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Associated skeletons of a new middle Triassic "Rauisuchia" from Brazil

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Abstract For more than 30 million years, in early Mesozoic Pangea, "rauisuchian" archosaurs were the apex predators in most terrestrial ecosystems, but their biology and evolutionary history remain poorly understood. We describe a new "rauisuchian" based on ten individuals found in a single locality from the Middle Triassic (Ladinian) Santa Maria Formation of southern Brazil. Nine articulated and associated skeletons were discovered, three of which have nearly complete skulls. Along with sedimentological and taphonomic data, this suggests that those highly successful predators exhibited some kind of intraspecific interaction. Other monotaxic assemblages of Triassic archosaurs are Late Triassic (Norian-Rhaetian) in age, approximately 10 million years younger than the material described here. Indeed, the studied assemblage may represent the earliest evidence of gregariousness among archosaurs, adding to our knowledge on the origin of a behavior pattern typical of extant taxa.

Keywords Santa Maria Formation · Archosauria · Rauisuchia · Behavior · Middle Triassic

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Introduction

"Rauisuchians" are a widespread group of crocodile-line archosaurs, first recognized by Huene (1942), based on fossils collected early in the last century by Gilherme Rau in the Middle Triassic of Rio Grande do Sul, southern Brazil. Since then, the group has been also recorded in Late Triassic and possibly Early Triassic rocks in all major parts of Pangea, except Australia and Antarctica (Gower 2000; Brusatte et al. 2010). With estimated lengths of up to 8 m (Barberena 1978; Bonaparte 1981), "rauisuchians" are generally regarded as the top terrestrial predators of their ecosystems. They are usually considered to be quadrupedal, but there were also partially (Chatterjee 1985; Long and Murry 1995) or fully (Nesbitt 2007) bipedal "rauisuchians". More recent discoveries revealed a previously unexpected morphological disparity for the group (Brusatte et al. 2010), including beaked forms, such as *Effigia okeeffeae* (Nesbitt 2007) and possibly aquatic animals, such as *Qianosuchus mixtus* (Li et al. 2006; Brusatte et al. 2010). The monophyly of "rauisuchians" is also disputed, and the group has been previously considered a paraphyletic array of taxa basal to other suchians (Benton and Clark 1988; Parrish 1993; Gower 2002; Weinbaum and Hungerbühler 2007). Otherwise, the monophyly of the group has been suggested in most recent studies (Benton 1999; Nesbitt 2003; Nesbitt and Norell 2006; Nesbitt 2007; Brusatte et al. 2010).

Despite their relative frequency in Triassic fossil faunas, only about ten of the nearly 50 known "rauisuchians" are based on informative cranial and postcranial remains. Therefore, the discovery of nine associated individuals (Fig. 1), three of which preserve virtually complete skulls, with cranial remains of a tenth individual found nearby is unique for the group and rare for basal archosaurs in
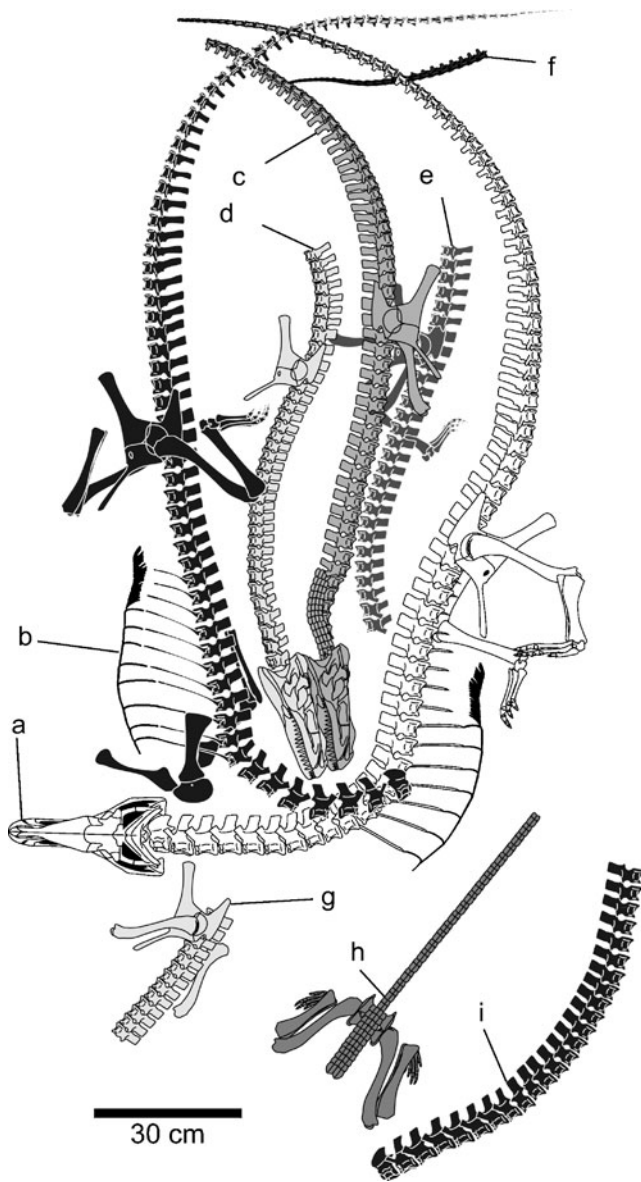
Fig. 1 Interpretive drawing of nine associated skeletons of *D. quartacolonia*, new genus and species. (**a–i**) corresponding to MCN PV10105a-i

general. The association of these specimens may correspond to a natural aggregation during life, a behavior also well recognized in triassic ornithosuchians.

Systematic paleontology

Archosauria Cope, 1869 (sensu Gauthier and Padian, 1985)
Pseudosuchia Zittel, 1887–1890 (sensu Parrish 1997)
Suchia Krebs, 1974 (sensu Benton and Clark 1988)
Rauisuchia Huene, 1942
Prestosuchidae Romer, 1966 (sensu Brusatte et al. 2010)
Decuriasuchus quartacolonia new genus and species

Etymology Decuriasuschus, after decury, groups of ten into which the Roman cavalry was divided (reference to the number of individuals in the site) and suchus, Greek name for the Egyptian crocodile-headed god; *quartacolonia*, after the "Quarta Colonia" region where the fossils were collected.

Holotype MCN PV10105a (Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul), articulated partial skeleton, lacking scapular girdle and limbs.

Paratypes Eight specimens (MCN PV10105b-i) associated with the holotype: b, nearly complete skeleton lacking skull and forelimb parts; c, skull and nearly complete postcranium; d, skull and presacral vertebrae; e, trunk and tail vertebrae, pelvic girdle and limbs; f, distal half of the tail (this is considered a unique individual because its vertebrae overlap in position with those of nearby specimens and does not fit their orientation pattern); g, tail vertebrae, pelvic girdle, and femora; h, tail vertebrae, pelvic girdle, and limbs; i, presacral vertebrae. Cranial remains from a different spot in the same locality represent the tenth specimen (MCN PV10004) of *D. quartacolonia*.
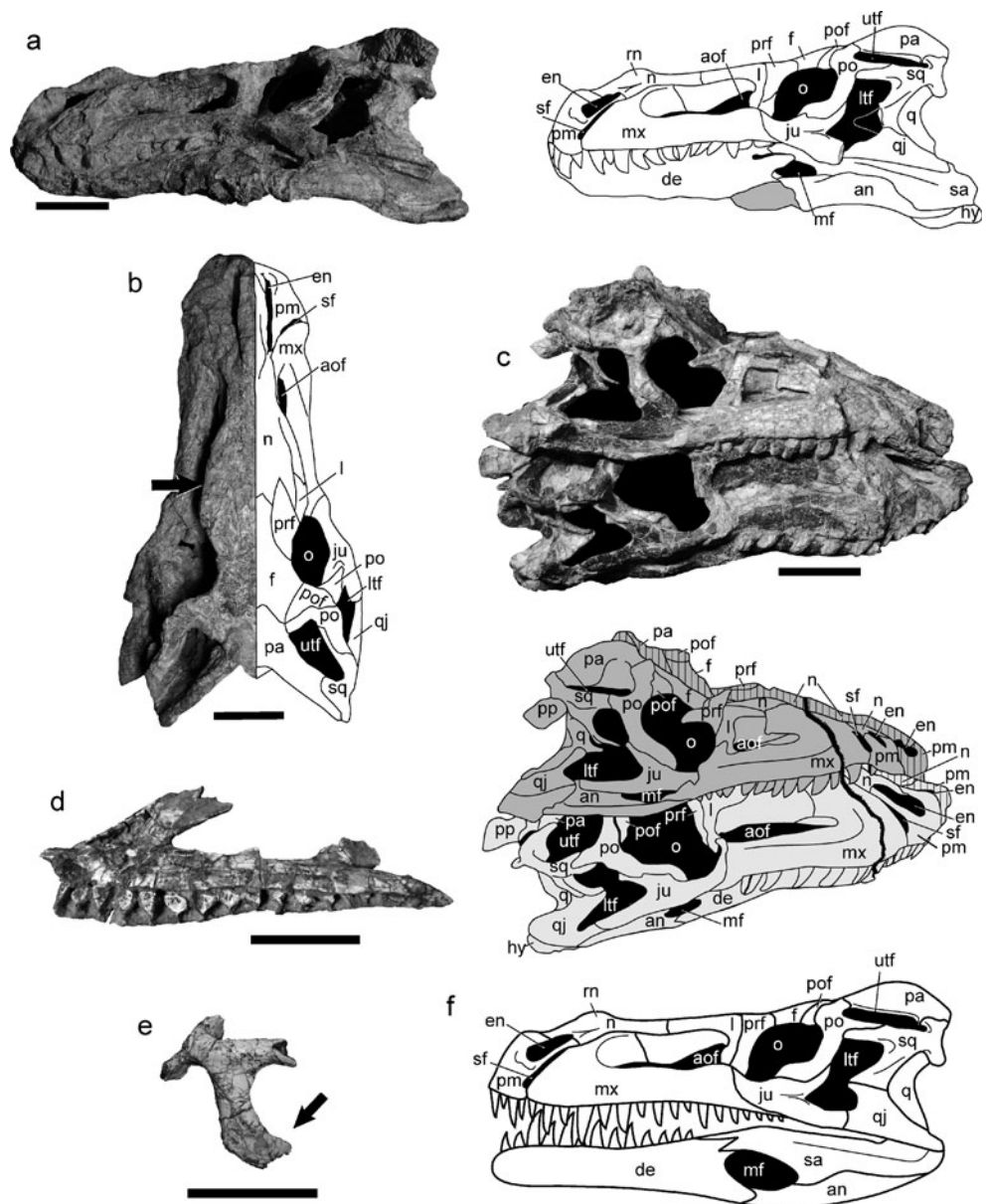
Type locality and horizon Alemoa Member, Santa Maria Formation, Rosário do Sul Group, transgressive systems tract of Santa Maria 1 Sequence (Zerfass et al. 2003), exposed at the site known as "Posto", located about 200 m north of RS 348 road, within the western outskirts of Dona Francisca, Rio Grande do Sul, Brazil (Langer et al. 2007). The type series of *D. quartacolonia* comes from two different large ravines: 29°37'38"S 53°22'07 W (MCN PV10105) and 29°37'36"S 53°22'02 W (MCN PV10004). Based on the occurrence of index-fossils such as *Dinodontosaurus* and *Massetognathus*, the site can be assigned to the Middle Triassic (Ladinian) *Dinodontosaurus* Biozone (Abdala and Ribeiro 2010); ca. 240–235 Ma.

Diagnosis Medium-sized "rauisuchian" distinguishable from all other members of the group, except *Q. mixtus*, by the possession of more than 15 maxillary teeth, and characterized by the following autapomorphies (arrows in Fig. 2): lacrimal and nasal form a lateral expansion of the skull roof that overhangs most of the antorbital fenestra; rostrally extended dorsal margin of quadratojugal and ventral margin of squamosal form the ventral portion of a subtriangular expansion that enters the lower temporal fenestra.

Description

The holotype and paratypes (Fig. 1) are all adult individuals, based on their similar size, and closed neurocranial

Fig. 2 Skulls preserved in *D. quartacolonia*, new genus and species. **a** Photograph (*left*) and line drawing (*right*) of holotype skull (MCN PV10105a), left lateral view (sediment cover represented in grey). **b** Photograph (*left*) and line drawing (*right*) of holotype skull (MCN PV10105a), dorsal view. **c** Photograph (*above*) and line drawing (*below*) of paratype skulls (MCN PV10105c, above; MCN PV10105d, below), right lateral view (hatched areas indicate bones from the left side). **d** Right maxilla (MCN PV10004), medial view. **e** Right squamosal (MCN PV10004), lateral view. **f** Reconstruction of skull and lower jaw, left lateral view. *Abbreviations*: *an* angular, *aof* antobital fenestra, *de* dentary, *en* external naris, *f* frontal, *hy* hyoid, *ju* jugal, *l* lacrimal, *ltf* lateral temporal fenestra, *mf* mandibular fenestra, *mx* maxilla, *n* nasal, *o* orbit, *pp* paraoccipital process of opisthotic, *pa* parietal, *pof* postfrontal, *po* postorbital, *prf* prefrontal, *pm* premaxilla, *q* quadrate, *qj* quadratojugal, *rn* "roman nose", *sa* surangular, *sq* squamosal, *sf* subnarial fenestra, *utf* upper temporal fenestra. Autapomorphies are noted by an *arrow*. Scale bar = 5 cm

and neurocentral sutures (Irmis 2007). The external naris is obliquely elongated and posteriorly tapering. Its margin is formed only by the premaxilla and nasal (Fig. 2a, b), differing from *Effigia* and *Batrachotomus*, in which the maxilla enters into the margin of the naris. The premaxilla has four teeth and lacks the posterior excavation seen in *Luperosuchus*. The obliquely elongated subnarial fenestra is neither dorsally displaced as in *Luperosuchus* nor small as in *Postosuchus*, *Batrachotomus*, *Polonosuchus*, and *Effigia*, but resembles the condition of *Saurosuchus*. In *Prestosuchus chiniquensis*, absence of the fenestra (Gower 2000) is probably a preservational artifact. *D. quartacolonia* shares a "U-shaped" maxilla (Fig. 2a, c, d) with *Postosuchus*, *Saurosuchus*, *Polonosuchus*, and *P. chiniquensis*, whereas a "Y-shaped" bone is seen in

Ticinosuchus, *Effigia*, *Batrachotomus*, *Fasolasuchus*, and *Yarasuchus*. Both sides of MCN PV10004 (Fig. 2d), and a CT-scan of MCN PV10105a reveal 17 maxillary tooth positions.

The nasals of *D. quartacolonia* ascend at the midline to contact one another, and the skull has a convex outline between the naris and antorbital fenesta. A more extreme version of this condition was termed "roman nose" in *Luperosuchus* (Romer 1971), whereas a subtler expansion is seen in *Batrachotomus* (Gower 1999) and *P. chiniquensis*. Caudal to that, the nasal and lacrimal form a lateral expansion that overhangs most of the antorbital fenestra (Fig. 2b). In other "rauisuchians" (*Batrachotomus*, *Luperosuchus*, *Saurosuchus*, *Postosuchus*, *P. chiniquensis*), this expansion is either absent or located more posteriorly. The

orbits of *Luperosuchus* and poposaurids have a rounded posterior margin, whereas a rostral expansion of the ventral ramus of the postorbital enters the orbit of *D. quartacolonia*. This defines a "key-hole" shape, typical of "rauisuchians", but the aperture is not anteroposteriorly narrow as in *P. chiniquensis*. Equally, the posterior margin of the lower temporal fenestra is invaded by a subtriangular expansion formed by the conjoined squamosal and quadratojugal (Fig. 2a, c, e). This differs from the condition in other "rauisuchians", where this expansion is either composed solely of the squamosal (*P. chiniquensis*, *Saurosuchus*) or extends to the anterior margin of the fenestra (*Polonosuchus*, *Postosuchus*). Except for a reduced mandibular fenestra, the lower jaw of *D. quartacolonia* resembles those of most "rauisuchians", but the rostral end of the dentary is not expanded as in *Postosuchus* and *Batrachotomus*.

D. quartacolonia and *Ticinosuchus* share elongated postaxial cervical vertebrae (Fig. 3a); differing from both the shorter elements of most "rauisuchians" and the more slender neck vertebrae of poposaurids. Neural spines of

vertebrae 4–7 are anteroposteriorly expanded, as in *Yarasuchus* and *Prestosuchus loricatus*. Spine tables are seen in both trunk and posterior neck vertebrae, whereas accessory articulations (hyposphene-hypantrum) are restricted to the former. *D. quartacolonia* also has fewer sacral vertebrae (Fig. 3c) than *Batrachotomus* and most poposaurids. Vertebrae from the mid-portion of the tail bear accessory neural spines (Fig. 3d, f), as in *Polonosuchus*, *Rauisuchus*, and *Ticinosuchus*. A prominent supracetabular buttress, typical of most "rauisuchian" ilia, is absent in *D. quartacolonia*. The ankle joint is typical "crocodile-normal" (Fig. 3g, h), and the pes includes a metatarsal III that is significantly longer than the neighboring elements and a robust "hook-like" metatarsal V. This differs from the subequal metatarsals III and IV in *P. chiniquensis* and the slender metatarsal V of *Ticinosuchus*. The dermal cover comprises two paramedian rows of osteoderms along the back (with two pairs per vertebra), a median row on the back of the tail (one pair per vertebra) (Fig. 3b–d), and scattered smaller osteoderms along the ventral surface of the tail (Fig. 3e).
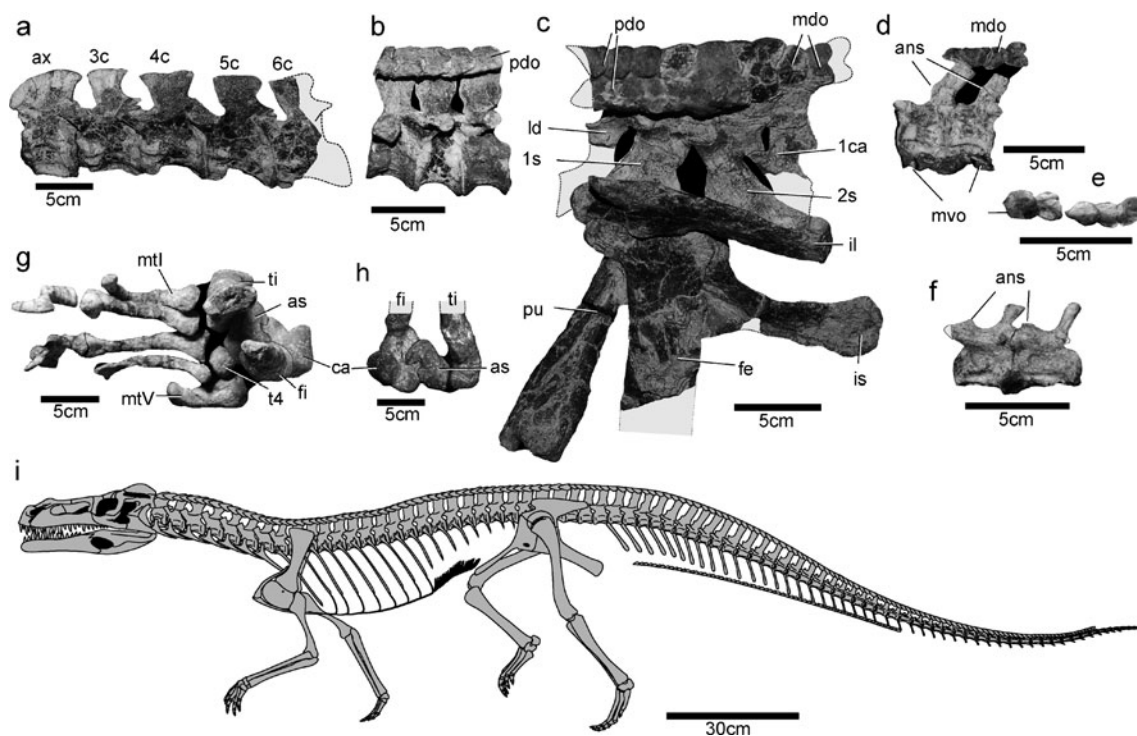

Fig. 3 Skeletal anatomy of *D. quartacolonia*, new genus and species. **a** Anterior cervical vertebrae (MCN PV10105i), right lateral view (reversed). **b** Middle trunk vertebrae (MCN PV10105i), right lateral view (reversed). **c** Sacrum and pelvis (MCN PV10105c), right lateral view (reversed). **d** Proximal caudal vertebrae (MCN PV10105c), right lateral view (reversed). **e** Details of ventral osteoderms (MCN PV10105c), ventral view. **f** Middle caudal vertebrae (MCN PV10105a), right lateral view (reversed). **g** Left ankle and pes (MCN PV10105a), dorsal view. **h** Left ankle (MCN PV10105a), posterior view. **i** Skull and skeletal anatomy reconstruction. *Abbreviations*: *1ca* first caudal vertebrae, *1s 2s* first and second sacral vertebrae, *3c–6c* third–sixth cervical vertebrae, *ans* accessory neural spine, *as* astragalus, *ax* axis, *ca* calcaneum, *fe* femur, *fi* fibula, *il* ilium, *is* ischium, *ld* last dorsal vertebrae, *mdo* median dorsal osteoderms, *mvo* median ventral osteoderms, *mtI* metatarsal I, *mtV* metatarsal V, *pdo* paramedian dorsal osteoderms, *pu* pubis, *t4* tarsal 4, *ti* tibia

Discussion

The data-matrix of Brusatte et al. (2010) was used to test the relationships of *D. quartacolonia*, and the search parameters employed were identical to those of the original analysis (see Electronic supplementary material). The phylogenetic analysis was conducted using TNT1.1 (Goloboff et al. 2008a, b) and resulted in 1,005 most parsimonious trees (MPTs) with 753 steps (see Electronic supplementary material). Their strict consensus revealed a poorly resolved Pseudosuchia, including a polytomic clade in which only the more "well established" groups show as monophyletic (e.g., Aetosauria, Phytosauria, Crocodylomorpha+*Erpetosuchus*+*Gracilisuchus*). "Rauisuchians" do not form a monophyletic group, but its paraphyly is also not unambiguously supported. In this context, *Decuriasuchus* represents one of the terminal taxa within the polytomic Pseudosuchia. Additionally, the majority consensus tree (see Electronic supplementary material) indicates that 85% of MPTs includes a clade composed of Ornithosuchidae and all taxa usually assigned to "Rauisuchia", a relation never recovered before. In this context, *Decuriasuchus* along with *Prestosuchus*, *Batrachotomus*, and *Saurosuchus* forms Prestosuchidae. Only one morphological trait is unique to these four taxa among archosaurs: a well-developed crest along the posterior margin of the ventral ramus of the squamosal. A reduced consensus analysis was carried out following the protocol of Pol and Escapa (2009). After four iterations, the analysis identified *Revueltosaurus*, *Fasolasuchus*, *Arganasuchus*, *Yarasuchus*, and *Stagonosuchus* as unstable taxa (Fig. 4). The reduced consensus tree places Phytosauria as the most basal group of pseudosuchians and Aetosauria as the sister group to *Gracilisuchus*+*Erpetosuchus*+Crocodylomorpha, forming the sister group to the clade including "rauisuchians" and ornithosuchids. Again, "Rauisuchia" may include Ornithosuchidae or represent its sister group. Less inclusive groups include Poposauridae and a clade comprising *Tikisuchus*, *Saurosuchus*, *Rauisuchus*, *Teratosaurus*, *Postosuchus*, *Decuriasuchus*, *Prestosuchus*, and *Batrachotomus*. Among these, *Decuriasuchus* represents the sister taxon of *Batrachotomus*+*Prestosuchus*. A more comprehensive phylogenetic analysis of pseudosuchians is necessary to define monophyly or paraphyly of "rauisuchians" and the position of *Decuriasuchus*.

The understanding of monotaxic accumulations of multiple individuals follows a rationale summarized by three questions (Fiorillo and Hebert 2004): Did the individuals live together or die together? Is there evidence for post-mortem transport? To what extent can gregarious behavior be inferred? Although sorting by size has apparently favored adults in the mass assemblage of *D. quartacolonia*, there is no evidence (heads rising/upright specimens, preservation bias for hindlimbs), for miring as
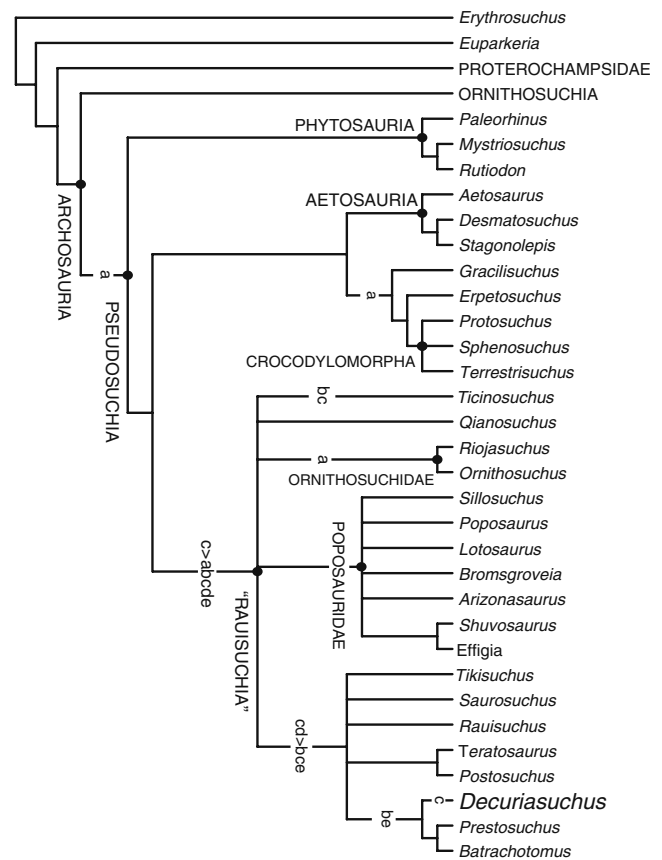

Fig. 4 Phylogenetic relationships of *D. quartacolonia*, new genus and species among Archosauria [see Electronic supplementary material for details of the analysis]. Reduced Consensus tree, based on 1,005 MPTs with 753 steps, after four iterations. The alternative positions of the unstable taxa are indicated in the tree as: *a* Revueltosaurus, *b* Fasolasuchus, *c* Stagonosuchus, *d* Yarasuchus, *e* Arganasuchus. Those on the right of the symbol ">" belong to the clade apical to the branch but in positions not possible to depict because collapsed in the shown topology

the concentration mechanism (Sander 1992). Likewise, there is no sedimentological support (differences in the composition/structure of the sediments surrounding the specimens) for preservation in confined spaces, which typically results in side-by-side alignment of individuals (Abdala et al. 2006). Instead, subparallel orientation of the vertebral column of most specimens and curvature of the neck and tail (Fig. 1) suggest current flow in an open environment (Faux and Padian 2007). This may also account for the loss of skeletal parts, notably skulls and limb elements, given that the completeness of the specimens precludes a long or distant transport (Hill and Behrensmeyer 1984). This scenario fits the geology of the site, which is composed of massive reddish mudstones with carbonate nodules and mudcrack infilling (Da Rosa 2005). The sedimentological setting and comparison to other localities of the Alemoa Member indicate that the site was located in the distal portion of a floodplain, at some

distance from the river channel. Precipitation of carbonate cement on previously exposed deposits during episodes of high phreatic level suggests contrasting dry and wet seasons (Rubert and Schultz 2004; Da Rosa 2005). This corroborates the idea that these individuals of *D. quartacolonia* were transported a short distance and buried rapidly. Moreover, the overlapping of some skeletal parts, e.g., MCN PV 10.105b with neck above and tail below MCN PV 10.105a (Fig. 1), suggests that some of the individuals were deposited at the same time.

Cynodonts and dicynodonts, rather than "rauisuchians", are the most common tetrapods in the Middle Triassic deposits of southern Brazil (Langer et al. 2007). The monotaxic composition of the *D. quartacolonia* site rules out significant time-averaging (Fiorillo and Hebert 2004), which would result in the incorporation of other taxa of similar size to the assemblage. In this context, two possible scenarios can explain the mass assemblage: 1—a group of animals was caught and killed by a flash flood that carried their bodies for a short period of time, prior to deposition on the floodplain; 2—they clustered due to early influences of the event that eventually caused their death (Fiorillo and Hebert 2004) and the carcasses were then reworked by current flow. Both hypotheses require a certain degree of interaction among individuals, but there is no evidence that this was more complex than that seen among extant crocodiles.

Except for the renowned *Coelophysis bauri* assemblage of Ghost Ranch, New Mexico (Schwartz and Gillette 1994) and those yielding sauropodomorph dinosaurs from Central Europe (Sander 1992), monotaxic association of articulated and nearly complete skeletons is rare for Triassic archosaurs. Previous records among pseudosuchians include only a group of about 20 individuals of *Aetosaurus ferratus* found in southern Germany in the late nineteenth century (Schoch 2007). Cross-correlation of biostratigraphic and radioisotopic data (Currie et al. 2009; Paul et al. 2009; Langer et al. 2010; Irmis et al. 2010) indicates that *D. quartacolonia* predates the Norian-Rhaetian (Late Triassic) "Siltstone Member" of the Chinle Formation, which yielded *C. bauri*, and the sauropodomorph/*A. ferratus*-bearing Löwenstein Formation by at least 10 million years, representing the earliest evidence of possible group behavior among archosaurs.

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