REDESCRIPTION AND PHYLOGENETIC RELATIONSHIPS OF THE PROTEROCHAMPSID *RHADINOSUCHUS GRACILIS* (DIAPSIDA: ARCHOSAURIFORMES) FROM THE EARLY LATE TRIASSIC OF SOUTHERN BRAZIL

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Abstract. The proterochampsids are small to medium-sized, quadrupedal and probable semi-aquatic reptiles that were part of the evolutionary radiation of Archosauromorpha during the Triassic. The group is restricted to the Middle and Late Triassic of South America with eight nominal species. *Rhadinosuchus gracilis* Huene was the first described proterochampsid and comes from the late Carnian−earliest Norian of southern Brazil. This genus and species is currently the most enigmatic and poorly known member of the group. For this reason we redescribe here its anatomy and discuss its phylogenetic relationships. We found that this species can be distinguished from other proterochampsids and we dismiss the proposed synonymy with *Cerritosaurus binsfeldi* Price. Our quantitative phylogenetic analysis found *Rhadinosuchus gracilis* more closely related to *Gualosuchus reigi* Romer and *Chanaresuchus bonapartei* Romer than to other proterochampsids, together forming the subfamily Rhadinosuchinae. Characters supporting this assignment include a maxilla with a distinct longitudinal change in slope between lateral and dorsal surfaces, and dorsal surface of nasal and frontal ornamented by ridges showing a radial pattern. In addition, *Rhadinosuchus gracilis* was recognized as the sister taxon of *Chanaresuchus bonapartei* based on a lacrimal with an antorbital fossa that occupies almost half or more of the anteroposterior length of the ventral process. The topology of the phylogenetic analysis shows that the Brazilian species do not form a monophyletic clade and favours multiple dispersal events between the Ischigualasto-Villa Unión (northwestern Argentina) and the Paraná (southern Brazil) basins.

Key words. Archosauromorpha. Proterochampsidae. Carnian. South America. Phylogeny. Biogeography.

Resumen. REDESCRIPCIÓN Y RELACIONES FILOGENÉTICAS DEL PROTEROCHÁMPSIDO *RHADINOSUCHUS GRACILIS* (DIAPSIDA: ARCHOSAU-RIFORMES) DEL TRIÁSICO TARDÍO TEMPRANO DEL SUR DE BRASIL. Los proterochámpsidos son reptiles cuadrúpedos, de pequeño a mediano tamaño y probablemente semiacuáticos que fueron parte de la radiación evolutiva de los Archosauromorpha durante el Triásico. El grupo esta restringido al Triásico Medio y Tardío de América del Sur, con ocho especies nominales. *Rhadinosuchus gracilis* Huene fue el primer protero-chámpsido descripto y proviene del Carniano tardío−Noriano más temprano del sur de Brasil. Este género y especie es actualmente el más enig-mático y menos conocido de los miembros del grupo y, como resultado, redescribimos aquí su anatomía y discutimos sus relaciones filogenéticas. Encontramos que esta especie puede ser distinguida de otros proterochámpsidos y rechazamos su supuesta sinonimia con *Cerritosaurus binsfeldi* Price. Nuestro análisis filogenético cuantitativo encontró a *Rhadinosuchus gracilis* como más cercanamente relacionado a *Gualosuchus reigi* Romer y *Chanaresuchus bonapartei* Romer que a otros proterochámpsidos, juntos formado la subfamilia Rhadinosuchinae. Los caracteres que soportan esta asignación incluyen un maxilar con un claro cambio de pendiente entre las superficies lateral y dorsal, y un nasal y frontal con superficies dorsales ornamentadas por crestas dispuestas en un patrón radial. Adicionalmente, *Rhadinosuchus gracilis* fue encontrado como el taxón hermano de *Chanaresuchus bonapartei* basado en un lacrimal con una fosa anteorbitaria que ocupa casi la mitad o más del largo anteroposterior del proceso ventral. La topología del análisis filogenético muestra que las especies brasileñas no forman un clado monofilético entre sí e indica la presencia de múltiples eventos dispersivos entre las cuencas de Ischigualasto-Villa Unión (noroeste de Argentina) y de Paraná (sur de Brasil).

Palabras clave. Archosauromorpha. Proterochampsidae. Carniano. América del Sur. Filogenia. Biogeografía.

PROTEROCHAMPSIDS are a group of small to medium-sized quadruped and semi-aquatic (at least *Proterochampsa* Reig, 1959) archosauriforms with an overall crocodile-like aspect (Trotteyn *et al.*, 2013). Proterochampsids were part of the evolutionary radiation of Archosauromorpha during the Triassic and they have been regarded as close relatives (Benton and Clark, 1988; Dilkes and Sues, 2009; Ezcurra *et al.*, 2010; Desojo *et al.*, 2011; Nesbitt, 2011; Dilkes and Arucci, 2012) or the immediate sister-taxon of crown-archosaurs (Gauthier, 1984; Sereno and Arcucci, 1990; Sereno, 1991; Parrish, 1993; Juul, 1994). Proterochampsids differ from most other archosauromorphs in the presence of dorsally facing external nares, strongly ornamented skull roofs, very long snouts (ca. 50– 55% of total skull length; *e.g.*, *Chanaresuchus bonapartei* Romer, 1971: MCZ 4037, 4039) and–particularly in some species– a strongly dorso-ventrally compressed skull with dorsally facing antorbital fenestrae and orbits (Trotteyn *et al.*, 2013). The fossil record of the group is currently restricted to eight nominal species from the Middle and Late Triassic Ischigualasto-Villa Unión and Paraná basins of northwestern Argentina and southern Brazil, respectively (Reig, 1959; Romer, 1971; Kischlat, 2000;

Figure 1. Map of the Brazilian region showing the Zahn Zanga locality yielded the holotype of **Rhadinosuchus gracilis** (modified from Reichel *et al.*, 2009). Scale bar for the Rio Grande do Sul State= 500 km, and for the close up= 50 km.

Dilkes and Arcucci, 2012; Trotteyn *et al.*, 2013). Several papers have improved our anatomical and phylogenetic knowledge of proterochampsids in the last few years (*e.g.*, Trotteyn, 2011; Trotteyn and Haro, 2011, 2012; Dilkes and Arcucci, 2012; Trotteyn *et al.*, 2012, 2013; Raugust *et al.*, 2013; Trotteyn and Ezcurra, 2014), but there are still some poorly known species that constitute a gap in the knowledge of the group. One of these poorly known species is *Rhadinosuchus gracilis* Huene, 1938, from the early Late Triassic Santa Maria Sequence 2 of southern Brazil (Fig. 1). *Rhadinosuchus gracilis* was the first described proterochampsid (although originally not described as a proterochampsid, but as a pseudosuchian; Huene, 1938), but as yet there is no detailed description of the single known specimen of this taxon. As a result, several aspects of the anatomy and the phylogenetic relationships of the species remain uncertain (Desojo *et al.*, 2010; Trotteyn *et al.*, 2013). Here we describe and compare the holotype of *Rhadinosuchus gracilis* in detail and discuss its phylogenetic relationships among proterochampsids and its implications for the taxonomy and palaeobiogeography of the group.

GEOLOGICAL AND PALAEONTOLOGICAL SETTING

The holotype and only known specimen of *Rhadinosuchus gracilis* was found in quarry 17 of the Sanga 6 or 'Zahn Sanga' in the site of São José (Huene, 1938, 1942; Langer *et al.*, 2007) (Fig. 1). The locality is part of the outcrops of the Santa Maria Sequence 2 in the Paraná Basin. The predominant lithofacies in the Santa Maria Sequence 2 is non-laminated to finely laminated reddish mudstones, with some sandy inclusions (Zerfass *et al.*, 2003). The 'Zahn Sanga' also yielded the holoype of *Rauisuchus tiradentes* Huene, 1942; and an indeterminate rhynchosaur (Huene, 1938, 1942). The 'Zahn Sanga' is placed in the Acme Zone of the *Hyperodapedon* Assemblage Zone, which was correlated with the lower levels of the Argentinean Ischigualasto Formation of late Carnian–early Norian age (Langer *et al.*, 2007). The Santa Maria *Hyperodapedon* Acme Zone also contains the following species: the rhynchosaurs *Hyperodapedon sanjuanensis* (Sill, 1970); *Hyperodapedon huenei* Langer and Schultz, 2000; *Hyperodapedon mariensis* (Tupí-Caldas, 1933), and *Hyperodapedon* sp., the pseudosuchians *Aetosauroides scagliai* Casamiquela, 1960, and *Aetobarbakinoides brasiliensis* Desojo Ezcurra and Kischlat 2012, the
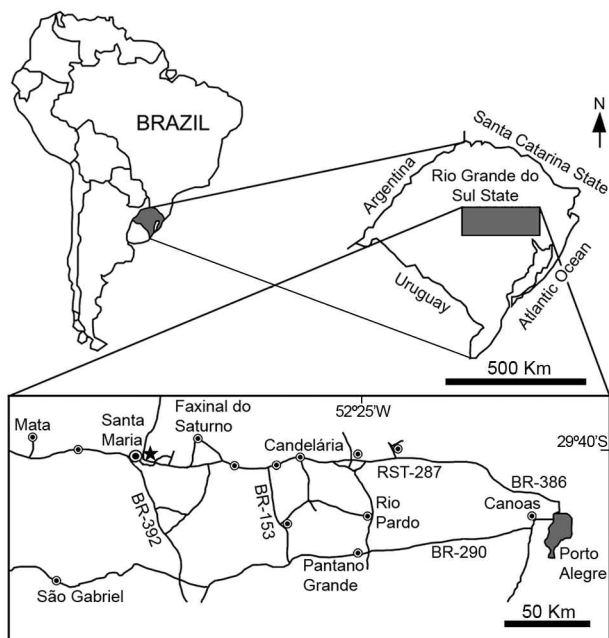
cynodonts *Therioherpeton cargnini* Bonaparte and Barberena, 1975; *Prozostrodon brasiliensis* (Barberena *et al.*, 1987), and *Gomphodontosuchus brasiliensis* Huene, 1928, the parareptile *Candelaria barbouri* Cisneros Damiani, Schultz, da Rosa, Schwanke, Neto and Aurelio 2004, and the dinosaurs *Staurikosaurus pricei* Colbert, 1970, and *Saturnalia tupiniquim* Langer Abdala, Richter and Benton, 1999 (Langer, 2005; Langer *et al.*, 2007; Desojo and Ezcurra, 2011; Desojo *et al.*, 2012).

A recent study of the chronostratigraphy of the Ischigualasto Formation indicates that the rhynchosaur biozone (*Scaphonyx-Exaeretodon-Herrerasaurus* biozone) and the younger *Exaeretodon* biozone (in which *Hyperodapedon* and *Herrerasaurus* are not recorded) can be constrained between 231.4 and 225.9 Ma based on radioisotopic dates (Martínez *et al.*, 2011). The age of the boundary between both biozones of the Ischigualasto Formation cannot be confidently assessed. Associations present in the Santa Maria Sequence 2 at most localities are the *Hyperodapedon-Exaeretodon* associations. In the cases in which a locality only yields *Exaeretodon* (*e.g.*, the *Sacisaurus* site; Langer *et al.*, 2007), it cannot be assigned unambiguously to the *Exaeretodon* biozone because the assessment is based on negative evidence (*i.e.*, supposed absence of Hyperodapedon; Desojo *et al.*, 2012). Accordingly, Desojo *et al.* (2012) proposed considering the entire *Hyperodapedon* Assemblage Zone constrained between the 231.4 and 225.9 Ma. Accordingly, the age of *Rhadinosuchus gracilis* can be constrained to the late Carnian–earliest Norian.

Institutional abbreviations. **BP,** Bernard Price Institute for Palaeontological Research, University of the Witswatersrand, Johannesburg, South Africa; **BSPG,** Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; **CA,** Colégio Anchieta, Porto Alegre, Brazil; **CPEZ,** Coleção Municipal, São Pedro do Sul, Brazil; **IVPP,** Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; **MACN-Pv,** Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires, Argentina; **MCP,** Museo de Ciencias e Tecnologia, Porto Alegre, Brazil; **MCZ,** Museum of Comparative Zoology, Harvard University, Boston, USA; **NM,** National Museum, Bloemfontein, South Africa; **PIN,** Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia; **PULR,** Paleontología, Universidad Nacional de La Rioja, La Rioja, Argentina; **PVL,** Paleontología de Vertebrados, Instituto 'Miguel Lillo', San Miguel de Tucumán, Argentina; **RC,** Rubidge Collection, Wellwood, Graaff-Reinet, South Africa; **SAM-PK,** Iziko South African Museum, Cape Town, South Africa; **SMNS,** Staatliches Museum für Naturkunde, Stuttgart, Germany; **TM,** Ditsong National Museum of Natural History (formerly Transvaal Museum), Pretoria, South Africa; **UFRGS,** Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil; **UMZC,** University Museum of Zoology, Cambridge, UK; **USNM,** National Museum of Natural History (formerly United States National Museum), Smithsonian Institution, Washington DC, USA.

SYSTEMATIC PALAEONTOLOGY

Diapsida Osborn, 1903 *sensu* Laurin (1991)
Archosauromorpha Huene, 1946 *sensu* Dilkes (1998)
Archosauriformes Gauthier *et al.*, 1988 *sensu* Gauthier *et al.* (1988)
Proterochampsia Bonaparte, 1971 *sensu* Kischlat (2000)
Proterochampsidae Sill, 1967 *sensu* Trotteyn (2011)
Rhadinosuchinae Hofstetter, 1955 (new definition)

Comment. Hofstetter (1955) erected the family Rhadinosuchidae for the taxa *Rhadinosuchus* and *Cerritosaurus* Price, 1946, which he considered to be possible synonym with each other. Later, Sill (1967) coined the family Proterochampsidae for the genus *Proterochampsa*. Although Rhadinosuchidae thus has formal priority to Proterochampsidae, the former family has rarely been mentioned in the literature (*e.g.*, Krebs, 1976), whereas the family Proterochampsidae has been commonly used to refer to this clade since its original designation (*e.g.*, Romer, 1971, 1972a,b; Arcucci, 1990; Kischlat, 2000; Langer 2005; Trotteyn and Haro, 2011; Dilkes and Arcucci, 2012; Trotteyn *et al.*, 2013; Trotteyn and Ezcurra, 2014). Thus, in accordance with article 35.5 of the ICZN, we prefer to retain the family name Proterochampsidae, with Rhadinosuchidae being subsumed under this name as Rhadinosuchinae. Rhadinosuchinae is defined here as a stem-based clade including all archosauriforms more closely related to *Rhadinosuchus gracilis* Huene, 1938, and *Chanaresuchus bonapartei* Romer, 1971, than to *Cerritosaurus binsfeldi* Price, 1946; *Tropidosuchus romeri* Arcucci, 1990, and *Doswellia kaltenbachi* Weems, 1980.

Rhadinosuchus gracilis Huene, 1938

Figures 2–5

Holotype. BSPG AS XXV 50, 51, partial skull and postcranium originally preserved in two blocks of red mudstone. The skull includes both premaxillae and dentaries, right maxilla, nasal, lacrimal and anterior tip of frontal, left jugal, quadratojugal, opisthotic, exoccipital, prootic and splenial. The postcranium is represented by a posterior cervical centrum, two partial cervical ribs, several gastralia, two dorsal osteoderms, and a probable left metatarsal II (Figs. 2–5). In addition, a possible partial neural arch of the axis (Fig. 2: ana?) and an indeterminate bone are preserved in the main block (Fig. 2: ?). The holotype was found below a rhynchosaur angular and the bones were in close association with each other (Huene, 1942).

Horizon and locality. Quarry 17 of the Sanga 6 or 'Zahn Sanga', Alemoa Member, Santa Maria Sequence 2 (*Hyperodapedon* Acme Zone: late Carnian to earliest Norian), Rosário do Sul Group, Paraná Basin, São José, Rio Grande do Sul State, southern Brazil (Huene, 1938, 1942; Langer *et al.*, 2007) (Fig. 1).

Emended diagnosis. *Rhadinosuchus gracilis* is a proterochampsian distinguished from other basal archosauriforms by the following combination of characters (autapomorphy indicated with an asterisk): maxilla with a dorsoventrally low antorbital fossa on the horizontal process; nasal with an anteroposteriorly elongated narial fossa and strongly ornamented dorsal surface composed of mainly longitudinally oriented ridges (also present in other proterochampsids); lacrimal with a very well anteroposteriorly developed antorbital fossa on the ventral process; and dentary with a large, anterodorsally opening foramen on the anterior surface*; and more than 22 dentary tooth positions.

DESCRIPTION

The holotype of *Rhadinosuchus gracilis* is preserved in two blocks of red mudstone. The larger block originally contained the skull bones, the cervical remains and the dorsal osteoderms (Fig. 2). The smaller block currently bears gastralia and a metatarsal (Fig. 5.10). The latter bone seems to have been completely removed from the matrix and fully prepared at some point [probably before Huene's (1942) description], but now it is glued back into the block. The

borders of the two blocks of mudstone do not match. The similar preservation and size of the bones from both blocks is consistent with the hypothesis that they belong to a single individual (cf. Huene, 1938, 1942). The holotype of *Rhadinosuchus gracilis* has received additional preparation for the purpose of this research, including the lateral and medial surface of the right dentary, medial surface of left dentary, areas surrounding the partial braincase, and the cervical centrum and osteoderms were removed from the main block of mudstone and fully prepared (Fig. 5.1–8).

Previous authors suggested that the holotype of *Rhadinosuchus gracilis* belonged to a juvenile specimen because of its small size (Kischlat, 2000). This interpretation is consistent with the presence of a completely unfused cervical centrum to the missing neural arch (Fig. 5: fna) (Brochu, 1996; Irmis, 2007) and the probable presence of a relatively large orbit (Ezcurra and Butler, 2015a). However, the evidence currently available to establish the ontogenetic stage of the specimen is weak and should be tested in the future with other lines of evidence (*e.g.*, palaeohistology).

Cranium

The right premaxilla, maxilla and anterior portion of nasal, right lacrimal are preserved in articulation with each other (Huene, 1942) (Fig. 2). However, the remaining bones of the snout (*i.e.*, both dentaries, left premaxilla, posterior portion of the right nasal in articulation with the anterior tip of the frontal) are preserved in semi-articulation close to their original position. In particular, the left premaxilla is posteriorly displaced from its counterpart and is rotated about 180° around the dorsoventral plane (Fig. 2: lpmx). As a result, the lateral surface of the left premaxilla is exposed in the right lateral view of the skull and its alveolar margin is facing upwards (Huene, 1942). There is one partial tooth, missing most of its root, preserved between the posterior end of the horizontal process of the maxilla and the posterior end of the right dentary (Fig. 2.3: t). Additionally, there are three maxillary tooth crowns preserved on the lateral surface of the right dentary (Figs. 2.4: t, 3.6), indicating that the lower jaws were in full occlusion with the cranium during and immediately after the death of the animal and the dentaries were displaced from their original position after burial. There are only a few teeth preserved *in situ*, mainly in the anterior halves of the right maxilla and den-
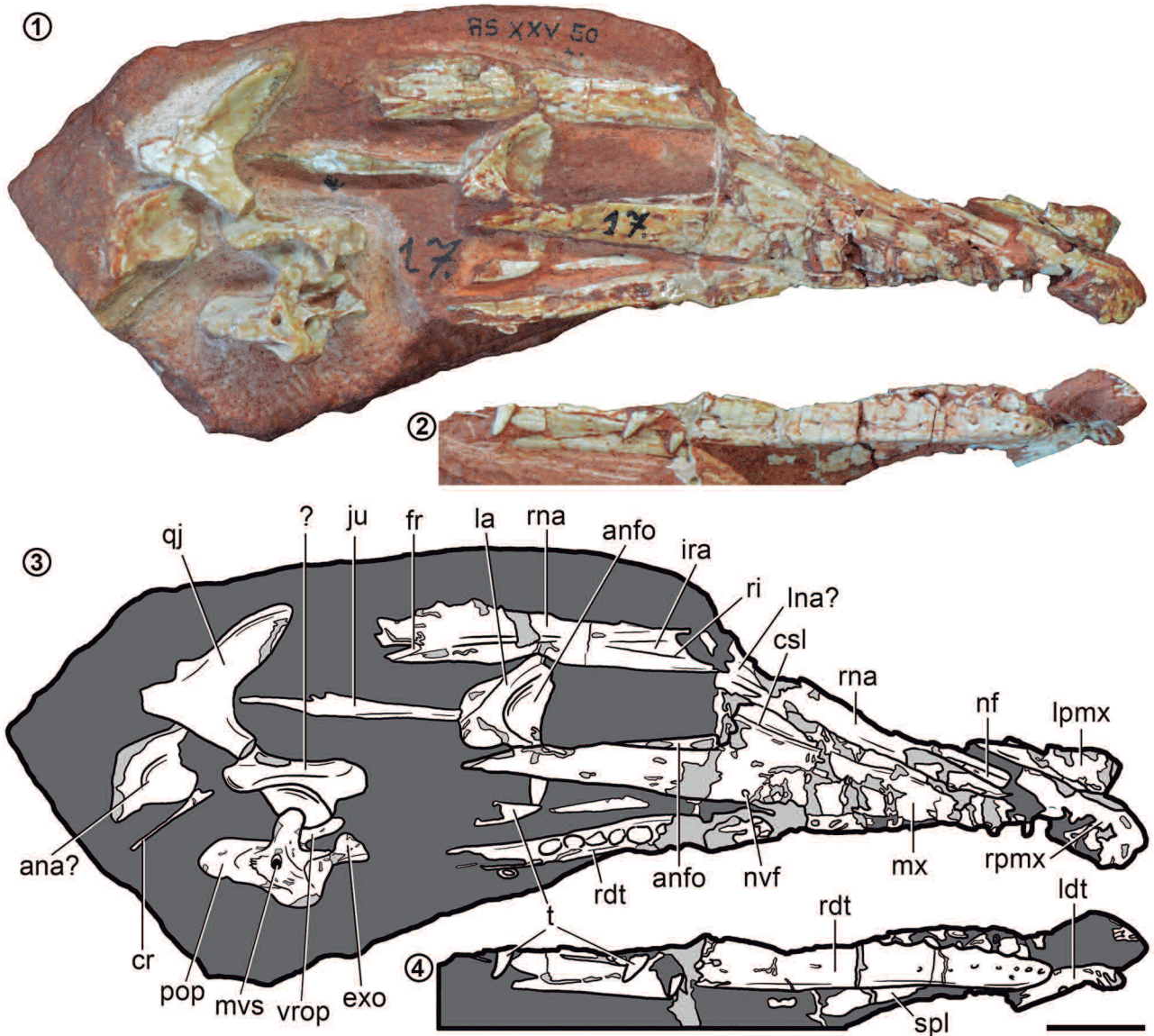
Figure 2. *Rhadinosuchus gracilis*, BSPG AS XXV 50, cranial remains. **1, 3,** Snout in right lateral view; **2, 4,** right hemimandible in lateral view. Abbreviations: **?,** indeterminate bone; **ana?,** possible axial neural arch; **anfo,** antorbital fossa; **cr,** cervical rib; **exo,** exoccipital; **csl,** change in slope; **fr,** frontal; **ira,** inter-ridges area; **ju,** jugal; **la,** lacrimal; **ldt,** left dentary; **lna?,** possible left nasal; **lpmx,** left premaxilla; **mvs,** mid-cerebral vein sinus; **mx,** maxilla; **nf,** narial facet; **nvf,** neurovascular foramen; **pop,** paroccipital process; **qj,** quadratojugal; **rdt,** right dentary; **rpmx,** right premaxilla; **rna,** right nasal; **ri,** ridge; **spl,** probable left splenial; **t,** teeth; **vrop,** ventral ramus of the opisthotic. Scale bar= 1 cm.

tary, but they are mostly represented by the roots implanted in alveoli. The most complete teeth preserved *in situ* are those occupying the third and fifth left dentary alveoli. The partial braincase is preserved posteriorly around 1.5 cm from the snout and originally in close association with the cervical centrum and two osteoderms (originally interpreted by Huene [1938, 1942] as a cervical centrum). A partial left jugal is exposed in medial view immediately posterior to the snout and its main axis is aligned with that of the snout (Fig. 2: ju). Below the left quadratojugal (originally interpreted by Huene [1938, 1942] as a right postorbital) (Figs. 2: qj, 3.5) there are two additional indeterminate bones (interpreted by Huene [1938, 1942] as possible quadrates) (Fig. 2: ?). The most posterior of these bones might be a partial neural arch of the axis. The surface of the premaxillae, dentaries, right maxilla and anterior portion of right nasal is

generally heavily cracked, which obscures some aspects of the morphology of the bones. The preserved bones of BSPG AS XXV 50, 51 did not suffer substantial post-mortem distortion. The braincase is mainly exposed in anterolateral view, in which the left prootic is severely damaged and, as a result, its internal structures are partially visible (*e.g.*, floccular recess).

General morphology. The total length of the skull of *Rhadinosuchus gracilis* is approximately 110 mm, based on the length of the maxilla (Tab. 1) and a linear regression based on the total skull and maxilla length of the *Chanaresuchus bonapartei* specimens MCZ 4037 (skull length: 243 mm, maxilla length: 105.7 mm) and MCZ 4039 (skull length: 162.4 mm, maxilla length: 79.1 mm) (we use this species for estimation of the total skull length because it was found to be the taxon most closely related to *Rhadinosuchus gracilis*; see below). The snout of *Rhadinosuchus gracilis* is considerably elongated anteroposteriorly with respect to its dorsoventral height (Fig. 2; Tab. 1), as also occurs in other proterochampsids (*e.g.*, *Chanaresuchus bonapartei*; *Gualosuchus reigi*

Romer, 1971; *Tropidosuchus romeri* Arcucci, 1990; *Proterochampsa nodosa* Barberena, 1982; *Proterochampsa barrionuevoi* Reig, 1959; Romer, 1971; Arcucci, 1990; Dilkes and Arcucci, 2012; Trotteyn *et al.*, 2013). The premaxilla is slightly downturned with respect to the main axis of the snout (Figs. 2.1, 3.1), resembling the condition seen in other archosauriforms, such as erythrosuchids (*e.g.*, *Erythrosuchus africanus* Broom, 1905: BP/1/5207; *Garjainia prima* Ochev, 1958: PIN 2394/5), some ornithosuchids (*e.g.*, *Ornithosuchus longidens* (Huxley, 1877): Walker, 1964) and other proterochampsids (*e.g.*, *Chanaresuchus bonapartei*: PULR 07, MCZ 4037, 4039; *Gualosuchus reigi*: PULR 05; *Proterochampsa barrionuevoi*: Dilkes and Arcucci, 2012). However, the degree of downturning of the premaxilla of *Rhadinosuchus gracilis* is considerably lower than those of some early archosauriforms (*e.g.*, *Proterosuchus fergusi* Broom, 1903: BP/1/3993, TM 201; possibly *Sarmatosuchus otschevi* Sennikov, 1994: Gower and Sennikov, 1997) and some ornithosuchids (*e.g.*, *Riojasuchus tenuiceps* Bonaparte, 1967: PVL 3827). The external naris is oval, strongly elongated anteroposteriorly

TABLE *1. Measurements of snout and mandible of* Rhadinosuchus gracilis *(BSPG AS XXV 50) in millimetres.*

| Measurement	Length	Width	Height
Snout	76.8	-	-
External naris	[15.6]	3.3	-
Antorbital fenestra	22.1	-	-
Premaxilla - body†	(14.7)	-	(6.5)
Premaxilla - prenarial process†	(13.2)	-	-
Maxilla	[61.0]	-	(11.0)
Maxilla - anterior process	[32.0]	-	-
Maxilla - horizontal process	28.5	-	-
Nasal	(56.6)	(6.9)	-
Lacrimal	(10.0)	-	(9.4)
Lacrimal - antorbital fossa	-	-	4.6
Dentary†	(66.6)	-	5.0^/(5.8)^^
Third dentary crown†	1.1*	-	(2.3)

Values between brackets indicate incomplete measurements (due to post-mortem damage), square brackets indicate estimate measurements, and the value given is the maximum measurable. Maximum deviation of the calliper is 0.02 mm but measurements were rounded to the nearest 0.1 millimetre.
 *Mesiodistal length at base.
 †Right.
 ^Anterior end.
 ^^Posterior end.
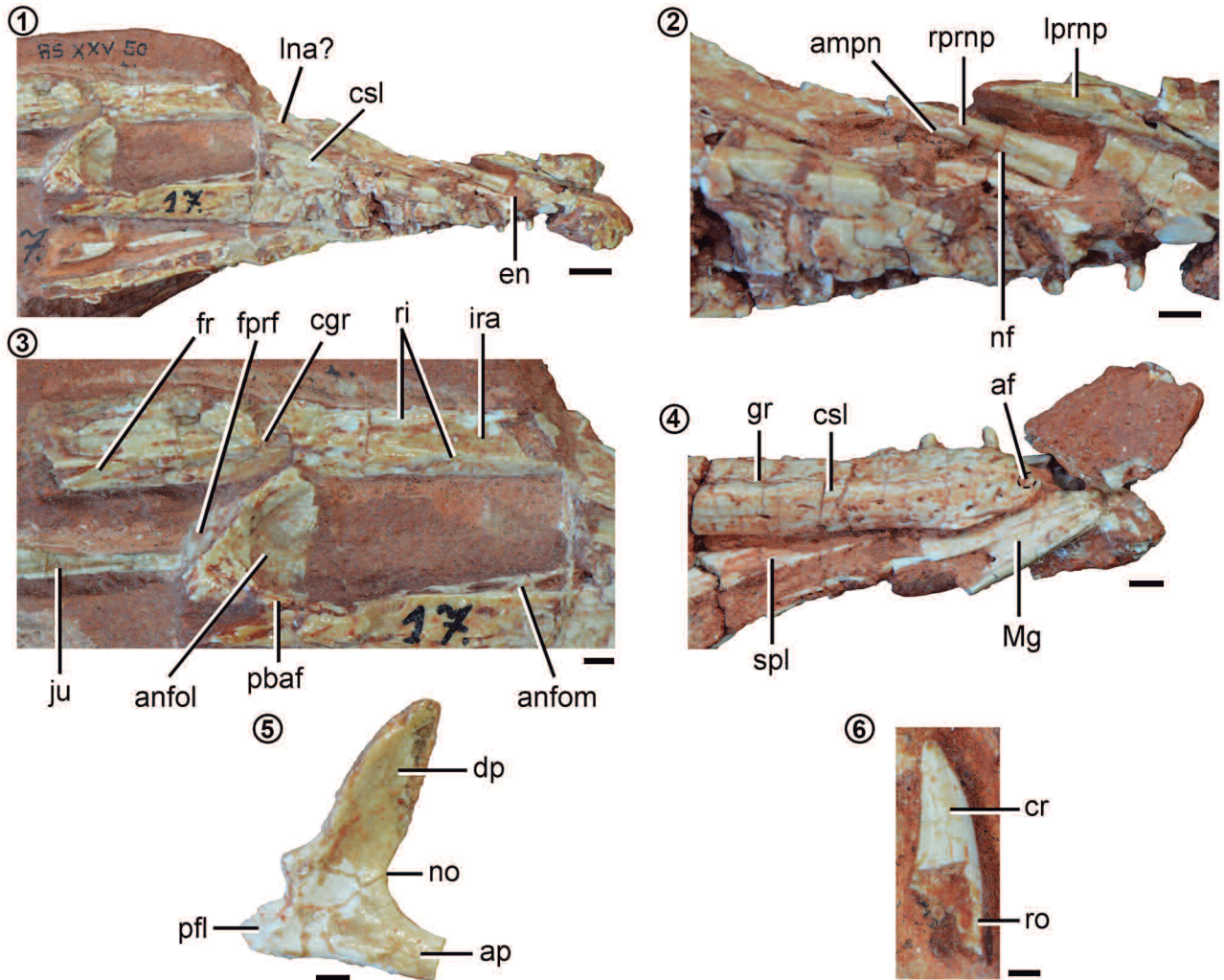
Figure 3. *Rhadinosuchus gracilis*, BSPG AS XXV 50, close-ups of cranial features. **1,** Snout in right lateral view; **2,** right premaxilla-nasal suture in lateral and slightly dorsal views; **3,** right nasal and maxilla in dorsal views and right lacrimal and maxilla in lateral views; **4,** anterior end of right dentaries in ventrolateral view and anterior end of left dentary in ventromedial view; **5,** left quadratojugal in medial view; **6,** tooth in side view. Abbreviations: **af,** anterior foramen; **ampn,** anteromedial process of the nasal; **anfol,** antorbital fossa of the lacrimal; **anfom,** antorbital fossa of the maxilla; **ap,** anterior process; **cgr,** centre of growth; **cr,** crown; **csl,** change in slope; **dp,** dorsal process; **en,** external naris; **fprf,** facet for prefrontal; **fr,** frontal; **gr,** groove; **ira,** inter-ridges area; **ju,** jugal; **lna?,** possible left nasal; **lprnp,** left prenarial process; **Mg,** Meckelian groove; **nf,** narial facet; **no,** notch; **pbaf,** posterior border of the antorbital fossa; **pfl,** posterior flange; **ri,** ridge; **ro,** root; **rprnp,** right prenarial process; **spl,** probable left splenial. Scale bars= 5 mm in (**1**), 2 mm in (**2–5**) and 1 mm in (**6**).

and mainly dorsally oriented, but with a low lateral component (Fig. 3.1: en), as also occurs in other proterochampsids (*e.g.*, *Chanaresuchus bonapartei*: PULR 07, MCZ 4037, 4039; *Pseudochampsa ischigualastensis* (Trotteyn *et al.*, 2012); *Gualosuchus reigi*: PULR 05; *Cerritosaurus binsfeldi*: cast of CA unnumbered; *Tropidosuchus romeri*: PVL 4601; *Proterochampsa barrionuevoi*: Dilkes and Arcucci, 2012; *Proterochampsa nodosa*: MCP 1694 PV). The shape of the antorbital fenestra cannot be confidently established because its dorsal border is missing and the lacrimal has been some-

what displaced posteriorly and slightly rotated. However, the preserved portions of the lacrimal and ascending process of the maxilla suggest that the opening was subtriangular in lateral view, with an anteriorly pointing apex (Figs. 2, 3.1). The antorbital fenestra is anteroposteriorly very long and represents around 32% of the total length of the maxilla, resembling the condition in the holotype of *Tropidosuchus romeri* (PVL 4601: ca. 40%) and some specimens of *Chanaresuchus bonapartei* (PULR 07: 31%; MCZ 4039: 29%). However, the size of the antorbital fenestra

seems to be intraspecifically variable, at least in *Chanare-suchus bonapartei*, in which some specimens have an antor-bital fenestra length representing 22% of the total length of the maxilla (MCZ 4037). The long and slender anterior ramus of the jugal indicates a proportionally large and rounded orbit, which would be consistent with a possible juvenile condition and resembles the condition in *Tropidosuchus romeri* (PVL 4601). The posterior end of the dermal skull is represented by a left quadratojugal (Fig. 3.5). The shape of this bone indicates that the posteroventral corner of the in-fratemporal fenestra was squared and possesses a notch (Fig. 3.5: no), as occurs in other proterochampsids (Dilkes and Arcucci, 2012). The relation between the dorsoventral height of the quadratojugal and the height of the snout is similar to that observed in *Chanaresuchus bonapartei* (PULR 07, MCZ 4039).

Premaxilla. The right premaxilla lacks the anterior tip and posterior end of the premaxillary body and the postnarial process, and has a heavily cracked lateral surface (Fig. 2: rpmx; Tab. 1). The bone is mainly exposed in lateral view and partially in dorsal and ventral views. The medial surface of the bone is covered by matrix, obscuring the palatal region. The left premaxilla is represented by part of the premaxillary body and proximal end of the prenarial process, both ex-posed in lateral view (Fig. 2: lpmx). The premaxillary body is anteroposteriorly long, resembling the condition in most proterochampsids (*e.g.*, *Chanaresuchus bonapartei*: PULR 07; MCZ 4037, 4039; *Gualosuchus reigi*: PULR 05; *Pseudo-champsa ischigualastensis*: Trotteyn and Ezcurra, 2014; *Proterochampsa barrionuevoi*: Dilkes and Arcucci, 2012; *Pro-terochampsa nodosa*: MCP 1694 PV), but contrasting with the possibly dorsoventrally deeper premaxillary body of *Cerritosaurus binsfeldi* (cast of CA unnumbered). At least most of the lateral surface of the premaxillary body lacks bone remodelling. It is not possible to determine the presence or absence of neurovascular foramina. The lateral margin of the premaxillary body is continuously convex anteroposte-riorly in ventral view, which resulted in a U-shaped anterior end of the snout. The prenarial process is anteroposteriorly very long and gently tapers posteriorly in dorsal view (Fig. 3.2: lprnp, rprnp), as also occurs in *Chanaresuchus bonapartei* (PULR 07; MCZ 4037, 4039) and *Gualosuchus reigi* (PULR 05). The area of transition between the premaxillary body and the prenarial process has a shallow and not well-defined

narial fossa, with an unornamented surface. The lateroven-tral surface of the prenarial process bears a slightly dorso-ventrally concave facet for reception of the anteromedial process of the nasal, which is dorsally delimited by a sharp longitudinal edge (Figs. 2, 3: nf). As a result, both prenarial processes of the premaxilla articulated with each other in the median line along their entire extension, as it is also the case in other proterochampsids (*e.g.*, *Pseudochampsa is-chigualastensis*: Trotteyn and Ezcurra, 2014; *Chanaresuchus bonapartei*: PULR 07; MCZ 4037; *Gualosuchus reigi*: PULR 05). Only the anterior portion of the alveolar margins is pre-served in the premaxillae and, as a consequence, the tooth count of the bone cannot be determined. In the right pre-maxilla there is one severely broken root preserved in the probable second tooth position. In the left premaxilla there is a better-preserved root in cross-section, which seems to belong to the first tooth position. The root is oval in cross-section, being labiolingually compressed, and possesses an oval pulp cavity. A clear distinction between the tooth and the bone exists, implying that the tooth was not ankylosed to the premaxilla.

Maxilla. The right maxilla is dorsoventrally low and antero-posteriorly very long (around 5.5 times longer than tall as preserved; Tab. 1), mainly as the result of an elongated an-terior process (Figs. 2, 3.1), resembling the overall mor-phology present in other proterochampsids and doswelliids (*e.g.*, Romer, 1971; Dilkes and Arcucci, 2012; Schoch and Sues, 2013; Trotteyn *et al.*, 2013). The anterior process is slightly longer than the length of the antorbital fenestra (Tab. 1) and is not differentiated along its dorsal margin from the base of the ascending process. The anterior process tapers strongly anteriorly, resulting in the anterior portion of the snout being considerably lower dorsoventrally than that at the level of the anterior border of the orbit. The anterior tip of the anterior process is not preserved and the morphology of its contact with the premaxilla cannot be determined. The lateral surface of the anterior process is heavily cracked and, as a result, only one neurovascular foramen can be confidently discerned (Fig. 2.3: nvf). The foramen is situated immediately above the alveolar margin of the bone and immediately anterior to the level of the anterior border of the antorbital fenestra, placed in a more ventral position than the maxillary alveolar foramina of *Chanaresuchus bonapartei* (PULR 07) and *Gualosuchus reigi*

(PULR 05). The foramen is sub-circular, relatively large (1 mm diameter) and opens lateroventrally. There is no evidence of ornamentation on the lateral surface of the anterior process. The anterior half of the anterior process is laterally inflated, resulting in a wide, anteroposteriorly convex surface, which is absent in the vast majority of proterochampsids (*i.e.*, *Chanaresuchus bonapartei*: PULR 07, MCZ 4037, 4039; *Pseudochampsa ischigualastensis*: Trotteyn and Ezcurra, 2014; *Gualosuchus reigi*: PULR 07; *Cerritosaurus binsfeldi*: cast of CA unnumbered; *Tropidosuchus romeri*: PVL 4601; *Proterochampsa barrionuevoi*: MACN-Pv 18165, Dilkes and Arcucci, 2012; *Proterochampsa nodosa*: MCP 1694 PV) and doswelliids (*e.g.*, *Jaxtasuchus salomoni* Schoch and Sues, 2013: SMNS 91083). However, the laterally inflated area of the maxilla of *Rhadinosuchus gracilis* may be an artefact as a result of damage suffered by the bone in that area. The dorsal portion of the anterior and ascending processes shows a distinct change in slope, which separates a laterally facing surface from a mainly dorsally facing one (Figs. 2, 3.1: csl). The laterally facing surface shows a shallow, dorsoventral concavity immediately below this change in slope, which results in a very low and rounded longitudinal ridge along the separation between both surfaces. The concavity becomes deeper posteriorly and extends at least slightly onto the surface of the ascending process. The edge between the two distinctly facing surfaces converges anteriorly with the dorsal margin of the bone and, as a result, the transverse width of the dorsally facing surface decreases gradually anteriorly. These two distinctly facing surfaces of the anterior process of the maxilla are also present in *Chanaresuchus bonapartei* and *Gualosuchus reigi*, but not in other proterochampsids (Dilkes and Arcucci, 2012) and doswelliids (*e.g.*, *Jaxtasuchus salomoni*: SMNS 91083). The dorsomedial margin of the maxilla shows an extensive, longitudinal suture with the nasal (Fig. 2.1, 2.3). The ventral margin of the anterior process is severely damaged, but it seems to curve slightly dorsally towards its anterior tip.

Only the base of the ascending process is preserved and is mainly posteriorly oriented, but with a very low dorsal component, in lateral view. The anterior border of the antorbital fenestra is acute and it is not possible to determine if the ascending process had an antorbital fossa because the area adjacent to the border of the opening is covered by matrix. The horizontal process seems to be fairly complete and with a relatively well preserved lateral surface. The horizontal process tapers posteriorly in lateral view, with a straight ventral margin and a posteroventrally sloping dorsal margin (Figs. 2.1, 2.3, 3.1). The lateral surface of the process lacks ornamentation and no neurovascular foramen can be confidently discerned. The horizontal process forms the entire ventral border of the antorbital fenestra. At the border of the fenestra, it forms a shelf that is transversely widened and dorsally slightly concave. Dorsoventrally there is a very low antorbital fossa, which is restricted to the anteroventral portion of the antorbital fenestra (Figs. 2.1, 2.3, 3.3: anfo), resembling the condition in some archosaurs (Nesbitt, 2011). It cannot be completely ruled out that part of the extension of the antorbital fossa is exaggerated, because the medial margin of the bone is slightly pressed upwards and some alveoli are visible in lateral view due to breakage. By contrast, in other proterochampsids the horizontal process lacks an antorbital fossa (*e.g.*, *Chanaresuchus bonapartei*: PULR 07, MCZ 4037, 4039; *Gualosuchus reigi*: PULR 05; *Pseudochampsa ischigualastensis*: Trotteyn and Ezcurra, 2014; *Cerritosaurus binsfeldi*: cast of CA unnumbered; *Tropidosuchus romeri*: PVL 4601; *Proterochampsa barrionuevoi*: Dilkes and Arcucci, 2012; *Proterochampsa nodosa*, MCP 1694 PV). The surface of the antorbital fossa has three sub-oval and equally separated openings. These openings correspond to the alveoli probably exposed because of damaging of the base of the alveolous. The posterior end of the horizontal process should have contacted the lacrimal at least medially (Fig. 2.1, 2.3: la), although the exact position of the contact remains unclear due to the displacement of the lacrimal. It is not possible to discern the facet for reception of the jugal.

The alveolar margin of the maxilla is strongly damaged along the anterior process of the bone and completely obscured by matrix along the horizontal process. As a result, it is not possible to determine the total number of tooth positions of the maxilla. Seven tooth positions are preserved along the anterior process, and the entire anterior process might have included eight or nine alveoli. The exposed alveoli are oval, being labiolingually compressed, and open ventrally. There are some maxillary teeth preserved *in situ*, with the roots implanted in their alveoli being exposed in labial view in some cases due to damage of the lateral surface of the bone. In addition, there are four right maxillary

teeth preserved detached from the bone. One of the teeth is preserved between the right maxilla and dentary and preserves the base of the root and an entire crown (Figs. 2.1, 2.3: t, 3.6). The other three teeth are found on the lateral surface of the right dentary and only have their crowns preserved (Fig. 2.2, 2.4: t). The position of the last maxillary tooth preserved on the lateral surface of the dentary (see above) indicates that the upper tooth row extended backwards more than that of the mandible, as occurs in other archosauromorphs (*e.g.*, *Prolacerta broomi* Parrington, 1935: BP/1/471; *Proterosuchus fergusi*: SAM-PK-11208; *Garjainia prima*: PIN 2394/5). The teeth are deeply implanted in the alveoli and are not fused to the maxilla. The bases of the crowns are oval, labiolingually compressed, and show a large pulp cavity in cross-section. The maxillary crowns are gently curved distally–with an apex placed slightly behind the distal margin of the base of the crown– to straight (Fig. 2.1, 2.3: t). However, in both cases the crowns are asymmetric in labial or lingual views, with an apicobasally convex mesial margin and a slightly concave or straight distal one. Both margins of the crown bear carinae and serrations. The distal serrations extend along the entire margin of the crown whereas the mesial serrations are restricted to the apical two-thirds of the crown. The mesial serrations are apicobasally and mesiodistally smaller and more densely packed than the distal serrations. The distal serrations are separated by wider interdenticle notches than those of the mesial carina and have a density of 10 serrations per mm close to the base of the crown. By contrast, along the mesial margin there are 12 serrations per mm. The serrations of both margins are subrectangular to chisel-like and perpendicular to the main axis of the crown. The crowns lack blood grooves, wrinkles and wear facets. Two of the preserved maxillary crowns have a faint enamel ornamentation. One maxillary crown, which is preserved between the right maxilla and dentary, has a gentle change in slope separating the distal portion of the crown from the rest of its surface. This change in slope is apicobasally oriented and curves slightly distally, following the concavity of the distal margin of the crown. The other ornamented crown is the best posteriorly preserved tooth that lies on the lateral surface of the dentary, which has an inflated, longitudinal area on its labial surface, with a slightly mesiodistally concave area distal to it.

Nasal. The right nasal is preserved in two portions. The anterior third of the bone is preserved in articulation with the right maxilla and premaxilla and the posterior two-thirds are preserved detached from the rest of the snout, but in articulation with the anterior tip of the frontal (Fig. 2.1, 2.3: rna; Tab. 1). The posterior portion of the nasal is interpreted as belonging to the right element because the margin of the bone that is artificially bordering the antorbital fenestra curves ventrally and would have articulated laterally with the prefrontal and maxilla. The opposite margin is broken, but it is dorsoventrally very thin, in agreement with that expected for the medial border of the bone. Moreover, the longer ridges of the dorsal ornamentation of the nasal are placed laterally, as expected in a right nasal (Fig. 2.1, 2.3: ri). Both fragments of the right nasal are exposed in dorsal view. Between the two fragments of bone there is another partial bone posteriorly covered by matrix and anteriorly overlapped by the anterior portion of nasal (Figs. 2.3, 3.1: lna?). The surface of the bone is slightly damaged and shows at least one low, thick ridge, suggesting that it may represent a skull roof element. However, it is not possible to determine if it also belonged to the right nasal or if it might be a fragment of the left nasal. Nevertheless, this fragment of bone lies in a different plane than those of the right nasal, and if it is considered as part of the latter element the right nasal would be longer than expected. As a result, we consider that it is more likely that it belongs to the left nasal.

The anterior portion of the right nasal preserves the posterior border of the external naris, which is situated approximately at the level of the mid-length of the anterior process of the maxilla. Only the base of the anterolateral process of the nasal is preserved, and the anteromedial process is more complete, but missing its anterior tip (Fig. 3.2: ampn). The anteromedial process forms the posterior half of the medial border of the external naris as far as is preserved. The facet for reception of this process in the premaxilla (Fig. 3.2: nf) indicates that it extended at least 2 mm further anteriorly than preserved and, as a result, the nasal formed most of the medial border of the narial opening, as also occurs in *Gualosuchus reigi* (PULR 05) and *Chanaresuchus bonapartei* (MCZ 4037). The nasal possesses a shallow, unornamented and posteriorly well-developed narial fossa behind the external naris (Fig. 3.3: ira), resembling the condition in *Gualosuchus reigi* (PULR 05), *Chanare-*

suchus bonapartei (PULR 07, MCZ 4037), *Pseudochampsa ischigualastensis* (Trotteyn and Ezcurra, 2014), *Cerritosaurus binsfeldi* (cast of CA unnumbered; Dilkes and Arcucci, 2012), *Tropidosuchus romeri* (Dilkes and Arcucci, 2012) and *Proterochampsa nodosa* (MCP 1694 PV). The lateral and medial borders of the narial fossa are delimited by thick ridges that increase in height posteriorly (Figs. 2.1, 2.3, 3.3: ri). These ridges show a mainly longitudinal orientation, but they converge posteriorly together with posterior ridges into a single centre of growth in the posterior third of the nasal. This pattern of radial skull roof ornamentation is also present in *Chanaresuchus bonapartei* (PULR 07, MCZ 4037, 4039; Romer, 1971), *Pseudochampsa ischigualastensis* (Trotteyn *et al.*, 2012; Trotteyn and Ezcurra, 2014) and *Gualosuchus reigi* (PULR 07; Romer, 1971), but it differs from the longitudinal ridges and tubercles present in other proterochampsids (*e.g.*, *Cerritosaurus binsfeldi*, *Tropidosuchus romeri*, *Proterochampsa nodosa*, *Proterochampsa barrionuevoi*; Romer, 1971; Arcucci, 1990; Dilkes and Arcucci, 2012; Trotteyn *et al.*, 2013). The posterior ridges radiate from the centre of growth and extend onto the dorsal surface of the preserved portion of the frontal. As mentioned above, the lateral margin of the nasal folds ventrally to contact the prefrontal and maxilla, resembling the condition in other proterochampsids (*e.g.*, *Chanaresuchus bonapartei*: MCZ 4039; *Gualosuchus bonapartei*: PULR 05). There is no discernable facet along the lateral border of the nasal for contact with the prefrontal.

Lacrimal. The right lacrimal is almost complete, but rotated, so that the ventral process is oriented strongly anteroventrally and the anterior process projects anterodorsally (Figs. 2.1, 2.3: la, 3.3; Tab. 1). In its original position, the ventral process of the lacrimal should have had a rather vertically oriented main axis, as occurs in other proterochampsids (*e.g.*, *Chanaresuchus bonapartei*: MCZ 4039). The ventral process becomes more massive dorsally and forms a rounded posterodorsal knob at the confluence with the anterior process. No lacrimal foramen is discernable. The anterior process is slightly flexed anteroventrally and of subequal width throughout its preserved length. As preserved, both processes are subequal in length, but it cannot be excluded that parts are missing, especially of the anterior process. The angle between the two processes is approximately 65–70°. The antorbital fossa is well developed and occupies a medial lamina spanning from the anterior end of

the anterior process to the upper third of the ventral process (Figs. 2.1, 2.3, 3.3: anfo), thus resembling the condition in *Chanaresuchus bonapartei* (PULR 07; MCZ 4039). By contrast, the lacrimal antorbital fossa is strongly restricted anteriorly in *Gualosuchus reigi* (PULR 05), *Cerritosaurus binsfeldi* (cast of CA unnumbered; Dilkes and Arcucci, 2012) and *Tropidosuchus romeri* (PVL 4601), and absent in *Pseudochampsa ischigualastensis* (Trotteyn and Ezcurra, 2014), *Proterochampsa barrionuevoi* (Dilkes and Arcucci, 2012) and *Proterochampsa nodosa* (MCP 1694 PV). The thickened dorsal rim of the fossa curves posteroventrally onto the ventral process. Anteroventral to the posterodorsal knob of the lacrimal, a very slight depression is present on the lateral side of the lacrimal main body just posterodorsal to the antorbital fossa. The dorsal rim of the anterior process and the main body of the lacrimal at the confluence of the processes forms a low but sharply defined laterodorsal crest. This crest separates the lateral surface of the lacrimal from the medially expanded horizontal facet for the articulation with the prefrontal, which is slightly depressed below the dorsal surface of the crest (Fig. 3: fpfr). As preserved, the facet is semioval in outline and restricted to the posterior two thirds of the lacrimal. The facet for articulation with the prefrontal along the posterior surface of the lacrimal is covered by matrix. As a result, it is not possible to determine the degree of participation of the lacrimal in the anterior border of the orbit.

Frontal. Only the anterolateral tip of the right frontal in articulation with the nasal is preserved (Figs. 2.1, 2.3, 3.3: fr). The suture with the nasal is interdigitated and the frontal shows two anterior projections in its preserved portion, resembling the condition present in other basal archosauriforms (*e.g.*, *Proterosuchus fergusi*: RC 59, BP/1/4016; *Proterochampsa barrionuevoi*: Dilkes and Arcucci, 2012; *Chanaresuchus bonapartei*: MCZ 4039). The dorsal surface of the anterior tip of the frontal is ornamented by ridges extended from a centre of growth in the posterior end of the nasal.

Jugal. The left jugal is partially preserved and exposed in medial view. It is very slender, with long anterior and posterior processes, as in *Tropidosuchus romeri* (Arcucci, 1990; Dilkes and Arcucci, 2012), but contrary to the situation in *Proterochampsa barrionuevoi*, *Pseudochampsa ischigualastensis*, *Chanaresuchus bonapartei* and *Gualosuchus reigi* (Dilkes and Arcucci, 2012; Trotteyn and Ezcurra, 2014). The anterior

process tapers over its posterior half and shows a slight twist at about its mid-length, so that the anterior portion is oriented slightly dorsomedially. The dorsal margin of this process is very gently concave, indicating a large and ventrally rounded orbit. The ventral margin of the bone is somewhat thickened, and the medial surface of the element is slightly concave dorsoventrally at the base of the anterior process. Only the base of the ascending process is preserved and is relatively short anteroposteriorly. The posterior process is poorly preserved and covered posteriorly by the quadratojugal, so that its exact length cannot be determined. As preserved, the posterior process appears to be very low dorsoventrally. However, the proportionally taller preserved portion of the anterior process of the quadratojugal indicates that it is probably an artefact due to damage. The medial surface of the posterior process is flat and faces slightly ventromedially as preserved, although it is unclear if this might be an artifact of preservation.

Quadratojugal. An L-shaped bone is preserved approximately 1 cm posterior to the frontal and nasal and was originally interpreted by Huene (1938, 1942) as a right postorbital (Figs. 2.1, 2.3: qj, 3.5; Tab. 2). The bone is interpreted as a quadratojugal here because it possesses a medial folding in the posterior margin of the dorsal process to contact the quadrate, a notch in the posteroventral corner of the infratemporal fenestra (Fig. 3.5: no) –as also present in other proterochampsids (Dilkes and Arcucci, 2012)– and a small posterior flange (Fig. 3.5: pfl) that in lateral view

usually covers partially the distal quadrate condyles in other basal archosauriforms (*e.g.*, *Erythrosuchus africanus*: BP/1/5207; *Euparkeria capensis* Broom, 1913: SAM-PK-5867). In addition, the bone is not a postorbital because if the longest preserved process is interpreted as a ventral process it lacks a facet for articulation with the jugal. On the other hand, if the longest preserved process is interpreted as a posterior process, the ventral process should be posteroventrally oriented and is too long and plate-like for an anterior process (*contra* Huene, 1938, 1942). The direction of the folding of the posterior margin of the dorsal process indicates that the quadratojugal is exposed in medial view. Only the base of the anterior process is preserved, which is straight and with a slightly dorsoventrally convex medial surface (Fig. 3.5: ap). The margins of the dorsal and anterior processes form a widely concave notch in the posteroventral corner of the infratemporal fenestra, which was interpreted as a synapomorphy of Proterochampsia/Proterochampsidae by Dilkes and Arcucci (2012). The notch of *Rhadinosuchus gracilis* seems to be shallower than in most members of the clade (*e.g.*, *Gualosuchus reigi*: PULR 05; *Chanaresuchus bonapartei*: PULR 07, MCZ 4039). By contrast, the posteroventral corner of the infratemporal fenestra of *Proterochampsa nodosa* lacks a notch (MCP 1694 PV). The dorsal process is plate-like and mainly perpendicular to the anterior process, but with a low anterior orientation (Fig. 3.5: dp). The anterodorsal margin of the process is broken. The medial surface of the dorsal process is anteropos-

TABLE 2. Measurements of quadratojugal and braincase of **Rhadinosuchus gracilis** *(BSPG AS XXV 50) in millimetres.*

Measurement	Length	Width	Height
Quadratojugal	(13.5)	-	18.2
Quadratojugal - dorsal process	-	-	13.7
Paraoccipital process	(9.0)	-	6.2*
Exoccipital	-	3.5**	-
Prootic	(11.3)	-	(9.9)
Mid-cerebral vein sinus	1.3	-	-
Crista prootica	-	-	(4.7)

Values between brackets indicate incomplete measurements (due to post-mortem damage), and the value given is the maximum measurable. Maximum deviation of the calliper is 0.02 mm but measurements were rounded to the nearest 0.1 millimetre.
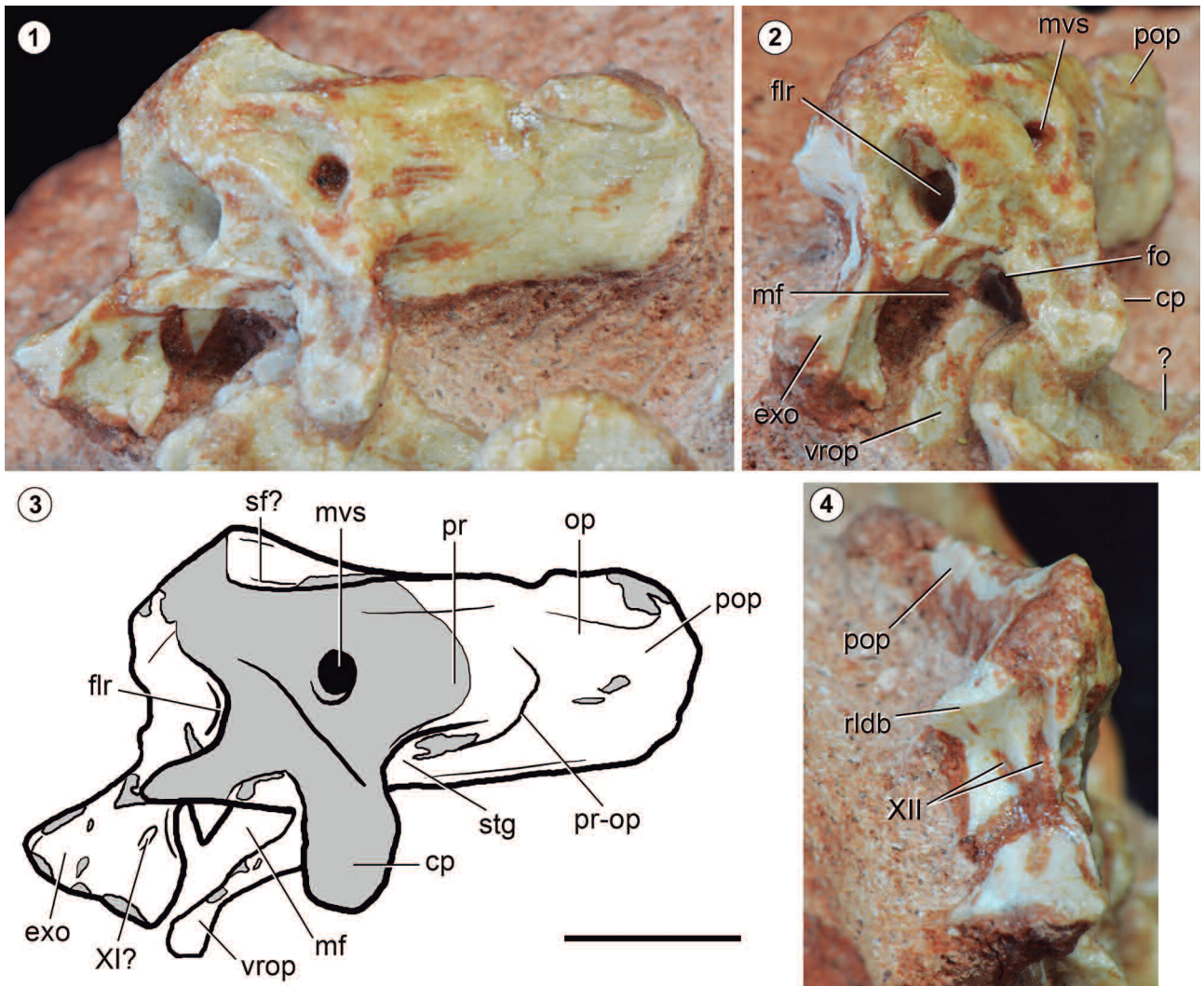*At its base.
**At its distal end.

Figure 4. *Rhadinosuchus gracilis*, **BSPG AS** XXV 50, left partial braincase. **1, 3,** anterior view; **2,** anteromedial view; **4,** exoccipital and opisthotic in medial view. Abbreviations: **?,** indeterminate bone; **XI?,** possible foramen for the accessory cranial nerve; **XII,** foramina for the hypoglossal cranial nerve; **cp,** crista prootica; **exo,** exoccipital; **flr,** floccular recess; **fo,** fenestra ovalis; **mvs,** mid-cerebral vein sinus; **mf,** metotic foramen; **op,** opisthotic; **pop,** paroccipital process; **pr,** prootic; **pr-op,** prootic-opisthotic suture; **rldb,** raised laterodorsal border of the foramen magnum; **sf?,** probable supraoccipital and possible parietal facet; **stg,** stapedial groove; **vrop,** ventral ramus of the opisthotic. Scale bar= 5 mm.

teriorly concave as a result of the medial folding of the posterior margin. Most of the posterior flange of the quadratojugal is broken off, but it can be assumed that it partially covered the distal condyles of the quadrate. There is no distinct facet for reception of the quadrate on the medial surface of the quadratojugal.

Opisthotic. The left opisthotic is preserved in articulation with the prootic and exoccipital (Fig. 4: op; Tab. 2). However, it is not possible to establish if the opisthotic was fused to the exoccipital (= otoccipital) because the occipital surface of the partial braincase is mostly covered by matrix. The

opisthotic possesses a posteriorly raised laterodorsal border of the foramen magnum, probably for articulation with the proatlas (Fig. 4.4: rldb). At the dorsal apex of the bone there is a facet, well defined ventrally by a shelf that probably represents the area of reception for the supraoccipital and possibly parietal (Fig. 4.1, 4.3: sf?). The base of the left paroccipital process shows parallel dorsal and ventral margins (Fig. 4.1, 4.3: pop). The suture between the opisthotic and the prootic can be seen on the anterolateral surface of the paroccipital process, which is continuously laterally convex, as also occurs in other archosauriforms (Gower and

Sennikov, 1996). The ventral margin of the paroccipital process leads anteromedially to the ventral ramus of the opisthotic (= crista metotica, = crista interfenestralis), which separates the fenestra ovalis and the metotic foramen and is exposed in anterior view as preserved (Fig. 4: vrop). On the anteroventral side of the paroccipital process, and dorsally partially bordered by the prootic, is the stapedial groove, which leads anteromedially to the fenestra ovalis. The ventral ramus is well developed, extending ventrally far beyond the level of the metotic foramen and fenestra ovalis, resembling the condition present in basal archosauriforms (Gower and Sennikov, 1996). The ventral ramus is also very thin transversely, resembling the condition present in, for example, *Euparkeria capensis* (Gower and Weber, 1998), *Chanaresuchus bonapartei* (PULR 07), *Proterochampsa barrionuevoi* (Dilkes and Arcucci, 2012), and *Archeopelta arborensis* Desojo, Ezcurra and Schultz, 2011 (CPEZ-239a). By contrast, in some less crownward archosauriforms (*e.g.*, "*Chasmatosaurus*" *yuani* Young, 1936: IVPP V2719; *Garjainia triplicostata* (Huene, 1960): PIN 951/ 60) the distal half of the ventral ramus of the opisthotic is considerably more robust and cylindrical in cross-section. The fenestra ovalis lies anterior to the ventral ramus of the opisthotic and is mostly obscured by the crista prootica in anterolateral view (Fig. 4.2: fo). The metotic foramen lies posteromedially to the ventral ramus and is preserved between this structure and the exoccipital (Fig. 4: mf).

Exoccipital. The exoccipital is mostly exposed in medial and anterior to anterolateral views (Figs. 2.1, 2.3, 4: exo; Tab. 2). The medial surface of the bone is almost flat at its ventral end and becomes anteroposteriorly concave dorsally. The medial surface has a shallow, moderately defined vertical groove that slightly curves posteriorly. This surface is separated from the internal wall of the brain cavity by a marked rim, as it also occurs in other archosaurs. The medial surface of the bone, which in life would have formed the lateral rim of the foramen magnum, possesses two oval foramina, with a major dorsoventral axis, which are interpreted to have conducted the branches of the hypoglossal cranial nerve (CN XII) (Fig. 4.4: XII). The presence of a pair of foramina for the hypoglossal nerve is also observed in the proterochampsid *Proterochampsa barrionuevoi* (Trotteyn and Haro, 2011) and several crown-archosaurs (*e.g.*, *Silesaurus opolensis*: Dzik, 2003). By contrast, in doswelliids (*i.e.*, *Dos-*

wellia kaltenbachi Weems, 1980: Dilkes and Sues, 2009; *Archeopelta arborensis*: Desojo *et al.*, 2011; *Jaxtasuchus salomoni*: Schoch and Sues, 2013) there is a single exit for the hypoglossal nerve. The anterolateral surface of the bone shows a large, apparently ventromedially directed foramen in a somewhat more ventral position than the foramina for the hypoglossal nerve; this foramen might have transmitted the accessory cranial nerve (CN XI) (Fig. 4.3: XI?). The occipital surface of the bone is covered by matrix and the anterior surface has a sharp vertical edge.

Prootic. The left prootic is preserved in articulation with the opisthotic and is exposed in anterior to anteromedial view in a broken approximately transverse section, showing internal structures of the braincase (*e.g.*, floccular recess) (Fig. 4: pr; Tab. 2). The posterior region of the prootic forms the anterior portion of the base of the paroccipital process and the dorsal margin of the stapedial groove, as also occurs in other basal archosauriforms (Gower and Sennikov, 1996). The lateral surface of the prootic is dorsoventrally convex at the base of the paroccipital process. The preserved portion of the crista prootica is ventrally oriented and forms the anterior margin of the fenestra ovalis (Gower and Sennikov, 1996). Immediately dorsal to the base of the crista prootica there is a large, rounded pit on the internal surface of the prootic. From this pit, a well-developed furrow extends posteromedially towards the (unpreserved) suture of the opisthotic with the supraoccipital. Another somewhat narrower furrow extends anteroventrally from it onto the base of the crista prootica. These furrows most probably mark the course of the mid-cerebral vein, with the pit representing the posterodorsal sinus formed by this vein (Figs. 2.1, 2.3, 4.1–3: mvs). Posteromedial to the sinus, a large, conical recess opens posterolaterally into the prootic from medial, which represents the floccular recess.

Mandible

Both dentaries are preserved in contact with each other, but the right bone is displaced posteriorly with respect to the left element and, as a result, the symphyseal region of the left dentary is exposed (Figs. 2, 3.1, 3.4). A transversely thin bone lies between both dentaries, but anteriorly it becomes adjacent to the medial surface of the left dentary up to the point that it is completely covered by matrix. Accordingly, the plate-like bone is interpreted as a left

splenial (Fig. 3.4: spl). No post-dentary bones are preserved in the holotype of *Rhadinosuchus gracilis*.

Dentary. The right dentary is almost complete, but the posterior end of the bone is not exposed, neither are the borders of the external mandibular fenestra (Fig. 2: rdt; Tab. 1). The right dentary is exposed mainly in dorsal and lateral views, and the anterior two-thirds of the bone are also exposed in ventral view. Only the anterior end of the left dentary is exposed in medial and ventral views (Figs. 2.2, 2.4: ldt, 3.4). The dentary is a very long and dorsoventrally low bone, at least more than 12 times longer than its height at the anterior end, resembling the condition in *Chanaresuchus bonapartei* (MCZ 4037, ratio >13.8; PULR 07, ratio 16), *Tropidosuchus romeri* (PVL 4601), *Proterochampsa barrionuevoi* (Dilkes and Arucci, 2012), and *Doswellia kaltenbachi* (USNM 186989), but contrasting with the proportionally more robust dentary of *Cerritosaurus binsfeldi* (cast of CA unnumbered). The dentary of *Rhadinosuchus gracilis* is straight along its entire length, as is also the case in *Chanaresuchus bonapartei* (PULR 07, MCZ 4037) and *Tropidosuchus romeri* (PVL 4601). By contrast, in *Proterosuchus fergusi* (TM 201, SAM-PK-11208) and *Euparkeria capensis* (SAM-PK-5867) the dentary curves dorsally, and in *Doswellia kaltenbachi* (USNM 186989) the dentary curves ventrally in lateral view. The dentary also curves slightly laterally in dorsal and ventral views. The lateral surface of the anterior end of the dentary is dorsoventrally convex, but it becomes flat along the rest of the bone. The lateral and ventral surfaces of the bone are not ornamented and they are separated from each other by a distinct change in slope of around 90° that results in a rounded and well-developed lateroventral longitudinal edge along at least the anterior two-thirds of the bone (Fig. 3.4: csl). As a result, the planes of the lateral and ventral surfaces of the bone meet each other at an orthogonal angle, with exception of the anterior end of the bone, in which the transition between the surfaces is more gradual. The latter condition is also present in *Chanaresuchus bonapartei* (PULR 07, MCZ 4037) and *Gualosuchus reigi* (PVL 4576), but not in *Proterochampsa nodosa* (MCP 1694 PV), *Cerritosaurus binsfeldi* (cast of CA unnumbered), *Tropidosuchus romeri* (PVL 4601), *Doswellia kaltenbachi* (USNM 186989), and other basal archosauriforms (*e.g.*, *Proterosuchus fergusi*: TM 201, BP/1/3993, SAM-PK-11208; *Erythrosuchus africanus*: BP/1/5207; *Euparkeria capensis*, SAM-PK-5867). The presence of this distinct change in slope between the lateral and ventral surfaces of the dentary might be correlated with a similar change of slope of the lateral and dorsal surfaces of the maxilla.

The anterior margin of the dentary is acute (ca. 60°), the result of a gentle ventral curvature of the alveolar margin of the bone along the first three alveoli (Figs. 2.2, 2.4, 3.4). The anterior tip of the dentary has a very large and mainly anterodorsally opening foramen (Fig. 3.4: af), which is absent in *Chanaresuchus bonapartei* (PULR 07, MCZ 4037), *Tropidosuchus romeri* (PVL 4601), *Proterochampsa nodosa* (MCP 1694 PV) and *Doswellia kaltenbachi* (USNM 186989). In addition, the lateral and ventral surfaces of the dentary show at least nine neurovascular foramina along the anterior half of the bone (Figs. 2.2, 2.4, 3.4). These foramina are aligned in four longitudinal rows, two on the lateral surface and two on the ventral one. The foramina show a variable morphology, from circular openings to oval ones, with a dorsoventral or an anteroposterior main axis. The foramina belonging to the most dorsal row, the first foramen of the second row (from dorsal to ventral) and the first two foramina of the most ventral row are the largest. From the level of the seventh tooth position there is a longitudinal and very shallow groove placed at mid-height on the lateral surface of the dentary (Fig. 3.4: gr). The groove finishes at the level of the tenth tooth position in an anteroposteirorly elongated and posterolaterally opening foramen. The lateral surface of the dentary lacks foramina or grooves posterior to the level of the tenth tooth position. The ventral surface of the bone is gently convex transversely at its anterior end and flat posteriorly, lacking foramina posterior to the level of the ninth tooth position. The most posterior foramen of the ventral surface is placed at mid-width of the bone and is not aligned with the rows at the anterior end of the dentary. This foramen is anteroposteriorly elongated and extends posteriorly as a groove that gradually fades into the ventral surface of the bone.

The medial surface of the anterior end of the bone has a deep and well-defined Meckelian groove, which extends anteriorly up to the anteriormost preserved portion of the left dentary (Fig. 3.4: Mg). The Meckelian groove is restricted to the ventral half of the dentary, as is also the case in *Chanaresuchus bonapartei* (PULR 07, MCZ 4037). By contrast, in *Doswellia kaltenbachi* the Meckelian groove is placed at

mid-height along the medial surface of the dentary (USNM 186989). The Meckelian groove is placed immediately above the ventral margin of the bone in the exposed area. The medial surface of the dentary dorsal to the Meckelian groove is flat. The symphysis cannot be distinguished or it was restricted to the missing anterior tip of the bone. As a result, it cannot be determined if the Meckelian groove extended onto the symphyseal region.

The alveolar margin of the right dentary is complete, but damaged in its central part. It preserves 21 alveoli and a total of 23 tooth positions can be estimated. The number of dentary tooth positions in *Rhadinosuchus gracilis* is considerably higher than in other proterochampsids (*e.g.*, *Chanaresuchus bonapartei*, ca. 18 tooth positions; *Tropidosuchus romeri*, ca. 15 tooth positions; Romer, 1971; Arcucci, 1990), but it is lower than that observed in *Doswellia kaltenbachi* (Dilkes and Sues, 2009, 35 tooth positions). It should be noted that in other archosauriforms the number of tooth positions increases through ontogeny (*e.g.*, *Proterosuchus fergusi*: Ezcurra and Butler, 2015a; *Coelophysis bauri*: Colbert, 1989). Thus, a higher number of dentary tooth positions might be expected if the holotype of *Rhadinosuchus gracilis* is actually a juvenile individual (Kischlat, 2000). Therefore the difference in the number of dentary tooth positions between *Rhadinosuchus gracilis* and other proterochampsids would be larger in adult stages of the Brazilian species. The alveoli are oval, being anteroposteriorly longer than wide transversely, and medially closed, resulting in a thecodont tooth implantation. Seven teeth are preserved *in situ* in their respective alveoli and four of them preserve partial crowns. The roots and crowns are labiolingually compressed in cross-section. The crowns are not constricted at their base and are curved distally. The third crown and the preserved portions of the other dentary crowns are devoid of serrations in both margins, contrasting with the condition present in the maxillary crowns.

Splenial. A transversely very thin bone, partially exposed in medial view between both dentaries, represents the left splenial (see above) (Figs. 2.1, 2.3, 3.4: spl). The bone curves gently laterally, following the contour of the left dentary, and the medial surface is flat and unornamented.

Postcranium

Neural arch of the axis(?). A fragment of bone exposed pos-

terior to the quadratojugal might represent part of an axial neural arch. The element is slightly longer than the preserved postaxial cervical centrum and has a short anterior and better developed posterior process. The anterior process is directed slightly anterodorsally and has a lateral thickening at the level of the anterior end of the neural spine, which might represent the axial prezygapophysis. The posterior process is flat horizontally and tapers posteriorly and probably represents the dorsal surface of the postzygapophysis, which is devoid of epipophyses, as in most other basal archosauriforms. The neural spine is relatively low, but considerably higher than that of *Proterochampsa barrionuevoi* (Dilkes and Arcucci, 2012) and *Doswellia kaltenbachi* (Dilkes and Sues, 2009). The dorsal margin of the axial neural spine of *Rhadinosuchus gracilis* is rounded anteroposteriorly, rising gradually from the anterior end, but with a straight posterior margin. The neural spine lacks completely a spine table or a distal thickening.

Postaxial cervical vertebra. A single cervical centrum is preserved in the holotype of *Rhadinosuchus gracilis* (Fig. 5.1–4; Tab. 3). The centrum is interpreted to belong to a posterior cervical vertebra because the parapophyses are situated in the anterodorsal corner of the centrum and possibly extended slightly onto the neural arch (Fig. 5.1–2: pa). The centrum is longer than tall and slightly compressed transversely in ventral view (Fig. 5.4), resembling the condition in other proterochampsids (*e.g.*, *Proterochampsa barrionuevoi*: Dilkes and Arcucci, 2012; *Tropidosuchus romeri*: PVL 4601; *Gualosuchus reigi*: PULR 05; *Chanaresuchus bonapartei*: PULR 07, MCZ 4037). The point of maximum transverse constriction is placed anterior to the mid-length of the centrum (Fig. 5.3). The ventral surface possesses a sharp and well-developed median keel that extends along the posterior three-quarters of the centrum (Fig. 5.3: vk), resembling the condition in the cervical vertebrae of *Proterochampsa barrionuevoi* (Dilkes and Arcucci, 2012), *Tropidosuchus romeri* (Arcucci, 1990), *Gualosuchus reigi* (PULR 05), *Chanaresuchus bonapartei* (PULR 07, MCZ 4037), *Doswellia kaltenbachi* (Dilkes and Sues, 2009), and *Jaxtasuchus salomoni* (Schoch and Sues, 2013). The ventral surface of the centrum is wide and transversely convex anterior to the median keel. The anterior and posterior articular surfaces are gently concave and oval, being transversely wider than tall, as also occurs in *Doswellia kaltenbachi* (Dilkes and Sues, 2009). There is

TABLE 3. Measurements of postcranial bones of Rhadinosuchus gracilis *(BSPG AS XXV 50) in millimetres.*

Measurement	Length	Width	Height
Postaxial cervical centrum	7.4	6.3*/5.9**	3.9*/4.2**
Cervical rib	11.2	-	-
Metatarsal II	23.4	8.6^/6.8^^	3.6^^
Metatarsal II - lateral condyle	-	4.2^^	-
Metatarsal II - medial condyle	-	2.5^^	-
Osteoderm	6.4	7.7	2.8†

Maximum deviation of the calliper is 0.02 mm but measurements were rounded to the nearest 0.1 millimetre.
*Anterior surface.
**Posterior surface.
^Proximal end.
^^Distal end.
†Thickness.

no bevelling in the ventral margin of the anterior and posterior surfaces (Fig. 5.1), suggesting the absence of intercentra in at least the posterior cervical series, as is also the case in *Chanaresuchus bonapartei* (PULR 07, MCZ 4037), *Tropidosuchus romeri* (PVL 4061), *Proterochampsa barrionuevoi* (Dilkes and Arcucci, 2012), and *Jaxtasuchus salomoni* (SMNS 91083). The ventral margin of the posterior surface of the centrum extends slightly more ventrally than the anterior one, resembling the condition in the posterior cervical vertebrae of other basal archosauriforms (*e.g.*, *Tropidosuchus romeri*: PVL 4601; *Jaxtasuchus salomoni*: SMNS 91083). The lateral surface possesses a very shallow and not well-defined lateral depression (Fig. 5.1, 5.3: d). Dorsal to the depression, the centrum expands laterally and possesses a facet for articulation with the neural arch on its laterodorsal surface (Fig. 5.1: fna). The facet is saddle-shaped in lateral view, but it is slightly asymmetric, extending more ventrally anteriorly than posteriorly. The articular surface of the facet is well preserved and was clearly unfused to the neural arch. The parapophysis is not raised in a peduncle and its circular articular facet faces anterolaterally. The floor of the neural canal (Fig. 5.2: nc) has a median depression with a tapering anterior margin. The posterior end of the depression is covered by a partial cervical rib shaft (Fig. 5.2, 5.4: cr) and matrix.

Cervical rib. An almost complete anterior or middle cervical rib is preserved 5 mm away from the partial braincase, but exposed on only one side (Figs. 2.1–2: cr, 5.9; Tab. 3). The rib

is approximately twice as long as the preserved cervical centrum, but an unknown length is missing at its posterior end. The proximal end has a short and tapering anterior process (Fig. 5.9: ap). Only one of the peduncles bearing the articular facets is exposed, but its distal end is covered by matrix. The peduncle is orthogonal to the main axis of the anterior process and shaft, indicating that the shaft was mainly parallel to the main axis of the neck, as in all archosauriforms. It is not possible to determine if the peduncle represents the capitulum or tuberculum and thus neither to which side the rib belongs. The shaft is straight and very thin.

Gastralia. Several gastralia are present in the block that also contains the metatarsal, six of which are preserved in natural position with each other (Fig. 5.10: ga). The gastralia present several breakages and, as a result, is not possible to determine the presence of more than one gastral segment. The gastralia are rod-like and at least some of them are gently curved posteriorly, as also occurs in the middle dorsal region of the gastral basket of *Proterosuchus alexanderi* (Hoffman, 1965) (NM QR 1484). One of the gastralia seems to have an anteroposteriorly expanded and plate-like end, resembling the condition in *Proterochampsa barrionuevoi* (Trotteyn, 2011).

Metatarsal II. The single preserved metatarsal is complete, but the proximal three-quarters of its dorsal surface are obscured by matrix (Fig. 5.10: mtt II, 5.11–14; Tab. 3). The metatarsal is a moderately robust bone that contrasts
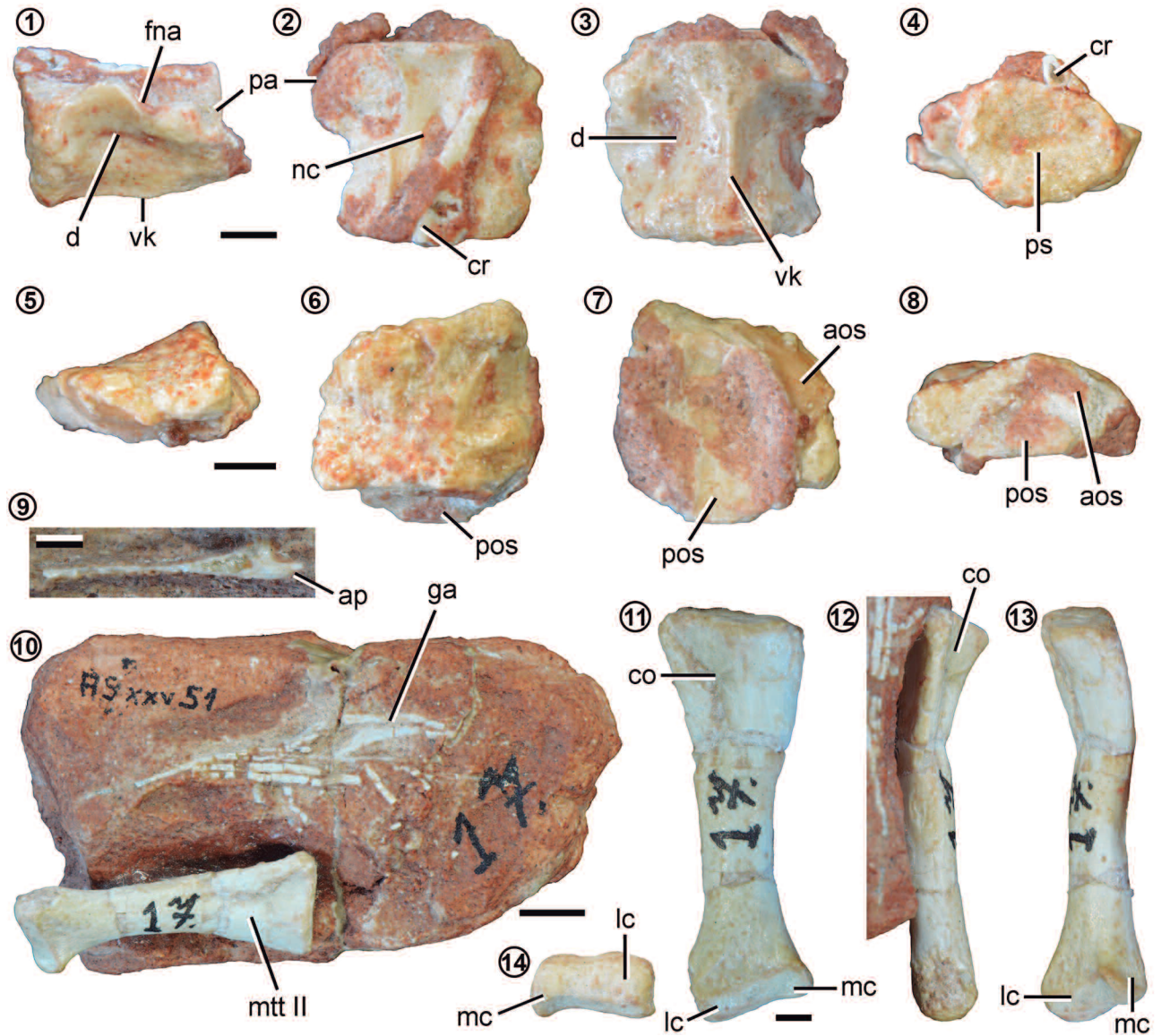
Figure 5. *Rhadinosuchus gracilis*, **BSPG AS** XXV 50, postcranial bones. **1–4,** Cervical centrum; **5–8,** osteoderms; **9,** cervical rib; **10,** block with gastralia and left metatarsal II; **11–14,** left metatarsal II. **1,** Right lateral; **2, 6,** dorsal; **3, 7, 11,** ventral; **4, 8,** posterior; **5,** left lateral; **9,** side; **12,** lateral; **13,** medial; and **14,** distal views. Abbreviations: **aos,** anterior osteoderm; **ap,** anterior process; **co,** concavity; **cr,** cervical rib; **d,** depression; **fna,** facet for reception of the neural arch; **ga,** gastralia; **lc,** lateral condyle; **mc,** medial condyle; **mtt II,** metatarsal II; **nc,** neural canal; **pa,** parapophysis; **pos,** posterior osteoderm; **ps,** posterior surface; **vk;** ventral keel. Scale bars= 2 mm in (**1–9, 11–14**) and 5 mm in (**10**).

with the considerably more gracile metatarsals III and IV of *Chanaresuchus bonapartei* (Romer, 1972a, MCZ 4035) and *Tropidosuchus romeri* (PVL 4601). The bone is proportionally too large to represent metatarsal I and the shaft is proportionally longer than those of the metatarsal I of other proterochampsids (*e.g.*, *Chanaresuchus bonapartei*: Romer, 1972a, MCZ 4035; *Tropidosuchus romeri*: PVL 4601). This element also differs from the metatarsal V of *Chanaresuchus bonapartei* (Romer, 1972a) by the presence of a long shaft

and well-developed distal articular surface. The metatarsal of *Rhadinosuchus gracilis* matches the overall proportions of metatarsal II of *Chanaresuchus bonapartei* (Romer, 1972a, MCZ 4035). In particular, the proximal end of the bone is trapezoidal in outline with a concave ventrolateral margin (Fig. 5.11–12: co), being almost identical to metatarsal II of *Chanaresuchus bonapartei* (MCZ 4035). Accordingly, the autopodial bone of *Rhadinosuchus gracilis* is interpreted as a metatarsal II. The concave ventral margin in the proximal

end of the bone corresponds to the margin contacting metatarsal III and as a result this metatarsal II is interpreted as a left element.

Metatarsal II of *Rhadinosuchus gracilis* is proportionally more robust than that of *Tropidosuchus romeri* (PVL 4601). As mentioned above, the element is trapezoidal in proximal view, with an almost straight ventromedial margin and a concave ventrolateral one. The proximal surface of the bone is flat and very gently inclined medially in ventral view with respect to the main axis of the shaft. The ventromedial surface of the proximal end of the bone is gently convex transversely. The ventrolateral surface is damaged by the collapse of cortical bone, but it seems to have been –at least proximally– transversely concave to receive the proximal end of the metatarsal III, as it is also the case in *Chanaresuchus bonapartei* (MCZ 4035). The shaft is oval in cross-section, being wider transversely than deep dorsoventrally. The medial margin of the shaft is slightly concave dorsoventrally and the lateral margin straight and. As a result, the shaft is very gently bowed medially in ventral view. The distal end of the bone is slightly expanded transversely with respect to the shaft, but less than the proximal end. The main axis of the distal end is rotated at about 30° with respect to the main axis of the proximal end of the bone, resembling the condition in *Chanaresuchus bonapartei* (MCZ 4035). The distal end is not ginglymoid, but it has two ventrally developed condyles that are poorly differentiated from each other (Fig. 5.11, 5.13–14: lc, mc). The distal condyles are asymmetric, with the lateral condyle being more ventrally extended and transversely wider than the medial one. As a result, the proximal phalanx of the digit would have been oriented medially with respect to the main axis of the metatarsal shaft. The distal articular surface is continuously convex dorsoventrally and gently concave transversely in dorsal or ventral views. The distal articular facet extends onto the distal –and part of the ventral– surface of the bone. The dorsal surface of the distal end shows a semilunate extensor fossa, which is laterally bounded by a proximomedially oriented and rugose ridge, resembling the condition in *Chanaresuchus bonapartei* (MCZ 4035). The medial surface lacks a collateral pit, whereas the lateral surface is damaged and the presence or absence of a collateral pit cannot be confirmed.

Osteoderms. Two osteoderms are preserved in articulation with each other (Fig. 5.5–8; Tab. 3). The most posterior osteoderm is only represented by its anterior tip (Fig. 5.6–8: pos), which lies almost completely below the more anterior and complete osteoderm (Fig. 5.7–8: aos). Imbricated osteoderms, in which the anterior element dorsally overlaps the posterior one, are also present in *Chanaresuchus bonapartei* (PULR 07, MCZ 4037) and *Tropidosuchus romeri* (PVL 4601). The presence of imbrication in the osteoderms of *Cerritosaurus binsfeldi* cannot be determined confidently (cast of CA unnumbered). By contrast, *Proterochampsa barrionuevoi* lacks dermal armor (Trotteyn, 2011; Dilkes and Arcucci, 2012). The posterior margin of the osteoderm is in a more dorsal position than the anterior one. The lateral margin of the osteoderm folds ventrally, which may indicate that a single median row of dorsal osteoderms was present in *Rhadinosuchus gracilis*, resembling the condition in *Chanaresuchus bonapartei* (PULR 07, MCZ 4037) and *Tropidosuchus romeri* (PVL 4601). However, the latter interpretation is tentative. The osteoderm is subrectangular in dorsal view, being wider transversely than long anteroposteriorly, and without an anterior apex (Fig. 5.6). The osteoderm is dorsoventrally thick, but the element is considerably thinner than in *Archeopelta arborensis* and *Tarjadia ruthae* Arcucci and Marsicano, 1998 (Desojo *et al.*, 2011). The dorsal surface is transversely convex and gently concave anteroposteriorly in lateral view (Fig. 5.5). This surface is not very well preserved, but it seems that it has a few anteriorly and laterally oriented ridges radiating from a centre of growth adjacent to the posterior margin of the element. However, the osteoderm lacks a clear, single median keel, resembling the condition in *Tropidosuchus romeri* (PVL 4601). The ventral surface of the most complete osteoderm is partially covered by matrix and the more posterior element, but it seems to be unornamented and moderately transversely concave. The lateral margins of the bone are not crenulated, contrasting with the condition present in *Euparkeria capensis* (UMZC T6921).

Indeterminate bone. The main block of mudstone preserves one bone that could not be identified here (Fig. 2.1, 2.3: ?). The bone is preserved between the left quadratojugal and the partial braincase, and Huene (1938, 1942) originally interpreted it as a possible left quadrate. It is composed of a thin main body and a flange that are connected by a curved ridge at one of the ends of the bone. The bone has a maxi-

mum linear measurement (*i.e.*, along the main body) of 16.3 mm. The presence of a large, teardrop-shaped foramen in the main body of the bone is an artifact resulting from breakage. The element is too large to represent the basal articulation area of a partial pterygoid and lacks any evidence of thickening of the main body towards its ends, as it should be expected for a quadrate (*contra* Huene, 1938, 1942). Accordingly, this bone is interpreted as an indeterminate element.

DISCUSSION

Taxonomy of Rhadinosuchus gracilis

Hoffstetter (1955) considered *Rhadinosuchus gracilis* as a probable senior synonym of the chronostratigraphically older archosauriform *Cerritosaurus binsfeldi*, and he considered both species to be members of its own family, Rhadinosuchidae. Certain subsequent authors followed this idea (Kuhn, 1966; Reig, 1970; Bonaparte, 1971), but others dismissed the proposal of synonymy between these Brazilian species (Huene, 1956; Romer, 1956; Bonaparte, 1970). Subsequently, Kischlat and Schultz (1999) and Kischlat (2000) proposed that *Rhadinosuchus gracilis* was more closely related to *Chanaresuchus bonapartei* and *Gualosuchus reigi* than to other proterochampsids, but representing different species.

In the present redescription we found several differences between *Rhadinosuchus gracilis* and other proterochampsids. In particular, *Rhadinosuchus gracilis* differs from *Proterochampsa barrionuevoi* and *Proterochampsa nodosa* by the absence of a skull strongly compressed dorsoventrally with a dorsally facing antorbital fenestra and the absence of well-developed nodular prominences on the lateral surface of the maxilla. *Rhadinosuchus graclis* also differs from *Cerritosaurus binsfeldi* by the presence of a proportionally lower premaxilla and maxilla, considerably longer antorbital fenestra, dorsal surface of nasals and/or frontals ornamented by ridges arranged in a radial pattern, and maxilla and dentary with distinct changes in slope between the lateral and dorsal and ventral surfaces, respectively. These differences, which are unlikely to be simply ontogenetic, undermine previous claims about a putative synonymy between *Cerritosaurus binsfeldi* and *Rhadinosuchus gracilis* (Hoffstetter, 1955; Kuhn, 1966; Reig, 1970; Bonaparte, 1971). *Rhadinosuchus gracilis* can be distinguished from *Tropido-*

suchus romeri by the pattern of skull roof ornamentation, the changes in slope in the surfaces of the maxilla and dentary, and the presence of considerably higher dentary tooth count. The Brazilian species shows several resemblances with *Pseudochampsa ischigualastensis* and *Gualosuchus reigi*, but it differs from them by the presence of a maxilla with an antorbital fossa in the horizontal process and a lacrimal with a very extensive antorbital fossa between the two processes. Finally, *Rhadinosuchus gracilis* can be distinguished from *Chanaresuchus bonapartei* by the presence of a maxilla with an antorbital fossa in the horizontal process, a dentary with a large and anterodorsally opening foramen on its anterior surface, and a considerably higher dentary tooth count. Accordingly, *Rhadinosuchus gracilis* can be considered a valid species of proterochampsid archosauriform.

Phylogenetic relationships of Rhadinosuchus gracilis

The phylogenetic relationships of *Rhadinosuchus gracilis* have been debated since its description. Huene (1938) originally classified *Rhadinosuchus gracilis* within the order-grade group Pseudosuchia, and subsequently Romer (1945) considered it as a member of Stagonolepididae. Hoffstetter (1955) transferred *Rhadinosuchus gracilis* to its own family, Rhadinosuchidae (together with *Cerritosaurus binsfeldi*). Subsequently, Romer (1956) reconsidered both *Rhadinosuchus gracilisi* and *Cerritosaurus binsfeldi* as members of the family Ornithosuchidae. Kuhn (1961) and Reig (1961, 1970) followed the interpretation proposed by Hoffstetter (1955). Romer (1966) reinterpreted the Brazilian species as members of Erpetosuchidae and Bonaparte (1970) considered *Rhadinosuchus gracilis* as a thecodont of uncertain relationships, but probably closely related to *Cerritosaurus binsfeldi*. Nevertheless, after the description of *Chanaresuchus bonapartei* and *Gualosuchus reigi* (Romer, 1971, 1972a), Romer (1972b) proposed that *Rhadinosuchus gracilis* was a member of the family Proterochampsidae, together with the former Argentinean species and *Proterochampsa barrionuevoi* and *Cerritosaurus binsfeldi*. However, Sill (1974) re-adopted the original idea of Huene (1938) of *Rhadinosuchus gracilis* as a pseudosuchian, and Krebs (1976) even considered it to be a basal crocodilian. Kischlat and Schultz (1999) and Kischlat (2000) agreed with Romer's (1972b) concept of Proterochampsidae and, in particular, proposed that *Rhadi-*

nosuchus gracilis was more closely related to *Gualosuchus reigi* and *Chanaresuchus bonapartei* than to other proterochampsids (*i.e.*, *Cerritosaurus binsfeldi*, *Tropidosuchus romeri*, *Proterochampsa barrionuevoi*, *Proterochampsa nodosa*). All subsequent authors followed the hypothesis supporting a placement of *Rhadinosuchus gracilis* within Proterochampsidae (Dilkes and Arcucci, 2012; Raugust *et al.*, 2013; Trotteyn *et al.*, 2013; Trotteyn and Ezcurra, 2014), but the species has not been included in a numerical cladistics analysis so far and its phylogenetic relationships within the group remain untested.

In order to test the phylogenetic relationships of *Rhadinosuchus gracilis* we included the Brazilian species in the data matrix published by Trotteyn and Ezcurra (2014), which is a modification of the most comprehensive analysis focused on proterochampsids by Dilkes and Arcucci (2012). We have furthermore added *Proterochampsa nodosa*, resulting in a new data matrix composed of 18 taxa and 110 characters (see Appendices). This data matrix includes for the first time all currently known nominal species of proterochampsids. The outgroup taxon was relabelled as *Proterosuchus* spp. instead of *Proterosuchus fergusi* because of a recent taxonomic revision of the genus (Ezcurra and Butler, 2015b), but the scorings of the terminal are the same as in Trotteyn and Ezcurra (2014). The data matrix was analysed under equally weighted parsimony using TNT 1.1 (Goloboff *et al.*, 2008) using the implicit enumeration algorithm. Zero length branches among any of the recovered MPTs were collapsed (rule 1 of Coddington and Scharff, 1994). Character 21 was treated as additive (ordered) following Dilkes and Arcucci (2012) and Trotteyn and Ezcurra (2014). As measures of tree support, decay indices (= Bremer supports) were calculated and a bootstrap resampling analysis —with 10,000 pseudoreplicates— was performed, reporting both absolute and GC (*i.e.*, difference between the frequency that the original group and the most frequent contradictory group are recovered in the pseudoreplicates) frequencies.

The search recovered two most parsimonious trees of 203 steps, with a consistency index of 0.5862 and a retention index of 0.7021. The overall topology of the strict consensus tree (Fig. 6) is completely consistent with that obtained by Trotteyn and Ezcurra (2014). Proterochampsia was recovered as a monophyletic group and the two newly added taxa (*Rhadinosuchus gracilis* and *Proterochampsa*

nodosa) were found within this clade, in agreement with previous qualitative studies (Kischlat and Schultz, 1999; Kischlat, 2000) (Fig. 6). The monophyly of Proterochampsia is supported by 11 synapomorphies (characters 1, 7, 9–11, 15, 20, 39, 42–44) that were already discussed in detail by Dilkes and Arcucci (2012) and its support metrics (Bremer index and bootstrap frequencies) are very high (Fig. 6). However, contrasting with Dilkes and Arcucci (2012), the presence of a distinct notch in the quadratojugal at the posteroventral corner of the infratemporal fenestra (character-state 26-1) was found as an ambiguous possible apomorphy of Proterochampsia and not as an unambiguous synapomorphy because of its absence in *Proterochampsa nodosa*. Within Proterochampsia, *Proterochampsa nodosa* was recovered as the sister-taxon of *Proterochampsa barrionuevoi* due to the presence of a skull strongly compressed dorsoventrally with dorsally facing antorbital fenestrae and mainly dorsally facing orbits (character-state 104-1); well developed nodular prominences on the lateral surface of maxilla, jugal, quadratojugal, squamosal and angular (character-state 105-1); absence of supratemporal fossa (character-state 107-0); lower jaw lacking retroarticular process (character-state 109-0); and angular with a distinctly ventrally developed thick, longitudinal lamina on the ventral surface between the levels of the external mandibular fenestra and the mandibular glenoid fossa (character-state 110-1).

The clade composed of *Cerritosaurus binsfeldi*, *Tropidosuchus romeri*, *Pseudochampsa ischigualastensis*, *Chanaresuchus bonapartei*, *Gualosuchus reigi* and *Rhadinosuchus gracilis* has two synapomorphies (characters 23 and 24) that were already discussed by Dilkes and Arcucci (2012), but their condition cannot be established in *Rhadinosuchus gracilis*. It should be noted that Dilkes and Arcucci (2012) also found character 8 (*i.e.*, depression lacking dermal sculpturing present on nasal around posterior border of external naris) as a synapomorphy of this node. However, the presence of this trait in *Proterochampsa nodosa* resulted in an ambiguous optimization of the character. The node that includes *Tropidosuchus romeri*, *Pseudochampsa ischigualastensis*, *Chanaresuchus bonapartei*, *Gualosuchus reigi* and *Rhadinosuchus gracilis* has three synapomorphies (character-states 19-1, 45-1 and 46-1) that were already discussed by Dilkes and Arcucci (2012).
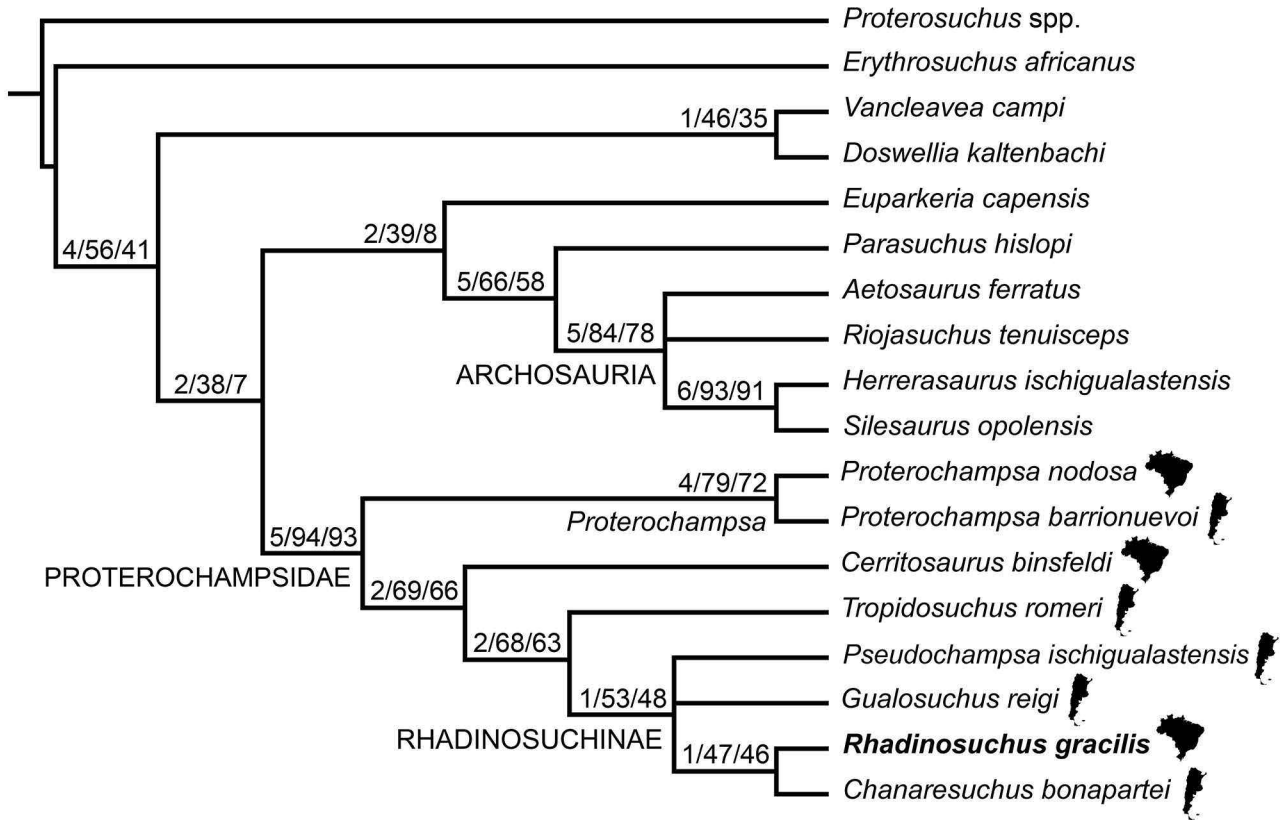
Figure 6. Phylogenetic relationships of ***Rhadinosuchus gracilis*** and other proterochampsians among basal archosauriforms. Numbers above nodes are Bremer support, absolute and GC bootstrap frequencies, respectively. The sillouetes immediately to the right of the proterochampsian species indicate their geographic occurrence (*i.e.*, Argentina or Brazil).

In agreement with Kischlat and Schultz (1999) and Kischlat (2000), *Rhadinosuchus gracilis*, *Chanaresuchus bonapartei* and *Gualosuchus reigi* were found as more closely related taxa with each other than with other proterochampsians, but also including the recently described species *Pseudochampsa ischigualastensis*. This clade is referred here as the subfamily Rhadinosuchinae Hofstetter, 1955 (derived from Rhadinosuchidae Hofstetter, 1955; keeping Proterochampsidae as the name of the family following the International Code of Zoological Nomenclature Article 35.5) and the hypothesis of Machado and Kischlat (2003) considering *Rhadinosuchus gracilis*, *Chanaresuchus bonapartei* and *Gualosuchus reigi* as members of Rhadinosuchidae (see Systematic Palaeontology for definition of Rhadinosuchinae; Fig. 6). Rhadinosuchinae is diagnosed by a skull with a lateral margin of the rostrum anterior to prefrontal formed by the nasal and maxilla with a sharp edge along maxilla between lateral and dorsal sides of this bone

(character-state 11-2) and dorsal surface of nasals and/or frontals ornamented by ridges arranged in a radial pattern (character-state 106-1). Finally, *Rhadinosuchus gracilis* is found to be the sister-taxon of *Chanaresuchus bonapartei* because of the presence of a lacrimal with an antorbital fossa that occupies almost half or more of the anteroposterior length of the ventral process (character-state 108-1). Under constrain searches two extra steps were required (TL= 205 steps) to find *Rhadinosuchus gracilis* as the sister-taxon of *Cerritosaurus binsfeldi* (*i.e.*, Hoffstetter's hypothesis of close relationships or even synonymy) and three extra steps (TL= 206 steps) are necessary to find *Rhadinosuchus gracilis* outside Proterochampsidae (*i.e.*, Huene's hypothesis), as the sister-taxon of crown-Archosauria. In summary, *Rhadinosuchus gracilis* is found here as a derived member of Proterochampsia and Proterochampsidae, contained within the subfamily Rhadinosuchinae and sister-taxon of *Chanaresuchus bonapartei*.

The Brazilian proterochampsid record and the palaeo-biogeography of the group

Proterochampsids are particularly interesting and a unique group among basal archosauriforms because it is the only group of the clade that underwent evolutionary radiation in a very restricted geographic area. Indeed, the current proterochampsid record is restricted to the Ischigualasto-Villa Unión Basin of northwestern Argentina and the Paraná Basin of southern Brazil, which are separated from each other by approximately 1,300 kilometres. The Ladinian–earliest Carnian (*Dinodontosaurus* and *Santacruzodon* Assemblages Zones) proterochampsid record of Brazil is represented by several specimens that were originally assigned to *Chanaresuchus bonapartei* (MCP 4195 PV, UFRGS-PV-0877-T), *Chanaresuchus* sp. (UFRGS-PV-0464-T) and ?*Gualosuchus* (UFRGS-PV-0465-T) (Barberena, 1978, 1982; Barberena *et al*., 1985; Dornelles, 1992, 1995; Hsiou *et al*., 2002; Raugust *et al*., 2013). *Rhadinosuchus gracilis* was found here as a species closely related to *Gualosuchus reigi* and *Chanaresuchus bonapartei* and, as a result, the taxonomic assignment of the above mentioned Brazilian specimens should be reconsidered in the light of the new evidence presented here.

The specimen originally assigned to *Chanaresuchus* sp. (UFRGS-PV-0464-T, Dornelles, 1992, 1995) was reinterpreted by Kischlat (2000) as an indeterminate proterochampsid more closely related to *Gualosuchus reigi* and *Chanaresuchus bonapartei* than to other members of the clade (*i.e.*, Rhadinosuchinae) because of the presence of a radial pattern of ornamentation in the skull roof. In addition, UFRGS-PV-0464-T shows a distinct longitudinal change in slope between the lateral and dorsal surfaces of the maxilla, bolstering its assignment to Rhadinosuchinae, but more detailed studies are necessary to assess the taxonomic identity and precise phylogenetic position for the specimen. In addition, we also agree with Kischlat (2000) in considering a partial skull (UFRGS-PV-065-T) from the same locality as UFRGS-PV-0464-T as an indeterminate rhadinosuchine because of the presence of a distinct change in slope between the lateral and dorsal surfaces of the snout. The partial skull MCP 4195 PV that was originally interpreted as *Chanaresuchus bonapartei* resembles this species rather than other proterochampsids in the presence of posteriorly divergent and subtriangular supratemporal fenestrae (Hsiou *et al*.,

2002). However, the condition of this character is unknown in *Rhadinosuchus gracilis*. As a result, MCP 4195 PV should be considered an indeterminate rhadinosuchine. Kischlat (2000) considered that the skull tentatively referred to *Gualosuchus* (UFRGS-PV-0465-T, Barberena, 1978, 1982; Barberena *et al*., 1985) was also very similar to *Rhadinosuchus gracilis*. UFRGS-PV-0465-T shows a distinct change in slope between the lateral and dorsal surfaces of the maxilla and thus can be referred to Rhadinosuchinae. However, UFRGS-PV-0465-T seems to differ from *Rhadinosuchus gracilis* by the presence of a possible lower maxillo-dentary tooth count (*i.e.*, around 12 maxillary tooth positions and should be expected a slightly higher dentary tooth count). UFRGS-PV-0465-T resembles both *Rhadinosuchus gracilis* and *Chanaresuchus bonapartei* in the presence of a well-developed antorbital fossa in the ventral process of the lacrimal. Accordingly, the combination of characters present in UFRGS-PV-0465-T suggests closer affinities with the *Chanaresuchus bonapartei* + *Rhadinosuchus gracilis* clade rather than with *Gualosuchus reigi*.

A specimen from the *Santacruzodon* Assemblage Zone was recently referred to *Chanaresuchus bonapartei* (UFRGS-PV-0877-T; Raugust *et al*., 2013). UFRGS-PV-0877-T has a limited number of bones overlapping with the holotype of *Rhadinosuchus gracilis* (*i.e.*, nasal and dentary) and it shows a morphology consistent with both *Chanaresuchus bonapartei* and *Rhadinosuchus gracilis*, including the presence of a skull roof ornamented by ridges arranged in a radial pattern and a dentary with a distinct change in slope of around 90° between the lateral and ventral surfaces (UFRGS-PV-0877-T). The dentary of UFRGS-PV-0877-T is missing its anterior tip and posterior end (Raugust *et al*., 2013) and, as a result, the complete number of tooth positions cannot be determined, but there are at least 17 dentary tooth positions. Accordingly, UFRGS-PV-0877-T should be considered an indeterminate rhadinosuchine until more evidence becomes available.

The three proterochampsid species endemic from Brazil are from the late Carnian–earliest Norian *Hyperodapedon* Assemblage Zone (Langer *et al*., 2007; Trotteyn *et al*., 2013) and they are nested as sister taxa (*i.e.*, *Proterochampsa nodosa*, *Rhadinosuchus gracilis*) or in pectinate positions (*i.e.*, *Cerritosaurus binsfeldi*) with respect to the Argentinean species (*i.e.*, *Proterochampsa barrionuevoi*, *Tropidosuchus*

romeri, *Gualosuchus reigi*) in our phylogenetic analysis (Fig. 6). This topology favours the hypothesis of multiple dispersal events between the Ischigualasto-Villa Unión and the Paraná basins, at least during the late Carnian–earliest Norian (*i.e.*, *Hyperodapedon* Assemblage Zone), and there is no current evidence for an endemic radiation of proterochampsids produced by sympatric cladogenetic events restricted to the Paraná Basin. The endemism of proterochampsids in South America has been previously recognized by most previous authors (see Trotteyn *et al.*, 2013). However, the possible causes for this endemism remain fairly unexplored. Proterochampsids and phytosaurs were partially contemporaneous and probably semi-aquatic archosauriforms, but they had non-overlapping geographic distributions during the Late Triassic. It was proposed that the distribution of phytosaurs coincides closely with the 'summerwet' (tropical, humid summer) biome reconstructed by the climatic modelling of Sellwood and Valdes (2006: fig. 2b) (Buffetaut, 1993; Brusatte *et al.*, 2013; Stocker and Butler, 2013). The geographic range of proterochampsids was located approximately at the northern rim of the temperate biome of Sellwood and Valdes (2006) and separated from the geographic range of phytosaurs by a large desert biome located between 40° S and the Palaeo-Equator. The presence of this large desert area may have prevented the dispersal of proterochampsids to more northern latitudes (*e.g.*, 'summerwet' biome). It should be further noted that phytosaurs only occur in the Paraná Basin after the extinction of proterochampsids (Kischlat and Lucas, 2003), suggesting the possibility of a competitive exclusion between these clades or, alternatively, the disappearance of a possible dispersal barrier during the middle Norian.

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