 2018). The Purple Claystone Fm is mainly  
38 composed of homogeneous silty-claystones, silts, and more rarely clays (Bercovici et  
39 al., 2012). The formation also comprises volcanoclastic siltstones and sandstones,  
40 with millimetric to centimetric rounded and highly-weathered volcanoclasts (up to  
41 about 20 vol.%). These volcanoclasts exhibit a variety of volcanic textures (microlithic,  
42 trachytic, porphyritic), and are sometimes embedded within lithic fragments, attesting  
43 to multiple reworking events for these volcanoclasts (Bercovici et al., 2012; Blanchard  
44 et al., 2013). The Purple Claystone Fm also contains subordinate amounts of coarser  
45 deposits, including sandstone and conglomeratic facies with 3D megaripples typical  
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3 of braided river deposits. Conglomeratic levels consist of rounded pebbles of highly  
4 fossiliferous limestones (foraminifers, corals, bryozoans), sub-angular to rounded  
5 pebbles of volcanic rocks, black cherts, red quartzites, red sandstones, and  
6 siltstones. Paleosols, sometimes exhibiting vertical root traces, are developed within  
7 this formation (Bercovici et al., 2012). The sedimentary facies association indicates  
8 braided river depositional environments, evolving vertically to alluvial plain  
9 environments, probably including ponds (Bercovici et al., 2012).

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19 Three samples from the Purple Claystone Fm, including one collected at the  
20 dicynodont site (Fig. 1C), were dated using U–Pb geochronology on detrital zircon  
21 (Rossignol et al., 2016). The sample collected at the dicynodont fossil site yielded a  
22 maximum depositional age of  $252.0 \pm 2.6$  Ma, whereas the other volcanoclastic  
23 samples collected in the same formation yield maximum depositional ages of  $251.0 \pm$   
24  $1.4$  Ma and  $300.5 \pm 3.7$  Ma (Table 1). The various volcanoclastic textures, their  
25 roundness, the relatively low volcanoclast content (below 20%) implying an important  
26 and protracted mixing with other detrital particles, as well as the fact that some of the  
27 volcanoclasts underwent at least two sedimentary cycles (Bercovici et al., 2012;  
28 Blanchard et al., 2013), suggest that these dates, obtained from zircon grains  
29 interpreted as being detrital in origin, represent maximum depositional ages. The  
30 actual age of deposition of the Purple Claystone Fm is therefore likely to be younger.  
31 Both youngest maximum depositional ages (i.e.,  $252.0 \pm 2.6$  Ma and  $251.0 \pm 1.4$  Ma)  
32 encompass the P–Tr boundary ( $251.902 \pm 0.024$  Ma; Burgess et al., 2014) within  
33 uncertainties. The consideration of a late Permian age, potentially plausible, would  
34 nonetheless imply that the reworking of the zircon grains took place within an unlikely  
35 brief time span. Given the age of the overlying formation ( $224.9 \pm 1.0$  Ma; Blanchard  
36 et al., 2013), an age up to the Carnian could be proposed as the theoretical upper  
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3 age limit for the Purple Claystone Fm. However, the occurrence of a regional Middle  
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5 Triassic unconformity (e.g., Racey, 2009), probably superimposed onto the reverse  
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7 fault separating the Purple Claystone Fm from other sedimentary units to the SE (Fig.  
8  
9 1B), reduces the likely time span for the deposition of the Purple Claystone Fm. As a  
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11 consequence, an Early Triassic age for the Purple Claystone Fm and its enclosed  
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13 fossils is considered as the most likely.  
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## 18 SYSTEMATIC PALEONTOLOGY 19

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24 The interpretation of the cranial bone contacts is based either on direct observations  
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26 of the scarce preserved sutures or on relief differences. When possible, some  
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28 sutures were deduced from the contacts between the surrounding bones.  
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33 THERAPSIDA Broom, 1905

34  
35 ANOMODONTIA Owen, 1860

36  
37 DICYNODONTIA Owen, 1860

38  
39 DICYNODONTOIDEA Olson, 1944

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42 *COUNILLONIA* gen. nov.  
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47 **Type Species**—*Counillonias superoculis* gen. et sp. nov., monotypic.

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49 **Etymology**—In honour of the French geologist Jean-Baptiste-Henri Counillon,  
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51 member of the Pavie Missions, who was the first to mention the occurrence of  
52  
53 dicynodonts in the Luang Prabang Basin (Counillon, 1896; see Steyer, 2009 for a  
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55 biography).  
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58 **Diagnosis**—See diagnosis of the type species.  
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*COUNILLONIA SUPEROCULIS* gen. et sp. nov.

(Fig. 2)

**Etymology**—From the Latin *oculis* (dative plural of *oculus*, eye) and *super* (upwards), referring to its largely dorsally opening orbits due to an especially narrow interorbital bar.

**Holotype**—LPB 1993-3, a skull without mandible (basal length: 16.02 cm, maximum width: 13.41 cm). The posterior side of the left orbit, the quadrates, and the stapes are missing. The dorsal surfaces of the premaxilla, nasals, prefrontals, and frontals are partially eroded. The preparietal, prootic, and epipterygoid are poorly preserved.

**Geographic Distribution and Stratigraphic Range**—The specimen LPB 1993-3 (19° 55' 59" N, E 102° 07' 41" E) was discovered in the Purple Claystone Fm, Luang Prabang Basin (Laos). This formation was initially attributed to the Early Triassic by Counillon (1896) then to the late Permian by Battail (2009). Recent geochronological (U–Pb on detrital zircon; Rossignol et al., 2016) analyses suggest a maximum depositional age of  $251.0 \pm 1.4$  Ma (see “Geological setting” above).

**Diagnosis**—Medium-sized dicynodontoid characterized by the unique combination of the following character states: a reduced premaxillary secondary palate; a naso-frontal suture with a distinct posterior process; a narrow intertemporal bar; a reduced temporal fenestra; a pineal foramen located in the posterior quarter of the dorsal skull length; an acute angle of the squamosal wings in lateral view; zygomatic squamosal rami posteriorly inserted at mid-height of the occiput; a relatively large median pterygoid plate; high-angled posterior pterygoid rami; anterior

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3 rami of the pterygoids ventrally highly expanded; a long interpterygoid vacuity; no  
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5 intertuberal ridge; distinct exoccipital and basioccipital contributions to the occipital  
6  
7 condyle; a very sharp and posteriorly directed lateral edge of the paroccipital  
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9 process, which is distinctly offset from the surface of the occipital plate. The naso-  
10  
11 frontal suture with a distinct posterior process distinguishes *Counillonia* from the  
12  
13 Laotian *Repelinosaurus* and “*Dicynodon*”-grade taxa. Further distinguished from  
14  
15 closely related “*Dicynodon*”-grade taxa by a pineal foramen located far posteriorly  
16  
17 and a large median pterygoid plate. Further distinguished from *Repelinosaurus* by an  
18  
19 anteriorly-directed caniniform process, a narrow interorbital bar, a triangular occiput,  
20  
21 and zygomatic squamosal rami posteriorly inserted at mid-height of the occiput.  
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26 **Description**—The skull is slender and short, with a short preorbital region and a  
27  
28 narrow snout. In dorsal view, the skull is relatively broad with zygomatic arches  
29  
30 laterally expanded. The combination of the laterally bowed zygomatic arches and  
31  
32 narrow interorbital result in notably dorsally-directed orbits (Fig. 2A). The surfaces of  
33  
34 the premaxilla, the maxillae, the nasals, the frontals, and the postorbitals are  
35  
36 weathered. Because of this, the mid-nasal, naso-premaxillary, preparieto-frontal, and  
37  
38 postorbital-parietal sutures are not visible (Fig. 2A). The absence of visible sutural  
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40 contacts in the weathered narial region precludes determination of the possible  
41  
42 presence of the septomaxillae (Fig. 2B). It is thus not clear whether the septomaxillae  
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44 form part of the ventrolateral margin of the nares, which seem to be formed only by  
45  
46 the premaxilla anteriorly, the nasals dorsolaterally, and the maxillae ventrolaterally. In  
47  
48 addition, the bone contacts cannot be discerned on the occiput, nor along the medial  
49  
50 partition of the temporal and orbital fossae (Fig. 2B, D).  
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56 The short premaxilla is fused and forms the anterior portion of the snout that  
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58 constricts and ends in a squared tip. The tip of the snout shows weak ventral  
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3 curvature in anterior view (not figured here) as in *Tropidostoma* and *Aulacephalodon*  
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5 (Kammerer and Smith, 2017). However, this curvature and possible ridges or  
6  
7 rugosities cannot be confirmed due to the poor preservation of the dorsal surface of  
8  
9 the premaxilla. The premaxilla contributes to the external anterior edge of the naris.  
10  
11 The large narial opening is situated near the anterior and ventral edges of the snout,  
12  
13 and contributes to more than a third of the surface of the snout (Fig. 2B). The  
14  
15 external ventral margin of the naris is visible in dorsal view (Fig. 2A). The premaxilla  
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17 contacts the nasals posterodorsally and the maxilla posterolaterally at the level of the  
18  
19 anterior third of the nares. In ventral view, the premaxilla bears two thin parallel  
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21 longitudinal ridges (the anterior palatal ridges) that surround a wide, median  
22  
23 longitudinal depression and extend beyond the anterior third of the palatal surface  
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25 (Fig. 2C). This depression turns posteriorly into a sharp crest (the median palatal  
26  
27 ridge), which extends to the vomer posteriorly and is flanked on either side by flat  
28  
29 depressions. The height of this longitudinal ridge increases posteriorly. On the palatal  
30  
31 surface, the premaxilla contacts the maxillae laterally. The absence of visible sutures  
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33 between the premaxilla and the palatines yields no information about a potential  
34  
35 contact (Fig. 2C). The nasals bear a median, rugose and well-developed boss, which  
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37 extends onto the bones bordered by two wide elongated depressions that broaden  
38  
39 posteriorly and terminate on the frontals (Fig. 2A). However, as mentioned above, the  
40  
41 poor preservation of the snout surface precludes firm conclusions to be reached  
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43 about the original external relief of the nasals. The nasals are surrounded by the  
44  
45 frontals and the prefrontals posteriorly, the premaxilla anteriorly, and the maxillae and  
46  
47 lacrimals laterally (Fig. 2A, B).

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49 The prefrontals form the anterodorsal edge of the orbits. On the external surface of  
50  
51 the skull, they contact the frontals medially, the lacrimals laterally, and the nasals  
52  
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1  
2  
3 anteriorly (Fig. 2A). A single rugose boss is visible on each prefrontal. However, as  
4  
5 already noted for the nasals, there is no reliable information about the original relief  
6  
7 of the bones due to the poor preservation of their external surfaces.  
8

9  
10 The frontals form the major part of the skull roof (Fig. 2A). The sutures of the  
11  
12 frontals can be discerned along their contact with the postorbitals, the prefrontals,  
13  
14 and the nasals, as well as the interfrontal one (Fig. 2A). The external surface of the  
15  
16 skull roof is poorly preserved; the presence of postfrontals cannot be confirmed in  
17  
18 LPB 1993-3. The naso-frontal suture has a distinct posterior process. The dorsal  
19  
20 margin of the orbits seems to be largely made up of the frontals. Apart from a small  
21  
22 chip of bone missing on the right dorsal margin of the orbit, the rest of its margin  
23  
24 appears to be preserved, with a symmetry of the lateral margins of the orbits and  
25  
26 continuous lateral borders. The interorbital region is broader than the intertemporal  
27  
28 bar (Fig. 2A).  
29  
30  
31

32  
33 The preparietal is strongly weathered and its anterior part is missing. However, its  
34  
35 posterior region displays a small bulge anterior to the pineal foramen, the relief  
36  
37 possibly being due to its poor preservation (Fig. 2A). The contact between the  
38  
39 preparietal and the nearby bone (the postorbitals, the frontals, and the preparietal)  
40  
41 cannot be determined.  
42

43  
44 The dorsal exposure of the parietals is limited to a midline groove between the  
45  
46 posterior postorbital processes (Fig. 2A). The parietals then contact the postorbitals  
47  
48 laterally and dorsally. External sutural contacts between the parietals and the frontals  
49  
50 are invisible due to the poor preservation of the preparietal and the eroded external  
51  
52 surface of the skull roof. The pineal foramen is surrounded by the parietals  
53  
54 posteriorly, and by the preparietal anteriorly. The oval pineal foramen, with a length of  
55  
56 1.36 cm and a width of 0.96 cm (Table 2), has its long axis perpendicular to the axis  
57  
58  
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1  
2  
3 of the intertemporal bar. It is located in the posterior quarter of the skull roof  
4  
5 (continuous character 7, Appendix 1).  
6  
7

8 The slender postorbitals have lateral and posterior processes. The posterior  
9  
10 postorbital process merges along the intertemporal bar, posterior to the pineal  
11  
12 foramen (Fig. 2A). The temporal portion of the postorbitals appears to be oblique with  
13  
14 a dorsolateral orientation. However, the poor preservation of the external surface of  
15  
16 the postorbital does not allow confirmation of this orientation with certainty. The  
17  
18 posterior postorbital region is thinner than the preorbital one (Fig. 2A). The  
19  
20 postorbitals extend along almost the entire intertemporal bar, bordering the temporal  
21  
22 fossae medially and anteriorly (Fig. 2A). They thus constitute the posterior margin of  
23  
24 the orbits. On their external surface, the posterior postorbital processes contact  
25  
26 mainly the squamosals and to a lesser degree the interparietal posteriorly, the  
27  
28 parietals medially, and the frontals anteriorly. As mentioned above, no reliable  
29  
30 information can be provided on the contact between the postorbitals, the frontals, and  
31  
32 the preparietal. The lateral postorbital processes have a sutural contact with the  
33  
34 jugals anteroventrally and the zygomatic squamosal processes posteroventrally (Fig.  
35  
36 2B).  
37  
38  
39  
40

41 The maxillae form the largest part of the lateral surface of the snout. They contact  
42  
43 the premaxilla anteriorly, the lacrimals and the nasals dorsally (Fig. 2B). The maxillo-  
44  
45 nasal suture lies on the dorsal edge of the nares. There is no sutural contact between  
46  
47 the maxillae and the prefrontals due to the anterior expansion of the lacrimals that  
48  
49 contacts the nasals. The maxillary zygomatic process is posteriorly pointed, and  
50  
51 contacts the squamosal posteriorly and the jugal dorsally (Fig. 2B). The maxillae bear  
52  
53 short caniniform processes housing tusks. The dorsal edge of the erupted portion of  
54  
55 the tusk is anterior to the anterior edge of the orbits. The caniniform processes and  
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57  
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1  
2  
3 the tusks face anteriorly. The tusks have a sub-circular basal section (Fig. 2C; Table  
4  
5 2). On the ventral surface, no maxillary teeth are observed except the tusks (Fig. 2C).  
6  
7  
8 The maxillae contact the anterior rami of the pterygoids and the ectopterygoids  
9  
10 posteriorly, and the jugals and the squamosals laterally. No boundaries are visible in  
11  
12 front of the palatines, and nothing can be confirmed about the extension of medial  
13  
14 maxillary processes posterior to the premaxilla. In *Lystrosaurus* (e.g., Cluver, 1971)  
15  
16 and *Kannemeyeria lophorhinus* (e.g., the holotype, BP/1/3638, and the specimen  
17  
18 formerly referred to *Rechnisaurus cristarhynchus*, NHMUK R11955 [Renaut et al.,  
19  
20 2003; C. Olivier, pers. obs., 2018]), these processes exclude the contact between the  
21  
22 premaxilla and the palatines. A depression lies on the suture between the maxillae  
23  
24 and the pterygoids (Fig. 2B). A broad labial fossa opens posterior to the tusk (Fig.  
25  
26 2C). Its boundaries cannot be discerned; however, it is usually surrounded by the  
27  
28 maxillae ventrally, the jugals dorsolaterally, and the palatines medially (e.g., Cluver  
29  
30 1971). It is therefore not certain whether *Counillonia* has a true labial fossa  
31  
32 (circumscribed by the maxillae, the palatines, and the jugals) or a comparable  
33  
34 structure to the foramen in dicynodonts such as *Diictodon*, *Endothiodon* or  
35  
36 *Dicynodontoides* (e.g., Angielczyk and Kurkin, 2003).  
37  
38  
39  
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41  
42

43 The lacrimals are relatively triangular in lateral view (Fig. 2B). They contact the  
44  
45 nasals and prefrontals dorsally, the maxillae ventrally, and the jugals posteriorly.  
46  
47 Their anterior well-developed expansions exclude a maxillo-prefrontal sutural contact.  
48  
49 Their sutures within the orbits are not visible. The lacrimals constitute the anterior  
50  
51 margin of the orbits with the jugals anteroventrally and the prefrontals anterodorsally  
52  
53 (Fig. 2B). Within the orbit, each lacrimal is perforated by a single foramen (Fig. 2A).  
54  
55

56 The jugals are longitudinally elongated and form the ventral edge of the orbits (Fig.  
57  
58 2B). However, their expansion within the orbits and their natural limits cannot be  
59  
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1  
2  
3 discerned due to the absence of visible sutures, as noted above. Visible sutures on  
4  
5 the lateral side of the skull show a long scarf joint with the maxillae ventrally, a jugal  
6  
7 posterior process contacting the postorbitals posteriorly, and a small contact with the  
8  
9 zygomatic squamosal processes ventroposteriorly and the lacrimals anterodorsally  
10  
11 (Fig. 2B).  
12

13  
14 The squamosals are triradiate with zygomatic, temporal, and quadrate rami. The  
15  
16 zygomatic ramus shapes the posterior region of the zygomatic arch (Fig. 2B). In  
17  
18 dorsal view (Fig. 2A), it widens posteriorly into a wing-shaped structure without a  
19  
20 folded edge. It becomes narrow in the pointed anterior region, without dorsoventral  
21  
22 expansion posterior to the postorbital bar (Fig. 2B). The squamosal zygomatic  
23  
24 processes contact the jugals, the postorbitals, and the maxillae anteriorly (Fig. 2B).  
25  
26 They circumscribe laterally and partly posteriorly the temporal fossae. The zygomatic  
27  
28 squamosal rami show a relatively ventral insertion on the back of the skull, at mid-  
29  
30 height on the occiput (Fig. 2D). On the lateral side, they do not reach the dorsal  
31  
32 region of the occiput. The temporal processes delimit the temporal fossae  
33  
34 posteromedially. On their external surface, they contact the postorbitals dorsally. On  
35  
36 their occipital side, no contact between bones is visible (Fig. 2D). The absence of the  
37  
38 limits of the tabulars does not allow us to determine whether the squamosals are  
39  
40 separated from supraoccipitals by the tabulars. The steep angle between the  
41  
42 temporal and zygomatic processes of the squamosal slightly exceeds  $90^\circ$  (Fig. 2D).  
43  
44 The wide lateral extensions of the squamosal make an angle of less than  $90^\circ$  with the  
45  
46 occipital side. A part of the lateral edge of the occiput is thus hidden. The squamosals  
47  
48 extend posterior to the occipital condyle (Fig. 2C).  
49  
50  
51  
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55  
56 The lateral surface of the braincase is strongly eroded but bone structures can be  
57  
58 noted. Although the sutural contacts of the prootics are not visible, the basal part of  
59  
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1  
2  
3 the left pila antotica (not figured here) is preserved. Only the dorsal region of the long  
4 and narrow epipterygoids, which contacts the ventral process of the parietals, is  
5 preserved. A strong anteroventral depression in the squamosals indicates the  
6 connection with the missing quadrates (Fig. 2B).  
7  
8  
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11 The vomer displays a tuberosity turning into a vertical blade, which narrows  
12 posteriorly and separates the two choanae (Fig. 2C). The width of the median blade  
13 is constant along its length. The vomer contacts the premaxilla anteriorly and the  
14 pterygoids posteriorly. It forms the anterior margin of an elongated and ovoid  
15 interpterygoid vacuity (Fig. 2C).  
16  
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24 The palatines border the choanae anterolaterally. The anterior palatine expansions  
25 form rugose and textured pads indicating a keratinized covering (Fig. 2C). They  
26 narrow posteriorly to form relatively smooth processes. The palatines contact the  
27 anterior rami of the pterygoids along their entire lateral scarf joint and are anteriorly  
28 bordered by the maxillae. However, as mentioned above, due to the uncertainties  
29 about their anterior sutural contact, it is not clear whether they contact the premaxilla.  
30  
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37  
38 A lateral palatine foramen is present alongside each anterior expanded pad (Fig. 2C).  
39

40 Each pterygoid has an anterior ramus and a posterior (or quadrate) ramus. A  
41 single median plate connects the two bones and links the four rami. The pterygoids  
42 contact the secondary palate and the basicranium (Fig. 2C). Their ventral projections  
43 extend strongly anteroventrally, such that they form an anterior depression with the  
44 maxillae (Fig. 2B). These anterior pterygoid keels extend along most of the length of  
45 the anterior rami. Nevertheless, this extension cannot be precisely measured  
46 because the sutures are not visible laterally (Fig. 2B). The anterior rami of the  
47 pterygoids merge from the median plate, posterior to the interpterygoid vacuity. The  
48 interpterygoid vacuity is thus bordered by the pterygoids posteriorly and the vomer  
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3 anteriorly. The posterior margin of the vacuity rises flush with the median plate of the  
4  
5 pterygoids. The ventral surface of the narrow median plate bears a thin crista  
6  
7 oesophagea (Fig. 2C). The median plate of the pterygoids contacts the  
8  
9 parabasisphenoid posteriorly and the vomer anteriorly. In addition, a possible  
10  
11 contribution of the parabasisphenoid to the interpterygoid vacuity cannot be proved.  
12  
13  
14 Two posterior rami of the pterygoids contact the squamosal fossa posteriorly and  
15  
16 probably the medial condyles of the quadrates laterally.  
17

18  
19 Despite the absence of visible sutural contacts on the lateral side of the skull, the  
20  
21 presence of the ectopterygoids is indicated by a variation in bone texture on the  
22  
23 lateral border of the anterior rami of the pterygoids (Fig. 2B). The ectopterygoids  
24  
25 have a slender leaf shape and expand laterally along the anterior rami of the  
26  
27 pterygoids. They do not expand posterior to the palatines in palatal view (Fig. 2C).  
28  
29  
30

31  
32 The crista oesophagea continues onto the parabasisphenoid and then diverges  
33  
34 posteriorly to form the ridges leading to the basitubera (Fig. 2C). The contribution of  
35  
36 the parabasisphenoid to the fenestra ovalis of the tubera is considerably restricted in  
37  
38 comparison with the basioccipital. The stapedial facet is ventrolaterally directed and  
39  
40 its narrow margin mostly extends anteroposteriorly. The paired carotid canals,  
41  
42 located in the anterior region of the parabasisphenoid in many dicynodonts (e.g.,  
43  
44 Maisch, 2002; Surkov and Benton, 2004), are not visible here. No intertuberal ridge is  
45  
46 visible. The basioccipital extends onto the occipital plate and with the exoccipitals  
47  
48 forms a tripartite occipital condyle (Fig. 2D). The exoccipitals and the basioccipital  
49  
50 appear not to be fused in the condyle. A circular central depression is located  
51  
52 between the three occipital sub-condyles. Medially, the exoccipitals border the  
53  
54 aperture of the vagus nerves (Dutuit, 1988).  
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3 The contacts between the interparietal and the other bones, forming the occipital  
4 side and the posterior region of the skull roof, cannot be discerned (Fig. 2D). Despite  
5 the eroded surface of the posterior postorbital processes, the interparietal does not  
6 seem to contribute to the skull roof (Fig. 2A).  
7

8  
9  
10  
11 The occiput is triangular in posterior view (Fig. 2D). Although sutures are not  
12 clearly preserved, the overall similarity of the occiputs of the *Counillonia* type  
13 specimens to those of other dicynodonts (Cluver, 1971: *Lystrosaurus*; Cluver &  
14 Hotton III, 1981: *Dicynodon* and *Diictodon*) suggests that they shared a similar  
15 construction of the occiput. The teardrop-shaped foramen magnum may be laterally  
16 bordered by the exoccipitals, which overhang the basioccipital as in other  
17 dicynodonts. They would also contact the supraoccipital dorsally, the opisthotics  
18 laterally, and the basioccipital ventrally. A central depression on the supraoccipitals  
19 overhangs the foramen magnum and is dorsally bordered by a weak transverse  
20 nuchal crest, which extends upwards towards the interparietal. The extent of the  
21 tabulars cannot be determined. The broad oval post-temporal fenestrae are located  
22 dorsal to the level of the occipital condyle, at the transverse level of the mid-height of  
23 the foramen magnum (Fig. 2D). They are oriented in the ventromedial-dorsolateral  
24 axis and would be delimited by the squamosal laterally, the supraoccipital  
25 dorsomedially, and the opisthotic ventromedially as in most dicynodonts. An oblique  
26 ridge on the supraoccipital extends over the fenestra. This ridge continues, below the  
27 fenestra, on the opisthotics and terminates in a sharp tuberosity.  
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54 KANNEMEYERIFORMES Maisch, 2001

55 *REPELINOSAURUS* gen. nov.  
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3 **Type Species**—*Repelinosaurus robustus* gen. et sp. nov., monotypic.

4  
5 **Etymology**— In honour of the French geologist Joseph R epelin, member of the  
6  
7 Pavi e Missions, who described and named Counillon’s dicynodont skull “*Dicynodon*  
8  
9 *incisivum*” (R epelin, 1923; see Steyer, 2009 for a biography). Also from the latinized  
10  
11 Greek saurus (a lizard) often used for non-mammalian synapsids, colloquially known  
12  
13 as ‘mammal-like reptiles’.

14  
15  
16  
17 **Diagnosis**—See diagnosis of the type species

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20  
21 *REPELINOSAURUS ROBUSTUS* gen. et sp. nov.

22  
23  
24 (Figs. 3–5)

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26  
27  
28 **Etymology**—From the Latin robustus (robust) referring to its robust cranial  
29  
30 appearance.

31  
32 **Holotype**—LPB 1993-2, a partial skull without mandible (basal length: 19 cm).  
33  
34 The left postorbital bar, the zygomatic arch, the dorsolateral wing of the squamosal,  
35  
36 the left quadratojugals, the quadrates, more than half of the left part of the occipital  
37  
38 side, the external portion of the tusks, and the stapes are missing. The palatal  
39  
40 surface is strongly eroded: most of the sutures cannot be made out and some bones  
41  
42 are poorly preserved or are missing.

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44  
45  
46 **Referred Material**—LPB 1995-9 is a skull (basal length: 15.72 cm) lacking the  
47  
48 mandible, the right quadrate ramus of the pterygoid, the left stapes, the quadrates,  
49  
50 and the left quadratojugal. The right stapes and the epipterygoids are poorly  
51  
52 preserved. The specimen was subjected to lateral compression. However, the left  
53  
54 orbit seems to have maintained its original shape.

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2  
3 **Geographic Distribution and Stratigraphic Range**—Same as for *Counillonia*  
4  
5 (see above), LPB 1993-2 (19° 55' 59" N, 102° 07' 41" E) and LPB 1995-9 (19° 55'  
6  
7 16" N, 102° 06' 27" E) were collected in the Purple Claystone Fm, Luang Prabang  
8  
9 Basin (Laos).  
10

11 **Diagnosis**—Medium-sized dicynodontoid characterized by the unique  
12  
13 combination of the following character states: a reduced preorbital region; a notch on  
14  
15 the dorsal edge of the narial opening; nasal bosses present as a median swelling  
16  
17 with a continuous posterior margin; a straight fronto-nasal suture; parietals exposed  
18  
19 in midline groove; a relatively flat temporal portion of the postorbital, so that most of  
20  
21 the exterior surface of the bone faces dorsally; a vertical caniniform process; high  
22  
23 insertion of the zygomatic squamosal rami on the occiput posteriorly. Distinguished  
24  
25 from all dicynodontoids by a very small preorbital region. Further distinguished from  
26  
27 all kannemeyeriiforms by a median nasal swelling with a continuous posterior margin  
28  
29 and a flat temporal portion of the postorbital. Further distinguished from the Laotian  
30  
31 *Counillonia* by a wide interorbital bar, a straight fronto-nasal suture, a vertical  
32  
33 caniniform process, a rectangular occiput, and a high insertion of the zygomatic  
34  
35 squamosal rami on the occiput posteriorly.  
36  
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41 **Remarks**—Some differences distinguish LPB 1993-2 and LPB 1995-9 such as (1)  
42  
43 the position of the pineal foramen on the skull roof more posterior in LPB 1993-2  
44  
45 (continuous character 6, Appendix 1); (2) a higher angulation between the occiput  
46  
47 and the palate in LPB 1993-2 (continuous character 13, Appendix 1); (3) a relatively  
48  
49 flat palatal surface of the premaxilla in LPB 1993-2 or with marked depressions on  
50  
51 either side of the median crest in LPB 1995-9 (discrete character 29, Appendix 1); (4)  
52  
53 a sutural contact between the maxillae and the prefrontals present in LPB 1995-9  
54  
55 and absent in LPB 1993-2 (discrete character 49, Appendix 1); (5) a preparietal  
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3 depressed in LPB 1993-2 or flush with the skull roof in LPB 1995-9 (discrete  
4  
5 character 68, Appendix 1); (6) a bigger pineal foramen in LPB 1995-9 (Table 2); (7) a  
6  
7 tusk basal section compressed mediolaterally in LPB 1995-9 and anteroposteriorly in  
8  
9 LPB 1993-2 (Table 2); and (8) more-developed ornamentation on the frontals in LPB  
10  
11 1993-2. However, each character state variation noted could be due to taphonomic  
12  
13 deformation, ontogeny, sexual dimorphism or other intraspecific variability (discussed  
14  
15 below). Moreover, LPB 1995-9 and LPB 1993-2 were found in the same geological  
16  
17 formation, suggesting conspecificity.  
18  
19

20  
21 **Description**—The skulls are narrow and robust with a wide and short snout that  
22  
23 narrows slightly anteriorly, and terminates in a squared tip. *Repelinosaurus* has a  
24  
25 wider interorbital region (Figs. 3A; 4A) than *Counillonina* (Fig. 2A). The orbits are thus  
26  
27 open mainly laterally. The dorsal surfaces of the premaxilla, maxillae, and nasals of  
28  
29 LPB 1995-9 are weathered, but the preservation of these surfaces in LPB 1993-2  
30  
31 displays strong rugosities on the snout (Figs. 3A; 4A). Nevertheless, the naso-  
32  
33 premaxillary and the mid-nasal sutures cannot be traced in LPB 1993-2. The  
34  
35 septomaxilla is well preserved in LPB 1995-9 unlike LPB 1993-2 where the poor  
36  
37 preservation of the naris does not yield information about this bone (Figs. 3B; 4B; 5).  
38  
39 Sutures are not visible on the occiput of either specimen, except for the connection of  
40  
41 the right quadrate in LPB 1995-9. The scarf joints also cannot be discerned on the  
42  
43 medial portion of the temporal and orbital fossae, but the dorsal head of the  
44  
45 epipterygoid and the basal region of the pila antotica are preserved in LPB 1995-9  
46  
47 (Fig. 4B). The palatal surface of LPB 1993-2 is poorly preserved; few sutures are  
48  
49 thus visible.  
50  
51  
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55  
56 As mentioned above, lots of pits and strong rugosities mark the dorsal surface of  
57  
58 the premaxilla in LPB 1993-2 and extend onto the nasals before stopping abruptly at  
59  
60

1  
2  
3 the naso-prefrontal and naso-frontal sutures (Fig. 3A). These rugosities are thought  
4  
5 to indicate a keratinized covering (e.g., Angielczyk et al., 2018). The premaxilla  
6  
7 contributes to the external anterior edge of the nares. In lateral view, the well-  
8  
9 developed nares of both LPB 1995-9 and 1993-2 represent more than half of the  
10  
11 length of the snout (Figs. 3B; 4B). Their ventral edges are close to the ventral border  
12  
13 of the snout. The premaxilla is toothless and anteriorly bears two short parallel  
14  
15 longitudinal ridges, which are separated by a shallow depression and overlie the  
16  
17 anterior quarter of the premaxilla (Figs. 3C; 4C). An anterior rounded pit of medium  
18  
19 size in LPB 1993-2, visible posterior to the premaxillary longitudinal crest, could be of  
20  
21 taphonomic origin (Fig. 3C). Posterior to this depression, a sharp median ridge  
22  
23 extends onto two-thirds of the premaxilla. In LPB 1993-2, the premaxilla is relatively  
24  
25 flat. However, this median ridge is surrounded by two depressions, which deepen in  
26  
27 the posterior region of the secondary palate in LPB 1995-9. These depressions may  
28  
29 be caused by taphonomic lateral compression (discussed below). The premaxilla  
30  
31 contacts the nasals posterodorsally and the maxillae posterolaterally at the level of  
32  
33 the anterior third of the nares in LPB 1995-9 (Figs. 3B; 4B). However, the sutures of  
34  
35 the premaxilla with the nasals and maxillae are not visible in LPB 1993-2. In both  
36  
37 LPB 1995-9 and 1993-2, on the palatal surface, the premaxilla contacts the maxillae  
38  
39 and their caniniform processes laterally. However, the suture between the premaxilla,  
40  
41 maxillae, and palatines are not clearly preserved (Figs. 3C; 4C).  
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49 The well-developed nasal bosses terminate laterally in a posterodorsal notch at  
50  
51 the dorsal edge of the nares, and are separated from the frontals and prefrontals by a  
52  
53 shallow depression (Figs. 3B; 4B). The notch on the posterodorsal edge of the naris  
54  
55 is formed by a thick expansion of the nasal bosses, which hides the external ventral  
56  
57 narial edge in dorsal view. The bosses form a median swelling that is more marked in  
58  
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2  
3 LPB 1993-2 than in LPB 1995-9 (Figs. 3B; 4B). The nasals are bordered by the  
4  
5 frontals and the prefrontals posteriorly, the premaxilla anteriorly, and the maxillae  
6  
7 laterally. However, the nasals do not contact the lacrimals in LPB 1995-9, in contrast  
8  
9 to LPB 1993-2 (Figs. 3B; 4B; 5).  
10

11  
12 The prefrontals form the edge of the orbits with the lacrimals anteriorly, the jugals  
13  
14 ventrally, the postorbitals posteriorly, and the frontals dorsally (Figs. 3A, B; 4A, B). As  
15  
16 for the nasals, the prefrontal extension is broader in dorsal than in lateral view. The  
17  
18 prefrontals bear a weak boss, distinct from the nasals. The prefrontals contact the  
19  
20 maxillae ventrally in LPB 1995-9 (Figs. 4B; 5).  
21  
22

23  
24 The interorbital region of *Repelinosaurus* (Figs. 3A; 4A) is clearly wider than that of  
25  
26 *Counillonia* (Fig. 2A). In *Repelinosaurus*, it is mainly formed by the frontals  
27  
28 constituting the dorsal margin of the orbits, which rise slightly laterally. In addition, as  
29  
30 mentioned above, the prefrontals bear bosses in both specimens. The interorbital  
31  
32 region obscures the orbits in dorsal view, their orientation is thus mainly lateral while  
33  
34 it is dorsolateral in *Counillonia*. In LPB 1993-2, the frontals are separated by a sharp  
35  
36 median ridge bordered by two deep depressions (Fig. 3A). In LPB 1995-9 the  
37  
38 preparietal, the parietals, and the posterior region of the frontals show a depression.  
39  
40 The frontals contact the nasals anteromedially, the prefrontals laterally, the  
41  
42 postorbitals posterolaterally, and the preparietal posteromedially (Figs. 3A; 4A). The  
43  
44 naso-frontal suture is relatively straight in *Repelinosaurus* (Figs. 3A; 4A), whereas it  
45  
46 has a distinct posterior process in *Counillonia* (Fig. 2A). No postfrontals are observed  
47  
48 in LPB 1995-9 (Fig. 4A) but as in *Counillonia*, we cannot determine whether they  
49  
50 were absent or present in LPB 1993-2 because of the eroded external bone surface  
51  
52 (Figs. 2A; 3A).  
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3 In LPB 1993-2, the preparietal is depressed and bordered anteriorly by a ridge  
4 (Fig. 3A), which continues into the median frontal ridge. The surface of the preparietal  
5 is flush with the depressed surface of the frontals in LPB 1995-9 (Fig. 4A). The  
6 preparietal contacts the postorbitals posterolaterally, the short parietals posteriorly,  
7 and the frontals anteriorly (Figs. 3A; 4A).  
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13  
14 The parietal contribution of the skull roof in LPB 1993-2 is limited to a midline  
15 groove between the posterior postorbital processes (Fig. 3A). These posterior  
16 parietal processes are thus slender. Noticeable lateral compression has modified the  
17 angulation of the postorbitals in LPB 1995-9. This taphonomic deformation may have  
18 resulted in artificial contact of the postorbitals in the midline of the intertemporal bar  
19 (Fig. 4A). The posterior expansion of the parietals is dorsally hidden by the posterior  
20 processes of the postorbitals or cannot be determined due to the lack of a clear  
21 suture between the parietal and interparietal. However, the anterior part of the  
22 parietals is preserved. In both specimens of *Repelinosaurus*, the anterolateral  
23 processes of the parietals, bordering the pineal foramen, are more anteroposteriorly  
24 elongate than broad (Figs. 3A; 4A), but their posterior end is not visible. The external  
25 dorsal surface of the parietals contacts the interparietal posteriorly, the postorbitals  
26 posterolaterally, and the preparietal anteriorly. The parietals surround the pineal  
27 foramen posteriorly with the preparietal anteriorly. The oval pineal foramen is clearly  
28 smaller in LPB 1993-2 (0.96 cm of length and 0.66 cm of width) than in LPB 1995-9  
29 (1.33 cm of length and 0.87 cm of width) (Table 2). In both specimens, the foramen is  
30 perpendicular to the intertemporal bar and flush with the skull roof. The pineal  
31 foramen is also more anterior in LPB 1995-9 than in LPB 1993-2 (continuous  
32 character 6, Appendix 1). In ventral view, the preservation of the specimens of  
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3 *Repelinosaurus* does not allow observation of the sutural contact between the  
4  
5 parietals and the prootic (Figs. 3B; 4B).  
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8 The lateral postorbital bars possess tuberosities in LPB 1993-2, in contrast to LPB  
9  
10 1995-9 (Figs. 3A, B; 4A, B). The posterior postorbital processes of *Repelinosaurus*  
11  
12 extend over the entire narrow intertemporal bar as in *Counillonia* (Figs. 2D; 3B; 4B).  
13

14 The temporal portion of the postorbitals is flat and dorsally directed in LPB 1993-2  
15  
16 (Fig. 3A). We consider that its slightly oblique direction in LPB 1995-9 is due to lateral  
17  
18 compression (Fig. 4A). This horizontal expansion of the posterior processes of the  
19  
20 postorbitals in *Repelinosaurus* is linked to a large fossa formed by the postorbitals  
21  
22 and the parietals below the intertemporal bar. The posterior processes of the  
23  
24 postorbitals, widened in both LPB 1993-2 and LPB 1995-9, contact the squamosals  
25  
26 and the interparietal posteriorly. Anteriorly, they are separated from the preparietal  
27  
28 and the parietals by a sharp ridge in LPB 1995-9 (Fig. 4A). The postorbital surface  
29  
30 has a triangular depression between the posterior and lateral processes (Figs. 3A;  
31  
32 4A). The lateral process of the postorbitals constitutes the posterior margin of the  
33  
34 orbits. They are wider in LPB 1993-2 than in LPB 1995-9 (Figs. 3B; 4B). In LPB  
35  
36 1995-9, they have a sutural contact with the jugals anteroventrally and the zygomatic  
37  
38 squamosal processes posteroventrally (Fig. 4A). The state of preservation of the  
39  
40 zygomatic arches of LPB 1993-2 does not provide information about the location of  
41  
42 the scarf joints. In dorsal view, the lateral expansion of the postorbital bars is smaller  
43  
44 in *Repelinosaurus* than in *Counillonia*, giving the skull of *Repelinosaurus* a narrower  
45  
46 appearance (Figs. 2A; 3A; 4A).  
47  
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54 The lateral surface of the maxilla displays stronger rugosities in LPB 1993-2 than  
55  
56 in LPB 1995-9 (Figs. 3B; 4B), but it is difficult to determine the degree to which these  
57  
58 rugosities are a real feature. In both skulls, the maxillae contact the premaxilla  
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3 anteriorly, and the lacrimals and nasals dorsally. However, in LPB 1993-2, the  
4  
5 maxillae do not contact the prefrontals because the anterior process of the lacrimals  
6  
7 intervenes, in contrast to LPB 1995-9 (Figs. 3B; 4B; 5). In LPB 1993-2, a notch on the  
8  
9 palatal rim is visible on the right side of the skull but not on its left, suggesting a  
10  
11 taphonomic origin. The poor preservation of the lateral surface of LPB 1993-2 does  
12  
13 not provide information about the sutures in the zygomatic arch. Nevertheless, these  
14  
15 contacts are visible in LPB 1995-9 (Fig. 4B). The zygomatic processes of the  
16  
17 maxillae comprise a bifid tip embedded in the squamosals and dorsally bordered by  
18  
19 the jugals. The maxillae are relatively robust, especially in LPB 1993-2. In addition,  
20  
21 the caniniform process is more developed in LPB 1993-2 than in 1995-9 (Figs. 3B;  
22  
23 4B). In *Repelinosaurus* (Figs. 3B; 4B), the caniniform process is vertical, whereas it is  
24  
25 anteriorly directed in *Counillonia* (Fig. 2B). The external part of the tusks is missing in  
26  
27 LPB 1993-2 but the tusk roots are anteroposteriorly flattened, while they are  
28  
29 mediolaterally compressed in LPB 1995-9 (Table 2). In LPB 1995-9, the tusks are  
30  
31 posteriorly directed and turn medially, forming a medial concavity (Fig. 4B). The lack  
32  
33 of fractures and the direction of the main taphonomic distortion (see above) suggest  
34  
35 that the tusks have not been deformed, but the space left between the tusks would  
36  
37 not be sufficient to insert a jaw (J. Camp, pers. comm., 2017). Moreover, the distinct  
38  
39 wear facet (formed as the mandible slides, e.g., Cluver, 1971; K. Angielczyk, pers.  
40  
41 comm., 2018) observed on the inner surface of the left tusk, is backwardly directed,  
42  
43 indicating distortion. The distal part of the right tusk is too eroded to reach any  
44  
45 conclusion. On the ventral orbital edge, a rounded labial fossa is visible posterior to  
46  
47 the caniniform process (Figs. 3C; 4C). Nevertheless, as noted in *Counillonia*, the  
48  
49 sutural contacts cannot be discerned; therefore, we cannot conclude whether  
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3 *Repelinosaurus* has a true labial fossa (circumscribed by the maxillae, palatines, and  
4  
5 jugals) or just a labial foramen (e.g., Angielczyk and Kurkin, 2003).  
6  
7

8 In LPB 1995-9, the well-preserved septomaxillae form with the maxillae the  
9  
10 posteroventral part of the margin of the nares with nasals dorsally, and the premaxilla  
11  
12 anteriorly, where they bear a sharp ridge, which partly divides the nares (Figs. 4B; 5).  
13

14 The lacrimals are limited by the nasals anteriorly, the prefrontals dorsally, the  
15  
16 maxillae anteroventrally, and the jugals posterolaterally in LPB 1993-2 (Fig. 3B).  
17  
18 Their anterior well-developed expansion does not allow a sutural contact between the  
19  
20 maxillae and the prefrontals. On the lateral surface of LPB 1995-9, the lacrimals are  
21  
22 only limited by the maxillae anteriorly and slightly by the jugals posterolaterally (Fig.  
23  
24 4B). A sutural contact between the maxillae and the prefrontals is also reported in  
25  
26 some dicynodonts such as *Kombuisia* (e.g., Fröbisch, 2007) or *Kannemeyeria* (e.g.,  
27  
28 Renault, 2000). Nevertheless, the antorbital margin formed by the prefrontals, the  
29  
30 lacrimals, and the maxillae (Figs. 4B; 5) seems to be unique in LPB 1995-9 within  
31  
32 dicynodonts. We cannot therefore rule out the possibility that the limits of the  
33  
34 lacrimals may be inaccurate due to taphonomic deformation. Additionally, the left  
35  
36 lateral side of the skull is too eroded and this particular bone contact cannot be  
37  
38 confirmed. On both skulls of *Repelinosaurus*, the bone sutures of the orbits are not  
39  
40 visible (Figs. 3A; 4A). In LPB 1995-9, the lacrimals show a tuberosity on the antorbital  
41  
42 rim, which forms the anterior border of the lacrimal foramen.  
43  
44  
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48 The jugals make a small contribution to the lateral surface of the skulls (Figs. 3B;  
49  
50 4B). In LPB 1993-2, their sutures with the other bones on the zygomatic arches  
51  
52 (except the maxillae and lacrimals) cannot be determined because of poor  
53  
54 preservation. The zygomatic arches of LPB 1995-9 show a sutural contact between  
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3 the jugals and the postorbitals posteriorly, and the squamosals posteroventrally (Fig.  
4  
5 4B).

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8 The zygomatic squamosal processes form the posterior regions of the zygomatic  
9  
10 arches, and circumscribe the temporal fossae laterally and partly posteriorly. They  
11  
12 widen posteriorly into a wing-shaped processes and become narrow, without  
13  
14 dorsoventral expansion posterior to the postorbital bar (Fig. 3A, B). The right  
15  
16 zygomatic arch of LPB 1993-2 presents a ventral expansion at the intersection  
17  
18 between the descending bar of the postorbital and the zygomatic arch (Fig. 3B),  
19  
20 somewhat reminiscent of the ventrally directed convexity of the squamosal in  
21  
22 *Aulacephalodon* (e.g., Tollman et al., 1980). However, the lack of the left zygomatic  
23  
24 arch and of visible sutures in the right zygomatic arch does not permit us to conclude  
25  
26 whether it is of natural or taphonomic origin. LPB 1995-9 does not exhibit this type of  
27  
28 ventral expansion on its zygomatic arches (Fig. 4B). The edge of the zygomatic  
29  
30 squamosal wing is flat and straight in LPB 1993-2 (Fig. 3B). The lateral compression  
31  
32 affecting LPB 1995-9 has distorted the edge of the zygomatic arch. The squamosal  
33  
34 zygomatic processes of LPB 1995-9 contact the jugals and the postorbitals dorsally,  
35  
36 and the maxillae in the pointed anterior region (Fig. 4B). In contrast to *Counillonia*  
37  
38 (Fig. 2D), the squamosal zygomatic processes of *Repelinosaurus* are inserted  
39  
40 dorsally on the back of the skull, well above the dorsal edge of the foramen magnum  
41  
42 (Figs. 3D; 4D). They extend slightly onto the dorsal region of the occiput in LPB  
43  
44 1993-2 but not in LPB 1995-9 (Figs. 3B; 4B) because of lateral compression. This  
45  
46 compression also raised the intertemporal region and crushed the zygomatic  
47  
48 squamosal processes in LPB 1995-9. The temporal squamosal processes of  
49  
50 *Repelinosaurus*, delimiting the temporal fossae posteromedially, are shorter than in  
51  
52 *Counillonia*. They contact the postorbitals dorsally and the interparietal medially. As  
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3 already noted, the bone contact on the occipital side cannot be traced (Figs. 3D; 4D).  
4  
5 No conclusion is thus possible concerning the limits of the tabulars and the potential  
6  
7 separation of the squamosals and supraoccipitals. The quadrate rami of the  
8  
9 squamosals are laterally expanded in *Repelinosaurus*. Compared to *Counillonia* (Fig.  
10  
11 2D), they are in the same plane as the occiput surface in LPB 1993-2 (Fig. 3D). This  
12  
13 structure cannot be compared in LPB 1995-9 because of deformation and because of  
14  
15 the left quadrate ramus of the squamosal is missing.  
16  
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18  
19 The lateral surface of the skulls is eroded but some structures can be made out: a  
20  
21 deep anteroventral depression in the squamosal may indicate their contact with the  
22  
23 missing quadrate in LPB 1993-2 and in the left side in LPB 1995-9 (Figs. 3B; 4B). In  
24  
25 addition, the dorsal head of the epipterygoid contacting the parietals and the basal  
26  
27 region of the pila antotica are preserved in LPB 1995-9 (Fig. 4B).  
28  
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30  
31 The vomer is missing in LPB 1993-2 but its poorly-preserved anterior region can  
32  
33 be observed (Fig. 3C). It displays a median blade separating the choanae in LPB  
34  
35 1995-9 (Fig. 4C). The width of this blade is constant throughout its length. Anteriorly,  
36  
37 the vomer shows a tuberosity following the posteromedial ridge of the premaxilla  
38  
39 (Figs. 3C; 4C). The vomer is divided posteriorly and delimits the anterior edge of the  
40  
41 interpterygoid vacuity, where it contacts the median plate of the pterygoids (Fig. 4C).  
42  
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44  
45 The palatines are bordered by the anterior rami of the pterygoids laterally (Figs.  
46  
47 3C; 4C) and the maxillae anteriorly. Because of the poor preservation, the  
48  
49 morphology of the palato-premaxillary contact is uncertain. Only the wide anterior  
50  
51 region of the palatines is preserved in LPB 1993-2 (Fig. 3C), but their poor  
52  
53 preservation does not provide relevant information about their texture. In LPB 1995-  
54  
55 9, the palatines widen anteriorly, forming a rugose textured pad (Fig. 4C). No  
56  
57 foramen is observed within the palatines, and we cannot determine whether there is  
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3 a foramen between these palatines and the anterior rami of the pterygoids because  
4  
5 of lateral compression of the palate.  
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8 Due to the multiple breaks and the missing bone in some areas, nothing can be  
9 said about the presence of pterygoid keels in LPB 1993-2 (Fig. 3B). The ventral  
10 projection of the anterior rami of the pterygoids does not strongly extend ventrally in  
11 LPB 1995-9 (Fig. 4B), in contrast to *Counillonia* (Fig. 2B) where this extension  
12 projects strongly ventrally. However, as in *Counillonia*, the absence of sutures in  
13 lateral view prevents measurements of the ventral expansion of the pterygoid keel  
14 from being taken. The thin anterior rami of the pterygoids contact the ectopterygoids  
15 anterolaterally, in the form of a slender leaf in LPB 1995-9. The ectopterygoids do not  
16 expand further posterior to the palatines in palatal view. In LPB 1993-2, they are not  
17 preserved but a shallow depression on the anterolateral edge of the pterygoids  
18 marks their presence. In LPB 1995-9, the teardrop-shaped interpterygoid vacuity is  
19 bordered by the median plate of the pterygoids posteriorly and the vomer anteriorly  
20 (Fig. 4C). The anterior margin of the interpterygoid vacuity is not defined in LPB  
21 1993-2 because the major portion of the vomer is missing. As in *Counillonia*, the  
22 ventral surface of the median plate bears a thin crista oesophagea in LPB 1995-9,  
23 which turns into two ridges posteriorly on the parabasisphenoid (Fig. 4C). However,  
24 the bone surface of LPB 1993-2 is eroded. The preservation of the two skulls of  
25 *Repelinosaurus* excludes any comments about a potential contribution of the  
26 parabasisphenoid to the interpterygoid vacuity. The posterior rami of the pterygoids  
27 are poorly preserved in LPB 1993-2 and are missing in LPB 1995-9 (Figs. 3C; 4C).  
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54 Two ridges extend onto the parabasisphenoid, from the crista oesophagea, and  
55 widen posteriorly (Figs. 3C; 4C). They delimit a broad triangular intertuberal  
56 depression. The parabasisphenoid is mainly vertical and makes less contribution to  
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3 the fenestra ovalis than the basioccipital. The stapedial facet in LPB 1993-2 is  
4  
5 exposed ventrolaterally and its narrow margin extends anteroposteriorly (Fig. 3C). In  
6  
7 LPB 1995-9, the structure of the parabasisphenoid-basioccipital tubera is distorted,  
8  
9 probably because of taphonomic deformation. As in *Counillonia*, the paired carotid  
10  
11 canals, located in the anterior region of the parabasisphenoid, are not visible in either  
12  
13 of the specimens of *Repelinosaurus*. No intertuberal ridge is visible. In LPB 1993-2,  
14  
15 the basioccipital extends onto the occipital plate and with the exoccipital forms a  
16  
17 tripartite occipital condyle (Fig. 3D). The occipital condyle is too poorly preserved in  
18  
19 LPB 1995-9 to be precisely described (Fig. 4D).  
20  
21  
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23

24 Only the right quadrate is preserved in LPB 1995-9 (Fig. 4C, D). It is ventrally bifid,  
25  
26 with lateral and medial condyles separated by a median groove. The lateral condyle  
27  
28 is more anteroposteriorly elongated than the medial one. However, the dorsal lobe  
29  
30 was laterally crushed.  
31  
32

33 The contact between the interparietal and the other bones forming the occiput and  
34  
35 the posterior region of the skull roof cannot be discerned (Figs. 3D; 4D). However, it  
36  
37 seems that the interparietal does not contribute to the skull roof. In both LPB 1993-2  
38  
39 and LPB 1995-9, the interparietal seems to form a deep longitudinal notch, which is  
40  
41 mainly overhung by the postorbitals dorsally. However, the interparieto-parietal  
42  
43 suture is not clearly visible.  
44  
45  
46

47 The occiput is rectangular in LPB 1993-2 (Fig. 3D) but distorted in LPB 1995-9  
48  
49 (Fig. 4D). The insertion of the squamosals on the occiput makes an obtuse angle in  
50  
51 LPB 1993-2 (Fig. 3D): most of the lateral squamosal expansion is thus visible in  
52  
53 occipital view, in contrast to *Counillonia* (Fig. 2D). The lateral compression of LPB  
54  
55 1995-9 may explain the sharper angle of the lateral squamosal expansions and their  
56  
57 asymmetry. As mentioned above, sutures are not clearly preserved. Nevertheless, as  
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3 in *Counillonia*, the overall similarity of the occiputs of *Repelinosaurus* (Figs. 3D; 4D)  
4  
5 to *Lystrosaurus* (Cluver, 1971), *Dicynodon* or *Diictodon* (Cluver & Hotton III, 1981)  
6  
7 suggests that they shared a similar construction of the occiput. However, the  
8  
9 dorsoventral expansion of the tabular cannot be determined. In LPB 1995-9, a short  
10  
11 nuchal crest, which is ventrally bordered by a depression, extends onto the most  
12  
13 dorsal region of the supraoccipital (Fig. 4D). No nuchal crest is visible in LPB 1993-2.  
14  
15 A very wide triangular depression extends laterally to the foramen magnum and  
16  
17 surrounds the posttemporal fenestrae (Figs. 3D; 4D). The anterior tip of this  
18  
19 depression is located near the junction between the root of the squamosal wings and  
20  
21 the supraoccipital. Its ventral base extends between the basal tubera and the oblique  
22  
23 opisthotic crest, which turns into a sharp process.  
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## 33 PHYLOGENETIC ANALYSIS

### 34 35 36 37 **Methodology**

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39 A phylogenetic analysis is used to test the systematic position of the three Laotian  
40  
41 dicynodont specimens. This analysis is based on an augmented version of the matrix  
42  
43 of Angielczyk and Kammerer (2017), which is one of the most recent and  
44  
45 comprehensive analyses of dicynodonts. Our final data set thus includes 106  
46  
47 operational taxonomic units and 194 characters: 171 discrete characters (treated as  
48  
49 of equal weight and as unordered, except for characters 81, 84, 102, 163, 173, and  
50  
51 174 following Angielczyk and Kammerer, 2017), and 23 continuous characters  
52  
53 (Supplementary Data 1–2). All new measurements and codings, made for the Laotian  
54  
55 specimens studied (Appendix 1), are defined using procedures mentioned in  
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3 Kammerer et al. (2011) and personal comments from C. F. Kammerer (2017) and K.  
4  
5 D. Angielczyk (2017). The treatment of the continuous characters is additive,  
6  
7 following Goloboff et al. (2006). Unknown and/or inapplicable states of discrete and  
8  
9 continuous characters are coded as “?” (Strong and Lipscomb, 1999). In order to  
10  
11 treat the continuous characters with a continued and ordered evolution permitted by  
12  
13 Goloboff’s algorithm (Goloboff et al., 2006), we analyzed the data set using TNT 1.1  
14  
15 (December 2013 version) (Goloboff et al., 2008). We performed two analyses: a new  
16  
17 technology search that analyzes different parts of the tree separately (Goloboff,  
18  
19 1999) and a traditional search. In the first case, we did a driven search with the initial  
20  
21 search level set checked every three hits. One hundred replications were chosen as  
22  
23 a starting point for each hit and we required to search to find the most parsimonious  
24  
25 trees twenty times. We did the phylogenetic analysis using sectorial search (default  
26  
27 settings) and tree-drifting (default settings but the number of cycles was 3) to produce  
28  
29 a nearly optimal tree, which could be used for tree-fusing (default settings but a  
30  
31 global fuse every 3 hits was input; Goloboff, 1999). In the second search, we used a  
32  
33 traditional search of TBR branch swapping with 11,111 replications and 9 trees saved  
34  
35 per replications. *Biarmosuchus* was used as an outgroup. We obtained the same  
36  
37 most parsimonious tree with both methods (1156.346 steps, CI = 0.236, RI = 0.712)  
38  
39 (Fig. 6). We indicate the Bremer values as a node support index (Fig. 6; Bremer,  
40  
41 1988). According to the recommendations of Goloboff et al. (2008), we performed  
42  
43 successive traditional searches using the most parsimonious trees as a starting point.  
44  
45 We increased the value of suboptimal trees each step to avoid overestimation of the  
46  
47 value of the Bremer support. We saved successively larger sets of suboptimal trees  
48  
49 (“stop when maxtrees hit” ticked on). The resulting trees were checked to discard  
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51 duplicate cladograms each search. Once the optimal and suboptimal trees stored  
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3 (99,999 unique cladograms), we tested the score differences to lose each node using  
4  
5 “Bremer support” function.  
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## 10 **Results and Comparisons with Previous Dicynodont Phylogenies**

11 The most parsimonious tree obtained (Fig. 6) is completely resolved. The clade  
12  
13 Dicynodontoidea is weakly supported. However, some clades within Dicynodontoidea  
14  
15 are well supported, such as Rhachiocephalidae and Lystrosauridae (Fig. 6).  
16  
17

18 We hereafter follow the comprehensive taxonomy of Kammerer and Angielczyk  
19  
20 (2009). Our results are in accordance with the strict consensus cladogram of  
21  
22 Angielczyk and Kammerer (2017), except for some relationships within  
23  
24 Dicynodontoidea. Our phylogenetic analysis indicates that Pylaecephalidae are  
25  
26 distinct from Emydopoidea, not recovered within Therochelonia, and placed in a  
27  
28 comparable position to that proposed by Angielczyk and Kurkin (2003), Fröbisch  
29  
30 (2007), Angielczyk and Rubidge (2013), Boos et al. (2016), Angielczyk and  
31  
32 Kammerer (2017) and Angielczyk et al. (2018). Additionally, the Kingoriidae are here  
33  
34 included in the Kistecephalia within Emydopoidea as previously proposed (e.g.,  
35  
36 Angielczyk and Kurkin, 2003; Angielczyk and Rubidge, 2013; Castanhinha et al.,  
37  
38 2013; Cox and Angielczyk, 2015; Angielczyk et al., 2016; Angielczyk and Kammerer,  
39  
40 2017; Kammerer and Smith, 2017; Angielczyk et al., 2018). Within dicynodontoids,  
41  
42 the relationships within Cryptodontia (here compositionally equivalent to  
43  
44 Oudenodontidae), Rhachiocephalidae, and Lystrosauridae are consistent with the  
45  
46 results of Angielczyk and Kammerer (2017). In contrast to previous studies (e.g.,  
47  
48 Angielczyk and Rubidge, 2013; Castanhinha et al., 2013; Kammerer et al., 2013; Cox  
49  
50 and Angielczyk, 2015; Kammerer and Smith, 2017), Rhachiocephalidae and  
51  
52 Geikiidae are not included in Cryptodontia, but in Dicynodontoidea (as defined by  
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3 Kammerer and Angielczyk, 2009) as proposed by Boos et al. (2016), Angielczyk and  
4  
5 Kammerer (2017), and Angielczyk et al. (2018).

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7  
8 As mentioned by Kammerer and Angielczyk (2009), no consensus exists about a  
9  
10 taxonomic definition of Kannemeyeriiformes, probably because the alpha taxonomy  
11  
12 of the Triassic forms is still unresolved. If we consider the definition of  
13  
14 Kannemeyeriiformes sensu Maisch (2001) as the clade of Triassic non-lystrosaurid  
15  
16 dicynodontoids, in our current results, the Laotian *Repelinosaurus* may thus be  
17  
18 considered as a kannemeyeriiform. However, the other Laotian Triassic genus  
19  
20 *Counillonia* is a non-kannemeyeriiform dicynodontoid, closely related to Permian  
21  
22 “*Dicynodon*”-grade taxa (i.e., most taxa previously attributed to *Dicynodon* before the  
23  
24 taxonomic revision by Kammerer et al., 2011): *Daptocephalus*, *Peramodon*,  
25  
26 *Dinanomodon*, *Turfanodon*, *Euptychognathus*, *Sintocephalus*, *Jimusaria*, *Gordonia*,  
27  
28 *Delectosaurus*, *Vivaxosaurus*, and the two valid species of *Dicynodon* (Fig. 6;  
29  
30 Kammerer et al. 2011). The stratigraphic definition of Kannemeyeriiformes sensu  
31  
32 Maisch (2001) is thus challenged by the phylogenetic position of *Counillonia*. We  
33  
34 therefore follow the phylogenetic definition of Kannemeyeriiformes sensu Kammerer  
35  
36 et al. (2013) as the clade comprising *Kannemeyeria simocephalus* and all taxa more  
37  
38 closely related to it than to *Lystrosaurus murrayi* or *Dicynodon lacerticeps*. Under this  
39  
40 definition, *Repelinosaurus* is recovered as a kannemeyeriiform. In contrast to recent  
41  
42 studies, our phylogeny recovers a large clade of “*Dicynodon*”-grade taxa uniting  
43  
44 *Daptocephalus*, *Peramodon*, *Dinanomodon*, *Turfanodon*, *Euptychognathus*,  
45  
46 *Sintocephalus*, *Jimusaria*, *Gordonia*, *Delectosaurus*, *Vivaxosaurus*, and the two valid  
47  
48 species of *Dicynodon* (Kammerer et al. 2011). These “*Dicynodon*”-grade taxa and  
49  
50 *Counillonia* form a clade with Kannemeyeriiformes characterized by two non-  
51  
52 ambiguous synapomorphies: (1) a lacrimal not in contact with the septomaxilla  
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3 (60(0)) and (2) a dorsal process on the anterior end of the epipterygoid footplate  
4  
5 (127(1)). The results of Angielczyk and Kurkin (2003) also recovered *Peramodon* and  
6  
7 *Vivaxosaurus* as more closely related to Kannemeyeriiformes than to *Lystrosaurus*.  
8  
9 Within Kannemeyeriiformes, our phylogenetic results indicate that *Repelinosaurus* is  
10  
11 sister to the rest of kannemeyeriiform, which is divided into three relatively well-  
12  
13 supported clades: Shansiodontidae, Kannemeyeriidae, and Stahleckeriidae.  
14  
15 Shansiodontidae, as defined by Maisch (2001), includes *Shansiodon*, *Vinceria*,  
16  
17 *Rhinodicynodon*, and *Tetragonias*. They are sister group to all other  
18  
19 kannemeyeriiforms but *Repelinosaurus*, a position previously recovered by  
20  
21 Castanhinha et al. (2013), Kammerer et al. (2013), Cox and Angielczyk (2015), Boos  
22  
23 et al. (2016), and Kammerer and Smith (2017). Despite the fact that Shansiodontidae  
24  
25 sensu Maisch (2001) are paraphyletic in the analyses of Kammerer and Angielczyk  
26  
27 (2017) and Angielczyk et al. (2018), *Shansiodon*, *Vinceria*, *Rhinodicynodon*, and  
28  
29 *Tetragonias* are also more basal than all other kannemeyeriiforms in their studies.  
30  
31 The compositions of the clades Kannemeyeriidae and Stahleckeriidae are similar in  
32  
33 the current analysis to those of Kammerer and Angielczyk (2017) and Angielczyk et  
34  
35 al. (2018). Stahleckeriidae, as the last common ancestor of *Placerias hesternus* and  
36  
37 *Stahleckeria potens*, and all of its descendants, excluding *Shansiodon wangi* or  
38  
39 *Kannemeyeria simocephalus* (Kammerer et al., 2013), are characterized by six non-  
40  
41 ambiguous synapomorphies: (1) a short interpterygoid vacuity (continuous character  
42  
43 10); (2) a very reduced minimum width of the scapula (continuous character 17); (3) a  
44  
45 very long anterior iliac process (continuous character 21); (4) a smooth and flat  
46  
47 median pterygoid plate (115(1)); (5) the presence of six sacral vertebrae (165(3));  
48  
49 and (6) the *M. latissimus dorsi* inserted on a rugose tuberosity on the posteroventral  
50  
51 surface of the humerus (175(0)). Kannemeyeriidae may therefore be defined here as  
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3 the clade comprising *Kannemeyeria simocephalus* and all taxa more closely related  
4  
5 to it than to *Stahleckeria potens*, *Placerias hesternus*, or *Shansiodon wangi*. This  
6  
7 clade is supported by six non-ambiguous synapomorphies: (1) a high preorbital  
8  
9 region (continuous character 1); (2) a high trochanteric crest on the femur  
10  
11 (continuous character 22); (3) a very narrow scapula (the narrowest in  
12  
13 dicynodontoids; continuous character 23); (4) a dorsal edge of the erupted portion of  
14  
15 the canine tusk anterior to the anterorbital margin (55(0)); (5) a temporal portion of  
16  
17 the skull roof angled dorsally with a strong break in slope near its anterior end  
18  
19 (67(1)); and (6) a lateral edge of the paroccipital process distinctly offset from the  
20  
21 surface of the occipital plate (135(1)).  
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### 28 **Positions of the three Laotian specimens**

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31 Our results indicate that the Laotian specimens LPB 1993-2 and LPB 1995-9 form  
32  
33 a relatively well-supported clade, characterized by five non-ambiguous  
34  
35 synapomorphies: (1) the most reduced preorbital region in dicynodontoids  
36  
37 (continuous character 1); (2) a notch on the dorsal edge of the narial opening (41(1));  
38  
39 (3) nasal bosses present as a median swelling with a continuous posterior margin  
40  
41 (57(1)); (4) parietals exposed in the midline groove (72(1)); and (5) a relatively flat  
42  
43 temporal portion of the postorbitals, so that most of the external surface of the bone  
44  
45 faces dorsally (74(0)). This supports our attribution of these Laotian specimens to the  
46  
47 single new taxon *Repelinosaurus robustus* gen. et sp. nov. erected above. This  
48  
49 Laotian clade is included in Kannemeyeriiformes, which are thus defined by three  
50  
51 derived character states: (1) the absence of postfrontal (64(1)); (2) no converging  
52  
53 ventral keels on the posterior portion of the anterior pterygoid rami (114(0)); and (3)  
54  
55 the absence of the intertuberal ridge (126(0)).  
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3 As already mentioned, the third Laotian specimen LPB 1993-3 is close to some  
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5 “*Dicynodon*”-grade taxa: *Daptocephalus*, *Peramodon*, *Dinanomodon*, *Turfanodon*,  
6  
7 *Euptychognathus*, *Sintocephalus*, *Jimusaria*, *Gordonia*, *Delectosaurus*,  
8  
9 *Vivaxosaurus*, and the two valid species of *Dicynodon* (Kammerer et al. 2011). All  
10  
11 these taxa form a clade supported by four non-ambiguous synapomorphies: (1) the  
12  
13 highest temporal fenestra within dicynodontoids (continuous character 5); (2) a  
14  
15 weakly-developed distal end of the radius in contrast to the other dicynodontoids  
16  
17 (continuous character 19); (3) a rounded anterior tip of the snout (35(0)); and (4) a  
18  
19 raised circumorbital rim (62(1)). Within this clade, LPB 1993-3 is sister to the clade  
20  
21 formed by the late Permian South Gondwanan *Daptocephalus* and *Dinanomodon*,  
22  
23 Chinese *Turfanodon*, and Russian *Peramodon* (Fröbisch, 2009).  
24  
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28 Battail (2009) previously compared the three Laotian specimens with *Lystrosaurus*  
29  
30 and *Dicynodon*. Based on a morphological study, he attributed them to *Dicynodon* as  
31  
32 previously defined by Cluver & Hotton III (1981), before the taxonomic revision of  
33  
34 *Dicynodon* by Kammerer et al. (2011). Our phylogenetic results do not contradict this  
35  
36 preliminary assignment because the Laotian specimens show closer affinities with  
37  
38 “*Dicynodon*”-grade taxa and the two valid species of *Dicynodon* (Kammerer et al.  
39  
40 2011) than with *Lystrosaurus*.  
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## 47 DISCUSSION

### 51 Morphological Variation in *Repelinosaurus robustus*

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53 LPB 1995-9 and LPB 1993-2 are found in the same clade as *Repelinosaurus*,  
54  
55 which is an early kannemeyeriiform (Fig. 6). As noted above, a variety of features  
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3 distinguishes these two specimens. However, these differences could be related to  
4  
5 postmortem distortions, ontogeny, sexual dimorphism or other intraspecific variation.  
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8 LPB 1995-9 is distinguished by well-defined depressions lateral to the median  
9  
10 ridge of the premaxilla in contrast to the flat surface in LPB 1993-2 (discrete  
11  
12 character 29, Appendix 1). Nevertheless, it is clear that LPB 1995-9 was affected by  
13  
14 lateral compression, as indicated by the lack of symmetry in ventral view, the tusks  
15  
16 turned inward, the more anterior position of the left tusk with respect to the right one,  
17  
18 and breaks in the compressed zygomatic arches. In addition, the angulation between  
19  
20 the occipital plate and the palate is less in LPB 1995-9 than in LPB 1993-2  
21  
22 (continuous character 13, Appendix 1) and could be linked to taphonomic distortion.  
23  
24 This latter could also explain other differences such as (1) the direction of the  
25  
26 posterior processes of the postorbitals (slightly oblique in LPB 1995-9 but horizontal  
27  
28 in LPB 1993-2); (2) the insertion of the squamosal wings in the occipital plate  
29  
30 (reaching the dorsal margin of the occiput in LPB 1993-2 but not in LPB 1995-9); and  
31  
32 (3) the dorsal expansion of the parietals in the intertemporal bar (as a midline groove  
33  
34 in LPB 1993-2 but mostly overlapped by the postorbitals in LPB 1995-9). In addition,  
35  
36 although only two specimens of *Repelinosaurus* are currently known, it cannot  
37  
38 excluded that the other morphological differences between the two specimens could  
39  
40 be related to ontogenetic, dimorphic or other intraspecific variation.  
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47 Indeed, the negative allometry measured in the length of the pineal foramen  
48  
49 versus skull size in *Repelinosaurus* (Table 2) could be interpreted as ontogenetic  
50  
51 variability, as observed in *Colobodectes cluveri* (Angielczyk and Rubidge, 2009). In  
52  
53 this taxon, Angielczyk and Rubidge (2009) also noted well-developed caniniform  
54  
55 processes with a disappearance of the palatal rim notch in the largest skull. Here, the  
56  
57 large LPB 1993-2 shows a deeper lateral convexity of the caniniform processes, yet  
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3 no palatal rim notch is present. A greater length of the intertemporal bar posterior to  
4  
5 the pineal foramen is also noted in the smaller LPB 1995-9 (continuous character 6,  
6  
7 Appendix 1), as is the case in the Middle Triassic *Dolichuranus primaevus* (C. Olivier,  
8  
9 pers. obs., 2018, on BP/1/4570 vs. BP/1/4573). This could suggest that the position  
10  
11 of the pineal foramen may be related to ontogeny.  
12

13  
14 LPB 1995-9 is less robust than LPB 1993-2, which bears more developed  
15  
16 ornamentations: (1) its frontals bear a sharp frontal ridge; (2) high rugosities are  
17  
18 noted on its premaxilla, maxillae, lateral processes of the postorbitals, and the  
19  
20 squamosal zygomatic arch; and (3) its nasal bosses are more laterally developed.  
21  
22 Variations in width, depth, and rugosity of skulls of the Middle–Late Triassic  
23  
24 *Dinodontosaurus turpior* appear to be related to ontogeny (e.g., C. Olivier, pers. obs.,  
25  
26 2018; Lucas and Harris, 1996): the large specimen MCZ 1679 bears frontal,  
27  
28 prefrontal, and postorbital bosses, which contrast with the smaller MCZ 1677 (C.  
29  
30 Olivier, pers. obs., 2018). The development of cranial ridges and ornamentations are  
31  
32 indeed related to skull size in *Lystrosaurus*, but only up to a size threshold (Grine et  
33  
34 al., 2006). In addition, the size variation of ridges and ornamentations differs  
35  
36 according to the species of *Lystrosaurus* (Grine et al., 2006). More developed  
37  
38 ornamentations are also observed in the largest skulls of *Lystrosaurus*, but Ray  
39  
40 (2005) supposed a sexually dimorphic variation, with inferred male individuals more  
41  
42 ornamented than females. In addition, a more developed cranial ornamentation in  
43  
44 adult males has been evidenced in *Diictodon* (Sullivan et al., 2003) and in  
45  
46 *Pelanomodon*, which may be linked to the ‘armament’ in the context of sexual  
47  
48 selection (Kammerer et al., 2016). The relative form and size of the nasal bosses  
49  
50 also appears to be related to sexual dimorphism in the Permian *Aulacephalodon*  
51  
52 (e.g., Keyser, 1969; Tollman et al., 1980). However, the quantitative analyses of  
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3 Tollman et al. (1980) indicated a positive allometry in the width of the nasal bosses,  
4  
5 instead suggesting an ontogenetic effect on it in *Aulacephalodon*. Moreover, as seen  
6  
7 in LPB 1993-2, a ventrally directed convexity of the squamosal zygomatic arch in  
8  
9 large specimens of *Aulacephalodon* are observed only in males (e.g., Tollman et al.,  
10  
11 1980).  
12

13  
14 The basal section of the tusk of LPB 1993-2 (anteroposteriorly compressed) is  
15  
16 different from that of LPB 1995-9 (mediolaterally compressed) (Table 2). Angielczyk  
17  
18 and Rubidge (2009) noted the fact that the smallest specimen of *Colobodectes*  
19  
20 *cluveri* has less-developed and newly erupted tusks, is related to ontogeny. In  
21  
22 *Repelinosaurus*, the tusks of LPB 1995-9 are well erupted and in the same proportion  
23  
24 as in the larger LPB 1993-2. This variation in the basal section of the tusk thus  
25  
26 appears unlikely to be linked to ontogeny. The mediolateral compression of the tusks  
27  
28 in LPB 1995-9 could not be explained by lateral postmortem compression because of  
29  
30 the excellent preservation of the tusks. Another intraspecific variation (i.e. related  
31  
32 neither to sex nor to ontogeny) may thus explain the differences in tusk basal  
33  
34 sections. This may also be the case for the preparietal depressed or flush with the  
35  
36 skull roof (discrete character 68, Appendix 1) and for the maxillo-prefrontal suture,  
37  
38 which is either present only in some of the specimen (discrete character 49,  
39  
40 Appendix 1).  
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47 Most morphological variation within *Repelinosaurus robustus* may therefore be  
48  
49 related to ontogeny and/or sexual dimorphism demonstrated to occur in other  
50  
51 dicynodonts (e.g., Keyser, 1969; Tollman et al., 1980; Ray, 2005; Angielczyk and  
52  
53 Rubidge, 2009), taphonomic distortion or other intraspecific variation. Nevertheless,  
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55 as mentioned above, the number of specimens of *Repelinosaurus* is too low to  
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3 assess which kind of intraspecific variation (sexual dimorphism, ontogeny, etc.) is  
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5 present.  
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### 10 **Taxonomic validity of *Repelinosaurus* and *Counillonia***

11 Phylogenetic affinities are found between the Laotian *Counillonia* and the late  
12 Permian *Peramodon*, *Delectosaurus*, *Vivaxosaurus*, *Turfanodon*, *Jimusaria*,  
13  
14 *Gordonia*, *Euptychognathus*, *Daptocephalus*, *Dinanomodon*, *Sintocephalus*, and the  
15  
16 two valid species of *Dicynodon* (Fig. 6; Kammerer et al. 2011). Within the clade  
17  
18 formed by *Counillonia* and these “*Dicynodon*”-grade taxa, the following  
19  
20 autapomorphies distinguish the Laotian dicynodont: (1) a relatively large median  
21  
22 pterygoid plate (continuous character 8, Appendix 1), (2) the absence of an  
23  
24 intertuberal ridge; and (3) opisthotics with distinct posteriorly-directed processes  
25  
26 (Figs. 2C–D). As in *Delectosaurus*, the occipital condyle of *Counillonia* is not fused,  
27  
28 while the other cited “*Dicynodon*”-grade taxa have a co-ossified single unit. The naso-  
29  
30 frontal suture is either straight, as in *Dicynodon huenei* and *Jimusaria*, or has an  
31  
32 anterior process in the other cited “*Dicynodon*”-grade taxa, unlike the clear posterior  
33  
34 process in *Counillonia* (Fig. 2A). Overall, most morphological characters distinguish  
35  
36 *Counillonia* from its closely related “*Dicynodon*”-grade taxa. If we focus on the  
37  
38 geographically close taxa such as the Russian *Peramodon*, *Delectosaurus* and  
39  
40 *Vivaxosaurus*, and the Chinese *Turfanodon* and *Jimusaria*, other differences can be  
41  
42 highlighted. *Peramodon* and *Turfanodon* have a rounded dorsal margin of the  
43  
44 squamosal wings in lateral view (Kammerer et al., 2011), while it is more acute in  
45  
46 *Counillonia* because of a lower lateral opening (Fig. 2B). The interorbital region in  
47  
48 *Turfanodon* is wider than in *Counillonia* (Fig. 2A; Kammerer et al., 2011). *Counillonia*  
49  
50 also has an interpterygoid vacuity and temporal squamosal processes longer than in  
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3 *Jimusaria* (Kammerer et al. 2011); the squamosals therefore do not reach the dorsal  
4 region of the occiput in this Laotian genus (Fig. 2B). In contrast to *Vivaxosaurus*, the  
5 caniniform processes are less anteriorly projected in *Counillonia*, and its maxillae do  
6 not bear a rounded boss anterior to the tusks (Fig. 2B; Kammerer et al., 2011). In  
7 *Counillonia*, the anterior rami of the pterygoids are ventrally highly expanded and  
8 therefore not in the same plane as the more dorsal palatines (Fig. 2C), in contrast to  
9 *Delectosaurus*.

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19 *Repelinosaurus* is recovered as a kannemeyeriiform. Only one genus of  
20 kannemeyeriiform was previously known near the Permo–Triassic boundary: the  
21 Early Triassic *Sungeodon* (Maisch & Matzke, 2014). *Repelinosaurus* differs from all  
22 kannemeyeriiforms by the strong reduction of the preorbital region (Figs. 3A; 4A).  
23 This character state is shared to a lesser degree with *Counillonia* (Fig. 2A) and the  
24 kistecephalian *Kombuisia* (Fröbisch, 2007). As in the Early Triassic *Kombuisia* and  
25 *Myosaurus*, the nasal bosses of *Repelinosaurus* form a single median swelling in  
26 dorsal view (Figs. 3A; 4A), in contrast to currently known kannemeyeriiforms that  
27 have a pair of bosses. In *Repelinosaurus*, the parietals, weakly exposed on the skull  
28 roof, are inserted between the two wide posterior processes of the postorbitals (Figs.  
29 3A; 4A), in contrast with the majority of kannemeyeriiforms except *Sangusaurus*,  
30 *Uralokannemeyeria*, and *Rechnisaurus*. Kannemeyeriiformes are known for their  
31 temporal crest, generally associated with laterally-directed posterior processes of the  
32 postorbitals. This is not the case in *Repelinosaurus* (Figs. 3A–B; 4A–B), where the  
33 postorbitals mainly face dorsally.

## 54 55 56 **New Data Supporting the Survivorship of Multiple Lineages across the P–Tr** 57 58 **Boundary?** 59 60

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3 The latest Permian terrestrial biomes were dominated by herbivorous  
4  
5 pareiasaurs and dicynodonts, and carnivorous gorgonopsians and therocephalians  
6  
7 (e.g., Steyer, 2012; Benton and Newell, 2014). A recent study (Bernardi et al., 2017)  
8  
9 evidenced a link between the distribution of herbivore tetrapods, phytoprovinces and  
10  
11 latitudinal climatic zonation. More specifically, dicynodonts were predominant only in  
12  
13 high paleolatitudes biomes. The dicynodonts were strongly affected by the P–Tr crisis  
14  
15 (e.g., Fröbisch, 2007). The lystrosaurids are the emblematic clade to have survived  
16  
17 the P–Tr event (e.g., Fröbisch, 2007; Botha-Brink et al., 2016). However, as indicated  
18  
19 by the dicynodont phylogenetic relationships recovered herein (e.g., Angielczyk,  
20  
21 2001; Fröbisch, 2007, 2010; Kammerer et al., 2011), other lineages also appear to  
22  
23 cross the end-Permian boundary. Fröbisch (2007) previously highlighted the  
24  
25 interesting phylogenetic position of the Triassic *Kombuisia*, belonging to kingoriids  
26  
27 and closely related to the Permian *Dicynodontoides*. *Kombuisia* is known from the  
28  
29 probable Middle Triassic of South Africa and also the Early Triassic of Antarctica  
30  
31 (e.g., Fig. 6; Fröbisch, 2007, 2010). The stratigraphic positions of the two *Kombuisia*  
32  
33 species imply lengthy ghost lineages, stretching back into the Permian. The Early  
34  
35 Triassic *Myosaurus* is also closely related to Permian dicynodonts and is sister taxon  
36  
37 to the cistecephalids (e.g., Fig. 6; Fröbisch, 2007). In addition, most previous studies  
38  
39 assumed a ghost lineage for Kannemeyeriiformes (e.g., Fröbisch, 2007, 2010;  
40  
41 Kammerer et al., 2011). Kammerer et al. (2011) indeed inferred Permian forms (such  
42  
43 as lystrosaurids or “*Dicynodon*”-grade taxa) as sister groups to the  
44  
45 kannemeyeriiforms. They thus assumed a ghost lineage for the kannemeyeriiforms  
46  
47 that spans at least part of the late Permian and the earliest Triassic.

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49 Most previous studies noted the impact of a potential geographic bias on the  
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51 presence of ghost lineages in dicynodonts (e.g., Angielczyk, 2001; Fröbisch et al.,  
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3 2010; Kammerer et al., 2011). Their hypothesis was supported by the discovery of  
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5 specimens of *Kombuisia* (formerly known from the Karoo Basin in South Africa, dated  
6  
7 to the Middle Triassic) from the Early Triassic Fremouw Fm in Antarctica (Fröbisch,  
8  
9 2010). In addition, the assumption of Kammerer et al. (2013) that supposed the  
10  
11 occurrence of kannemeyeriiforms in the Early Triassic gained support by the recent  
12  
13 description of *Sungeodon* from the Junggar Basin in China (Maisch & Matzke, 2014).  
14  
15 Despite relatively weak node supports, the phylogenetic position of the Laotian  
16  
17 *Repelinosaurus* also helps to shorten the ghost lineage between the  
18  
19 kannemeyeriiforms and the other dicynodontoids, extending the first appearance of  
20  
21 Kannemeyeriiformes to near the P–Tr boundary. In addition, the discovery of the  
22  
23 earliest kannemeyeriiforms in an understudied geographic area such Laos, with  
24  
25 *Repelinosaurus* and China, with *Sungeodon* (Maisch & Matzke, 2014), strengthens  
26  
27 these suggestions, underlining a geographic bias in dicynodont sampling. The  
28  
29 phylogenetic position of *Counillonia* makes it the first known “*Dicynodon*”-grade  
30  
31 dicynodontoid that could have survived the P–Tr extinction (maximum depositional  
32  
33 age of  $251.0 \pm 1.4$  Ma). This supports the survivorship of multiple dicynodont lineages  
34  
35 across the P–Tr event, as previously suggested (e.g., Angielczyk, 2001; Fröbisch,  
36  
37 2007, 2010; Kammerer et al., 2011).  
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44 The dicynodont post-extinction recovery was thought to be have been relatively  
45  
46 delayed (e.g., Sahney and Benton, 2008; Chen and Benton, 2012), starting in the  
47  
48 Middle Triassic when the kannemeyeriiforms underwent a large adaptive radiation  
49  
50 (Fröbisch, 2009). Sun et al. (2012) described an “equatorial tetrapod gap” and  
51  
52 attributed the delayed recovery to excessive paleotemperatures during the Early  
53  
54 Triassic, especially at the warmer equatorial paleolatitudes. However, other studies  
55  
56 have supported a rapid recovery (e.g., Botha and Smith, 2006; Maisch and Matzke,  
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3 2014). The occurrence in the Early Triassic of the kannemeyeriiform *Sungeodon*  
4  
5 (Maisch and Matzke, 2014) and potentially of a new Laotian kannemeyeriiform  
6  
7 *Repelinosaurus* (maximum depositional age of  $251.0 \pm 1.4$  Ma; Rossignol et al.,  
8  
9 2016) would support a rapid recovery of the group after the P–Tr mass extinction  
10  
11 event. In addition, Bernardi et al. (2018) explained the “equatorial tetrapod gap”  
12  
13 defined by Sun et al. (2012) by invoking a northwards tetrapod distribution shift  
14  
15 during the Induan. Besides, as for Antarctica (Fröbisch et al., 2010), the presence of  
16  
17 dicynodonts (*Repelinosaurus* and *Counillonia*) and a chroniosuchian (*Laosuchus*  
18  
19 *naga*, Arbez et al., 2018) in Laos near the Permo–Triassic boundary may also  
20  
21 indicate a refuge zone where the dicynodont and chroniosuchian (and possibly other  
22  
23 tetrapod faunas) were not strongly affected by the P–Tr crisis. However, the available  
24  
25 data on the Laotian fauna of the Permo–Triassic period is not yet sufficient to draw  
26  
27 firm conclusions on this point.  
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32  
33 As mentioned above, Bernardi et al. (2017) demonstrated a significant correlation  
34  
35 between the distribution of the dicynodonts and phytoprovinces, indicating that the  
36  
37 resilience and survivorship of dicynodonts after the crisis may be linked to plant  
38  
39 diversity. Indeed, Gastaldo et al. (2017) described an uninterrupted plant cover of  
40  
41 glossopterids and sphenophytes in the *Lystrosaurus* Assemblage zone, across the  
42  
43 P–Tr boundary. A full recovery of plants is also attested from the Middle Triassic  
44  
45 (e.g., Benton and Newell, 2014). An Early Triassic flora is well documented in South  
46  
47 China, combining the late Permian relic *Gigantopteris* and pioneer taxa dominated by  
48  
49 the lycopsid *Annalepsis* (Yu et al., 2015). This Chinese paleoflora has been shown to  
50  
51 be stable across the P–Tr boundary, with the highest turnover rates occurring during  
52  
53 the Induan (Xiong and Wang, 2011). Even if documented in a distinct and somewhat  
54  
55 remote area from the Luang Prabang Basin at that time (Fig. 1), a rich and diversified  
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3 paleoflora (Bercovici et al., 2012) has been evidenced above the strata correlated to  
4  
5 the late Changhsingian (Blanchard et al., 2013) and below the Purple Claystone Fm  
6  
7 (Rossignol et al., 2016). The occurrence of paleosols with root traces (Bercovici et  
8  
9 al., 2012) attests to the presence of plants during the deposition of the Purple  
10  
11 Claystone Fm.  
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### 13 14 15 16 17 18 **Paleobiogeographical Implications of the Two Laotian Dicynodonts**

19  
20 The occurrence of new dicynodonts in the Luang Prabang Basin (Laos), located  
21  
22 in the Indochina Block (e.g., Fig. 1A; Cocks and Torsvik, 2013), provides interesting  
23  
24 new insights on the controverted paleogeography of Southeast Asia.  
25

26  
27 Like all the other East and Southeast Asian continental blocks, the Indochina  
28  
29 Block originates from the Eastern Gondwana margin (e.g., Metcalfe, 2013; Burrett et  
30  
31 al., 2014). The separation of this block from the Gondwana mainland, by the opening  
32  
33 of the Paleotethyan Ocean, is dated from the Early Ordovician (e.g., Cocks and  
34  
35 Torsvik, 2013) or the Devonian (e.g., Metcalfe, 2011, 2013; Thanh et al., 2011; Lai et  
36  
37 al., 2014). The collision between the Indochina and South China blocks has been  
38  
39 variously dated: Silurian to Devonian (e.g., Thanh et al., 2011), Carboniferous (e.g.,  
40  
41 Metcalfe, 2011; Vư֏ng et al., 2013; Zhang et al., 2014), late Permian to Early  
42  
43 Triassic (Halpin et al., 2016), Early Triassic (e.g., Lepvrier et al., 2004; Kamvong et  
44  
45 al., 2014), Middle Triassic (e.g., Nakano et al., 2008; Zhang et al., 2013, 2014; Faure  
46  
47 et al., 2014; Rossignol et al., 2018) or even Late Triassic (e.g., Liu et al., 2012).  
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52  
53 Microanatomical studies, analyzing the distribution of the bone tissues,  
54  
55 morphological and taphonomic evidence, support an essentially terrestrial lifestyle for  
56  
57 most of dicynodonts (e.g., Ray et al., 2005, 2010; 2012; Wall 1983; King and Cluver,  
58  
59 1990; Botha-Brink and Angielczyk, 2010). *Lystrosaurus* is one of the rare dicynodonts  
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2  
3 supposed to be semi-aquatic based on its microanatomy, morphology, and  
4  
5 taphonomic preservation (e.g., Germain and Laurin, 2005; Ray, 2006). However,  
6  
7 these conclusions have been questioned, and a terrestrial lifestyle has been  
8  
9 proposed for *Lystrosaurus* based on its microanatomy, associated faunas, and  
10  
11 paleoenvironment (e.g., King and Cluver, 1990; Botha-Brink and Angielczyk, 2010).  
12

13  
14 The bone microstructure in *Lystrosaurus* is similar to that of *Placerias*, *Wadisasaurus*,  
15  
16 and *Kannemeyeria* (Ray *et al.*, 2005, 2012; Wall 1983). However, whilst a semi-  
17  
18 aquatic lifestyle based on microanatomy is proposed for *Placerias* (Green *et al.*,  
19  
20 2010), *Kannemeyeria*, and *Wadisasaurus* were supposed to be terrestrial (Ray *et al.*,  
21  
22 2010, 2012). Evidence for dicynodont lifestyle remains equivocal, but even if some  
23  
24 taxa did have a semi-aquatic but freshwater lifestyle, this would be unlikely to allow  
25  
26 dispersal across a wide oceanic domain.  
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32 The presence of dicynodonts in Laos highlights a connection between the  
33  
34 Indochina Block and South China Block (SCB). U–Pb geochronology on detrital  
35  
36 zircon suggested that the connection may occur not later than  $251.0 \pm 1.4$  Ma, the  
37  
38 maximum depositional age. Two different hypotheses can be proposed to account for  
39  
40 such a connection.

41  
42 Firstly, the Indochina Block could have been connected with the North China  
43  
44 Block (NCB), via the SCB. This hypothesis requires that the contact between the  
45  
46 NCB and the SCB was effective at  $251.0 \pm 1.4$  Ma, i.e, slightly before the Middle to  
47  
48 Late Triassic age generally considered plausible for the collision between these  
49  
50 blocks (Li, 1994; Weislogel *et al.*, 2006; Chang and Zhao, 2012; Torsvik and Cocks,  
51  
52 2017). It also implies a connection between the Indochina Block and the SCB before  
53  
54 or during the latest Permian or earliest Triassic, as proposed by Lepvrier *et al.*  
55  
56 (2004), Metcalfe (2011), Kamvong *et al.* (2014), Scotese (2014), and Halpin *et al.*  
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3 (2016). However, other interpretations support a continental connection between the  
4  
5 SCB and the Indochina Block later than the Early Triassic (see references above). A  
6  
7 diachronous continental collision between the SCB and the Indochina Block (Halpin  
8  
9 et al., 2016), beginning during the late Permian to the East (present day coordinates)  
10  
11 and continuing toward the West up to the Middle Triassic, has recently been put  
12  
13 forward. Such a hypothesis reconciles an Early to Middle Triassic collision between  
14  
15 the SCB and the Indochina Block with the paleobiogeographic distribution of  
16  
17 dicynodonts. This is further corroborated with the discovery of a new chroniosuchian  
18  
19 in non-marine rocks in the Purple Claystone Fm (Arbez et al., 2018), which is inferred  
20  
21 to have had an amphibious lifestyle (e.g., Buchwitz et al, 2012; Golubev, 2015; Arbez  
22  
23 et al., 2018) and which supports a connection between Eurasia and the Indochina  
24  
25 Block at that time.  
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31 Secondly, another hypothesis to account for the presence of dicynodont remains  
32  
33 in the Indochina Block consists of an indirect connection with other landmasses via a  
34  
35 string of microcontinents. Indeed, a connection between Pangea and the Indochina  
36  
37 Block, involving the western Cimmerian continental strip before or during the Early  
38  
39 Triassic, was also suggested (Buffetaut, 1989; Metcalfe, 2006, 2011). Laos is  
40  
41 characterized by a Cathaysian flora, also found in China, Korea, Japan, Thailand,  
42  
43 Indonesia, and Malaysia (e.g., Bernardi et al., 2017). The high affinities between  
44  
45 Cathaysian and Cimmerian faunas and floras suggest geographical proximity (Wang  
46  
47 and Sugiyama, 2002; Torsvik and Cocks, 2017). Nevertheless, this proximity is  
48  
49 based on plants and marine faunas (Wang and Sugiyama, 2002; Ueno, 2003; Shen  
50  
51 et al., 2013; Torsvik and Cocks, 2017), which are less constrained for dispersion by  
52  
53 oceanic barriers than terrestrial faunas are. Moreover, the presence of marine faunas  
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55 and a majority of limestone deposits during the late Permian in the Sibumasu Block  
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3 (e.g., Ueno, 2003; Chaodumrong et al., 2007; Shen et al., 2013; Wang et al., 2013),  
4  
5 indicate a largely submerged land (Metcalf, 2011). Furthermore, the collision  
6  
7 between the Sibumasu or Simao blocks with the Indochina Block is considered to  
8  
9 have occurred after the Norian (e.g., Metcalfe, 2011; Rossignol et al., 2016). The  
10  
11 Cimmerian option also supposes proximity between the Cimmerian blocks and  
12  
13 Pangea. The collision between Iran and Eurasia is latest Triassic–Jurassic in age  
14  
15 (e.g., Wilmsen et al., 2009; Zanchi et al., 2009). However, Zanchi et al. (2015)  
16  
17 suggest an affinity and probable proximity between Eurasia and Central Iran as early  
18  
19 as late Paleozoic. These uncertainties render difficult the involvement of the  
20  
21 Cimmerian blocks during the Permian–Triassic in the role of an indirect connection,  
22  
23 and suggest the existence of other microcontinents to explain this second  
24  
25 hypothesis.  
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31 The aforementioned two hypotheses are based on a maximum depositional  
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33 age of  $251.0 \pm 1.4$  Ma for the Laotian dicynodonts. Such a maximum depositional  
34  
35 age is also compatible with a deposition of the Purple Claystone Fm in the Middle  
36  
37 Triassic (Rossignol et al., 2016). This maximum depositional age is therefore  
38  
39 consistent with paleogeographic results indicating collisions between NCB and SCB  
40  
41 (Li, 1994; Weislogel et al., 2006; Chang and Zhao, 2012; Torsvik and Cocks, 2017) in  
42  
43 the Middle Triassic, and between the Indochina Block and SCB in the Middle to Late  
44  
45 Triassic (e.g., Liu et al., 2012; Zhang et al., 2013; Faure et al., 2014; Rossignol et al.,  
46  
47 2018). This implies the survival of a “*Dicynodon*”-grade taxon *Counillonia superoculis*  
48  
49 to the P–Tr crisis. This work brings new insights to ongoing debates about the  
50  
51 paleobiogeographic and geodynamic evolution of Southeast Asia from the late  
52  
53 Paleozoic to the early Mesozoic. It warrants further field expeditions in late Permian  
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3 and Early Triassic formations in the former indochina block to confirm or reject our  
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5 hypotheses.  
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## 45 FIGURE AND TABLE CAPTIONS

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### 49 **Figures**

50  
51 FIGURE 1. Continental blocks of Southeast Asia and geological map of the Luang  
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53 Prabang Basin. **A**, Tectonic subdivisions of Southeast Asia after Metcalfe (2011); **B**,  
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55 geological map of the Luang Prabang Basin with the emplacement of fossil sites and  
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57 dated samples (modified after Blanchard et al., 2013). Sample LP03 was collected at  
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3 the dicynodont site, sample LP04 in an unfossiliferous site, and sample LP05 at the  
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5 chroniosuchian site (Arbez et al., 2018). **Abbreviations:** **AL**, Ailaoshan suture zone;  
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9 suture zone; **SK**, Sra Kaeo suture zone; **LP**, emplacement of the Luang Prabang  
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11 Basin. [Intended for 2/3 of a whole page width]  
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17 FIGURE 2. Photographs and interpretive drawings of LPB 1993-3, the holotype of  
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19 *Counillonia superoculis* gen. et sp. nov. Skull in **A**, dorsal; **B**, right lateral; **C**, ventral;  
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21 and **D**, occipital views. The thin grey lines represent the sutures and the bold black  
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23 ones represent the relief. The dotted line represents our interpretation of sutures  
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25 based on variation in bone texture. Scale bar equals 5 cm. [Intended for whole page  
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33 FIGURE 3. Photographs and interpretive drawings of LPB 1993-2, the holotype of  
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55 sutures based on variation in bone texture. Scale bar equals 5 cm. [Intended for  
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FIGURE 5. Close-up photograph and interpretive drawing of the lateral snout region of the referred skull LPB 1995-9, attributed to *Repelinosaurus robustus* gen. et sp. nov. The thin grey lines represent the sutures, and the bold black ones represent the relief. Scale bar equals 5 cm. [Intended for 2/3 of a whole page width]

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FIGURE 6. The most parsimonious cladogram (1156.346 steps, CI = 0.236, RI = 0.712). Numbers at nodes represent the Bremer supports. Capital letters indicate the following clades (Maisch, 2001; Kammerer and Angielczyk, 2009): A, Dicynodontia. B, Pylaecephalidae. C, Endothiodontia. D, Therochelonina. E, Emydopoidea. F, Emydopidae. G, Kistecephalia. H, Kingoriidae. I, Cistecephalidae. J, Bidentalina. K, Cryptodontia. L, Rhachiocephalidae. M, Geikiidae. N, Geikiinae. O, Lystrosauridae. P, Kannemeyeriiformes. Q, Shansiodontidae. R, Stahleckeriidae. S, Kannemeyeriidae. [Intended for whole page width]

## Tables

TABLE 1. Summary of the maximum depositional ages obtained by U–Pb Laser Ablation – Inductively Coupled – Mass Spectrometry dating on detrital zircon grains from volcanoclastic rocks of the samples collected in the Purple Claystone Formation (LP03, LP04, LP05) (Rossignol et al., 2016). LP03 was collected at the dicynodont fossil site. The MSWD and the probability given for the concordia ages are for both concordance and equivalence. **Abbreviations:** **MSWD**, mean square of weighted deviates; **n**, number of analyses used to calculate the maximum depositional age; **N**, number of concordant zircon grain; **N<sub>a</sub>**, number of analyses per sample; **N<sub>zr</sub>**, number of zircon grains analyzed per sample.

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5 TABLE 2. Cranial measurements (in cm, scaled with Image J 1.50i) of the three  
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8 Laotian dicynodont skulls attributed to *Counillonia superoculis* and *Repelinosaurus*  
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10 *robustus*.

## 11 12 13 14 **Appendices**

15  
16 APPENDIX 1. Continuous and discrete codings in the Laotian dicynodonts used in  
17  
18 the phylogenetic analysis. The whole character-taxon matrix is available online as  
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21 Supplementary Data 1.  
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## 25 26 **Supplementary Data**

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28 SUPPLEMENTARY DATA 1. Data matrix used in the phylogenetic analysis (modified  
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31 from Angielczyk and Kammerer, 2017) (Matrix.txt).  
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36 SUPPLEMENTARY DATA 2. List of characters (continuous and discrete) used in the  
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38 phylogenetic analysis (modified from Angielczyk and Kammerer, 2017).  
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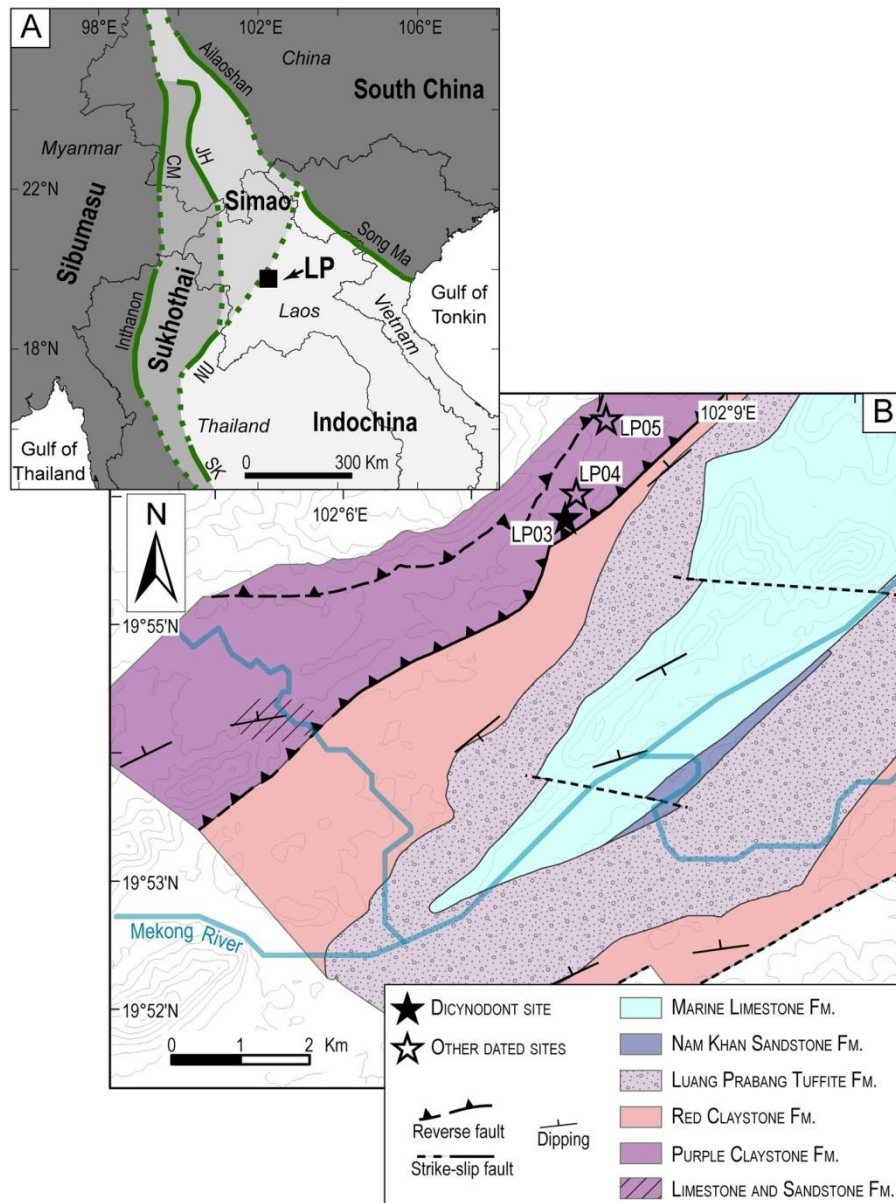


FIGURE 1. Continental blocks of Southeast Asia and geological map of the Luang Prabang Basin. **A**, Tectonic subdivisions of Southeast Asia after Metcalfe (2011); **B**, geological map of the Luang Prabang Basin with the emplacement of fossil sites and dated samples (modified after Blanchard et al., 2013). Sample LP03 was collected at the dicynodont site, sample LP04 in an unfossiliferous site, and sample LP05 at the chroniosuchian site (Arbez et al., 2018). **Abbreviations:** **AL**, Ailaoshan suture zone; **CM**, Changning Menglian suture zone; **JH**, Jinghong suture zone; **NU**, Nan Uttaradit suture zone; **SK**, Sra Kaeo suture zone; **LP**, emplacement of the Luang Prabang Basin. [Intended for 2/3 of a whole page width]

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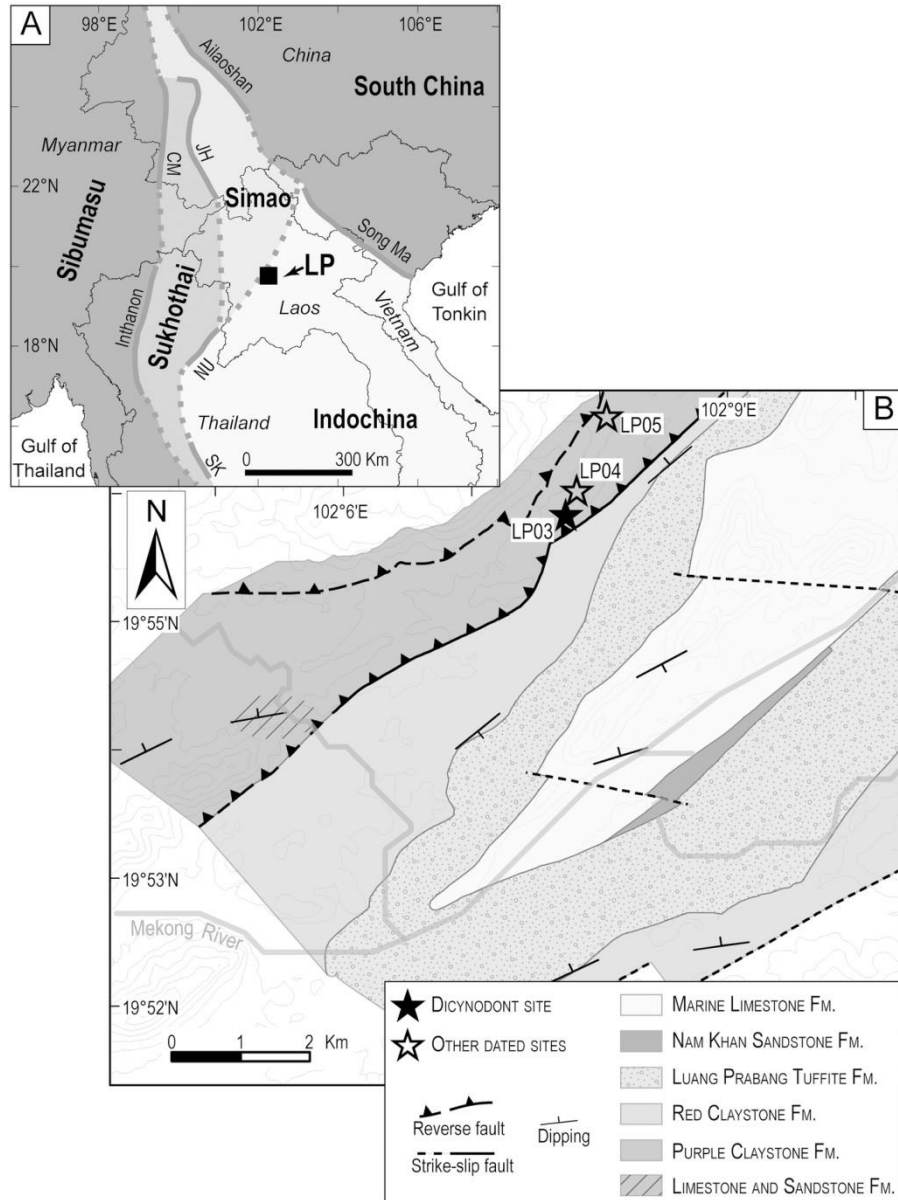


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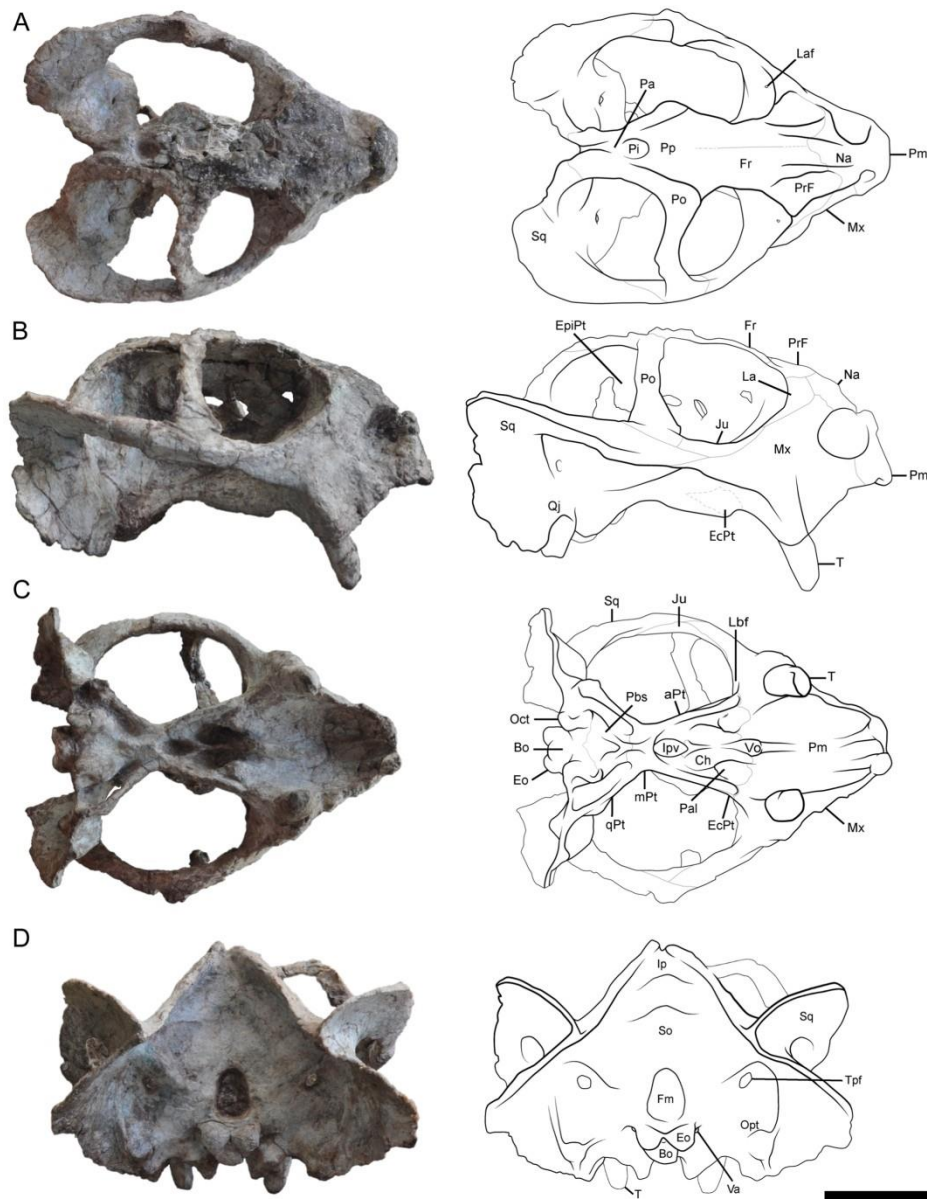


FIGURE 2. Photographs and interpretive drawings of LPB 1993-3, the holotype of *Counillonia superoculis* gen. et sp. nov. Skull in **A**, dorsal; **B**, right lateral; **C**, ventral; and **D**, occipital views. The thin grey lines represent the sutures and the bold black ones represent the relief. The dotted line represents our interpretation of sutures based on variation in bone texture. Scale bar equals 5 cm. [Intended for whole page width]

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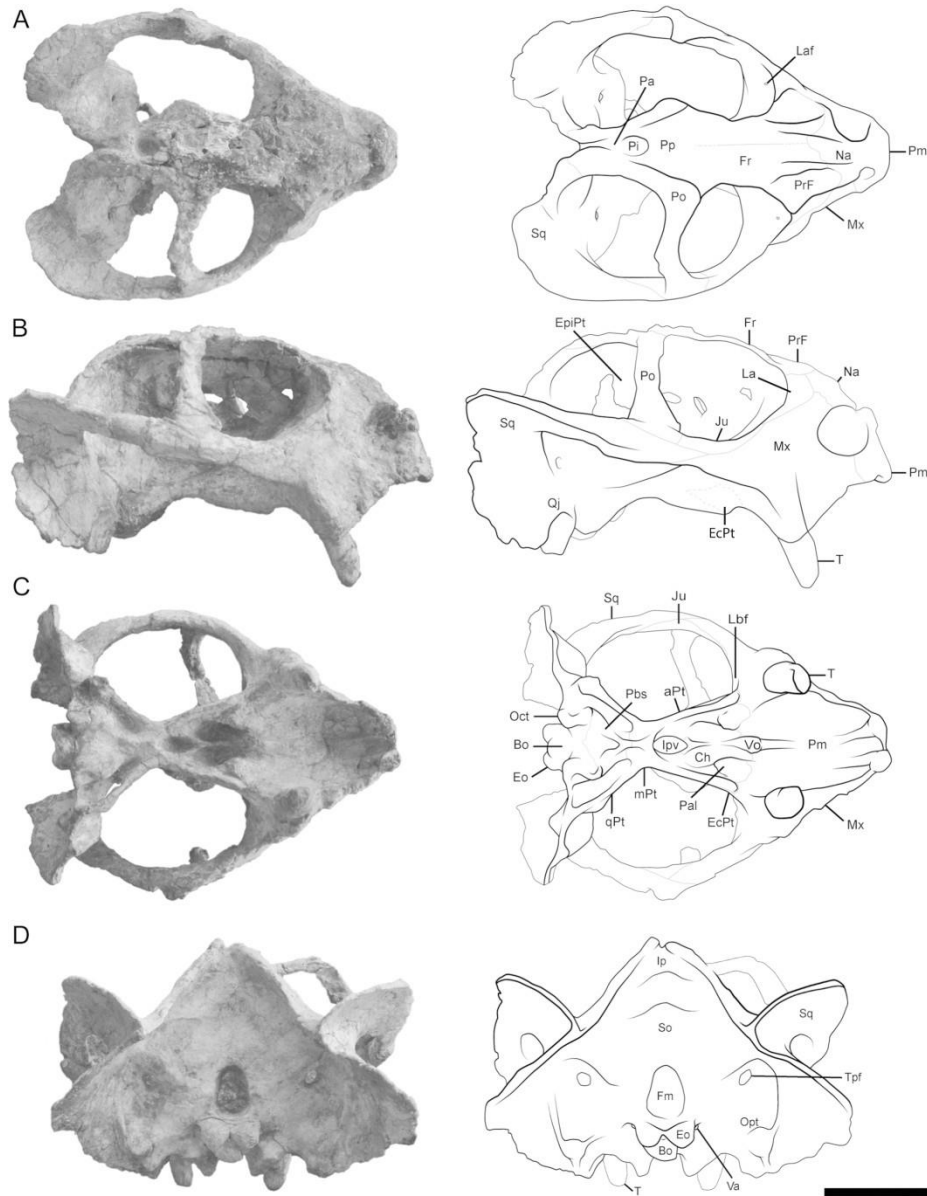


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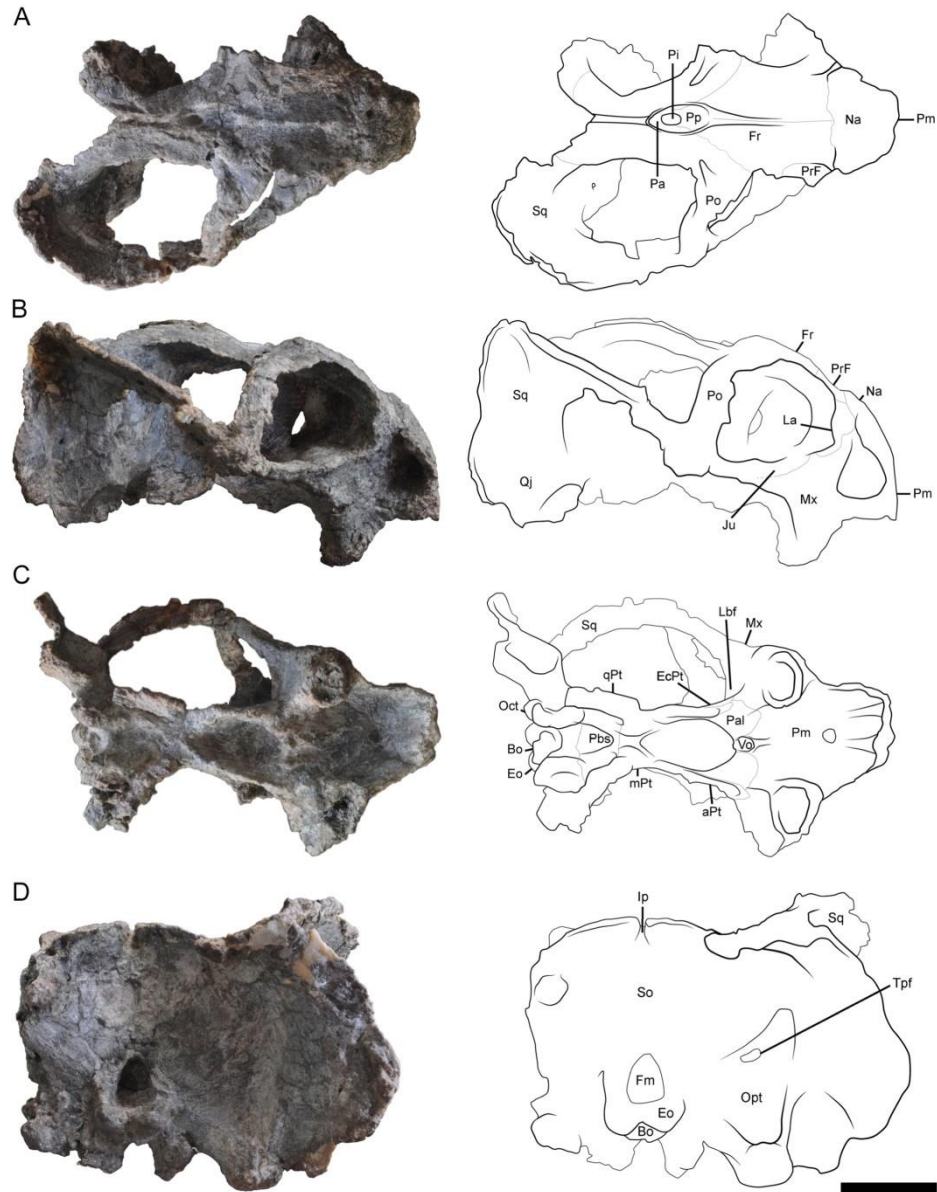


FIGURE 3. Photographs and interpretive drawings of LPB 1993-2, the holotype of *Repelinosaurus robustus* gen. et sp. nov. Skull in **A**, dorsal; **B**, right lateral; **C**, ventral; and **D**, occipital views. The thin grey lines represent the sutures and the bold black ones represent the relief. Scale bar equals 5 cm. [Intended for whole page width]

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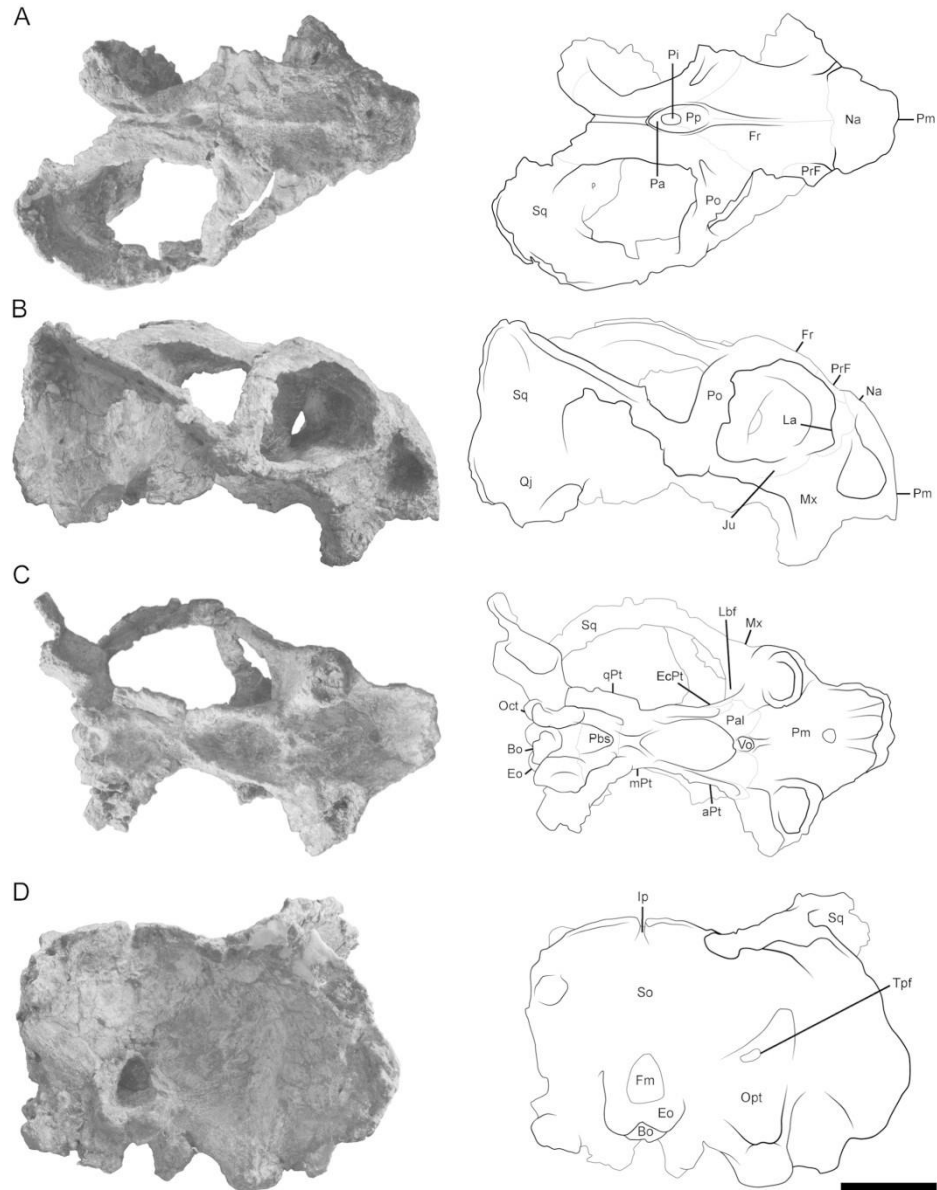


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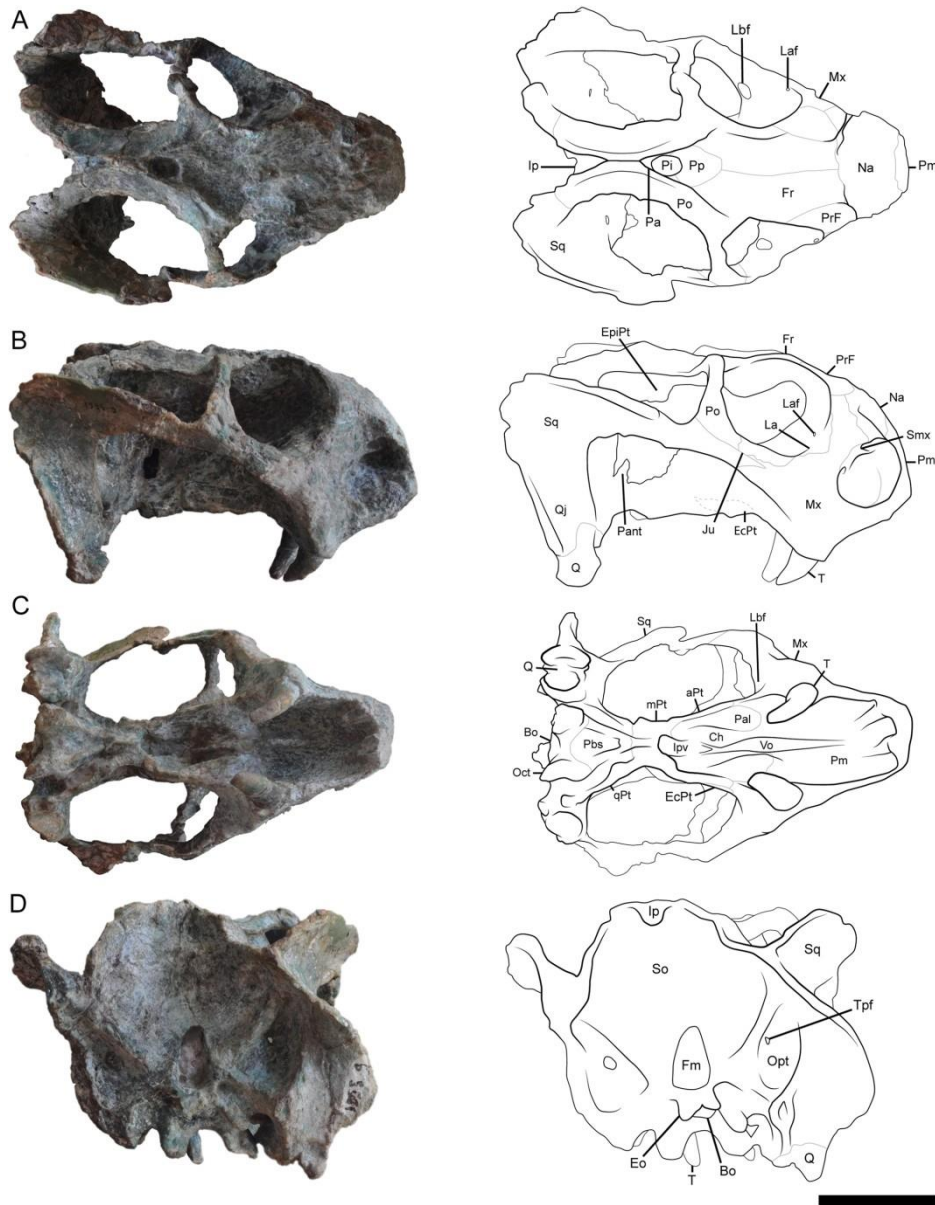


FIGURE 4. Photographs and interpretive drawings of LPB 1995-9, a skull referred to *Repelinosaurus robustus* gen. et sp. nov. Skull in **A**, dorsal; **B**, right lateral; **C**, ventral; and **D**, occipital views. The thin grey lines represent the sutures and the bold black ones represent the relief. The dotted line represents our interpretation of sutures based on variation in bone texture. Scale bar equals 5 cm. [Intended for whole page width]

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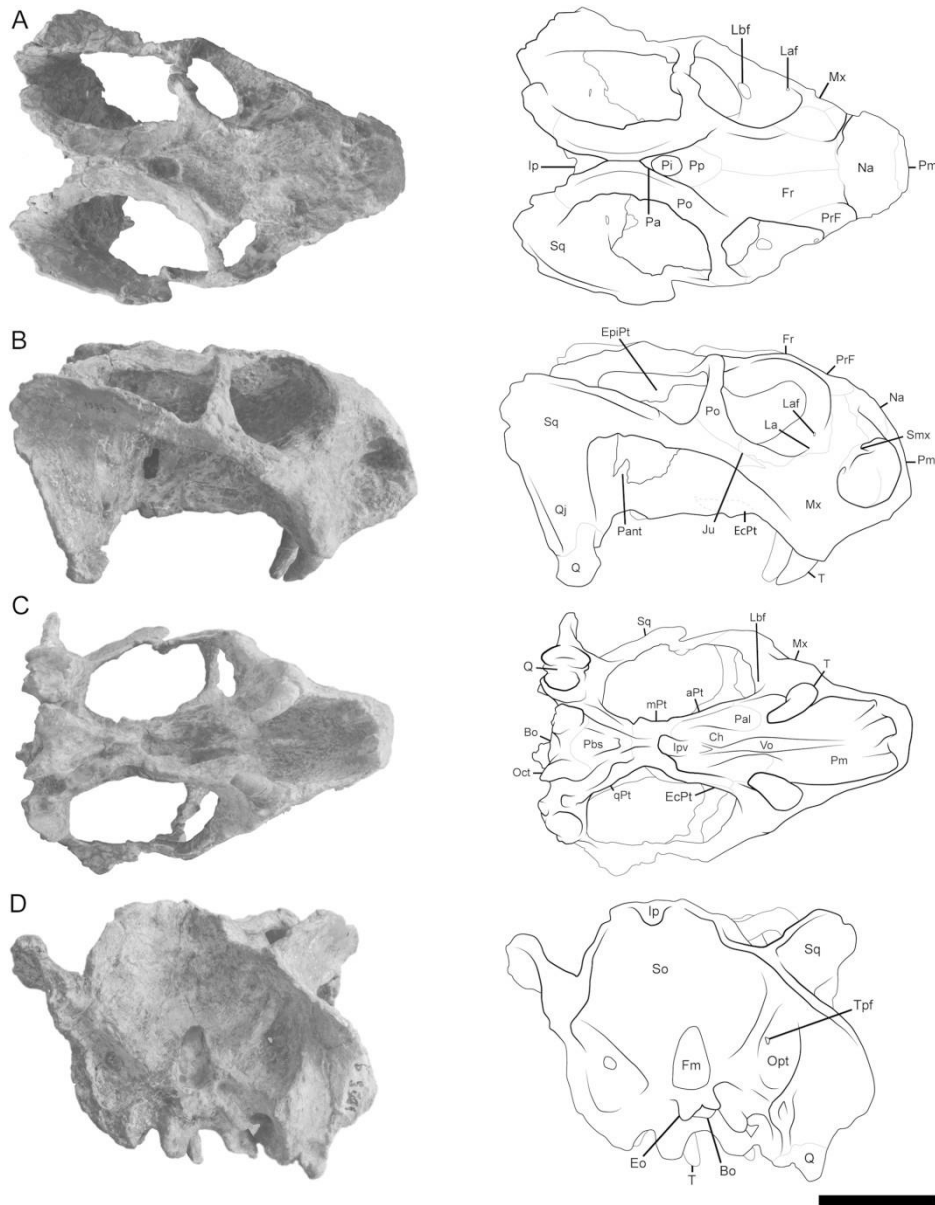


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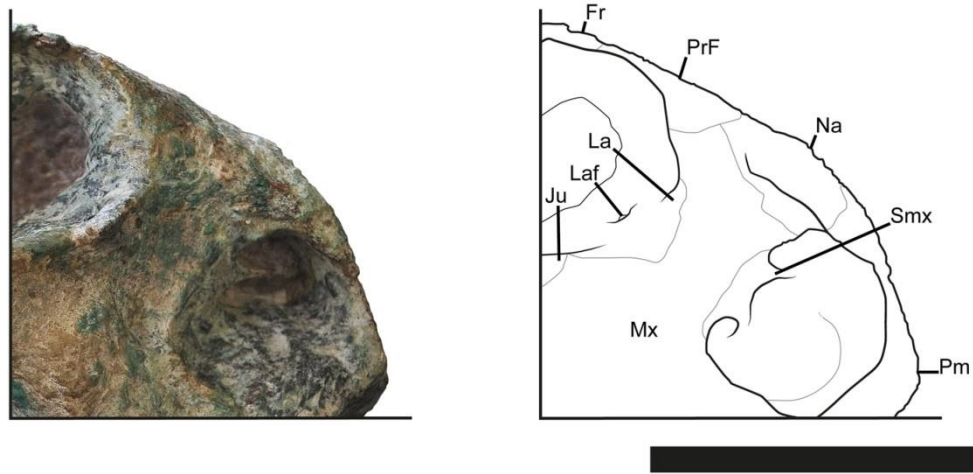


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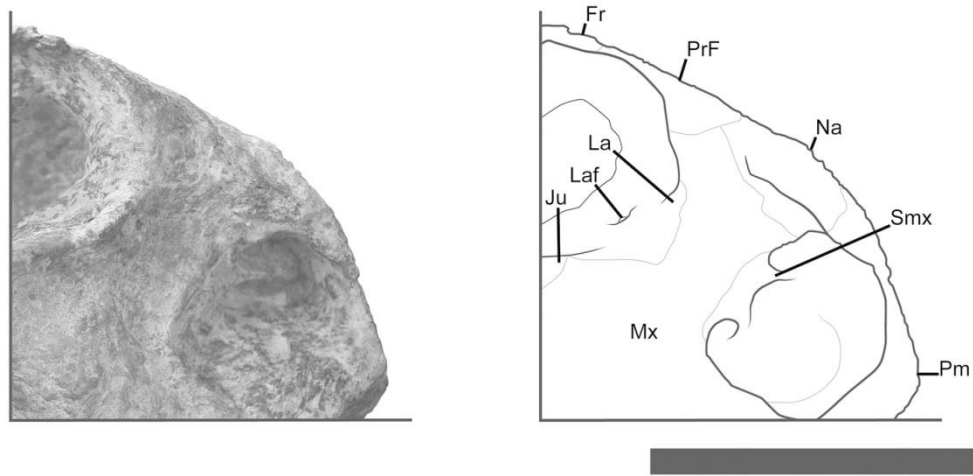


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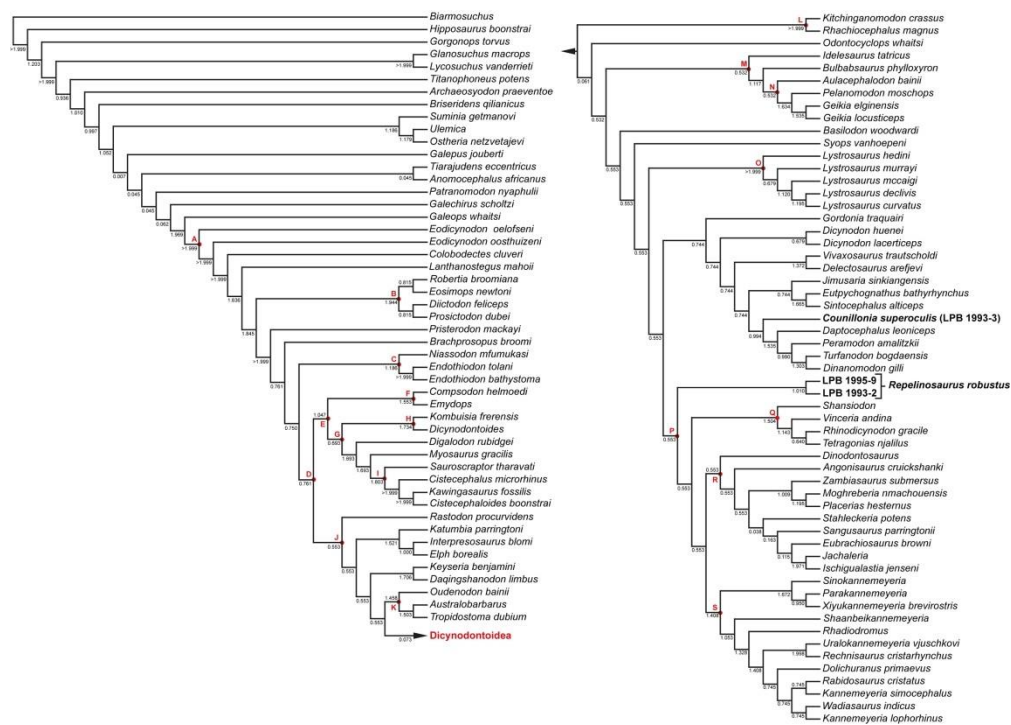


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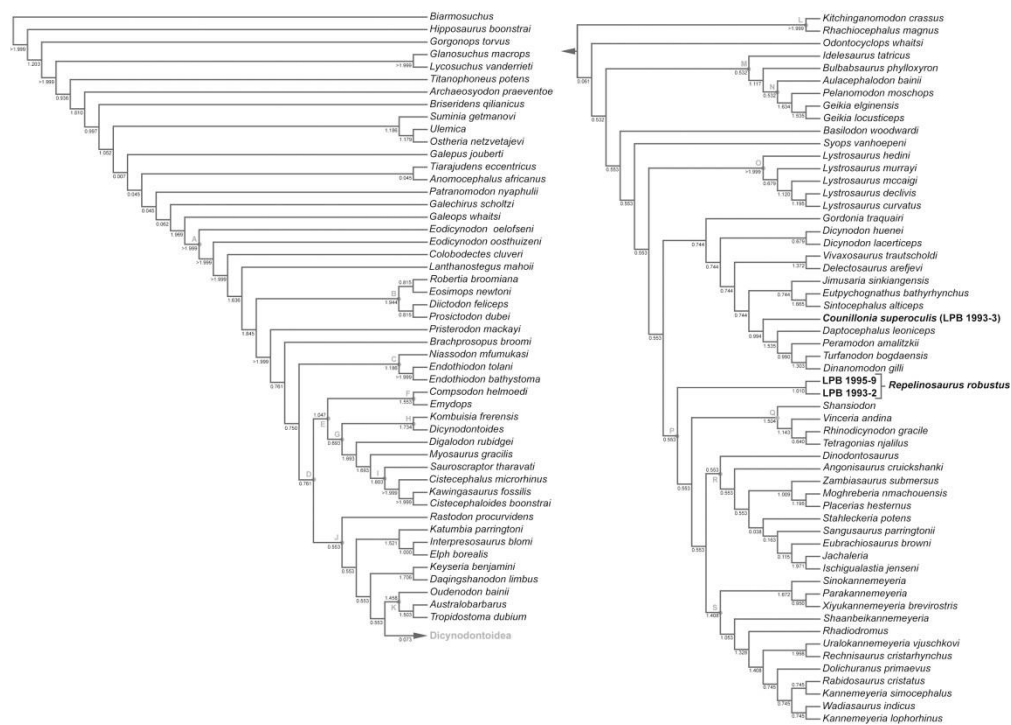


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	N <sub>a</sub>	N <sub>zr</sub>	N	Maximum depositional age				
				Concordia age	± (2σ)	n	MSWD	Probability
LP03	105	102	25	252.0	2.6	6	0.89	0.55
LP04	41	36	7	300.5	3.7	4	0.73	0.65
LP05	96	95	39	251.0	1.4	21	0.55	0.99

TABLE 2. Cranial measurements (in cm, scaled with Image J 1.50i) of the three Laotian dicynodont skulls attributed to *Counillonia superoculis* and *Repelinosaurus robustus*.

	<i>C. superoculis</i>		<i>R. robustus</i>	
	LPB 1993-3	LPB 1995-9	LPB 1993-2	
Basal length (from the tip of snout to the occipital condyle, in ventral view)	16.02	15.72	19.00	
Maximum width (in dorsal view)	13.41	NA	NA	
Maximum orbital height (in lateral view)	4.82	4.19	5.79	
Maximum orbital length (in lateral view)	5.67	4.73	6.82	
Mediolateral diameter of the tusk root (in ventral view)	1.27	1.46	2.02	
Anteroposterior diameter of the tusk root (in ventral view)	1.56	0.90	1.49	
Pineal foramen length (in dorsal view)	1.36	1.33	0.96	
Pineal foramen width (in dorsal view)	0.96	0.87	0.66	

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3 APPENDIX 1. Continuous and discrete codings in the Laotian dicynodonts  
4  
5 used in the phylogenetic analysis; en dash (-) indicates missing values. The whole  
6  
7 character-taxon matrix is available online as Supplementary Data 1.  
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12 **Continuous codings (characters 1 to 23)**

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14 LPB 1993-3 (holotype of *Counillonia superoculis*)

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16 0.2975.068 - - 0.276 0.134 - 0.131 8.333 0.140 - 9.616 0.876 - - - -  
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18  
19 - - - - - -  
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21  
22 LPB 1993-2 (holotype of *Repelinosaurus robustus*)

23  
24 0.200 - 0.295 - 0.408 0.281 - - - - - 14.698 0.829 - - - - - - - - -  
25  
26 -  
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28  
29 LPB 1995-9 (attributed to *Repelinosaurus robustus*)

30  
31 0.205 - 0.254 - - 0.316 - 0.124 - 0.101 - - 0.935 - - - - - - - - -  
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39 **Discrete codings (characters 24 to 194)**

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41 LPB 1993-3 (holotype of *Counillonia superoculis*)

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51 LPB 1993-2 (holotype of *Repelinosaurus robustus*)

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APPENDIX 1. (Continued)

LPB 1995-9 (attributed to *Repelinosaurus robustus*)

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