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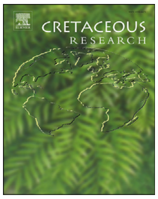

Re-description of the cranio-mandibular anatomy of *Notosuchus terrestris* (Crocodyliformes, Mesoeucrocodylia) from the Upper Cretaceous of Patagonia

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ABSTRACT

Notosuchus terrestris was the first notosuchian described worldwide and the most abundant crocodyliform species in Gondwana during the Late Cretaceous. Here, the lectotype and more than 60 complete and fragmentary specimens were studied allowing the most detailed description of the cranio-mandibular anatomy of this taxon, including poorly known regions as the braincase. Thirty-fourth characters were described and confirmed by the first time for *Notosuchus*. Possible autapomorphies include: frontal with olfactory tract groove convex posteriorly and with well marked furrows for laterosphenoid, small premaxillary knob fits a maxillary notch in the palate adjacent to the toothrow, small bilobate trigeminal fossa with grooves for the branches the CN V_{so}, CN V_2 and CN V_3, parietal and laterosphenoid highly pneumatic, post-temporal fenestra obliterated, presence of vestigial quadratojugal spine, ascending process of quadratojugal with posterior groove, vomer lateromedially broad, incisive foramen in heart-shaped delimited by premaxillae and maxillae, and choana with narrow pterygoid septum. We propose a *crista pseudo-tuberalis* separating the occiput from the braincase wall, as present in some notosuchians. Contrary to previous work, the carotid foramen and the metotic foramen open within a fossa lateral to the occipital condyle, a common feature in advanced notosuchians.

1. Introduction

Notosuchus terretris is one of the best known Crocodyliformes Mesoeucrocodylia (e.g., Clark, 1994; Pol et al., 2014) of the Cretaceous of Gondwana and the first Mesozoic crocodyliform described for South America still valid taxonomically (Pol and Gasparini, 2007). This species was first described by Woodward in 1896, from a set of 20 specimens (Giachino and Gurovich, 2001), collected by Santiago Roth in the red sandstone levels of the Bajo de la Carpa Formation (Santonian; sensu Garrido, 2010) at the campus of the Universidad Nacional del Comahue (traditionally Boca del Sapo locality), Neuquén City, Neuquén Province, Patagonia, Argentina (Fig. 1). Without designating a holotype, Woodward (1896) provided a description that includes anatomical information of the skull, mandible, teeth and the fragmentary postcranium, with emphasis on its terrestrial habit.

Dollo (1914) assigned the genus *Notosuchus* to a new family of "Mesosuchia", the Notosuchidae, in which were posteriorly also included the genera *Araripesuchus* Price, 1959 and *Uruguaysuchus* Rusconi, 1933 (Price, 1959). Dolgopol de Saez (1957) describe a new species, *Notosuchus lepidus*, based on a partial skull also collected by Santiago Roth at the same locality and horizon of *N. terrestris*.

In 1971, Gasparini assigned to the "Infraorder" Notosuchia the families Uruguaysuchidae (with *Araripesuchus* and *Uruguaysuchus*), and Notosuchidae (with *Notosuchus*). Gasparini (1971) also designed the specimen MLP 64-IV-16-5 (n ° 253 of Woodward, 1896, Fig. 2) as the lectotype of *N. terrestris*, refer to this species more than 20 specimens, all belonging to the same locality and horizon, and housed in the paleontological collection of the Museo

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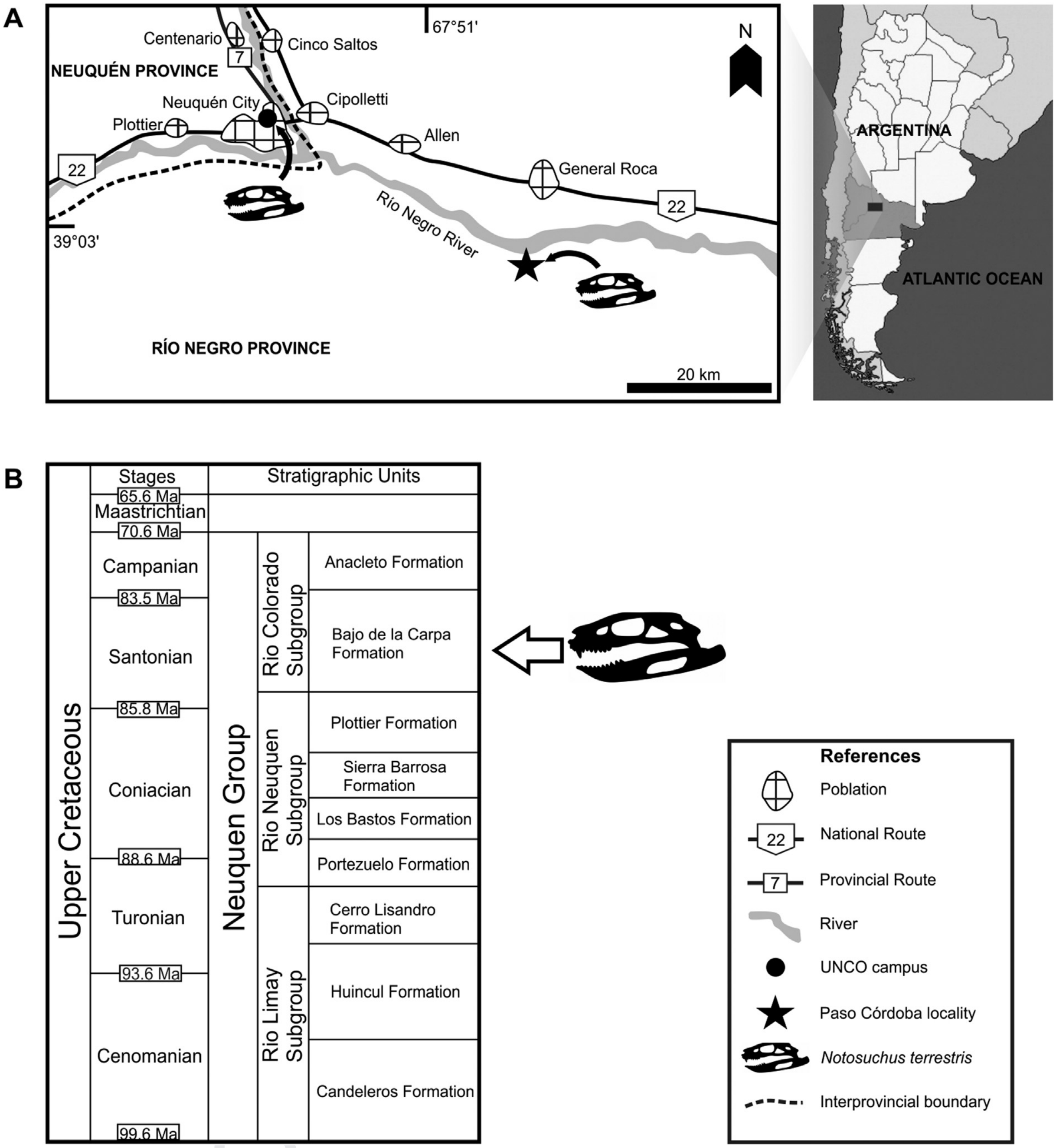

Fig. 1. **A**, Geographic and **B**, chronostratigraphic procedence of the specimens of *Notosuchus terrestris*.

de La Plata (MLP). She also consider *N. lepidus* as a synonym of *N. terrestris*, and provided a general description of its cranial and mandibular anatomy.

Despite these taxonomical approaches, several authors analyzed several cranial (pneumaticity, ontogeny, cranio-mandibular articulation and dentition) and postcranial features (corporal posture) of *Notosuchus*, which allowed to infer a terrestrial behavior for this species, with an upright posture, propalinal mandibular movements, and omnivorous or even herbivorous habits (e.g., Bonaparte, 1991; Pol, 2005; Fiorelli and Calvo, 2008; Lecuona and Pol, 2008; Coêlho et al., 2011; Ösi, 2013).

Recent phylogenetic approaches (e.g., Zaher et al., 2006; Fiorelli and Calvo, 2008; Andrade and Bertini, 2008a,b; Sereno and Larsson, 2009; Turner and Sertich, 2010; Pol et al., 2012, 2014; Leardi et al., 2015; Fiorelli et al., 2016) place *Notosuchus terrestris* as a sister taxa of Sphagesauridae (e.g., *Caipirasuchus* Iori and Carvalho, 2011, *Armadillosuchus* Marinho and Carvalho, 2009, *Yacarerani* Novas et al., 2009, *Sphagesaurus* Price, 1950), and other relative forming all together the a clade of advanced notosuchians (sensu Pol et al., 2014); Fig. 3.

Notosuchus terrestris has a unique combination of plesiomorphic characters, including: an oreinirostral skull shape (sensu Busbey, 1995), terminal nares with a perinarial depression, antorbital fenestra, neumatized basicranium, fenestrate quadrate, heterodont dentition (sensu Ösi, 2013); as well also apomorphies (e.g., maxillo-palatine fenestrae) (Pol and Gasparini, 2007). However, some important cranial features are still unknown or needs further exhaustive descriptions, as the palate, the orbital cavity, the

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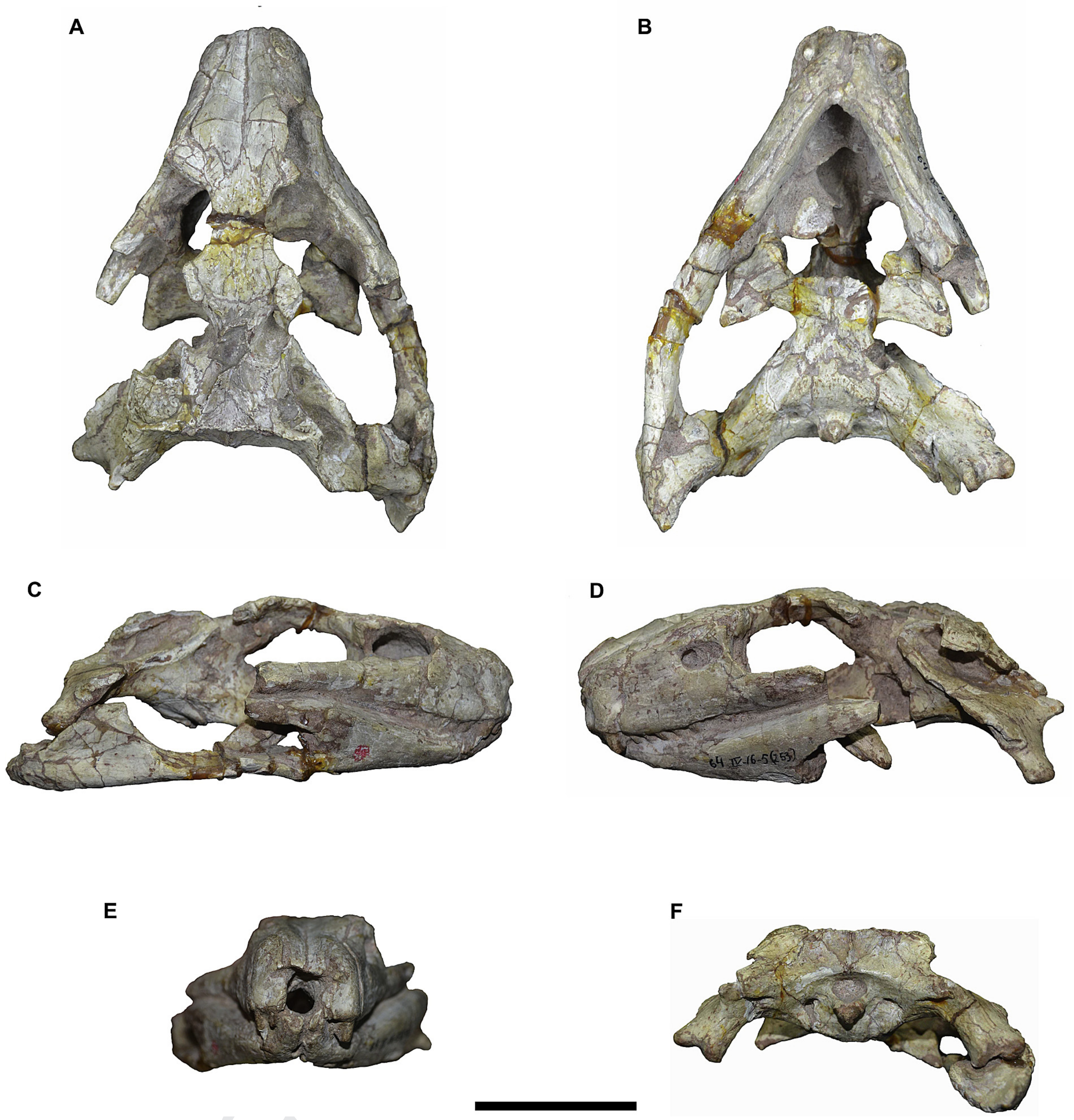

Fig. 2. *Notosuchus terrestris* MLP-64-IV-16-5 (lectotype), before mechanical preparation. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, left lateral; **E**, anterior; **F**, posterior views of the skull. Scale bar equals 5 cm.

braincase wall, the nerves and vascular foramina and several mandibular bones.

Interpretations given by previous authors about some anatomical structures of *Notosuchus* (e.g., the carotid foramen, the incisive foramen and the choanae) are controversial and, as a result, different cranial reconstructions of this species are found in the literature (Andrade et al., 2006, fig. 1 B p. 325; Bonaparte, 1991, fig. 3 p. 33, fig. 4 p. 35, fig. 5 p. 37, fig. 7 p. 39, fig. 9 p. 43, fig. 10 p. 44, fig. 11 B p.46, fig. 16 C p. 57; Fiorelli and Calvo, 2008, fig. 7 p. 92, fig. 15 p. 104; Fiorelli et al., 2016, fig. 7C p. 202; Gasparini, 1971, lámina I B p. 87, fig. 1 p. 88, lámina II B p.89, lámina III B p. 90; Martinelli, 2003, fig. 3 p. 564; Ortega et al., 2000, fig. 8; Ortega, 2004, fig. 3.8 p. 80, fig. 3.9 p. 81, fig. 3.10 p. 81, fig. 3.12 p. 84, fig. 3.13 B p. 85, fig. 7.8 p. 229; Pol and Gasparini, 2007, fig. 5.4 p. 127; Price, 1955, fig. 1 A p. 28, fig. 2 B p. 30, fig. 3 B p. 32, fig. 4C and D p. 34; Turner and Sertich, 2010, fig. 16 A).

Despite the great number of specimens of *Notosuchus* housed in several Argentinean paleontological collections, there are not complete skulls. In almost complete specimens, the mandible is always articulated with the skull, obscuring the anatomical features of palate and lower jaw.

The aim of this work is to increase the knowledge of the cranial and mandibular anatomy of *Notosuchus terrestris,* in order to clarify the paleobiology and the evolutionary history of this taxon. In this context, here we present a re-description of the skull of *N. terrestris* based on the study of more than 60 specimens that allowed the

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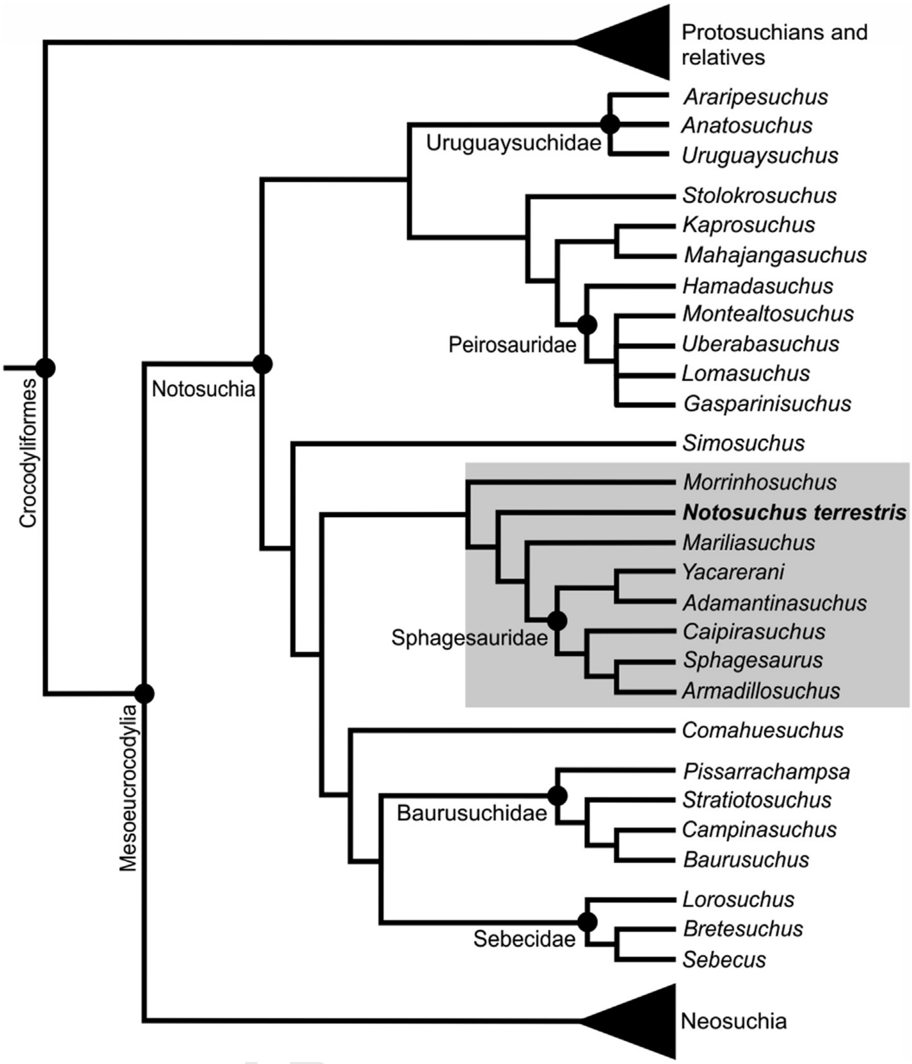

Fig. 3. Abbreviated cladogram showing the phylogenetic position of *Notosuchus terrestris* among the principal groups notosuchians considered in the comparative analyzes (modified from Pol et al., 2014, fig. 31, we left the taxa mentioned in this study). Advanced notosuchians are indicated in gray.

identification of several characters (including braincase characters) never mentioned for the taxon as well as a new reconstruction of its cranial and mandibular anatomy.

2. Materials and methods

2.1. Specimens of *Notosuchus terrestris*

The lectotype skull of *N. terrestris* (MLP 64-IV-16-5) was recently mechanically prepared allowing the observation of the braincase morphology and some internal structures in detail (e.g., pneumatic cavities, neurovascular foramina, endocranial cavity) (Figs. 5–7). Other specimens were also mechanically prepared: MLP 64-IV-16-30, MCF-PVPH-710, MPCA-Pv-237 and MPCA-Pv-791 (Fig. 4). In addition, more than 60 specimens of *Notosuchus*, hosted in seven Argentinean fossil collections were studied (Table S1, Figs. 8–20). The sample includes juvenile and adult individuals, consisting in complete and fragmented skulls and isolated skull bones and lower jaws (Table S1).

2.2. Taxa compared

For comparison purposes, the following notosuchians taxa were studied and photographed by first hand: *Araripesuchus patagonicus* Ortega et al., 2000, *A. buitreraensis* Pol and Apesteguia 2005, *Baurusuchus pachechoi* Price 1945, *Bretesuchus bonapartei* Gasparini et al., 1993, *Comahuesuchus brachybuccalis* Bonaparte 1991, *Gasparinisuchus peirosauroides* Martinelli et al., 2012, *Lorosuchus nodosus* Pol and Powell, 2011, *Uruguaysuchus aznarezi* Rusconi 1933, *Wargosuchus australis* Martinelli and Pais 2008, and *Yacarerani boliviensis* Novas et al., 2009; the “protosuchian” *Hemiprotosuchus leali* Bonaparte 1969 and eusuchians taxa *Crocodylus niloticus* Laurenti 1768, *Gavialis gangeticus* Gmelin 1789, *Caiman yacare* Daudin 1802, and *C. latirostris* Daudin 1802, were also studied (Table S2). Whereas, the following taxa were studied from the literature and, in some cases, with additional photographs shared by colleagues: *Adamantinasuchus navae* Nobre and Carvalho 2006, *Anatosuchus minor* Sereno et al., 2003, *Araripesuchus tsangatsangana* Turner, 2006, *Araripesuchus wegeneri* Buffetaut 1981, *Armadillosuchus arrudai* Marinho and Carvalho 2009, *Baurusuchus salgadoensis* Carvalho et al., 2005, *Baurusuchus albertoi* Nascimento and Zaher 2010, *Caipirasuchus montealtensis* (Andrade and Bertini, 2008b), *C. paulistanus* Iori and Carvalho 2011, *C. stenognathus* Pol et al., 2014, *Campinasuchus dinizi* Carvalho et al., 2011, *Libycosuchus brevirostris* Stromer 1914, *Mahajangasuchus insignis* Buckley and Brochu, 1999, *Mariliasuchus amarali* Carvalho and Bertini 1999, *Morrinhosuchus luziae* Iori and

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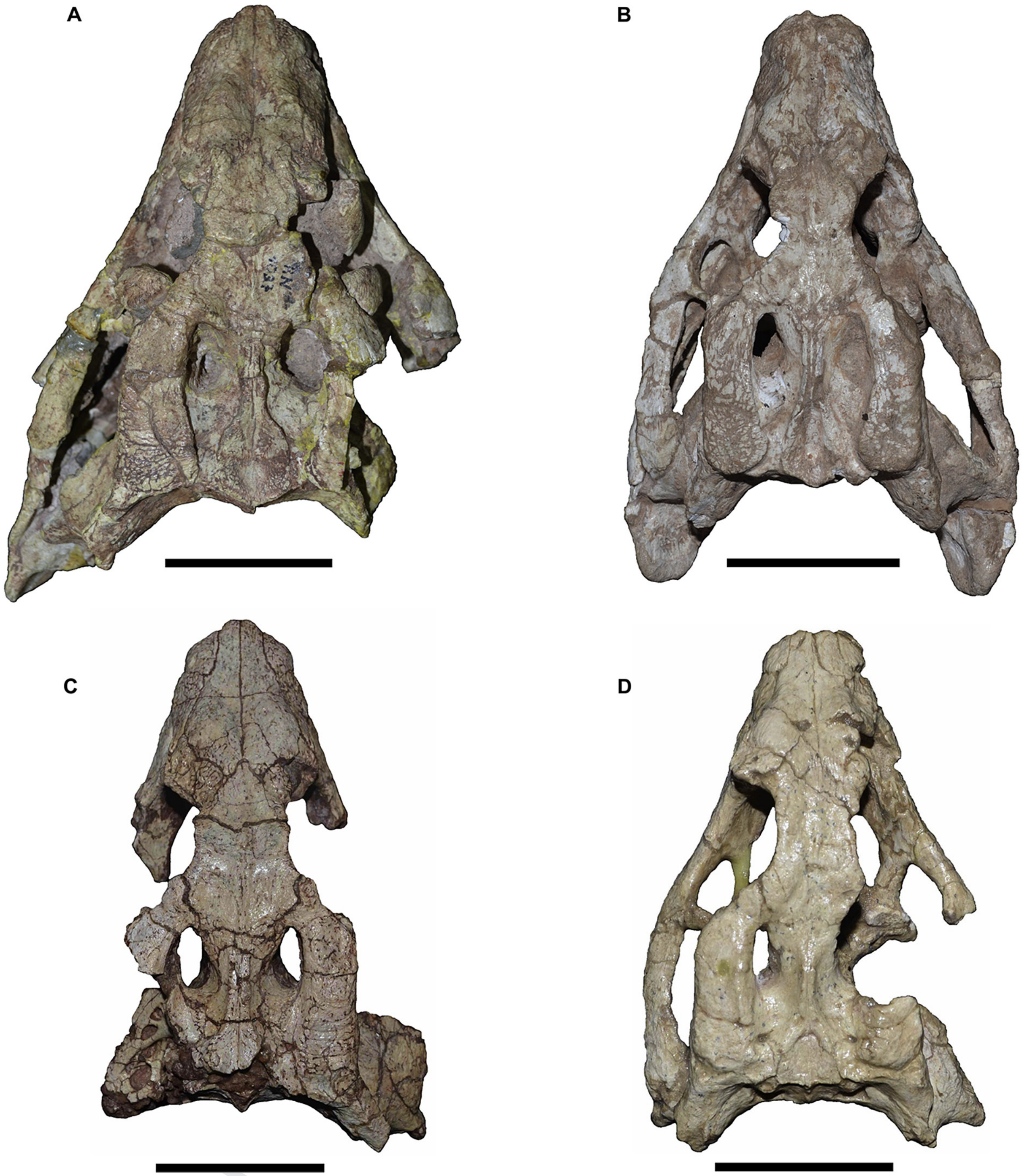

Fig. 4. *Notosuchus terrestris*, skulls of selected specimens in dorsal view: **A**, MACN-PV-RN-1037; **B**, MUCPv-147; **C**, MPCA-Pv-237; **D**, MCF-PVPH 710. Scale bar equals 5 cm.

Carvalho 2009, *Pissarrachampsa sera* Montefeltro et al., 2011, *Sahitisuchus fluminensis* Kellner et al., 2013, *Shamosuchus djadochtensis* Mook 1924, *Simosuchus clarki* Buckley et al., 2000, *Stolokrosuchus lapparenti* Larsson and Gado 2000, *Stratiotosuchus maxhechti* Campos et al., 2001, *Uruguaysuchus aznarezi* (Rusconi, 1933; Larsson and Gado, 2000; Riff, 2003; Carvalho et al., 2004, 2005; Pol et al., 2006; Turner, 2006; Zaher et al., 2006; Carvalho et al., 2007; Pinheiro et al., 2008; Turner and Buckley, 2008; Andrade and Bertini, 2008a; Marinho and Carvalho, 2009; Pol et al., 2009; Sereno et al., 2009; Kley et al., 2010; Carvalho et al., 2011; Montefeltro et al., 2011; Nascimento and Zaher, 2011; Soto et al., 2011; Augusta, 2013; Iori et al., 2013; Pol et al., 2014).

2.3. Institutional abbreviations

AMNH, American Museum Natural History, New York, U.S.A.; **CPPLIP**, Centro de Pesquisas Paleontológicas L.I. Price, Peirópolis, Brazil; **DGM**, Departamento de Produção Mineral, Rio de Janeiro, Brazil; **FC-DPV**, Facultad de Ciencias, Colección de Vertebrados Fósiles, Montevideo, Uruguay; **FMNH**, The Field Museum, Chicago, U.S.A.; **MACN**, Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; **MCF**, Museo Carmen Funes, Plaza Huincul, Argentina; **MLP**, Museo de La Plata, La Plata, Argentina; **MNK**, Museo de Historia Natural Noel Kempf Mercado, Santa Cruz de la Sierra, Bolivia; **MOZ**, Museo Provincial de Ciencias Naturales

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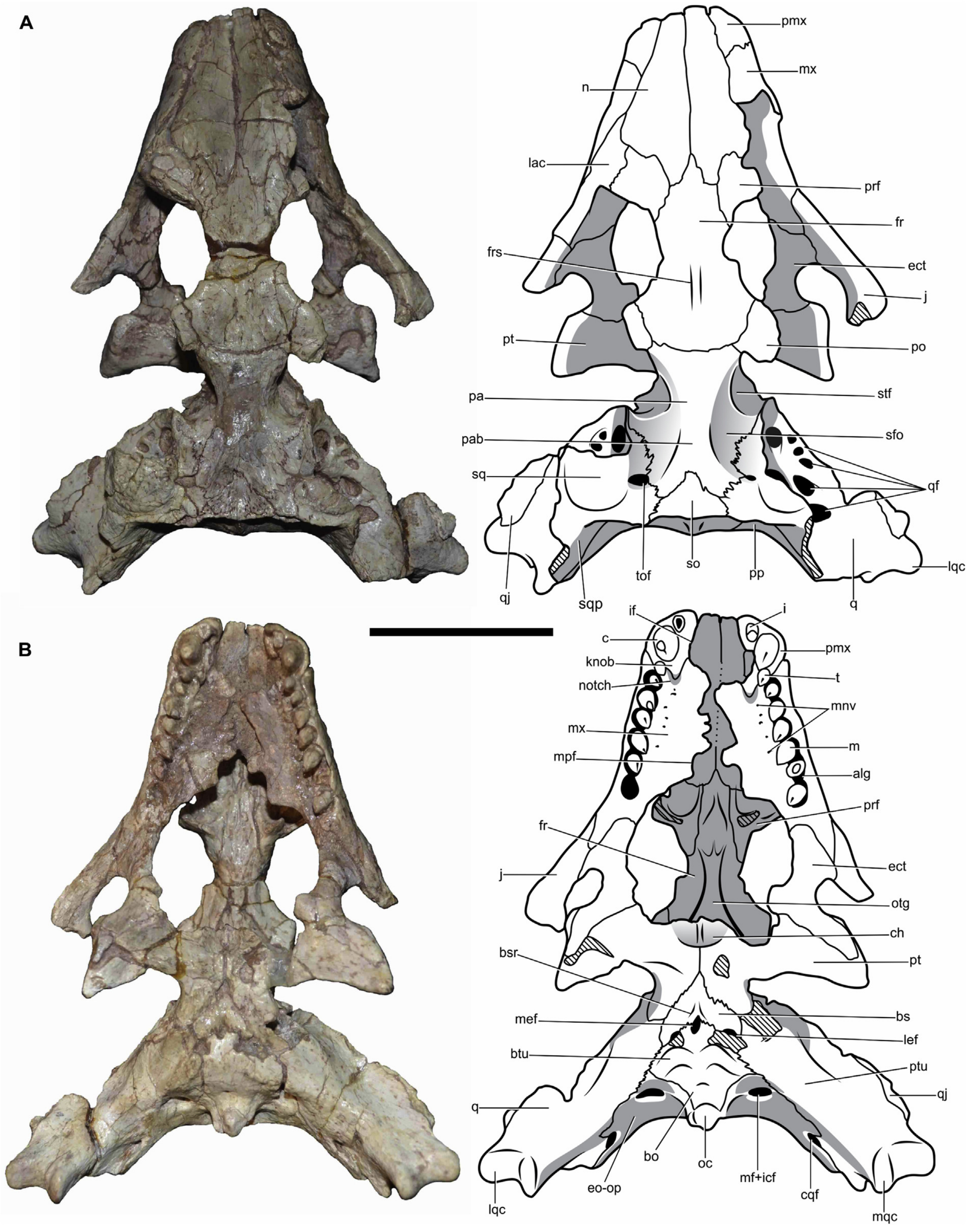

Fig. 5. *Notosuchus terrestris* MLP-64-IV-16-5 (lectotype), after mechanical preparation. **A**, dorsal; **B**, ventral views of the skull. Scale bar equals 5 cm.

Profesor J. Olsacher, Zapala, Argentina; **MPCA**, Museo Provincial Carlos Ameghino, Cipolletti, Argentina; **MPCN**, Museo Patagónico de Ciencias Naturales, Gral. Roca, Argentina; **MPMA**, Museu de Paleontologia de Monte Alto, Monte Alto, Brazil; **MUC**, Museo de la Universidad Nacional del Comahue, Neuquén, Argentina; **PVL**, Instituto Miguel Lillo, Tucumán, Argentina; **UA**, University of Antananarivo, Antananarivo, Madagascar; **UFRJ**, Museu de Paleontologia e Estratigrafia, Universidade Federal de Rio de Janeiro, Rio de Janeiro, Brazil; **ZSM**, Zoologische Staatssammlung, Munich, Germany.

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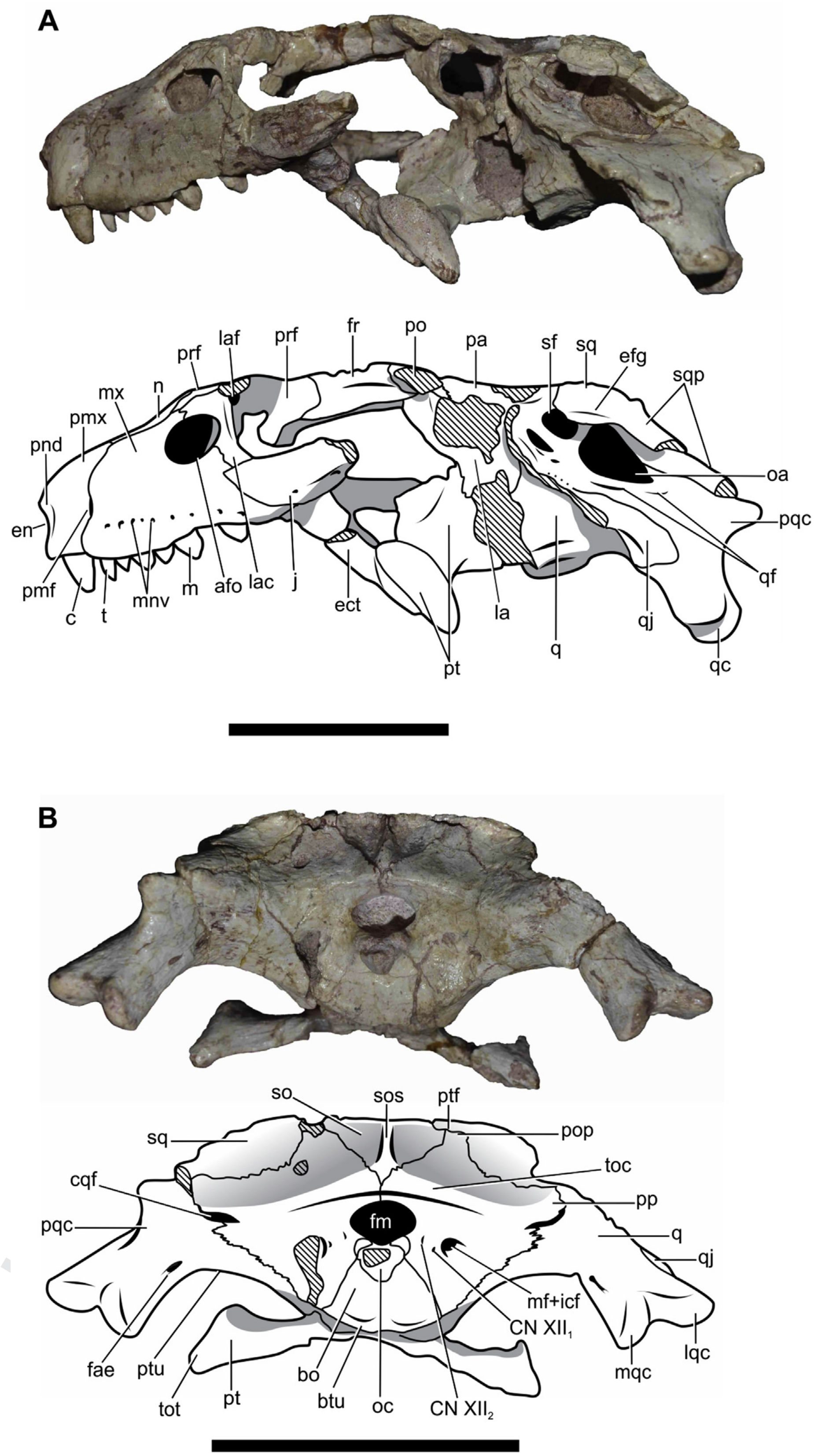

Fig. 6. *Notosuchus terrestris* MLP-64-IV-16-5 (lectotype), after mechanical preparation. **A**, left lateral; **B**, occipital views of the skull. Scale bar equals 5 cm.

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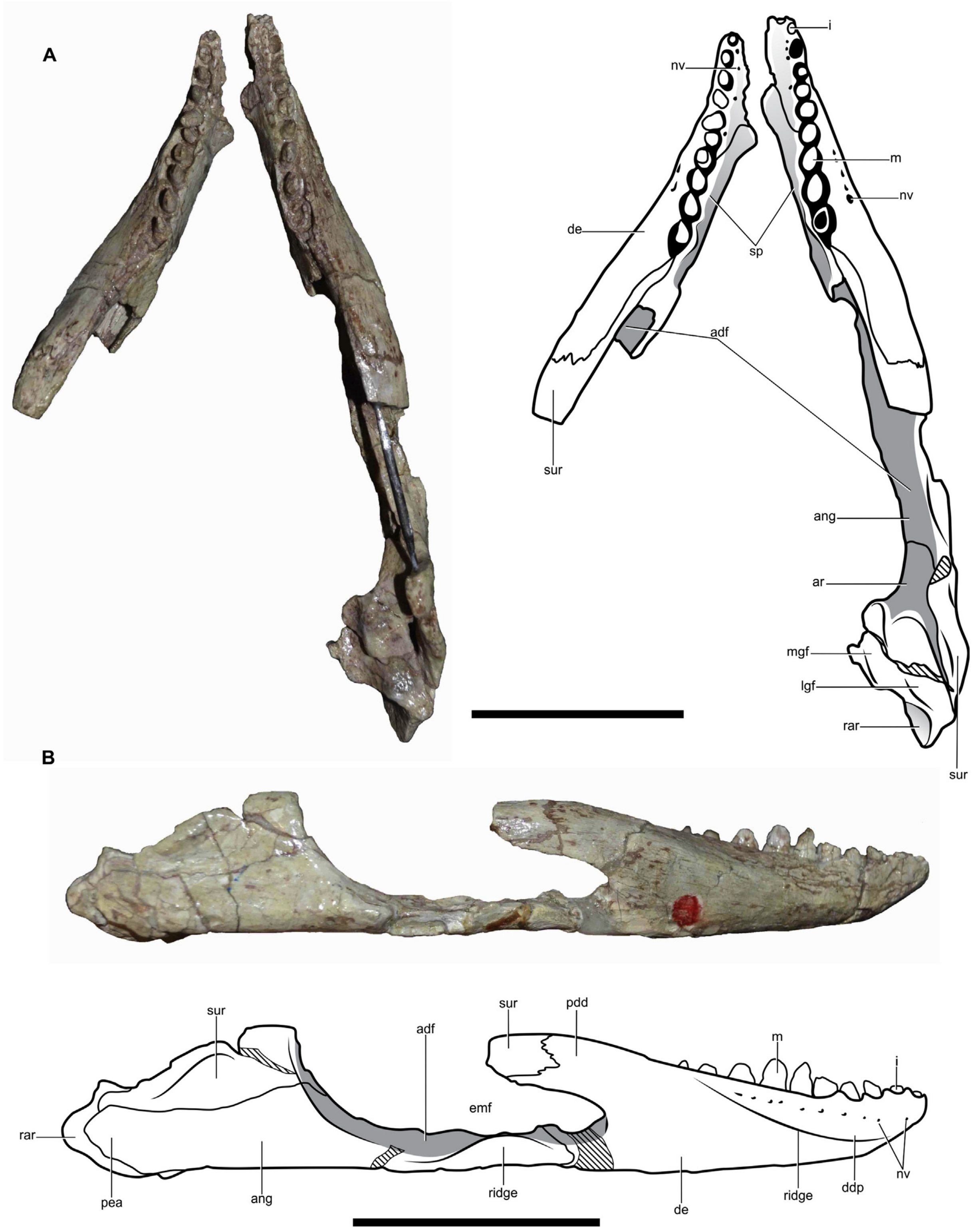

Fig. 7. *Notosuchus terrestris* MLP-64-IV-16-5 (lectotype), after mechanical preparation. **A**, dorsal; **B**, right lateral views of the mandible. Scale bar equals 5 cm.

2.4. *Anatomical abbreviations*

aar, anterior process of the articular; **adf**, aductor mandibular fossa; **afo**, antorbital fossa; **alg**, alveolar groove; **ang**, angular; **aof**, antorbital fenestra; **ap**, anterior palpebral; **app**, anterior process of the postorbital; **ar**, articular; **bo**, basioccipital; **bos**, basioccipital sagittal crest; **bs**, basisphenoid; **bsr**; basisphenoid ridge; **btu**, basal tubera; **c**, caniniform tooth; **ccr**, crista cranii; **CN I**, foramen for the olfactory cranial nerve; **CN II**, foramen for the optic cranial nerve; **CN III**, foramen for the oculomotor cranial nerve; **CN IV**, foramen for the troclear cranial nerve; **CN VI**, foramen for the abducens cranial nerve; **CN** $\mathbf{XII_1}$, foramen for the anterior ramus of

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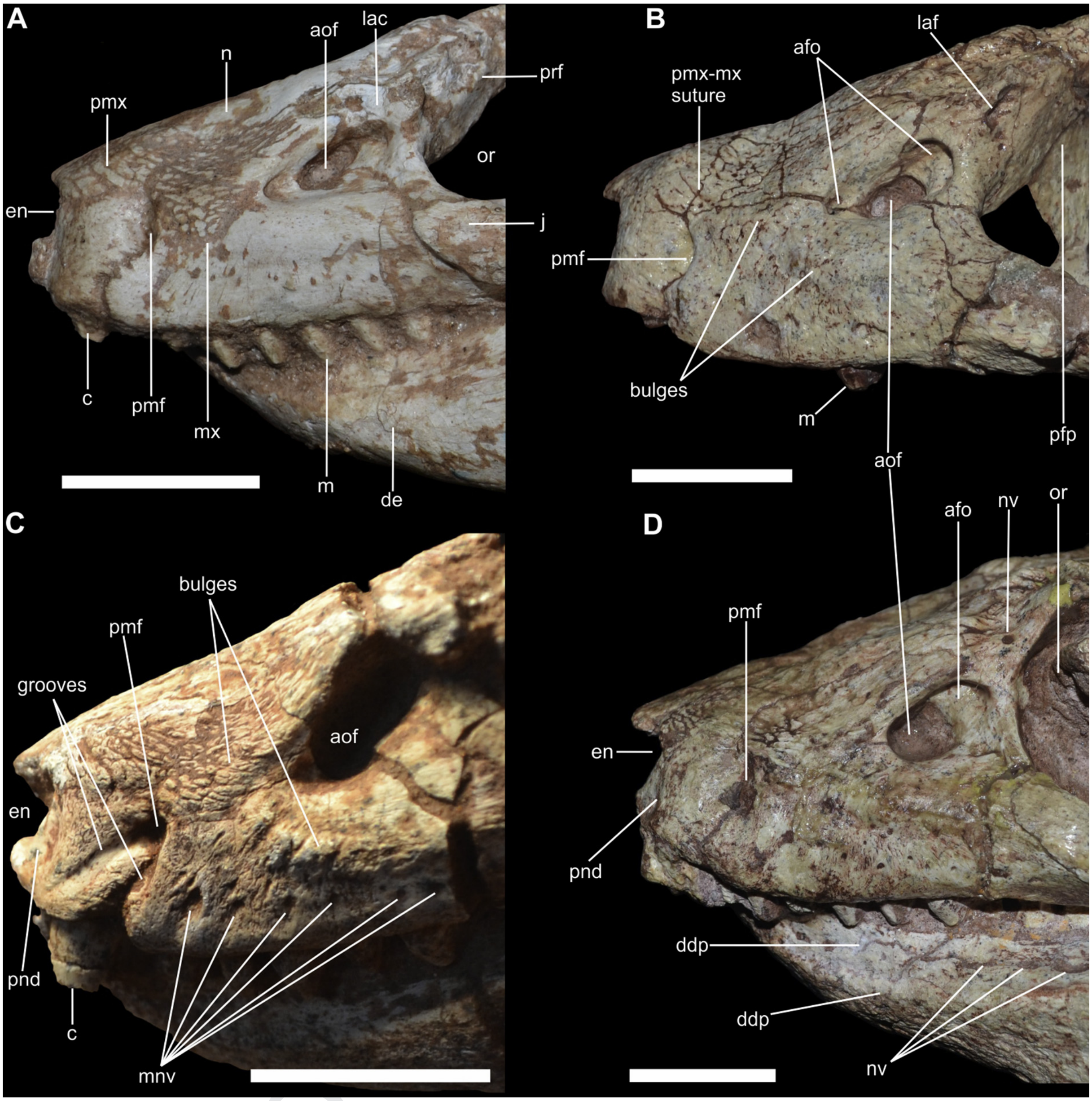

Fig. 8. Rostrum of *Notosuchus terrestris*. **A**, MUCPv 147; **B**, MPCA-Pv-237; **C**, MPCA-Pv-528; **D**, MACN-PV-RN-1037, left lateral view. Scale bar equals 2.5 cm.

hypoglossal cranial nerve; **CN XII$_2$**, foramen for the posterior ramus of hypoglossal cranial nerve; **CN V$_1$**, foramen for the ophthalmic trigeminal branch; **CN V$_2$**, groove for passage of the maxillary trigeminal branch; **CN V$_3$**, groove for passage of the mandibular trigeminal branch; **CN V$_{so}$**, groove for passage of the supraorbitary trigeminal branch; **cot**, cotylar crest; **cqf**, cranioquadrate foramen; **crf**, coronoid facet of the surangular; **ch**, choana; **chf**, choanal fenestra; **chg**, choanal groove; **chs**, choanal septum; **ddp**, dentary depression; **de**, dentary; **dil**, diverticulum laterosphenoid; **dip**, diverticulum parietal; **dpr**, diverticulum prootic; **dpt**, diverticulum pterygoid; **ect**, ectopterygoid; **efg**, ear-flap groove; **emf**, external mandibular fenestra; **en**, external nares; **enc**, endocranial cavity; **eo**, exoccipital; **eo-op**, exoccipital-ophistotic complex; **epb**, ectopterigoyd-palatine bar; **fae**, foramen aerum; **fio**, foramen intermandibularis oralis; **fm**, foramen magnum; **foV**, trigeminal fossa; **fpf**, facet of the prefrontal for the anterior palpebral; **fr**, frontal; **frs**, frontal sagital crest; **gc**, glenoid crest; **gcs**, groove of the choanal septum; **gla**, groove for the laterosphenoid; **i**, incisiviform tooth; **icf**, internal carotid foramen; **ie**, inner ear; **if**, incisive foramen; **itd**, intertympanic diverticulum; **itf**, infratemporal fenestra; **j**, jugal; **la**, laterosphenoid; **lac**, lacrimal; **laf**, lacrimal foramen; **lb**, lateral bridge; **lef**, lateral Eustachian foramen; **lfr**, lateral facet of the retroarticular process; **lgf**, lateral glenoid facet; **lqc**, lateral quadrate condyle; **m**, molariform tooth; **mef**, median Eustachian foramen; **mf**, metotic foramen; **mfr**, medial facet of the retroarticular process; **mgf**, medial glenoid facet; **mnv**, maxillary neurovascular foramina; **mx**, maxilla; **mpf**, maxilla-palatine fenestra; **mqc**, medial quadrate condyle; **n**, nasal; **nv**, neurovascular foramen; **oa**, otic aperture; **obc**, oblique crest of the retroarticular process; **oc**, occipital condyle; **ogc**, olfactory tract groove convexity; **ogd**, olfactory tract groove depression to the olfactory bulbs; **or**, orbit; **otg**, olfactory tract groove; **pa**, parietal; **pab**, parietal bar; **pal**, palatine; **pas**, contact surface to the parietal; **pb**, palatine bar; **pdd**, posterodorsal process of dentary; **pea**, posterior end of angular; **pfp**, prefrontal pillar; **pfs**, contact surface to the prefrontal; **pit**, pituitary fossa; **pmf**, premaxilla-maxillary foramen; **pmx**,

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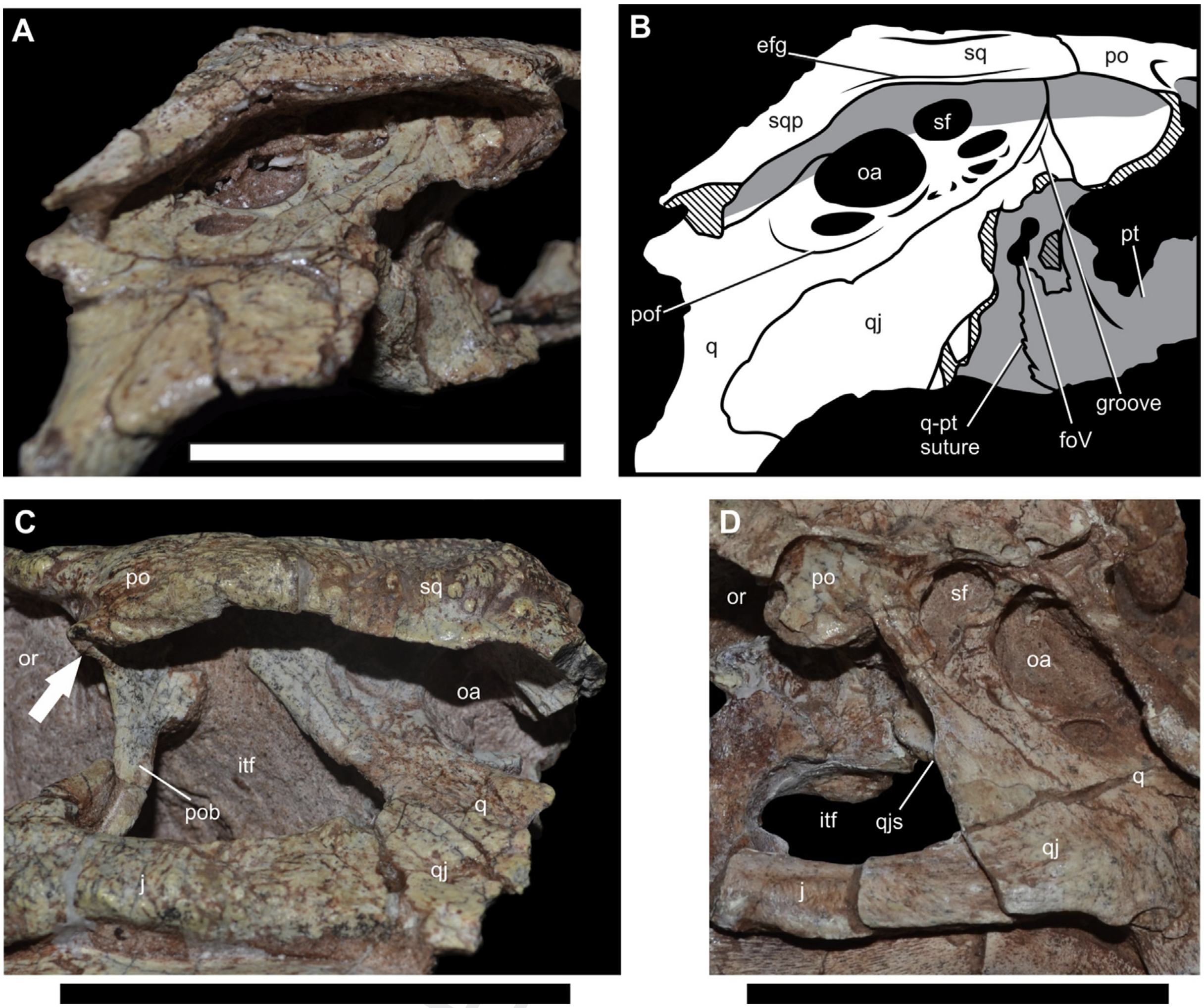

Fig. 9. Temporal region of *Notosuchus terrestris*. **A** and **B**, MPCA-Pv-237, right lateral view; **C**, MACN-PV-RN-1045; **D**, MPCA-Pv-528; C y D, left lateral view. In D, the arrow indicates the postorbital fold. Scale bar equals 5 cm.

premaxilla; **pnd**, perinarial depression; **po**, postorbital; **pob**, postorbital bar; **pof**, periotic fossa; **pop**, postoccipital process; **pos**, contact surface to the postorbital; **pp**, paraoccipital process; **ppl**, posterior palpebral; **ppp**, posterior process of the postorbital; **pqc**, posterior quadrate crest; **prf**, prefrontal; **pt**, pterygoid; **ptc**, pterygoid sagittal crest; **ptf**, posttemporal fenestra; **PTs**, pharyngotympanic sinus; **ptu**, crista pseudo-tuberalis; **ptw**, pterygoid wing; **rar**, retroarticular process; **q**, quadrate; **qc**, quadrate condyle; **qf**, quadrate foramina; **qj**, quadratojugal; **qjs**, quadratojugal spine; **sf**, siphonial foramen; **sfo**, supratemporal fossa; **so**, supraoccipital; **sof**, suborbital fenestra; **sos**, supraoccipital sagittal crest; **sp**, splenial; **sps**, splenial symphyseal; **sq**, squamosal; **sqp**, squamosal posterolateral process; **stf**, supratemporal fenestra; **sul**, sulcus septalis; **sur**, surangular; **t**, transitional tooth; **toc**, transversal occipital crest; **tof**, temporo-orbital foramen; **tog**, temporo-orbital groove; **tot**; torus transiliens; **tu**, crista tuberalis; **vo**, vomer.

3. Systematic palaeontology

Crocodyliformes Hay, 1930 (sensu Benton and Clark, 1988)
Mesoeucrocodylia Whetstone and Whybrow, 1983
Notosuchia Gasparini, 1971 (sensu Sereno et al., 2001)
Notosuchidae Dollo, 1914 (sensu Turner and Sertich, 2010)
Notosuchus terrestris Woodward, 1896

3.1 *Lectotype.* MLP 64-IV-16-5, skull and mandibles (Figs. 2, 5–7, Table S3), designated by Gasparini (1971).

3.2 *Referred material.* More than sixty specimens housed at MLP, MACN, MPCA, MUC, MCF, MPCN collections, which represent different ontogenetic stages with different degrees of preservation and preparation (Fig. 4, Table S1).

3.3 *Locality and age.* The lectotype and referred material described by Woodward (1896) and Gasparini (1971) are from the historical locality “Boca del Sapo”, corresponding to outcrops located north of Neuquén City, now the campus and vicinity of the Universidad Nacional del Comahue (UNCO), Neuquén Province, Argentina (Fig. 1A). The specimens housed at MACN-N, MUC and MCF collections were also found in the north sector of the Neuquén city. The specimens housed at the MACN-RN, MPCA and MPCN collections were found in the “Paso Córdoba (or Paso Córdova)” locality, Gral. Roca city, Río Negro Province, Argentina (Fig. 1A). All these outcrops are referred to Bajo de la Carpa Formation, Río Colorado Subgroup, Neuquén Group (Fig. 1B). This unit has been considered as Santonian in age (86-83 Ma.) (Garrido, 2010).

3.4 *Enmended diagnosis.* Snout short and high, with anterior external nares. Well-developed perinarial depressions. Well-developed bulge on the maxilla, anteroventral to the small antorbital fossa*. Ectopterygoid extended along the lateral

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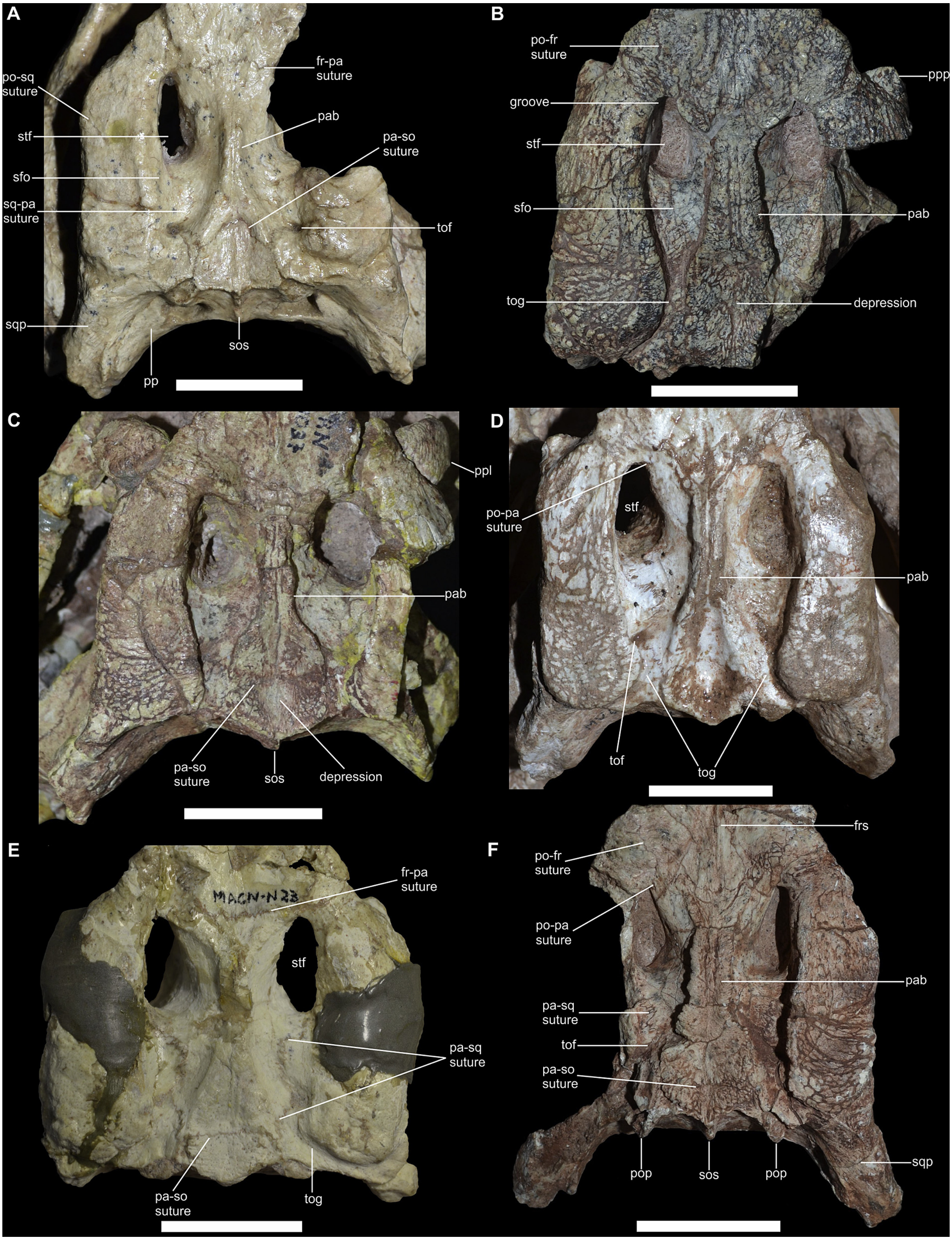

Fig. 10. Skull table of *Notosuchus terrestris*. **A**, MCF PVPH 710; **B**, MACN-PV-RN-1045; **C**, MACN-PV-RN-1037; **D**, MUCPv 147; **E**, MACN- PV-RN-23; **F**, MPCA-Pv-528. Scale bar equals 2.5 cm.

margin of the choanal opening*, contacting the palatine, and excluding the pterygoid from the suborbital fenestra. Extremely elongate articular facet for the quadrate condyles, being approximately three times as long as the condyles*, and lacking a posterior buttress. Five premaxillary teeth, being the fourth element notably hypertrophied. Seven maxillary teeth, subtriangular in cross-section, with major axis oriented posteromedially. Crista cranii frontalis poorly developed**. Frontal

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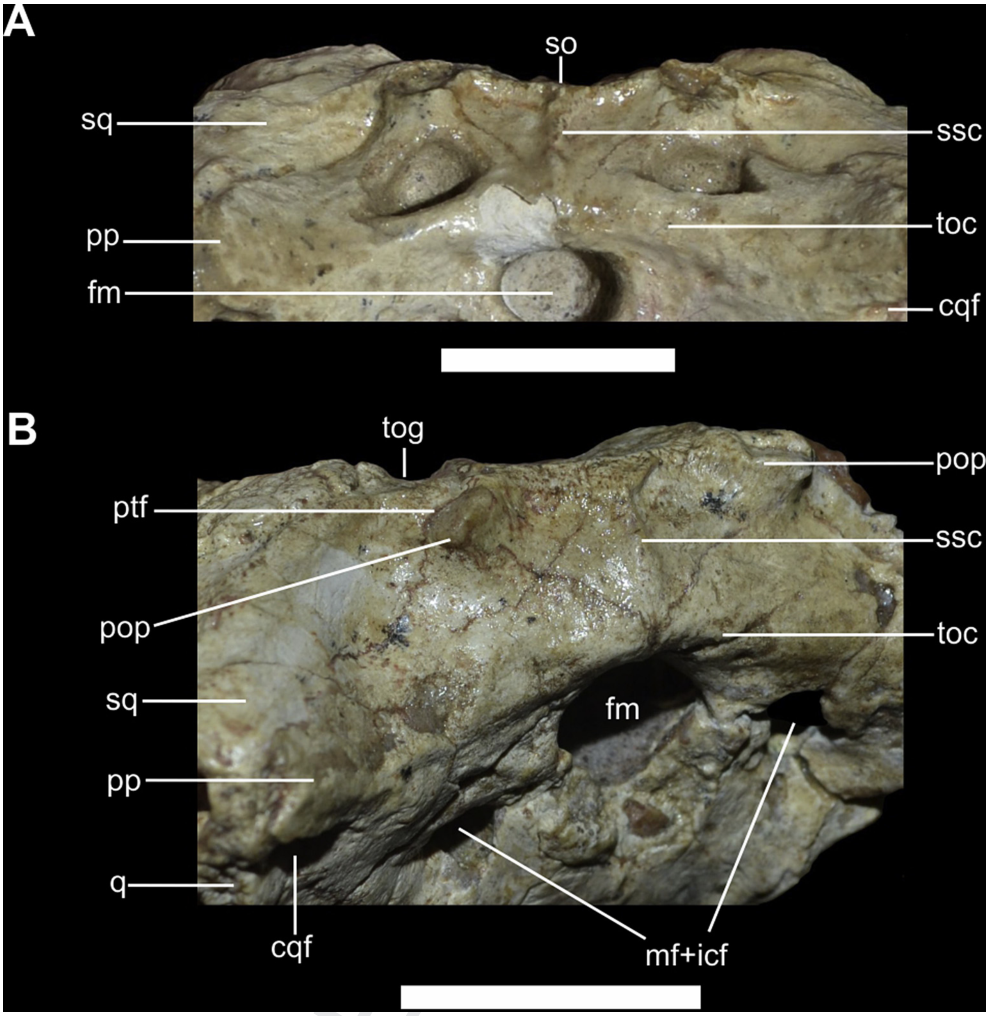

Fig. 11. Occiput of *Notosuchus terrestris*. **A**, MCF-PVPH 710; **B**, MLP 64-IV-16-30. Scale bar equals 2 cm.

with olfactory tract groove convex posteriorly and with well marked furrows for laterosphenoid**. Small bilobate trigeminal fossa with grooves for the branches of the CN V$_{so}$, CN V$_2$ and CN V$_3$**. Parietal and laterosphenoid highly pneumatic**. Post-temporal fenestrae obliterated**. Small premaxillary knob fits a maxillary notch in the palate adjacent to the toothrow**. Incisive foramen in heart-shaped delimited by premaxillae and maxillae**. Vomer lateromedially broad**. Choana with narrow pterygoid septum**. Ascending process of quadratojugal with groove adjacent and parallel to quadratojugal-quadrate suture**, vestigial quadratojugal spine**. Anteroposteriorly short axial neural spine. Three sacral vertebrae, two of which are fused to each other* (modified from Pol and Gasparini, 2007; *autapomorphies, **new autapomorphies).

4. Description

4.1. General skull morphology of Notosuchus terrestris

The cranium of *N. terrestris* is triangular in dorsal view, with preorbital and postorbital regions approximately similar in length (Figs. 5–6), as in non-mesoeucrocodylian protosuchians and others advanced notosuchians. The snout is tall, quadrangular in cross-section, with anterior external nares, as in protosuchians and most notosuchians (e.g., Gasparini, 1971; Bonaparte, 1991; Busbey, 1995). The external nares are delimited by premaxillae lateral and ventrally and by the nasals dorsally (Fig. 2E). They are terminal openings, quadrangular in contour and slightly oriented downwards, accompanied by a smooth perinarial depression also present in other notosuchians such as *Simosuchus clarki*, *Comahuesuchus brachybuccalis*, Sphagesauridae, Baurusuchidae, Peirosauridae and Sebecidae. The nares in *Notosuchus* are not divided by a naso-premaxillar bar, unlike the condition observed in other notosuchians such as *Simosuchus*, peirosaurids (e.g., *Hamadasuchus*, *Uberabasuchus*) and baurusuchids.

In both sides of the snout and anterior to the orbits are the antorbital fenestrae, which open within larger antorbital fossae (both delimited by the maxillae anteriorly and the lacrimals posteriorly) (Figs. 6A, 8). The antorbital fossa is oval-shaped, although its size is variable (Fig. 8). In the specimens MACN-PV-RN-1045, MLP 64-IV-16-6, MLP 64-IV-16-21, MPCA-Pv-237 and MUCPv-147, the antorbital fossa is elongated, oval shaped, excavated on the maxilla and the lacrimal, and the antorbital fenestra is in a central position within the fossa (Fig. 8A, B). In other specimens (e.g., MACN-PV-RN-1037, MLP 64-IV-16-5, MPCA-Pv-789), the antorbital fossa is subcircular and is mainly excavated on the lacrimal, and therefore the antorbital fenestra is more anteriorly located within the fossa (Figs. 6A and 8D). This variation on the relative location of the antorbital fenestra and development of the antorbital fossa is

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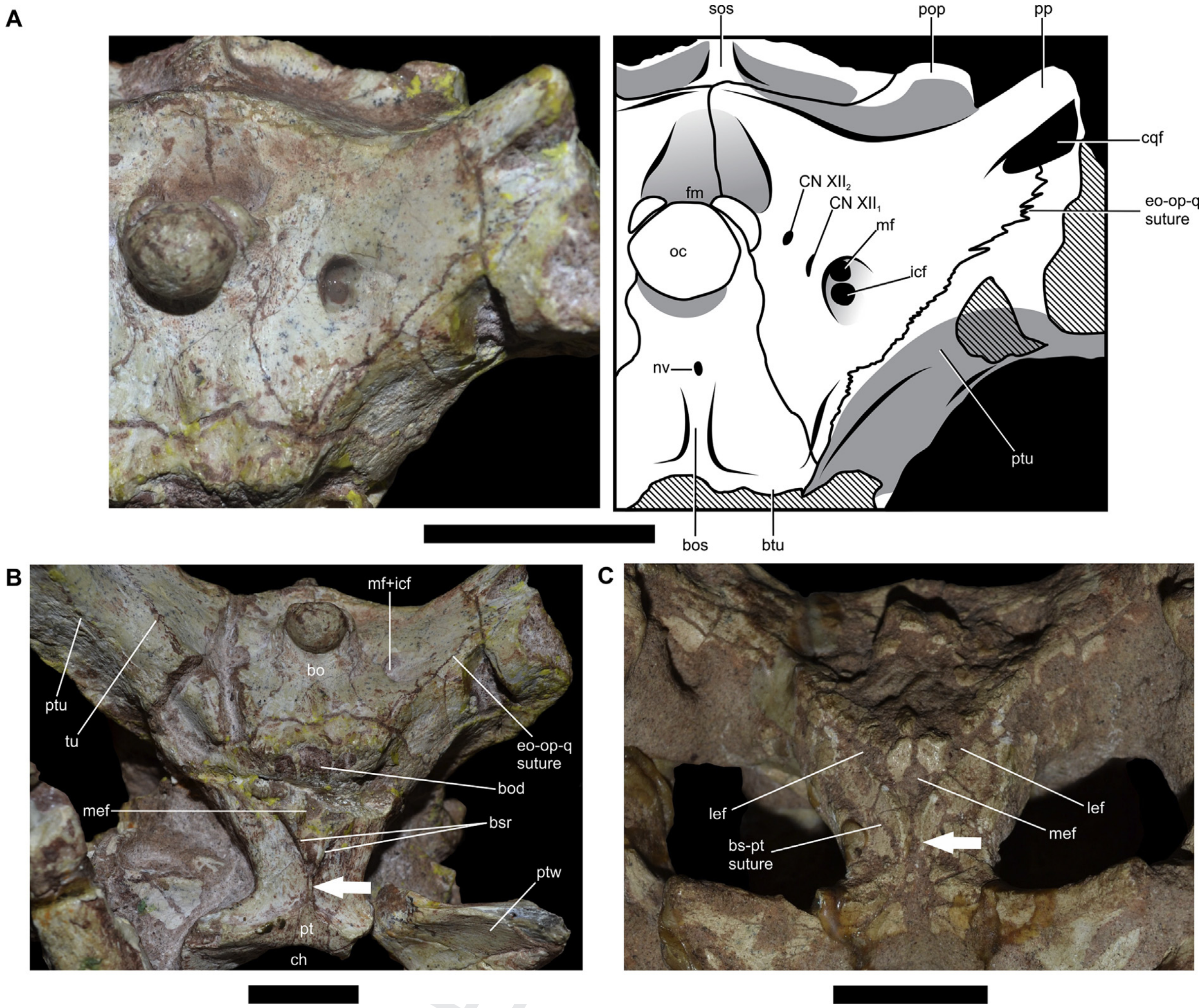

Fig. 12. Basicranium of *Notosuchus terrestris*. MACN-PV-RN-1037, **A** and **B**; **C**, MLP 64-IV-16-31. The arrow indicates the joined (B) or separated (C) basisphenoid ridges. Scale bar equals 2 cm.

not related to the size of the specimens. The antorbital fenestra and fossa are present in most notosuchians (e.g. *Araripesuchus*, *Simosuchus*, *Caipirasuchus*, peirosaurids, *Mahajangasuchus*), except in some sphagesaurids (e.g., *Marialiasuchus*, *Adamantisuchus*, *Armadillosuchus*, *Yacarerani*), and baurusuchids (e.g., *Baurusuchus*, *Stratiotosuchus* and *Pissarrachampsa*) (e.g. Campos et al., 2011; Zaher et al., 2006; Montefeltro et al., 2011; Pol et al., 2014). The snout of *Notosuchus* bears bulges developed anteriorly and anteroventrally to the antorbital fenestra, being the latter the most protuberant. Also anterior the orbit, the snout has a triangular depressed area – excavated on the maxilla and lacrimal-surrounding the antorbital fossa, and the posterior margin of this depressed area is markedly recurved as in most advanced notosuchians (except *Yacarerani*) and baurusuchids.

The infratemporal fenestra is dorsolaterally oriented and presents a triangular contour, the ventral margin has a slight convexity, and the posterior margin presents a vestigial quadratojugal spine (e.g., MPCA-Pv-528; Fig. 9). The margins of the infratemporal fenestra are formed by the postorbital anteriorly, the jugal anteroventrally and the quadratojugal posteriorly and its length is slightly shorter than the anteroposterior length of the orbits (Figs. 6A and 9). The postorbital bar that forms the anterior margin of the infratemporal fenestra is oval in transverse cross-section (e.g., MACN-PV-RN-1045, MUCPv-147).

The orbits are laterally displaced and over-hanged dorsally by the palpebral bones. They are elliptic to sub-rectangular in shape and bounded by the prefrontal and frontal dorsally, the lacrimal anteriorly, the postorbital and jugal posteriorly and the jugal ventrally. The orbits and the supratemporal fossae are subequal in length (Figs. 5A and 10).

The skull table is pentagonal in contour, having straight parallel lateral margins and a posterior margin that is mainly transversal in dorsal view. The posterior margin of the skull roof may have two notches of variable presence (e.g., in MCF PVPH-710 the notches are absent and the posterior margin is transversally straight; Figs. 4 and 10A). Osteoderms of rugose texture are fused to the dorsal surface of the postorbitals and squamosals, being the ornamentation more clearly marked in the latter. Enclosed between these osteoderms -and posterior to the supratemporal fossae-there are large vascular impressions left by the temporo-orbital vein (Holliday and Gardner, 2012; Bona et al., 2012) (Fig. 10).

The internal supratemporal fenestra and supratemporal fossa are elongated, oval-shaped and parallel to the sagittal plane (Figs. 4, 5A, and 10). The margins of the supratemporal fossa are formed by the postorbital anteriorly, the squamosal posterolaterally and the parietal posteromedially. In the skull table, the medial margins of both fossae are near to the midline forming a low sagittal crest. The

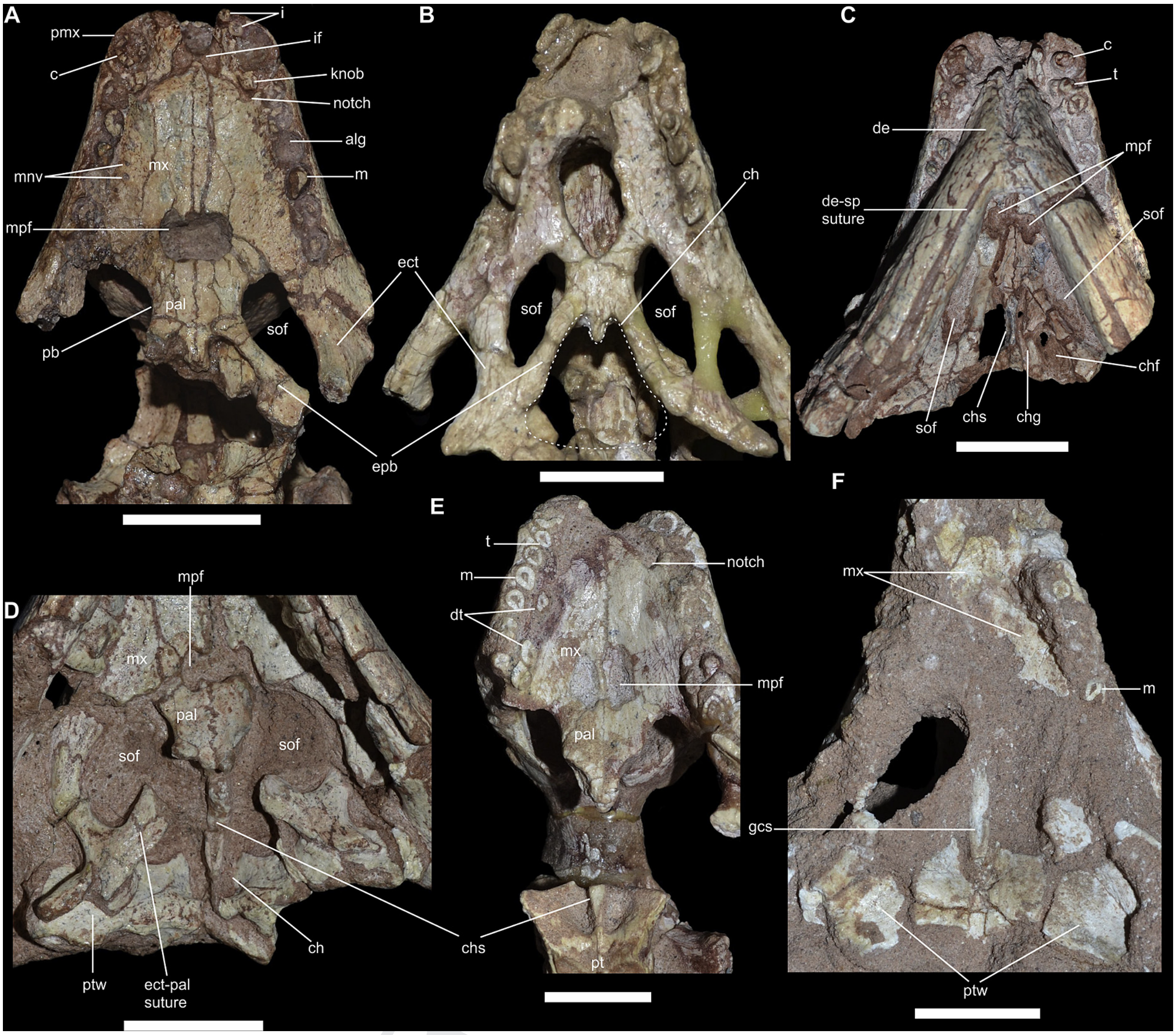

Fig. 13. Palate of *Notosuchus terrestirs*. **A**, MPCA-Pv-237; **B**, MCF PVPH 710; **C**, MPCA-Pv-791; **D**, MACN-PV-RN-1038; **E**, MUCPv-35; **F**, MUCPv 137. Scale bar equals 2.5 cm.

lateral margin is mainly straight and the medial margin is curved (convex).

The internal supratemporal fenestra is small and restricted to the anterior half of the supratemporal fossa. The margins of the internal supratemporal fenestrae are also formed by contributions of the laterosphenoid medially and the quadrate posteriorly. The posterior half of the supratemporal fossa bears a shelf formed by the descending lamina of the parietal and the medial lamina of the squamosal. On the shelf opens the temporo-orbital foramen (for the temporo-orbital artery and vein sensu Porter et al., 2016), which pierces mainly the squamosal (the parietal forms a small section of its medial margin).

The temporo-orbital foramen is small, oval, and faces dorsally, being completely visible in dorsal view, as in advanced notosuchians, *Mahajangasuchus*, and baurusuchids. In others notosuchians as uruguaysuchids, *Comahuesuchus*, *Simosuchus*, some baurusuchids (e.g., *Campinasuchus*, *Baurusuchus*, *Pissarrachampsa*), and peirosaurids, as well as in eusuchians, the temporo-orbital foramen is located on the parietal-squamosal suture. In advanced notosuchians (e.g., *Yacarerani*, *Mariliasuchus*, *Caipirasuchus*, *Armadillosuchus*) and the baurusuchid *Stratiotosuchus*, the temporo-orbital foramen is completely enclosed by the squamosal. In most peirosaurids (e.g., *Lomasuchus*, *Uberabasuchus*), and all crocodylians the temporo-orbital foramen is recessed posteriorly (Pol et al., 2014).

The posterior margin of the supratemporal fossa of *Notosuchus* is continuous with a vascular groove left by the temporo-orbital vein, which is a well-marked impression in adult specimens (e.g., MACN-PV-RN-1037, MACN-PV-RN-1045, MLP 64-IV-16-31, MPCA-Pv-528, MUCPv 147; Figs. 4 and 10). In all studied specimens of *Notosuchus*, the post-temporal fenestra is obliterated (e.g., MLP 64-IV-16-5, MLP 64-IV-16-30) (Figs. 6B and 11), a feature not mentioned for any crocodyliform so far (see Section 5).

In posterior view the occiput is triangular in contour, and is divided dorsoventrally by a wide transversal crest in two surfaces, slightly concave (the dorsal surface faces posterodorsally, whereas the ventral surface faces posteroventrally; Figs. 6B and 12). This crest is present, showing variable development, in all notosuchians (e.g., *Araripesuchus*, *Lomasuchus*, *Yacarerani*, *Caipirasuchus*, *Baurusuchus*, *Pissarrachampsa*, *Mariliasuchus*, *Stratiotosuchus*).

The occipital condyle is posteroventrally oriented and is not visible in dorsal view (Figs. 4, 5A and 10). The occipital transversal crest is dorsal to the foramen magnum and located between the paroccipital processes (Fig. 6B). The foramen magnum of *Notosuchus* is rhomboid contour, its margins are formed by the exoccipital-opisthotic bones dorsolaterally and the basioccipital

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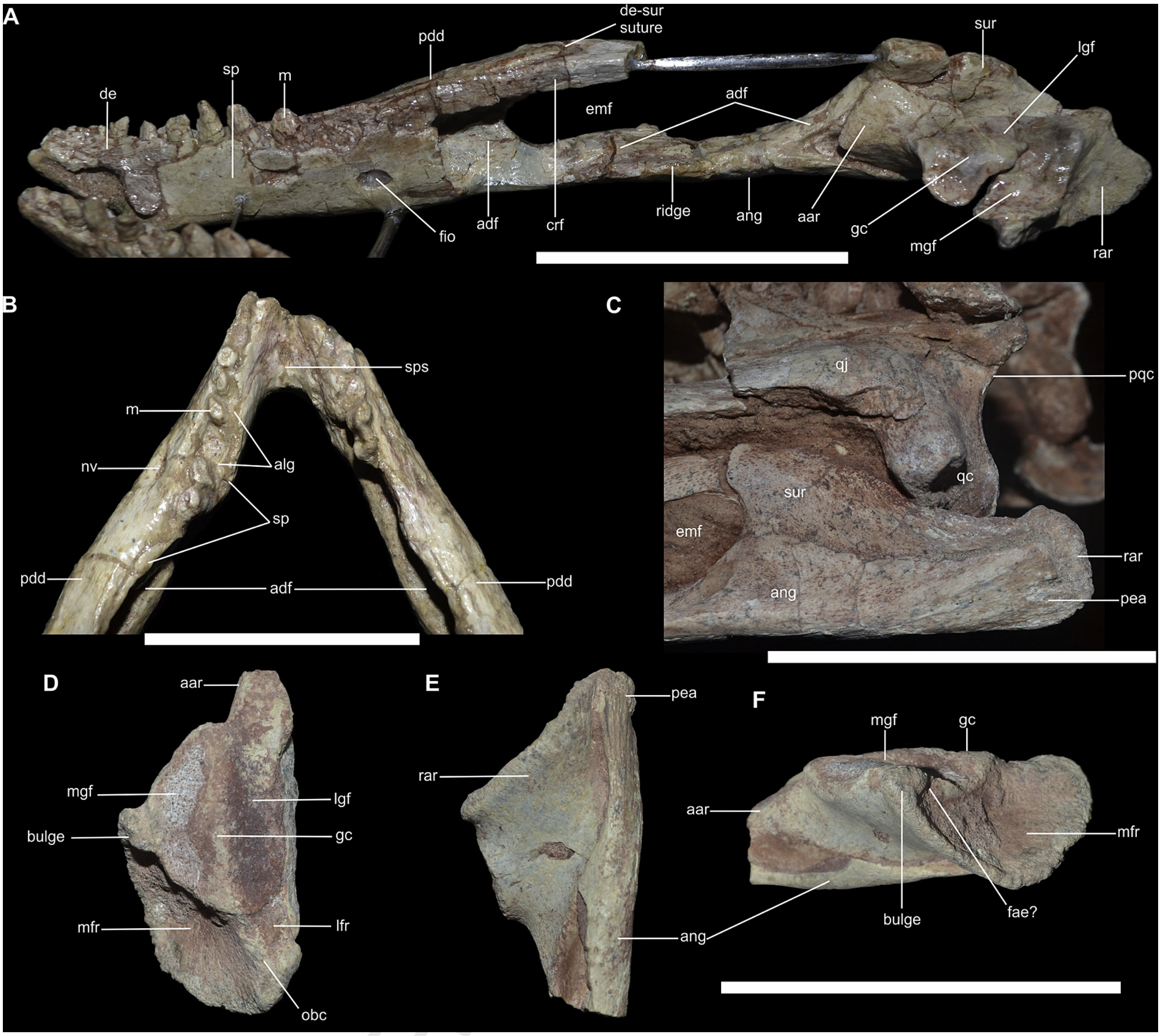

Fig. 14. Mandible of *Notosuchus terrestris*. **A**, MLP 64-IV-16-5 (lectotype) medial view; **B**, MCF-PVPH 710 symphyseal portion, dorsal view; **C**, MPCA-Pv-528 left posterior mandibular portion, lateral view; **D**–**F**, MACN-PV-sn right articular isolated, **D**, dorsal, **E**, ventral, **F**, medial views. Scale bar equals 5 cm.

ventrally as in all crocodyliforms (Benton and Clark, 1988). The supraoccipital (some specimens) and exoccipital-opisthotic complex are largely exposed dorsally, and therefore observed in dorsal view (Figs. 4, 5A and 10).

The bony secondary palate is formed mainly by the palatines and the maxillary palatal processes, and also by the premaxillae (Figs. 5B and 13). The palate is fenestrated by the incisive foramen, a pair of maxilla-palatine fenestrae, the suborbital fenestrae and the choanae. The incisive foramen is a small opening bounded by the premaxillary palatal processes anterolaterally. It is heart-shaped with the narrow tip oriented forward and the posterior margin divided by a small projection of the maxillary palatal processes (Fig. 13). The premaxillae do not joint behind the incisive foramen, a feature shared with most notosuchians (e.g., *Comahuesuchus*, *Stolokrosuchus*, *Montealtosuchus*, *Stratiotosuchus*, *Caipirasuchus*, *Sphagesaurus*). While *Mariliasuchus* and *Yacarerani* have an incisive foramen opened transversely between the premaxillar and maxillar. In other notosuchians (e.g., *Simosuchus, Hamadasuchus,* and *Lorosuchus*) and most neosuchians the premaxillae join behind the incisive foramen. The notosuchians *Araripesuchus wegeneri* and most baurusuchids (e.g., *Baurusuchus pachecoi, B. salgadoensis*, *Campinasuchus*) do not have incisive foramen. In each premaxilla, the incisive foramen of *Notosuchus* occupies the 50% of the width of the palatal process. This opening is observed in the specimens MACN-PV-RN-1038, MACN-PV-RN-40 (through the external nares) and MPCA-Pv-237 (Fig. 13A).

The maxillo-palatine fenestrae are small and oval openings, located close to each other and to the midline, and separated by a narrow inter-fenestral bridge. The maxillo-palatine fenestrae are delimited by the maxillae anterodorsally and the palatines posteromedially, and the inter-fenestral bridge is formed by the maxillae anteriorly and the palatines posteriorly, the latter forming most of the inter-fenestral bridge (about the 80% of the complete length of the bridge) (Fig. 13). The maxillo-palatine fenestrae are present in the advanced notosuchians *Mariliasuchus amarali* and *Caipirasuchus stenognathus* (Zaher et al., 2006; Pol et al., 2014; Martinelli et al., 2016). These fenestrae would be related to the vomeronasal or Jacobson's organ as suggested by Ösi (2013).

The pterygoid is excluded from the margins, as in the basal notosuchian *Comahuesuchus* (Martinelli, 2003), advanced notosuchians (e.g., *Mariliasuchus*, *Yacarerani*, *Caipirasuchus*) and baurusuchids (e.g., *Baurusuchus*, *Pissarrachampsa*). In the basal notosuchian *Simosuchus*, uruguaysuchids, peirosaurids, mahajangasuchids, sebecids and eusuchians the pterygoid forms part of the suborbital fenestra.

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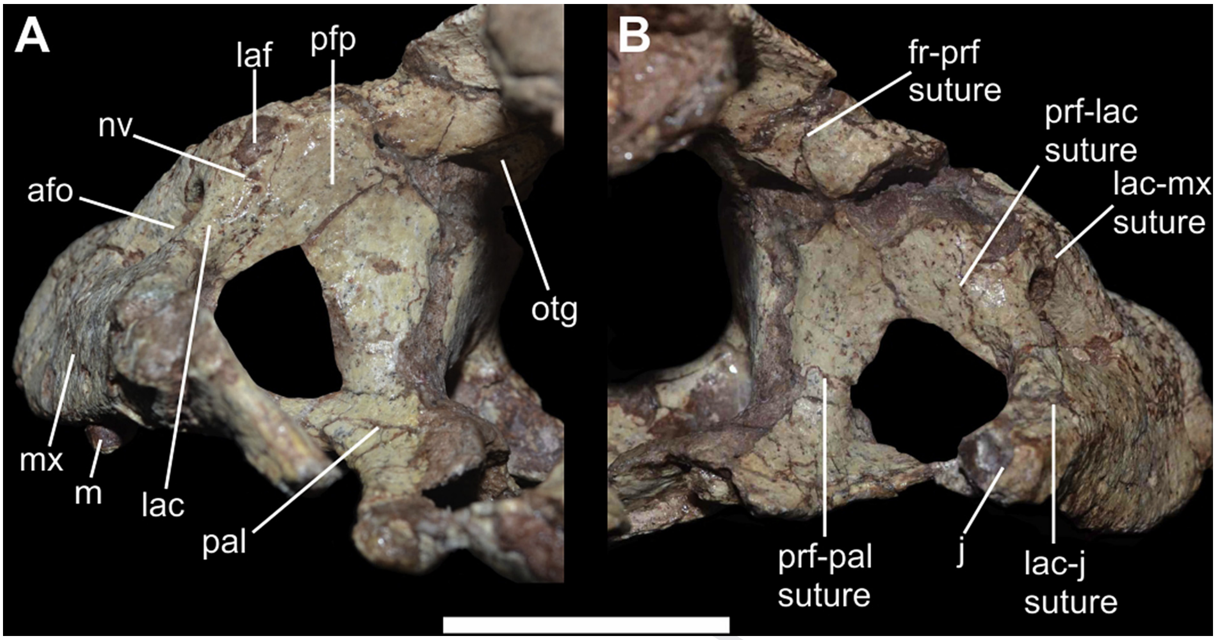

Fig. 15. Prefrontal pillars of *Notosuchus terrestris*. MPCA-Pv-237, left (**A**) and right (**B**) views. Scale bar equals 5 cm.

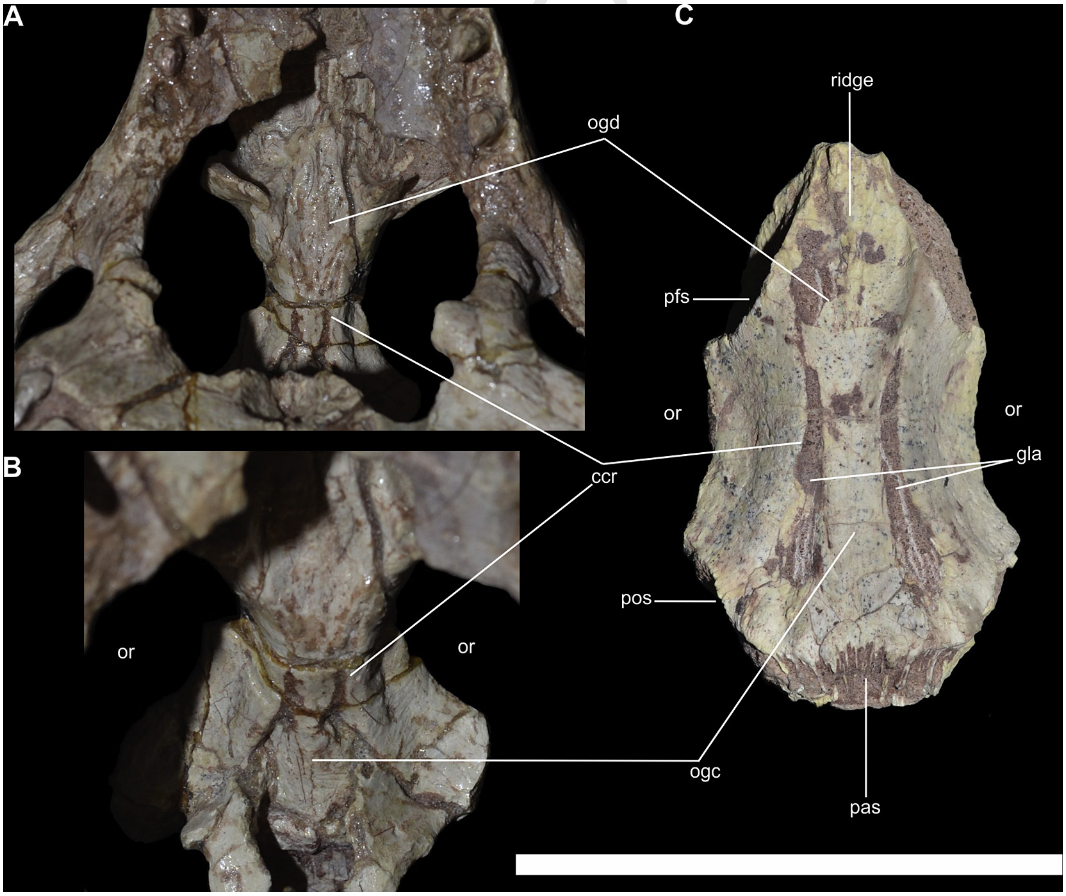

Fig. 16. Frontal of *Notosuchus terrestris* MLP-64-IV-16-5 (lectotype), **A**, ventral, **B**, anteroventral views; and **C**, MACN-PV-sn isolated bone in ventral view. Scale bar equals 5 cm in C.

The suborbital fenestrae are oval openings, anteroposteriorly elongate, with a slight lateral inclination of the sagittal axis, delimited by the maxillae anteriorly, the palatine medially, and the ectopterygoids posterolaterally. The suborbital fenestrae are larger than the maxillo-palatine fenestrae. A wide palatine bridge separates them medially, which is wider than the maximum transversal width of the suborbital fenestrae.

The choanae (internal nares) are large (anteroposteriorly longer than the suborbital fenestrae), triangular, and wider than the palatine bridge posteriorly (Fig. 13). They are bounded by the palatines

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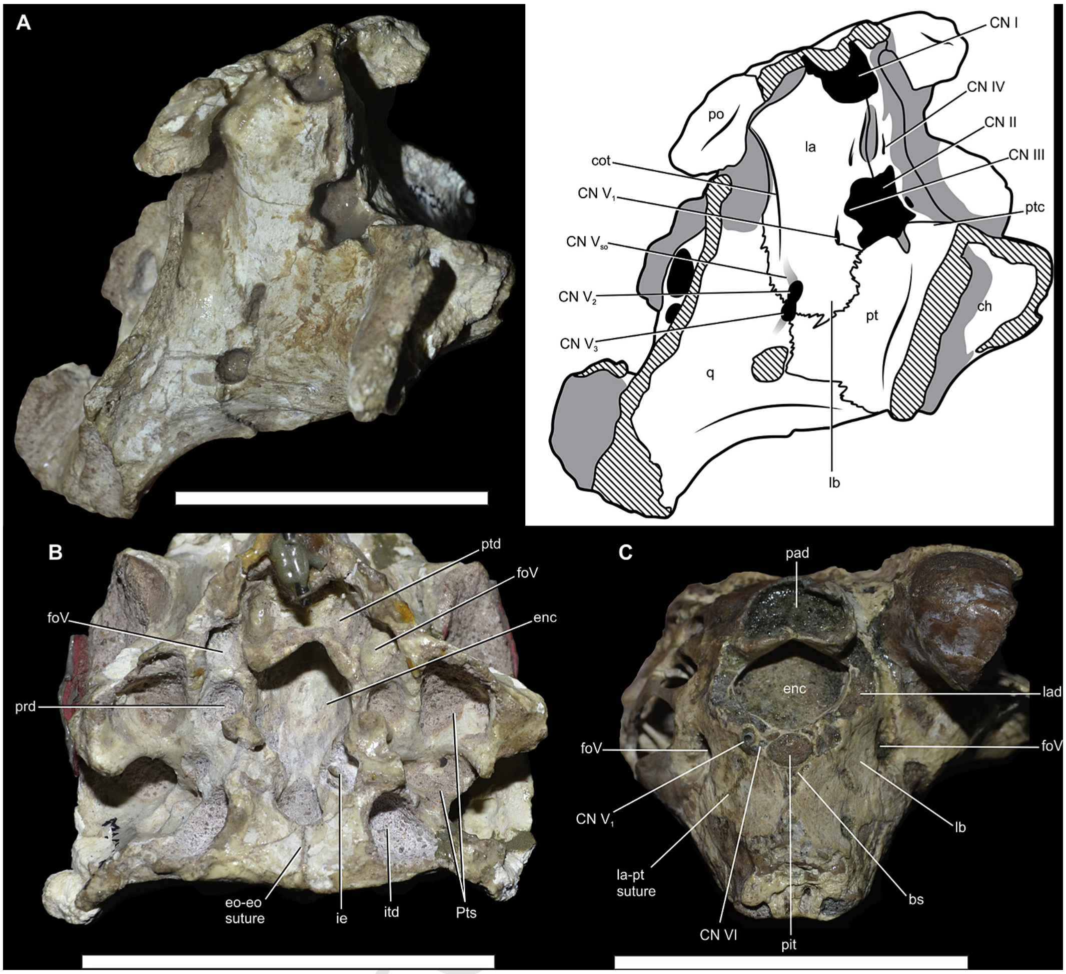

Fig. 17. Lateral wall of braincase of *Notosuchus terrestris*. **A**, MACN-PV-RN-1037 (anterolateral view); **B**, MACN-PV-N-23 (ventral view); **C**, MLP 64-IV-16-30 (anterior view). Scale bar equals 5 cm.

anterolaterally, the ectopterygoids laterally and the pterygoids posteriorly. Dorsally, palatines and pterygoids form the choanal groove. This palatal opening is divided by the choanal septum, as in other notosuchians (Andrade et al., 2006; Turner and Sertich, 2010; Pol et al., 2014). The choanal septum is formed by the palatines anteriorly and the pterygoids posteriorly, the later forming approximately the 90% of the length of the septum, which is formed by a dorsal lamina that reaches the choanal groove. The choana is internally divided along its total length. The ventral border of the anterior half of the choanal septum has a median longitudinal crest, and therefore the septum is rhomboid in cross-section (e.g., MPCA-Pv-791). Whereas, the ventral border of the posterior half of the choanal septum is slightly more transversely expanded and has a shallow longitudinal groove, and therefore the septum is drop-shaped in cross-section (e.g., MUCPv-137; Fig. 13). The posterior margin of the choanae has a notch with two parasagittal flanges that are larger in some specimens (e.g., MPCA-Pv-789/1) than in others (e.g., MACN-PV-RN-1045). The morphology of the choana is similar to the present in most notosuchians, but differs in the proportion of the elements forming its margins (e.g., *Baurusuchus*, *Pissarrachampsa*, *Caipirasuchus*, *Comahuesuchus*, *Yacarerani*, *Mariliasuchus*). The morphology of the choanal septum and the proportion of the maxillae and palatines forming it are highly variable within Notosuchia (see Section 5).

Dorsally the lower jaw of *Notosuchus terrestris* is triangular in outline. The symphyseal region is narrower than the post-alveolar region, the latter markedly curved dorsal and laterally. Each of the mandibular rami is narrow and anteroposteriorly elongated in dorsal view (Fig. 7). Laterally, the post-alveolar region of the mandibular ramus is dorsoventrally taller than in the symphyseal region. Dorsally, the mandibular rami diverge from each other behind the symphyseal region forming an acute angle of approximately 60°. The symphyseal region is relatively narrow, long, and presents a deep concavity along the midline; therefore, this region is U-shaped in cross-section. The mandibular symphysis is formed mainly by the dentary (approximately 75% of the symphyseal length) and in less proportion by the splenial (25% of the symphyseal length). The alveolar series comprehends the anterior 30% of the total mandibular length.

As in other notosuchians and non-eusuchian mesoeucrocodylians with preserved mandibles, there is no coronoid bone in the mandible of *Notosuchus* (Fig. 14A). This element is present in extant and extinct Crocodylia, forming the anterior border of the adductor mandibular fossa and bounding posteriorly the foramen intermandibular medius.

4.2. Skull bones

4.2.1. Nasal

The nasals form the dorsal margin of the external nares. They contact the dorsal process of the premaxilla anterolaterally, the maxilla laterally, the lacrimal and prefrontal posterolaterally and the frontal posteriorly (Fig. 5A). The nasals are as long as the snout. Posteriorly they have a process projected between the prefrontal

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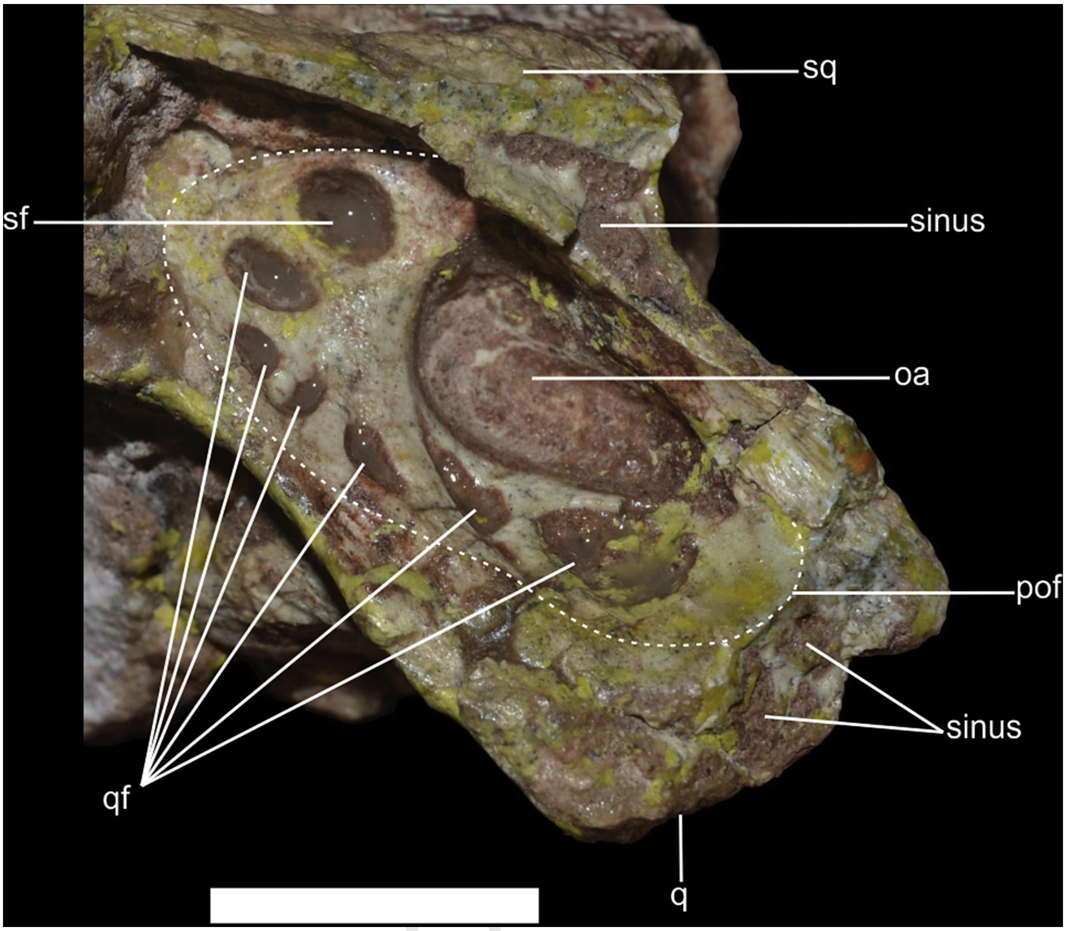

Fig. 18. Quadrate foramina of *Notosuchus terrestris*; lateral view of the left quadrate of MACN-PV-RN-1037. Scale bar equals 2 cm.

and the nasal process of the frontal. The posterior end of each nasal is separated from its counterpart by a median frontal projection. Its dorsal surface is mostly smooth, except for a dorsal bulge at the posterior half. Both nasals narrow anteriorly forming a process that curves ventrally towards the space of the nares (e.g., MACN-PV-RN-1037, Fig. 8).

4.2.2. *Lacrimal*

The lacrimal is mainly a vertical bone on the lateral side of the snout. It presents a well-developed anterior process that projects between the nasal and the maxilla, and delimits the posterodorsal margin of the antorbital fossa. It contacts with the maxilla anteriorly, the prefrontal dorsomedially, and the jugal ventrally through a process that forms the anteroventral margin of the orbit (Figs. 5A, 6A and 4). In dorsal view the lacrimal is lateromedially compressed between the prefrontal and the lateral wall of the snout.

There is a small oval lacrimal foramen, located at the laterodorsal border of the lacrimal, in the internal face of the orbital margin, near the contact with the prefrontal. Below and above the lacrimal foramen there is a pair of small vascular foramina (e.g., MPCA-Pv-237, Fig. 15). The lacrimal foramen communicates with the lacrimal duct, which extends anteriorly inside the maxilla, running dorsal to the antorbital fenestra. The lacrimal duct curves ventrally entering an oval recess (located anteroventrallly to the antorbital fenestra), approximately at the level of the 4° maxillary tooth. This recess manifests on the external surface of the maxilla as a small bulging (Fig. 8). The bulge is well marked in MACN-PV-RN-1045, MLP 64-IV-16-23 and MPCA-Pv-789/1, suggesting the presence of a large recess internally. In some specimens the natural cast of this recess is preserved exhibiting vascular impressions on its surface (e.g., MLP-64-IV-16-21). Ventrally, this recess is continuous with a passage running posteromedially that seems to lead into the maxilla-palatine fenestrae of the palate.

Dorsal to the lacrimal foramen, the lacrimal presents an oblique ridge separating its dorsal surface from its vertical lateral surface. The dorsal surface as a shelf of the lacrimal presents also a facet slightly rugose for the articulation of the anterior palpebral bone. In this surface and adjacent to the oblique ridge, both lacrimal bones present a tiny neurovascular foramen (MACN-PV-RN-1037, Fig. 8D); as in *Caipirasuchus stenognathus* (Pol et al., 2014).

4.2.3. *Prefrontal*

The prefrontal is an element exposed posterodorsally in the snout, contacting the nasal anteromedially, the frontal medially, and the lacrimal lateroventrally (Figs. 5A, 6A and 8). In the anterior wall of the orbit, the lacrimal-frontal suture is large and mainly vertical. Below this contact with the lacrimal, the prefrontal forms thin process oriented anteriorly towards the posterior region of the nasal cavity contacting the internal wall of the maxilla (MPCA-Pv-237, Fig. 15).

Dorsolaterally, the prefrontal has a facet for the anterior palpebral. Ventrally, the prefrontal has a lateromedially wide pillar, which form more than the 50% of the anterior wall of the orbital cavity. The prefrontal of the closely related *Mariliasuchus* also has wide prefrontal pillars (Zaher et al., 2006). These pillars in *Notosuchus* are transverse to the sagittal plane and projected vertically

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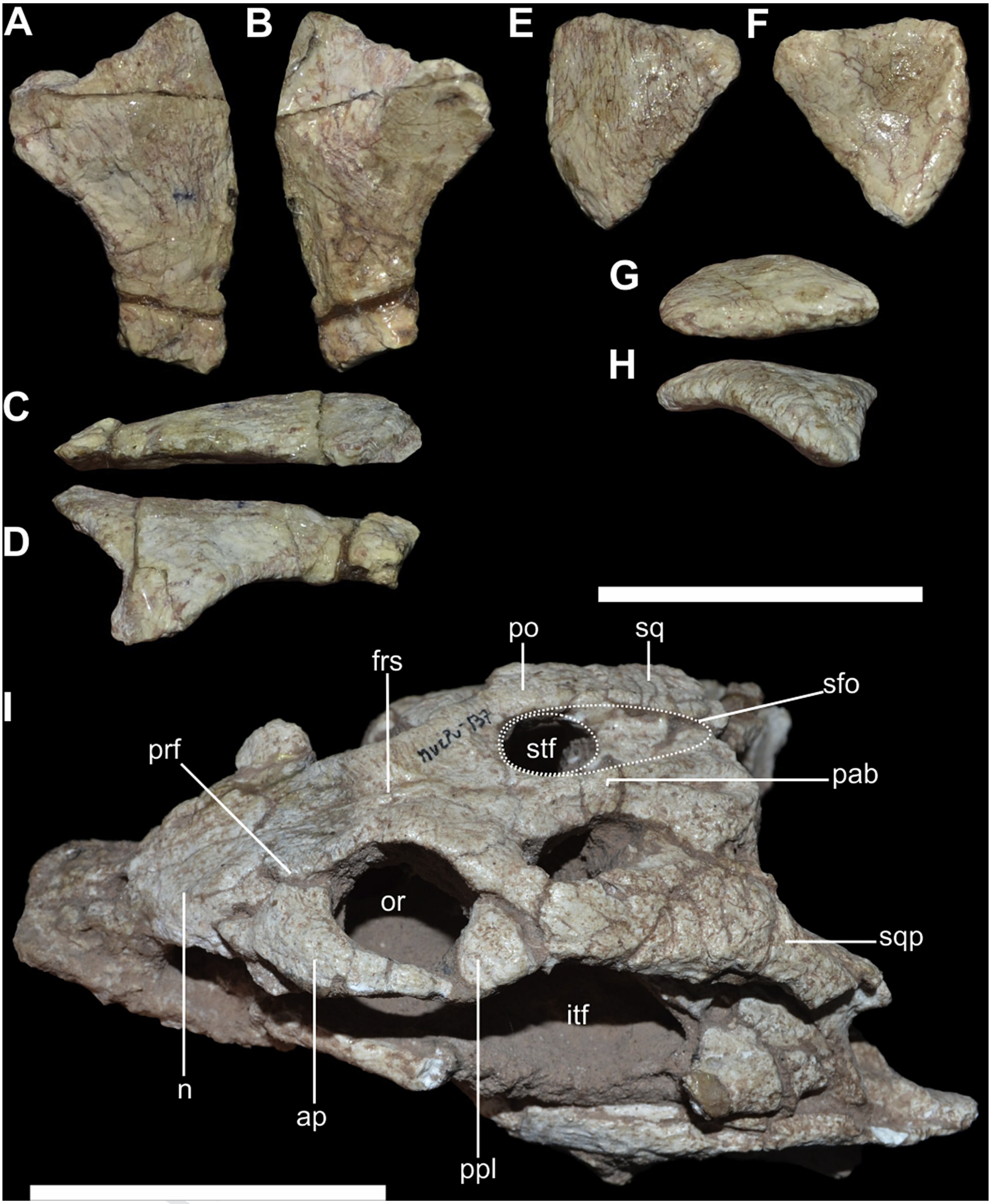

Fig. 19. Palpebral bones of *Notosuchus terrestris*. MLP-64-IV-16-5 (lectotype), right anterior palpebral, **A**, dorsal, **B**, ventral, **C**, lateral, **D**, medial views, and right posterior palpebral, **E**, dorsal, **F**, ventral, **G**, lateral, **H**, medial views, and specimen MUCPv -137 showing the palpebral bones in articulation, **I**, left side dorsolateral view. Scale bar equals 5 cm (A–H) and 2 cm, (I).

contacting the palatines. Both prefrontal pillars contact each other in the midline.

4.2.4. Postorbital

The postorbital contacts the frontal anteromedially, the squamosal posteriorly, the parietal medially (trough a narrow suture anterior to the supratemporal fenestra), the jugal ventrally (trough a descending process leveled to the postorbital bar), the quadratojugal posteroventrally (at the level of the dorsal corner of the infratemporal fenestra), the capitate process of the laterosphenoid (ventral and adjacent to the postorbital-frontal contact with), and the quadrate posteroventrally (within the external otic recess) (Figs. 4, 5A, 6A, 9, 10, 16 and 17).

The postorbital forms the posterior border of the orbit and the anterolateral margin of the supratemporal fenestra. The descending process (or descending lamina) of the postorbital is flat in cross-section and in its anterodorsal section opens the postorbital foramen (e.g., MACN-PV-RN-1045, MUCPv-35, MCF-PVPH-710). The

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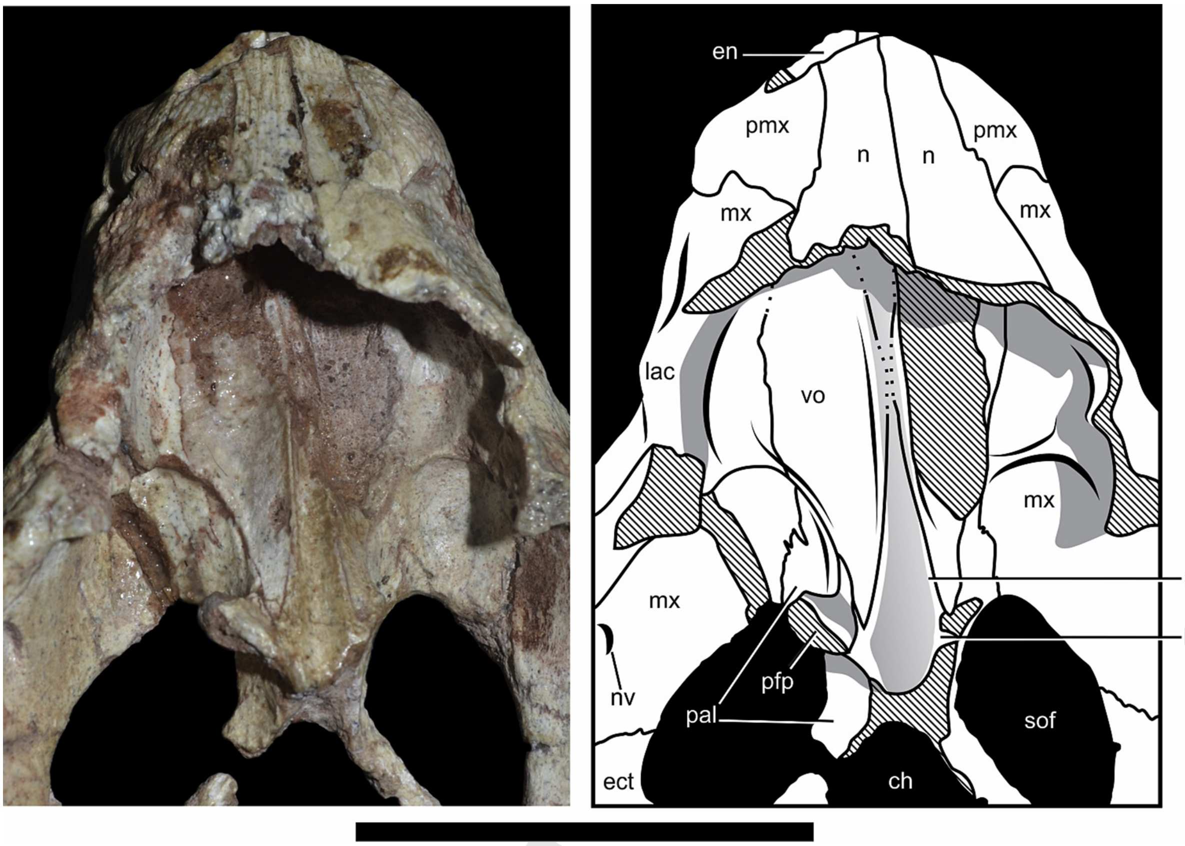

Fig. 20. Nasal cavity of *Notosuchus terrestris*; dorsal view of MACN-PV-RN-1040. Scale bar equals 5 cm.

postorbital presents in its anterior margin a smooth anterior process projected towards the orbit, for the articulation with the posterior palpebral bone. Ventrally, this anterior process is continuous with the descending process (forming the anterior limit of the external otic recess), and the postorbital bar. The external otic recess extends anteriorly up to the most anterior region of the postorbital, a condition present in all studied notosuchians (Pol et al., 2014). Between the anterior and descending processes a fold is formed laterally (e.g., MACN-PV-RN-1045, MUCPv-147) (Fig. 9C). Posteroventrally, the contact with quadratojugal is relatively broad (Fig. 9).

A postorbital-quadratojugal contact is present in all notosuchians (e.g., Pol et al., 2014; Sertich and O'Connor, 2014). This contact occurs in the posterodorsal margin of the fenestra infratemporal in baurusuchids, advanced notosuchians, and peirosaurids. In basal notosuchians (e.g., *Simosuchus*), advanced notosuchian *Sphagesaurus*, and uruguaysuchids this contact occurs in the dorsal corner of the fenestra. Particularly, in baurusuchids (e.g., *Campinasuchus*, *Pissarrachampsa*, *Baurusuchus*, *Stratiotosuchus*) the postorbital-quadratojugal contact is very broad (Campos et al., 2011; Carvalho et al., 2005, 2011; Montefeltro et al., 2011), while in others notosuchians this contact is relatively broad. In neosuchians (e.g., Crocodylia), the postorbital-quadratojugal contact is reduced or absent (e.g., Brochu, 1999).

In dorsal view, on the posterior half of the postorbital, a vascular groove delimits an anteriorly rounded ornamented structure reminiscent of an osteoderm. This feature is also present in *Caipirasuchus montealtensis*, *C. paulistanus*, and *C. stenognathus*, poorly developed in *Armadillosuchus*, and absent in basal notosuchians, uruguaysuchids, peirosaurids, *Yacarerani*, *Mariliasuchus*, and baurusuchids.

4.2.5. Squamosal

The squamosal is anteroposteriorly longer than wide (Figs. 4, 5A, 6, 9 and 10). It forms the posterior region of the supratemporal bar. The squamosal contacts with the postorbital anteriorly, parietal medially, supraoccipital posteromedially, exoccipital-opisthotic complex posteroventrally, and quadrate ventrally. With the latter bone, forms the posterior wall of the external otic recess (Figs. 6, 9 and 18).

In posterior view, the squamosal is projected laterally along the paroccipital process. The posterior contact with the parietal and the medial contact with the supraoccipital occur on the skull table at the level of the parietal-supraoccipital osteoderms. The squamosal-quadrate suture is anteroposteriorly wide, and it extends from the postorbital to the distal end of the posterolateral process of the squamosal. Laterally, the squamosal presents an elongated groove posterolaterally oriented, for the attachment of the muscles associated with an external ear-flap, as described in extinct and extant crocodyliforms (Barrios et al., 2015; Larsson and Sues, 2007; Shute and Bellairs, 1955).

The ornamentation of the squamosal of *Notosuchus* is irregular and formed by small rugosities delimited by shallow grooves (Figs. 5A and 10). The dorsal surface of the posterolateral process and the medial lamina (which forms part of the supratemporal fossa), do not present ornamentation except for the presence of a low and elongated crest separating the anterior surface of the occipital on the former. A smooth posterolateral process is present in advanced notosuchians as sphagesaurids (except *Armadillosuchus*), a deeply ornamented posterolateral process is present in the peirosaurids (e.g., *Lomasuchus*, *Montealtosuchus*, *Uberabasuchus*), and the basal notosuchian *Simosuchus*, whereas the ornamentation is poorly marked in uruguaysuchids and baurusuchids.

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The ornamented dorsal surface of the squamosal of *Notosuchus* is interrupted at the level of the posterior margin of the supratemporal fossa by an anteroposteriorly oriented vascular groove (Fig. 10). This groove delimits a posteriorly rounded structure similar to an osteoderm. This feature is poorly developed in *Caipirasuchus* species and absent in others notosuchians (Pol et al., 2014). In the posterior corner of the supratemporal fossa of *Notosuchus*, the temporo-orbital foramen is mainly enclosed by the squamosal as in others advanced notosuchians (e.g., *Yacarerani*, *Mariliasuchus*, *Caipirasuchus*), and baurusuchids (e.g., *Baurusuchus*).

4.2.6. Palpebral bones

Notosuchus terrestris presents two supraorbital ossifications (in MACN-PV-RN-1037, MPCA-Pv-789/1, and MUCPv-137 are best available), one anterior triangular in shape and another posterior circular to subtriangular in shape as the most notosuchians (e.g., *Mariliasuchus*, *Caipirasuchus*, *Armadillosuchus*, uruguaysuchids, baurusuchids, peirosaurids) (Fig. 19). The anterior palpebral is larger and leans on a depressed surface (articular facet) of the prefrontal and lacrimal, while the posterior palpebral is smaller and lean on the anterior process of the postorbital. The anterior palpebral is convex in dorsal and lateral views, and is overhanging most of the orbit. Its anterior end has two projections, one medial that leans on the prefrontal and another anterior that leans on the lacrimal and part of the prefrontal. Both, anterior and posterior palpebral bones have an ornamented convex dorsal surface and a smooth concave ventral surface.

4.2.7. Frontal

The frontal is a sub-rectangular to triangular plate-like bone in the skull roof (Figs. 4 and 5A). It contacts with the nasal anteriorly, the prefrontal anterolaterally, the postorbital posterolaterally, the parietal posteriorly and the laterosphenoid posteroventrally. The frontoparietal suture is interdigitate and varies from straight (MACN-PV-N-22, MACN-PV-N-23, MACN-PV-RN-1048, MACN-PV-RN-1118, MCF-PHPV-710, MLP 64-IV-16-1, MUCPv-137, MUCPv-147) to slightly concave-convex (MACN-PV-RN-1119, MLP 64-IV-16-5, MLP 64-IV-16-7, MLP 64-IV-16-31, MPCA-Pv-237, MPCN-Pv-96) (Fig. 10).

The frontal is longer than wide. The bone broadens backwards gradually from the posterior half of the orbit to the contact with the postorbital, where is its maximum width. The nasal process converges gradually between the nasals. The anterior end of the nasal process does not surpass the prefrontal. The frontal-postorbital contact is an oblique suture oriented from the lateral widening towards the level of the anterior corner of the supratemporal fenestra. The frontal does not participate of the supratemporal fenestra, except in the specimen MPCA-Pv-528, unlike most notosuchians (e.g., uruguaysuchids, peirosaurids, baurusuchids, sebecids, and advanced notosuchians).

The interorbital plate has curved lateral margins but does not forms an orbital crest, unlike the well-marked crest present in Eusuchia (e.g., *Caiman*). The dorsal surface of the frontal is mostly flat, with a slight anteroventral curvature. The frontal is ornamented with small rugosities and striations, with variable presence of a low sagittal crest that is more conspicuous in adult specimens (e.g., MACN-PV-N-106, MACN-PV-RN-1037, MACN-PV-RN-1045, MACN-PV-RN-1118, MLP 64-IV-16-5, MLP 64-IV-16-31, MPCA-Pv-528, MPCA-Pv-237, MPCA-Pv-789/1, MUCPv-35, MUCPv-137, MUCPv-147); as in most notosuchians (e.g., Baurusuchidae, Sebecidae, Sphagesauridae). This sagittal crest is more marked in the center of the interorbital plate.

The ventral surface of the frontal is smooth and the crista cranii is poorly developed (Fig. 16). The passage or groove delimited by right and left crests – hosting the olfactory tract-is slightly concave anteriorly and convex posteriorly (e.g., MACN-PV-N-23, MLP 64-IV-16-5); unlike most Crocodyliformes where the crista cranii frontalis is well defined, sharp-edged, dorsoventrally tall, delimiting a narrow groove, and is concave along its length. The olfactory tract groove presents posteriorly a pair of grooves parallel to the crista cranii, which indicate the contact with the rostral process of the laterosphenoids. These grooves are deeper posteriorly and extend anteriorly leaving a shallow mark that becomes diffuse at the level of the olfactory bulbs. Well-marked grooves for the laterosphenoids are also present in *Gavialis gangeticus* (pers. obs.).

The olfactory tract groove of *Notosuchus* expands anteriorly in well-defined depressions to house the olfactory bulbs; these depressions are oval and divergent from the midline anteriorly. Also the olfactory tract groove of *Notosuchus* expands posteriorly delimiting a convex surface at the level the anterior portion of the cerebral hemispheres. The studied Crocodylia (e.g., *Caiman*, *Crocodylus*, *Gavialis*), present a slight depression for the olfactory bulbs and present an olfactory tract groove expanded posteriorly with a well marked cerebral fossa to house the cerebral hemispheres (see Section 5). The dorsomedial surface to the orbit is concave and presents a series of vascular foramina aligned anteroposteriorly (Fig. 16).

4.2.8. Parietal

In dorsal view, the parietal is subrectangular contour, shorter than the frontal (Figs. 4, 5A, and 10). The parietal contacts with the frontal anteriorly, postorbital anterolaterally, squamosal posterolaterally, supraoccipital posteriorly, laterosphenoid anteroventrally, and quadrate posteroventrally. The parietal-frontal suture is interdigitated, transversely or slightly concave-convex. The contact with postorbital is short on the skull table but continues within the supratemporal fossa. The parietal-supraoccipital suture is V-shaped (e.g., MLP 64-IV-16-2, MLP 64-IV-16-5, MCF-PVPH-710), transversal (e.g., MACN-PV-N-23, MACN-PV-RN-1045, MACN-PV-RN-1048, MLP 64-IV-16-1, MLP 64-IV-16-10, MPCA-Pv-528), or an intermediate state between those two (e.g. MLP 64-IV-16-8, MACN-PV-N-108, MACN-PV-RN-1041, MLP 64-IV-16-30, MUCPv-147, MPCN-Pv-96) (Figs. 4, 5A, and 10). Together with the squamosal, the parietal form the supratemporal fossa largely. Posterior to this depression, the parietal participates in a point of the medial margin of the temporo-orbital foramen.

The dorsal surface of parietal is widely affected by the supratemporal fossae. The interfenestral plate is narrow, being its minimum width at the level of the posterior margin of the supratemporal fenestra. It forms a sagittal bar with divergent anterior and posterior ends, ornamented with a pair of parallel longitudinal grooves produced by the contact of the medial margins of the supratemporal fossae. The sagittal bar is wider and with parallel margins in most of the adult specimens (e.g., MACN-PV-N-22, MACN-PV-N-23, MACN-PV-RN-1037, MACN-PV-RN-1041, MACN-PV-RN-1045, MACN-PV-RN-1048, MACN-PV-RN-1118, MCF PVPH-710, MLP 64-IV-16-1, MPCA-Pv-528, MPCA-Pv-237, MUCPv-35, MUCPv-137, MUCPv-147) (Figs. 4 and 10). In juvenile specimens the space between the supratemporal fossae is wider than in adult specimens, and the sagittal bar is incipient (e.g., MLP 64-IV-16-7) or absent (MUCPv-118). The dorsal surface of the posterior end of the sagittal bar presents a median depression. The morphology of the sagittal bar is shared with *Simosuchus*, sphagesaurids (except *Yacarerani*) and other advanced notosuchians and baurusuchids. The descending lamina or crista cranii parietalis forms a depressed surface in the skull roof, transversely wide, concave and smooth, that constitute the medial wall of the supratemporal fenestra and fossa.

The parietal-supraoccipital osteoderms present two morphotypes, one of triangular contour (e.g., MACN-PV-N-108, MACN-PV-RN-1041,

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MACN-PV-RN-1048, MACN-PV-RN-1119, MLP 64-IV-16-1, MLP 64-IV-16-5, MLP 64-IV-16-8, MLP 64-IV-16-10, MLP 64-IV-16-31, MCF PVPH-710, MUCPv-35, MUCPv-137, MUCPv-147), and another of hexagonal or subrectangular contour (e.g., MACN-PV-N-22, MACN-PV-N-23, MACN-PV-N-108, MACN-PV-RN-1037, MACN-PV-RN-1045, MACN-PV-RN-1118, MLP 64-IV-16-7, MPCA-Pv-237, MPCA-Pv-528, MUCPv-198) (Fig. 10). These two morphotypes respond to the “triangular crest” and “paddle-shaped crest” of Andrade and Bertini (2008a) respectively. The parietal-supraoccipital osteoderms are also affected laterally by vascular grooves, impressions of the temporo-orbital vein. Principally in the osteoderms triangular morphotype, there is a depression projected forward on the parietal bar forming a narrow and shallow groove that is in turn occupied by a narrow longitudinal ridge.

Internally, the parietal is profusely pneumatized forward by the anterior ramification of the intertympanic diverticulum, the parietal diverticulum (sensu Dufeau and Witmer, 2015), as observed in MLP 64-IV-16-30 externally; in extant crocodylians (e.g., *Alligator*, *Caiman*), this diverticulum is posteriorly restricted (Dufeau and Witmer, 2015; pers. obs.).

4.2.9. Supraoccipital

The supraoccipital is a vertical element observed in both posterior and dorsal views of the skull, since it presents a dorsal projection that forms part of the skull table (Figs. 4, 5A, 6B, 10, 11). It contacts the parietal anteriorly and the squamosal laterally, whereas contacts the exoccipital-opisthotic posteroventrally. The supraoccipital of *Notosuchus* is excluded from the dorsal margin of the foramen magnum by the medial contact of the exoccipitals (Fig. 6B), as all crocodyliforms (Benton and Clark, 1988). Internally, the supraoccipital is invaded by intertympanicum diverticulum (e.g., MACN-PV-RN-1045), as in extant crocodylians (Dufeau and Witmer, 2015). As mentioned, the supraoccipital-parietal suture can be V-shaped, transversal, or an intermediate morphology between those two suture (Fig. 10). In most notosuchians, the dorsal exposure of the supraoccipital on the skull table is anteroposteriorly reduced (e.g., *Araripesuchus patagonicus*, *Mahajangasuchus*, *Yacarerani*, *Caipirasuchus montealtensis*, baurusuchids) or absent (e.g., peirosaurids).

The supraoccipital is dorsally affected by the parietal-supraoccipital osteoderms and also by the central depression that affects the posterior part of the parietal. In posterior view, the supraoccipital is triangular, smooth, and presents a median vertical crest along its complete dorsoventral extension. In the posterior margin of the skull table, the supraoccipital present a horizontal edge that separates the skull table from the occiput. In MCF PVPH-710, the vertical crest extends as a poorly developed longitudinal crest on the surface of the dorsal portion of the supraoccipital on the skull table (Fig. 10A). In dorsal view, the posterior margin of the supraoccipital presents a triangular caudal projection that is coincident with the vertical crest of the occipital plate (e.g., MACN-PV-N-22, MACN-PV-N-23, MACN-PV-RN-1037, MUCPv 147). In some specimens the posterior margin is rect, lack the caudal projection, and the body of the supraoccipital is visible mostly behind the skull table (e.g., MACN-PV-RN-1045, MCF PVPH-710, MLP 64-IV-16-5, MLP 64-IV-16-30) (Figs. 4, 5A and 10); the same condition is observed in *Araripesuchus patagonicus* and *A. tsangatsangana*.

In most studied specimens, the post-occipital processes are mainly formed by the supraoccipital and less by the exoccipital (e.g., MACN-PV-RN-1037, MACN-PV-RN-1045, MLP 64-IV-16-10, MLP 64-IV-16-30), as in others notosuchians (e.g., *Simosuchus*, *Araripesuchus*, *Baurusuchus*, peirosaurids, *Mahajangasuchus*, *Mariliasuchus*, *Sahitisuchus*, *Yacarerani*) and eusuchians (e.g., *Crocodylus*, *Gavialis*, *Alligator*, *Caiman*). However, in the specimens MACN-PV-RN-1048, MLP 64-IV-16-8, MLP 64-IV-16-5, MCF PVPH-710, and MPCA-Pv-528, the post-occipital processes are formed mainly by the exoccipital, a characteristic not described previously for *Notosuchus* and neither other described crocodyliforms (Fig. 11). In dorsal view, these processes are triangular shaped and posteriorly projected. They form the ventral margin of the post-temporal fenestra and have an oval surface dorsally oriented for the insertion of the M. transversospinalis capitis (as described for extant crocodilians, Cleuren and De Vree, 2000). This surface of insertion is level with the skull table and slightly inclined, as in several notosuchians (e.g., *Araripesuchus*, Peirosauridae), but unlike the condition observed in other Mesoeucrocodylia (e.g., *Simosuchus*, *Mahajangasuchus*, Crocodylia), which have a lateroventral inclination of the dorsal surface of post-occipital processes (Turner, 2006).

4.2.10. Exoccipital-opisthotic complex

The exoccipital-opisthotic complex contacts with the supraoccipital dorsomedially, the squamosal dorsolaterally (along the paroccipital process), the quadrate lateroventrally and the basioccipital ventromedially (Fig. 6B). The body of the element has two main planes, one dorsal and another ventral to the foramen magnum, separated by the occipital transversal crest. The dorsal plane if inclined postero-dorsally. At this level the exoccipital-opisthotic complex projects laterally forming the paroccipital processes that — together with the squamosal-form the concave surface for the insertion of the neck muscles M. epistropheo-capitis and M. depressor mandibulae as in extant crocodylians (Cleuren and De Vree, 2000; Iordansky, 2000). The ventral plane is oriented postero-ventrally.

The exoccipitals delimit the foramen magnum postero-laterally and form part of the neck of the occipital condyle. In addition, the exoccipitals form part of the body of occipital condyle laterally. Lateral to the occipital condyle there are two small foramina medially and one large foramen laterally (Figs. 6B and 12A). The smaller foramina are completely enclosed by the exoccipital and correspond to the exit of the anterior and posterior branches of the Cranial Nerve (CN) XII (XII$_1$ and XII$_2$ respectively), whereas the larger foramen corresponds to the metotic foramen (for CNs IX-XI and internal jugular vein). The foramen for CN XII$_1$ is small, oval (e.g., MCF-PVPH-710) or slit-shaped (e.g., MACN-PV-RN-1037), and located between the foramen for CN XII$_2$ and the metotic foramen. In some specimens, CN XII$_1$ is slit-shaped and opens on the medial wall of the metotic foramen (e.g., MACN-PV-RN-1045, MLP 64-IV-16-2, MLP 64-IV-16-10, MPCA-Pv-237). However, in the lectotype (MLP 64-IV-16-5), the left CN XII$_1$ is slit-shaped and is on the medial margin of the lateral larger foramen, whereas the right side these foramen is oval and away from the margin, suggesting that this character is highly variable (Fig. 6B). The foramen for CN XII$_2$ is oval.

The larger metotic foramen is delimited by the exoccipital medially and the opisthotic laterally. It opens within an oval recess (dorsomedially), together with the foramen for the internal carotid artery (lateroventrally) (e.g., MACN-PV-RN-1037, MLP 64-IV-16-2, MLP 64-IV-16-5, MPCA-Pv-237) (Fig. 12). This particular feature -metotic foramen plus internal carotid artery foramen within a common recess-is also present in other advanced notosuchians (e.g., *Caipirasuchus*, *Yacarerani*, *Mariliasuchus*). In the sebecosuchian *Baurusuchus pachecoi* and the peirosaurid *Montealtosuchus arrudacamposi*, the metotic foramen plus the internal carotid artery foramen open within in a shallow common recess; while in all neosuchians (e.g., Eusuchia), these foramina are considerably separated and the internal carotid foramen is displaced in a more ventral position (see Section 5).

Laterally and below the paroccipital process, the exoccipital-opisthotic complex delimits the medial margin of the external opening of the cranioquadrate passage (Figs. 6B and 12). Ventral to

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this opening, the crista tuberalis is not sharp, but poorly developed and is ventromedially oriented running from the cranioquadrate passage to the basal tubera. In most peirosaurids and neosuchians (e.g., Eusuchia), the crista tuberalis is sharp and forms the ventrolateral margin of the occiput, separating the posterior and lateral surfaces of the braincase.

Internally, the exoccipital-opisthotic complex is highly pneumatized by the otoccipital diverticulum (sensu Dufeau and Witmer, 2015) (e.g., MACN-PV-RN-1045). In extant crocodylians (e.g., *Alligator*) this diverticulum is reduced (Dufeau and Witmer, 2015).

4.2.11. *Basioccipital*

The basioccipital contacts the exoccipitals dorsolaterally and the basisphenoid and the quadrate anteroventrally (Fig. 6B). It forms the posterior section of the floor of the endocranial cavity. Between the basioccipital and the basisphenoid, there are the median opening and the paired lateral openings (Eustachian tubes) of the pneumatic pharyngotympanic system. These openings are not aligned transversely in ventral and posterior views as in some sphagesaurids (e.g., *Yacarerani*, *Mariliasuchus*), basal notosuchians (e.g., *Simosuchus*), and some crocodylians (e.g., *Gavialis gangeticus*, *Crocodylus niloticus*). Like in peirosaurids, *Notosuchus* has lateral Eustachian tubes slightly displaced posterior and dorsally respect to the median Eustachian tube (Figs. 5B and 12).

The basioccipital forms most of the occipital condyle and the ventral portion of the neck of the condyle. The occipital condyle is posteroventrally oriented forming an angle of approximately 45° with the dorsal occipital plane, whereas in neosuchians the same angle is wider than 50°. Ventral to the occipital condyle the basioccipital has a faintly developed sagittal ridge. The basal tubera are also poorly developed. Below the occipital condyle, there is a small vascular foramen (Fig. 12). In its lateroventral border the basioccipital plate forms briefly part of the crista tuberalis, together with the exoccipital and the quadrate, which extends ventrally and continues with the basal tubera (e.g., MUCPv-35, MPCA-Pv-237). In most studied specimens the basioccipital is of inverted pentagonal contour (e.g., MLP 64-IV-16-2, MLP 64-IV-16-5, MPCA-Pv-237), however some present a lateral constriction at the base of the occipital condyle neck (e.g., MACN-PV-RN-1037, MCF PHPV-710) (Fig. 12).

Internally the basioccipital is highly pneumatized by branches of the pharyngotympanic system, particularly the basioccipital diverticulum (sensu Dufeau and Witmer, 2015). Therefore, the posterior wall of the basioccipital is markedly thin (exposed fracture in MLP 64-IV-16-18, MACN-PV-1045, MACN-PV-1037), compared to extant crocodylians. This degree of pneumatization was not mentioned for any notosuchian so far, and contrast with the neosuchian condition (e.g., Eusuchia), only comparable to a lesser extent with the perinatal condition of *Alligator mississippiensis*, in which the basioccipital diverticulum invades the precondylar portion of the basioccipital bone (see Dufeau and Witmer, 2015).

4.2.12. *Basisphenoid*

The basisphenoid is exposed ventrally as a triangular plate, more precisely an inverted V-shaped, anteroposteriorly narrow (Figs. 5B and 12). The basisphenoid contacts with the pterygoids anteriorly, with the quadrate laterally and with the basioccipital posteriorly. The basisphenoid forms a large region of the floor of the endocranial cavity. Anteriorly, the ventral exposure of the basisphenoid is wedged between the dorsal processes of the pterygoids. Both the basisphenoid and basioccipital delimit the external openings of the pharyngotympanic system. As in all Crocodyliformes, these openings comprehend the median Eustachian foramen and the lateral Eustachian foramina, (the median pharyngeal tube and pharyngotympanic tube respectively sensu Dufeau and Witmer, 2015). The median pharyngeal tube is at the posterior end of a sagittal groove delimited by oblique ridges (Fig. 12C).

The large ventral exposition of the basisphenoid is similar to that in other notosuchians (e.g., *Araripesuchus patagonicus*, *Simosuchus*, *Baurusuchus salgadoensis*), but contrasts with the larger exposition observed in the closely related *Sphagesaurus*, *Mariliasuchus*, *Caipirasuchus* and *Yacarerani*. The ventral exposition of the basisphenoid in peirosaurids is anteroposteriorly narrow but not as much as in Neosuchia (e.g., Crocodylia). Also in peirosaurids, the basisphenoid is vertically exposed in posterior view.

The anterior and lateral portions of the basisphenoid are covered by the dorsal processes of the pterygoids and in any specimen the cultriform process (= basisphenoidal rostrum) is observed (Fig. 17). The ventral surface of the basisphenoid has two low oblique ridges that are continuous with the crista tuberalis of the exoccipital-opisthotic complex, and extend from the lateral margin of the pharyngotympanic tubes converging anteriorly. In the specimen MACN-PV-RN-1037 the basisphenoid ridges join with the ridges of the posterior margin of the pterygoid wings (which converge posteriorly) and form a short sagittal ridge; in the specimen MLP 64-IV-16-31 these ridges not join (Fig. 12A and B). Similar ridges are present in *Araripesuchus patagonicus* and baurusuchids, are poorly developed in *Mariliasuchus*, *Uruguaysuchus aznarezi* and *Caipirasuchus* (forming a deep sagittal groove), and are absent in other notosuchians such as *Yacarerani* and *Armadillosuchus*. In some neosuchians (e.g., crocodylians *Paleosuchus*, *Osteolaemus tetraspis*, *Alligator*), the ventral exposure of the basisphenoid is narrow antero-posteriorly and mainly vertically disposed with a pair of oblique ridges poorly developed.

4.2.13. *Laterosphenoid*

The laterosphenoid contacts the frontal dorsally, the postorbital dorsolaterally, the parietal dorsally, the quadrate posterolaterally, the prootic posteroventrally (internally), the pterygoid ventrally, the basisphenoid ventromedially, and its counterpart medially (Fig. 17A). Within studied specimens, only in MACN-PV-N-22, MACN-PV-N-23, MACNPV-RN-1045, MCF PVPH-710, MLP 64-IV-16-2, MLP 64-IV-16-5, MLP 64-IV-16-10, MLP 64-IV-16-30, MPCA-Pv-237, MUCPv-35 and MUCPv-147, the laterosphenoid (partial or completely preserved) is observed (Fig. 17).

The laterosphenoid forms the anterior portion of the lateral wall of the braincase. Dorsally, the laterosphenoid has an anterior and a posterior process. The anterior process (or rostral process) is short and dorsoventrally tall (e.g., MACN-PV-N-22, MACN-PV-N-23, MPCA-Pv-237). *Notosuchus* would have an elongated anterior process (from the level of the postorbital-frontal contact to the base of the olfactory bulbs), inferred from the furrows on the ventral surface of the frontal. The rostral end of the anterior process of the laterosphenoid is not preserved in any of the studied specimens, suggesting it may have been cartilaginous.

The posterior process (postorbitary process) contacts with the postorbital without a suture (synovial contact), as in Crocodylia and other derived mesoeucrocodylians (Holliday and Witmer, 2009). The laterosphenoid forms the anteromedial wall of the supratemporal fenestra, were contacts with the parietal dorsally. Posteriorly, the laterosphenoid delimits the anterior margin of the trigeminal foramen and fossa (foV).

In *Notosuchus*, the contact of the laterosphenoid with its counterpart is trough a vertical large suture ventral to CN I and dorsal to CN II, within a dorsoventrally elongated depression. Thick ridges with convergent ends delimit this depression. The foramen for CN II is dorsoventrally depressed between the medial contact of the laterosphenoid and the basisphenoid as in peirosaurids (e.g., *Lomasuchus*), and is partially preserved in the specimens MACN-PV-N-22

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and MPCA-Pv-237. Lateral to the foramen for CN II, there is a smaller foramen for CN III (MLP 64-IV-16-30, MPCA-Pv-237). Dorsal to the latter and in medial position on the laterosphenoid there is a tiny foramen for CN IV, located within a superficial groove.

The laterosphenoid of *Notosuchus* present a lateral bridge for the ophthalmic branch (CN V_1), but not a caudal bridge for the supraorbitary branch of the trigeminal nerve (CN V_{so}) (Fig. 17A). A caudal bridge of the laterosphenoid is present in the basal notosuchian *Araripesuchus*, the peirosaurid *Lomasuchus*, and more derived Mesoeucrocodylia (e.g., Crocodylia) (see Holliday and Witmer, 2009). In the specimen MACN-Pv-N-22, there is a groove on the laterosphenoid left by the supraorbitary branch (CN V_{so}), adjacent to the quadrate-laterosphenoid suture at the dorsal margin of the trigeminal fossa, and this margin is continuous. In the specimens MACN-PV-RN-1045 and MPCA-Pv-237, this groove left a notch at the dorsal margin of the trigeminal fossa (Fig. 17A). The lateral bridge of the laterosphenoid of *Notosuchus* delimits laterally the canal that transmitted the branch CN V_1 ending in a small oval foramen. This lateral bridge contacts ventrally with the pterygoid in a broad sutural contact. In the extant crocodylians, the lateral bridge delimits a dorsoventrally broad groove for the CN V_1, and has a relatively narrow sutural contact with pterygoid.

The opening for the exit of all the branches of the trigeminal nerve (CN V_2, CN V_3, and CN V_{so}), the trigeminal fossa (foV), is proportionally small in *Notosuchus*; the anteroposterior diameter is 50% smaller to the width of the lateral bridge of the laterosphenoid. In other notosuchians (e.g., *Lomasuchus*), the width of the trigeminal fossa is equal to the width of the lateral bridge (pers. obs.). In neosuchians (e.g., Crocodylia), the width of this opening is always wider (equal or larger than 50%) than the width of the bridge; derived mesoeucrocodylians present a relatively large trigeminal fossa (Holliday and Witmer, 2009; George and Holliday, 2013). In the specimen MACN-PV-RN-1045 the trigeminal fossa is oval contour for maxilla-mandibular branches (CN V_2 and CN V_3), whereas in the specimen MACN-PV-N-22 is bilobate contour with an anterior groove for CN V_2 and a posterior groove for CN V_3, anteroposteriorly oriented. This posterior groove continues caudally by a depression for CN V_3 on the quadrate (Fig. 17). In front view, in the specimen MLP 64-IV-16-30 the foramen for the CN VI is observed below the foramen CN III, and lateral to the pituitary fossa (Fig. 17C).

In the specimens MACN-PV-N-22, MACN-PV-N-23, MPCA-Pv-237, and MCF PVPH-710 is observed a cotylar crest slightly marked, which extends posteroventrally on the surface of the postorbitary process of the laterosphenoid from the capitate process to the surface behind of the posterior margin of the trigeminal fossa (Fig. 17A). This crest divides the anterior from the posterior surface of the laterosphenoid. Internally, the laterosphenoid is highly pneumatized by diverticulae of the pharhyngotympanic sinus, as was observed in the broken specimens (MLP 64-IV-16-30, MACN-PV-N-23) (Fig. 17B and C).

4.2.14. Prootic

The prootic forms the lateral wall of the braincase, contacting with the opisthotic posteriorly and the laterosphenoid anteriorly. As in the most crocodyliforms the medial branch of the quadrate obscures the posterior region of braincase and therefore the prootic is not manner complete externally exposed (e.g., Langston, 1973; Busbey and Cow, 1984; Holliday and Witmer, 2009). In the specimens MLP 64-IV-16-2, MLP 64-IV-16-30, and MPCA-Pv-237, a fragmentary and small prootic is observed within the trigeminal fossa forming the ventral and posterior margin of this opening as derived mesoeucrocodylians (e.g., crocodylians). Unlike *Notosuchus*, extinct and extant crocodylians have a relatively more exposed prootic forming a trigeminal fossa larger (Iordansky, 1973; Holliday and Witmer, 2009; George and Holliday, 2013).

4.2.15. Quadrate

The quadrate is a wide and robust bone sutured to the lateral walls of the braincase (Figs. 5, 6, 17). It contacts the squamosal dorsally, the pterygoid ventromedially covering the prootic posteriorly, the laterosphenoid anteromedially, the basisphenoid and basioccipital ventrally, the exoccipital-opisthotic complex posteromedially, and the quadratojugal laterally along the external otic recess. In the external otic recess, the quadrate contacts with the postorbital anteriorly. The quadrate forms the posterior margin of the trigeminal fossa, ventral and posterior to this forms part of the groove of CN V_3 (Fig. 17).

On the anterodorsal surface of the quadrate, a crescentic depressed area (periotic fossa sensu Montefeltro et al., 2016), indicates the surface where the tympanic membrane was supported. On this surface a series of foramina (up to 7) is arranged following a crescentic curvature, anterior and ventral to the otic aperture (Figs. 6A, 9 and 18). The most dorsal and large correspond to a subdivided sub-tympanic foramen (= periotic foramen or siphoneal foramen); there are up to three foramina in advanced notosuchians (e.g., *Marialisuchus*, *Yacarerani*) and Baurusuchidae. A periotic fossa with several pneumatic foramina is also present in “protosuchians”, whereas in most notosuchians (e.g., Peirosauridae, Sebecidae, *Araripesuchus*) and in Neosuchia there is a single foramen and the periotic fossa is reduced (Zaher et al., 2006; Carvalho et al., 2011; Montefeltro et al., 2011, 2016; Pol et al., 2014). The contour of the periotic fossa indicates that the tympanic membrane would have been wide, oval and inclined accompanying the orientation of the dorsal surface of the quadrate and covering laterally the mentioned pneumatic openings.

The quadrate delimits together with the lateroventral border of the paroccipital process the cranioquadrate canal (Fig. 12A). The quadrate and the exoccipital-opistothic complex form the crista tuberalis, which is low and restricted to the occiput (Fig. 6B). In other mesoeucrocodylians (e.g., Peirosauridae, Sebecidae and neosuchians), the crista tuberalis (sensu Bona and Paulina Carabajal, 2013) is relatively sharp and forms the ventrolateral margin of the occipital table. In *Yacarerani* and *Mariliasuchus*, the crista tuberalis is low and forms the ventral margin of the occiput.

The ventral or articular branch of the quadrate is ventrally oriented in lateral and occipital views (Fig. 6); perinatal alligators have similar ventral orientation of the articular branch of the quadrate (pers. obs.). Laterally, the ventral branch of the quadrate forms an angle of 120° with the the skull table. In other notosuchians this angle is less than (e.g., *Simosuchus*, *Yacarerani*, and *Montealtosuchus*) or equal (e.g., *Mariliasuchus*, *Baurusuchus*) to 120°, while in extant crocodylians the angle is greater (e.g., up to 140° in *Caiman*) and the articular branch is posteroventrally oriented.

The condyles of the articular branch of the quadrate of *Notosuchus* extends ventrally far beyond the quadrate-quadratojugal contact, below the level of the upper toothrow, as in baurusuchids and advanced notosuchians, but different from the condition of peirosaurids and neosuchians which have condyles at the level of the toothrow. The portion of the articular branch of quadrate without the quadratojugal has a height approximately equal to its anteroposterior length (Fig. 6A). Uruguaysuchids, peirosaurids, sebecids and neosuchians, have quadrate condyles that do not extend far beyond the quadrate-cuadratojugal contact. In occipital view, the quadrate condyles extends ventrally below the level of the occipital condyle to the level of the ventral margin of the basioccipital (Fig. 6B), as all notosuchians and some neosuchians (e.g, Thalattosuchia, *Shamosuchus*); in crocodylians these condyles do not exceed ventrally the level of the occipital condyle.

The condyles of the quadrate in *Notosuchus* are elongated and well defined, being the medial condyle slightly larger than the

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lateral (they are separated by an intercondylar groove) (Fig. 6), as in advanced notosuchians (e.g., *Marialisuchus*, *Yacarerani*), and some baurusuchids (e.g., *Campinasuchus*, *Pissarrachampsa*). In *Araripesuchus*, *Baurusuchus* and *Mahajangasuchus*, the lateral condyle is slightly larger than medial. Brevirostres crocodylians (e.g., *Crocodylus, Caiman*) have well differentiated and separate condyles, being the lateral condyle larger than the medial. In *Notosuchus,* the medial condyle is ventrally projected and faces ventrolaterally, whereas the lateral condyle is more dorsally developed and faces ventrally, as all others notosuchians. Therefore, the quadrate condyles are not transversally aligned as in crocodylians (e.g., *Caiman*), but show a laterodorsal inclination forming an angle of approximately 25° with the horizontal plane.

Internally, as in *Caipirasuchus montealtensis* (Andrade and Bertini, 2008b), the articular branch of the quadrate of *Notosuchus* is highly pneumatized by the quadrate diverticulum, a branching of the pharyngotympanic system sensu Dufeau and Witmer (2015). These pneumatic recesses are observed in the broken specimens MACN-PV-RN-1037, MACN-Pv-RN-1045, MPCA-Pv-237, and MLP 64-IV-16-sn. In extant crocodylians (e.g., *Caiman*), this diverticulum is reduced (pers. obs.).

Dorsoposteriorly, the quadrate has a prominent posterolaterally projected triangular process, forming a well-developed crest that extents from the distal end of the posterolateral process of the squamosal to the medial condyle of the quadrate (Figs. 6 and 9). This crest bounds a shallow triangular concavity on the posteromedially surface of the quadrate, as in other advanced notosuchians (Pol et al., 2014). Medially to this crest, the foramen aerum is located within a groove on the posteromedial surface, near the medial condyle of the quadrate, as in most notosuchians (e.g., *Yacarerani*, *Caipirasuchus*, *Montealtosuchus*). In *Araripesuchus*, baurusuchids and *Mariliasuchus*, the foramen aerum is dorsal to the medial quadrate condyle.

On the anteroventral surface of the quadrate there is a well developed broad blunt crest (similar relative position to the crest “B” of Iordansky, 1964), which extends caudolaterally from the medial condyle to the contact between the exoccipital-opisthotic, basioccipital and quadrate, forming the ventrolateral margin of the occiput (Figs. 5B and 6B). The poorly developed crista tuberalis (formed by exoccipital-opisthotic and quadrate) and broad crista pseudo-tuberalis (only formed by quadrate, crest B = ventral crest, Andrade and Bertini, 2008b) of *Notosuchus* converge ventromedially at the level of the exoccipital-opisthotic-quadrate contact with the basioccipital, and continues up to the basal tubera. Laterally to this point, the crista pseudo-tuberalis transmitted a branch that extends anteromedially to the quadrate-pterygoid-basisphenoid contact. Similarly, broad and blunt crista pseudo-tuberalis is present in *Simosuchus*, *Comahuesuchus*, *Baurusuchus*, *Mariliasuchus*, *Sphagesaurus*, and *Caipirasuchus*; *Yacarerani* lacks this crest but has a well-developed crista tuberalis (exoccipital-opisthotic-quadrate). Peirosaurid notosuchians (e.g., *Lomasuchus*) and *Mahajangasuchus* present both well developed crests which are relatively sharp, while eusuchians have a sharp crista tuberalis, but lack a crista pseudo-tuberalis (some taxa have a sharp crest “B”, specially Crocodylia). On the contact with the quadratojugal, the quadrate of *Notosuchus* presents a tuberosity that corresponds to the distal part of the crest “A” sensu Iordansky (1964).

4.2.16. Premaxilla

The premaxilla is oriented principally vertically, with a dorsal process that contacts with the nasals (Figs. 5A, 6A and 8). It contacts the maxilla posteriorly delimiting at this level the premaxilla-maxilla foramen, where two grooves converge. On of which is disposed on the wall of the caniniform tooth and the other on the premaxilla-maxilla suture, at this level laterally presents a slight notch. Grooves and ridges ornament the dorsal half of the premaxilla.

The premaxilla presents five alveoli, the fourth for a large caniniform tooth, unlike most advanced notosuchians and baurusuchids, which present four or three alveoli (e.g., Zaher et al., 2006; Carvalho et al., 2011; Montefeltro et al., 2011; Iori et al., 2013). The caniniform alveolus of *Notosuchus* extends as tall as the dorsal process of the premaxilla forming a bulging on the dorsal surface (e.g., MPCN-PV-97). The premaxilla projects ventral and medially forming the anterior region of the secondary palate (Figs. 5B, 13).

The palatal branch of the premaxilla is transversely short and presents neurovascular foramina parallel to the alveoli. The premaxilla delimits the incisive foramen anterolaterally, which is heart-shaped, and posteriorly divided by the anterior projection of the maxillae (MPCA-Pv-237, MACN-PV-RN-1038, and MACN-PV-RN-1040; Fig. 13A). In front of the incisive foramen, the premaxillae are medially close but without forming a narrow sutural contact between them. In its anterior end the premaxillae present a slight dorsal curvature laterally (as observed in MACN-PV-RN-1040). There is no narial bar dividing the external nares, unlike to other notosuchians that present a bony bar formed by the nasals and premaxillae (e.g., peirosaurids, baurusuchids, sebecids).

In anterior view, the premaxillae delimit the lateroventral margins of the external nares. Lateral to the nares there is a smooth perinarial depression, with a tiny neurovascular foramen ventrally located. Also within the external nares and anterior to the incisive foramen, there is a small foramen (e.g., MACN-PV-RN-1040, MACN-PV-1124). Similar foramina are anteroventrally located within the external nares in extant crocodylians (e.g., *Caiman*). The perinarial depression of *Notosuchus* is oriented anteriorly and it would work as support for a soft structure (Bonaparte, 1991; Fiorelli and Calvo, 2008). A similar perinarial depression is also present in other notosuchians (e.g., Baurusuchidae, Peirosauridae, Sphagesauridae). The premaxilla-maxilla foramen and associated grooves, as well as the foramen of the perinarial depression, would be related to the narial cavernous tissue associated with the fleshy nostril, as in extant crocodylians (Witmer, 2001). In extant crocodylians, the external anterior surface of the premaxillae is covered with small neurovascular foramina for branches of the CN V_2 (Leitch and Catania, 2012), unlike the condition of *Notosuchus* which lack of these foramina.

In the palatal surface, at the premaxillar-maxillar contact and medial to the transitional tooth (postcaniniform), there is a small knob (formed by premaxilla) fits into a notch of the maxilla also in this notch fits the dentary tooth (Figs. 5B and 13). This feature was not previously reported in *Notosuchus*.

4.2.17. Maxilla

The maxilla is a vertical bone in the snout. It contacts the premaxilla anteriorly, the nasal and lacrimal dorsomedially, and the lacrimal and jugal posteriorly (Figs. 5, 6A, 8, 13 and 20). The maxilla delimits the antorbital fossa and fenestra anteriorly. The dorsal sector of its lateral surface is ornamented by shallow grooves and striations, in contrast to its ventral half that is smooth (as in the premaxilla). Also in the lateral surface, the maxilla has a pair of bulges, one anterior and other anteroventral to the antorbital fossa respectively. The anteroventral bulge is well marked and internally corresponds to a recess for the lacrimal duct. In the specimen MLP 64-IV-16-21, the cast of this recess presents thin blood vessel impressions, indicating that the soft structure that housed was irrigated.

In palatal view each maxilla projects medially (maxillary branch) contacting its counterpart, forming the anterior and

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main parts of the secondary palate and delimiting the anterior border of the maxillo-palatine fenestrae (Fig. 5B and 13). These fenestrae, recognized in *Notosuchus* by Woodward (1896), are also present in *Mariliasuchus* (Andrade and Bertini, 2008a) and *Caipirasuchus stenognathus* (Zaher et al., 2006; Pol et al., 2014), located parallel to the midline of the palate. On the lateral surface and palatal branch of the maxilla there is a series of foramina located dorsal and parallel line to the alveolar row. In extant crocodylians, these foramina are more numerous and related to the sensitive system innervated by CN V_2 (e.g., Soares, 2002; Leitch and Catania, 2012). Anteriorly in the palate, the suture with the premaxilla is anteromedially oriented (MPCA-Pv-237). The anterior ends of the maxilla palate processes converge forward in the incisive foramen. This opening is divided posteriorly by the maxillae (Fig. 13).

In the palate, the maxilla contacts posterolaterally with the ectopterygoid. There are six teeth in sub-equal sized alveoli, without complete septa and disposed in an alveolar groove (Fig. 5B). The teeth row extends no further the anterior margin of the suborbital fenestra, as in other advanced notosuchians (e.g., sphagesaurids) and baurusuchids, but unlike the condition observed in uruguaysuchids, peirosaurids and neosuchians, where it extends further than the same margin. On the internal face of the posterior process of the maxilla, and at the level with the suture with the jugal and the ectopterygoid, there is a neurovascular foramen that is also related to the CN V_2 (e.g., MACN-PV-RN-1039, MACN-PV-RN-1040, MLP 64-IV-16-15, MLP 64-IV-16-19), as observed in extant crocodylians (e.g. Iordansky, 1973; Holliday and Witmer, 2007).

4.2.18. Jugal

The jugal is a three-radiate bone, slightly ornamented with rugosities laterally. It is elongated and narrow, formed by two branches: the anterior branch (or suborbital) and the posterior branch (or infratemporal) (Fig. 4). These branches are separate by the ascending process that forms part of the postorbital bar. This ascending process is posterodorsally oriented and continued with lateral surface of the jugal as in basal crocodyliforms, *Simosuchus*, advanced notosuchians, baurusuchids, and some neosuchians (e.g., metriorhynchids) (e.g., Clark, 1994; Pol and Gasparini, 2009; Kley et al., 2010; Pol et al., 2014). Others mesoeucrocodylians (e.g., uruguaysuchids, peirosaurids, eusuchians) present an ascending process medially displaced to the lateral surface of the jugal (e.g., Iordansky, 1973; Ortega et al., 2000; Carvalho et al., 2004; Larsson and Sues, 2007).

The anterior branch of the jugal contacts the maxilla anteriorly, the lacrimal anterodorsally, and the ectopterygoid medioventrally. In *Notosuchus* as well as in others notosuchians (e.g., *Simosuchus*, *Yacarerani*, *Caipirasuchus*, baurusuchids), the jugal-ectopterygoid contact occurs in front of the postorbital bar, while in peirosaurids and Crocodylia occurs at the base of this bar. The anterior branch of the jugal of *Notosuchus* is oriented horizontally and presents a vertical lateral surface. On the ventrolateral margin of the anterior branch there are small foramina disposed in a superficial groove that correspond to the exit of branches of CN V_2; the most anterior foramen is larger and corresponds to the jugal foramen also present in sphagesaurids and other advanced notosuchians (Pol et al., 2014). A low ridge separates the vertical lateral surface of the foramina as in others advanced notosuchians (Pol et al., 2014). The end of the anterior branch reaches the level of anterior margin of the orbit and does not overpass it, as in most notosuchians but unlike neosuchians (e.g., Crocodylia) in which it extends more forward that orbital margin. The posterior branch contacts with the quadratojugal, and is dorsoventrally depressed. This branch is dorsoventrally compressed and dorsolaterally oriented. In dorsal view, the jugal describes a large curvature (Fig. 4); a similar condition is observed in *Araripesuchus* and *Mariliasuchus*.

4.2.19. Quadratojugal

The quadratojugal contacts the jugal anterolateraly, the quadrate ventral and posterodorsally, and the postorbital anterodorsally (Fig. 9). It extends as a narrow process (ascending process) along the posterodorsal margin of the infratemporal fenestra, forming its posterior margin to reach the dorsal corner of it. In the advanced notosuchian *Yacarerani*, *Mahajangasuchus*, baurusuchids, and peirosaurids, the ascending process of the quadratojugal does not reach this corner; in *Mariliasuchus*, the dorsal extension of the quadratojugal is variable (Augusta, 2013). In this point, the ascending process of the quadratojugal of *Notosuchus* contacts with the postorbital dorsally as observed in MPCA-Pv-237, a shared feature with others notosuchians (e.g., *Simosuchus*, uruguaysuchids, *Sphagesaurus*).

Adjacent to the contact with the quadrate, the dorsal end of the ascending process presents a shallow vertical groove posteriorly (MPCA-Pv-237). In the specimen MPCA-Pv-528 and MACN-PV-RN-1118 (Fig. 9), the ascending process of the quadratojugal has a vestigial quadratojugal spine in the posterior margin of the infratemporal fenestra, a character not mentioned for notosuchians but present in some neosuchians (several clades of Eusuchia; e.g., Brochu, 1999).

The quadratojugal extends ventrolaterally over the dorsal and anterior surfaces of the quadrate and does not reach the lateral lobe of the articular condyle of the quadrate, as in advanced notosuchians and baurusuchids. In most basal notosuchians, as well as in peirosaurids and sebecids, the quadratojugal reaches this lateral lobe (Pol et al., 2014). Between the jugal and the quadrate, the quadratojugal presents small rugosities as ornamentation. In the internal side of this surface it presents a small foramen that corresponds to the exit of one of the ramifications of the CN V_2, as in extant crocodylians.

4.2.20. Vomer (Prevomer)

In the specimen MACN-PV-RN-1040 the floor of the nasal cavity is exposed by fractures, allowing the observation of the posterior half of the vomer (Fig. 20). It is a laminar and long bone, particularly wide lateromedially at the level of the contact with its counterpart in the midline. This morphology has not been described in other mesoeucrocodyians where generally it is a delicate bone, lateromedially narrow, and restricted to the midline (Witmer, 1995).

The vomer extends from its contact with the palatine and the palatal process (= anterior) of the pterygoid (where its narrow) forward contacting mainly with the maxilla and its counterpart. It forms the floor of the nasal cavity, and together with the anterior process of the pterygoid covers dorsally the maxilla-palatine fenestrae of the palate. In the midline there is a groove (= sulcus septalis) for the cartilaginous internasal septum as in extant crocodylians (Witmer, 1995). This sulcus septalis extends forward from the anterior process of the pteygoid. The vomer in *Notosuchus* does not have a palatal exposure as the present in the basal notosuchian *Simosuchus* and other derived mesoeucrocodylians (e.g., *Tomistoma* and *Melanosuchus*) (Kley et al., 2010).

4.2.21. Palatine

The palatine is a triradiate bone restricted to the mid-central part of the secondary palate (Fig. 13). It contacts the maxilla anterolaterally, the ectopterygoid posterolaterally and the pterygoid posteromedially. Both palatines form the posterior and part of the medial margins of the maxillo-palatine fenestrae anteriorly. The anterior ends of the palatines, together with the palatal process of the maxilla, form a narrow septum that separates the maxillo-

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palatine fenestrae; the palatines have larger contribution in the formation of the septum. In the closely related *Mariliasuchus*, the septum that separates the maxillo-palatine is wider than in *Notosuchus*.

Posteriorly the palatines form the anterolateral margin of the internal choanae. The palatines and the pterygoids form the choanal septum; the participation of the palatines to that septum is minimum. Posterolaterally the palatines are narrow and divergent, projecting a barlike process (palatine bar) that contacts the ectopterygoids. The palatine bars are also present in *Comahuesuchus*, most advanced notosuchians (e.g., *Mariliasuchus*, *Yacarerani*, *Caipirasuchus*), and baurusuchids. In *Comahuesuchus*, *Mariliasuchus*, *Yacarerani*, and *Caipirasuchus*, the palatine bars stand posteriorly to the suborbital fenestrae, whereas in *Notosuchus* and bauruschids these bars are much shorter contacting an anteromedially directed process of the ectopterygoid at the level of the suborbital fenestrae. The anteromedial process of the ectopterygoid contributes to the palatine bar in *Notosuchus* and baurusuchids; in *Comahuesuchus* and most advanced notosuchians, the ectopterygoid does not contribute to this bar. The lateral borders of the palatine form the median margin of the elongated suborbital fenestrae.

The palatine processes form a septum with the maxilla that separates the maxillo-palatine fenestrae, a bar with the maxilla that separates the suborbital fenestra from the maxillo-palatine fenestra, a bar with the ectopterygoid that separates the suborbital fenestra from the choana, and a septum with the ptergyoid that separates the choanae. The main body of the palatines separates the suborbital fenestrae. This palatine morphology is similar in *Mariliasuchus* (Zaher et al., 2006).

4.2.22. Pterygoid

The pterygoid contacts the palatine anteriorly, the ectopterygoid laterally, the basisphenoid posteriorly, and the quadrate and laterosphenoid posterodorsally. It probably contacts the prootic posterodorsally within the trigeminal fossa (Figs. 5B and 13). In *Notosuchus*, the pterygoids are completely fused as in other notosuchians. In extant crocodylians, the interpterygoid suture persists anterior to the choanae (Iordansky, 1973). The pterygoids are wide bones delimiting the choanae posteriorly and medially, and forming – together with the palatines-the choanal septum (Fig. 13).

Within the interorbital space, each pterygoid extends dorsomedially and converge at the midline to form a longitudinal crest (e.g., MLP 64-IV-16-5, MLP 64-IV-16-10, MACN-PV-RN-1039, MUCPv-147) (Figs. 6A and 17). Posterodorsally, the posterior ascending process of the pterygoids form a conspicuous neck linking the palate with the braincase; to this level, the bone is pneumatized internally as seen in specimen MACN-PV-RN-1039, probably by the pterygoid diverticulum as in extant crocodylians (Dufeau and Witmer, 2015).

On the ventrolateral surface of the braincase, the left and right posterior ascending processes are separated. At this level, the pterygoid contacts with the lateral bridge of the laterosphenoid (trough a broad sutural contact), the quadrate, and the prootic (presumably), forming the ventral margin of the trigeminal fossa (foV) (Fig. 17). The pterygoid wings are narrow anteroposteriorly and do not participate on the border of the suborbital fenestra, which is delimited by the ectopterygoid, the palatine and the maxilla, as in advanced notosuchians, *Comahuesuchus*, and baurusuchids. In uruguaysuchids, *Simosuchus*, *Mahanjangasuchus*, peirosaurids and neosuchians, the pterygoid participates on the border of the suborbital fenestra (e.g., Martinelli, 2003; Andrade et al., 2006), and the pterygoid wings are wide anteroposteriorly (except in *Simosuchus* and *Mahajangasuchus*, which have pterygoid wings narrower than *Notosuchus*).

In the dorsal surface of the lateral edge of the ptergyoid wings there is a semicircular mark, porous in texture probably related to the contact with the cartilago transiliens (Schumacher, 1973), associated to the adductor musculature (see Holliday and Witmer, 2007). The posterior end of the ptergyoid wing extends caudally towards the level of the postorbital bar, as in other notosuchians (uruguaysuchids, baurusuchids, peirosaurids, sphagesaurids); except *Simosuchus*. In neosuchians (e.g., Crocodylia), the posterior end of the pterygoid extends to the level of the posterior margin of the infratemporal fenestra. The lateral edge of the pterygoid wings (torus transiliens, sensu Hua and Jouve, 2004), is dorsoventrally tall (as in all Mesoeucrocodylia), although relatively short anteroposteriorly.

Dorsally to the choanae, the pterygoid projects a trough-shaped process (anterior branch) that extends anteriorly forming the choanal groove, and more anteriorlythe roof of the nasopharyngeal duct. The anterior branch of the pterygoid is an elongated pointed process wedged between the vomers, extended forward beyond the level prefrontal pillars (Fig. 20); unlike the condition exhibited by the eusuchian *Caiman* where this end of the pterygoid contacts with the vomer anteriorly and the palatine laterally. At this level the anterior branch of the pterygoid is trough-shaped (= sulcus septalis) for cartilaginous internasalis septum as extant crocodylians (Witmer, 1995).

Within the choanal groove the pterygoid bears a sagittaly oriented choanal septum that is relatively narrow, as in *Mariliasuchus*, but differing from the relatively broad septum of *Caipirasuchus*. In the anterolateral portion of the pterygoid, *Notosuchus* present a choanal fenestra on both sides of the choanal groove (Fig. 13). Ventrally, this fenestra is bounded by the palatine anteriorly, the ectopterygoid laterally, and the pterygoid. The same configuration is observed in the bauruschid *Pissarrachampsa sera*, differing from the condition of both *Mariliasuchus* and *Caipirasuchus* where the ectopterygoid is excluded from the margin of the choanal fenestra. Posterior to the choana, *Notosuchus* lacks of pterygoid chamber present in the closely related *Caipirasuchus montealtensis* (Iori et al., 2013).

4.2.23. Ectopterygoid

The ectoptergyoid is a trirradiate bone formed by an anterodorsal, ventral and medial processes (Fig. 5B and 13). The anterodorsal process contacts the maxilla anterolaterally and the jugal laterally. It is directed forward without contacting the postorbital bar, as in most advanced notosuchians and baurusuchids, but unlike the condition exhibited by peirosaurids and crocodylians (where the ectopterygoid contact the base of the postorbital bar).

The anterodorsal process of the ectopterygoid of *Notosuchus* does not reach the last maxillary alveolus. Unlikely, this contact is found in most advanced notosuchians (e.g., *Yacarerani*, *Caipirasuchus*), and even in the peirosaurid *Montealtosuchus*. The ventral process is lanceolated and overlaps the ventral surface of the anterolateral corner of the ptergyoid wing. The medial process contacts with the palatine forming a bar, and the posterior margin of the suborbital fenestra. The ectopterygoid excludes the ptergyoid from the margin of this fenestra. The ectopterygoid-palatine bar separates the choana from the suborbital fenestra. Therefore, the ectoptergyoids contribute laterally in the margin of the choanae as in baurusuchids.

In the studied specimens the anterior process of the ectoptergyoid does not reaches the palatine, as is observed in other advanced notosuchians such as *Yacarerani* and *Mariliasuchus*. An ectopterygoid-palatine contact that excludes the pterygoid from the suborbital fenestra is also present in other notosuchians (e.g., *Comahuesuchus*, advanced notosuchians, and baurusuchids), differing from the condition observed in basal notosuchians (e.g.,

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Simosuchus, uruguaysuchids and peirosaurids) and neosuchians (e.g., Crocodylia).

4.2.24. Dentary

The dentary is an elongated bone contacting the surangular posterodorsally, the angular posteroventrally, the splenial medially and its counterpart anteromedially through a long symphysis that extends forward from the 6°–7° alveoli (Figs. 7 and 14). In the symphyseal region, anteriorly the dentaries narrow dorsoventrally and mediolaterally. Dorsally, there is a concavity along midline, and this region is U-shaped in cross-section (e.g., MACN-PV-RN-1127, MLP 64-IV-16-5, MCF-PVPH-710) (Fig. 14B). A similar condition observed in *Araripesuchus*, *Uruguaysuchus*, *Baurusuchus*, and *Mariliasuchus*; whereas the sphagesaurids notosuchians *Sphagesaurus*, *Armadillosuchus*, *Caipirasuchus* and *Yacarerani* lack this concavity. In the ventral surface of the symphysial region, the dentaries have a shallow groove disposed along midline (MACN-PV-RN-1037, MACN-PV-RN-1040, MACN-PV-RN-1041, MPCA Pv-791, MUCPv-147, MLP 64-IV-16-11, MLP 64-IV-16-23); *Araripesuchus buitreraensis* and *Caipirasuchus stenognathus* present a similar groove but is less marked.

Posteriorly the dentary forms the anterior and anterodorsal margin of the external mandibular fenestra. The external mandibular fenestra is large, anteroposteriorly elongated, and subrectangular in shape; whereas in *Baurusuchus*, sphagesaurids and basal notosuchians (e.g., *Uruguaysuchus*, *Araripesuchus*, *Simosuchus*), the contour of the fenestra is oval. This fenestra is delimited by the angular ventrally, the dentary anterodorsally, the surangular dorsally and posteriorly by the surangular dorsally and angular ventrally (Fig. 7B).

The posterodorsal branch of the dentary overlies the anterior branch of the surangular, having a broad U-shaped concavity in cross-section. In the most mesoeucrocodylians, the posterodorsal branch of the dentary underlies the anterior branch of the surangular. Posteroventrally, the dentary-angular contact runs posterolaterally on the ventral surface of the mandibular ramus and turns dorsally on its lateral surface, at the level behind the anterior margin of the external mandibular fenestra. Here the dentary projects as a short triangular posteroventral process, as in uruguaysuchids, peirosaurids and no-longirrostrine neosuchians. While, in other notosuchians (e.g., *Simosuchus*, baurusuchids, sphagesaurids), the dentary is not projected posteriorly along the ventral margin of the external mandibular fenestra.

The ventral surface of the dentary is ornamented by thin grooves separated by shallow ridges, mainly in the anterior portion. The anterior portion of the dentary, above the ornamentated area and ventral to the alveolar margin, bears a smooth semicircular depression (e.g., MACN-PV-RN-1037, MACN-PV-RN-1038, MACN-PV-RN-1045, MACN-PV-RN-1127, MLP 64-IV-16-5, MPCA-Pv-528). A broad ridge extended from the first alveolous to the last alveoli separates the smooth and the ornamented areas. Within the smooth depression, and parallel to the ridge, there is a series of neurovascular foramina (up to eight foramina), probably related with sensitive structures associated to CN V$_3$ as occurs in extant crocodylians (but these foramina are more numerous) (e.g., Soares, 2002; Leitch and Catania, 2012). In *Notosuchus* these foramina particularly decrease in size anteriorly (e.g., MACN-PV-RN-1127, MUCPv-147). A similar condition is observed in advanced notosuchians (e.g., *Yacarerani*, *Mariliasuchus*, *Caipirasuchus*), as well as in the basal notosuchian *Comahuesuchus*. In *Yacarerani* the anterior foramen is larger. In extant crocodylians (e.g., *Caiman*, *Crocodylus*, *Gavialis*), external surface of the anterior end of the dentary bears numerous small foramina for CN V$_3$. The external posterolateral surface of the dentary of *Notosuchus* is unornamented.

The dentaries present ten alveoli, being the last ones confluent. There are three complete alveoli located in the symphyseal region; from 4° to, 7° the alveoli are confluent, and backward the 7° alveolous the dentary teeth are implanted in an alveolar groove (e.g., MLP 64-IV-16-5) (Fig. 7A). The alveoli are aligned in dorsal view in an angle of 25° respect the symphyseal plane. The alveolar margin describes a single wave well marked laterally, whereas in dorsal view the lateral margin of the dentaries is curved (Fig. 7). Laterally, the first four alveolar margins are festooned. At the level of the posterior teeth, the dentary develops a lateral horizontal surface, forming ashelf that widens posteriorly (e.g., MACN-PV-RN-1127, MLP 64-IV-16-5, MCF-PVPH-710), as in other advanced notosuchians but unlike the condition in uruguaysuchids, peirosaurids, baurusuchids, sebecids and neosuchians (e.g., crocodylians) where the dentary is lateromedially narrow posteriorly.

4.2.25. Splenial

The splenials are laminar bones, dorsoventrally tall that cover the medial surface of the mandibular rami, and forms part of the mandibular symphysis extending anteriorly to the level of the 4°–5° dentary alveoli (Figs. 7A and 14). The splenial contacts with the dentary laterally and its counterpart anteromedially forming the splenial symphysis, the surangular posterodorsally and the angular posteroventrally (below the adductor mandibular fossa) (Fig. 21).

The anterior end of the splenial is convex in dorsal and ventral views; thus the splenial-dentary suture is a curved line as in *Uruguaysuchus*, not tapered as in other notosuchians (e.g., peirosaurids). In *Notosuchus* the ventral exposition of the splenial in the symphyseal region is reduced (approximately the 15% of the symphyseal length or less), as in *Comahuesuchus* and sphagesaurids, but unlike the condition observed in *Araripesuchus buitreraensis*, peirosaurids (e.g., *Montealtosuchus*, *Uberabasuchus*) and baurusuchids (*Baurusuchus*, *Campinasuchus*) (approximately the 30% of the symphyseal length).

Posteriorly the splenials delimit the anterior margin of the adductor mandibular fossa, which has subrectangular shape (Fig. 21). This fossa is delimited by the angular ventrally, the dentary and splenial anteriorly, the surangular dorsally and the articular posteriorly. As in all notosuchians there is no coronoid bone delimiting the fossa anteriorly, as occurs in Neosuchia (e.g., Crocodylia).

The splenial forms the medial wall of the alveolar groove posteriorly, together with the dentary. In its medial face, the single foramen intermandibularis oralis is exposed in a central position, at the level of the last dentary tooth (e.g., MLP 64-IV-16-5, MLP 64-IV-16-20, MACN-PV-RN-1037, MACN-PV-RN-1045). This foramen is oval, relatively small, and located in a central position (Fig. 14). In extant crocodylians this foramen is markedly smaller. The position of this foramen on the medial face of the splenial is variable within Notosuchia; in basal notosuchians (e.g., *Simosuchus*, uruguaysuchids), peirosaurids and baurusuchids it has an anterior position adjacent to the symphysis, whereas in advanced notosuchians it has a central position (e.g., *Mariliasuchus* and *Yacarerani*).

As all other observed notosuchian, the posterior margin of the splenial of *Notosuchus* is smoothly concave, has no notches for the intermandibularis caudalis nor intermandibularis medius foramina. These foramina are present in Crocodylia for branches of the CN V$_3$, and posteriorly delimited by the coronoid and angular, respectively (Iordansky, 1963; Schumacher, 1973). The posterior margin of the splenial of *Notosuchus* curves near the suture with the angular, anteriorly to the adductor mandibular fossa. This curvature would correspond to the groove left by the Ramus intermandibularis caudalis (a branch of the CN V$_3$) that would exit directly from the adductor mandibular fossa as was suggested also

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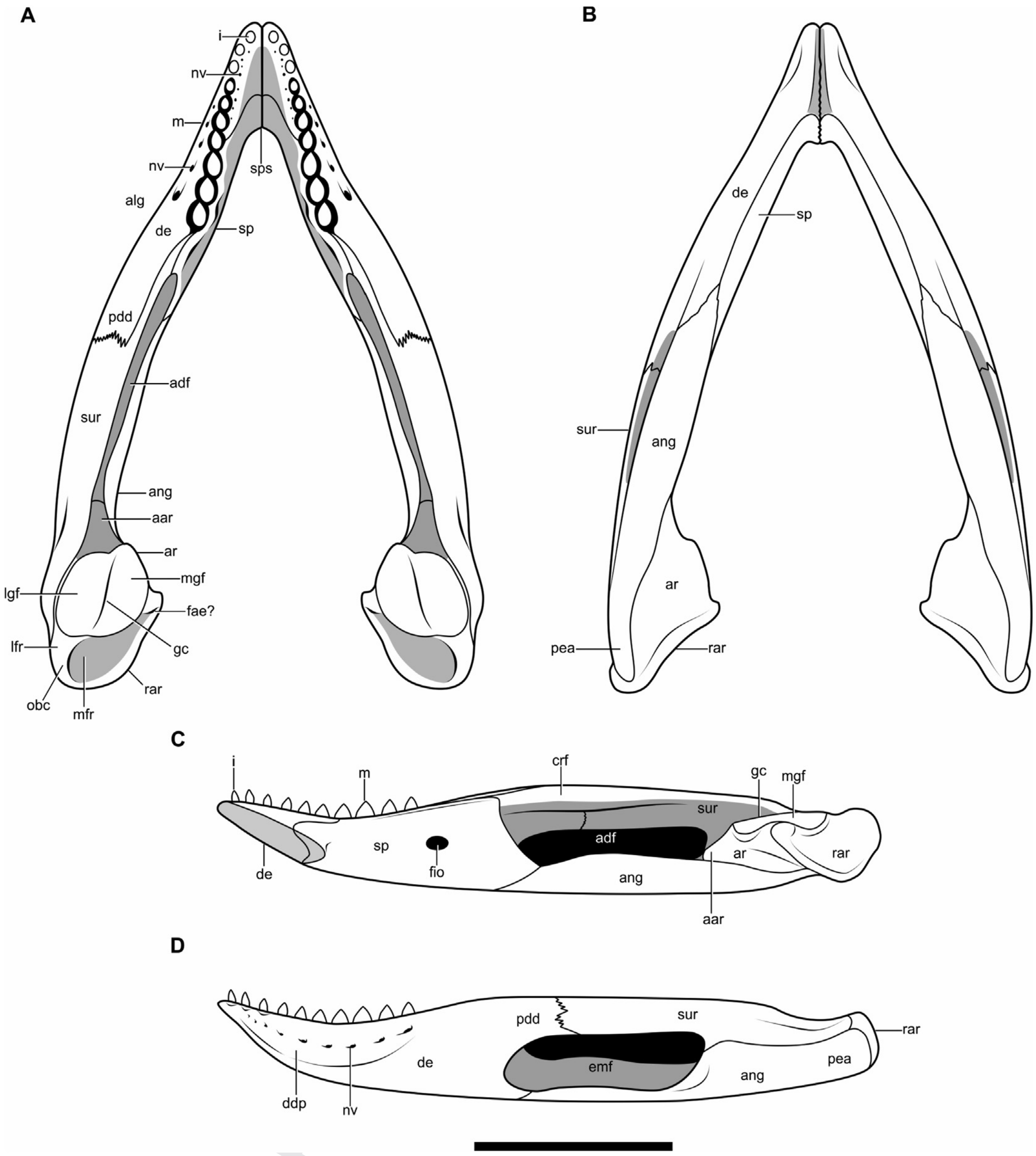

Fig. 21. Reconstruction of the mandible of *Notosuchus terrestris*. **A**, dorsal, **B**, ventral, **C**, medial, and **D**, lateral views. Scale bar equals 5 cm.

for the advanced notosuchians *Caipirasuchus stenognathus* (Pol et al., 2014).

On the ventral surface of the mandibular symphysis, there is a large peg, a feature also present in basal notosuchians (e.g., *Uruguaysuchus* and *Araripesuchus buitreraensis*), but unlike the smaller peg located on the posterior surface of the mandibular symphysis of *Comahuesuchus*, sphagesaurids and baurusuchids (Pol et al., 2014).

4.2.26. Surangular

The surangular is an anteroposteriorly elongated bone that contacts with the dentary anteriorly, the splenial medially, the articular posteromedially and the angular ventrally (Figs. 7 and 14). The surangular-dentary contact occurs above the external mandibular fenestra, which posterodorsal margin is formed by the surangular. Posterior to this fenestra the surangular-angular contact is a subhorizontal anteroposterior suture.

The surangular does not reaches the distal end of the retroarticular process, but forms the lateral margin of the articular glenoid fossa where there is a lateral ridge oriented anteroposteriorly. At this level, the posterior end of the surangular narrows gradually backwards ending in a blunt tip (MPCA-Pv-528, MACN-PV-RN-1037), as in notosuchians that have preserved this region except *Yacarerani*, in which the posterior end of the surangular is dorsoventrally twice as high at the anterior end. In neosuchians (e.g., Crocodylia) the posterior end is pointed.

In dorsal view, the anterior branch of the surangular underlies the posterodorsal branch of the dentary and wedges between it and the splenial. Superficially, it extends forward reaching the alveolar groove (Fig. 7A). This morphology is also observed in other notosuchians as *Simosuchus*, *Uruguaysuchus*, sphagesaurids (e.g., *Yacarerani*, *Caipirasuchus*), and *Baurusuchus*. Unlikely, *Mariliasuchus* and peirosaurids (e.g., *Lomasuchus*, *Montealtosuchus*) have an anterior branch of the surangular that overlies the posterodorsal branch of the dentary, as in crocodylians. The anterior branch of the surangular has not dorsal and ventral processes, as those observed in baurusuchids, peirosaurids, and crocodylians. In cross-section, the anterior branch of the surangular of *Notosuchus* is a broad

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inverted U-shaped concavity along its total length; whereas in *Baurusuchus*, peirosaurids and crocodylians this branch is lateromedially narrow bar.

The anterior branch of the surangular, together with the posterodorsal branch of the dentary, forms a longitudinal bridge lateromedially wide above the external mandibular fenestra. This bridge is an inverted U in cross-section and is dorsally convex for the insertion of the M. adductor mandibulae externus superficialis (Cleuren and De Vree, 2000). In the dorsal surface of the anterior branch of the surangular of *Notosuchus* there are no neurovascular foramina for CN V$_3$. These foramina are present in most notosuchians (e.g., *Simosuchus*, *Uruguaysuchus*, *Mariliasuchus*, *Caipirasuchusstenognathus*, peirosaurids, baurusuchids), and crocodylians; whereas in *Yacarerani* and *Caipirasuchus montealtensis*, there is a single foramen near to the splenial-dentary suture. Medially, the surangular presents a lingual foramen near of the contact with the articular (e.g., MCF-PVPH-710), as observed in *Mariliasuchus* and *Yacarerani*.

Like in other notosuchians (e.g., *Simosuchus*, *Mariliasuchus*, *Caipirasuchus*, *Yacarerani*, *Baurusuchus*, *Montealtosuchus*, *Uruguaysuchus*), the medial surface of the anterior branch of the surangular of *Notosuchus* has a large longitudinal facet (tuberosities sensu Pol et al., 2014) (Fig. 14A). In extant crocodylians, the contact with the posterodorsal process of the coronoid is within this facet and overlies the transiliens cartilage (Iordansky, 1973).

4.2.27. Angular

The angular is an elongate bone that extends anteroposteriorly forming the posteroventral angle of the mandibule, which is obtuse or subhorizontal (15°) (Fig. 7B). The angular contacts with the dentary anterolaterally, the splenial anteromedially, the surangular posterodorsally, and the articular posteromedially. The anterior end of the angular is U-shaped in cross-section forming the floor of the adductor mandibular fossa (Fig. 7A). The angular projects backwards further the surangular but does not reaches the distal end of the retroarticular process (e.g., MACN-PV-RN-1037, MPCA-Pv-528).

Anteriorly, the medial wall of the angular is dorsoventrally tall and contacts with the splenial in the anteroventral margin of the adductor mandibular fossa. Laterally, the angular form the ventral margin of the external mandibular fenestra. At this level, the angular has a smooth shallow fossa and its ventral margin is a laterally projected ridge, as in *Baurusuchus* and advanced notosuchians. In uruguaysuchids, peirosaurids, sebecids, *Mahajangasuchus*, and Crocodylia, the angular has a relatively tall and sharp ridge that form the ventral margin of the external mandibular fenestra.

The smooth surface within the posteroventral margin of the external mandibular fenestra in extant crocodylians serves as area of insertion for the lateral portion of the M. pterygoideus posterior (Iordansky, 1964; Schumacher, 1973; Holliday and Witmer, 2007); the fossa and ridge additional in this mandibular region of *Notosuchus* serves as increased insertion area for this adductor musculature. In addition, the ventral margin of the adductor mandibular fossa of *Notosuchus* has a vertically projected ridge (Fig. 7A). These lateral and vertical ridges delimit the groove that forms the floor of the fossa; the medial ridge is taller than the lateral.

Laterally, the posterior end of the angular is laminar, vertically and dorsoventrally tall (e.g., MPCA-Pv-528, MACN-PV-RN-1037) (Fig. 14C); a similar condition observed in *Mariliasuchus* and *Baurusuchus*, unlike some advanced notosuchians. In *Caipirasuchus* and *Yacarerani*, the posterior end of the angular is laminar but subhorizontally arranged. Ventrally the angular is wedged between the dentary and the splenial. In the specimen MLP 64-IV-16-5, there is a small neurovascular foramen on the floor of the adductor mandibular fossa, related to the branch of CN V$_3$ as in extant crocodylians; this foramen also is present in other notosuchians.

4.2.28. Articular

The articular is a roughly triangular bone that contacts the angular ventrolaterally and the surangular laterally (Figs. 7 and 14). It presents and anterior process, a glenoid region and a retroarticular process. The anterior process is short, triangular and anteroventrally oriented. A short anterior process is present in *Simosuchus* and advanced notosuchians (e.g., *Yacarerani*, *Caipirasuchus*), whereas in peirosaurids and *Baurusuchus* it is elongated as in crocodylians. The dorsal surface of the anterior process in *Notosuchus* is slightly concave and delimited medially by a longitudinal ridge that extent from the anteromedial margin of the medial glenoid facet, and serves as area of insertion of the M. adductor mandibulae posterior as in extant crocodylians (Schumacher, 1973). The anterior process of the articular in *Notosuchus* extents to the level of the posterior margin of the external mandibular fenestra (Fig. 14).

The glenoid region of the articular is oval in outline, laterally delimited by the surangular, and has two distinct facets for the medial and lateral condyles of the quadrate (Figs. 7A and 14D). A longitudinal crest with a slight anteromedial inclination separates both facets. This lateral and medial facets of the articular are anteroposteriorly elongated, being approximately twice as large as the condyles of the quadrate. A similar morphology of the glenoid region of the articular shared with other advanced notosuchians (e.g., *Mariliasuchus* and *Yacarerani*), for a propalinal movement of mandibular occlusion (Ösi, 2013 and references therein). Q10 The glenoid region of baurusuchids, peirosaurids, sebecids, *Uruguaysuchus*, and crocodylians is kidney shaped and relatively narrower than in advanced notosuchians, are at the most 50% longer than the articular surface of the quadrate condyles (Pol et al., 2014).

The glenoid facets in *Notosuchus* are unequal being the medial slightly longer. In dorsal view, the lateral facet is slightly dorsolateraly oriented whereas the medial facet is dorsomedially inclined. The posterior margin of the medial facet is separated from the medial flange of the retroarticular process, while the lateral facet is continuous with the dorsal surface of the anterior articular process (anteriorly) and the lateral flange of the retroarticular process (posteriorly); a feature shared with *Simosuchus* and advanced notosuchians (e.g., *Mariliasuchus*, *Yacarerani* and *Caipirasuchus*). As in the basal notosuchians (e.g., *Simosuchus* and *Uruguaysuchus*), and other advanced notosuchians, the lateral and medial glenoid facets of *Notosuchus* lack an elevated posterior buttress, which is present in peirosaurids, baurusuchids, sebecids and crocodylian neosuchians.

The retroarticular process is relatively short, broad, medially round and has a concave surface that projects posteroventrally from the glenoid region and faces dorsomedially, almost vertically (Figs. 7A and 14). A similar disposition of the retroarticular process observed in other notosuchians (e.g., *Uruguaysuchus*, *Simosuchus*, sphagesaurids, baurusuchids and peirosaurids), while in Crocodylia this process projects posteriorly and faces slightly dorsomedially. This concave surface of the retroarticular process serves for the insertion of the M. depressor mandibulae in extant crocodylians (Iordansky, 1964; Cleuren and De Vree, 2000). However, the morphology of the retroarticular process is variable within Notosuchia (e.g., the retroarticular process is markedly anteroposteriorly short and small in *Yacarerani*, has a robust ventral projection in baurusuchids, with strong dorsal curvature in peirosaurids, is anteroposteriorly short and robust in *Simosuchus*). In crocodylians, the retroarticular process is relatively anteroposteriorly elongated.

Dorsally, the anteroposterior length of the retroarticular process of *Notosuchus* is lesser than the anteroposterior length of the

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glenoid facets, as most the notosuchians (e.g., *Simosuchus*, baurusuchids and advanced notosuchians); in peirosaurids, sebecids and neosuchians, the anteroposterior length of the retroarticular process is greater than the the anteroposterior length of the glenoid facet of the articular. The posterior end of the retroarticular of *Notosuchus* is oriented posteriorly as in most notosuchians (sphagesaurids, baurusuchids) and some crocodylians (e.g., *Caiman*), and not dorsally as in sebecids, peirosaurid and long-snouted crocodylians (e.g., *Tomistoma* and *Gavialis*).

The retroarticular process of *Notosuchus* is divided by an oblique crest that extends posterolaterally from the posterior end of the longitudinal crest (that separates the lateral and medial glenoid facets of the articular) to a rugose bulge of its posterolateral corner. This oblique crest separates the retroarticular process in lateral and medial flanges; as in most the notosuchians (e.g., *Simosuchus*, *Mariliasuchus*, *Caipirasuchus*, and *Baurusuchus*). In peirosaurids, sebecids and crocodylians the crest on retroarticular process is anteroposteriorly oriented, and laterally has some contribution of the surangular.

The lateral flange of the retroarticular process of *Notosuchus* is anteroposteriorly short, triangular shaped with its apex pointing posteriorly, and faces dorsally. This flange extends posteriorly from the lateral glenoid facet to the bulge of the posterolateral corner of the retroarticular process. The dorsal surface of the lateral flange is slightly concave and its posterior apex slightly elevates dorsally at the level of the bulge. The medial flange is wider than the lateral flange, forms a markedly concave paddle-shaped lamina with its medial margin recurved, and faces posteromedially and slightly dorsally; as in all known notosuchians (Pol et al., 2014).

The posterior margin of the medial flange of the retroarticular process of *Notosuchus* runs ventromedially from the bulge of the posterior end of the lateral flange to the level of the posterior margin of the glenoid facet. From this level it turns anterodorsally forming an extensive arch and ending in a small rugose bulge (a structure not observed in other notosuchians) at the anteroposterior midpoint of medial margin of the glenoid facet. The anteromedial margin of the medial flange of the retroarticular process lack of a distinct anterior process. This anterior process is present in others advanced notosuchians (e.g., *Mariliasuchus* and *Caipirasuchus*).

The foramen aerum is not present in any studied specimen. However, in the specimen MACN-PV-RN-1037 there is a groove infilled with sediment between the posteromedial margin of the medial glenoid facet and anterodorsal margin of the medial flange of the retroarticular process. Within that groove probably opens foramen aerum, in a similar position to the observed in the closely related *Yacarerani*.

5. Final remarks

Previously to this study, the skull morphology of *Notosuchus terrestris* was known from relatively fragmentary materials and its cranial morphological variation has not been fully described (Woodward, 1896; Gasparini, 1971; Bonaparte, 1991; Fiorelli and Calvo, 2008; Andrade and Bertini, 2008a). Within the Cretaceous Notosuchia, detailed descriptions of the skull morphology were made for *Simosuchus*, *Araripesuchus*, *Anatosuchus*, *Hamadasuchus*, *Mahajangasuchus*, *Kaprosuchus*, *Pissarrachampsa*, *Campinasuchus*, *Mariliasuchus*, and *Caipirasuchus* (Turner, 2006; Zaher et al., 2006; Larsson and Sues, 2007; Sereno and Larsson, 2009; Kley et al., 2010; Carvalho et al., 2011; Montefeltro et al., 2011; Pol et al., 2014). Particularly, detailed and fully descriptions of the notosuchian braincase and its neurovascular foramina are scarce, known only for *Simosuchus*, *Araripesuchus*, *Hamadasuchus*, and *Rukwasuchus* (Turner, 2006; Holliday and Witmer, 2009; Sertich and O'Connor, 2014).

Characters here described by the first time for *Notosuchus terrestris* include: crista cranii frontalis poorly developed, frontal with olfactory tract groove posteriorly convex and well marked depression for the olfactory bulbs, prefrontal pillars lateromedially wide and laminar, palatines that form most of the bar between the maxillo-palatine fenestra, metotic foramen and carotid foramen open together within a deep fossa lateral to the occipital condyle, relatively broad postorbital-quadratojugal contact near the dorsal corner of the infratemporal fenestra, ascending process of the quadratojugal with posterior groove and parallel to the quadratojugal-quadrate suture, vestigial quadratojugal spine, heart-shaped incisive foramen delimited by the premaxillae anterolaterally and the maxillae posteriorly, small premaxillary knob fits in a maxillary notch in the palate adjacent to the toothrow, choanal septum relatively narrow and formed mainly by pterygoid, choana with choanal groove and choanal fenestra, symphsyseal región in U-shaped cross-section and sagittal groove on its ventral surface, osteoderms on the squamosal affected by temporo-orbital vein grooves, temporo-orbital foramen enclosed by squamosal facing dorsally, post-temporal fenestra dorsoventrally compressed at the level of the posterior margin of the skull table, the exoccipital forming most of the post-occipital processes, crista tuberalis poorly developed and excluded from the ventrolateral margin of the occiput, presence of a broad and blunt crista pseudo-tuberalis formed by quadrate, laterosphenoid without caudal bridge but with shallow groove for the CN V_{so}, small bilobate trigeminal fossa with grooves for CN V_2 and CN V_3, robust lateral bridge of the laterosphenoid for CN V_1 with relatively broad sutural contact with pterygoid, foramen for the CN V_1 is relatively small and oval, articular branch of the quadrate extends ventrally beyond the contact with the quadratojugal and is positioned below of the toothrow, braincase bones (parietal, laterosphenoid, quadrate, basioccipital) highly pneumatic, vomer lateromedially broad and forming most of the floor of the nasal cavity, anterior process of the pterygoid elongated wedged between vomers and extending forward beyond the prefrontal pillars, posterior end of the angular dorsoventrally broad and vertical, surangular with coronoid tuberosity, the surangular anterior branch reaches the alveolar groove, foramen intermandibularis oralis oval and located centrally in the splenial lamina, lingual foramen adjacent to the surangular-articular suture, quadrate with foramen aerum into shallow groove and dorsomedially located to the medial condyle, articular foramen aerum located ventral to the medial margin of the glenoid facet, and retroarticular process relatively short facing dorsomedially with posterior end directed posteriorly. Although most of these characters were at least mentioned (and/or scored in phylogenetic analyzes) in the literature (e.g., Gasparini, 1971; Bonaparte, 1991; Andrade et al., 2006; Turner, 2006; Fiorelli and Calvo, 2008; Andrade and Bertini, 2008a,b; Holliday and Witmer, 2009; Kley et al., 2010; Turner and Sertich, 2010; Montefeltro et al., 2011; Ösi, 2013; Pol et al., 2014; Sertich and O'Connor, 2014), some of they were not described for any other notosuchians (e.g., crista cranii frontalis poorly developed, frontal with olfactory tract groove convex posteriorly and with well marked furrows for laterosphenoid, small bilobate trigeminal fossa with grooves for the branches of the CN V_{so}, CN V_2 and CN V_3, parietal and laterosphenoid highly pneumatic, post-temporal fenestrae obliterated, small premaxillary knob fits a maxillary notch in the palate adjacent to the toothrow, incisive foramen in heart-shaped delimited by premaxillae and maxillae, vomer lateromedially broad, choana with narrow pterygoid septum, ascending process of quadratojugal with groove adjacent and parallel to quadratojugal-quadrate suture, vestigial quadratojugal spine), and should regarded as autapomorphies of *N. terrestris*. The impact of these new characters on the

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phylogenetic relationships of *N. terrestris* and amongst other notosuchians have to be tested in further studies. Final comments on possible autapomorphies of *N. terrestris*, and the identification of internal carotid artery entrance foramen in notosuchians are discussed below.

5.1. *Quadratojugal spine and vertical groove (Fig. 9D)*

A quadratojugal spine in the posterior margin of the infratemporal fenestra is present in several neosuchians (e.g., *Goniopholis*, *Shamosuchus*, Eusuchia), is very developed in long-snouted taxa (e.g. *Gavialis*, *Tomistoma*), and is reduced or absent in some crocodylians (e.g., Alligatoroidea, *Osteolaemus*) (Kälin, 1933; Iordansky, 1973; Norell, 1989; Brochu, 1999; Larsson and Sues, 2007; Pol et al., 2009; Andrade et al., 2011). Nevertheless it presence was never reported in any notosuchian and phylogenetic analyzes this feature was always scored as absent in non-neosuchian crocodyliforms (e.g., Pol et al., 2014). Instead, most notosuchians have a relatively straight or slightly concave posterior margin of the infratemporal fenestra (e.g., *Montealtosuchus arrudacamposi*, *Simosuchus clarki*, *Araripesuchus patagonicus*), or slight convexity or bump in that margin (e.g., *Mariliasuchus amarali, Araripesuchus wegeneri, Libycosuchus brevirostris,* baurusuchids). This last condition as in some basal crocodyliforms (e.g., *Protosuchus richardsoni*) (e.g., Norell, 1989).

Surprisingly, in one of the all specimens of *Notosuchus* here study (MPCA-Pv-528), a vestigial quadratojugal spine was observed, with similar morphology to that of some alligatoroids (e.g., *Leidyosuchus*, *Diplocynodon*, *Caiman*) (Kälin, 1933; Norell, 1989; Brochu, 1999; Wu et al., 2001). The feature here described of a vestigial quadratojugal spine present in *Notosuchus* has phylogenetic and probably morphofunctional implications. The quadratojugal spine is related to the M. levator bulbi (e.g., Larsson and Sues, 2007), but its functional implications is beyond the scope of work. Finally, an ascending process of the quadratojugal with groove adjacent and parallel to the quadratojugal-quadrate suture as observed in *Notosuchus* (MPCA-Pv-237), was also not reported for notosuchians.

5.2. *Trigeminal fossa (Fig. 17)*

The trigeminal fossa and the passages for the CN V branches (V$_{so}$, V$_1$, V$_2$, and V$_3$) exhibit marked variation in size and shape among extant and extinct mesoeucrocodylians (see Holliday and Witmer, 2009). Among notosuchians, the trigeminal fossa morphology and associated structures were briefly described for few taxa, *Araripesuchus*, *Simosuchus*, *Hamadasuchus*, and *Rukwasuchus* (Holliday and Witmer, 2009; Kley et al., 2010; Sertich and O'Connor, 2014).

In *Notosuchus*, the morphology of this fossa and its surrounding structures are unique among mesoeucrocodylians; probably shared with the closely related *Mariliasuchus*, based on figure 4 G of Sertich and O'Connor (2014). *Notosuchus* presents a robust lateral bridge of the laterosphenoid separating the passage of CN V$_1$, grooves of CN V$_2$ and CN V$_3$, but lacks of caudal bridge separating the passage of CN V$_{so}$, and an epipterygoid (sensu Holliday and Witmer, 2009). Some notosuchians have an epipterygoid and lack of lateral bridge of the laterosphenoid (e.g., *Araripesuchus wegeneri, Simosuchus*), others have a rudimentary or absent epipterygoid but with lateral bridge (e.g., *Hamadasuchus, Lomasuchus, Rukwasuchus*) (Holliday and Witmer, 2009; Kley et al., 2010; Sertich and O'Connor, 2014, pers. obs.).

The caudal bridge of the laterosphenoid for CN V$_{so}$ is present in the basal notosuchian *Araripesuchus*, peirosaurids, and most crocodylians (Holliday and Witmer, 2009; pers. obs.). Absence of the caudal bridge in *Notosuchus* is probably the primitive condition for Mesoeucrocodylia, contrary partly to the hypothesis of Holliday and Witmer (2009), on the phylogenetically early appearance of the caudal bridge with respect to the lateral bridge of the laterosphenoid in the group. However, these authors also indicated that the appearance of the caudal bridge might be highly variable and homoplastic among mesoeucrocodylians.

The trigeminal fossa size of *Notosuchus* is relatively small, bilobate-shaped, and with grooves of CN V$_2$ and CN V$_3$ anteroposteriorly oriented. This feature differs from others mesoeucrocodylians, that present a large trigeminal fossa, and grooves of CN V$_2$, and CN V$_3$ posterolaterally or anterolaterally oriented. The trigeminal fossa size in *Notosuchus*, would indicate a relatively small trigeminal ganglion, reflecting a diminished facial sensitivity compared to extant crocodylians (e.g., *Alligator*) (Leitch and Catania, 2012; George and Holliday, 2013). This last feature would be related to the small number of neurovascular foramina in the face and lower jaw of *Notosuchus terrestris*, which can be related to the terrestrial habits of the species. A similar condition for the peirosaurid *Hamadasuchus*, unlike modern crocodylians that have dense array of facial neurovascular foramina and semi-aquatic habits (see George and Holliday, 2013).

5.3. *Incisive foramen (Fig. 13A)*

The incisive foramen in notosuchians is variable in morphology and size. In *Notosuchus,* the foramen is heart-shaped and closed posteriorly by the palatal branch of the maxilla. Several notosuchians and some eusuchians (e.g., basal alligatoroids, Brochu, 1999), also present an incisive foramen posteriorly closed by maxilla. This foramen is larger and circular in *Comahuesuchus*, broad transversally in advanced notosuchian *Yacarerani* and *Mariliasuchus*, small and triangular in *Sphagesaurus*, small and oval in the peirosaurid *Montealtosuchus*, and the sphagesaurid *Caipirasuchus* (Martinelli, 2003; Pol, 2003; Iori et al., 2013; Pol et al., 2014). In the basal notosuchian *Simosuchus*, peirosaurid *Hamadasuchus*, sebecids, and neosuchians (e.g., Eusuchia), the incisive foramen is closed posteriorly by the premaxilla (e.g., Brochu, 1999; Larsson and Sues, 2007; Kley et al., 2010; Pol and Powell, 2011). The uruguaysuchid *Araripesuchus wegeneri* and some baurusuchids (*Baurusuchus* and *Campinasuchus*) lack of incisive foramen (Price, 1945; Sereno and Larsson, 2009; Carvalho et al., 2011).

5.4. *Premaxillary knob and maxillary notch (Fig. 13A and E)*

The palate of *Notosuchus terrestris*, about of the premaxillary-maxillary suture, presents a premaxillary knob (medial to transitional alveolous) which fits in a maxillary notch (medial to first maxillary alveolous); this notch is dorsally closed. In the same position others notosuchians present a large and dorsolaterally open notch for reception of the large fourth dentary tooth (baurusuchids, some peirosaurids and sebecids) (Carvalho et al., 2004, 2005, 2007, 2011; Gasparini et al., 1993; Montefeltro et al., 2011; Price, 1945; Riff and Kellner, 2001, 2011). A small and dorsally closed notch in the maxilla is presents in *Araripesuchus wegeneri* and peirosaurid *Hamadasuchus rebouli* (Larsson and Sues, 2007; Sereno and Larsson, 2009). The basal notosuchian *Simosuchus* presents a small and dorsally open notch in the premaxilla-maxilla suture (Kley et al., 2010). Others advanced notosuchians (e.g., sphagesaurids) lack of maxillary notch in the palatal premaxilla-maxilla suture (e.g., Pol et al., 2014).

5.5. *Vomer (Fig. 20)*

The vomer was only described in two notosuchians so far, *Araripesuchus tsangatsangana* and *Simosuchus clarki* (Turner, 2009; Kley et al., 2010). In the former the vomer is long, narrow and restringed to the midline of the palate within the nasal cavity as most mesoeucrocodylians (e.g., crocodylians) (Iordansky, 1973). In basal notosuchian *Simosuchus* the vomer is relatively broad, pneumatized, and present an ascending process within nasal cavity, unlike known crocodyliforms. In addition, the vomer of *Simosuchus* has palatal exposure as the crocodylian *Melanosuchus niger* (Kley et al., 2010). *Notosuchus terrestris* has a distinctive long and lateromedially broad vomer forming most of floor of the nasal cavity. The vomer is unknown in almost all other notosuchians.

5.6. Choana (Figs. 13 and 22C)

The internal morphology of the choana and the choanal septum of *Notosuchus* where not fully described or interpreted in previous works (e.g., Woodward, 1896; Rusconi, 1933; Gasparini, 1971; Bonaparte, 1991; Andrade et al., 2006; Fiorelli and Calvo, 2008; Andrade and Bertini, 2008a; Pol et al., 2014). The choanal morphology of this taxon (i.e., triangular-shaped contour with choanal groove and choanal fenestrae), is similar to the closely related advanced notosuchians, *Mariliasuchus* and *Caipirasuchus* greatly; unlike *Yacarerani* which has rhomboid-shaped contour.

In any specimen analized here, the choanal septum is completely preserved, and therefore it was reconstructed from the specimens MACN-PV-RN-1038, MPCA-Pv-791, and MUCPv-137. The choanal septum of *Notosuchus* is formed mainly by pterygoid. It is T-shaped in cross-section, and in ventral view is relatively thin, with slightly convex lateral margins, slight anterior constriction and marked posterior constriction, and a posteriorly shallow longitudinal groove. This septum is similar to *Mariliasuchus*, but different to that present in *Caipirasuchus* (which is posteriorly broadand robust septum), and *Yacarerani* (which is markedly thin posteriorly with the palatines forming approximately half of it). As it was seen, the morphology of the choanal septum within Notosuchia is highly variable at low taxonomic levels and probably a great source of phylogenetic information, as mentioned Andrade et al. (2006) and Pol et al. (2014).

5.7. Olfactory tract groove (Fig. 16)

The ventral surface of the frontal of *Notosuchus* was not previously described. In most notosuchians, the sediment obscures the

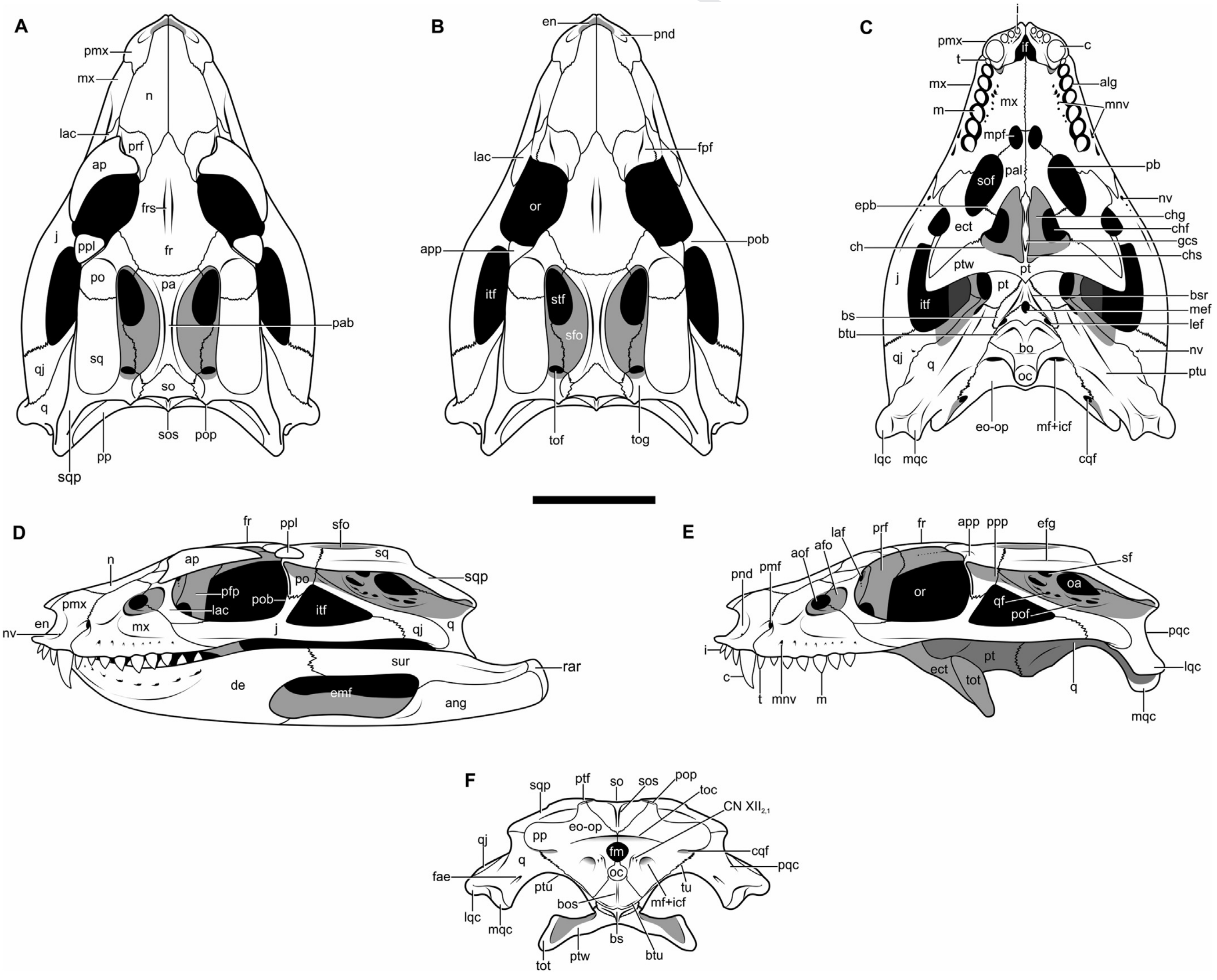

Fig. 22. Reconstruction of the skull of *Notosuchus terrestris*. **A** and **B** in dorsal view, **C**, ventral view, **D** and **E** in left lateral view, and **F**, occipital view. **A** and **D** with articulated palpebrals. Also **D** with lower jaw articulated. Scale bar equals 5 cm.

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ventral surface of the frontal preventing the observation of its morphology. Some aspects for the ventral surface of the frontal were briefly described (not comparatively) in some notosuchians, such as *Stratiotosuchus maxhechti*, *Araripesuchus tsangatsangana*, *Mariliasuchus amarali*, *Hamadasuchus rebouli*, *Mahajangasuchus insignis*, *Wargosuchus australis*, *Simosuchus clarki*, *Caipirasuchus stenognathus*, and *Rukwasuchus yajabalijekundu* (Riff, 2003; Turner, 2006; Turner and Buckley, 2006; Zaher et al., 2006; Larsson and Sues, 2007; Martinelli and Pais, 2008; Kley et al., 2010; Pol et al., 2014; Sertich and O'Connor, 2014).

Notosuchus terrestris presents a crista cranii frontalis poorly developed bounding the single passage of the olfactory tract, which is anteriorly concave and posteriorly convex, and accompanied laterally by a groove for the rostral end of the laterosphenoid. Others notosuchians, such as *Comahuesuchus*, *Caipirasuchus*, *Mariliasuchus*, *Simosuchus*, uruguaysuchids, baurusuchids, and peirosaurids have a developed crista cranii (e.g., Pol et al., 2014; pers. obs.). A well-developed crista cranii frontalis is present in extinct and extant crocodylians (e.g., Iordansky, 1973).

Anteriorly to the olfactory tract impression, there are two marked oval impressions for the olfactory bulbs, which were separated by a shallow longitudinal ridge (a median septum). The olfactory bulbs of Notosuchus were well developed, and relatively more anteroposteriorly elongated than those present in extant crocodylians did. In extant crocodylians (e.g., *Crocodylus*, *Gavialis*, *Caiman*), the anterior ventral surface of the frontal has not well-defined depressions for olfactory bulbs, and the groove of the olfactory tract loses gradually forward. A greater olfactory acuity is related to a greater olfactory bulbs volume (e.g., Zelenitsky et al., 2009; Kavoi and Jameela, 2011). The relatively larger size of the olfactory bulbs suggests a greater olfactory acuity in *Notosuchus* compared to extant crocodylians, as suggested Martinelli and Pais (2008). However, these researchers mistakenly identified the posterior recesses of the nasal cavity (postconcha sensu Witmer, 1995), as depressions for the olfactory bulbs in the baurusuchid *Wargosuchus australis*. A well-developed olfactory system is an adaptation of the notosuchians to terrestrial habitats (e.g., Gasparini, 1971; Bonaparte, 1991; Fiorelli and Calvo, 2008; Martinelli and Pais, 2008; Sereno and Larsson, 2009; Ösi, 2013).

5.8. *Braincase pneumaticity (Fig. 17B and C)*

Protosuchian basal crocodyliforms have a highly pneumatized braincase, mainly in the middle ear region and quadrate region (e.g., *Baroqueosuchus*, Busbey and Cow, 1984), and similar pneumaticity is observed in *Notosuchus* (e.g., quadrate foramina; Fig. 18). For this reason, some researchers considered *Notosuchus* closely related to the protosuchian lineage (Hecht and Tarsitano, 1983; Bonaparte, 1991). However, in addition with the supraoccipital, exoccipital-opisthotic, basioccipital, basisphenoid, pterygoid, and quadrate bones, the pneumatic sinuses of *Notosuchus* greatly invade the parietals, prootics, and laterosphenoids.

The tympanic pneumaticity in adult modern crocodylians is relatively reduced and posteriorly restricted (e.g., reduced laterosphenoid, prootic, parietal, and quadrate diverticula) (Dufeau and Witmer, 2007, 2015). The tympanic pneumaticity of the braincase and suspensorium of *Notosuchus* (as well as protosuchians), resembles that of young alligators (Dufeau and Witmer, 2007; pers. obs.). This pneumaticity would correspond to the greater auditory capacity of the middle ear (Dufeau and Witmer, 2015), as an adaptation to the terrestrial mode of life inferred for *Notosuchus*. Studies using CT scan (under preparation) will provide new information of the endocranial anatomy (paleoneurology) and paleobiology of *Notosuchus*.

5.9. *Post-temporal fenestra obliterated (Fig. 11)*

In extant eusuchians (e.g., *Caiman*, *Crocodylus*), the post-temporal fenestra is reduced to narrow recessed posterior opening of the orbitotemporal passage, that also opens anteriorly at the supratemporal fossa by the temporo-orbital foramen (Miall, 1878; Mansharamani, 1965). The post-temporal fenestra (delimited by squamosal, supraoccipital, exoccipital-opisthotic complex, and parietal in some case) is located above the post-occipital process, and ventral to the posterior margin of the skull table (Iordansky, 1973).

In the basal notosuchian *Simosuchus*, advanced notosuchians (e.g., *Mariliasuchus*, *Yacarerani*), *Mahajangasuchus*, and baurusuchids (e.g., *Baurusuchus*, *Stratiotosuchus*), this fenestra is located among the squamosal, supraoccipital and exoccipital-opisthotic complex (e.g., Pinheiro et al., 2008; Turner and Buckley, 2008; Q12 Kley et al., 2010). In the peirosaurids (e.g., *Montealtosuchus*, *Lomasuchus*, *Hamadasuchus*), the sebecid *Sahitisuchus*, *Comahuesuchus*, and uruguaysuchids (e.g., *Araripesuchus*), the parietal also forms part of the margin of the post-temporal fenestra (e.g., Gasparini et al., 1991; Ortega et al., 2000; Turner, 2006; Larsson and Sues, 2007; Kellner et al., 2013; Sertich and O'Connor, 2014).

In all notosuchians the post-temporal fenestra is at the level of the posterior margin of the skull table, dorsoventrally compressed, latero-ventrally slightly inclined, and not recessed; in peirosaurids the fenestra is slightly recessed (Pol et al., 2014; pers. obs.). Distinctively, in *Notosuchus terrestris* post-temporal fenestra is obliterated by squamosal and post-occipital process (supraoccipital + exoccipital-opisthotic complex), and the dorsal surface of these processes is located at the level of the skull table.

5.10. *Carotid foramen and metotic foramen (Fig. 12)*

The foramen for the internal carotid artery in the occiput was hardly identifiable in some notosuchians (e.g., Zaher et al., 2006). Particularly in *Notosuchus terrestris*, a foramen ventrally located in the basisphenoid and adjacent to the lateral Eustachian canal (pharyngotympanic tube sensu Dufeau and Witmer, 2015), mistakenly identified as the carotid foramen by some authors (Gasparini, 1971; Bonaparte, 1991; Fiorelli and Calvo, 2008). Here, we identified and confirm the internal carotid foramen of *Notosuchus*, which open together with the metotic foramen within a deep fossa, lateral to the occipital condyle. The same feature identified in the closely related notosuchians *Mariliasuchus*, *Yacarerani*, and *Caipirasuchus* (Pol et al., 2014). In *Baurusuchus*, *Montealtosuchus* and *Mahajangasuchus*, these foramina are situated together in a shallow fossa. Uruguaysuchids, *Simosuchus*, some peirosaurids and neosuchians have an internal carotid foramen located ventral or ventromedially to the metotic foramen (e.g., Brochu, 1999; Turner, 2006; Turner and Buckley, 2008; Pol and Gasparini, 2009; Kley et al., 2010; Sertich and O'Connor, 2014; Pol et al., 2014). This evidence indicates that a deep fossa containing the metotic and carotid foramina would be a putative synapomorphy for advanced notosuchians.

6. Conclusions

As result of this study, the revision of more than 60 specimens of *Notosuchus terrestris* provided a new and more complete interpretation of its cranial and mandibular osteology (Figs. 21 and 22). The cranio-mandibular description here presented for specie is the most complete hypothesis so far. In particular, the braincase morphology and the pattern of neurovascular foramina were not described in detail so far. Numerous and new characters are described for the first time for *Notosuchus*, some of these potential

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autapomorphies (e.g., quadratojugal spine, crista pseudo-tuberalis, laterosphenoid without caudal bridge, postorbital-quadratojugal contact, small palatal premaxillary knob, morphology of the crista cranii frontalis, olfactory tract groove, trigeminal fossa, vomer, choana), adding a significant amount information to test in a phylogenetic analyzes. Others cranial features here analyzed are probably synapomorphies of Notosuchia (e.g., frontal with well-marked depressions for olfactory bulbs, small trigeminal fossa size), and probably related to terrestriality. *Notosuchus* presents cranial characters with intraspecific variation (e.g., antorbital fossa contour, supraoccipital-parietal suture, number of quadrate foramina, frontal-parietal suture, shape of the parietal bar, trigeminal fossa size, ornamentation), that could correspond to ontogenetic stages as well as its sexual dimorphism (additional studies based on more complete and prepared materials will clarify this). In addition, comparisons with other notosuchians of poorly explored cranial regions are necessary.

Uncited references

Q14 Andrade and Bertini, 2008c, Walker, 1970.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.cretres.2017.08.016.

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