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The osteology of the holotype of the early erythrosuchid *Garjainia prima* Ochev, 1958 (Diapsida: Archosauromorpha) from the upper Lower Triassic of European Russia

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Running title: Osteology of the erythrosuchid *Garjainia prima*

Abstract. Erythrosuchids are Early–Middle Triassic bulky, quadrupedal archosauromorphs with proportionally large heads, and they were among the first archosauromorphs to occupy the role of terrestrial hypercarnivores. Recent work has expanded anatomical and phylogenetic knowledge of erythrosuchids, but a thorough understanding is still lacking and *Erythrosuchus africanus* is the only species for which a thorough anatomical description of most of the skeleton has been published. *Garjainia prima*, from the upper Olenekian of Russia, represents one of the oldest known erythrosuchids and includes the best-preserved skull of an Early Triassic erythrosuchid. Here we expand understanding of erythrosuchid anatomy by providing the first detailed and comprehensive description of the holotype of *Garjainia prima*. We consider “*Vjushkovia triplicostata*” to be a junior synonym of *Garjainia prima* because of their extremely similar morphology, with the two character states that differ between them being variable intraspecifically in some other diapsids. A new phylogenetic analysis recovered a monophyletic *Garjainia* as sister to Middle Triassic erythrosuchids, and recovered *Fugusuchus hejiapanensis* as the earliest branching erythrosuchid. Branch support for Erythrosuchidae is low, but the Middle Triassic erythrosuchid clade is well supported by characters with low homoplasy, indicating that their morphology was specialized in ways rarely explored by other Triassic archosauromorphs.

Key words: Archosauriformes, Erythrosuchidae, Olenekian, phylogeny, skull, Yarengian Supergorizont

INTRODUCTION

The Triassic Period (ca. 252–201 mya) witnessed a broad evolutionary radiation of archosauromorphs (all diapsids closer to crocodylians and dinosaurs than to lepidosaurs) after the Permo-Triassic mass extinction, which resulted in the appearance of multiple, very disparate ecomorphotypes (Charig & Reig, 1970; Reig, 1970; Charig & Sues 1976; Sennikov, 1996; Gower & Sennikov, 2000; Nesbitt, 2011; Ezcurra, 2016). The erythrosuchids were quadrupedal, likely sprawling and bulky predatory archosauromorphs with proportionally large heads, and they were among the first archosauromorphs, together with the poposauroid archosaurs, to occupy the role of terrestrial hypercarnivores during the Early–Middle Triassic (Charig & Reig, 1970; Reig, 1970; Charig & Sues 1976; Sennikov, 1996; Butler *et al.*, 2011; Ezcurra, Butler & Gower, 2013). The oldest known erythrosuchids come from the late Olenekian (late Early Triassic) of Russia, South Africa, and probably China, and the youngest are recorded from the Ladinian (late Middle Triassic) of Russia and China (Gower & Sennikov, 2000; Ezcurra, 2016; Liu & Sullivan, 2017). Recent work on erythrosuchids has expanded our anatomical and phylogenetic knowledge of the group (Gower, 2003; Wang *et al.*, 2013; Gower *et al.*, 2014; Ezcurra, 2016), but a thorough understanding is hampered by the lack of precise anatomical descriptions of several species (Ezcurra *et al.*, 2013). The erythrosuchid *Garjainia prima* from the Olenekian of Russia (Ochev, 1958) is one of those species in need of detailed revision. *Garjainia prima* is particularly relevant because it represents one of the oldest known erythrosuchid species and its holotype includes the most complete and best-preserved skull available for an Early Triassic erythrosuchid.

Ochev (1958) erected the species *Garjainia prima* based on a fairly complete skull and associated partial postcranium collected close to the village of Andreevka (Belyaevka district, Orenburg Province, Russia) in outcrops of the Petropavlovskaya Svita of the Yarengian (=Yarenskian) Supergorizont, Fedorovkian Gorizont (Early Triassic: late Olenekian). Subsequently, Huene (1960) named another erythrosuchid species, “*Vjushkovia triplicostata*”, from the Rassypnaya locality (Ilek district, Orenburg Province) of the Yarengian Supergorizont (Gamian Gorizont, Early Triassic: late Olenekian), at a level somewhat stratigraphically younger than that of the *Garjainia prima* type locality. This new species was based on at least five, very well-preserved, disarticulated specimens including cranial and postcranial bones (Huene, 1960). Tatarinov (1961) proposed that both *Garjainia* and “*Vjushkovia*” were subjective junior synonyms of the South African genus *Erythrosuchus*, and this hypothesis was followed by several subsequent authors (e.g. Hughes, 1963; Ewer, 1965; Romer, 1966; Romer, 1972; Cruickshank, 1972). However, this synonymy was rejected by Young (1964) and Charig & Reig (1970), and by more recent authors (e.g. Parrish, 1992; Sennikov, 1995a, b, 2008; Gower & Sennikov, 1996, 1997, 2000; Desojo, Arcucci & Marsicano, 2002; Ezcurra, Lecuona & Martinelli, 2010; Ezcurra *et al.*, 2013; Ezcurra, 2014, 2016; Gower *et al.*, 2014; Ezcurra & Butler, 2015a). Gower & Sennikov (2000) concluded that “*Vjushkovia*” is a subjective junior synonym of *Garjainia*, a hypothesis previously proposed by Kalandadze & Sennikov (1985), Ochev & Shishkin (1988), Sennikov (1995a), and Sennikov (1995b), and that “*Garjainia triplicostata*” is a subjective junior synonym of *Garjainia prima*. These hypotheses of synonymy have been followed more recently by Gower *et al.* (2014) and Ezcurra (2016). Another species of the genus, *Garjainia madiba*, has been described recently by Gower *et al.* (2014) from the Olenekian of South Africa.

Here we expand knowledge of erythrosuchid anatomy by providing a detailed redescription of the craniodental and postcranial osteological anatomy of the holotype of *Garjainia prima*. The diagnosis, taxonomy, phylogenetic relationships, and some palaeobiological aspects of this species are discussed based on the new anatomical information provided here. The paper of Huene (1960) still represents the most complete source of published information for “*Vjushkovia triplicostata*”, but this description is not very detailed and the figures are limited to line drawings. A full revision of the complete hypodigm of *Garjainia prima* (including the material referred to “*Vjushkovia triplicostata*”) is beyond the scope of this publication, this is intended to be published elsewhere.

INSTITUTIONAL ABBREVIATIONS

BP, Evolutionary Studies Institute (formerly Bernard Price Institute for Palaeontological Research), University of the Witwatersrand, Johannesburg, South Africa; BSPG, Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; CRILAR-Pv, Centro Regional de Investigaciones y Transferencia Tecnológica de La Rioja, Paleontología de Vertebrados, Anillaco, La Rioja, Argentina; GHG, Geological Survey, Pretoria, South Africa; GMB, Geological Institute, Beijing, China; GPIT, Paläontologische Sammlung der Universität Tübingen, Tübingen, Germany; ISIR, Indian Statistical Institute, Kolkata, India; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; MACN-Pv, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Paleontología de Vertebrados, Buenos Aires, Argentina; MB, Museum für Naturkunde – Leibniz-Institut für Evolutions- und Biodiversitätsforschung, Berlin, Germany; MCNAM, Museo de Ciencias Naturales y Antropológicas de Mendoza (J. C. Moyano), Mendoza,

Argentina; MCZ, Museum of Comparative Zoology, Cambridge, USA; NHMUK, Natural History Museum, London, UK; NMK, Naturkundemuseum im Ottoneum, Kassel, Germany; NM QR, National Museum, Bloemfontein, South Africa; PIMUZ, Paläontologisches Institut und Museum der Universität Zürich, Zurich, Switzerland; PIN, Borissiak Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia; PULR, Paleontología, Universidad Nacional de La Rioja, La Rioja, Argentina; PVL, Paleontología de Vertebrados, Instituto ‘Miguel Lillo’, San Miguel de Tucumán, Argentina; RC, Rubidge Collection, Wellwood, Graaff-Reinet, South Africa; SAM-PK, Iziko South African Museum, Cape Town, South Africa; SMNS, Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany; TM, Ditsong National Museum of Natural History (formerly Transvaal Museum), Pretoria, South Africa; UA, University of Antananarivo, Antananarivo, Madagascar; UCMP, University of California Museum of Paleontology, Berkeley, USA; UFRGS, Universidade Federal do Rio Grande do Sul, Porto Alegre, RS, Brazil; UMZC, University Museum of Zoology, Cambridge, UK; UNIPAMPA, Universidade Federal do Pampa, São Gabriel, Brazil; USNM, National Museum of Natural History (formerly United States National Museum), Smithsonian Institution, Washington, D.C., USA; UTGD, School of Earth Sciences, University of Tasmania, Hobart, Australia; ZPAL, Institute of Paleobiology of the Polish Academy of Sciences, Warsaw, Poland.

MATERIALS AND METHODS

PHYLOGENETIC DATA MATRIX

The phylogenetic relationships of *Garjainia prima* were analysed using the most extensive phylogenetic dataset currently available for Permian and Triassic archosauromorphs

(Ezcurra, 2016) as modified by subsequent authors (Ezcurra & Butler, in press; Ezcurra *et al.*, 2017; Nesbitt *et al.*, 2017; Sengupta, Ezcurra & Bandyopadhyay, 2017; Stocker *et al.*, 2017). Here, we modified character 386 and added six additional characters (690–695) as a result of the comparisons made between the holotype of *Garjainia prima* and other early archosauriforms (see Appendix). We also modified some of the scorings of the original versions of this data matrix (see Appendix). The expansion of the taxonomic sample conducted by Ezcurra and Butler (in press) was an attempt to include all known Permian to early Late Triassic archosauromorphs in a single data matrix, but was intended for assessing disparity and evolutionary rates, and not for detailed reconstruction of phylogenetic relationships. Thus, we deactivated 35 terminals (see Appendix), resulting in a data set of 116 active terminals and 695 characters.

ANALYTICAL PROTOCOL

The data matrix was analysed under equally weighted maximum parsimony using TNT v.1.5 (Goloboff, Farris & Nixon, 2008a; Goloboff & Catalano, 2016). The search strategy started using a combination of the tree-search algorithms Wagner trees, TBR branch swapping, sectorial searches, Ratchet (perturbation phase stopped after 20 substitutions) and Tree Fusing (5 rounds), until 100 hits of the same minimum tree length were achieved. The best trees obtained were subjected to a final round of TBR branch swapping. Zero length branches in any of the recovered most parsimonious trees were collapsed. The following characters were considered additive (ordered) during the searches: 1, 2, 7, 10, 17, 19–21, 28, 29, 36, 40, 42, 50, 54, 66, 71, 74–76, 122, 127, 146, 153, 156, 157, 171, 176, 177, 187, 202, 221, 227, 263, 266, 278, 279, 283, 324, 327, 331, 337, 345, 351, 352, 354, 361, 365, 370, 377, 379, 386, 387, 398, 410, 424, 430, 435, 446, 448, 454, 458, 460, 463,

470, 472, 478, 482, 483, 485, 489, 490, 504, 510, 516, 529, 537, 546, 552, 556, 557, 567, 569, 571, 574, 581, 582, 588, 648, 652 and 662 because they are considered to represent nested sets of homologies. Character 119 was deactivated before the tree searches, following Ezcurra *et al.* (2017). Branch support was quantified using decay indices (Bremer support values) and a bootstrap resampling analysis, using 1,000 pseudoreplicates and reporting both absolute and GC (that is, the difference between the frequencies of recovery in pseudoreplicates of the clade in question and the most frequently recovered contradictory clade) frequencies (Goloboff *et al.*, 2003). The minimum number of additional steps necessary to generate alternative, suboptimal tree topologies was calculated when constraining the positions of *Garjainia prima* and *Fugusuchus hejiapanensis* in different parts of the tree and rerunning the analysis. *Garjainia madiba* was considered as a floating taxon in all suboptimal searches that constrained the position of *Garjainia prima*.

In order to evaluate the effect of homoplasy on the recovered phylogenetic relationships of erythrosuchids we also analysed the data matrix using implied weights (Goloboff *et al.*, 2008b) with a constant k from 3 to 18. These sensitivity analyses used the same search strategy, parameters, and character treatments detailed above. The results of these 15 analyses are reported as a colour-coded grid in a subset of the strict consensus tree focused on ‘proterosuchian’ archosauriforms.

CHANGES TO THE CHARACTER LIST

The following change was made to the character list of Ezcurra (2016), as modified by subsequent authors (Ezcurra & Butler, in press; Ezcurra *et al.*, 2017; Nesbitt *et al.*, 2017; Sengupta *et al.*, 2017; Stocker *et al.*, 2017):

Character 386) Scapula-coracoid, glenoid fossa orientation: mainly lateral, being more laterally facing than posteriorly and without a posteriorly prominent supraglenoid lip in lateral view (0); slightly posterolateral, being more posteriorly facing than laterally and resulting in a posteriorly prominent supraglenoid lip in lateral view (1); posteroventral (2), ORDERED.

We added an intermediate state between the two character states present in the original formulation of Ezcurra (2016) (i.e. posterolateral versus posteroventral) to capture the variation in orientation of the glenoid fossa present in early archosauromorphs (mainly lateral, e.g. rhynchosaurs, prolacertids, proterosuchids, *Sarmatosuchus otschevi*) (Ezcurra, 2016: fig. 36a, b) and erythrosuchids and early eucrocopod archosauriforms (slightly posterolateral) (Ezcurra, 2016: fig. 36c–e). The third character state—posteroventral orientation—occurs in the rauisuchid *Postosuchus*, early crocodylomorphs, and dinosauriforms (Nesbitt, 2011; Ezcurra, 2016: fig. 36f).

The following characters were added to the character list of Ezcurra (2016), as modified by subsequent authors (Ezcurra & Butler, in press; Ezcurra *et al.*, 2017; Nesbitt *et al.*, 2017; Sengupta *et al.*, 2017; Stocker *et al.*, 2017):

Character 690) Premaxilla, alveolar margin in lateral view: straight (0); distinctly convex (1). This character is inapplicable in terminals with a premaxilla restricted to the anterior half of the external naris or with a premaxilla modified as a downturned edentulous beak (e.g. rhynchosaurids).

The alveolar margin of the premaxilla of the holotype and referred specimens of *Garjainia prima* is straight in lateral view (PIN 2394/5, 951/63), as also occurs in most Triassic archosauromorphs (e.g. *Macrocnemus bassanii*: PIMUZ 4822; allokokotosaurians:

Flynn *et al.*, 2010; Sengupta *et al.*, 2017; *Mesosuchus browni*: SAM-PK-6536; *Prolacerta broomi*: BP/1/471; *Teyujagua paradoxa*: Pinheiro *et al.*, 2016; *Tasmaniosaurus triassicus*: UTGD 54655; proterosuchids: Ezcurra & Butler, 2015a; *Sarmatosuchus otschevi*: PIN 2865/68-9; *Garjainia madiba*: BP/1/5760a, 6232l; *Euparkeria capensis*: SAM-PK-5867; *Chanaresuchus bonapartei*: MCZ 4037, PVL 4575; *Tarjadia ruthae*: CRILAR-Pv 495; ornithosuchids: Walker, 1964; early avemetatarsalians: Dzik, 2003). By contrast, the alveolar margin of the premaxilla is distinctly convex ventrally, resulting in an upturned anteroventral corner of the bone in lateral view, in the erythrosuchids *Erythrosuchus africanus* (BP/1/5207) and *Shansisuchus shansisuchus* (Young, 1964; Wang *et al.*, 2013). This condition resembles that of some phylogenetically disparate archosauromorphs, such as *Dinocephalosaurus orientalis* (Li, 2003), *Pectodens zhenyuensis* (Li *et al.*, 2017), *Asperoris mnyama* (NHMUK PV R36615), *Proterochampsia* spp. (Dilkes & Arcucci, 2012), and some pseudosuchians (e.g. *Diandongosuchus fuyuanensis*: Stocker *et al.*, 2017; *Qianosuchus mixtus*: Li *et al.*, 2006; *Xilousuchus sapingensis*: Nesbitt, Liu & Li, 2011; *Batrachotomus kupferzellensis*: SMNS 52970, 80260). Thus, this character seems to be rather homoplastic among major archosauromorph lineages, but it may be phylogenetically informative at lower taxonomic levels.

Character 691) Nasal, small lateral process that excludes the anteriormost tip of the prefrontal from the lateral margin of the skull roof: absent (0); present (1). This character is inapplicable in terminals lacking a nasal-prefrontal contact.

In most Triassic archosauromorphs the entire lateral margin of the prefrontal forms the lateral edge of the skull roof. However, in *Fugusuchus hejiapanensis* (Cheng, 1980; photographs of GMB V 313), *Garjainia prima* (PIN 2394/5), *Erythrosuchus africanus*

(Gower, 2003; BP/1/5207), *Shansisuchus shansisuchus* (Young, 1964), *Youngosuchus sinensis* (IVPP V3239), *Vancleavea campi* (Nesbitt *et al.*, 2009), *Diandongosuchus fuyuanensis* (Stocker *et al.*, 2017), *Qianosuchus mixtus* (Li *et al.*, 2006), and *Decuriasuchus quartacolonias* (França, Langer & Ferigolo, 2013) the anterior end of the prefrontal is excluded from the lateral edge of the skull roof by a small posterolateral process of the nasal. This process results in a V-shaped notch that receives the tapering anterior end of the prefrontal in dorsal view. This condition resembles that present in several saurischian dinosaurs, in which a posterolateral process of the nasal forms a notch to receive the anterior end of the lacrimal (Serenio, 1999).

Character 692) Postfrontal, suture with postorbital in dorsal view: mainly transverse, may have a minor anteromedial-to-posterolateral orientation (0); mainly longitudinal, with an angle of 45° or greater to the transverse axis (1). This character is inapplicable in terminals with a bifid medial process of the postfrontal or lacking a postfrontal bone.

The postfrontal possesses a long and tapering lateral process that contributes to the posterodorsal border of the orbit laterally and forms a mainly transverse (sometimes slightly anteromedial-to-posterolateral) suture with the postorbital medially in most Triassic archosauromorphs. However, the lateral process of the postfrontal is reduced, resulting in a mainly longitudinal suture with the postorbital—at an angle of 45° or greater to the transverse axis—in *Pamelaria dolichotrachela* (ISIR 316/1), *Fugusuchus hejiapanensis* (Cheng, 1980), *Garjainia prima* (PIN 2394/5), *Garjainia madiba* (BP/1/5525), *Erythrosuchus africanus* (Gower, 2003; BP/1/5207), *Shansisuchus shansisuchus* (Young, 1964; Wang *et al.*, 2013), some phytosaurs (Hungerbühler, 1998), *Luperosuchus fractus* (Nesbitt & Desojo, 2017), and *Batrachotomus kupferzellensis* (Gower, 1999).

Character 693) Postorbital, sub-triangular to oval fossa on the dorsal surface of the main body and base of the anterior process (distinctly separated from the edge of the supratemporal fenestra): absent (0); present (1).

The dorsal surface of the postorbital of most archosauromorphs is flat to slightly convex or possesses a well-rimmed supratemporal fossa adjacent to the border of the supratemporal fenestra. By contrast, the postorbital has a dorsal fossa at the base of the ascending or anterior process and the main body of the bone, which is distinctly separated from the rim of the supratemporal fenestra, in *Erythrosuchus africanus* (Gower, 2003), *Garjainia prima* (PIN 2394/5), and *Garjainia madiba* (Gower *et al.*, 2014).

Character 694) Prootic, separation between the inferior and superior anterior processes in lateral view: well separated from each other anteriorly, not contributing to the anterior border of the trigeminal foramen (for cranial nerve V) (0); closely approach or join together to form most or the entire anterior border of the trigeminal foramen (for cranial nerve V) (1). This character is scored as inapplicable in taxa that lack an inferior anterior process.

The inferior and superior anterior processes of the prootic form the dorsal, posterior, and ventral borders of the foramen for the passage of the trigeminal cranial nerve in most Triassic archosauromorphs. However, these processes converge and nearly contact each other, thus contributing to the anterior border of the trigeminal foramen, or the prootic completely encloses the trigeminal foramen, in *Fugusuchus hejiapanensis* (Gower & Sennikov, 1996), *Garjainia prima* (PIN 2394/5), and *Erythrosuchus africanus* (Gower, 1997). *Shansisuchus shansisuchus* possesses inferior and superior anterior processes of the

prootic that are widely separated from each other (Gower & Sennikov, 1996), resembling the condition most widespread among early archosauromorphs.

Character 695) Axis, neural spine posterior margin: convex or acute, placed anterior or approximately level to the posterior tip of the postzygapophyses (0); acute, posterodorsally oriented apex extending posteriorly beyond the postzygapophyses for a distance equal to or longer than the length of the postzygapophyses (1).

The neural spine of the axis of *Shansisuchus shansisuchus* is distinctly more posteriorly developed, extending beyond the level of the postzygapophyses, than in the holotype and referred specimens of *Garjainia prima* (PIN 2394/5; Huene, 1960). The presence of an acute posterior margin of the neural spine that extends beyond the postzygapophyses for a distance equal to or longer than the length of the postzygapophyses of the axis also occurs in other, disparate Triassic archosauromorphs, such as *Mesosuchus browni* (SAM-PK-5882), *Stenaulorhynchus stockleyi* (Huene, 1938), *Proterosuchus fergusi* (BSPG 1934 VIII 514), proterochampsids (e.g. *Proterochampsia barrionuevoi*: Dilkes & Arcucci, 2012; *Chanaresuchus bonapartei*: MCZ 4037), *Riojasuchus tenuisiceps* (PVL 3827), and *Heterodontosaurus tucki* (SAM-PK-K1332). By contrast, the neural spine of the axis is placed anterior to or approximately level to the posterior tips of the postzygapophyses in several other taxa, including tanystropheids (e.g. Nosotti, 2007), allokotosaurians (e.g. Nesbitt *et al.*, 2015), *Prolacerta broomi* (BP/1/2675), *Sarmatosuchus otschevi* (PIN 2865/68-22), *Euparkeria capensis* (SAM-PK-5867), *Doswellia kaltenbachii* (USNM 244214), *Parasuchus hislopi* (ISIR 42), *Turfanosuchus dabanensis* (IVPP V3237), *Batrachotomus kupferzellensis* (Gower & Schoch, 2009), aphanosaurs (e.g. Nesbitt *et al.*,

2017), and non-dinosaurian dinosauriforms (e.g. Bittencourt *et al.*, 2014; Piechowsky & Dzik, 2010).

SYSTEMATIC PALAEONTOLOGY

DIAPSIDA Osborn, 1903 sensu Laurin (1991)

SAURIA Gauthier, 1984 sensu Gauthier, Kluge & Rowe (1988)

ARCHOSAUIROMORPHA Huene, 1946 sensu Dilkes (1998)

ARCHOSAURIFORMES Gauthier, Kluge & Rowe (1988)

ERYTHROSUCHIDAE Watson, 1917 sensu Ezcurra *et al.* (2010)

Garjainia prima Ochev, 1958

Synonymy list

Erythrosuchus primus, *Vjushkovia triplicostata*, *Garjainia triplicostata*.

Holotype

PIN 2394/5 (formerly SGU 104/3-43), partial skeleton of a single individual, including an almost complete skull (PIN 2394/5-1–5-7) and lower jaws (PIN 2394/5-8, 5-9), second to fifth cervical vertebrae (PIN 2394/5-10–5-13), two posterior cervical or anterior dorsal vertebrae (PIN 2394/5-16), at least four dorsal vertebrae (PIN 2394/5-14, 5-15, 5-17–5-19), both scapulae and coracoids (PIN 2394/5-32, 5-33), right clavicle (PIN 2394/5-35), interclavicle (PIN 2394/5-34), left fourth metatarsal (PIN 2394/5-36), several presacral ribs (PIN 2394/5-21–5-31), probable gastralia (PIN 2394/5-37), and some indeterminate fragments of bone (PIN 2394/5-37).

Type horizon and locality

Kzyl-Sai (=Kzyl-Say) II 2 locality (Fig. 1), Petropavlovskaya Svita of the Yarengian (=Yarenskian) Supergorizont, Fedorovkian Gorizont (Early Triassic: late Olenekian), 0.5–1 km west of the village Andreevka, Akbulak district, Orenburg Province, Russia (Ochev, 1958; Sennikov, 1995, 2008; Gower & Sennikov, 2000; locality 29 of Tverdokhlebov *et al.*, 2003).

Referred specimens

The hypodigm of “*Vjushkovia triplicostata*”, which includes the lectotype (a skull roof, PIN 951/59) and isolated skull and postcranial bones (PIN 951/1–40, 46, 54–64, 69, 70, 78–105) (Gamian Gorizont).

Probable referred specimens

The following specimens may belong to *Garjainia prima*, but a more definitive assignment requires a revision of the complete hypodigm of the species (including the material referred to “*Vjushkovia triplicostata*”).

Gamian Gorizont: PIN 4596/3, 4, two fragments of tibiae, Bakas locality (Bashkortosata, Kuyurgazinsky district); PIN 4187/27, dorsal vertebra, PIN 4187/28, fragment of tibia, Donguz IX locality (Orenburg Province, Sol-Iletsk district); PIN 2431/2, fragment of left premaxilla, PIN 2431/3, dorsal vertebra, Astrakhanovka II locality (Orenburg Province, Tulgan district); PIN 4365/1, fragment of left maxilla; PIN 4365/2, fragment of right humerus, Petropavlovka I locality (Orenburg Province, Sakmara district).

Fedorovkian Gorizont: PIN 2394/21, 23, 24, 26, 28, 29, 35-40, teeth, Kzyl-Say II 2 locality; PIN 2394/10, right scapula, Kzyl-Say II 1 locality; PIN 2394/6, right femur, PIN 2394/7, 33, dorsal vertebrae, PIN 2394/8, right palatine, PIN 2394/34, intercentra, Kzyl-Say II 3 locality; PIN 2394/9, dorsal vertebra, PIN 2394/48, fragment of left femur, PIN 2394/49, left jugal, Kzyl-Say I 2 locality; PIN 2394/51, fragment of vertebral centrum, Kzyl-Say I 3 locality; PIN 4172/2, neural spine of vertebra, Kzyl-Say III 1 locality; PIN 4375/1, neural arch of dorsal vertebra, PIN 4375/2, 3, two fragments of tibiae, Muraptalovo II locality (Bashkortostan, Kuyurgazinsky district); PIN 4789/1, right postorbital, Elshanskoye locality (Orenburg Province, Sol-Iletsk district).

Diagnosis

Garjainia prima (= "*Vjushkovia triplicostata*") is a medium-sized erythrosuchid (holotype skull 440 mm long) differentiated from other archosauromorphs by the following unique combination of character states (autapomorphies indicated with an asterisk): premaxilla with a longitudinal groove on the lateral surface of the premaxillary body (also present in *Garjainia madiba*), palatal process gently curved ventrally with its main axis sub-parallel to the alveolar margin of the bone (long axis of the process posteriorly intercepts that of the alveolar margin in *Garjainia madiba*), and five tooth positions (six in *Garjainia madiba*); nasal with an anteroposteriorly long descending process that forms an extensive longitudinal suture with the maxilla* (unknown in *Garjainia madiba*); antorbital fossa absent on the horizontal process of the maxilla (the same condition probably occurs in *Garjainia madiba*); antorbital fenestra trapezoidal with its main axis orientated from anteroventrally to posterodorsally, in association with the horizontal process of the maxilla being much taller posteriorly* (unknown in *Garjainia madiba*); prefrontal strongly flared

laterally in dorsal view* (unknown in *Garjainia madiba*); skull roof with a longitudinal fossa on its dorsal surface that harbours a longitudinal median prominence in its posterior half* (unknown in *Garjainia madiba*); straight suture between postfrontal and postorbital (possibly present in some specimens of *Shansisuchus shansisuchus*); jugal and postorbital without a ball-like boss on their external surface (ball-like boss is present in *Garjainia madiba*); basioccipital with a median tuberosity on its ventral surface*; and interclavicle with a rhomboidal posterior ramus* (unknown in *Erythrosuchus africanus* and *Garjainia madiba*). This list of character states was originally proposed by Ezcurra (2016) and is expanded here to form a differential diagnosis. In addition, referred specimens of *Garjainia prima* also differ from those of *Garjainia madiba* in the presence of a postacetabular process that is shorter than the acetabular portion of the ilium (unknown in the holotype of *Garjainia prima*) (Gower *et al.*, 2014).

DESCRIPTION OF THE HOLOTYPE

The holotype of *Garjainia prima* consists of a partial skeleton of a single individual (Ochev, 1958, 1975, 1981; Sennikov, 1995, 2008; Gower & Sennikov, 2000). The state of preservation of the specimen is generally good, but most of the bones suffered moderate post-mortem transverse compression and fracturing and parts of several elements have broken away. The osteological description follows anatomical limb orientations of sprawling animals (i.e. limbs are considered projected orthogonal to the sagittal plane of the axial skeleton). Accordingly, the limb orientations used here are equivalent to the following orientations of an animal with parasagittally-oriented limbs (parasagittal orientations within brackets): dorsal (= posterior), ventral (= anterior), anterior (= lateral), posterior (= medial),

proximal (= proximal), and distal (= distal). Comparisons with specimens that belong to the hypodigm of “*Vjushkovia triplicostata*” are indicated as comparisons with referred specimens of *Garjainia prima*. The holotype and only known specimen of *Fugusuchus hejiapanensis* could not be studied at first-hand by M.D.E. and R.J.B., because it could not be located by the GMB when access was requested in May 2013. However, comparisons and observation of this species are made here based on the original description of Cheng (1980) and additional information in Gower (1994), personal observations by D.J.G. (1993), and unpublished photographs provided by J.M. Parrish (hereafter quoted as ‘GMB V 313 photographs’).

General state of preservation of the skull

The skull and lower jaws of PIN 2394/5 are fairly complete, lacking most of the prenasal processes of the premaxillae and anteriormost portions of the nasals, part of the distal end of the postnasal process of the left premaxilla, the posterior end of the left maxilla, part of the anterior process of the left jugal and the proximal end of the left quadrate, most of the ventral process of the right squamosal, the medial half of the left ectopterygoid and the lateral process of right ectopterygoid, fragments of the posterolateral processes (= occipital wings) of the parietals, and the right quadrate, as well as several premaxillary, maxillary and dentary teeth (Figs. 2, 3). The vomers are not exposed or preserved. Parts of the premaxilla-nasal bar, the posterior end of the horizontal process of the left maxilla, the anterior process of the left jugal and the proximal end of the left quadrate are reconstructed with white plaster and painted over (Figs. 4–7).

The surfaces of the cranial bones are generally heavily cracked and some areas are eroded (Figs. 4, 6). The combination of these taphonomic conditions complicates or

prevents the clear assessment of the position of several sutures (e.g. those on the right side of the skull and skull roof). The external naris is bordered mostly by the premaxilla, but it cannot be determined if the nasal formed part of its dorsal margin. The cranium is asymmetrically transversely compressed, with the right side of the skull being flatter and slightly displaced anteriorly relative to the left side. As a result of post-mortem compression, the right pterygoid and palatine are ventrally displaced from their original positions and the left basipterygoid process dislocated from its articular socket in the pterygoid. Several bones are currently preserved detached from the articulated skull, including the right premaxilla, the posterior process of the right jugal, the right quadratojugal, the distal end of the posterolateral process of the right pterygoid, the distal part of the posterior end of the right ectopterygoid, and both epipterygoids (Figs. 8, 9). Most of the right side and part of the left side of the braincase are exposed through the respective infratemporal fenestrae.

General morphology of the skull

The skull of the holotype of *Garjainia prima* is 440 mm long from the tip of the snout to the distal condyles of the quadrate, and has a maximum height—at the level of the temporal region—of 173 mm. The skull is subtriangular in lateral and dorsal views, being dorsoventrally lower and transversely narrower at the level of the external naris than at the level of the infratemporal and supratemporal fenestrae (Ochev, 1981) (Figs. 2–7). The snout (= preorbital region) is 243 mm long and represents 55.2% of the total length of the skull, resembling the condition present in some early archosauromorphs (e.g. 56.4% in *Protorosaurus speneri*: USNM 442453, cast of NMK S 180; 57.9% in *Macrocnemus bassanii*: PIMUZ T4822; 46.9% in *Prolacerta broomi*: BP/1/471; 41.9% in *Teyujagua*

paradoxa: UNIPAMPA 653 cast) and several non-archosaurian archosauriforms, such as *Proterosuchus fergusi* (50.4% in RC 96; 50.8% in SAM-PK-11208), “*Chasmatosaurus*” *yuani* (51.8% in IVPP V4067), *Erythrosuchus africanus* (51.6% in BP/1/5207), *Fugusuchus hejiapanensis* (43.4%: Cheng, 1980: fig. 22), *Euparkeria capensis* (47.0% in SAM-PK-5867) and *Chanaresuchus bonapartei* (53.7% in MCZ 4039; 54.9% in MCZ 4037). The skull of PIN 2394/5 is 2.5 times longer anteroposteriorly than its maximum dorsoventral height, representing a ratio intermediate between those present in *Erythrosuchus africanus* (ratio of 2.0 in BP/1/5207) and *Teyujagua paradoxa* (ratio 3.3 in UNIPAMPA 653 cast) and proterosuchids (e.g. *Proterosuchus fergusi*: ratios of 3.3 in RC 96, 3.4 in BSPG 1934 VIII 514, 3.2 in GHG 231; “*Chasmatosaurus*” *yuani* ratio of 3.4 in IVPP V4067).

The external naris is situated near the anterior tip of the snout and approximately level with the mid-height of the skull, and its ventral margin extends ventral to the level of the ventral border of the antorbital fenestra (Ochev, 1981). By contrast, in *Erythrosuchus africanus* (Gower, 2003; BP/1/5207) and *Shansisuchus shansisuchus* (Wang *et al.*, 2013: fig. 2) the external naris is situated above the level of the mid-height of the skull and its ventral margin is level with the ventral border of the antorbital fenestra. The complete outline of the external naris of PIN 2394/5 cannot be determined because the anterior end of the nasal is missing (Ochev, 1981: fig. 3; contra Ochev, 1958: fig. 1). However, the preserved premaxillary part of the opening suggests that the naris was oval, with its main axis oriented from anteroventral to posterodorsal, as also occurs but with a lower degree of diagonal orientation in *Erythrosuchus africanus* (Gower, 2003; BP/1/5207) and *Shansisuchus shansisuchus* (Wang *et al.*, 2013: fig. 2). The large and plate-like postnarial process of the premaxilla excludes the maxilla from participation in the border of the

external naris (Ochev, 1981), resembling the condition of several early archosauromorphs (e.g. *Shringasaurus indicus*: Sengupta *et al.*, 2017, ISIR 793; *Teyujagua paradoxa*: Pinheiro *et al.*, 2016, UNIPAMPA 653 cast; *Proterosuchus fergusi*: RC 96; *Erythrosuchus africanus*: BP/1/5207; *Euparkeria capensis*: Ewer, 1965). It is not possible to determine the absence or presence of a septomaxilla because the relevant area of the skull is severely damaged in PIN 2394/5.

A notch interrupts the alveolar margin of the cranium between the premaxilla and the maxilla (contra Ochev, 1958: fig. 1, 1981: fig. 3) (Figs. 2, 4, 5). The antorbital fenestra is 70.8 mm long and 53.4 mm high, and its anteroposterior length is 16.1% of the total length of the skull, resembling the condition in *Proterosuchus fergusi* (16.2% in SAM-PK-11208; 15.3% in BP/1/3993; 15.7% in RC 96; 15.2% in BSPG 1934 VIII 514), “*Chasmatosaurus*” *yuani* (15.8% in IVPP V4067), *Fugusuchus hejiapanensis* (16.9%: Cheng, 1980: fig. 22), *Erythrosuchus africanus* (18.2% in BP/1/5207) and *Chanaresuchus bonapartei* (14.0% in MCZ 4038), but contrasting with the proportionally longer antorbital fenestra of *Euparkeria capensis* (26.7% in SAM-PK-5867). The opening is trapezoidal, with the main axis oriented from anteroventral to posterodorsal (Ochev, 1981). This unusual outline of the antorbital fenestra is associated with the strong increase in the dorsoventral height of the horizontal process of the maxilla towards its posterior end. By contrast, in *Erythrosuchus africanus* (BP/1/5207), *Proterosuchus fergusi* (BP/1/4016, RC 96), “*Chasmatosaurus*” *yuani* (IVPP V2719, V4067), *Fugusuchus hejiapanensis* (Cheng, 1980: fig. 22; GMB V 313 photographs), *Euparkeria capensis* (SAM-PK-5867), and *Tasmaniosaurus triassicus* (UTGD 54655) the main axis of the antorbital fenestra is approximately horizontal. The antorbital fenestra of the holotype of *Garjainia prima* is bordered by the maxilla anteriorly, ventrally and anterodorsally and by the lacrimal posterodorsally (Ochev, 1981: fig. 3). The

jugal does not participate in the border of the antorbital fenestra. The jugal is also excluded from the border of the fenestra in *Erythrosuchus africanus* (Gower, 2003: fig. 1a; BP/1/5207), but participates in the posteroventral border of the opening in *Proterosuchus fergusi* (RC 96), “*Chasamatosaurus*” *yuani* (IVPP V4067), and *Euparkeria capensis* (SAM-PK-5867).

The orbit is oval, considerably dorsoventrally taller (98.6 mm) than anteroposteriorly long (ca. 52 mm), resembling the condition in *Erythrosuchus africanus* (BP/1/5207), *Proterosuchus fergusi* (RC 96), “*Chasamatosaurus*” *yuani* (IVPP V4067) and *Fugusuchus hejiapanensis* (Cheng, 1980: fig. 22), but contrasting with the sub-circular orbits of *Prolacerta broomi* (BP/1/471), *Teyujagua paradoxa* (UNIPAMPA 653 cast), and *Euparkeria capensis* (SAM-PK-5867). The main axis of the orbit of the holotype of *Garjainia prima* is mainly dorsoventrally oriented, but with a minor posterior component, as also occurs in other early archosauriforms (e.g. *Erythrosuchus africanus*: BP/1/5207; *Proterosuchus fergusi*: SAM-PK-11208, RC 96; “*Chasamatosaurus*” *yuani*: IVPP V4067; *Fugusuchus hejiapanensis*: Cheng, 1980: fig. 22). The border of the orbit is formed primarily by the jugal, lacrimal, prefrontal, and postorbital with minor contributions from the frontal and postfrontal (Ochev, 1981), resembling the condition in *Erythrosuchus africanus* (Gower, 2003; BP/1/5207). In *Proterosuchus fergusi* (BP/1/4016, SAM-PK-K10603, BSPG 1934 VIII 514), *Guchengosuchus shiguaiensis* (IVPP V8808), and *Euparkeria capensis* (SAM-PK-5867) the frontals participate more broadly in the dorsal border of the orbit than in the holotype of *Garjainia prima* and in *Erythrosuchus africanus* (Gower, 2003).

The infratemporal fenestra is the largest opening of the skull, with an anteroposterior length of 95.3 mm and a height of 99.2 mm. It is trapezoidal and occupies

most of the lateral surface of the postorbital area of the skull in lateral view, as is also the case in other early archosauromorphs (e.g. *Teyujagua paradoxa*: UNIPAMPA 653 cast; *Proterosuchus fergusi*: BP/1/4016, RC 96; “*Chasmatosaurus*” *yuani*: IVPP V4067; *Euparkeria capensis*: SAM-PK-5867; *Prolacerta broomi*: BP/1/471; *Fugusuchus hejiapanensis*: Cheng, 1980: fig. 22). The maximum anteroposterior length of the infratemporal fenestra of the holotype of *Garjainia prima* is 21.6% of the total length of the skull, and the opening is only slightly dorsoventrally taller than anteroposteriorly long. By contrast, in *Teyujagua paradoxa* (Pinheiro *et al.*, 2016: fig. 2), *Proterosuchus fergusi* (BP/1/4016, 4224, SAM-PK-11208, RC 96, BSPG 1934 VIII 514, GHG 231), “*Chasmatosaurus*” *yuani* (Young, 1978: fig. 3), and *Fugusuchus hejiapanensis* (Cheng, 1980: fig. 22) the infratemporal fenestra is considerably longer than tall. Conversely, in *Erythrosuchus africanus* (BP/1/5207) and *Euparkeria capensis* (SAM-PK-5867) the infratemporal fenestra is considerably taller than long. The infratemporal fenestra of the holotype of *Garjainia prima* is bordered by the jugal, quadratojugal, squamosal and postorbital, and the quadrate does not participate in the posterior border of the opening because of the contact between the ventral process of the squamosal and the dorsal process of the quadratojugal (Ochev, 1981), as also occurs in other early archosauriforms (e.g. *Erythrosuchus africanus*: BP/1/5207; *Euparkeria capensis*: SAM-PK-5867).

The supratemporal fenestra is 47.4 mm long and 33.4 mm wide, subtriangular in dorsal view, with a lateral border that is parallel to the anteroposterior midline axis of the skull (Figs. 6, 7), contrasting with the anteromedially to posterolaterally oriented lateral border reconstructed by Ochev (1981). The supratemporal fenestra is bordered by the squamosal, postorbital and parietal, without participation of the postfrontal anteriorly (Ochev, 1981). Supratemporals are absent in PIN 2394/5, and also in *Erythrosuchus*

africanus (Gower, 2003; BP/1/5207), *Euparkeria capensis* (Ewer, 1965; SAM-PK-5867), and all more crownward archosauriforms (character 13 in Dilkes & Sues, 2009; character 145 in Nesbitt, 2011).

Dermal skull roof

Premaxilla. The left premaxilla is preserved in articulation (Figs. 4, 5) and the right element is detached from the rest of the skull (Fig. 8). The left premaxilla lacks most of its prenasal process, and its alveolar margin is severely damaged. The right premaxilla lacks the distal ends of the prenasal and postnasal processes. The premaxillary body is subrectangular and moderately anteroposteriorly long, being 1.82 times longer than the distance between the alveolar margin and the ventral border of the external naris. The ratio observed in PIN 2394/5 is only slightly greater than that of the proportionately slightly shorter premaxillae in the erythrosuchids *Erythrosuchus africanus* (1.50 in BP/1/5207; 1.65 in BP/1/4526) and *Shansisuchus shansisuchus* (1.07–1.33, Young, 1964: figs. 8, 9). By contrast, the ratio is considerably greater in *Tasmaniosaurus triassicus* (>2.21 in UTGD 54655), *Teyujagua paradoxa* (2.33 in UNIPAMPA 653 cast), *Sarmatosuchus otschevi* (2.29 in PIN 2865/68), *Euparkeria capensis* (2.61 in UMZC T6921), *Garjainia madiba* (2.27 in BP/1/6232l; 2.23 in BP/1/6232n), and, in particular, *Prolacerta broomi* (3.80 in BP/1/471), *Archosaurus rossicus* (3.72 in PIN 1100/55) and *Proterosuchus fergusi* (3.50 in RC 59; 3.19 in SAM-PK-11208; 3.03 in BP/1/3993; 3.03 in TM 201). The main axis of the premaxillary body of PIN 2394/5 is moderately downturned in comparison with the main axis of the skull, resembling the condition of *Prolacerta broomi* (BP/1/471), *Teyujagua paradoxa* (Pinheiro *et al.*, 2016: fig. 2), *Erythrosuchus africanus* (BP/1/5207), and probably *Tasmaniosaurus triassicus* (UTGD 54655). By contrast, in *Proterosuchus fergusi*

(RC 59, 96, BP/1/3993, 4016, BSPG 1934 VIII 514, GHG 231, SAM-PK-11208, TM 201), “*Chasmatosaurus*” *yuani* (IVPP V4067, V90002), and probably *Sarmatosuchus otschevi* (Gower & Sennikov, 1997) and *Archosaurus rossicus* (Tatarinov, 1960) the premaxillary body is strongly downturned and extended far below the level of the alveolar margin of the maxilla (Figs. 2, 4, 5). In *Euparkeria capensis* the main axis of the premaxillary body is parallel to the main axis of the skull (SAM-PK-5867). The alveolar margin of the right premaxilla of the holotype of *Garjainia prima* is slightly damaged, but it was clearly approximately straight in lateral view. The condition in the left premaxilla cannot be determined because of breakage of the alveolar margin, primarily at its anterior and posterior ends. The straight premaxillary alveolar margin of PIN 2394/5 closely resembles the condition present in a referred specimen of *Garjainia prima* (PIN 951/63) and *Garjainia madiba* (BP/1/5760a, 62321), but differs from the convex alveolar margin in *Erythrosuchus africanus* (BP/1/5207) and *Shansisuchus shansisuchus* (Young, 1964: figs. 8, 9) in lateral view. The anterior margin of the premaxillary body forms almost a right angle with the alveolar margin of the bone, resembling the condition present in a referred specimen of *Garjainia prima* (PIN 951/63), *Erythrosuchus africanus* (Gower, 2003: fig. 4), *Sarmatosuchus otschevi* (PIN 2865/68), and at least some specimens of *Shansisuchus shansisuchus* (Young, 1964: fig. 9). In ventral view, the alveolar margin of the premaxilla of the holotype of *Garjainia prima* is only weakly convex laterally, but the degree of curvature was probably greater in life and has been modified by post-mortem compression.

The body of the right premaxilla of PIN 2394/5 has two mainly anteriorly opening neurovascular foramina on its anterior surface, but only one is partially visible in lateral view (Fig. 8A: ‘f’). The equivalent area of the left premaxilla is not preserved. The more ventral foramen is situated well below the mid-height of the premaxillary body and is

subcircular. The more dorsal foramen is immediately above the mid-height of the premaxillary body, anteroventrally opening and oval, with a dorsoventrally extending main axis. A similar condition is present in the premaxillae of a referred specimen of *Garjainia prima* (PIN 951/63), in which the positions of the foramina are the same, but the dorsal foramen is subcircular rather than oval. The lateral surface of the premaxillary body of the holotype of *Garjainia prima* is anteroposteriorly convex above the first and last three alveoli. These two convexities are separated by a shallow concavity above the second alveolus. This concavity does not reach the ventral margin of the bone, where the lateral surface of the bone is also convex. The same concavity above the second alveolus is present in a referred specimen of *Garjainia prima* (PIN 951/63). The right premaxillary body of the holotype of *Garjainia prima* possesses a faint longitudinal groove along most of its lateral surface, but not reaching the anterior surface of the bone (Fig. 8A: 'lg'). The groove is also present on the left premaxilla, seen mainly in the posterior region of the premaxillary body because the rest of the lateral surface of the bone is not well preserved. The groove extends primarily anteroposteriorly and is dorsoventrally narrow (3 mm) along most of its length, being slightly deeper at its posterior end. The groove is straight along most of its length and curves dorsally at its most anterior portion, slightly anterior to the level of the posterior margin of the first alveolus. A referred specimen of *Garjainia prima* (PIN 951/63) and at least some specimens of *Garjainia madiba* (BP/1/62321) possess a groove that is very similar in morphology and position, but slightly more deeply impressed into the surface of the premaxilla, to that of the holotype of *Garjainia prima*. By contrast, a similar longitudinal groove is not present on the premaxillary body of *Prolacerta broomi* (BP/1/471), *Proterosuchus fergusi* (RC 59, SAM-PK-11208, BP/1/3993, TM 201), *Archosaurus rossicus* (PIN 1100/55), *Sarmatosuchus otschevi* (PIN 2865/68),

Erythrosuchus africanus (BP/1/5207, 4526), *Shansisuchus shansisuchus* (IVPP V2501, V2504), or *Euparkeria capensis* (UMZC T6921). The groove in *Garjainia* does not contact the posterior margin of the premaxillary body, contrasting with the premaxillary groove of *Azendohsaurus madagaskarensis* (Flynn *et al.*, 2010).

The lateral surface of the premaxilla of PIN 2394/5 possesses two oval neurovascular foramina situated considerably below the mid-height of the premaxillary body above the posterior half of the third alveolus and slightly posterior to the mid-length of the second alveolus. Both foramina are extended ventrally as short sulci that open into the longitudinal groove described above. Similar foramina are present in a referred specimen of *Garjainia prima* (PIN 951/63), but in this specimen the sulci are deeper and broader and the first of these two foramina (i.e. the foramen that is positioned above the third alveolus in the holotype of *Garjainia prima*) is level with the posterior half of the fourth alveolus. In the referred specimen of *Garjainia prima* the sulcus extending from the foramen above the second alveolus extends ventrally beyond the level of the longitudinal groove (PIN 951/63). The same condition seems to be present in the holotype of *Garjainia prima*, but this cannot be determined with certainty because of poor preservation of the lateral surfaces of the premaxillae. The narial fossa is poorly developed ventrally and weakly defined on the lateral surface of the premaxillary body (Fig. 8: 'nf'), resembling the condition observed in most early archosauromorphs (e.g. *Teyujagua paradoxa*: UNIPAMPA 653 cast; *Prolacerta broomi*: BP/1/471; *Proterosuchus fergusi*: RC 59, 96, SAM-PK-11208, TM 201; *Sarmatosuchus otschevi*: PIN 2865/68; *Erythrosuchus africanus*: BP/1/5207, 4526). The lateral surfaces of the anteroventral corners of both premaxillary bodies of PIN 2394/5 are damaged, and their morphologies cannot be accurately determined.

The prenarial (= ascending) process of the premaxilla of the holotype of *Garjainia prima* has an anteroposteriorly narrow base in lateral view, associated with a shallow, weakly anteriorly extended narial fossa (Fig. 8: 'prnp'), resembling the condition in *Prolacerta broomi* (BP/1/471), *Sarmatosuchus otschevi* (PIN 2865/68), *Erythrosuchus africanus* (BP/1/5207, 4526), *Shansisuchus shansisuchus* (Young, 1964: figs. 8, 9), *Garjainia madiba* (NM QR 3257), and a referred specimen of *Garjainia prima* (PIN 951/63). By contrast, the base of the prenarial process is proportionally broader and the narial fossa is considerably more extended anteriorly in the proterosuchids *Proterosuchus fergusi* (RC 59, 96, SAM-PK-11208, TM 201) and *Archosaurus rossicus* (PIN 1100/55) the base of the prenarial process is proportionally broader and the narial fossa is considerably more extended anteriorly. In PIN 2394/5 the narial fossa is well defined anteriorly by a thickening that extends along the lateral surface of the prenarial process (Fig. 8A: 'nf'). The narial fossa is concave at the base of the prenarial process and becomes gradually planar towards the distal end of the process. On the portion of the narial fossa at the base of the prenarial process there are two small foramina, one anterior and one posterior to the level of the anterior margin of the external naris. The more anterior foramen is sub-circular and the more posterior is oval. The more anterior foramen is present in a referred specimen of *Garjainia prima* (PIN 951/63), but the posterior foramen is absent. The prenarial process in PIN 2394/5 is elongate and forms at least the majority of the dorsal border of the external naris, resembling the condition in *Proterosuchus fergusi* (RC 59, 96, TM 201), *Garjainia madiba* (NM QR 3257), and *Erythrosuchus africanus* (BP/1/5207). However, the distal end of the process is missing in both of the premaxillae of PIN 2394/5 and the posterodorsal limit of the bone cannot be determined. The prenarial process curves posteriorly along its preserved length. The prenarial and postnarial processes do not intersect one another

posterodorsal to the naris in lateral view, similar to the condition in *Erythrosuchus africanus* (BP/1/5207) and *Euparkeria capensis* (SAM-PK-5867), and contrasting with *Proterosuchus fergusi* (RC 59, 96, TM 201), “*Chasmatosaurus*” *yuani* (IVPP V90002) and probably *Sarmatosuchus otschevi* (Gower & Sennikov, 1997) and *Archosaurus rossicus* (PIN 1100/55). The contact between the prenarial process of the premaxilla and the nasal is not preserved.

There is a clear inflexion between the alveolar margin and the base of the postnarial process of the premaxilla of PIN 2394/5, forming an angle of approximately 120°, resembling the condition in *Erythrosuchus africanus* (BP/1/4226, 5207), referred specimens of *Garjainia prima* (PIN 951/63), *Garjainia madiba* (BP/1/5760a, 6232n), and *Euparkeria capensis* (SAM-PK-5867, UMZC T921). By contrast, in *Shansisuchus shansisuchus* the transition between the premaxillary body and the postnarial process is marked by a strongly dorsoventrally developed and posteriorly facing concavity that results in a more dorsally positioned and dorsoventrally narrower postnarial process (Young, 1964: figs. 8, 9). In *Prolacerta broomi* (BP/1/471), *Teyujagua paradoxa* (UNIPAMPA 653 cast), *Proterosuchus fergusi* (RC 59, SAM-PK-11208, TM 201), *Archosaurus rossicus* (PIN 1100/55), and *Sarmatosuchus otschevi* (PIN 2865/68) the alveolar margin and the ventral margin of the postnarial process are continuous without a clear inflexion. The postnarial process of PIN 2394/5 is posterodorsally oriented with respect to the long axis of the skull (Fig. 8: ‘ponp’), resembling the condition in *Erythrosuchus africanus* (BP/1/5207). The postnarial process forms the posteroventral border of the external naris and tapers posteriorly, ending in a sub-triangular tip. This process extends considerably posterior to the posterior border of the external naris. The lateral surface of the postnarial process of the

right premaxilla is mostly covered by matrix and the postnarial process of the left side is missing. Thus, it is not possible to describe details of the lateral surface of the process.

The medial surface of the premaxilla possesses a subtriangular and slightly rugose symphyseal area on the preserved portion of the prenasal process and the anterior half of the premaxillary body (Fig. 8B: ‘sy’), which tapers onto the palatal process (Fig. 8B: ‘pp’). As a result, the bases of the palatal processes would have contacted each other, as occurs in other archosauriforms (e.g. *Erythrosuchus africanus*: NHMUK R3592; a referred specimen of *Garjainia prima*: PIN 951/63). The posterior half of the palatal process curves laterally in dorsal or ventral view, representing the point at which the palatal processes diverged from each other. The base of the palatal process is placed above the posterior margin of the third alveolus. The process tapers both in dorsoventral height and transverse width towards its posterior end. The process is gently curved ventrally in medial view and its main axis is sub-parallel to the alveolar margin of the bone, resembling the condition in *Erythrosuchus africanus* (NHMUK R3592). By contrast, in *Proterosuchus fergusi* (TM 201), “*Chasmatosaurus*” *yuani* (IVPP V90002), *Sarmatosuchus otschevi* (PIN 2865/68), *Archosaurus rossicus* (PIN 1100/55), and *Garjainia madiba* (BP/1/5760a) the long axis of the palatal process of the premaxilla posteriorly intercepts that of the alveolar margin (Gower & Sennikov, 1997). The palatal process of PIN 2394/5 extends posteriorly very slightly beyond the posterior end of the alveolar margin of the premaxillary body. This clearly differs from the considerably more posteriorly extended palatal processes of *Proterosuchus fergusi* (TM 201) and *Sarmatosuchus otschevi* (PIN 2865/68), the tips of which are visible in lateral view when the premaxilla is disarticulated from the rest of the skull. The relative lengths of the palatal processes of the premaxilla and maxilla in PIN 2394/5 suggest that the processes would have contacted each other, with the premaxillary

process lying dorsal to the maxillary process. The medial surface of the postnarial process of the premaxilla is almost flat and makes extensive contact with the nasal.

The alveolar margin of the premaxilla bears five tooth positions (Fig. 8C), as also occurs in small specimens of *Proterosuchus fergusi* (Ezcurra & Butler, 2015b; RC 59), and in *Prolacerta broomi* (Modesto & Sues, 2004), a referred specimen of *Garjainia prima* (PIN 951/63), *Shansisuchus shansisuchus* (Young, 1964) and *Erythrosuchus africanus* (Gower, 2003). By contrast, in medium to large-sized specimens of *Proterosuchus fergusi* specimens (Ezcurra & Butler, 2015b; BP/1/3993, SAM-PK-K140, TM 201), and in “*Chasmatosaurus*” *yuani* (IVPP V90002, V4067), *Sarmatosuchus otschevi* (Gower & Sennikov, 1997; PIN 2865/68), *Archosaurus rossicus* (Tatarinov, 1960; PIN 1100/55), *Tasmaniosaurus triassicus* (Ezcurra, 2014; UTGD 54655), and *Garjainia madiba* (Gower *et al.*, 2014; BP/1/62321) the premaxilla has six or more tooth positions. An almost complete tooth is preserved in PIN 2394/5 in the fifth alveolus of the left premaxilla, whereas in the right premaxilla an erupting tooth is preserved in the second alveolus and the base of a crown in the fifth. The teeth possess a typical thecodont tooth implantation, with a root that fits into a deep socket and a clear distinction between the base of the crown and the tooth-bearing bone, as occurs in *Erythrosuchus africanus* (Gower, 2003; NHMUK R3592). By contrast, *Prolacerta broomi* (Modesto & Sues, 2004), *Proterosuchus fergusi* (BSPG 1934 VIII 514, RC 59, SAM-PK-11208, TM 201), *Tasmaniosaurus triassicus* (UTGD 54655), *Sarmatosuchus otschevi* (PIN 2865/68), referred specimens of *Garjainia prima* (PIN 951/63), and some teeth of *Azendohsaurus madagaskariensis* (UA 8-7-98-284) possess an ankylothecodont tooth implantation, in which the crowns are fused to the alveolar margin of the premaxilla via thin bony ridges. The posterior end of the alveolar

margin of the premaxilla is edentulous; the length of this edentulous region is equal to the length of one alveolus.

The premaxillary tooth crowns are labiolingually compressed and slightly distally curved. The most complete, fully erupted crown has a convex mesial margin and a concave distal margin in labial or lingual view, but both margins of the erupting crown are convex close to its apex. The latter condition may be correlated with the more anterior position of this crown within the premaxillary tooth row. The preserved crowns possess a carina and denticles on both mesial and distal margins. The denticles are subrectangular in labial view and perpendicular to the main axis of the crown, as occurs in *Teyujagua paradoxa*, *Tasmaniosaurus triassicus*, and usually in carnivorous archosauriforms (Nesbitt, 2011; Ezcurra, 2014, 2016; Pinheiro *et al.*, 2016). By contrast, the teeth of most non-archosauriform diapsids are completely devoid of mesial or distal denticles (e.g. *Youngina capensis*: GHG K106; *Protorosaurus speneri*: Gottman-Quesada & Sander, 2009; *Macrocnemus bassanii*: PIMUZ T4822; *Prolacerta broomi*: BP/1/471). The preserved premaxillary tooth crowns lack enamel ornamentation or ridges on their labial and lingual surfaces, similar to the condition in other early archosauromorphs (e.g. *Macrocnemus bassanii*: PIMUZ T4822; *Prolacerta broomi*: BP/1/471; *Proterosuchus fergusi*: SAM-PK-11208; *Erythrosuchus africanus*: BP/1/5207, NHMUK R3592; referred specimens of *Garjainia prima*: PIN 951/63).

Maxilla. The maxillae are exposed in lateral and ventral views, but small portions of their medial surfaces, adjacent to the alveolar margin, are also exposed (Figs. 4–7). The lateral surface of the maxilla is ornamented by multiple anastomosing grooves that extend onto the lateral surface of the lacrimal. This ornamentation is absent on the lateral surface of the

anterior tip of the maxilla and the maxillary and lacrimal surfaces within the antorbital fossa. The maxilla possesses a subrectangular anterior process (= the part of the maxilla anterior to the ascending or dorsal process), which is slightly dorsoventrally taller (at its tallest point, adjacent to its base) than anteroposteriorly long. The anterior process is very well differentiated from the ascending process by a clear inflexion (Figs. 2, 4, 5), resembling the condition in referred specimens of *Garjainia prima* (PIN 951/32), *Erythrosuchus africanus* (Gower, 2003; BP/1/2529, 5207), *Shansisuchus shansisuchus* (Young, 1964: figs. 10, 11), and *Chalishevia cothurnata* (PIN 4366/1). By contrast, in *Proterosuchus fergusi* (BSPG 1934 VIII 514, RC 59, 96, SAM-PK-11208, TM 201), *Tasmaniosaurus triassicus* (UTGD 54655), *Fugusuchus hejiapanensis* (Cheng, 1980: fig. 22), “*Chasmatosaurus*” *yuani* (IVPP V4067, V90002), and *Guchengosuchus shiguaiensis* (IVPP V8808) the dorsal margin of the anterior process is smoothly continuous with that of the ascending process, with no sharp inflexion. In PIN 2394/5, referred specimens of *Garjainia prima* (PIN 951/32), *Shansisuchus shansisuchus* (Young, 1964: figs. 10, 11), and, at least partially, in *Chalishevia cothurnata* (PIN 4366/1) the dorsal margin of the anterior process is subparallel to the longitudinal axis of the skull. By contrast, the latter character state seems to be variable in *Erythrosuchus africanus*, in which the dorsal margin of the process has either a strong anteroventral slope (BP/1/5207, SAM-PK-1098), is almost horizontal (BP/1/2529), or possesses an intermediate condition (NHMUK R3592). The dorsal half of the anterior process of the maxillae of PIN 2394/5, referred specimens of *Garjainia prima* (PIN 951/32), and *Erythrosuchus africanus* (BP/1/5207, SAM-PK-K1098, NHMUK R3592) lacks the large, well-defined fossa that extends along the entire ventral border of the second antorbital fenestra in *Chalishevia cothurnata* (PIN 4366/1) and *Shansisuchus shansisuchus* (IVPP V2504, V2505).

The anteriormost portion of the ventral margin of the maxilla possesses an edentulous region approximately 1.2 cm long (Figs. 2, 4, 5), resembling the condition in *Chalishevia cothurnata* (PIN 4366/1), “*Chasmatosaurus*” *yuani* (IVPP V4067, V90002), *Proterosuchus goweri* (NM QR 880), and probably *Erythrosuchus africanus* (BP/1/5207). The anterior margins of the anterior processes of both maxillae possess an anteriorly opening notch situated below the mid-height of the process that extends onto the lateral surface of the bone as a sulcus that is oriented mainly longitudinally and slightly posterodorsally (Figs. 2, 4, 5B: ‘lg’). The sulcus is slightly dorsoventrally higher anteriorly and extends posteriorly to the level of the posterior margin of the second maxillary alveolus. The sulcus is deeper and better defined on the right maxilla of PIN 2394/5. An extremely similar condition is present in *Chalishevia cothurnata* (PIN 4366/1), in which the notch is deeper at its posterior end and the sulcus is more dorsally oriented than in PIN 2394/5. In a referred specimen of *Garjainia prima* (PIN 951/32) the sulcus is also present, but is posterodorsally oriented, as in *Chalishevia cothurnata*. The presence of the anterior notch cannot be determined in available maxillae of the referred specimens of *Garjainia prima* (PIN 951/32, 34, 55) due to damage. Both the notch and the sulcus are absent in *Erythrosuchus africanus* (BP/1/5207, SAM-PK-1098).

A series of five neurovascular foramina are present on the lateral surface of the anterior and horizontal processes (= main body of the maxilla), lying 1 to 2 cm above the alveolar margin of the bone (Fig. 2, 4, 5). The series possibly also included additional foramina that are not discernable due to damage to the lateral surfaces of the maxillae. Similar neurovascular foramina are widespread taxonomically among other early archosauromorphs (e.g. *Proterosuchus fergusi*: BP/1/4016, RC 59, 96, SAM-PK-11208; *Fugusuchus hejiapanensis*: GMB V 313 photographs; *Guchengosuchus shiguaiensis*: IVPP

V8808; *Erythrosuchus africanus*: BP/1/5207; referred specimens of *Garjainia prima*: PIN 951/34; *Chalishevia cothurnata*: PIN 4366/1; *Shansisuchus shansisuchus*: IVPP V2501, V2503; *Euparkeria capensis*: SAM-PK-5867). In particular, in the holotype and referred specimens of *Garjainia prima*, *Guchengosuchus shiguaiensis*, *Erythrosuchus africanus*, *Shansisuchus shansisuchus*, and *Chalishevia cothurnata* the neurovascular foramina open lateroventrally. By contrast, in *Proterosuchus fergusi*, *Fugusuchus hejiapanensis*, and *Euparkeria capensis* the neurovascular foramina are circular pits that open directly laterally. At the level above the third and fourth alveolus of the holotype of *Garjainia prima* there is a foramen that is ventrally extended as a pair of well-defined sulci, forming an inverted V-shaped structure. This resembles the condition in referred specimens of *Garjainia prima* (PIN 951/34) and may be a less strongly developed version of the broader and longer sulci that extend ventrally from neurovascular foramina in *Erythrosuchus africanus* (BP/1/5207), *Shansisuchus shansisuchus* (IVPP V2503), and *Chalishevia cothurnata* (PIN 4366/1). The more posterior neurovascular foramina of PIN 2394/5 are not ventrally extended as sulci. The anterior process of the maxilla lacks the large, oval neurovascular foramen that it is next to the anterior margin of the bone in some non-archosaurian archosauromorphs, such as *Protorosaurus speneri* (Gottman-Quesada & Sander, 2009), *Prolacerta broomi* (Modesto & Sues, 2004), and some specimens of *Proterosuchus fergusi* (SAM-PK-11208).

The ascending process of the maxilla of PIN 2394/5 is almost vertical and anteroposteriorly short at its base. It possesses a strongly anteroposteriorly convex lateral surface, which forms a vertical tuberosity (also extending onto the nasal and hereafter referred to as the maxillo-nasal tuberosity) that defines the anterior margin of the antorbital fossa (Figs. 2, 4, 5: 'mnt'). As a result, the ascending process is a pillar-like structure, as

also occurs in referred specimens of *Garjainia prima* (PIN 951/32), *Erythrosuchus africanus* (BP/1/2529, 5207), *Shansisuchus shansisuchus* (IVPP V2501, V2503), and *Chalishevia cothurnata* (PIN 4366/1). By contrast, in other archosauromorphs the ascending process of the maxilla is plate-like, with a planar or slightly convex external surface (e.g. *Prolacerta broomi*: BP/1/471; *Proterosuchus fergusi*: BP/1/4016, BSPG 1934 VIII 514; *Fugusuchus hejiapanensis*: Cheng, 1980: fig. 22, GMB V 313 photographs; *Euparkeria capensis*: SAM-PK-5867). The maxillo-nasal tuberosity extends ventrally well beyond the level of the ventral border of the antorbital fenestra and delimits posteriorly the anterior process of the maxilla along its dorsal half. The ventralmost portion of the maxillo-nasal tuberosity also defines, along its posterior margin, a shallow oval—considerably taller than long—depression beneath the antorbital fenestra.

The ascending process of PIN 2394/5 curves posteriorly and delimits a concave anterodorsal border of the antorbital fenestra. The antorbital fossa is broadly extended onto the lateral surface of the ascending process posterior to the maxillo-nasal tuberosity (Figs. 2, 4, 5: ‘anfo’). As a result, the antorbital fossa extends along the dorsal two-thirds of the ascending process, resembling the condition in *Euparkeria capensis* (SAM-PK-5867). By contrast, in *Erythrosuchus africanus* (BP/1/5207), *Shansisuchus shansisuchus* (IVPP V2501, V2503), and *Chalishevia cothurnata* (PIN 4366/1) the antorbital fossa extends along the entire posterior margin of the ascending process. In the available maxillae of referred specimens of *Garjainia prima* only the base of the ascending process is preserved (PIN 951/32) and the antorbital fossa is absent on its lateral surface. Accordingly, as far as can be determined, the condition in these referred specimens is in agreement with the holotype. The maxillary antorbital fossa continues dorsally onto the lateral surface of the anterior process of the lacrimal and is roofed dorsally by the lateral extension of the nasal,

as also occurs in *Erythrosuchus africanus* (BP/1/5207) and *Euparkeria capensis* (SAM-PK-5867). The ascending process of the maxilla possesses a partially interlaced contact with the nasal, in which the nasal folds medially onto the ascending process of the maxilla and part of the posterodistal tip of the nasal is covered laterally by the maxilla, as is also the case in *Chalishevia cothurnata* (PIN 4366/1) and *Erythrosuchus africanus* (BP/1/5207). A diagonal, slightly ventrally curved change in level of the surface of the antorbital fossa probably represents the suture between the ascending process of the maxilla and the anterior process of the lacrimal. The shape and position of this probable suture is the same on both sides of the skull and is in agreement with the condition in *Erythrosuchus africanus* (BP/1/5207). Although we cannot rule out completely the possibility that this is an artefact due to breakage, we consider it likely represents the maxilla-lacrimal contact.

The horizontal process of the maxilla increases in dorsoventral height dramatically towards its contact with the ventral process of the lacrimal. As a result, the ventral border of the antorbital fenestra slopes from anteroventral to posterodorsal at approximately 45° to the horizontal. This condition differs from the much more moderate increase in dorsoventral height of the horizontal process of *Proterosuchus fergusi* (BSPG 1934 VIII 514, RC 96, SAM-PK-11208), *Fugusuchus hejiapanensis* (Cheng, 1980: fig. 22), *Tasmaniosaurus triassicus* (UTGD 54655), *Guchengosuchus shiguaiensis* (IVPP V8808), *Erythrosuchus africanus* (BP/1/5207), *Shansisuchus shansisuchus* (IVPP V2505), and *Chalishevia cothurnata* (PIN 4366/1). It is striking to note that the morphology of the ventral border of the antorbital fenestra of *Garjainia prima* is almost identical to that of the ventral border of the antorbital fossa of *Chalishevia cothurnata* (PIN 4366/1), suggesting a potential homology between both structures in these species. The dorsal margin of the horizontal process is not preserved in any of the preserved maxillae of the referred

specimens of *Garjainia prima* (PIN 951/32, 34, 55). The horizontal process of PIN 2394/5 completely lacks an antorbital fossa, resembling the condition in *Euparkeria capensis* (SAM-PK-5867). By contrast, in *Erythrosuchus africanus* (Gower, 2003; BP/1/4680, 5207), *Chalishevia cothurnata* (PIN 4366/1), and *Shansisuchus shansisuchus* (IVPP V2503) the antorbital fossa is present on the maxillary horizontal process.

The alveolar margin of the horizontal process of PIN 2394/5 is sigmoid in lateral view, with an anteroposteriorly convex anterior half and a concave posterior one, as also occurs in referred specimens of *Garjainia prima* (PIN 951/34), *Erythrosuchus africanus* (BP/1/4680, 5207), and *Chalishevia cothurnata* (PIN 4366/1). The horizontal process of the maxilla extends posteriorly up to the level of the posterior three-quarters of the orbit, and the ventral margin of its posteriormost tip has a 1.9 cm long edentulous region, equivalent to the length of the three most posterior maxillary tooth positions. The posterior tip of the horizontal process of PIN 2394/5 is obscured by the jugal in lateral view (Fig. 5). The sutures between the maxilla and lacrimal and jugal, respectively, are entirely visible on the right side of the skull and partially on the left side (Figs. 4, 5). The suture between the horizontal process of the maxilla and the lacrimal is posteroventrally oriented and lies well above the level of the ventral border of the antorbital fenestra, resembling the condition in *Euparkeria capensis* (Ewer, 1965). By contrast, in *Proterosuchus fergusi* (BP/1/4016, BSPG 1934 VIII 514, RC 96) and *Erythrosuchus africanus* (BP/1/5207) the contact between the lacrimal and maxilla is level with the ventral border of the antorbital fenestra. The horizontal process of the maxilla of PIN 2394/5 contacts the anterior margin of the jugal in an extensive sub-vertical and slightly interdigitated suture. The jugal completely excludes the maxilla from the orbital margin, as also occurs in several non-archosauriform archosauromorphs (e.g. *Protorosaurus speneri*: Gottman-Quesada & Sander, 2009;

Prolacerta broomi: Modesto & Sues, 2004) and archosauriforms (e.g. *Proterosuchus fergusi*: BP/1/4016, BSPG 1934 VIII 514, RC 96; *Erythrosuchus africanus*: Gower, 2003; *Euparkeria capensis*: Ewer, 1965). The maxilla extends posteriorly below the anterior process and part of the main body of the jugal. The posteriormost tip of the maxilla is covered laterally by the main body of the jugal and contacts the ectopterygoid medially (Fig. 11A, B).

The palatal process of the maxilla extends anteriorly by approximately 1 cm beyond the level of the lateral surface of the anterior process of the maxilla and, as a result, is partially visible in lateral view below the premaxilla-maxilla suture. The anterior half of the palatal process contacts its counterpart medially along the mid-line (Figs. 6, 7: 'mx.pal'), but this contact is likely an artefact of the transverse compression that the skull suffered after burial given that midline contact between maxillary palatal processes is typically restricted to archosaurs (character 32 in Nesbitt 2011). The exposed region of the palatal process has a long axis that is almost parallel to the main longitudinal axis of the skull, but it slopes gently from posterodorsal to anteroventral. It is not possible to determine the dorsoventral height of the palatal process because the process is obscured by the rest of the snout.

The maxillary tooth row extends posteriorly to a point immediately anterior to the level of the mid-length of the orbit, resembling the condition in *Shansisuchus shansisuchus* (Wang *et al.*, 2013: fig. 2). By contrast, in *Erythrosuchus africanus* the maxillary tooth row ends level with the anterior border of the orbit (BP/1/5207). The maxilla of PIN 2394/5 has 14 or possibly 13 tooth positions, resembling the relatively low maxillary tooth counts of *Guchengosuchus shiguaiensis* (IVPP V8808: maxillary tooth count 14 or 15), *Erythrosuchus africanus* (BP/1/5207: maxillary tooth count 11), *Chalishevia cothurnata*

(PIN 4366/1; maxillary tooth count 12 or possibly 13), *Shansisuchus shansisuchus* (Young [1964] described 9 or possibly 10 tooth positions and Wang *et al.* [2013] probably 13 maxillary teeth), and *Euparkeria capensis* (Ewer, 1965; maxillary tooth count 13). By contrast, higher maxillary tooth counts are present in *Tasmaniosaurus triassicus* (UTGD 54655; >21), *Proterosuchus fergusi* (BP/1/3993, BSPG 1934 VIII 514, GHG 231 RC 59, 96, SAM-PK-11208, K140, K10603; maxillary tooth count 20–31, depending of ontogenetic stage, Ezcurra & Butler [2015b]), “*Chasmatosaurus*” *yuani* (>23 in IVPP V90002 and ≥ 29 in IVPP V2719) and *Prolacerta broomi* (BP/1/471, Modesto & Sues, 2004; tooth count 24–25). The largest maxillary teeth of PIN 2394/5 are level with the maxillo-nasal tuberosity. Maxillary interdental plates cannot be observed, but this is likely a result of lack of preservation in the holotype because they are present in referred specimens of *Garjainia prima* (PIN 951/55).

The maxillary tooth implantation of the holotype is fully thecodont, similar to the condition in *Erythrosuchus africanus* (BP/1/2529, 4680). By contrast, in referred specimens of *Garjainia prima* (PIN 951/32, 34, 55) and *Garjainia madiba* (BP/1/5525) at least some maxillary teeth possess an ankylotheodont tooth implantation, resembling the condition in *Prolacerta broomi* (Modesto & Sues, 2004), *Proterosuchus fergusi* (e.g. BSPG 1934 VIII 514, RC 59, TM 201), and *Guchengosuchus shiguaiensis* (IVPP V8808). The maxillary teeth of PIN 2394/5 resemble those of other carnivorous archosauriforms (e.g. *Erythrosuchus africanus*: NHMUK R3592), with distally curved (convex mesially and concave distally) and labiolingually compressed crowns. Both mesial and distal margins of the crown are finely serrated and the denticles are perpendicular to the main axis of the crown. The enamel lacks ornamentation.

Nasal. The nasal extends for approximately half of the total length of the skull (Figs. 3, 6, 7). The lateral surface of the anterior end of the nasal possesses a large, well-defined and sub-triangular facet for reception of the postnarial process of the premaxilla (Fig. 5B: ‘pnf’). A ventral projection, forming the descending process of the nasal, is well developed between the postnarial process of the premaxilla and the ascending process of the maxilla and forms the dorsal half of the snout immediately posterior to the premaxilla-maxilla suture in lateral view (Fig. 5: ‘dpn’). As a result, the posteroventral margin of the postnarial process of the premaxilla contacts the nasal rather than the maxilla, resembling the condition in *Guchengosuchus shiguaiensis* (IVPP V8808), *Erythrosuchus africanus* (BP/1/5207), *Chalishevia cothurnata* (PIN 4366/1), *Shansisuchus shansisuchus* (Young, 1964: figs. 6, 7c), and *Euparkeria capensis* (SAM-PK-5867; Ewer, 1965: fig. 2a). By contrast, in *Proterosuchus fergusi* (RC 59, 96, SAM-PK-11208), *Teyujagua paradoxa* (Pinheiro *et al.*, 2016), and *Prolacerta broomi* (BP/1/471) the entire length of the posteroventral margin of the postnarial process of the premaxilla contacts the maxilla. The ventral projection of the nasal immediately anterior to the ascending process of the maxilla is truncated ventrally in *Chalishevia cothurnata* (PIN 4366/1) and *Shansisuchus shansisuchus* (Young, 1964: figs. 6, 7c) and allows the development of a large secondary antorbital fenestra that it is absent in the holotype of *Garjainia prima* and *Erythrosuchus africanus* (Gower, 2003; BP/1/5207). A secondary antorbital fenestra seems to have been also present in *Guchengosuchus shiguaiensis* because the anterior margin of the ascending process of the maxilla is distinctly concave and lacks a facet for reception of the postnarial process of the premaxilla (Peng, 1991). The maxilla-nasal tuberosity of the ascending process of the maxilla continues on the lateral surface of the nasal and in dorsal view forms a well-developed and rounded lateral projection anterior to the lateral flaring of the

prefrontals on the skull roof, as also occurs in *Erythrosuchus africanus* (BP/1/5207) and *Shansisuchus shansisuchus* (Young, 1964: fig. 6). The portion of the maxillo-nasal tuberosity on the nasal expands anteroposteriorly at the level of the lateral margin of the skull roof. Its anterior extension is very short and posteriorly it roofs the anterodorsal corner of the antorbital fossa and is continuous with the lateral flaring of the lateral margin of the prefrontal.

The dorsal surfaces of the nasals are ornamented by rugosities formed by small, rounded nodules along their preserved portions. The presence or absence of ornamentation on the anteriormost portions of the bones cannot be determined due to damage to the dorsal surfaces. The dorsal ornamentation present on the nasals extends onto the anterior half of the dorsal surfaces of the prefrontals and the median longitudinal fossa of the frontals (see below). The median suture between the nasals is partially discernable along their anterior half and the portion posterior to the level of the maxillo-nasal tuberosity. The suture between the left nasal and prefrontal is only partially discernable, but it is not possible to determine its position on the right side. The nasal has a small lateral process that excludes the anteriormost tip of the prefrontal from the lateral margin of the skull roof, resembling the condition in *Fugusuchus hejiapanensis* (Cheng, 1980: fig. 22; GMB V 313 photographs), *Erythrosuchus africanus* (BP/1/5207, NHMUK R3592), and *Shansisuchus shansisuchus* (Young, 1964: fig. 6). As a result, the nasal possesses a V-shaped suture with the prefrontal anteriorly whereas posteriorly the suture is almost parallel to the sagittal axis of the skull, but with a very low anterolateral-to-posteromedial component. The nasal-frontal suture is strongly interdigitated. A sub-rectangular, well-defined and moderately deep median fossa on the nasals extends from the level of the posterior margin of the maxillo-nasal tuberosity and continues posteriorly onto the anterior two-thirds of the dorsal

surface of the frontals. At the posteriormost end of the nasals is the anterior end of a median, longitudinal tuberosity that divides the surface of the fossa into two concavities. A median fossa in the same position and with the same morphology is also present in skull roofs of referred specimens of *Garjainia prima* (PIN 951).

Lacrima. The lacrimal of the holotype of *Garjainia prima* is an inverted L-shape in lateral view (Figs. 2, 4, 5), resembling that of *Proterosuchus fergusi* (BSPG 1934 VIII 514, SAM-PK-11208, K10603), *Tasmaniosaurus triassicus* (UTGD 54655), *Fugusuchus hejiapanensis* (Cheng, 1980: fig. 22; GMB V 313 photographs), and *Erythrosuchus africanus* (BP/1/5207). By contrast, in the lacrimal of *Euparkeria capensis* (SAM-PK-5867) the anterior and ventral processes merge more smoothly into one another. The lacrimal forms a proportionally smaller dorsoventral component of the lateral surface of the skull than in *Erythrosuchus africanus* (Gower, 2003; BP/1/5207), as result of the dorsoventrally high horizontal process of the maxilla and anterior process of the jugal in *Garjainia prima*. The anterior process of the lacrimal forms at least the posterodorsal border of the antorbital fenestra and its lateral surface houses the lacrimal antorbital fossa (Fig. 5: 'anfo'), as also occurs in *Erythrosuchus africanus* (Gower, 2003; BP/1/5207). A lacrimal antorbital fossa that is similar but considerably shallower and less well defined posteriorly and dorsally is present in *Proterosuchus fergusi* (BSPG 1934 VIII 514, RC 96). The contact between the anterior process of the lacrimal and the maxilla is not clear (see above) and it is not possible to provide information on the anterior end of the process. The ventral process of the lacrimal possesses an anteroposteriorly convex lateral surface and a concave posterior surface, visible on the right side, which forms the anterior border of the orbit. There is no antorbital fossa on the lateral surface of the ventral process of the

lacrimal, similar to the condition in *Erythrosuchus africanus* (Gower, 2003; BP/1/5207), but contrasting with the condition in which the antorbital fossa extends on both anterior and ventral processes of *Euparkeria capensis* (SAM-PK-5867) and *Proterosuchus fergusi* (BSPG 1934 VIII 514, RC 96). A deep sulcus is present adjacent to the anterior border of the orbit in PIN 2394/5, level with the dorsal border of the antorbital fenestra. The sulcus is oriented almost parallel to the main axis of the skull, but with a low anterodorsal-to-posteroventral component, and probably represents the medial wall of the nasolacrimal duct with the lateral wall having broken away (Fig. 5A: 'nld'). We are unable to determine confidently the course of the suture between the lacrimal and the ventral process of the prefrontal. The lacrimal is overhung by the lateral preorbital projection of the prefrontal, but the suture between the bones cannot be identified. The distal end of the ventral process of the lacrimal is anteroposteriorly expanded at its contact with the maxilla and jugal, with the posterior expansion being considerably more developed than the anterior one.

Jugal. The jugal possesses the typical triradiate morphology observed in other Triassic archosauriforms, with anterior, ascending (= dorsal or postorbital process), and posterior processes (Figs. 2, 4, 5). The anterior process is anteroposteriorly short and delimits the anteroventral border of the orbit, resembling the condition in *Erythrosuchus africanus* (Gower, 2003; BP/1/5207). The anterior process is dorsoventrally narrow at its base, representing the ventralmost end of the orbit. From here, the anterior process increases dramatically in height anteriorly and forms a dorsoventrally extensive and almost vertical suture with the horizontal process of the maxilla (see above). This process also contacts the posteroventral corner of the ventral process of the lacrimal in a posteroventral to anterodorsal suture. The anterior and ascending processes of the jugal together form the

ventral third of the border of the orbit. The bases of the orbital margins of these processes form an acute angle with each other and, as a result, the ventral end of the orbit is subtriangular. The same condition is present in *Erythrosuchus africanus* (Gower, 2003; BP/1/5207), contrasting with the obtuse or right-angle between the anterior and ascending processes in *Prolacerta broomi* (BP/1/471), *Teyujagua paradoxa* (Pinheiro *et al.*, 2016), *Proterosuchus fergusi* (BP/1/4016, BSPG 1934 VIII 514, RC 96, SAM-PK-11208, TM 201), *Sarmatosuchus otschevi* (PIN 2865/68-6), *Fugusuchus hejiapanensis* (Cheng, 1980: fig. 22), *Shansisuchus shansisuchus* (Young, 1964: fig. 12a, b, d), and *Euparkeria capensis* (SAM-PK-5867).

The ascending process of the jugal is mainly dorsally oriented, but with a slight posterior component (such that it extends from anteroventral to posterodorsal) with respect to the longitudinal axis of the skull. However, the ascending process is set at approximately 90° to the main axis of the posterior process, resembling the condition in *Erythrosuchus africanus* (Gower, 2003; BP/1/5207), and contrasting with the slightly more acute angle between the processes in *Garjainia madiba* (Gower *et al.*, 2104; BP/1/5760). The ascending process forms a little less than the half of the anterior border of the infratemporal fenestra. Immediately adjacent to the posteroventral corner of the orbit, a thick, diagonal tuberosity extends across the lateral surface of the ascending process of the jugal (Fig. 5B: 't'). The diagonal tuberosity crosses the lateral surface of the ascending process posterodorsally from its anterior margin and reaches the anterior border of the infratemporal fenestra at the ventral end of the ventral process of the postorbital, resembling the condition present in *Erythrosuchus africanus* (BP/1/5207) and *Garjainia madiba* (BP/1/5760). The suture between the ascending process of the jugal and the postorbital is interlaced, with the ventral process of the postorbital folding medially over

the jugal and being covered laterally by the latter at its ventralmost end (Fig. 11A, B), as also occurs in other early basal archosauriforms (e.g. *Erythrosuchus africanus*: BP/1/5207; *Fugusuchus hejiapanensis*: GMB V 313 photographs; *Proterosuchus fergusi*: BP/1/4106, BSPG 1934 VIII 514). The suture between the jugal and postorbital is diagonal (anteroventral–posterodorsal) and is harboured partially by the diagonal tuberosity on both bones.

The lateral surface of the main body of the jugal possesses a dorsoventrally thick and well-developed, lateral tuberosity that also extends along the mid-height of the anterior half of the posterior process of the bone, reaching posterior to the level of the anterior tip of the quadratojugal (Fig. 5: ‘jt’). The tuberosity is subparallel to the main axis of the posterior process of the jugal, with a slight anterodorsal to posteroventral slope. The tuberosity is most prominent at a point level with the anterior margin of the infratemporal fenestra. The tuberosity possesses the same kind of ornamentation observed on the dorsal surfaces of the nasal and frontals. An identical longitudinal tuberosity is present in referred specimens of *Garjainia prima* (PIN 951/23). The tuberosity in *Garjainia prima* is in the same position as the massive knob-like jugal boss of *Garjainia madiba* (Gower *et al.*, 2014; BP/1/5760) that continues posteriorly and anteriorly as longitudinal tuberosities, resembling the condition in *Garjainia prima*. As a result, the boss and tuberosities present in *Garjainia* species probably represent different conditions of the same homologous structure. In *Erythrosuchus africanus* (BP/1/5207) there is a well-developed tuberosity in the same position as in *Garjainia prima*, but it is lateroventrally directed and forms a thick and distinctly convex ventral edge of the anterior half of the posterior process of the jugal in lateral view. A tuberosity that extends through the main body and the base of the posterior process of the jugal is present also in *Fugusuchus hejiapanensis* (GMB V 313 photographs). Some

specimens of *Proterosuchus fergusi* possess a similar tuberosity to that of *Erythrosuchus africanus*, although it is less strongly developed lateroventrally (RC 96, SAM-PK-K10603). The proterochampsid *Chanaresuchus bonapartei* has a longitudinal tuberosity on the lateral surface of the jugal, but it also extends along the posterior half of the anterior process of the jugal (MCZ 4039), contrasting with that of *Garjainia prima*. The jugals of *Prolacerta broomi* (BP/1/471), *Teyujagua paradoxa* (UNIPAMPA 653 cast), and *Euparkeria capensis* (SAM-PK-5867) lack a tuberosity.

The posterior process of the jugal of PIN 2394/5 is anteroposteriorly very long and forms most of the ventral border of the infratemporal fenestra, as occurs in other non-archosaurian archosauriforms (e.g. *Proterosuchus fergusi*: RC 96, TM 201, BP/1/3993, 4016, BSPG 1934 VIII 514, SAM-PK-11208, K10603; *Erythrosuchus fergusi*: BP/1/5207; *Fugusuchus hejiapanensis*: Cheng, 1980: fig. 22). The posterior process of the jugal of PIN 2394/5 extends posteriorly up to at least the level of the posterior border of the infratemporal fenestra but it is not possible to determine how much further because of damage on both sides of the skull. In referred specimens of *Garjainia prima* (PIN 951/17, 23) and *Erythrosuchus africanus* (Gower, 2003; BP/1/5207) the jugal extends posteriorly far beyond the posterior end of the infratemporal fenestra. The posterior process of the jugal of PIN 2394/5 tapers posteriorly and extensively contacts the anterior process of the quadratojugal, resulting in an infratemporal fenestra with a completely closed ventral margin, as also occurs in *Erythrosuchus africanus* (Gower, 2003; BP/1/5207), referred specimens of *Garjainia prima* (PIN 951/17, 23), at least two specimens of *Proterosuchus fergusi* (Ezcurra & Butler, 2015b; BP/1/3993, 4016), and more crownward archosauriforms (e.g. *Euparkeria capensis*: Ewer, 1965; SAM-PK-5867).

The medial surface of the jugal bears a flat articular facet for articulation with the lateral process of the ectopterygoid. This facet extends posteriorly beyond the anterior end of the infratemporal fenestra. The facet for reception of the anterior process of the quadratojugal extends along most of the medial surface of the posterior process of the jugal and lies adjacent to the ventral margin of the process. This facet occupies the entire height of the process posteriorly and tapers gradually towards its anterior end. The anterior tip of the facet is slightly below the mid-height of the process. The anterior end of the quadratojugal facet is separated from the ectopterygoid facet by a dorsoventrally concave area.

Prefrontal. The prefrontal is a large, subtriangular bone in dorsal view that expands laterally on the skull roof anterior to the orbit (Figs. 3, 6, 7), resembling the condition present in other early archosauriforms (e.g. *Proterosuchus fergusi*: BPSG 1934 VIII 514; *Erythrosuchus africanus*: BP/1/5207; *Shansisuchus shansisuchus*: Young, 1964: figs. 1–3, 5; *Euparkeria capensis*: SAM-PK-5867). The lateral expansion of the prefrontal roofs the antorbital fossa and is continuous with the posterior expansion of the maxillo-nasal tuberosity on the lateral margin of the skull roof (Figs. 2, 4, 5). The prefrontal possesses an anteroposteriorly extensive and slightly sinusoidal suture with the nasal and frontal. The anterior end of the prefrontal tapers in dorsal view and at its tip does not form the lateral margin of the skull roof, but lies instead slightly medial to it. The posterior end of the prefrontal is squared off in dorsal view, and forms a slightly posteriorly concave transverse suture with the frontal. The lateral margin of the prefrontal is formed by two straight edges, the anterior of which is the longest, that meet at an obtuse angle, resembling the condition present in some specimens of *Shansisuchus shansisuchus* (Young, 1964: fig. 1). By

contrast, in *Erythrosuchus africanus* (Gower, 2003; BP/1/5207, NHMUK R3592, NM QR 1473) and other specimens of *Shansisuchus shansisuchus* (Young, 1964: figs. 2, 3) the lateral margin of the prefrontal is more rounded. The contact between the two straight lateral edges in PIN 2394/5 forms the most lateral point of the prefrontal, lying level with the anterior border of the orbit. The lateral projection of the prefrontal is dorsoventrally thick in lateral view, with a longitudinal and well-rimmed groove on its lateral surface (Fig. 5: 'g'), resembling the condition in *Erythrosuchus africanus* (Gower, 2003; BP/1/5207) and *Garjainia madiba* (Gower *et al.*, 2014; BP/1/6226a). By contrast, this groove is absent in *Proterosuchus fergusi* (BP/1/4016, RC 96, SAM-PK-K10603), *Fugusuchus hajiapanensis* (GMB V 313 photographs), and *Euparkeria capensis* (SAM-PK-5867). The prefrontal forms the anterodorsal border of the orbit in lateral view, but the ventral extent of the element is unclear because there is no discernable suture with the lacrimal.

Frontal. The sutures of the frontals with nasals, prefrontals, and postfrontals are discernable, but part of the suture with the parietals at the midline and most of the median suture with its counterpart are not identifiable (Figs. 3, 6, 7). The midline suture between the frontals can be identified at the very anterior ends of the bones. The apparent absence of this suture posteriorly may be a result of bone remodelling on the dorsal surface of the skull roof and/or poor preservation. As a result, it is not known whether the frontals were partially fused (incomplete synostosis) with each other or with the parietals. The paired frontals are wider than long, contrasting with the longer than wide paired frontals of *Prolacerta broomi* (BP/1/471), *Teyujagua paradoxa* (Pinheiro *et al.*, 2016), *Proterosuchus fergusi* (RC 59, 96, BP/1/3993, SAM-PK-K10603), *Tasmaniosaurus triassicus* (Ezcurra, 2014; UTGD 54655), *Fugusuchus hejiapanensis* (Cheng, 1980: fig. 22; GMB V 313

photographs), *Erythrosuchus africanus* (Gower, 2003; NHMUK R3592, NM QR 1473), *Shansisuchus shansisuchus* (Young, 1964: figs. 1–6), and *Euparkeria capensis* (SAM-PK-5867). The frontal-nasal suture is strongly interdigitated in PIN 2394/5, with moderately well-developed projections, resembling the condition observed in medium to large specimens of *Proterosuchus fergusi* (e.g. RC 96) (see Ezcurra & Butler, 2015b). By contrast, in small specimens of *Proterosuchus fergusi* (Ezcurra & Butler, 2015b; RC 59, SAM-PK-K10603) and medium to large specimens of *Erythrosuchus africanus* (Gower, 2003; NHMUK R3592, NM QR 1473) the projections of the interdigitated suture are proportionally longer anteroposteriorly. Each frontal has three anterior projections that articulate with the nasal: one adjacent to the suture with the prefrontal and the other two medially displaced from the mid-width of the posterior end of the nasal and extending slightly further anteriorly than the most lateral projection. A similar pattern is present in *Erythrosuchus africanus* (BP/1/5207), but with a single medial projection. The suture in *Proterosuchus fergusi* possesses a median projection formed by both frontals (RC 59, 96, SAM-PK-K10603) that is absent in the holotype of *Garjainia prima* and in *Erythrosuchus africanus*.

The frontal of PIN 2394/5 has a small participation in the rim of the orbit in dorsal view, as also occurs in at least one specimen of *Erythrosuchus africanus* (NHMUK R3592). By contrast, the frontals of *Shansisuchus shansisuchus* (e.g. Young, 1964: fig. 5) and another specimen of *Erythrosuchus africanus* (NM QR 1473) have either only an incipient participation in the external border of the orbit or are excluded by contact between the prefrontal and postfrontal in lateral and dorsal views (e.g. Young, 1964: figs. 1–4). The suture of the frontal with the postfrontal is oriented from anterolaterally to posteromedially and is slightly concave anteromedially. The preserved part of the fronto-parietal suture is

not interdigitated, but slightly sinuous, and transverse. The shape of the suture is similar to that of *Proterosuchus fergusi* (SAM-PK-K10603) and some specimens of *Shansisuchus shansisuchus* (e.g. Young, 1964: fig. 6). The anterior two-thirds of the combined dorsal surface of the frontals of PIN 2394/5 bears a median longitudinal fossa that extends back from that on the nasals (Figs. 3, 6, 7), a feature that is also present in referred specimens of *Garjainia prima* (PIN 951), but is absent in *Fugusuchus hejiapanensis* (GMB V 313 photographs), *Erythrosuchus africanus* (NM QR 1473, NHMUK R3592), and *Shansisuchus shansisuchus* (Young, 1964: figs. 2, 4). The fossa extends posteriorly to a point level with the posterior participation of the frontal in the orbit in dorsal view. The fossa on the frontals has a median longitudinal ridge, transversely thicker posteriorly, which is shallower in dorsoventral height than the depth of the fossa. The fossa and ridge are ornamented, as are the external surfaces of the nasals. The shape and position of this median ornamented ridge closely resembles that of *Guchengosuchus shiguaensis* (IVPP V8808), but in that species the ridge is not within a fossa. The posterior ends of the frontals, immediately posterior to and separated from the median longitudinal fossa, possess a subrectangular pineal fossa that continues on the dorsal surfaces of the parietals, resembling the condition in *Erythrosuchus africanus* (NM QR 1473, NHMUK R3592) and some specimens of *Proterosuchus fergusi* (e.g. BP/1/3993, SAM-PK-K10603). However, in *Proterosuchus fergusi* the pineal fossa has a smaller extension onto the frontals and a rounded anterior margin, rather than being well extended onto the frontals with a squared anterior margin as occurs in *Garjainia prima* and *Erythrosuchus africanus*. In *Shansisuchus shansisuchus* (IVPP V2503; Young, 1964: figs. 1–4, 6) and *Fugusuchus hejiapanensis* (Cheng, 1980: fig. 22) the pineal fossa is restricted to the parietals.

The ventral surface of the frontal has a concave orbital depression, delimited medially by contact with the taenia medialis of the laterosphenoid, resembling the condition present in other early archosauriforms (Clark *et al.*, 1993). The morphology of the impressions of the olfactory tract and bulbs cannot be determined in PIN 2394/5 because the relevant area is covered by the laterosphenoids and matrix.

Postfrontal. The postfrontal is visible mainly in dorsal view and only slightly in lateral view in the posterodorsal corner of the orbit (Figs. 2–7). In dorsal view, the postfrontal is subrectangular to semilunate with a concave medial margin and its main axis extending from anterolateral to posteromedial, resembling the condition in *Erythrosuchus africanus* (NHMUK R3592, NM QR 1473) and *Shansisuchus shansisuchus* (Young, 1964: figs. 1, 2, 4, 5). By contrast, in *Prolacerta broomi* (BP/1/471, 2675, UMZC T2003.41R), *Proterosuchus fergusi* (RC 59, BP/1/3993, 4016, SAM-PK-K10603), *Fugusuchus hejiapanensis* (Cheng, 1980: fig. 22; GMB V 313 photographs), and *Euparkeria capensis* (SAM-PK-5867) the postfrontal is subtriangular or semilunate with the main axis of the bone oriented posterolaterally to anteromedially. The suture between the postfrontal and postorbital extends from anterolateral to posteromedial in PIN 2394/5, *Garjainia madiba* (BP/1/5760), *Fugusuchus hejiapanensis* (Cheng, 1980: fig. 22; GMB V 313 photographs), *Erythrosuchus africanus* (Gower, 2003; NM QR 1473), and *Shansisuchus shansisuchus* (Young, 1964: figs. 2, 4, 5), but from anteromedial to posterolateral in most other archosauromorphs. In addition, the postfrontal-postorbital suture is almost straight in PIN 2394/5, contrasting with the strongly convex suture in *Erythrosuchus africanus* (BP/1/5207) and the more complex, sigmoid suture in *Garjainia madiba* (BP/1/5760). The exposed dorsal surface of the postfrontal in PIN 2394/5 is slightly transversely wider

anteriorly than posteriorly. The postfrontal has a small participation in the posterodorsal border of the orbit and it lacks a ventral process, contrasting with that of *Prolacerta broomi* (BP/1/471), in which the postfrontal widely participates in the posterodorsal border of the orbit via a well developed, tapering ventral process. The postfrontal is excluded from the anterior border of the supratemporal fenestra by parietal-postorbital contact, as occurs in other early archosauromorphs (e.g. *Prolacerta broomi*: BP/1/471; *Proterosuchus fergusi*: BP/1/3993, SAM-PK-K10603; *Erythrosuchus africanus*: NM QR 1473).

Postorbital. The tridiadate postorbital has an anterodorsally directed anterior process, an almost horizontal posterior process parallel to the long axis of the skull, and an anteroventrally oriented ventral process (Figs. 2, 4, 5). The short anterior process forms most of the posterodorsal border of the orbit and contacts the postfrontal and a small portion of the parietal medially. The ventral process forms most of the posterior border of the orbit and approximately half of the anterior border of the infratemporal fenestra. By contrast, in *Proterosuchus fergusi* (BP/1/4016, BSPG 1934 VIII 514), *Fugusuchus hejiapanensis* (Cheng, 1980: fig. 22; GMB V 313 photographs), *Erythrosuchus fergusi* (Gower, 2003; BP/1/5207), and *Euparkeria capensis* (Ewer, 1965; SAM-PK-5867) the ascending process of the jugal forms most of the anterior border of the infratemporal fenestra. The ventral process of the postorbital of PIN 2394/5 tapers distally and folds medially to partially wrap the ascending process of the jugal (see above). The anterior margin of the ventral process has a low, rounded anterior projection into the orbit, situated approximately at mid-height of the opening (Fig. 5A: ‘sof’), resembling the condition in *Shansisuchus shansisuchus* (Young, 1964: fig. 7a) and *Garjainia madiba* (BP/1/5760). The anterior projection is reminiscent of a similar condition, with various degrees of

development, in some ‘rauisuchian’ pseudosuchians (e.g. *Prestosuchus chiniquensis*: UFRGS PV 0156; *Postosuchus kirkpatricki*: Weinbaum, 2011) and theropod dinosaurs (e.g. *Carnotaurus sastrei*: MACN- Pv-CH 894; *Sinraptor dongi*: Currie & Zhao, 1993), which is usually termed the suborbital flange in the latter group (Sereno *et al.*, 1996). By contrast, *Prolacerta broomi* (BP/1/471), *Teyujagua paradoxa* (UNIPAMPA 653 cast), *Proterosuchus fergusi* (BP/1/4016, BSPG 1934 VIII 514, RC 96), *Erythrosuchus africanus* (BP/1/5207), *Fugusuchus hejiapanensis* (Cheng, 1980: fig. 22; GMB V 313 photographs), and *Euparkeria capensis* (SAM-PK-5867) lack a suborbital flange on the postorbital. The anterior surface of the ventral process of PIN 2394/5 possesses a wide pocket immediately ventral to the suborbital flange, as also occurs in *Garjainia madiba* (Gower *et al.*, 2104; BP/1/5760).

The posterior and ventral processes of the postorbital merge smoothly into one another, defining a widely rounded anterodorsal border of the infratemporal fenestra, as occurs in *Erythrosuchus africanus* (BP/1/5207) and *Garjainia madiba* (BP/1/5760). The posterior process of the postorbital is moderately long and tapers posteriorly to fit into a very deep cleft on the lateral surface of the anterior process of the squamosal, resembling the condition in *Erythrosuchus africanus* (BP/1/5207) and *Fugusuchus hejiapanensis* (Parrish, 1992; GMB V 313 photographs). In *Prolacerta broomi* (BP/1/471), *Proterosuchus fergusi* (BP/1/4016, SAM-PK-K10603), and *Sarmatosuchus otschevi* (PIN 2865/68, where the condition is inferred based on the postorbital facet of the squamosal) the extension and shape of this contact is similar but the postorbital does not fit deeply into the squamosal facet. The anterior and posterior processes of the postorbital form the anterolateral border of the supratemporal fenestra and the dorsal surface of the postorbital lacks a supratemporal fossa, as in *Erythrosuchus africanus* (Gower, 2003; BP/1/5207), *Garjainia madiba* (Gower

et al., 2014; BP/1/5760), *Fugusuchus hejiapanensis* (Cheng, 1980: fig. 22; GMB V 313 photographs), and *Proterosuchus fergusi* (BP/1/4016, BSPG 1934 VIII 514; SAM-PK-K10603).

The lateral surface of the main body of the postorbital (i.e. the region in which the three processes merge) possesses a dorsoventrally thick and laterally well-developed tuberosity, the anterior end of which is boss-like and adjacent to the posterodorsal border of the orbit (Fig. 5: 'pok'). This tuberosity is in the same position as the more pronounced knob-like postorbital boss of *Garjainia madiba* (Gower *et al.*, 2014; BP/1/5760) and, as a result, they probably represent different conditions of the same homologous structure. A similar tuberosity is present also in *Erythrosuchus africanus* (Gower, 2003; BP/1/5207), the proterochampsid *Chanaresuchus bonapartei* (MCZ 4039), and a lower, knob-like tuberosity occurs in *Fugusuchus hejiapanensis* (Cheng, 1980: fig. 22; GMB V 313 photographs). By contrast, a postorbital lateral tuberosity or boss is absent in *Shansisuchus shansisuchus* (Young, 1964: fig. 7a) and other non-archosaurian archosauromorphs (e.g. *Prolacerta broomi*: BP/1/471; *Teyujagua paradoxa*: UNIPAMPA 653 cast; *Proterosuchus fergusi*: BP/1/4016, RC 96, SAM-PK-K10603; *Euparkeria capensis*: SAM-PK-5867). The main axis of this tuberosity is mainly longitudinal, with a low posterodorsal to anteroventral component, and the tuberosity also extends along the anterior half of the posterior process of the postorbital. The tuberosity curves slightly dorsally towards its posterior end and possesses a moderately deep longitudinal depression on the lateral surface of its anterior half, as in *Erythrosuchus africanus* (BP/1/5207). The longitudinal tuberosity is adjacent to the dorsal margin of the posterior process and delimits a shallow longitudinal depression on the ventral half of the lateral surface of the process. A posteriorly tapering, sub-triangular fossa is present on the dorsal surface of the tuberosity (Fig. 5: 'f'), as also

occurs in *Erythrosuchus africanus* (BP/1/5207) and resembling the subcircular fossa present on the dorsal surface of the postorbital boss of *Garjainia madiba* (BP/1/5760). The lateral tuberosity of the postorbital in PIN 2394/5 is rugose like the dorsal surface of the nasals and frontals and the longitudinal tuberosity of the jugal.

Squamosal. The anterior and ventral processes of the approximately semilunate squamosal merge smoothly into one another and from a widely concave posterodorsal border of the infratemporal fenestra (Figs. 2, 4, 5). The anterior process forms the posterior half of the dorsal border of the infratemporal fenestra and slightly more than half of the lateral border of the supratemporal fenestra. The latter condition contrasts with that in *Proterosuchus fergusi* (SAM-PK-K10603) and *Euparkeria capensis* (SAM-PK-5867), in which the anterior process of the squamosal has an extensive anteroposterior contact with the posterior process of the postorbital and forms most of the dorsal border of the infratemporal fenestra. The lateral surface of the squamosal bears a dorsoventrally thick tuberosity adjacent to the dorsal margin of the bone, which curves ventrally and extends posteriorly onto the base of the posterior process of the squamosal, resembling the condition in *Erythrosuchus africanus* (BP/1/5207). The squamosal has a transversely short and dorsoventrally broad medial process that articulates with the posterolateral process of the parietal (= occipital wing) and contacts the distal tip of the paroccipital process of the otooccipital. The squamosal has a very anteroposteriorly short posterior process that lies well below the level of the dorsal border of the infratemporal fenestra (Fig. 5B: 'pps'). This process curves ventrally and its strongly concave ventral surface receives the quadrate head. The posterior process of the squamosal is similarly developed in *Proterosuchus fergusi* (BP/1/4016), *Sarmatosuchus otschevi* (PIN 2865/68), *Fugusuchus hejiapanensis*

(Cheng, 1980: fig. 22; GMB V 313 photographs), and *Shansisuchus shansisuchus* (Young, 1964: fig. 14a), but it is absent in *Erythrosuchus africanus* (BP/1/4680, 5207). In *Prolacerta broomi* (Modesto & Sues, 2004) and *Euparkeria capensis* (SAM-PK-5867) the posterior process is considerably more strongly developed posteriorly than in PIN 2394/5. The long ventral process of the squamosal forms most of the posterior border of the infratemporal fenestra (Fig. 5A: ‘vps’), as occurs in several other early archosauromorphs (e.g. *Prolacerta broomi*: Modesto & Sues, 2004; *Teyujagua paradoxa*: Pinheiro *et al.*, 2016; *Proterosuchus fergusi*: RC 96, SAM-PK-K10603; *Fugusuchus hejiapanensis*: Cheng, 1980: fig. 22). The process is gently sigmoid in lateral view, being posteriorly curved along its proximal (dorsal) half and anteriorly curved distally (ventrally). The lateral surface of the ventral process is slightly convex anteroposteriorly. The medial surface of the squamosal articulates with the quadrate at the base of the ventral process and with the dorsal process of the quadratojugal along the ventral two-thirds of the ventral process.

The dorsal surface of the squamosal lacks a facet for a supratemporal and we infer that this bone was absent in PIN 2394/5, as is the case in *Erythrosuchus africanus* (Gower, 2003; BP/1/5207), *Euparkeria capensis* (Ewer, 1965), and more crownward archosauriforms (Nesbitt, 2011). By contrast, *Prolacerta broomi* (Modesto & Sues, 2004), *Teyujagua paradoxa* (Pinheiro *et al.*, 2016), and *Proterosuchus fergusi* (SAM-PK-K10603) have splint-like supratemporals.

Quadratojugal. The quadratojugal is V-shaped in lateral view (Figs. 2, 4, 5, 9A, B). It has a very long anterior process (Figs. 5A, 9B: ‘apqj’), as in *Erythrosuchus africanus* (Gower, 2003; BP/1/5207), referred specimens of *Garjainia prima* (PIN 951/23), *Garjainia madiba* (Gower *et al.*, 2014; BP/1/6735), *Shansisuchus shansisuchus* (Young, 1964: figs. 13d–g),

and more crownward archosauriforms. By contrast, in *Prolacerta broomi* (Modesto & Sues, 2004) and *Proterosuchus fergusi* (BP/1/3993, 4016, SAM-PK-11208, K10603, RC 96) the anterior process of the quadratojugal is absent or incipient (Ezcurra & Butler, 2015a). The quadratojugal forms a small portion of the posteroventral border of the infratemporal fenestra and its lateral surface possesses an infratemporal fossa adjacent to the posteroventral corner of the fenestra. A similar fossa is present in some specimens of *Proterosuchus fergusi* (e.g. BP/1/4016), and proterochampsids (e.g. *Chanaresuchus bonapartei*: PULR 07) and its presence is variable on left and right sides of the same individual in a referred specimen of *Garjainia prima* (PIN 951/23). The posteroventral margin of the infratemporal fossa is well delimited by a shelf on the lateral surface of the quadratojugal that separates the fossa from an area close to the posteroventral corner of the quadratojugal that is covered with longitudinal and dorsally curved, parallel ridges (Figs. 5A, 9A: ‘sh’). A similar condition is present in referred specimens of *Garjainia prima* (PIN 951/17, 23) and in *Garjainia madiba* (BP/1/7215). The posteroventral corner of the quadratojugal possesses a short, transversely thin, and posteriorly rounded posterior flange (Figs. 5, 9A: ‘pf’), resembling the condition in *Proterosuchus fergusi* (RC 96, BSPG 1934 VIII 514, BP/1/4016, SAM-PK-K10603), *Erythrosuchus africanus* (Gower, 2003; BP/1/5207, NHMUK R3592), *Shansisuchus shansisuchus* (Young, 1964: fig. 13d–g), referred specimens of *Garjainia prima* (PIN 951/23), *Garjainia madiba* (Gower *et al.*, 2014; BP/1/6735, 7215), and *Euparkeria capensis* (SAM-PK-5867). The posterior process is mainly posteriorly directed, but also slightly medially, and covers most of the lateral distal condyle of the quadrate in lateral view (Figs. 2, 9B: ‘qf’).

The anterior process of the quadratojugal forms an extensive longitudinal suture with the jugal (see above). The dorsal margin of the process is transversely thin, but the

ventral margin is considerably thicker and, as a result, the ventral surface is strongly convex. The ventral margin of the anterior process is slightly anteroposteriorly convex in lateral view and forms the most ventral level of the skull, extending below the level of the alveolar margin of the maxilla. The medial surface of the anterior process is almost flat. The dorsal process of the quadratojugal is partially covered by the ventral process of the squamosal in lateral view and its distal tip is surrounded by the squamosal laterally and the quadrate medially in occipital view. The quadratojugal contacts the quadrate extensively along three-quarters of the height of the latter bone. The lateral surface of the anterior half of the dorsal process of the quadratojugal is gently anteroposteriorly convex, whereas the posterior half is extensively invaded by a depression with a gently anteroposteriorly concave surface, as occurs in referred specimens of *Garjainia prima* (PIN 951/23), *Erythrosuchus africanus*, and *Shansisuchus shansisuchus* (Ezcurra, 2016).

Quadrate. The quadrate is posteriorly bowed in lateral view and the posterior margins of its dorsal and ventral ends form an angle of 120° (Figs. 2, 4, 5), closely resembling the condition in *Erythrosuchus africanus* (BP/1/5207: 120°). *Prolacerta broomi* (BP/1/471, UCMP 37151: $106\text{--}110^\circ$) has a slightly lower equivalent angle and *Proterosuchus fergusi* (BP/1/4016, 4224, BSPG 1934 VIII 514, GHG 231, RC 96, SAM-PK-K11208, K140, K10603: $128\text{--}137^\circ$) and *Shansisuchus shansisuchus* (Young, 1964: fig. 13a: 130°) have slightly greater angles. The ventral condyles of the quadrate of PIN 2394/5 lie further posteriorly than the quadrate head (Figs. 2, 4A, 5A). The quadrate head articulates with a deep socket on the squamosal and is covered by the latter bone in lateral view. A vertical and strongly transversely convex ridge extends along the posterior surface of the quadrate, from the base of the quadrate head to the base of the medial distal condyle of the bone. The

quadrate foramen is preserved only on the left side of the skull. Its borders are damaged, but at least its medial and ventral borders were formed by the quadrate and the lateral border was formed by the quadratojugal (Fig. 10: 'qf'), as in other early archosauromorphs (e.g. *Prolacerta broomi*: Modesto & Sues, 2004; *Proterosuchus fergusi*: SAM-PK-K10603, RC 96). The quadrates of PIN 2394/5 and *Proterosuchus fergusi* (SAM-PK-K10603, RC 96) lack the laterally opening pit that lies next to the medial border of the quadrate foramen in *Sarmatosuchus otschevi* and *Erythrosuchus africanus* (Gower & Sennikov, 1997; Gower, 2003).

The ventral end of the quadrate is L-shaped in distal view because of the strong anterior projection of the medial ventral condyle, which is approximately 1.8 times longer anteroposteriorly than the lateral condyle (Fig. 10A). The ventral condyles are subequal in transverse width, but the medial condyle extends considerably further distally. The ventral condyles of the quadrate and, as a result, the cranio-mandibular joint are situated considerably posterior to the level of the posterior margin of the occipital condyle, a condition that is widespread among archosauromorphs (Dilkes, 1998). The dorsal end of the pterygoid ala of the quadrate arises dorsoventrally along most of the height of the quadrate, and the medial surface of the ala is concave (Fig. 5A: 'paq'). The dorsal margin and ventral ends of the pterygoid ala are broken off or severely damaged and, as a result, it is not possible to determine the morphology of the contact between the quadrate and the palate.

Parietal. There is no discernable median interparietal suture, but it cannot be ruled out that it is a result of preservational artefact rather than an actual synostosis (Figs. 3, 6, 7). In *Erythrosuchus africanus* the parietals are firmly articulated with one another but the median

suture is still distinct (Gower, 2003). In the holotype of *Garjainia prima* the anterior ends of the dorsal surfaces of the parietals bear the continuation of the pineal fossa that also extends onto the frontals (described above). The surface of this fossa is not ornamented and has a small, circular pit that is slightly displaced to the left of the sagittal midline of the skull. This pit may represent a vestigial pineal foramen (Figs. 3, 6, 7), resembling the condition present in one specimen of *Proterosuchus fergusi* (BP/1/3993), but this interpretation should be considered tentative. Similarly, there is no conclusive evidence as to the presence or absence of a pineal foramen in *Erythrosuchus africanus* (Gower, 2003). The parietal forms the medial border of the supratemporal fenestra. A transversely narrow and moderately dorsoventrally deep supratemporal fossa extends onto the posterolateral process (= occipital wing) of the parietal. The medial border of the supratemporal fenestra and the posterolateral parietal process are raised dorsally above the rest of the skull roof. As a result, the dorsal surface of the parietals has a deep median concavity between the raised medial borders of the supratemporal fenestrae.

The posterolateral process of the parietal is long and has a sharp dorsal edge along the posterior margin of its dorsal surface (Fig. 5: 'pvpp'), as occurs in other archosauromorphs (e.g. *Protorosaurus speneri*: Gottmann-Quesada & Sander, 2009; *Prolacerta broomi*: BP/1/471; *Teyujagua paradoxa*: UNIPAMPA 653 cast; *Proterosuchus fergusi*: SAM-PK-K10603; *Erythrosuchus africanus*: BP/1/5207; *Euparkeria capensis*: SAM-PK-5867). The posterolateral process of the parietal of PIN 2394/5 is anteriorly curved towards its distal end, with a continuously convex posterior margin in dorsal view, but this may be an artefact of transverse compression, because it contrasts with the straight process in dorsal view that is present in archosauromorphs (e.g. *Mesosuchus browni*: SAM-PK-6536; *Prolacerta broomi*: BP/1/471; *Proterosuchus fergusi*: SAM-PK-K10603;

Fugusuchus hejiapanensis: Cheng, 1980: fig. 22; *Shansisuchus shansisuchus*: Young, 1964: figs. 1, 2, 4; *Erythrosuchus africanus*: NM QR 1473; referred specimens of *Garjainia prima*: Huene, 1960: plate 11, fig. 1; *Euparkeria capensis*: SAM-PK-5867). The wing-like posterolateral processes are dorsally strongly convex, forming a deep median cleft between them in occipital view (Fig. 10: 'pa.wi'), resembling the condition in *Erythrosuchus africanus* (NM QR 1473, NHMUK R3592). By contrast, in *Prolacerta broomi* (BP/1/471), *Teyujagua paradoxa* (UNIPAMPA 653 cast), *Proterosuchus fergusi* (SAM-PK-K10603), *Fugusuchus hejiapanensis* (GMB V 313 photographs), *Guchengosuchus shiguaiensis* (IVPP V8808), *Shansisuchus shansisuchus* (Young, 1964: fig. 6), and *Euparkeria capensis* (SAM-PK-5867) the posterolateral processes of the parietal do not flare strongly dorsally and their dorsal margins are straight to slightly convex in occipital view.

In occipital view, the posterolateral process is dorsoventrally taller than the supraoccipital (Fig. 10). The ventral margins of the parietals together form a median, subtriangular notch to receive the supraoccipital. The contact between the parietals and the paroccipital process of the otoccipital (opisthotic + exoccipital) is not completely discernable on the right side of the skull and is probably completely missing on the left side. However, the ventral margin of the posterolateral process of the parietal lies close to the dorsal margin of the paroccipital process of the otoccipital, suggesting that the posttemporal fenestra was extremely small, as in other early archosauriforms (e.g. *Proterosuchus fergusi*: SAM-PK-K10603; referred specimens of *Garjainia prima*: Gower & Sennikov, 1996; *Erythrosuchus africanus*: UMZC T700). The posterior surface of the posterolateral process of the parietal is not well preserved, but it seems to lack the tuberosity adjacent to the dorsal margin of the process that is present in *Erythrosuchus*

africanus (Gower, 2003) and *Garjainia madiba* (Gower *et al.*, 2104; BP/1/6739). The ventral surface of the main body of the parietal articulates with the prootic and probably with the base of the laterosphenoid.

Interparietal. There is an anteroposteriorly short and dorsoventrally low, vertical median ridge on the posterior surface of the parietals that may represent an interparietal that is either fused to, or lacks a discernable suture with, the parietals. The position and morphology of this possible interparietal is in agreement with that described for *Erythrosuchus africanus* (Gower, 2003).

Braincase

General morphology. The basicranium is almost vertical (*sensu* Gower & Sennikov, 1996) in lateral view, with the basiptyergoid processes situated far ventral to the level of the basal tubera (Figs. 4, 5, 10, 11C, D), resembling the condition in *Sarmatosuchus otschevi* (Gower & Sennikov, 1997; PIN 2865/68), a referred specimen of *Garjainia prima* (Gower & Sennikov, 1996; PIN 951/60), *Erythrosuchus africanus* (Gower, 1997; NHMUK R3592), and *Shansisuchus shansisuchus* (Gower & Sennikov, 1996). By contrast, in *Prolacerta broomi* (BP/1/2675), *Proterosuchus fergusi* (BSPG 1934 VIII 514), and *Fugusuchus hejiapensis* (Gower & Sennikov, 1996) the basicranium is approximately horizontal in lateral view, with the basiptyergoid processes in front of the basal tubera.

Supraoccipital. The supraoccipital contacts the parietals dorsally and the otoccipitals ventrally (Fig. 10). It is not possible to determine whether or not the supraoccipital contacted the interparietal, if present. As preserved, part of the supraoccipital is covered by

the parietals in occipital view because of the anterior displacement of the dorsal part of the bone. As a result, it is not possible to determine the presence or absence of the markedly rugose posterodorsal surface of the supraoccipital described for a referred specimen of *Garjainia prima* by Gower & Sennikov (1996). The sutures between the supraoccipital and the otoccipitals are only partially preserved along the median portion of the braincase, so it is not possible to determine the lateral extensions of the former. The supraoccipital lacks a median prominent vertical crest on the exposed occipital surface of the bone, thus resembling the condition of *Prolacerta broomi* (SAM-PK-K10797), *Proterosuchus fergusi* (SAM-PK-K10603), *Fugusuchus hejiapensis* (Gower & Sennikov, 1996), *Erythrosuchus africanus* (BP/1/4645), and referred specimens of *Garjainia prima* (PIN 951/60). By contrast, a well-developed median vertical crest is present on the occipital surface of the supraoccipital of *Shansisuchus shansisuchus* (Gower & Sennikov, 1996) and *Guchengosuchus shiguaiensis* (IVPP V8808). The supraoccipital of PIN 2394/5 is excluded from the dorsal border of the foramen magnum by median contact between the otoccipitals, as also occurs in *Proterosuchus fergusi* (SAM-PK-K10603), a referred specimen of *Garjainia prima*, *Fugusuchus hejiapensis*, *Erythrosuchus africanus*, and *Shansisuchus shansisuchus* (Gower, 1997; Gower & Sennikov, 1996).

Otoccipital (opisthotic + exoccipital). The opisthotic and exoccipitals are fused with one another in a complete synostosis, and, as a result, we refer to them as the otoccipital (sensu Clark, 1986). As a result of post-mortem transverse compression, the paroccipital processes are more posteriorly directed and the posteroventral processes of the otoccipitals are closer to one another and to the midline than they would have been in life. As a result, the foramen magnum is distorted and artificially appears to be considerably dorsoventrally

taller than transversely wide. The distal end of the left paroccipital process is broken off (Fig. 10).

The base of the paroccipital process lies above the level of the dorsal margin of the occipital condyle, resembling the condition in other early archosauriforms (e.g. *Proterosuchus fergusi*: SAM-PK-K10603; *Sarmatosuchus otschevi*: PIN 2865/68; *Erythrosuchus africanus*: UMZC T700; *Euparkeria capensis*: SAM-PK-5867). The paroccipital process has a weak ventral expansion at its distal end, as also occurs in *Fugusuchus hejiapanensis* (GMB V 313 photographs), *Garjainia madiba* (BP/1/5760), *Erythrosuchus africanus* (UMZC T700), and *Shansisuchus shansisuchus* (Young, 1964: fig. 6), and has a continuous ventral curvature along its length, with a convex dorsal margin in occipital view. The ventral curvature is probably an artefact of the transverse post-mortem compression. The distal end of the paroccipital process is damaged, but it seems to have been rounded in occipital view. The distal end of the process is heavily longitudinally striated on its posterior surface, and anteriorly it loosely contacts the medial process of the squamosal. The proximal half of the ventral surface of the paroccipital process possesses a very deep, well-defined stapedial groove. The stapedial groove lacks the bulge described for *Erythrosuchus africanus* (Gower, 1997). At the base of the stapedial groove the base of the ventral ramus of the opisthotic separates the metotic foramen from the fenestra ovalis (Fig. 11C, D: ‘mf’, ‘vrop’). The metotic foramen is oval, being transversely wider than anteroposteriorly deep. The fenestra ovalis is anterodorsally delimited by the well-developed crista prootica (Fig. 5A: ‘fo’). The ventral half of the ventral ramus of the opisthotic is not preserved and it is not possible to determine if it possessed the strong degree of ventral development and robustness present in some non-archosaurian archosauriforms, such as “*Chasmatosaurus*” *yuani* (IVPP V2719), a referred specimen of

Garjainia prima (Gower & Sennikov, 1996), and *Garjainia madiba* (Gower *et al.*, 2014; BP/1/5525). The posteroventral process of the otoccipital (= base of the exoccipital pillar) seems to have a single opening for the exit of the hypoglossal nerve (cranial nerve XII) next to the contact with the basioccipital, as also occurs in a referred specimen of *Garjainia prima* (Gower & Sennikov, 1996), *Erythrosuchus africanus* (Gower, 1997), and *Fugusuchus hejiapensis* (Gower & Sennikov, 1996). Nevertheless, the area is partially covered by matrix on both sides of the braincase and it is not possible to rule out the presence of additional exits for the hypoglossal nerve.

Both otoccipitals possess an oval, transversely wider than tall, well-defined and deep fossa next to the dorsolateral border of the foramen magnum and below the suture with the supraoccipital (Fig. 10: 'f'). A similar fossa is also present in referred specimens of *Garjainia prima* (PIN 951/60), *Garjainia madiba* (Gower *et al.*, 2014; BP/1/5760), *Fugusuchus hejiapensis* (Gower & Sennikov, 1996: fig. 4b), *Sarmatosuchus otschevi* (Gower & Sennikov, 1997), and *Erythrosuchus africanus* (UMZC T700). By contrast, this fossa is absent in *Proterosuchus fergusi* (SAM-PK-K10603), *Guchengosuchus shiguaiensis* (IVPP V8808), *Shansisuchus shansisuchus* (Gower & Sennikov, 1996: fig. 6a), and *Euparkeria capensis* (SAM-PK-5867). The otoccipital forms the ventrolateral border of the foramen magnum. It seems that the otoccipitals do not contact each other at the midline on the dorsal surface of the occipital condyle, similar to the condition in a referred specimen of *Garjainia prima* (PIN 951/60), in *Garjainia madiba* (BP/1/5525), and in *Fugusuchus hejiapensis* (Gower & Sennikov, 1996: fig. 4b). By contrast, in *Erythrosuchus africanus* (Gower, 1997; SAM-PK-3612) and *Shansisuchus shansisuchus* (Gower & Sennikov, 1996: fig. 6b) the otoccipitals extend together far posteriorly on the dorsal surface of the occipital condyle. It is not possible to determine in PIN 2394/5 if the otoccipitals contacted each

other further anteriorly, on the floor of the endocranial cavity, as commonly occurs in early archosauriforms (Gower & Sennikov, 1996), because the area is covered by matrix. The suture between the otoccipital and the prootic is partially discernable on the exposed left side of the braincase, showing the contribution of the prootic to the anterior surface of the base of the paroccipital process, as also occurs in *Erythrosuchus africanus* (Gower, 1997). It is not possible to determine the presence or absence of the pseudolagenar recess described by Gower & Sennikov (1996) for a referred specimen of *Garjainia prima* because the area is heavily covered by matrix on both sides of the braincase.

Basioccipital. The basioccipital forms the entire articular surface of the occipital condyle (Fig. 10). The occipital condyle is wider than tall and bears a dorsally displaced, median notochordal pit on its articular surface, as occurs in other early archosauriforms (e.g. “*Chasmatosaurus*” *yuani*: IVPP V2719; *Erythrosuchus africanus*: Gower, 1997; a referred specimen of *Garjainia prima*: PIN 951/60; *Garjainia madiba*: BP/1/5525). The occipital condyle is separated from the rest of the basioccipital by a constricted area that results in a moderately well-developed occipital neck (Fig. 5A: ‘oc’), resembling the condition in a referred specimen of *Garjainia prima* (PIN 951/60), *Garjainia madiba* (BP/1/5525), *Erythrosuchus africanus* (NHMUK R3592, SAM-PK-3612), *Fugusuchus hejiapanensis* (GMB V 313 photographs), and *Proterosuchus fergusi* (BSPG 1934 VIII 514). The basal tubera of the basioccipital project ventrally, are anteroposteriorly short and are completely separated from each other at the midline of the bone. The basal tubera are moderately developed ventrally and are widely visible in occipital view lateroventral to the occipital condyle. The tubera have a main axis that extends from anteromedial to posterolateral in ventral view, resembling the condition in referred specimens of *Garjainia prima* (PIN

951/60) and *Garjainia madiba* (BP/1/5525). Between the basal tubera there is an autapomorphic stout median tubercle, as also occurs in referred specimens of *Garjainia prima* (PIN 951/60; Gower & Sennikov, 1996). By contrast, this tubercle is absent in *Garjainia madiba* (BP/1/5525), *Prolacerta broomi* (BP/1/2675), *Proterosuchus fergusi* (BSPG 1934 VIII 514), *Sarmatosuchus otschevi* (PIN 2865/68), and *Erythrosuchus africanus* (NHMUK R3592). Both lateral surfaces of the basioccipital are covered by matrix.

Parabasisphenoid. The basisphenoid and parasphenoid are indistinguishable from each other and, as a result, they are described here together as a single element (= parabasisphenoid). The posterolateral corners of the parabasisphenoid contribute to the anterior portions of the basal tubera. The ventral surface between the basal tubera harbours a gently concave basioccipital-basisphenoid fossa (Fig. 10). A thick, transverse intertuberal plate connects the parabasisphenoidal portions of the basal tubera (Fig. 10: 'itp'), resembling the condition in referred specimens of *Garjainia prima* (PIN 951/60), *Garjainia madiba* (BP/1/5525), *Sarmatosuchus otschevi* (PIN 2865/68), *Fugusuchus hejiapensis* (Gower & Sennikov, 1996: fig. 4a), as well as the less well-developed structure present in *Erythrosuchus africanus* (Gower, 1997), *Proterosuchus fergusi* (BSPG 1934 VIII 514), and *Prolacerta broomi* (BP/1/2675). The ventral surface of the main body of the parabasisphenoid is concave, bearing a shallow basisphenoid fossa. The ventrolateral margins of the basisphenoid fossa are not preserved and the foramina that transmitted the cerebral branches of the internal carotid arteries are not discernable, probably because the area is partially covered by matrix. The posterior half of the lateral surface of the main body of the parabasisphenoid is not exposed and, as a result, is not possible to determine the

presence or absence of the semilunar depression described for a referred specimen of *Garjainia prima* by Gower & Sennikov (1996). The anterior half of the main body of the parabasisphenoid is exposed through the infratemporal fenestra in left lateral view. The lateral surface of the posterodorsal region of the clinoid process possesses a deep, ventrally curved groove, which would have transmitted the palatine branch of the facial nerve (cranial nerve VII) (Gower & Sennikov, 1996), resembling the condition in referred specimens of *Garjainia prima* (PIN 951/60), *Sarmatosuchus otschevi* (PIN 2865/68), *Fugusuchus hejiapensis* (Gower & Sennikov, 1996), and *Shansisuchus shansisuchus* (Gower & Sennikov, 1996). It is not possible to observe the notch between the basipterygoid process and basal tuber in lateral view because the area is covered by plaster and matrix. The left basipterygoid process is posteroventrally directed in lateral view (Fig. 5A: 'bsp'), as also occurs in referred specimens of *Garjainia prima* (PIN 951/60) and *Garjainia madiba* (BP/1/5525). The anterior half of the cultriform process is exposed in left lateral view (Fig. 11C, D: 'culp'). Its main axis in lateral view is approximately parallel to the longitudinal axis of the skull, and there is no evidence for a dorsoventral constriction at the base of the process, as occurs in *Prolacerta broomi* (Gow, 1975) and the erythrosuchids *Erythrosuchus africanus*, *Shansisuchus shansisuchus*, and a referred specimen of *Garjainia prima* (Gower & Sennikov, 1996). By contrast, the base of the cultriform process is dorsoventrally constricted in *Proterosuchus fergusi*, *Fugusuchus hejiapensis*, and *Euparkeria capensis* (Gower & Sennikov, 1996). The ventral margin of the cultriform process is level with the base of the basipterygoid process in lateral view. The dorsal region of the clinoid process of the basisphenoid is damaged and the suture with the prootic is not discernable.

Prootic. Only the left prootic is exposed, in lateral view through the infratemporal fenestra (Fig. 11C, D). The dorsal margin of the prootic contacts the parietal, forming part of the internal medial wall of the supratemporal opening. The prootic possesses a posterior projection that overlaps the otoccipital and forms part of the base of the paroccipital process (Fig. 11C, D: ‘ot-pr’). The crista prootica is well developed, sinusoidal, and its main axis is oriented from anteroventrally to posterodorsally. The crista prootica forms the anterolateral margin of the fenestra ovalis and the base of the stapedial groove. There is an anteroposteriorly long recess on the edge of the crista prootica, situated posterodorsally to the fenestra ovalis, which may harbour the exit foramen for the facial nerve (cranial nerve VII) and the groove that indicates the route of the chorda tympani branch of this cranial nerve (Fig. 11C, D: ‘gr’). A similar condition is possibly present in *Erythrosuchus africanus* (Gower, 1997). On the lateral surface of the prootic it is not possible to determine the likely route of the hyomandibular branch of the facial nerve because of poor preservation. The position of the preserved portion of the laterosphenoid-prootic suture indicates that the foramen for the exit of the trigeminal nerve (cranial nerve V) is completely enclosed by the prootic (Fig. 11C, D: ‘V’). This condition contrasts with that present in *Proterosuchus fergusi* (Cruickshank, 1972; BP/1/3993), *Proterosuchus goweri* (NM QR 880), *Proterosuchus alexanderi* (NM QR 1484), *Sarmatosuchus otschevi* (Gower & Sennikov, 1997; PIN 2865/68), a referred specimen of *Erythrosuchus africanus* (Gower, 1997; UMZC T700), *Shansisuchus shansisuchus* (Gower & Sennikov, 1996: fig. 6b), and possibly *Fugusuchus hejiapensis* (Gower & Sennikov, 1996), in which the exit of the trigeminal nerve is enclosed by both laterosphenoid and prootic. Gower & Sennikov (1996) and Gower (1997) suggested that in a referred specimen of *Garjainia prima* and in at least one specimen of *Erythrosuchus africanus* (NHMUK PV R3592) the exit of the trigeminal

nerve is probably completely enclosed by the prootic, but this interpretation is not certain. Nevertheless, it is clear that *Erythrosuchus africanus* and *Fugusuchus hejiapanensis* more closely resemble *Garjainia prima* than other archosauriforms in the presence of inferior and superior anterior processes of the prootic that closely approach each other. The exit foramen of the trigeminal nerve in PIN 2394/5 appears to open anteriorly into a groove that may have transmitted the ophthalmic branch of the trigeminal nerve (see Clark *et al.*, 1993). However, the identification of this groove in PIN 2394/5 should be considered tentative because the area is damaged. The inferior anterior process (= pila antotica) of the prootic possesses a ridge that is possibly for attachment of the *M. protractor pterygoidei* (Gower & Sennikov, 1996), situated anterior to the exit foramen of the trigeminal nerve (Fig. 11C, D: 'ppt'), resembling the condition in other early archosauriforms (e.g. *Fugusuchus hejiapensis*: Gower & Sennikov, 1996; *Sarmatosuchus otschevi*: Gower & Sennikov, 1997). The sutures between the prootic inferior anterior process and the clinoid process of the parabasisphenoid and the laterosphenoid are not preserved. The superior anterior process of the prootic possesses a dorsoventrally convex lateral surface and an extensive, slightly sigmoid suture (oriented mostly from anteroventral to posterodorsal) with the base of the laterosphenoid (Fig. 11C, D: 'ltp-pr').

Laterosphenoid. The left laterosphenoid is ossified and exposed in lateral view through the infratemporal fenestra and the orbit (Fig. 11C–E). Its base possesses extensive sutures with the prootic posteroventrally and the parietal posterodorsally. Two posteriorly curved ridges are present on the lateral surface of the laterosphenoid. The more posterior ridge is posterior to the medial projection of the capitate process of the laterosphenoid and reaches the suture with the prootic, resembling the condition in other erythrosuchids (e.g. a referred

specimen of *Garjainia prima*, *Shansisuchus shansisuchus*, *Erythrosuchus africanus*: Gower & Sennikov, 1996; Gower, 1997). This ridge is not present in *Proterosuchus fergusi* (Clark *et al.*, 1993). The more anterior ridge, the cotylar crest, extends along the capitate process. Although the area is partly damaged, it seems that the capitate process contacted the parietal, postfrontal, frontal and possibly postorbital. However, there is no conclusive evidence for the presence of a postorbital-laterosphenoid contact (cf. Gower & Sennikov [1996] for a referred specimen of *Garjainia prima*). A groove bound by the two ridges possibly transmitted the ophthalmic branch of the trigeminal nerve, as interpreted for a referred specimen of *Garjainia prima*, *Shansisuchus shansisuchus* (see Gower & Sennikov, 1996), and *Erythrosuchus africanus* (Gower, 1997). A probably homologous groove is also present in *Proterosuchus fergusi* but is not delimited by a posterior ridge (Clark *et al.*, 1993). Several breakages on the lateral surface of the anterior process of the laterosphenoid mean that it is not possible to discern (assuming that it was present) the foramen for the passage of the ophthalmic artery or the surface for contact with the dorsal process of the epipteryoid. The anterior process of the laterosphenoid tapers anteriorly and is considerably shorter than that present in *Proterosuchus alexanderi* (NM QR 1484), but resembles the condition in *Erythrosuchus africanus* (Gower, 1997) and a referred specimen of *Garjainia prima* (Gower & Sennikov, 1996). The frontal receives the anterior process of the laterosphenoid along an extensive, sagittally oriented contact.

Palatal complex

Post-mortem transverse compression of the skull displaced the preserved palatal bones from their original positions (Ochev, 1975; see above) (Figs. 4–7, 11F). Moreover, several areas of the palate are heavily covered by matrix and, as a result, it is not currently possible

to observe the morphology and position of the choanae. Only part of the probable right suborbital fenestra can be recognised in ventral view. The vomers, if preserved, are not exposed.

Palatine. The right palatine is preserved in articulation with the pterygoid and is exposed in ventral and partially lateral views (Figs. 4–7, 11F: ‘pal’). The palatine has an extensive anteroposterior suture with the pterygoid (Ochev, 1975). A thick, anterolateral to posteromedial ridge on the ventral surface of the palatine separates two concave areas, and continues onto the ventral margin of the anterior process (= palatine ramus) of the pterygoid (Ochev, 1975; Fig. 11F: ‘ri’), as also occurs in *Sarmatosuchus otschevi* (PIN 2865/68), *Proterosuchus fergusi* (RC 59), and a referred specimen of *Garjainia prima* (PIN 951/18). The palatine contacted the medial surface of the maxilla, but it seems very likely that it did not contact the jugal, as interpreted by Ochev (1975). The ventral surface of the palatine is well-preserved and bears no indication of palatal teeth, resembling the condition in *Erythrosuchus africanus* (Gower, 2003; NHMUK R3592) and *Shansisuchus shansisuchus* (Young, 1964: fig. 15b, c). By contrast, *Prolacerta broomi* (Gow, 1975), *Proterosuchus fergusi* (RC 59; Welman, 1998), *Sarmatosuchus otschevi* (PIN 2865/68), a referred specimen of *Garjainia prima* (PIN 951/18), and *Euparkeria capensis* (Ewer, 1965) have palatal teeth on the ventral surface of the palatine.

Pterygoid. The right pterygoid is almost complete and the left element is partially preserved in semi-articulation with the rest of the skull (Figs. 6, 7, 11F), with part of the ventrolateral process (= ectopterygoid ramus) of the left pterygoid preserved separately (Fig. 9C, D). The anterior process of the pterygoid is anteroposteriorly long, with an almost

flat medial surface. A thick, rounded ridge runs along the dorsal margin of the preserved portion of the anterior process (Ochev, 1975). A similar ridge is present on the ventral margin of the posterior half of the anterior process, but this ridge continues onto the palatine rather than along the suture between the pterygoid and palatine (Ochev, 1975). The ventrolateral process is posterolateroventrally directed and proportionately long, resembling that of *Erythrosuchus africanus* (NHMUK R3592), *Shansisuchus shansisuchus* (Young, 1964: fig. 15a), *Uralosaurus magnus* (PIN 2973/70), and *Sarmatosuchus otschevi* (PIN 2865/68). This process in PIN 2394/5 possesses a ridge that is thicker than those present on the anterior process and that is restricted to the posteromedial margin of the ventrolateral process. This ridge delimits posteriorly a concave area. The ventrolateral process tapers distally and possesses a long facet, with a slightly concave and striated surface, to articulate with the ectopterygoid (Fig. 9D: 'ecf'). It is not possible to discern most of the suture between the pterygoid and the ectopterygoid on the right side of the palate. The facet for the basal articulation is not exposed on either pterygoid. The pterygoid posterolateral process (= quadrate ramus) is long, transversely thin and increases in dorsoventral height posteriorly. The contact with the pterygoid ala of the quadrate is not well preserved. The pterygoid of PIN 2394/5 also bears no indication of palatal teeth, resembling the condition in *Erythrosuchus africanus* (Gower, 2003), *Uralosaurus magnus* (PIN 2973/70), and *Shansisuchus shansisuchus* (Young, 1964: fig. 15a). By contrast, a referred specimen of *Garjainia prima* possesses two anteroposteriorly short rows of palatal teeth on a ridge that is placed on the anterior process of the pterygoid and continues onto the palatine (PIN 951/18). The palatal teeth on the pterygoids of *Prolacerta broomi* (BP/1/471), *Proterosuchus fergusi* (RC 59, SAM-PK-11208), *Sarmatosuchus otschevi* (PIN 2865/68),

and *Euparkeria capensis* (Ewer, 1965) are considerably more numerous and extend over a greater anteroposterior distance than in referred specimens of *Garjainia prima*.

Ectopterygoid. Part of the main body and the base of the lateral process of the right ectopterygoid and the lateral process of the left ectopterygoid are preserved (Figs. 4, 5B, 11A, B: 'ec'). The ectopterygoid has an anteroposteriorly long medial body, indicating an extensive contact with the ventrolateral process of the pterygoid (Ochev, 1975). The lateral process curves strongly posteriorly, acquiring a hook shape in ventral view, as occurs in other archosauriforms (e.g. *Proterosuchus fergusi*: SAM-PK-11208). The anteriormost portion of the lateral surface of this process articulates with the distal tip of the horizontal process of the maxilla. The remainder of the lateral process possesses an anteroposteriorly extensive contact with the medial surface of the jugal.

Epipterygoid. Both epipterygoids are partially preserved, lacking their distal ends and parts of their bases (Fig. 9E, F). These bones are currently detached from the rest of the skull but originally they were preserved in articulation with the ascending process of the pterygoids (Ochev, 1975). The base of the epipterygoid is anteroposteriorly expanded, more so posteriorly than anteriorly (Fig. 9: 'ae', 'pe'), resembling the condition in *Proterosuchus fergusi* (BSPG 1934 VIII 514, RC 96). The medial surface of the base of the bone has a well-defined and dorsoventrally broad facet for an extensive articulation with the dorsolateral surface of the pterygoid. However, it is not possible to detect the facet for the epipterygoid on the right pterygoid. The dorsal process of the epipterygoid is rod like and is directed mainly dorsally, but also slightly anteriorly (Fig. 9: 'dp'). The dorsal process of the

right epipterygoid is posteriorly curved, probably artefactually. There is no clear area for reception of the epipterygoid on the lateral surface of the laterosphenoid.

Lower jaw

General morphology. Both hemimandibles have suffered post-mortem transverse compression, as also occurs in the skull. The right hemimandible is preserved in articulation with the skull and is almost complete (Fig. 12). The left hemimandible is incomplete; the preserved parts consist of the posterior end of the dentary in articulation with the anterior halves of the surangular and angular and most of the prearticular (Fig. 13), as well as the incomplete glenoid and postglenoid region (Fig. 14). When the lower jaw is in complete occlusion with the skull the preserved anterior margin of the dentary (which is damaged but only a small portion of the bone appears to be missing) extends to the level of the mid-length of the premaxillary body (Fig. 2), resembling the condition in *Prolacerta broomi* (Modesto & Sues, 2004: fig. 1), *Erythrosuchus africanus* (BP/1/5207), and probably *Tasmaniosaurus triassicus* (UTGD 54655), and contrasting with the proportionally shorter hemimandible of *Proterosuchus fergusi* (BP/1/4016, RC 96, SAM-PK-11208). The external mandibular fenestra lies in the posterior half of the lower jaw and is delimited anteriorly by the dentary, ventrally by the angular and dorsally by the surangular in lateral view (Figs. 2, 12). This fenestra is oval, being anteroposteriorly longer (67 mm) than dorsoventrally tall (23 mm) and representing 15.8% of the total length of the lower jaw, being proportionally shorter than that of *Erythrosuchus africanus* (BP/1/5207: 21.7%) and slightly shorter than that of *Euparkeria capensis* (SAM-PK-5867: 18.0%), but much longer than in *Proterosuchus fergusi* (3.7% to 10.1% of the total length of the lower jaw; RC 59, 96, BSPG 1934 VIII 514, GHG 231). The adductor fossa on the medial surface

of the lower jaw opens dorsolaterally and is bound by the prearticular ventromedially, the articular posteriorly, the surangular dorsolaterally and the coronoid anterodorsally (Figs. 12B, E, 13B, E). The anteriormost border of the adductor fossa is not preserved because the ventral margin of the posterior end of the coronoid and the dorsal margin of the anterior end of the prearticular are broken off.

Dentary. The dentary is approximately 60% of the length of the lower jaw in lateral view (Figs. 2, 12), similar to that in *Proterosuchus fergusi* (RC 59: 58.2%; SAM-PK-11208: 60.3%; BP/1/3993: 60.8%; RC 96: 63.4%; BSPG 1934 VIII 514: 60.1%; GHG 231: 63.9%), *Erythrosuchus africanus* (BP/1/5207: 54.6%), and *Euparkeria capensis* (SAM-PK-5867: 53.5%). In addition, the dentary of PIN 2394/5 is a rather robust bone, being 5.4 times longer than the dorsoventral height of its anterior end, similar to *Erythrosuchus africanus* (BP/1/5207: ratio 5.0) and probably *Shansisuchus shansisuchus* (Young, 1964: figs. 17, 18) and more robust than in *Proterosuchus fergusi* (BP/1/4016: ratio 10.4; SAM-PK-K10603: ratio 11.6; RC 96: ratio 10.6; GHG 231: ratio 10.5), *Tasmaniosaurus triassicus* (UTGD 54655: ratio ca. 11.1), *Prolacerta broomi* (BP/1/2675), “*Chasmatosaurus*” *yuani* (IVPP V2719), and, to a lesser degree, *Euparkeria capensis* (SAM-PK-5867: ratio 7.8). The dentary of PIN 2394/5 is gently dorsally bowed, resembling the condition of *Sarmatosuchus otschevi* (PIN 2865/68), but to a lesser degree than the stronger dorsal bowing in *Proterosuchus fergusi* (RC 59, 96, SAM-PK-11208, TM 201), “*Chasmatosaurus*” *yuani* (Young, 1936), a dentary referred to *Uralosaurus magnus* (PIN 2973/71), and *Euparkeria capensis* (SAM-PK-5867). By contrast, the dentary is almost straight in lateral view, with a straight ventral margin, in *Prolacerta broomi* (BP/1/471), *Teyujagua paradoxa* (UNIPAMPA 653 cast), *Tasmaniosaurus triassicus*

(Ezcurra, 2014; UTGD 54655), *Erythrosuchus africanus* (Gower, 2003; BP/1/5207), and *Shansisuchus shansisuchus* (Young, 1964: figs. 17, 18). The anterior margin of the dentary of PIN 2394/5 is damaged, but likely only its anteriormost tip is missing (Fig. 2), with the apparently rounded anterior margin of the dentary probably a preservational artefact. The anterior end of the bone is slightly dorsally and transversely expanded, as also occurs in other early archosauriforms (e.g. *Sarmatosuchus otschevi*: PIN 2865/68; *Erythrosuchus africanus*: BP/1/5207; *Shansisuchus shansisuchus*: Young, 1964: figs. 17, 18). The posterior end of the dentary is dorsoventrally expanded, such that the dorsal margin of the dentary is continuously concave in lateral view and is shortest dorsoventrally at the level of the eighth alveolus. The lateral surface of the anteroventral corner of the dentary is ornamented by a series of anastomosing grooves with a main alignment subparallel to the alveolar margin of the bone. The lateral surface of the anterior end of the right dentary is damaged, but at least one anterodorsally opening neurovascular foramen is visible at the level of the second alveolus (Fig. 12A, D: ‘f’). A similar foramen is present in a referred specimen of *Garjainia prima* (PIN 951/30), and in this specimen it forms part of a row of anterodorsally opening foramina that runs parallel to the alveolar margin along the anterodorsal corner of the bone. The lateral surface of the dentary of the holotype of *Garjainia prima* possesses two short parallel grooves that are oriented from anteroventral to posterodorsal (Fig. 12A, D: ‘g’). These grooves are slightly above the mid-height of the bone and begin at the level of the eighth and ninth alveoli. The posterior groove is considerably longer than the anterior one, extending from the level of the ninth to the eleventh alveolus. The grooves are deeper anteroventrally and shallower posterodorsally where they merge with the remainder of the lateral surface of the bone. These parallel grooves are present in the same position in a referred specimen of *Garjainia prima* (PIN

951/30), and anteroventrally the grooves terminate in foramina. In PIN 2394/5 it is not possible to determine the presence of these foramina because the anteroventral ends of the grooves are filled with matrix. The lateral surface of the posterior two-thirds of the dentary possesses a longitudinal, sub-triangular depression that is dorsoventrally taller towards its posterior end.

The dentary possesses three posterior processes: posterodorsal and posterior central processes that articulate with the surangular, and a posteroventral process that articulates with the angular (Figs. 2, 12, 13: 'pdp', 'pcp', 'pvp'). This condition is also present in *Erythrosuchus africanus* (Gower, 2003), *Shansisuchus shansisuchus* (Young, 1964: fig. 16c), and referred specimens of *Garjainia prima* (PIN 951/30, 951/46). By contrast, in *Proterosuchus fergusi* a posteroventral process is absent (RC 96, SAM-PK-K10603). In PIN 2394/5 the preserved portion of the right and most complete posterodorsal process extends posteriorly to the same level as the posterior extension of the posterior central process and articulates with a deep and well-defined facet on the lateral surface of the surangular. This facet is extremely similar to that of *Erythrosuchus africanus* (BP/1/5207) and indicates that when complete the posterodorsal process of both species extended posteriorly beyond the posterior extension of the posterior central process (Figs. 2, 13A, D: 'pdpf'), as also occurs in referred specimens of *Garjainia prima* (PIN 951/30, 951/46) and probably in *Shansisuchus shansisuchus* (Young, 1964: fig. 16c). The facet on the surangular indicates that the posterodorsal process of PIN 2394/5 was a dorsoventrally short and slightly ventrally curved finger-like projection. The height of the right posterodorsal process is probably exaggerated by breakage. The posterior central process of the dentary is subtriangular and forms the anterodorsal border of the external mandibular fenestra, resembling the condition in *Proterosuchus fergusi* (RC 96), *Erythrosuchus*

africanus (BP/1/5207), and *Shansisuchus shansisuchus* (Young, 1964: fig 16c). The medial surface of this process articulates with the anterior end of the prearticular, forming part of the anterolateral border of the adductor fossa. Only the base of the posteroventral process is preserved on each of the dentaries and it is not possible to identify confidently the facet for its articulation on either angular. However, the base of the posteroventral process on the left dentary indicates that it did not participate in the anteroventral border of the external mandibular fenestra (contra Ochev, 1981: fig. 3) (Fig. 2). The posteroventral process is also excluded from the border of the external mandibular fenestra in referred specimens of *Garjainia prima* (PIN 951/46), in *Erythrosuchus africanus* (BP/1/5207), and *Shansisuchus shansisuchus* (Young, 1964: fig. 16c).

Only the anterior end of the right dentary (the rest of the bone is covered by the splenial) and the posterior end of the left element are exposed in medial view (Fig. 12B, E). The medial surface of the anterior end of the dentary is almost flat and it is not possible to describe the symphyseal facet, because it was possibly located mostly on the missing portion of the dentary and/or because of poor preservation. The anterior end of the Meckelian groove is dorsoventrally low and closer to the ventral edge of the dentary than the dorsal (Fig. 12B, E: ‘Mg’), resembling the condition in *Erythrosuchus africanus* (NHMUK R2790), *Shansisuchus shansisuchus* (Young, 1964: fig. 17c), *Sarmatosuchus otschevi* (PIN 2865/68), *Garjainia madiba* (NM QR 3051), and a dentary referred to *Uralosaurus magnus* (PIN 2973/71). The medial surface of the posterior end of the dentary possesses a dorsoventrally tall Meckelian canal that is ventrally defined by a longitudinal ridge adjacent to the ventral margin of the bone. This ridge possesses a flat medial surface for contact with the splenial. Some poorly preserved interdental plates on the anterior end of the right dentary are subtriangular to pentagonal in medial view and are not fused with

each other, resembling the condition in dentaries referred to *Garjainia madiba* (Gower *et al.*, 2014) and *Uralosaurus magnus* (Ochev, 1980; PIN 2973/71). The dorsal margin of the dentary of PIN 2394/5 is edentulous along its posterior 14.5 cm.

The dentary teeth of PIN 2394/5 possess a thecodont implantation with no evidence of an ankylothecodont implantation, as also occurs in *Erythrosuchus africanus* (Gower, 2003) and a dentary referred to *Uralosaurus magnus* (PIN 2973/71). The dentary of PIN 2394/5 has either 13 or, less likely, 14 tooth positions, resembling the condition in a referred specimen of *Garjainia prima* (PIN 951/30: 13 tooth positions), *Garjainia madiba* (NM QR 3051: 14 tooth positions), *Sarmatosuchus otschevi* (Gower & Sennikov, 1997: 14 tooth positions), and probably *Shansisuchus shansisuchus* (Young, 1964: fig. 17a). By contrast, *Prolacerta broomi* (Gow, 1975; Modesto & Sues, 2004), *Proterosuchus fergusi* (BSPG 1934 VIII 514, GHG 231, SAM-PK-11208, RC 59, 96), “*Chasmatosaurus*” *yuani* (IVPP V2719), and *Tasmaniosaurus triassicus* (UTGD 54655) all have at least 18 dentary tooth positions. Only two tooth crowns are fairly complete in the right dentary of PIN 2394/5, the morphology of which is completely congruent with those of the maxillary teeth (see above).

Coronoid. The right coronoid is preserved in articulation with the right dentary and surangular but its anterior two-thirds are missing (broken at level of the ninth dentary tooth position) and the posterior end is damaged. The coronoid is a transversely thin, plate-like and anteroposteriorly elongated bone. The posterior end is slightly spatulate, with a dorsoventrally convex medial surface and a concave lateral surface (Fig. 12B, E: ‘co’). The anterior two-thirds of the coronoid articulate with a longitudinal groove on the dorsomedial surface of the dentary, immediately medial to the alveolar margin. The coronoid covers the

bases of the dentary crowns in medial view and is visible in lateral view along its entire preserved region (Figs. 2, 12A, D), resembling the condition in *Erythrosuchus africanus* (BP/1/3893). The posterodorsal end of the coronoid folds laterally and extends onto the dorsal surface of the surangular. The surangular possesses an articular facet to receive the missing posterior end of the coronoid and this indicates that the coronoid extended for approximately 1 cm further posteriorly than is currently preserved. As a result, the coronoid would have extended slightly posterior to the mid-length of the external mandibular fenestra. The posteroventral margin of the coronoid is concave and forms the anterodorsal border of the adductor fossa in medial view. The ventral margin of the posterior end of the coronoid is damaged and the nature of the probable articulation with the prearticular is unclear. Nevertheless, the anterior end of the left prearticular is complete, indicating that it probably contacted the posteroventral end of the coronoid, closing the anterior border of the adductor fossa.

Splénial. The right splénial is preserved in articulation with the dentary and angular, and lacks its anterior end and most of the posterior tip (Fig. 12: ‘sp’), and its posterodorsal corner, anterior to the prearticular, is severely damaged. The splénial is transversely compressed and extends dorsally to the level of the ventral margin of the coronoid. The anterior two-thirds of the preserved portion of the splénial cover most of the medial surface of the dentary, with the exception of the most ventromedial surface of the dentary. The splénial gradually expands ventrally towards its posterior end. As a result, the posterior end of the bone covers completely the medial surface of the dentary, and the most lateroventral surface of the splénial is visible in lateral view, as also occurs in referred specimens of *Garjainia prima* (PIN 951/46). A facet for reception of the posterior process of the splénial

on the medial surface of the angular indicates that the posterior end of the former bone was dorsoventrally short and tapered strongly posteriorly. The posteriormost portion of the splenial is not visible in lateral view because the angular folds medially and covers it, as is also the case in referred specimens of *Garjainia prima* (PIN 951/46).

Surangular. The right surangular is almost completely preserved (Fig. 12: 'sa'), but the left is broken in two pieces and lacks most of its ventral margin (Figs. 13, 14: 'sa'). The anterior end of the surangular possesses on its lateral surface a dorsoventrally thick ridge that delimits dorsally the facet for the posterodorsal process of the dentary. This ridge becomes increasingly prominent posterior to the level of the facet and forms a laterally well developed and dorsoventrally thick longitudinal shelf on the dorsolateral surface of the bone (Figs. 12, 14: 'ssh'), resembling the condition in *Erythrosuchus africanus* (BP/1/5207, NHMUK R3592), referred specimens of *Garjainia prima* (PIN 951/46), *Garjainia madiba* (BP/1/5760), *Guchengosuchus shiguaiensis* (IVPP V8808), and *Euparkeria capensis* (SAM-PK-5867). By contrast, the surangular shelf is considerably less well developed laterally in *Prolacerta broomi* (BP/1/471, 2675), *Teyujagua paradoxa* (UNIPAMPA 653 cast), and *Proterosuchus fergusi* (BP/1/4016, RC 96, SAM-PK-11208, K10603). The longitudinal surangular shelf of PIN 2394/5 appears to be less laterally developed than those of *Erythrosuchus africanus*, referred specimens of *Garjainia prima*, and *Garjainia madiba*, probably because of post-mortem transverse compression. The surangular shelf bows gently ventrally in lateral view, following the shape of the dorsal margin of the surangular, and reaches its maximum lateral development immediately anterior to the level of the glenoid fossa. The posterior end of the shelf curves dorsally and merges with the lateral surface of the postglenoid process (Fig. 12A, D, 14A). The dorsolateral area of the

longitudinal shelf harbours an anteroposteriorly elongated flat surface and the soft tissue that covered it would likely have received the lower temporal bar and its associated soft tissue during complete occlusion of the jaws (Figs. 2, 12D: 'qjf'), as likely also occurred in other archosauriforms (e.g. *Proterosuchus fergusi*: RC 96). The holotype and a referred specimen (PIN 951/33) of *Garjainia prima* lack a posterior surangular foramen (= surangular foramen of Gower, 2003) below the longitudinal shelf on the lateral surface of the surangular. By contrast, in *Prolacerta broomi* (Modesto & Sues, 2004), *Proterosuchus fergusi* (RC 96, SAM-PK-K10603), *Erythrosuchus africanus* (NHMUK R3592), *Garjainia madiba* (NM QR 3051), and *Euparkeria capensis* (SAM-PK-5867) there is a small posterior surangular foramen situated level with the preglenoid lip and immediately below the longitudinal shelf. The surangular of PIN 2394/5 possesses an anteroposteriorly extensive, slightly sinusoidal suture with the angular (Figs. 2, 12), closely resembling the condition in referred specimens of *Garjainia prima* (PIN 951/46). This suture is mainly longitudinally oriented, but with a low anteroventral to posterodorsal component. The angular excludes the surangular from most of the ventral margin of the lower jaw, with the probable exception of its posteriormost region. The anteroventral margin of the surangular is concave and forms two-thirds of the dorsal border of the external mandibular fenestra. The dorsal surface of the surangular is widely anteroposteriostrongly convex in lateral view.

The medial surface of the surangular is concave and forms the medial wall of the large adductor fossa (Figs. 12, 13: 'adf'). The dorsal margin of the adductor fossa is clearly defined by a longitudinal, thick ridge on the dorsomedial surface of the surangular. The adductor fossa invades the ventral surface of the anterior end of this ridge and becomes shallower posteriorly. This dorsomedial ridge merges with the preglenoid process. The

preglenoid lip is dorsoventrally very low (Fig. 14: 'prgl') and the surangular portion of the postglenoid lip is considerably taller. The surangular forms the lateral half of the mandibular glenoid fossa (Figs. 12, 14: 'gf'). The surangular-articular suture runs from immediately anterior to the base of the preglenoid process, and is oriented from anterolateral to posteromedial; more posteriorly it curves medially and is almost longitudinal, running along the pre- and postglenoid lips, glenoid fossa and retroarticular process. The surangular region of the retroarticular process is posteriorly directed, anteroposteriorly short, and has a rounded posterior margin (Fig. 12).

Angular. The angular is boomerang-shaped in lateral view, with a continuously convex ventral margin (Figs. 2, 12, 13). Its anterior end forms the entire ventral border of the external mandibular fenestra. The lateral surface of the bone is almost flat, although this is probably exaggerated by transverse post-mortem compression. The ventral surface of the angular folds strongly dorsomedially and forms the floor of the adductor fossa and articulates with the prearticular. This folding is not present in the most anterior portion of the bone and, as a result, the splenial is visible in lateral view. The ventral surface of the angular is strongly transversely convex. The angular extends posteriorly slightly beyond the level of the posterior margin of the postglenoid process and thus forms most of the ventral margin of the post-dentary region of the lower jaw.

Preatticular. The right prearticular is damaged at its anterior and posterior ends and the left prearticular lacks the posterior end. The prearticular is constricted at mid-length in medial view, with dorsally expanded anterior and posterior ends (Fig. 12B, E, 13B, E), closely resembling the condition in other archosauriforms (e.g. *Proterosuchus fergusi*:

BSPG 1934 VIII 514; referred specimens of *Garjainia prima*: PIN 951/46). The dorsoventrally narrowest region of the prearticular is posteriorly displaced from the mid-length of the bone. The prearticular is dorsoventrally narrow at that point, contributing to the formation of a dorsomedially open adductor fossa. The spatulate anterior end of the prearticular, which is medially convex and laterally concave, forms the medioventral wall of the anterior region of the adductor fossa. The prearticular partially covers the angular and, as a result, the ventromedial surface of the angular is exposed in medial view. Part of the prearticular-articular suture is preserved at the posterior end of the right prearticular.

Articular. The left articular is partially preserved, lacking its anterior and medial margins and with damaged ventral and posterior surfaces (Fig. 14). Only a small and severely damaged portion of the lateral part of the right articular is preserved. Both articulars are preserved in articulation with the surangular. The articular formed a small medial portion of the preglenoid lip (Fig. 14: 'prgl'). The medial portion of the articular is not preserved, but in referred specimens of *Garjainia prima* this bone forms most of the glenoid fossa and possesses a laterally directed and anteroposteriorly long medial process (PIN 951/33). The postglenoid lip of PIN 2394/5 is formed by two dorsal projections; a lateral one formed by the surangular and a taller and more anterior one formed by the articular (Fig. 14: 'pogl'). The retroarticular process is mainly formed by the articular, with the surangular restricted to the lateralmost portion of the postglenoid region (Fig. 14: 'rap'). The portion of the retroarticular process formed by the articular is transversely wider than anteroposteriorly long. The base of the retroarticular process bears a deeply concave and dorsomedially facing surface that is anteriorly delimited by the postglenoid lip (Fig. 14: 'con'), resembling the condition in *Proterosuchus fergusi* (BSPG 1934 VIII 514), *Guchengosuchus*

shiguaiensis (IVPP V8808), referred specimens of *Garjainia prima* (PIN 951/33), and in *Garjainia madiba* (NM QR 3051). It is not possible to determine confidently the position (if present) of the foramen for the passage of the *chorda tympani* nerve because of surface damage. The posterior end of the retroarticular process possesses a pyramidal dorsomedial process (Fig. 14: ‘dmp’), as also occurs in *Proterosuchus fergusi* (BSPG 1934 VIII 514), referred specimens of *Garjainia prima* (PIN 951/33), and in *Garjainia madiba* (NM QR 3051). The ventral surface of the articular is strongly transversely convex and considerably transversely narrower than the dorsal surface.

Postcranium

The holotype of *Garjainia prima* includes a very incomplete postcranium (Figs. 15–22), comprising an axis, three anterior and middle cervical vertebrae, two posterior cervical or anterior dorsal vertebrae and four dorsal vertebrae, two distal ends of postaxial neural spines, multiple cervico-dorsal ribs, fairly complete pectoral girdles (with the exception of the left clavicle, which is missing) and an autopodial bone. Most of the postcranial bones suffered strong transverse post-mortem compression, similar to that seen in the skull. The transverse compression is particularly evident in the vertebrae, in which the crushed neural canals are slit-like in anterior and posterior views. There are no osteoderms preserved in the holotype or multiple referred specimens of *Garjainia prima* (PIN 951). Accordingly, although we cannot completely rule out the possibility of the presence of osteoderms, we consider that they were likely to be absent in *Garjainia prima*. A few possible osteoderms are associated with a specimen of *Erythrosuchus africanus* (NHMUK PV R3592), but the identification of these bones is debated (Gower, 2003; but see Nesbitt, 2011). It was not possible to determine the region of the axial skeleton to which the two isolated distal ends

of neural spine (PIN 2394/5-19–20) belong. However, these spines possess a morphology that is consistent with that of the other preserved postaxial vertebrae and, as a result, will not be described here separately.

Axis. The axis is almost completely preserved, but the centrum has damaged anterior and posterior articular surfaces (Fig. 15). The centrum is not fused to the axial intercentrum or the odontoid process, resembling the condition in *Prolacerta broomi* (BP/1/2675), *Proterosuchus fergusi* (BSPG 1934 VIII 514), *Sarmatosuchus otschevi* (PIN 2865/68), *Erythrosuchus africanus* (BP/1/5207), and *Shansisuchus shansisuchus* (Young, 1964: fig. 20a). The centrum is slightly longer than tall in lateral view, as occurs in *Sarmatosuchus otschevi* (PIN 2865/68). By contrast, the centrum is considerably longer than tall in *Prolacerta broomi* (BP/1/2675) and *Proterosuchus fergusi* (BSPG 1934 VIII 514), slightly shorter than tall in *Erythrosuchus africanus* (BP/1/5207), and strongly anteroposteriorly compressed in *Shansisuchus shansisuchus* (Young, 1964: fig. 20a). The axial centrum of PIN 2394/5 possesses a strong transverse compression close to its mid-length, resulting in an hourglass-shaped centrum in ventral view. The ventral surface of the centrum is continuously transversely convex, without any distinct median keel, as also occurs in *Sarmatosuchus otschevi* (PIN 2865/68). By contrast, *Prolacerta broomi* (BP/1/2675) and *Proterosuchus fergusi* (BSPG 1934 VIII 514; SAM-PK-11208) have a very well developed and sharp, ventral median keel on the axial centrum. The anterior surface of the centrum is damaged and partially covered by matrix, but the preserved area indicates that it was probably subvertical (Fig. 15: ‘af’), as also occurs in *Sarmatosuchus otschevi* (but with a strong ventral bevelling, PIN 2865/68) and *Shansisuchus shansisuchus* (Young, 1964: fig. 20a). By contrast, in *Prolacerta broomi* (BP/1/2675), *Proterosuchus fergusi* (BSPG 1934

VIII 514), and *Erythrosuchus africanus* (BP/1/5207) the anterior margin of the axial centrum slopes from anteroventral to posterodorsal in lateral view. The posterior articular facet of the centrum of PIN 2394/5 is gently concave and considerably higher than wide, but this condition is probably exaggerated by post-mortem compression (Fig. 15: 'pf'). However, the outline of the element probably differed from the wider than tall posterior surface of the centrum present in *Prolacerta broomi* (BP/1/2675). The posteroventral corner of the centrum is not complete, so it is not possible to determine the presence of a bevelling or facet for articulation with a postaxial intercentrum. The lateral surface of the centrum possesses two concavities separated on the posterior half of the centrum by a low, rounded ridge (Fig. 15: 'sr'), closely resembling the condition in *Prolacerta broomi* (BP/1/2675). In PIN 2394/5 this ridge is mainly horizontally oriented, but with a low anterodorsal to posteroventral component, and is situated slightly below the mid-height of the centrum. In *Proterosuchus fergusi* (BSPG 1934 VIII 514) and *Sarmatosuchus otschevi* (PIN 2865/68) there is a single, poorly defined shallow concavity on the lateral surface of the centrum. The right side of the centrum possesses a single, small and circular nutrient foramen within the dorsal concavity. There is a single apophysis for articulation with the proximal end of the axial rib in PIN 2394/5 and there is no indication of a second one, resembling the condition in *Prolacerta broomi* (BP/1/2675), *Proterosuchus fergusi* (BSPG 1934 VIII 514), and *Erythrosuchus africanus* (BP/1/5207). This apophysis is next to the anterior margin of the centrum and is shared between the base of the neural arch and the dorsal end of the centrum. Its position suggests that it would be a serial homolog of the postaxial diapophyses (Fig. 15: 'dp'). As a result, the second head of the axial rib (if present) possibly articulated on the lateral surface of the axial intercentrum, as in *Proterosuchus fergusi* (BSPG 1934 VIII 514). There is no visible neurocentral suture.

The dorsoventral height of the neural arch up to the base of the neural spine is slightly lower than that of the centrum. The prezygapophyses are dorsoventrally low and anteroposteriorly short (Fig. 15: 'prz'), as also occurs in other archosauromorphs (e.g. *Prolacerta broomi*: BP/2675; *Proterosuchus fergusi*: BSPG 1934 VIII 514; *Sarmatosuchus otschevi*: PIN 2865/68; *Erythrosuchus africanus*: BP/1/5207). The postzygapophyses are prominent, posteriorly extending far beyond the posterior margin of the centrum (Fig. 15: 'poz'). The postzygapophysis has a ventrolaterally facing, oval to subcircular articular facet. A thick ridge extends from the base of the postzygapophysis; this ridge is mainly horizontally oriented, but with a low anteroventral component (Fig. 15: 'r'), resembling the condition in other archosauromorphs (e.g. *Prolacerta broomi*: BP/1/2675; *Sarmatosuchus otschevi*: PIN 2865/68). The ridge ends before reaching the base of the prezygapophysis. The ridge on the left side of the vertebra is slightly better developed than that of the right side, but this difference is probably a post-mortem artefact. The neural arch bears a moderately deep depression immediately lateral to the base of the neural spine (Fig. 15: 'dn'), as also occurs in other early archosauriforms (e.g. *Proterosuchus fergusi*: GHG 231; *Sarmatosuchus otschevi*: PIN 2865/68). This depression extends dorsally as a shallow concavity onto the lateral surface of the base of the neural spine, is better developed on the right side of the vertebra, and is situated close to the mid-length of the base of the neural spine. The axis lacks a prespinal fossa, but possesses a very deep postspinal fossa between the postzygapophyses that extends onto the base of the neural spine (Fig. 15: 'psf'), resembling the condition in other early archosauromorphs (e.g. *Prolacerta broomi*: BP/1/2675; *Sarmatosuchus otschevi*: PIN 2865/68; *Shansisuchus shansisuchus*: Young, 1964: fig. 20a; *Euparkeria capensis*: SAM-PK-5867). The postspinal fossa becomes shallower dorsally and does not reach the distal tip of the neural spine. The postspinal fossa

is ventrally closed by the median contact between the postzygapophyses. A thick ridge connects the base of the postzygapophysis with the neural spine and forms the lateral wall of the postspinal fossa. This condition is also observed in other early archosauromorphs (e.g. *Prolacerta broomi*: BP/1/2675; *Proterosuchus fergusi*: BSPG 1934 VIII 514). The neural spine is blade-like, with a subtriangular anterior projection that extends anteriorly considerably beyond the level of the anterior margin of the centrum (Fig. 15: 'ap'), as also occurs in *Prolacerta broomi* (BP/1/2675), *Teyujagua paradoxa* (UNIPAMPA 653 cast), *Proterosuchus fergusi* (BSPG 1934 VIII 514), *Sarmatosuchus otschevi* (PIN 2865/68), *Shansisuchus shansisuchus* (Young, 1964: fig. 20a), and *Euparkeria capensis* (SAM-PK-5867). The dorsal margin of the neural spine is slightly convex in lateral view, resembling the condition in *Shansisuchus shansisuchus* (Young, 1964: fig. 20a) and *Euparkeria capensis* (SAM-PK-5867). The posterior end of the neural spine is moderately posterodorsally expanded and extends posteriorly a short distance beyond the posterior margin of the centrum and approximately to the level of the posterior tips of the postzygapophyses, resembling the condition in *Sarmatosuchus otschevi* (PIN 2865/68). In *Prolacerta broomi* (BP/1/2675) and *Teyujagua paradoxa* (UNIPAMPA 653 cast) the posterior margin of the neural spine does not extend beyond the posterior margin of the centrum or the tips of the postzygapophyses, and in *Proterosuchus fergusi* (BSPG 1934 VIII 514) and *Shansisuchus shansisuchus* (Young, 1964: fig. 20a, b) the posterior margin of the neural spine extends posteriorly considerably beyond the remainder of the vertebra. The neural spine of PIN 2394/5 is transversely thicker anteriorly and posteriorly than at mid-length. The posterior end of the neural spine is considerably more transversely expanded than the anterior end, but the degree of transverse expansion is probably considerably lower than it was originally because of the post-mortem compression. The

original expansion was probably more similar to the condition in *Shansisuchus shansisuchus* (Young, 1964: fig. 20a). The neural spine lacks a spine table.

Anterior postaxial cervical vertebrae. There are three postaxial anterior cervical vertebrae, which are possibly a consecutive series following the axis (i.e. PIN 2394/5-11: third cervical; PIN 2394/5-12 fourth cervical; PIN 2394/5-13: fifth cervical). The third and fifth cervical vertebrae are fairly complete, with some damaged margins of the centra, zygapophyses and neural spine; and lacking most of the diapophyses (Fig. 16A–D, I–L). The fourth cervical lacks the anteroventral half of the centrum and most of the diapophyses (Fig. 16E–H). The vertebrae all possess a very similar morphology and, as a result, they are described together. The centrum is non-notochordal and parallelogram-shaped in lateral view, with the anterior articular facet situated more dorsally than the posterior one, similar to the condition in other early archosauromorphs (e.g. *Prolacerta broomi*: BP/1/2675; *Sarmatosuchus otschevi*: PIN 2865/68; *Garjainia madiba*: BP/1/5360). The centrum is slightly longer than tall, resembling the condition in *Sarmatosuchus otschevi* (PIN 2865/68). By contrast, the centra of the anterior postaxial cervicals of *Erythrosuchus africanus* (Gower, 2003; SAM-PK-3028) and *Shansisuchus shansisuchus* (Young, 1964: fig. 20e) are considerably anteroposteriorly shorter than tall, and in *Prolacerta broomi* (BP/1/2675), *Teyujagua paradoxa* (UNIPAMPA 653 cast), *Proterosuchus fergusi* (BSPG 1934 VIII 514, SAM-PK-11208), *Guchengosuchus shiguaiensis* (IVPP V8808), and *Euparkeria capensis* (SAM-PK-5867) the centra are considerably longer than tall. The centrum is moderately compressed at mid-length and has an hourglass-shape in ventral view. The ventral surface of the centrum has a low and sharp median keel that becomes flatter posteriorly, resembling the condition in *Sarmatosuchus otschevi* (PIN 2865/68),

Guchengosuchus shiguaiensis (IVPP V8808), *Prolacerta broomi* (BP/1/2675), *Proterosuchus fergusi* (BSPG 1934 VIII 514), and *Euparkeria capensis* (SAM-PK-5867). *Erythrosuchus africanus* has a low median ventral keel (BP/1/4680), but it is considerably transversely thicker than in the holotype of *Garjainia prima*. The anterior and posterior articular facets of the centrum are concave and higher than wide, but the transversely compressed outlines of the centrum faces are exaggerated by post-mortem compression. Nevertheless, it seems that the condition of PIN 2394/5 differed from the transversely wider than tall articular surfaces of the anterior cervical centra of *Prolacerta broomi* (BP/1/2675). The ventral margins of the anterior and posterior facets are not sufficiently preserved to determine the presence of bevelled surfaces for articulation with postaxial intercentra. The lateral surface of the centrum possesses two concave areas partially separated by a subhorizontal ridge (Fig. 16: 'sr'), a similar feature to that present in the axis and which resembles the condition in *Erythrosuchus africanus* (SAM-PK-3028) and *Garjainia madiba* (BP/1/5360). The parapophysis is placed on a low peduncle that is situated on the anterior margin of the centrum, immediately below the level of mid-height of the centrum (Fig. 16: 'pa'). The subhorizontal ridge of the centrum extends posteriorly from the base of the peduncle of the parapophysis. Thus, this ridge extends further anteriorly than in the axis. The probable fourth cervical vertebra possesses one small nutrient foramen on the left side of the centrum, but the foramen seems to be absent in the other postaxial anterior cervical vertebrae. There are some traces of the neurocentral suture, but most of the suture seems to be closed on both sides of the vertebrae. Only the bases of the diapophyses are preserved, and are situated on the anterior edge of the centrum (Fig. 16: 'dp'). The diapophyses are situated immediately above the mid-height of the centrum in the

third cervical and level with the dorsal margin of the centrum and extending partially onto the base of the neural arch in the fourth and fifth cervical vertebrae.

The height of the neural arch up to the base of the neural spine is considerably dorsoventrally lower than the height of the centrum. There are no laminae on the surface of the neural arch, similar to the condition in the anterior cervical vertebrae of proterosuchids (NM QR 1484) and *Erythrosuchus africanus* (SAM-PK-3028). The base of the neural arch bears a shallow depression immediately below the base of the postzygapophysis (Fig. 16: 'd'), a feature that is widespread among early archosauriforms (e.g. *Erythrosuchus africanus*: SAM-PK-3028). The zygapophyses are anteroposteriorly well developed, with the prezygapophyses extending far beyond the anterior margins of the centra and the postzygapophyses extending slightly beyond the posterior margins of the centra (Fig. 16: 'poz', 'prz'). The prezygapophyses are anterodorsally directed in lateral view and the articular facets face dorsomedially at an angle of 45° (third cervical), to slightly lower than 45° (fourth cervical), to the horizontal. The postzygapophyses are directed almost straight posteriorly in lateral view and the articular facets face lateroventrally at angles congruent with those observed in the prezygapophyses. The articular facets of the zygapophyses are oval to subcircular. There is no hyposphene or hypantrum. A subtle ridge extends anteroventrally from the base of the postzygapophysis along the lateral surface of the neural arch (Fig. 16: 'r'). This ridge is less well developed than the ridge present in the axis, and resembles the condition in other archosauriforms (e.g. *Proterosuchus fergusi*: BSPG 1934 VIII 514; *Erythrosuchus africanus*: SAM-PK-3028). There is a shallow depression placed immediately lateral to the base of the neural spine, as also occurs in other archosauriforms (e.g. *Proterosuchus fergusi*; SAM-PK-11208; *Euparkeria capensis*: SAM-PK-5867). The neural spine is sub-vertical and considerably taller than anteroposteriorly long, being taller

than the height of the centrum (Fig. 16: 'ns'), resembling the condition in *Sarmatosuchus otschevi* (PIN 2865/68), *Teyujagua paradoxa* (UNIPAMPA 653 cast), some specimens of *Proterosuchus fergusi* (BSPG 1934 VIII 514; SAM-PK-11208), and *Euparkeria capensis* (SAM-PK-5867). The neural spines of the anterior postaxial cervical vertebrae of *Guchengosuchus shiguaiensis* are also taller than the centrum, but slightly anteriorly oriented and with an anteroposterior expansion of the distal end (IVPP V8808). By contrast, in *Prolacerta broomi* the neural spine is anteroposteriorly longer than tall and lower than the height of the centrum (BP/1/2675). There are deep pre- and postspinal fossae, but these are restricted to the base of the neural spine (Fig. 16: 'posf', 'prsf'). The anterior surface of the neural spine has a thin vertical edge that probably served as a point of attachment for intervertebral ligaments. The anteroposterior length of the neural spine increases slightly towards its distal end, resulting in a somewhat trapezoidal outline of the neural spine in lateral view. The distal end of the neural spine is slightly transversely expanded, but without a spine table or a lateral process. These neural spines are less transversely expanded and rugose than in *Guchengosuchus shiguaiensis* (IVPP V8808). The distal surface of the neural spine is convex and differs from the flat surface present in *Euparkeria capensis* (SAM-PK-5867), which articulates with osteoderms. The distal end of the neural spine of the holotype of *Garjainia prima* is oval, with an anteroposterior main axis, in dorsal view.

Cervico-dorsal (= pectoral) vertebrae. The two cervico-dorsal vertebrae are preserved in articulation (PIN 2394/5-16) (Fig. 17). The parapophyses are situated on the anterodorsal corner of the centrum and the anteroventral portion of the neural arch and the transverse processes are well developed and situated level with the zygapophyses (Fig. 17: 'tp', 'pa').

This combination of features indicates that these elements correspond to cervico-dorsal vertebrae, based on comparisons with other archosauriforms (e.g. *Proterosuchus alexanderi*: NM QR 1484; *Sarmatosuchus otschevi*: Gower & Sennikov, 1997; *Erythrosuchus africanus*: Gower, 2003). The left sides of these vertebrae are poorly preserved and they lack the distal ends of the diapophyses. The right diapophysis of the more anterior of the two vertebrae is complete, and the subsequent vertebra preserves the base of the right diapophysis. The zygapophyses of the anterior vertebra are relatively complete, lacking only the anterior ends of the prezygapophyses. In the posterior vertebra, the prezygapophyses are complete and the postzygapophyses completely lost. The neural spines are fairly complete. There is no preserved intercentrum between the centra of the two cervico-dorsal vertebrae, but this could simply result from lack of preservation because there are isolated intercentra preserved in referred specimens of *Garjainia prima* (PIN 951).

The centrum is non-notochordal and slightly parallelogram shaped in lateral view, with the anterior articular facet slightly dorsal to the posterior one, as also occurs in other early archosauromorphs (e.g. *Prolacerta broomi*: BP/1/2675; *Sarmatosuchus otschevi*: PIN 2865/68; *Euparkeria capensis*: UMZC T921; *Garjainia madiba*: BP/1/5360). In lateral view, the centrum is anteroposteriorly shorter than tall, resembling the posterior cervicals and anterior dorsals of *Sarmatosuchus otschevi* (Gower & Sennikov, 1997; PIN 2865/68), *Garjainia madiba* (Gower *et al.*, 2014; BP/1/5360), *Erythrosuchus africanus* (Gower, 2003; NHMUK R3592), and *Shansisuchus shansisuchus* (Young, 1964: fig. 20). By contrast, in *Prolacerta broomi* (BP/1/2675), *Proterosuchus alexanderi* (NM QR 1484), *Cuyosuchus huenei* (MCNAM 2669), and *Euparkeria capensis* (UMZC T921) the cervico-dorsal centra are longer than tall. The centrum is transversely compressed at mid-length in ventral view, as occurs in the more anterior cervical vertebrae. The ventral surface of the

centrum possesses a low and sharp median ventral keel, resembling the condition in *Proterosuchus alexanderi* (NM QR 1484), *Garjainia madiba* (BP/1/5360), and *Erythrosuchus africanus* (NHMUK R3592), but it is not possible to determine if this keel also extended onto the posterior end of the centrum because the area is not preserved. By contrast, the posterior cervical vertebrae of *Sarmatosuchus otschevi* (PIN 2865/68) and *Cuyosuchus huenei* (MCNAM 2669) lack a ventral keel. The anterior and posterior articular surfaces of the centrum are oval, taller than wide, and concave. There is possibly a slight bevelling on the anteroventral surface of the more anterior vertebra. The lateral surface of the centrum bears two concave areas separated by a more poorly developed subhorizontal ridge than in the anterior cervical vertebrae. The neurocentral suture is not visible in these vertebrae and was probably completely closed. The parapophysis is on a short but prominent pedicel, and has an oval articular facet. This pedicel is more strongly developed laterally at its dorsal margin and, as a result, the parapophyseal facet faces mainly laterally, but with a low ventral component.

The neural arches of the cervico-dorsal vertebrae of the holotype of *Garjainia prima* are proportionally tall when compared with the heights of the centra. The neural arch up to the base of the neural spine is subequal in height to the centrum, resembling the condition in *Proterosuchus fergusi* (SAM-PK-11208), *Tasmaniosaurus triassicus* (UTGD 54655), and *Euparkeria capensis* (SAM-PK-5867). By contrast, the height of this region of the neural arch is proportionately lower in *Prolacerta broomi* (BP/1/2675). The base of the neural arch possesses an inflated and mainly vertical area on the lateral surface, which is situated below the level of the diapophysis and curves anteriorly to reach the base of the parapophysis (Fig. 17: 'ia'), closely resembling the condition in the dorsal vertebrae of "*Chasmatosaurus*" *yuani* (IVPP V2719) and *Sarmatosuchus otschevi* (PIN 2865/68). As a

result, this inflated area delimits a concavity that is positioned posteroventral to the paradiapophyseal lamina. The transverse process is very long and posterolaterally directed, forming an angle of approximately 45° with the anteroposterior axis of the axial skeleton (Fig. 17: 'tp'). However, the strong posterior orientation of the transverse process may be an artefact of the post-mortem transverse compression. The transverse process is subrectangular in dorsal view and with a subtriangular articular facet (with a sub-horizontal dorsal margin) that faces mainly laterally, and slightly ventrally. The ventral surface of the transverse process possesses a well-developed and very sharp ridge that extends along the length of the process. As a result, the transverse process is subtriangular in cross-section. From the base of the transverse process extend paradiapophyseal, posterior centrodiapophyseal and prezygodiapophyseal laminae (Fig. 17: 'pcdl', 'pdl', 'prdl'), as also occurs in the non-crocopod archosauromorphs *Tanystropheus longobardicus* (Wild, 1973: figs. 52–54) and *Protorosaurus speneri* (BSPG 1995 I 5), and the early archosauriforms *Cuyosuchus huenei* (MCNAM 2669), *Erythrosuchus africanus* (NHMUK R3592, Gower, 2003), *Shansisuchus shansisuchus* (Young, 1964: fig. 21), and *Euparkeria capensis* (UMZC T921). By contrast, the cervico-dorsal vertebrae of *Proterosuchus fergusi* (SAM-PK-K140, GHG 363) and "*Chasmatosaurus*" *yuani* (IVPP V2719) lack posterior centrodiapophyseal and prezygodiapophyseal laminae, and *Prolacerta broomi* (BP/1/2675) and *Sarmatosuchus otschevi* (PIN 2865/68) lack posterior centrodiapophyseal laminae. These laminae in *Garjainia prima* define moderately deep centrodiapophyseal and prezygapophyseal and postzygapophyseal centrodiapophyseal fossae (sensu Wilson *et al.*, 2011). These fossae are partially filled by matrix, but there is no evidence of subdivisions or the presence of foramina within them. In addition, although the area is not completely preserved in either vertebra, there is evidence of a spinoprezygapophyseal lamina.

The prezygapophysis projects anterodorsally and extends anteriorly beyond the anterior margin of the centrum (Fig. 17: 'prz'). The postzygapophysis is directed straight posteriorly and does not extend beyond the posterior margin of the centrum (Fig. 17: 'poz'). The zygapophyseal facets are oval to subcircular and are set at an angle of approximately 45° to the horizontal, resembling the condition in the anterior cervical vertebrae. There is a shallow depression lateral to the base of the neural spine (Fig. 17: 'dn'), also resembling the condition present in the anterior cervical vertebrae. The neural spine is mainly dorsally directed, but with a low posterior component, and is taller than the centrum (Fig. 17: 'ns'). Tall neural spines also occur in *Proterosuchus alexanderi* (NM QR 1484), *Tasmaniosaurus triassicus* (UTGD 54655), *Cuyosuchus huenei* (MCNAM 2669), and *Euparkeria capensis* (UMZC T921). By contrast, in *Sarmatosuchus otschevi* (PIN 2865/68), and especially *Prolacerta broomi* (BP/1/2675), the cervico-dorsal neural spines are dorsoventrally shorter than the centrum. The neural spine in *Garjainia prima* is trapezoidal in lateral view as a result of a considerable and continuous increase in its anteroposterior length towards its distal end. There are deep pre- and postspinal fossae, but these are restricted to the base of the neural spine (Fig. 17: 'prsf'). The distal end of the neural spine has an incipient posterodorsal projection (Fig. 17: 'pdp') and is slightly transversely expanded, but does not have a spine table or lateral prominences. Spine tables and lateral prominences are also absent in *Erythrosuchus africanus* (Gower, 2003). By contrast, the cervico-dorsal neural spines of *Prolacerta broomi* (BP/1/2675), *Proterosuchus alexanderi* (NM QR 1484), and "*Chasmatosaurus*" *yuani* (IVPP V2719) possess distinct lateral prominences (mammillary processes sensu Ezcurra & Butler [2015a], which are morphologically distinct from the distally restricted spine tables present in some other taxa) on the lateral surfaces of the distal ends of the neural spines. Both anterior and posterior surfaces of the neural spine of

Garjainia prima have a thin vertical edge and grooves probably indicating the attachment of intervertebral ligaments. The distal surface of the neural spine is slightly convex in lateral view and lacks any indication of an osteoderm facet, contrasting with the oval and planar surfaces of the distal ends of the neural spines of *Euparkeria capensis* (SAM-PK-5867), *Cuyosuchus huenei* (MCNAM 2669), and several archosaurs (Nesbitt, 2011).

Dorsal vertebrae. The holotype has four partial dorsal vertebrae (PIN 2394/5-14, 15, 17, 18). Two of these (PIN 2394/5-14, 15) are similar to the cervico-dorsal vertebrae (Fig. 18A–I), but the parapophyses are more dorsal on the neurocentral boundary, so these elements are interpreted as very anterior dorsal vertebrae. The other two vertebrae (PIN 2394/5-17, 18) possess more dorsally situated parapophyses, placed completely or mostly on the neural arch, and they are interpreted as anterior or middle dorsal vertebrae (Fig. 18J–M).

PIN 2394/5-14 is fairly complete, lacking the ventral margin of the posterior articular surface of the centrum, most of the left transverse process and the distal tip of the neural spine (Fig. 18A–D, I). PIN 2394/5-15 is more damaged, lacking the posterior ends of the centrum and base of the neural arch (including both postzygapophyses) and the distal tip of the neural spine (Fig. 18E–H). As mentioned above, these very anterior dorsal vertebrae do not differ substantially from the cervico-dorsal vertebrae, and, as a result, they will not be described in detail here. Nevertheless, we note that the surfaces of the fossae that lie below the base of the transverse process are better exposed than in the cervico-dorsal vertebrae and it can be more confidently determined that they lack foramina. The damaged posterior ends of the centra means that it is not possible to determine if the centra

had parallelogram-shaped outlines in lateral view. There are no traces of the neurocentral suture in the very anterior dorsal vertebrae.

The anterior or middle dorsal vertebrae (PIN 2394/5-17, 18) are similar to each other and are less complete than the cervico-dorsal and most anterior dorsal vertebrae. PIN 2394/5-17 lacks the anterior end of the centrum, both prezygapophyses, part of the left lateral surface of the neural arch and most of the neural spine (Fig. 18J–L). PIN 2394/5-18 lacks both anterior and posterior ends of the centrum, the left side of the base of the neural arch, both postzygapophyses and the neural spine (Fig. 18M). The posterior articular surface of the centrum is oval, dorsoventrally taller than wide, and slightly concave. The ventral margin of the posterior surface of the centrum is bevelled. The preserved portion of the ventral surface of the centrum lacks a ventral keel. The lateral surface of the centrum is anteroposteriorly concave, but it lacks the sub-horizontal ridge that subdivides the concavity in more anterior vertebrae. The parapophysis is on a low peduncle that lies mostly or completely on the neural arch (Fig. 18J, M: ‘pa’). The articular facet of the parapophysis faces ventrolaterally and is oval, being dorsoventrally taller than anteroposteriorly long, similar to the condition in more anterior vertebrae. There is no trace of a neurocentral suture, indicating that it was probably fully closed in this region of the trunk. The raised area below the diapophysis is still present in the anterior or middle dorsal vertebrae, but it is more restricted anteroposteriorly and more ridge like than in more anterior vertebrae (Fig. 18M: ‘ia’). The raised area lacks an anterior curvature and ends below the posterior centrodiaiphyseal lamina. The parapophysis is still connected to the diapophysis by a paradiapophyseal lamina, but the posterior centrodiaiphyseal lamina is considerably shorter than in more anterior vertebrae.

The neural canal is subrectangular, considerably higher than wide in posterior view (Fig. 18L: 'nc'). The shape of the neural canal seems to have been less affected by post-mortem distortion in PIN 2394/5-17 than in more anterior dorsal vertebrae. The fossae that lie below the base of the transverse process are shallower than in cervico-dorsal and more anterior dorsal vertebrae, but they also lack foramina on their surfaces. The transverse process is shorter and less sharply triangular than in the cervico-dorsal vertebrae (Fig. 18L: 'tp'). Instead, the transverse process has a more subcircular cross-section and the diapophysis a suboval distal articular facet. The transverse process is anteroposteriorly short and ventrolaterally directed. The diapophyseal facet is orthogonal to the main axis of the transverse process, facing lateroventrally (Fig. 18J: 'dp'). The postzygapophysis is directed straight posteriorly and projects very slightly beyond the level of the posterior margin of the centrum (Fig. 18J–L: 'poz'). The articular facets are oval, longer than wide, and face lateroventrally at an angle of approximately 45° to the horizontal. The postzygapophyses are connected ventrally at the midline (Fig. 18L: 'poz'), but without forming a hyposphene. There is a shallow, poorly defined depression placed lateral to the base of the neural spine that is set anterior to the mid-length of the neural arch, resembling the condition in several early archosauromorphs (e.g. *Protorosaurus speneri*: BSPG 1995 I 5; *Prolacerta broomi*: BP/1/2675; *Proterosuchus fergusi*: GHG 231; *Tasmaniosaurus triassicus*: UTGD 54655). The neural arch has deep pre- and post-spinal fossae, but only the ventral half of the pre-spinal fossa is preserved (Fig. 18: 'posf', 'prsf'). The more complete post-spinal fossa is fusiform in posterior view and tapers abruptly dorsally, seemingly restricted to between the postzygapophyses and not extending onto the posterior surface of the neural spine. The base of the neural spine is anteroposteriorly long and the spine is mainly dorsally directed, but with a low posterior component, as also occurs in the

dorsal vertebrae of *Proterosuchus fergusi* (SAM-PK-11208), *Tasmaniosaurus triassicus* (UTGD 54655), *Shansisuchus shansisuchus* (Young, 1964: fig. 21d, f), and *Erythrosuchus africanus* (NHMUK R3592).

Cervical and dorsal ribs. There are multiple ribs preserved in the holotype of *Garjainia prima* (PIN 2394/5-21–31). An anterior or middle cervical rib (PIN 2394/5-21) is dichocoepalous, but lacks most of the capitulum (Fig. 19A, B). There is no preserved three-headed rib in PIN 2394/5, but anterior dorsal ribs with three articular facets are present in referred specimens of *Garjainia prima* (Huene, 1960). The anterior or middle cervical rib of the holotype of *Garjainia prima* possesses a straight shaft and a moderately long, tapering anterior process that is set between the proximal peduncles (Fig. 19: A, B: ‘ap’). The proximal peduncles are strongly transversely compressed and the tuberculum is subrectangular in lateral view (Fig. 19A, B: ‘tu’). The shaft tapers gradually distally. The lateral surfaces of the main body of the proximal end (i.e. without the proximal peduncles) and the shaft are dorsoventrally convex and the medial surfaces are concave (Fig. 19B: ‘con’), but the shaft becomes flatter on its medial surface towards its distal end. Posterior cervical and dorsal ribs (e.g. PIN 2394/5-24, 26, 28) are longer elements, with a clear medial curvature between the bases of the proximal peduncles and the shaft. All the preserved proximal ends are dichocoepalous and possess differing degrees of development of the capitulum and tuberculum, corresponding to elements of different regions of the presacral axial skeleton. However, the presence of some holocephalous ribs in the posterior region of the trunk cannot be ruled out. The capitulum and tuberculum of the posterior cervical and dorsal ribs are strongly transversely compressed and subrectangular to trapezoidal in lateral view, being slightly expanded towards their distal ends in the latter

case. The articular facet of the capitulum is considerably dorsoventrally taller than that of the tuberculum in some ribs (e.g. PIN 2394/5-28), but in other elements both facets are subequal in size (e.g. PIN 2394/5-26). Distal to its initial curvature, the shaft is mostly straight. The anterior surface of the shaft is transversely convex and possesses a narrow, well-delimited longitudinal groove. The groove runs distally from the base of the shaft, where it has a median position, and distally it becomes gradually more medially situated. The posterior surface of the base of the shaft is transversely concave and becomes shallower distally, merging with the rest of the bone. The medial surface of most of the shaft is gently transversely convex and, as a result, the shaft acquires a rod-like shape towards its distal end.

Gastralia? There are several rod-like partial bones of 1 cm or less (PIN 2394/5-37). These fragments are very thin (ca. 2 mm in diameter), thinner than would be expected for ribs or hyoids, and they are perhaps partial gastralia.

Scapula. Both left (PIN 2394/5-32) and right (PIN 2394/5-33) scapulae are almost complete, although the right scapular blade has a partially damaged anterior margin (Fig. 20). Both scapulae are preserved in articulation with their respective coracoids, with the sutures between the bones clearly visible. The scapula is anteroposteriorly expanded at both proximal and distal ends, and medially curved such that the lateral surface is dorsoventrally convex and the medial surface concave in anterior or posterior views. At its proximal end the scapula is strongly transversely expanded posteriorly, where it forms the scapular contribution to the glenoid fossa (Fig. 20: 'gf'). This expansion is asymmetric in posterior view, being more expanded medially than laterally. The lateral 60% of the transverse

expansion forms the scapular portion of the glenoid fossa, which is mainly posteriorly facing, but with a small lateral component, as also occurs in *Erythrosuchus africanus* (NHMUK R3762a, SAM-PK-905), *Garjainia madiba* (NM QR 3051), *Shansisuchus shansisuchus* (Young, 1964: fig. 26a), and *Euparkeria capensis* (SAM-PK-5867). By contrast, in *Prolacerta broomi* (BP/1/2675), *Proterosuchus alexanderi* (NM QR 1484), “*Chasmatosaurus*” *yuani* (IVPP V2719), and *Sarmatosuchus otschevi* (PIN 2865/68) the glenoid fossa faces posterolaterally, implying a more laterally projecting humerus than in erythrosuchids and eucrocopods. The proximal end of the scapula tapers transversely toward its anterior margin along the suture with the coracoid, forming a transversely compressed acromion process. The acromion process is relatively low, not well differentiated from the base of the scapular blade, and its anterior margin is broadly rounded in lateral view (Fig. 20: ‘acp’), resembling the condition in *Garjainia madiba* (Gower *et al.*, 2014; BP/1/7152), a referred specimen of *Garjainia prima* (Huene, 1960: plate 14, fig. 10), *Erythrosuchus africanus* (Gower, 2003; NHMUK R3762a), and *Shansisuchus shansisuchus* (Young, 1964: fig. 26a, b). By contrast, *Prolacerta broomi* (Gow, 1975; BP/1/2675), *Proterosuchus alexanderi* (Cruickshank, 1972; NM QR 1484), and *Sarmatosuchus otschevi* (Gower & Sennikov, 1997; PIN 2865/68) lack a distinctly raised acromion process. The most anteroproximal portion of the scapula curves posteriorly and forms a deep notch with the coracoid at the suture between both bones (Fig. 20: ‘no’), as also occurs in *Sarmatosuchus otschevi* (PIN 2865/68), *Erythrosuchus africanus* (SAM-PK-905), referred specimens of *Garjainia prima* (Huene, 1960: plate 14, fig. 10), and *Shansisuchus shansisuchus* (Young, 1964: fig. 26a, b). However, in *Proterosuchus alexanderi* the scapula and coracoid lack a notch on the anterior margin of the pectoral girdle (NM QR 1484). The lateral surface of the acromion is not distinctly laterally raised

along its anterior margin, resembling the condition in other non-eucrocopodan archosauriforms (e.g. *Prolacerta broomi*: BP/1/2675; *Proterosuchus alexanderi*: NM QR 1484; *Sarmatosuchus otschevi*: PIN 2865/68; *Erythrosuchus africanus*: SAM-PK-905). The lateral surface of the proximal end of the bone is depressed between the anterior border of the acromion process and the posterior expansion of the bone. The depressed area is dorsoventrally and anteroposteriorly concave and is adjacent to the contact with the coracoid. The anterior three-quarters of the medial surface of the proximal end are concave anteroposteriorly, as a result of the strong medial expansion of the glenoid region. A roughened area is present on the posterior half of the medial surface of the proximal end of the bone, adjacent to the border of the glenoid fossa. The supraglenoid lip of the glenoid fossa is subtriangular in lateral view and strongly posteriorly developed (Fig. 20: 'sugl'), resembling the condition in *Erythrosuchus africanus* (NHMUK R3762a, SAM-PK-905), a referred specimen of *Garjainia prima* (Huene, 1960: plate 14, fig. 10), *Garjainia madiba* (BP/1/7152), *Shansisuchus shansisuchus* (Young, 1964: fig. 26a, b), and *Euparkeria capensis* (SAM-PK-5867). By contrast, the supraglenoid lip is very poorly posteriorly developed in lateral view in *Prolacerta broomi* (BP/1/2675), *Proterosuchus alexanderi* (NM QR 1484), and *Sarmatosuchus otschevi* (PIN 2865/68), which seems to be associated with the mainly lateral orientation of the glenoid fossa. There is no distinct tubercle or ridge for the likely origin of the *M. triceps* on the posterolateral surface of the base of the supraglenoid lip, contrasting with the condition present in several archosaurs (Nesbitt, 2011).

The scapular blade is relatively dorsoventrally short (around 2.7 times longer than its minimum anteroposterior depth) and set at nearly 90° to the main anteroposterior axis of the proximal end of the bone. The anterior margin of the scapular blade is strongly concave

in lateral view, whereas the posterior margin is almost straight, with a very gently convex margin at its distal end, as also occurs in *Euparkeria capensis* (SAM-PK-5867), referred specimens of *Garjainia prima* (Huene, 1960: plate 14, fig. 10), *Guchengosuchus shiguaiensis* (Peng, 1991), and in some specimens of *Erythrosuchus africanus* (e.g. NHMUK R3762a), and *Shansisuchus shansisuchus* (Young, 1964: fig. 26a). By contrast, in *Prolacerta broomi* (BP/1/2575), *Proterosuchus alexanderi* (NM QR 1484), “*Chasmatosaurus*” *yuani* (IVPP V2719), *Sarmatosuchus otschevi* (PIN 2865/68), and *Cuyosuchus huenei* (MCNAM 2669) the anterior margin of the scapular blade is convex and the posterior margin is orientated from anteroproximal to posterodistal. The scapular blade of the holotype of *Garjainia prima* reaches its minimum anteroposterior width a few centimetres above its base and expands gradually anteriorly towards its distal end. At its base, the posterior border of the scapular blade is transversely expanded and continuous with the transverse expansion of the glenoid region. The posterior surface is depressed and transversely concave along this expanded base of the blade. The anterior border of the base of the scapular blade tapers anteriorly. The anterior margin of the blade is a sharp ridge continuous with the transversely compressed acromion process. The lateral surface of the blade is convex anteroposteriorly, with this convexity strongest at the base of the blade. The medial surface of the blade is anteroposteriorly concave at its base, becoming flattened and then slightly convex anteroposteriorly toward the distal end. A gentle break-in-slope extends diagonally across the element from the roughened area on the posterior part of the proximal end to the anterodistal margin of the bone. This break-in-slope divides the medial surface into two surfaces, one anterior and proximal and the other distal and posterior. There is a diagonal, short and thick ridge on the medial surface close to the mid-length of the scapular blade (Fig. 20: ‘r’), extending from anterodistal to posteroproximal and

terminating distally next to the anterior margin of the scapular blade, as also occurs in *Erythrosuchus africanus* (SAM-PK-905) and *Garjainia madiba* (Gower *et al.*, 2014; BP/1/7152). The distal end of the scapular blade is transversely flattened and trapezoidal in lateral view, more expanded anteriorly than posteriorly. The distal margin of the bone is oriented at an angle of approximately 20° with respect to the axis of the scapula-coracoid suture, resembling the condition in referred specimens of *Garjainia prima* (Huene, 1960: plate 14, fig. 10) and some specimens of *Erythrosuchus africanus* (NHMUK R3762a) and *Shansisuchus shansisuchus* (Young, 1964: fig. 26a, b).

Coracoid. The left coracoid (PIN 2394/5-32) is complete (Fig. 20D–F) whereas the right (PIN 2394/5-33) lacks a semi-oval portion of its distal half close to the anteroposterior mid-length of the bone (Fig. 20A–C). The coracoid is suboval in lateral view, considerably anteroposteriorly longer than proximodistally tall. The proximal margin of the bone is relatively straight along its suture with the scapula, and the anterior and distal margins are broadly convex in lateral view. The lateral surface of the bone is mainly convex anteroposteriorly and proximodistally. However, the lateral surface of the anterior half of the coracoid is concave proximally and convex distally, being thicker transversely at the apex of the convexity. As a result, the anterior edge of the bone is slightly sigmoidal in anterior view. The medial surface of the coracoid is mostly concave proximodistally and anteroposteriorly, but with a slightly convex area anterior to the coracoid foramen. The coracoid foramen is oval, proximodistally taller than anteroposteriorly long, opening posterolaterally on the lateral surface of the bone (Fig. 20: ‘cf’). The foramen is situated approximately at the mid-length of the bone and level with the subglenoid lip of the glenoid fossa, clearly below the scapula-coracoid suture. The subglenoid lip, slightly damaged in

both coracoids, is moderately developed in the posterior region of the glenoid fossa and becomes lower anteriorly (Fig. 20: 'sbg1'). The coracoid forms approximately two-thirds of the glenoid fossa and the articular surface is simple and concave. The coracoid has a very low, rounded posterior process that extends slightly beyond the posterior margin of the glenoid fossa (Fig. 20: 'pp'), resembling the condition in several early archosauromorphs (e.g. *Prolacerta broomi*: BP/1/2675; *Proterosuchus alexanderi*: NM QR 1484; "*Chasmatosaurus*" *yuani*: IVPP V2719; *Sarmatosuchus otschevi*: PIN 2865/68; *Cuyosuchus huenei*: MCNAM 2669; referred specimens of *Garjainia prima*: Huene, 1960: plate 14, fig. 10; *Garjainia madiba*: NM QR 3051; *Erythrosuchus africanus*: NHMUK R3592, SAM-PK-905; *Euparkeria capensis*: SAM-PK-5867). The lateral surface of the coracoid has a shallow, sub-circular and anteroposteriorly concave depression between the glenoid fossa and the coracoid foramen. A low, rounded tuberosity situated distal to the anterior half of the glenoid fossa (Fig. 20: 'accp') seems to be topologically equivalent to the acrocoracoidal tuberosity of non-avian theropods (Carpenter, 2002), and resembles the condition in *Garjainia madiba* (NM QR 3051). The right coracoid has a small, pit-like depression on the lateral surface immediately below the posterior end of the subglenoid lip, very close to the posterior margin of the posterior process of the bone (Fig. 20: 'p'), as also occurs in *Garjainia madiba* (NM QR 3051) and some dinosaurs (e.g. *Liliensternus liliensterni*: MB.R 2175). The same depression on the left coracoids is very weakly developed. The distal half of the coracoid thins transversely below the level of the acrocoracoidal tuberosity.

Clavicle. The right clavicle is preserved (PIN 2394/5-35), but lacking its distal end and with a damaged proximal end (Fig. 21D–G). The clavicle is posteriorly bowed in dorsal

view, being considerably longer distal to the point of maximum curvature of the element. The curvature of the bone closely matches the contour of the anterior margin of the coracoid. The proximal end of the bone is moderately anteroposteriorly expanded and flattened (Fig. 21: 'pe'), but with a shallowly concave dorsal surface (Fig. 21: 'con') and a convex ventral surface. As a result, the proximal end of the bone is spoon-like, with the concave dorsal surface articulating with the lateral process of the interclavicle, resembling the condition in *Prolacerta broomi* (BP/1/2675), *Proterosuchus alexanderi* (NM QR 1484), and "*Chasmatosaurus*" *yuani* (IVPP V2719, V4067). The anterior margin of the proximal end of the clavicle of the holotype of *Garjainia prima* is slightly dorsoventrally thicker than the posterior one. The clavicle becomes rod-like distally, with a sub-circular cross-section along the base of its shaft. At the point of maximum curvature of the shaft, the cross-section of the bone becomes sub-triangular, with a flat dorsal surface and a strongly anteroposteriorly convex ventral surface. The shaft becomes dorsoventrally (= transversely, if the clavicle is oriented as in life) flatter distal to the point of maximum curvature where, as a result, it acquires an oval cross-section. The shaft is very long, strongly posteriorly bowed at its base, and tapers gently towards its distal end in anterior or posterior view, as also occurs in referred specimens of *Garjainia prima* (Huene, 1960). By contrast, in *Prolacerta broomi* (BP/1/2675) and "*Chasmatosaurus*" *yuani* (IVPP V4067) the shaft of the clavicle is proportionally shorter, less posteriorly curved and tapers more strongly toward the distal end in anterior view. The shaft of the clavicle of the holotype of *Garjainia prima* expands slightly and gradually anteroposteriorly towards its distal end, at least along the preserved portion of the bone. The dorsal surface of the shaft bears a longitudinal groove next to the anterior margin of the bone (Fig. 21: 'g'). This groove becomes is shallower distally, fading out onto the dorsal surface of the shaft. The groove receives the

lateral process of the interclavicle and part of the anteroproximal border of the coracoid. The groove is delimited anteriorly by a longitudinal and anteroposteriorly convex surface adjacent to the anterior margin of the shaft.

Interclavicle. The interclavicle has a partially preserved anterior end and a fairly complete posterior ramus with damaged lateral and posterior borders (PIN 2394/5-34) (Fig. 21A–C). The anterior margin and most of the lateral processes of the interclavicle are not preserved. Although the borders of the posterior half of the interclavicle are damaged, it is likely that they preserve the approximate original shape of the bone because the preserved margins are extremely thin dorsoventrally. The proximal end of the interclavicle is straight in lateral view, but the posterior ramus (Fig. 21: ‘pr’) is continuously dorsally concave along its long axis (Fig. 21C). Part of the base of the right lateral process has a complete border and shows that the process gradually diverges from the posterior ramus and that the anterior end of the bone was not T-shaped (Fig. 21: ‘lp’), contrasting with the condition in *Proterosuchus fergusi* (GHG 363), *Proterosuchus alexanderi* (NM QR 1484), “*Chasmatosaurus*” *yuani* (IVPP V2719), and a small referred specimen of *Garjainia prima* (Huene, 1960: plate 14, fig. 8). Conversely, the anterior end of the interclavicle was probably diamond shaped, more closely resembling the condition in *Prolacerta broomi* (BP/1/2675) and *Tasmaniosaurus triassicus* (UTGD 54655), but with a lower angle of divergence between the lateral processes. The preserved portion of the anterior end of the interclavicle of PIN 2394/5 is almost identical to that of a large referred specimen of *Garjainia prima* (Huene, 1960: plate 14, fig. 7). The ventral surface of the anterior end of the interclavicle bears a pair of ridges on each side that are sub-parallel to the lateral

margins of the bone. The more lateral ridge reaches almost to the base of the posterior ramus of the interclavicle, whereas the medial ridge is less posteriorly extensive.

The interclavicles of the holotype and referred specimens of *Garjainia prima* (Huene, 1960: plate 14, fig. 7) are constricted transversely immediately posterior to the anterior end and along the anterior one-third of the posterior ramus, resulting in concave lateral margins in dorsal view (Fig. 21: 'tc'). A similar but less well developed constriction of the posterior ramus is also present in *Prolacerta broomi* (BP/1/2675) and possibly *Tasmaniosaurus triassicus* (UTGD 54655). In addition, in the holotype of *Garjainia prima* the maximum constriction point is situated at the anterior portion of the posterior ramus whereas in *Prolacerta broomi* it is more posterior, being situated slightly anterior to the mid-length of the posterior ramus. By contrast, *Proterosuchus fergusi* (GHG 363), *Proterosuchus alexanderi* (NM QR 1484), and "*Chasmatosaurus*" *yuani* (IVPP V2719) lack a transverse constriction of the posterior ramus. Immediately posterior to the narrowest point of the posterior ramus, the interclavicle of the holotype of *Garjainia prima* reaches the apex of its anteroposterior curvature and at that point it is slightly ventrally inflated (Fig. 21: 'dvt'). Posterior to the constriction, the posterior ramus expands steadily transversely, being widest at approximately two-thirds along the length of the ramus (Fig. 21: 'te'), and posteriorly it tapers to a point (Fig. 21: 'pt'). As a result, the posterior two-thirds of the posterior ramus acquire a rhomboidal-shape in dorsal view. A considerably less well-developed transverse expansion of the posterior half of the interclavicle is present in several early archosauromorphs (e.g. *Trilophosaurus buettneri*: Spielmann *et al.*, 2008; *Tasmaniosaurus triassicus*: UTGD 54655; *Prolacerta broomi*: BP/1/2675; *Mesosuchus browni*: Dilkes, 1998; *Euparkeria capensis*: SAM-PK-5867) and an expansion is absent in *Proterosuchus fergusi* (GHG 363), *Proterosuchus alexanderi* (NM QR 1484), and

“*Chasmatosaurus*” *yuani* (IVPP V2719). The dorsal surface of the posterior ramus of *Garjainia prima* is gently concave transversely and the ventral surface gently convex. Both dorsal and ventral surfaces of the posterior end of the interclavicle bear longitudinal striations, better developed on the ventral surface.

Metatarsal IV. Only one autopodial bone is preserved in the holotype of *Garjainia prima* (PIN 2394/5-36) (Fig. 22). The bone is fairly complete, but the distal end is severely damaged. The absence of a concave proximal articular surface and the presence of a strongly transversely expanded proximal end and a strong torsion between the main axes of the proximal and distal ends indicate that the element does not represent a phalanx. In addition, the bone is proportionally more proximodistally elongated than the metacarpals of *Erythrosuchus africanus* (NHMUK R3592) and *Shansisuchus shansisuchus* (Young, 1964: fig. 33). Instead, PIN 2394/5-36 closely resembles in proportions metatarsals II–IV of *Erythrosuchus africanus* (Gower, 1996; BP/1/2096) and *Shansisuchus shansisuchus* (Young, 1964: fig. 36) and so the bone is identified a metatarsal. PIN 2394/5-36 differs from the proportionally more robust metatarsal I and from the hook-shaped metatarsal V of other erythrosuchids (BP/1/2096; Young, 1964: fig. 36). The proximal outline of PIN 2394/5-36 is subtriangular, with an extensive straight ventral margin and two shorter dorsal margins that meet at a very wide angle (Fig. 22E). In *Erythrosuchus africanus* (BP/1/2096), the proximal end of metatarsal II is subrectangular and that of metatarsal III trapezoidal, clearly contrasting with the condition in PIN 2394/5-36. However, the outline of the proximal end and the degree of proximal transverse expansion in PIN 2394/5-36 match those observed in metatarsal IV of *Proterosuchus fergusi* (SAM-PK-K140) and

Erythrosuchus africanus (BP/1/2096). Accordingly, PIN 2394/5-36 is interpreted as a left metatarsal IV.

As mentioned above, the metatarsal IV of PIN 2394/5 resembles in robustness that of other erythrosuchids, and is proportionally more robust than those of *Prolacerta broomi* (BP/1/2676), *Proterosuchus fergusi* (SAM-PK-K140) and *Euparkeria capensis* (GPIT 1681/1). The proximal surface of the bone is rugose and slightly transversely convex. The anteromedial margin of the bone received metatarsal III and is straight and considerably longer than the slightly convex anterolateral margin in proximal view. There are no discrete facets for articulation with metatarsals III and V. The main axis of the proximal end of the bone is strongly rotated from that of the distal end, indicating the presence of an extensive overlap by metatarsal IV in dorsal view, resembling the condition in other early archosauriforms (e.g. *Proterosuchus fergusi*: SAM-PK-K140; *Erythrosuchus africanus*: BP/1/2096; *Euparkeria capensis*: GPIT 1681/1). The proximal end of the bone is asymmetrically expanded transversely, with a stronger medial than lateral expansion. The dorsal surface of the proximal end of the bone is slightly proximodistally concave and the ventral surface is flat. Both lateral and medial surfaces are convex at the proximal end, with the medial surface being more strongly convex and possessing a sharper edge. The shaft of the metatarsal is straight in dorsal and lateral views, resembling the condition in *Proterosuchus fergusi* (SAM-PK-K140), *Erythrosuchus africanus* (Gower, 1996; BP/1/2096) and *Shansisuchus shansisuchus* (Young, 1964: fig. 33a, b). By contrast, in *Euparkeria capensis* the shaft of metatarsal IV is slightly laterally curved in dorsal view (GPIT 1681/1), as also occurs in dinosauriforms (Novas, 1996). The distal end of the bone is not ginglymoid (i.e. it lacks a distal trochlea) and is weakly and symmetrically expanded transversely, resembling the condition in other early archosauriforms (e.g. *Proterosuchus*

fergusi: SAM-PK-K140; *Erythrosuchus africanus*: BP/1/2096; *Euparkeria capensis*: GPIT 1681/1). The lateral and medial surfaces of the distal end lack collateral pits, also absent in *Proterosuchus fergusi* (SAM-PK-K140) and *Erythrosuchus africanus* (BP/1/2096). The distal end possesses a weak ventral expansion that contributes to the articular surface for the proximal phalanx. It is not possible to determine the shape of the distal articular surface of the bone due to damage.

Phylogenetic analysis

Our phylogenetic analysis using equal weights recovered 27 most parsimonious trees (MPTs) of 3580 steps, with a consistency index (CI) of 0.2517 and a retention index (RI) of 0.6476. The strict consensus tree (SCT; Fig. 23) generated from the MPTs shows a topology congruent with that found by Ezcurra (2016) and subsequent modifications of this data set (e.g. Ezcurra *et al.*, 2017; Nesbitt *et al.*, 2017; Sengupta *et al.*, 2017; Stocker *et al.*, 2017). As a result, the overall topology of the SCT will not be described in detail.

Garjainia prima is nested within Erythrosuchidae and as more closely related to *Garjainia madiba* than to other species (see also Gower *et al.*, 2014; Ezcurra, 2016). *Garjainia* is the sister-taxon of a clade composed of the stratigraphically younger erythrosuchids *Erythrosuchus africanus*, *Shansisuchus shansisuchus*, and *Chalishevia cothurnata*. The erythrosuchid *Guchengosuchus shiguaiensis* is found as the sister-taxon of all the above mentioned species of the clade. Contrasting with the result found by Ezcurra (2016), *Fugusuchus hejiapanensis* is recovered as the earliest branching Erythrosuchidae (sensu Ezcurra *et al.*, 2010) and not as one of the successive sister-taxa of Erythrosuchidae + Eurocopoda. The optimal trees found under implied weights ($k=3-18$) show the same relationships among erythrosuchids as that described above.

DISCUSSION

Diagnosis of Garjainia prima and its synonymy with “Garjainia triplicostata”

The genus *Garjainia* can be distinguished from other erythrosuchids based on multiple character states (see Diagnosis), several of them preserved in the holotype of *Garjainia prima*. The general morphology of the holotype of *Garjainia prima* is very similar to the hypodigm of *Garjainia madiba* despite the large geographic distance separating them, the former being known from European Russia and the latter from South Africa (Gower *et al.*, 2014). The presence of such similar species in localities so distant from one another is consistent with the hypothesis of a high degree of global cosmopolitanism among tetrapod land assemblages during the Early Triassic (Shishkin *et al.*, 2006; Button *et al.*, 2017). The distinction between the holotypes of *Garjainia prima* and *Garjainia madiba* is complicated by the low number of overlapping elements for direct comparison. However, the holotype of *Garjainia prima* differs from *Garjainia madiba* in possessing a premaxilla with a palatal process that is gently curved ventrally and five tooth positions, jugal and postorbital bones without ball-like bosses on their external surfaces, and a basioccipital with a median tuberosity on its ventral surface (see also Gower *et al.*, 2014).

The erythrosuchid “*Vjushkovia triplicostata*” had historically been considered as closely related to or a subjective junior synonym of *Garjainia prima* (Gower & Sennikov, 2000). The specimens that form the hypodigm of “*Vjushkovia triplicostata*” share with the holotype of *Garjainia prima* and/or the hypodigm of *Garjainia madiba*, but not with other erythrosuchids, the presence of a longitudinal groove on the lateral surface of the premaxillary body, basioccipital with basal tubera clearly separated from each other,

anterior and middle postaxial cervical vertebrae with a distinct longitudinal lamina extending along the lateral surface of the centrum at mid-height, interclavicle with a rhomboidal posterior ramus, ilium with semicircular preacetabular process in lateral view, and pubis with prominent tuberosity for the attachment of the ambiens muscle in mature individuals. In addition, “*Vjushkovia triplicostata*” shares with the holotype of *Garjainia prima*, but not with *Garjainia madiba*, the presence of a premaxilla with five tooth positions, jugal without a ball-like boss on its external surface, and basioccipital with a median tuberosity on its ventral surface. As a result, “*Vjushkovia triplicostata*” is more similar to the holotype of *Garjainia prima* than to any other described taxon.

The morphology of the holotype of *Garjainia prima* is mostly identical to that of the hypodigm of “*Vjushkovia triplicostata*”, but the two differ in that the former specimen lacks palatal teeth on the palatine and pterygoid and possesses a completely thecodont tooth implantation. These two character states have been shown to be informative in several phylogenetic analyses focused on non-archosaurian archosauromorphs, including the present one, and may support a species-level distinction between *Garjainia prima* and “*Vjushkovia triplicostata*”. However, the extremely similar overall morphology of these two nominal species means that these two potentially distinguishing characters might be intraspecifically variable in this case. The Permian and Triassic archosauromorphs that we have examined at first hand do not show intraspecific variation in the presence or absence of palatal teeth, but assessing variation in this character is complicated by the very small number of individuals sampled for the vast majority of these species. Additionally, the presence of palatal teeth is intraspecifically variable in several species of extant iguanid, teiid, lacertid, scincid, anguid, helodermatid, boid, and colubrid lepidosaurs (Mahler & Kearney, 2006).

Regarding the difference in tooth implantation, the condition of this character is difficult to determine in some non-archosaurian archosauromorphs. For example, in the holotype of the Early Triassic proterosuchid “*Chasmatosaurus*” *yuani* there is a single tooth ankylosed to the bone, whereas all other teeth are not ankylosed (IVPP V36315). Gower *et al.* (2014: 18) noted that in *Garjainia madiba* that “the instances of close bone-tooth association are not prevalent or strongly developed enough for the implantation as a whole to be considered ankylothecondont, and the dentition is overall more thecodont than in, for example, *Proterosuchus* and *Sarmatosuchus*”. Within Erythrosuchidae, Middle Triassic species (e.g. *Erythrosuchus africanus*, *Shansisuchus shansisuchus*) possess a completely thecodont tooth implantation, whereas early erythrosuchids retain an ankylothecondont condition (e.g. *Guchengosuchus shiguaiensis*) (Ezcurra, 2016). Thus, it is possible that the genus *Garjainia* shows an intermediate condition, with a perhaps relictual ankylothecondont condition in some individuals and a polymorphic tooth implantation in others, before thecodonty finally fixed in the phenotype of Middle Triassic erythrosuchids.

In conclusion, we consider here (in agreement with Gower & Sennikov, 2000) that “*Vjuskovia*” and “*Vjushkovia triplicostata*” are junior synonyms of *Garjainia* and *Garjainia prima*, respectively, based on the observation in other diapsids of intraspecific variability in the characters that differ between them and the unique combination of character-states that they share among Permian and Triassic archosauromorphs.

The phylogenetic relationships of the erythrosuchids

Garjainia prima has been considered to be closely related to the South African species *Erythrosuchus africanus* and, therefore, within the family Erythrosuchidae, ever since the former species was erected in the late 1950s. The earliest quantitative phylogenetic analysis

that focused on erythrosuchids (Parrish, 1992) found *Garjainia prima* as the sister-taxon of a clade composed of *Erythrosuchus africanus*, the Chinese *Shansisuchus shansisuchus*, and the Russian “*Vjushkovia triplicostata*” (Parrish, 1992). However, the latter species is considered here and by several previous authors (e.g. Gower & Sennikov, 2000; Gower *et al.*, 2014; Ezcurra, 2016) as a junior synonym of *Garjainia prima*. More recently, “*Vjushkovia triplicostata*” was recovered as more closely related to *Erythrosuchus africanus* than to *Shansisuchus shansisuchus* (Ezcurra *et al.*, 2010). The phylogenetic analysis of Ezcurra (2016), which scored *Garjainia prima* based on the holotype and referred specimens of the species (i.e. including the hypodigm of “*Vjushkovia triplicostata*”), recovered *Garjainia prima* as the sister-taxon of the clade composed of *Erythrosuchus africanus*, *Shansisuchus shansisuchus*, and the Russian *Chalishevia cothurnata*, thus being more in agreement with the results of Gower & Sennikoiv (1996: analysis of braincase data only) than Parrish (1992).

Our analysis recovered the same phylogenetic interrelationships between erythrosuchids as in Ezcurra (2016), with the exception of the position of *Fugusuchus hejiapanensis* as the earliest branching Erythrosuchidae (this family is defined as a stem-based clade that includes all taxa more closely related to *Erythrosuchus africanus* Broom, 1905 than to *Proterosuchus fergusi* Broom, 1903, or *Passer domesticus* Linnaeus, 1758 sensu Ezcurra *et al.* [2010]; therefore, *Fugusuchus hejiapanensis* lies within Erythrosuchidae) (Fig. 23). The phylogenetic position of the latter species at the base of Erythrosuchidae was recovered also by Parrish (1992), but contrasts with the results of Gower & Sennikov (1996, 1997) where *Fugusuchus hejiapanensis* was found as a proterosuchid. The following unambiguous synapomorphies of Erythrosuchidae, which support the position of *Fugusuchus hejiapanensis* within the clade, are optimized in our

analysis: postorbital with a lateral boss adjacent to orbital margin (128:0→1; Fig. 23B–D), supraoccipital excluded from the dorsal border of the foramen magnum (209:1→0), exoccipital with one foramen for the passage of the hypoglossal cranial nerve (222:0→1), nasal with small lateral process that excludes the anteriormost tip of the prefrontal from the lateral margin of the skull roof (691:0→1; Fig. 23B, C), postfrontal-postorbital suture mainly longitudinal in dorsal view, with an angle of 45° or greater to the transverse axis of the skull (692:0→1), and inferior and superior anterior processes of prootic closely approaching or joining together to form most or the entire anterior border of the foramen for the trigeminal cranial nerve (694:0→1). It is interesting that none of these character states were found as synapomorphies of Erythrosuchidae by Ezcurra (2016), showing that the position of *Fugusuchus hejiapanensis* at the base of the clade strongly modifies of the ancestral synapomorphies of Erythrosuchidae. Branch support for Erythrosuchidae is low, with a minimal Bremer support and absolute and GC bootstrap frequencies of 21% and 4%, respectively.

In our analysis, the clade that includes *Guchengosuchus shiguaiensis*, *Garjainia* spp., *Erythrosuchus africanus*, *Shansisuchus shansisuchus*, and *Chalishevia cothurnata* possesses the following unambiguous synapomorphies: maxilla with neurovascular foramina lateroventrally facing and extending ventrally as deep, well-defined grooves on the lateral surface of the anterior and horizontal processes (53: 0→1), maxillary alveolar margin distinctly upturned in the anterior third of the bone (70: 0→1), parietal with a strongly transversely convex dorsal margin of the posterolateral process, which is elevated from the median line of the posterior margin of the skull roof (169: 0→1), and distal end of the radius strongly anteroposteriorly expanded (438: 0→1). The latter character-states were optimized as synapomorphies of Erythrosuchidae by Ezcurra (2016), but the first one was

recovered as a synapomorphy of the clade in only some trees. The Bremer support of this branch is minimal, but the bootstrap frequencies are considerably higher than those of Erythrosuchidae, with absolute and GC frequencies of 50% and 45%, respectively. These bootstrap frequencies are higher than those calculated for the same branch in the analysis of Ezcurra (2016).

The clade that includes *Garjainia* spp., *Erythrosuchus africanus*, *Shansisuchus shansisuchus*, and *Chalishevia cothurnata* is supported by the following unambiguous synapomorphies: maxillo-nasal tuberosity delimiting anteriorly the antorbital fossa (46:0→1; Fig. 23C, D), maxilla with an antorbital fossa on the lateral surface of the bone (54: 0→1), anterior margin of the base of the ascending process of the maxilla sub-vertical (58:1→2), edentulous anterior portion of the ventral margin of the maxilla (69:0→1), ventral surface of the frontal with a median longitudinal canal for the passage of the olfactory tract only slightly constricted and without olfactory bulb impressions and distinct semilunate posteromedially-to-anterolaterally oriented ridges on the orbital roof (120:0→1), pineal fossa on the midline of the dorsal surface of the parietal (162:0→1), lateral surface of the surangular with a laterally projecting shelf that possesses a strongly convex lateral edge (286:2→3), anterior cervical vertebrae with a median longitudinal keel on the ventral surface of the centrum that extends ventral to the centrum rim in at least one vertebra (327:1→2), postaxial cervical vertebrae with a shallow, posterolaterally facing fossa on the posterior portion of the neural arch ventral to the postzygapophysis (335:0→1), and articular with a dorsomedial projection separated from glenoid fossa by a clear concave surface (652: 0→1). Characters 54 and 652 represent new synapomorphies added to those already recognised for this clade in the analysis of Ezcurra (2016). This branch is well supported, with a Bremer support of 4 and absolute and GC bootstrap

frequencies of 86% and 84%, respectively, slightly higher support values than those in Ezcurra (2016).

In our analysis, *Garjainia* possesses the following unambiguous synapomorphies: supratemporal fossa immediately medial or anterior to the supratemporal fenestra on the dorsal surface of the skull roof (8:0→1), premaxilla with a longitudinal groove placed approximately at mid-height and extending along most of the length of the lateral surface of the main body of the bone (31: 0→1), quadrate medial condyle distinctly more distally projected than the lateral one (183: 0→1), opisthotic with fossa immediately lateral to the foramen magnum on the occipital surface (216: 0→1), basioccipital with basal tubera clearly separated from each other (227: 1→0), anterior and middle postaxial cervical vertebrae with a distinct longitudinal lamina extending along the lateral surface of the centrum at mid-height (340: 0→1), ilium with semicircular preacetabular process in lateral view (461: 1→0), and pubis with prominent tuberosity for the attachment of the ambiens muscle in mature individuals (474: 1→0; also proposed as apomorphic for *Garjainia* by Gower *et al.* [2014]). Ezcurra (2016) found a single unambiguous synapomorphy for *Garjainia* (character 8), whereas all the other synapomorphies were recovered in only some optimal trees. Here, the number of unambiguous apomorphies for *Garjainia* is greater because GHG 7433MI, a still undescribed small erythrosuchid specimen from the *Cynognathus* Assemblage Zone of South Africa (see Ezcurra, 2016), was not included in the analysis. GHG 7433MI possesses a high proportion of missing data that generated several ambiguous optimizations for the genus *Garjainia* in the results of Ezcurra (2016). As a result of the exclusion of this specimen, branch support for *Garjainia* is greater than found by Ezcurra (2016), with a Bremer support of 3 and absolute and GC bootstrap frequencies of 85% and 79%, respectively.

The clade comprising the Middle Triassic erythrosuchids *Erythrosuchus africanus*, *Shansisuchus shansisuchus*, and *Chalishevia cothurnata* has the following unambiguous synapomorphies in our analysis: premaxilla with a peg on the posterior edge of the main body (33: 0→1), nasal contributing to the dorsal border of the antorbital fossa (83: 0→1), jugal with posterior process extending beyond the level of the infratemporal fenestra (106: 0→1), squamosal with sharp transition between the anterior and ventral processes and the posterodorsal border of the infratemporal fenestra acquires a square outline (139: 1→0), squamosal with ventral process forming almost the entire posterior border of the infratemporal fenestra (146: 1→2), squamosal with a posterodorsally-to-anteroventrally oriented tuck on the lateral surface of the ventral process (147: 0→1), opisthotic with ventral ramus covered by the lateralmost edge of the exoccipital in posterior view (218: 0→1), exoccipital with distal end contacting its counterpart along the entire dorsal surface of the basioccipital, excluding the basioccipital from the floor of the endocranial cavity and the dorsal surface of the occipital condyle (221: 1→2), braincase without pseudolagenar recess (223: 0→1), parabasisphenoid with base of the cultriform process tall, with the dorsal edge extending between the clinoid processes and the ventral part of the crista prootica (243: 0→1), external foramina for the passage of the abducens nerves (CN VI) open anteriorly (251: 1→0), prootic with a ridge on the lateral surface of the inferior anterior process ventral to the trigeminal foramen (256: 0→1), dentary with mostly straight tooth bearing portion: (267: 1→0), cervico-dorsal transition with a very strong anteroposterior compression of the centra, being considerably anteroposteriorly shorter than tall (311: 0→1), ulna with lateral tuber (= radius tuber) on the proximal portion (433: 0→1), calcaneum with an expanded distal end of the calcaneal tuber in proximal or distal view (549: 0→1), ilium with subtriangular, tapering posteriorly postacetabular process in

lateral view (688: 0→1), and premaxilla with distinctly convex alveolar margin in lateral view (690: 0→1). Characters 139, 433, 688, and 690 are newly identified synapomorphies for this clade found in our analysis. The Bremer support of this clade is 2 and the bootstrap absolute and GC frequencies are 68% and 58%, respectively, being slightly higher than those recovered by Ezcurra (2016).

The clade composed of *Shansisuchus shansisuchus* and *Chalishevia cothurnata* possesses the same two synapomorphies found by Ezcurra (2016): secondary antorbital fenestra immediately anterior to the antorbital fenestra (15: 0→1) and postaxial cervical vertebrae without excavation immediately lateral to the base of the neural spine (337: 1→0). The branch supports calculated here for this clade are very similar to those of Ezcurra (2016), with a Bremer support of 1 and bootstrap absolute and GC frequencies of 61% and 33%, respectively.

Suboptimal searches constraining the position of *Garjainia prima* in different positions of the tree found that 28 additional steps are necessary to force its placement as an eucrocopod, 16 to be the earliest branching erythrosuchid, twelve extra steps to be the sister-taxon of *Erythrosuchus africanus*, and ten to be the sister-taxon of *Fugusuchus hejiapanensis*, *Guchengosuchus shiguaiensis*, and *Shansisuchus shansisuchus*. The floating taxon *Garjainia madiba* was found as the sister-taxon of *Garjainia prima* in all these suboptimal searches. Thus, the phylogenetic position of *Erythrosuchus africanus* as more closely related to *Garjainia prima* than to *Shansisuchus shansisuchus* proposed by Ezcurra *et al.* (2010) is very poorly supported in the context of the current data set.

Regarding *Fugusuchus hejiapanensis*, three additional steps are necessary to recover this species in the same position as found by Ezcurra (2016), four steps to be the sister-taxon of *Sarmatosuchus otschevi*, *Guchengosuchus shiguaiensis*, or of all the other

erythrosuchids with exception of *Guchengosuchus shiguaiensis*, five steps to force its placement as a proterosuchid, and six steps to be the sister-taxon of Archosauriformes. As a result, the phylogenetic position of *Fugusuchus hejiapanensis* as an erythrosuchid is moderately supported by our dataset.

The bootstrap GC frequencies calculated under implied weights are lower than those under equal weights for the entire range of used k values (3–18) in Proterosuchidae and the clade that includes *Sarmatosuchus otschevi* and more crownward archosauriforms, and Erythrosuchidae. The condition is similar for Erythrosuchidae, but with k values of 15 and 18 the frequencies are slightly higher under implied weights. In the case of the genus *Garjainia*, k values between 3 and 8 recovered lower frequencies than those under equal weights, whereas using higher k values the frequencies were higher. In contrast, the clade comprising *Erythrosuchus africanus*, *Shansisuchus shansisuchus*, and *Chalishevia cothurnata* possesses higher GC frequencies under implied weights than using equal weights, with exception of the extreme condition of a k constant equal to 3. As a result, weighting against homoplasy reduces the resampling support for higher-level clades among ‘proterosuchians’, indicating that characters with high levels of homoplasy contribute substantially to the monophyly of these groups. The condition is intermediate for the genus *Garjainia*, in which moderately low weighting produces a better supported branch. The clade that comprises Middle Triassic erythrosuchids is supported by characters with low homoplasy, and, as a result, implied weights increase its support. These results indicate that the morphology of Middle Triassic erythrosuchids was specialized in ways not generally explored by other Triassic archosauromorphs.

CONCLUSIONS

The holotype of *Garjainia prima* possesses a unique combination of character states that allow it to be distinguished from other Triassic archosauromorphs, including its sister-species *Garjainia madiba*. These character states, and the absence of substantial evidence supporting the taxonomic distinctiveness of “*Vjushkovia triplicostata*”, bolster the hypothesis that the latter species is a subjective junior synonym of *Garjainia prima*. The genus *Garjainia* is placed as the sister-taxon of Middle Triassic erythrosuchids, the latter showing a series of apomorphies with low degrees of homoplasy. Thus, Middle Triassic erythrosuchids acquired morphologies rarely explored by other early archosauromorphs. Our revision of the anatomy of *Garjainia prima* allowed us to identify phylogenetically informative characters that were used to expand a previously published phylogenetic dataset focused on Permo-Triassic archosauromorphs. The modifications of this data set resulted in the recovery of *Fugusuchus hejiapanensis* from the upper Lower Triassic of China as the earliest branching erythrosuchid, rather than as outside of the clade composed of Erythrosuchidae + Eurocopoda that was recovered by previous analyses. This new phylogenetic hypothesis resulted in a modification of the unambiguous ancestral synapomorphies of Erythrosuchidae.

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FIGURE LEGENDS

Figure 1. Photograph of the Kzyl-Say locality (taken in 2011) approximately 500 metres from the excavation site of the holotype of *Garjainia prima* (left: photo by A.G.S.) and photograph of V.G. Ochev in the Koltaevo 2 locality of the Donguz Gorizont (taken in 1995) (right: photo by M.J. Benton).

Figure 2. Skull reconstruction of holotype of *Garjainia prima* (PIN 2394/5) in lateral view based on both sides of the original skull and detached bones. Bones in pale grey are elements that are placed more medially than other bones. Scale bar equals 5 cm.

Figure 3. Skull reconstruction of holotype of *Garjainia prima* (PIN 2394/5) in dorsal view. The width of the skull was increased in order to match that of other erythrosuchids (e.g. *Erythrosuchus africanus*: NM QR 1473) because the original specimen suffered transverse post-mortem compression. Scale bar equals 5 cm.

Figure 4. Skull of holotype of *Garjainia prima* (PIN 2394/5-1) in left lateral (A) and right lateral (B) views. Scale bar equals 10 cm.

Figure 5. Line drawings of the skull of holotype of *Garjainia prima* (PIN 2394/5-1) in left lateral (A) and right lateral (B) views. Pale grey areas indicate matrix or damaged bone surface and dark grey areas represent portions reconstructed with plaster. Abbreviations: anfo, antorbital fossa; apqj, anterior process of the quadratojugal; bsp, basiptyergoid process; cp, cultriform process; dpn, descending process of the nasal; ec, ectopterygoid; f,

fossa; fr, frontal; fo, fenestra ovalis; g, groove; jt, jugal tuberosity; lg, longitudinal groove; ljqb, left jugal-quadratojugal bar; mnt, maxillo-nasal tuberosity; nld, naso-lacrimal duct; oc, occipital condyle; pal, palatine; paq, pterygoid ala of the quadrate; pf, posterior flange; pmx, premaxilla; pnp, postnarial process facet; pok, postorbital knob; ppm, palatal process of the maxilla; pps, posterior process of squamosal; pvpp, posteroventral process of the parietal; qdc, quadrate distal condyle; sh, shelf; sof, suborbital flange; t, tuberosity; vps, ventral process of the squamosal. Scale bar equals 10 cm.

Figure 6. Skull of holotype of *Garjainia prima* (PIN 2394/5-1) in dorsal (A) and ventral (B) views. Scale bar equals 10 cm.

Figure 7. Line drawing of the skull of holotype of *Garjainia prima* (PIN 2394/5-1) in dorsal (A) and ventral (B) views. Pale grey areas indicate matrix or damaged bone surface and dark grey areas represent portions reconstructed with plaster. Abbreviations: bo, basioccipital; ect, ectopterygoid; f, fossa; fr, frontal; ju, jugal; mnt, maxillo-nasal tuberosity; mx, maxilla; mx.pal, maxillary palatal process; na, nasal; pal, palatine; pbs, parabasisphenoid; pfor, pineal foramen; pfos, pineal fossa; pmx, premaxilla; po, postorbital; pof, postfrontal; pop, paroccipital process; prf, prefrontal; pt, pterygoid; q, quadrate; q.vc, quadrate ventral condyles; qj, quadratojugal; sq, squamosal; stfo, supratemporal fossa; tu, tuberosity. Scale bar equals 10 cm.

Figure 8. Right premaxilla of holotype of *Garjainia prima* (PIN 2394/5-2) in lateral (A), medial (B) and ventral (C) views. Abbreviations: 1–5, tooth positions 1–5; en, external naris; et, erupting tooth; f, foramen; lg, longitudinal groove; nf, narial fossa; ponp,

postnarial process; pp, palatal process; prnp, prenarial process; sy, symphysis. Scale bar equals 2 cm.

Figure 9. Quadratojugal and palatal bones of holotype of *Garjainia prima* (PIN 2394/5-3, 5-5, 5-7). Right quadratojugal in lateral (A) and medial (B) views; distal tip of the lateroventral process (= ectopterygoid ramus) of the left pterygoid in dorsal (C) and ventral (D) views; and left epipterygoid in medial (E) and lateral (F) views. Abbreviations: ae, anterior expansion; apqj, anterior process of the quadratojugal; dp, dorsal process; ecf, ectopterygoid facet; itf, infratemporal fenestra; jf, jugal facet; pe, posterior expansion; pf, posterior flange; qf, quadrate facet; sh, shelf. Scale bars equal 2cm in (A–D) and 1 cm in (E, F).

Figure 10. Photograph (A) and line drawing (B) of the skull of holotype of *Garjainia prima* (PIN 2394/5-1) in occipital view. Photograph (A) includes detail of the ventral condyles of the quadrate in ventral view. Abbreviations: bspp, basiptyergoid process; bt, basal tuber; f, fossa; itp, intertuberal plate; oc, occipital condyle; pa, parietal; pa.wi, parietal wing; pbs, parabasisphenoid; pop, paroccipital process; qf, quadrate foramen; qj, quadratojugal; qu.wi, quadrate pterygoid wing; so, supraoccipital; sq, squamosal. Scale bar equals 5 cm.

Figure 11. Close-ups of the skull of holotype of *Garjainia prima* (PIN 2394/5-1). Photograph (A) and drawing (B) of the articulation between the left maxilla, ectopterygoid, jugal, and postorbital in ventromedial view; photograph (C) and drawing (D) of the braincase in left lateral view; laterosphenoid and upper half of the orbit in anterolateral and

slightly ventral view (E); and right palate in ventral view (F). Pale grey areas indicate matrix or damaged bone surface and dark grey areas represent portions reconstructed with plaster. Abbreviations: V, foramen for the passage of the trigeminal cranial nerve; ar.pt, anterior ramus of the pterygoid; cpr, crista prootica; culp, cultriform process; ect, ectopterygoid; f.mx, facet for maxilla; fr, frontal; gr, groove; ju, jugal; ltp, laterosphenoid; ltp-pr, suture between prootic and laterosphenoid; mf, metotic foramen; mx, maxilla; ot-pr, suture between otoccipital and prootic; pa, parietal; pal, palatine; plr.pt, posterolateral ramus of the pterygoid; po, postorbital; pop, paroccipital process; ppt, attachment ridge for protactor pterygoidei muscle; pr, prootic; prf, prefrontal; pt, pterygoid; ri, ridge; s.pt-pal, suture between pterygoid and palatine; vrop, ventral ramus of the opisthotic. Not to scale.

Figure 12. Right lower jaw of holotype of *Garjainia prima* (PIN 2394/5-8) in lateral (A, D), medial (B, E) and dorsal (C) views. Abbreviations: adf, adductor fossa; an, angular; co, coronoid; f, foramen; g, groove; gf, glenoid fossa; Mc, Meckelian groove; pcp, posterior central process; pdp, posterior dorsal process; pgl, postglenoid lip; pra, prearticular; qjf, quadratojugal facet; rap, retroarticular process; sa, surangular; sp, splenial; ssh, surangular shelf. Scale bars equal 5 cm.

Figure 13. Left lower jaw of holotype of *Garjainia prima* (PIN 2394/5-9) in lateral (A, D), medial (B, E) and ventral (C) views. Abbreviations: adf, adductor fossa; an, angular; dt, dentary; pcp, posterior central process; pdpf, posterior dorsal process facet; pra, prearticular; pvp, posterior ventral process; sa, surangular. Scale bars equal 2 cm.

Figure 14. Posterior end of the left lower jaw of holotype of *Garjainia prima* (PIN 2394/5-9) in lateral (A), dorsal (B), posterior (C), medial (D) and ventral (E) views. Abbreviations: con, concavity; dmp, dorsomedial process; gf, glenoid fossa; pogl, postglenoid lip; prgl, preglenoid lip; rap, retroarticular process; ssh, surangular shelf. Scale bar equals 2 cm.

Figure 15. Axis of holotype of *Garjainia prima* (PIN 2394/5-10) in right lateral (A), dorsal (B), ventral (C), left lateral (D), anterior (E) and posterior (F) views. Abbreviations: af, anterior facet; ap, anterior projection; dn, depression lateral to the base of the neural spine; dp, diapophysis; nc, neural canal; ns, neural spine; pf, posterior facet; poz, postzygapophysis; prz, prezygapophysis; psf, post-spinal fossa; r, ridge; subhorizontal ridge. Scale bar equals 2 cm.

Figure 16. Third cervical (A–D), fourth cervical (E–H) and fifth cervical (I–L) vertebrae of holotype of *Garjainia prima* (PIN 2394/5-11–5-13) in right lateral (A, E, I), left lateral (B, F, J), anterior (C, G, K) and posterior (D, H, L) views. Abbreviations: af, anterior facet; d, depression; dn, depression lateral to neural spine; dp, diapophysis; nc, neural canal; ns, neural spine; pf, posterior facet; posf, postspinal fossa; poz, postzygapophysis; prsf, prespinal fossa; prz, prezygapophysis; r, ridge; sr, subhorizontal ridge. Scale bar equals 2 cm.

Figure 17. Cervico-dorsal vertebrae of holotype of *Garjainia prima* (PIN 2394/5-16) in right lateral (A), anterior (B), left lateral (C) and posterior (D) views. Abbreviations: af, anterior facet; dn, depression lateral to neural spine; dp, diapophysis; ia, inflated area; nc, neural canal; ns, neural spine; pa, parapophysis; pcdl, posterior centrodiapophyseal lamina;

pdl, paradiapophyseal lamina; pdp, posterodorsal projection; pf, posterior facet; poz, postzygapophysis; prdl, prezygodiapophyseal lamina; prsf, prespinal fossa; prz, prezygapophysis; tp, transverse process. Scale bar equals 2 cm.

Figure 18. Dorsal vertebrae of holotype of *Garjainia prima* (PIN 2394/5-14, 5-15, 5-17, 5-18) in right lateral (A, E, J, M), left lateral (B, F, K), anterior (C, G), posterior (D, H, L) and ventral (I) views. Abbreviations: af, anterior facet; dp, diapophysis; ia, inflated area; nc, neural canal; ns, neural spine; pa, parapophysis; pcdl, posterior centrodiapophyseal lamina; pdl, paradiapophyseal lamina; pf, posterior facet; posf, postspinal fossa; poz, postzygapophysis; prdl, prezygodiapophyseal lamina; prsf, prespinal fossa; prz, prezygapophysis; tp, transverse process; vk, ventral keel. Scale bar equals 2 cm.

Figure 19. Left cervical (A, B), left mid-dorsal (C, D) and right anterior dorsal (E–F) ribs of holotype of *Garjainia prima* (PIN 2394/5-21, 5-28, 5-30) in lateral (A), medial (B), anterior (D, F) and posterior (C, E) views. Abbreviations: ap, anterior process; ca, capitulum; con, concavity; g, groove; tu, tuberculum. Scale bar equals 2 cm.

Figure 20. Right (A–C) and left (D–F) scapulae and coracoids of holotype of *Garjainia prima* (PIN 2394/5-32, 5-33) in lateral (A, D), medial (B, E) and posterior (C, F) views. Abbreviations: accp, acrocoracoidal process; acp, acromion process; cf, coracoid foramen; gf, glenoid fossa; no, notch; p, pit; pp, posterior process; r, ridge; sbgl, subglenoid lip; sugl, supraglenoid lip. Scale bar equals 5 cm.

Figure 21. Interclavicle (A–C) and right clavicle (D–G) of holotype of *Garjainia prima* (PIN 2394/5-34, 5-35) in ventral (A), dorsal (B), left lateral (C), anterior (D), posterior (E), lateral (F) and medial (G) views. Abbreviations: con, concavity; dvt, dorsoventral thickening; g, groove; lp, lateral process; pe, proximal end; pr, posterior ramus; pt, posterior tapering; tc, transverse constriction; te, transverse expansion. Scale bar equals 2 cm.

Figure 22. Left metatarsal IV of holotype of *Garjainia prima* (PIN 2394/5-36) in dorsal (A), ventral (B), anterior (C), posterior (D) and proximal (E) views. Scale bar equals 1 cm.

Figure 23. Subset of the strict consensus tree showing the phylogenetic relationships of *Garjainia prima* and other ‘proterosuchian’ archosauromorphs recovered in our analyses (A) and line drawings of the skulls of an adult of *Proterosuchus fergusi* (B), *Fugusuchus hejiapanensis* (C), and *Garjainia prima* (D). A black square in the colour grids (A) means the non-monophyly of the clade under that search and the different colours represent the difference between the bootstrap GC frequencies under equal and implied weights (a white square means no difference between frequencies). The cells of the grids represent analyses with k of 3 to 18 from left to right and from top to bottom. Values above each branch in (A) are absolute (left) and GC (right) bootstrap frequencies and below the branches are Bremer supports values >1. Numbers in (B–D) indicate selected phylogenetically informative character-states among ‘proterosuchian’ archosauromorphs. (B) Modified from Ezcurra & Butler (2015b), (C) drawn from GMB V 313 photographs, and (D) drawn from PIN 2394/5-1 and modified from Gower (1994).

TABLES

Table 1. Measurements of premaxilla, maxilla, lacrimal and jugal of holotype of *Garjainia prima* (PIN 2394/5) in mm, made with a digital calliper set. Values between brackets indicate incomplete measurements (due to post-mortem damage) and the value given is the maximum measurable. Maximum deviation of the calliper is 0.02 mm but measurements were rounded to the nearest 0.1 mm.

<i>Right premaxilla</i>	
Body length	71.2
Body height	39
Largest crown length at base	8.6
<i>Right maxilla</i>	
Length	235
Height	113.6
Horizontal process minimum height	41
Horizontal process length	159.8
Ascending process height	68.6
Largest crown height	(20.2)
Largest crown length at base	13
<i>Right lacrimal</i>	
Length	65.2
Height (exposed in lateral view)	80
Anterior process length	36.4
Ventral process height	44.9
Ventral process minimum length	[18.5]
<i>Left jugal</i>	
Length	171.6
Height	85.7
Anterior process length	41.6
Anterior process height at base	23.6
Posterior process length	101.1
Posterior process height at mid-length	[19.7]
Ascending process height	61.5

Table 2. Measurements of skull roof bones of holotype of *Garjainia prima* (PIN 2394/5) in mm, made with a digital calliper. Values between brackets indicate incomplete

measurements (due to post-mortem damage) and the value given is the maximum measurable. Maximum deviation of the calliper is 0.02 mm but measurements were rounded to the nearest 0.1 mm.

<i>Nasals</i>	
Length	[226]
Pair maximum width	30.1
Pair minimum width	11.6
<i>Left prefrontal</i>	
Length	102.9
Width	41
Height	(35.3)
<i>Frontals</i>	
Length	82.3
Pair minimum width	37.5
<i>Right postfrontal</i>	
Length (oblique)	33.6
<i>Parietals</i>	
Length	66.8
Length up to posterior transverse crest	28.2
Pair maximum width	[98]
Pair minimum width	32.3
Pineal fossa length	38.4
Pineal fossa width	23.8

Table 3. Measurements of postorbital, squamosal, quadratojugal and quadrate of holotype of *Garjainia prima* (PIN 2394/5) in mm, made with a digital calliper. Values between brackets indicate incomplete measurements (due to post-mortem damage) and the value given is the maximum measurable. Maximum deviation of the calliper is 0.02 mm but measurements were rounded to the nearest 0.1 mm.

<i>Left postorbital</i>	
Length	[95.5]
Height	83.3
Maximum width	33.6
Ascending process length	(18.7)
Posterior process length	[47.8]
Ventral process length	47.7
<i>Left squamosal</i>	
Length	(72.7)

Height	116.1
Ventral process height	73.6
Ventral process length at base	26.3
<i>Left quadratojugal</i>	
Height	[99.0]
Length along ventral margin	107.1
<i>Left quadrate</i>	
Height	[107.1]
Quadrate foramen height	[9.5]
Quadrate foramen width	ca. 5.3
Distal end width	30.3
Distal end length	23.4
Lateral distal condyle width	14.2
Lateral distal condyle depth	13.1
Medial distal condyle width	13.3
Medial distal condyle depth	23.1

Table 4. Measurements of braincase bones of holotype of *Garjainia prima* (PIN 2394/5) in mm, made with a digital calliper. Values between brackets indicate incomplete measurements (due to post-mortem damage) and the value given is the maximum measurable. Maximum deviation of the calliper is 0.02 mm but measurements were rounded to the nearest 0.1 mm.

<i>Supraoccipital</i>	
Height	33.0*
Width	27.7*
<i>Otoccipitals</i>	
Width between paroccipital processes	89.4*
Foramen magnum lateral wall width	9
Foramen magnum height	19.3
Foramen magnum width	7.2*
<i>Basioccipital</i>	
Length	23.6
Width	29.5*
Occipital condyle height	19.1
Occipital condyle width	23.9
Basal tuber height	7.8
Basal tubera width at base	10.5
Width along basal tubera	29.5*
Minimum width between basal tubera	6.7
<i>Parabasisphenoid</i>	
Length up to base of basiptyergoid process	9.7

Width	[41.8]
Basipterygoid process length	18.5
<i>Left prootic</i>	
Height	[33.6]
<i>Laterosphenoid</i>	
Height	43.1

Table 5. Measurements of right lower jaw bones of holotype of *Garjainia prima* (PIN 2394/5) in mm, made with a digital calliper. Values between brackets indicate incomplete measurements (due to post-mortem damage) and the value given is the maximum measurable. Maximum deviation of the calliper is 0.02 mm but measurements were rounded to the nearest 0.1 mm.

<i>Dentary</i>	
Length	255*
Anterior height	47.1
Largest crown height	14.4*
Largest crown length at base	8.2
<i>Splénial</i>	
Length	234*
Height	[52.7]
<i>Surangular</i>	
Length	210
Height	47.7
<i>Angular</i>	
Length	204*
Height	37.3
<i>Prearticular</i>	
Length	151.5*
Minimum height	12.1

Table 6. Measurements of left scapula of holotype of *Garjainia prima* (PIN 2394/5) in mm, made with a digital calliper. Values between brackets indicate incomplete measurements (due to post-mortem damage) and the value given is the maximum measurable. Maximum deviation of the calliper is 0.02 mm but measurements were rounded to the nearest 0.1 mm.

Distal end depth	102.7
Proximal end depth	109.5
Minimum depth of blade	56

Table 7. Parameters calculated for the optimal phylogenetic trees recovered under implied weights.

<i>k value</i>	<i>Fit</i>	<i>Length</i>	<i>Consistency index</i>	<i>Retention index</i>
3	329.04059	3617	0.2488	0.6174
4	288.63867	3615	0.2490	0.6177
5	257.69835	3593	0.2505	0.6208
6	233.18091	3589	0.2508	0.6213
7	213.18138	3586	0.2510	0.6217
8	196.50817	3586	0.2510	0.6217
9	182.37132	3586	0.2510	0.6217
10	170.21341	3586	0.2510	0.6217
11	159.63334	3586	0.2510	0.6217
12	150.33377	3585	0.2510	0.6219
13	142.08837	3585	0.2510	0.6219
14	134.72450	3585	0.2510	0.6219
15	128.10318	3584	0.2511	0.6220
16	122.11672	3584	0.2511	0.6220
17	116.67633	3584	0.2511	0.6220
18	111.70927	3584	0.2511	0.6220

APPENDIX

Terminals deactivated from the data set of Ezcurra and Butler (in press)

Dinocephalosaurus, Macrocnemus obristi, Fuyuanosaurus, Pectodens, Protanystropheus, Trachelosaurus, Tanystropheus haasi, Eorasaurus, Prolacertoides, 'Archosaurus holotype', 'Archosaurus hypodigm', 'Panchet proterosuchid', Vonhuenia, Chasmatosuchus rossicus, Chasmatosuchus magnus, Chasmatosuchus vjushkovi, Koilamasuchus, Kalisuchus, NMQR 3570, Shansisuchus kuyeheensis, Uralosaurus, 'Osmolskina holotype', 'Osmolskina hypodigm', 'Otter Sandstone archosaur', Stagonosuchus, Dagasuchus, Hypselorhachis, 'Waldhaus poposauroid', Vysthegodosuchus, Bystrowisuchus, Bromsgroveia, 'Moenkopi poposauroid', Mandasuchus, Lutungutali, and Nyasasaurus.

Scorings changed from the data matrix of Ezcurra (2016) and its modified versions

Character 7) changed from (1) to (0) in *Luperosuchus fractus* (PULR 04).

Character 37) changed from (?) to (1) in *Luperosuchus fractus* following the scoring of this character by Nesbitt & Desojo (2017).

Character 39) changed from (?) to (0) in *Luperosuchus fractus* following the scoring of this character by Nesbitt & Desojo (2017).

Character 42) changed from (2) to (1) in *Silesaurus opolensis* because the holotype premaxilla preserves five alveoli (ZPAL Ab III/361/34).

Character 83) changed from (0) to (1) in *Luperosuchus fractus* following the scoring of this character by Nesbitt & Desojo (2017).

Character 111) changed from (1) to (0) in *Asperoris mnyama* because the rugosity on the prefrontal orbital margin of this species is distinctly less developed than in allokotosaurians and phytosaurs.

Character 115) changed from (0) to (1) in *Luperosuchus fractus* following the scoring of this character by Nesbitt & Desojo (2017).

Character 128) changed from (0) to (1) because the orbital border of the postorbital bone of *Fugusuchus hejiapanensis* possesses a low, rounded and rugose boss, contrasting with the smoothly concave surface present in, for example, *Proterosuchus fergusi*.

Character 155) changed from (0) to (1) in *Garjainia prima* and from (0) to (?) in *Garjainia madiba*.

Character 174) changed from (0) to (1) in *Prestosuchus chiniquensis* following the interpretation of Nesbitt & Desojo (2017) and their rescoring in the original data set of Nesbitt (2011).

Character 225) changed from (0) to (?) because the condition in *Fugusuchus hejiapanensis* cannot be determined because of the undetermined ontogenetic stage of the only known specimen of the species.

Character 382) changed from (1) to (2) in *Aetosauroides scagliai*, from (1) to (0) in *Aetosaurus ferratus*, and from (1/2) to (2) in *Stagonolepis robertsoni*.

Character 386) changed from (0) to (1) in *Pamelaria dolichotrachela*, *Azendohsaurus madagaskarensis*, *Shringasaurus indicus*, *Cuyosuchus huenei*, *Garjainia prima*, *Garjainia madiba*, *Erythrosuchus africanus*, *Shansisuchus shansisuchus*, *Shansisuchus kuyeheensis*, *Youngosuchus sinensis*, *Vancleavea campi*, *Euparkeria capensis*, *Halazhaisuchus qiaoensis*, *Osmolskina* complete hypodigm, *Yarasuchus deccanensis*, *Teleocrater rhadinus*, *Tropidosuchus romeri*, *Gualosuchus reigi*, *Chanaresuchus*

bonapartei, *Pseudochampsa ischigualastensis*, *Tarjadia ruthae*, *Erpetosuchus granti*,
Ornithosuchus woodwardi, *Riojasuchus tenuisiceps*, *Nundasuchus songeaensis*,
Parringtonia gracilis, *Aetosauroides scagliai*, *Aetosaurus ferratus*, *Stagonolepis*
robertsoni, *Stagonosuchus nyassicus*, *Arizonasaurus babbitti*, *Mandasuchus*
tanyauchen, *Batrachotomus kupferzellensis*, and *Prestosuchus chiniquensis*.

Changed from (0) to (0/1) in *Teraterpeton hrynewichorum*, *Rhynchosaurus articeps*,
and *Guchengosuchus shiguaiensis*, and *Ticinosuchus ferox*.

Changed from (?) to (1) in *Litorosuchus somnii*.

Changed from (0) to (?) in *Proterochampsa barrionuevoi*.

Changed from (1) to (2) in *Marasuchus lilloensis*, *Asilisaurus kongwe*, *Lewisuchus*
admixtus, *Silesaurus opolensis*, *Herrerasaurus ischigualastensis*, and
Heterodontosaurus tucki.

Character 673) changed from (1) to (0) in *Gracilisuchus stipanicorum*.

A

B

A

B

A **B** **C** **D** **E** **F**

A **B**

A **B** **C** **D** **E**