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Cranial morphology of *Jonkeria truculenta* (Therapsida, Dinocephalia) and a taxonomic reassessment of the family Titanosuchidae

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Titanosuchidae are a group of herbivorous, long-snouted dinocephalians with definitive records known only from the middle Permian *Tapinocephalus* Assemblage Zone of the Beaufort Group (Karoo Supergroup) of South Africa. Here, the taxonomy of this family is revised; of the nine species currently recognized, only two are found to be valid: *Titanosuchus ferox* and *Jonkeria truculenta*, which can be distinguished on the basis of appendicular proportions. *Jonkeria boonstrai*, *J. haughtoni*, *J. ingens*, *J. parva*, *J. rossouwi*, and *J. vanderbyli* are synonymized with *Jonkeria truculenta*, and *J. koupensis* is considered a *nomen dubium* (Titanosuchidae indet.). Several new cranial features are described for *J. truculenta*, such as pachyostosis of the prefrontals, postorbitals and parietals, and an ontogenetic series for the species is presented.

Keywords: Dinocephalia, Titanosuchidae, Beaufort Group, *Tapinocephalus* Assemblage Zone, taxonomy.

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INTRODUCTION

Dinocephalians, which lived during the Guadalupian Epoch of the Permian Period, are a group of mostly large-bodied therapsids characterized by intermeshing, 'heeled' incisors, reduction in size of the postcanine teeth, 'grooved' or 'excavated' vomers, anteriorization of the jaw articulation, and non-terminal nostrils (Boonstra 1969; Kemp 1982; King 1988), although these last two characters likely evolved independently in different dinocephalian groups (Kammerer 2011). Dinocephalia currently comprises six families, following synonymization of the previously-recognized seventh family ('Brithopidae') with Anteosauridae by Kammerer (2011). Four of these families (Anteosauridae, Titanosuchidae, Tapinocephalidae, and Styracocephalidae) have records in South Africa (Angielczyk & Kammerer 2018). Styracocephalidae is a rare family with only a single recognized species (Rubidge & van den Heever 1997; Fraser-King *et al*. 2019), but the other three families are represented by numerous specimens from the South African Karoo Basin (Smith *et al*. 2012). Anteosaurids, tapinocephalids, and titanosuchids all have complex taxonomic histories, with many named species, often based on fragmentary and poorly prepared specimens (see e.g. Broom 1932). Unfortunately, until recently there were few published papers attempting to resolve the alpha taxonomy of Karoo dinocephalians, with the 'last word' on the subject having been the review by Boonstra (1969). Because of the abundance of this group, and its importance both in terms of species richness and palaeoecology in understanding turnover during the end-Guadalupian mass extinction (Day & Rubidge 2021), it is important to have a well-supported taxonomic framework for Dinocephalia.

The first published record of a titanosuchid was that of Owen (1879), who described *Titanosuchus ferox* based on portions of a skull (NHMUK PV OR 49370) in the collections of the Natural History Museum, London. This specimen comprises an extremely weathered maxilla and a dentary with some poorly preserved tooth roots from the farm Klein Koedoeskop 310, near Beaufort West, South Africa.

Numerous other titanosuchid records from the Karoo Basin were published in the first half of the 20th century. Broom (1903a) described the anterior portion of a lower jaw (SAM-PK-731) from the Gamka River near Prince Albert and identified it as a new species, *Titanosuchus cloetei*. He later (Broom 1904) described a fragmentary jaw and a humerus (SAM-PK-769) from the lower Karoo beds of Prince Albert as another new species, *Scapanodon duplessisi*.

Watson (1914) examined all of the dinocephalian remains in the British Museum, and described a new species *Lamiasaurus newtoni* on the basis of a snout and occiput (NHMUK PV OR 49385) from Warmbad, Beaufort West. However, NHMUK PV OR 49385 was soon after recognized as chimerical by Williston (1925), who considered the occipital portion of the skull to represent a tapino-

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cephalid and the snout portion to represent a titanosuchid. In reviewing the history of this taxon, Kammerer (2011) stated that the holotype of *L. newtoni* should be restricted to the occiput, following Williston (1925) and considering *Lamiasaurus* a tapinocephalid. However, the actual first reviser of this species was Broom (1923, p. 662), who stated that 'it will be well to regard the snout as the type for *Lamiasaurus newtoni*', making *Lamiasaurus* a titanosuchid (see also Broom 1929, 1932). Boonstra (1953) synonymized *Lamiasaurus* with *Titanosuchus* but maintained the specific validity of *T. newtoni*, although he later (Boonstra 1969, p. 36) considered it dubious, with the snout fragment unable to 'be identified even as to family'. Kammerer (2011) demonstrated on the basis of vomerine morphology that the snout portion of NHMUK PV OR 49385 is indeed titanosuchid, but also considered *L. newtoni* to be a *nomen dubium*.

Haughton (1915) described the front half of a mandible (SAM-PK-2759) from Platfontein, Prince Albert, which he ascribed to a new species named *Titanosuchus dubius*. Broom (1929) placed this specimen in a new genus, *Dinocynodon*, based on flattening of the canine, which he considered unattributable to taphonomic crushing and unlike that of other titanosuchids. Boonstra (1962) later transferred this species to *Jonkeria*, but finally (Boonstra 1969) suggested that the holotype was too poorly preserved to identify beyond family level.

Van Hoepen (1916) established a new genus and species, *Jonkeria truculenta*, based on a specimen preserving a skull, jaws, and associated partial skeleton (TM 212) from Abrahamskraal, Prince Albert. However, he provided only a preliminary description of the specimen, and it would not be described in detail until the work of Broom (1929).

Broom (1923) reviewed the dinocephalians and divided them into the herbivorous suborder Tapinocephalia and (supposedly) carnivorous suborder Titanosuchia. He also suggested that the holotype of *Moschosaurus longiceps* (SAM-PK-3015) was an immature titanosuchid (although subsequent research has supported a tapinocephalid identity for this specimen, with Boonstra [1969] considering it to represent a juvenile *Struthiocephalus*). In the same work he named a new titanosuchian species, *Dinophoneus ingens*, based on two specimens from Kookfontein, Prince Albert (the holotype, AMNH FARB 5634, and a topotype, AMNH FARB 5608). Broom (1929) later removed the topotype specimen from *Dinophoneus* and placed it in the genus *Jonkeria*, as the new species *J. pugnax*. Boonstra (1936) argued that Broom's (1923) original diagnosis was correct, but attributed the two skulls to the same species and considered them referable to the genus *Jonkeria*. Hence, *Dinophoneus* was synonymized with *Jonkeria*, with both specimens placed in the new combination *Jonkeria ingens*. Broom (1923) also described a second new taxon, *Enobius strubeni*, based on the symphyseal region of two dentaries (MMK 4043) from Abrahamskraal, Prince Albert. Boonstra (1953) lumped this genus with *Titanosuchus*, since he could not find any distinguishing features in the poorly preserved holotype, and later decided that the *Enobius* material could be identified only as an indeterminate titanosuchid (Boonstra 1969). Finally, Broom (1923) described some cranial fragments from Abrahamskraal under the name *Dinartamus vanderbyli*. He placed this taxon in its own family (Dinartamidae) and considered it a titanosuchian. No specimen number or repository has ever been listed for these fragments and their current location is unknown. Boonstra (1969) considered the *D. vanderbyli* material to have features too indefinite for a generic diagnosis and considered it an indeterminate titanosuchian.

Broom (1929) reviewed Titanosuchidae, describing a number of new species. *Jonkeria vanderbyli* was based on a partial skull (AMNH FARB 5620) from Jan Willemsfontein, Prince Albert. He conceded that the skull agrees closely with that of *Jonkeria truculenta*; so much so, that it was only after some hesitation that he decided to ascribe it to a new species and not as the adult of *J. truculenta*. Broom noted a few differences between the two species, with *J. vanderbyli* featuring a shorter internasal process of the premaxillaries, a groove in the frontal region, and a much more flattened snout. Another of Broom's (1929) new species, *Scullya gigas*, was erected based on a poorly preserved snout that he stated has palatine teeth, which is not a titanosuchid character. Nevertheless, Haughton & Brink (1954) considered this species referable to *Titanosuchus* (as *T. gigas*). Boonstra (1969) suggested that if teeth are present on the palatine of this specimen, it may represent an anteosaurid, but in the absence of clear evidence it should be considered an indeterminable dinocephalian. No specimen number or repository information is available for the type material of *Scullya*, and it seems that no researchers other than Broom ever personally examined the holotype.

A more substantive new taxon described by Broom (1929), *Dinosphageus haughtoni*, was based on a skull, humerus, and ilium (SAM-PK-4343) found at Welgemoed (Kruidfontein 33) near Fraserburg Road (Leeu Gamka) Station. Boonstra (1969) noted that this specimen shows no features distinguishing it from *Jonkeria* and transferred it to that genus, as *J. haughtoni*. Broom (1929) described another new species, *Jonkeria crassus*, based on some dentary fragments, a scapula, a humerus, partial ulna, and a few partial vertebrae (AMNH FARB 5577) from Kruidfontein Station, Prince Albert. However, Boonstra (1969) observed that the humerus cannot be distinguished from that of *J. haughtoni* and considered it a synonym of that species. Finally, Broom (1929) described *Phoneosuchus angusticeps* based on a fragmentary jaw (AMNH FARB 5633) from Abrahamskraal, Prince Albert. Boonstra (1969) synonymized this species with *J. truculenta*. Broom (1929) also re-evaluated the taxonomy of *Titanosuchus cloetei*, represented by a fragmentary lower jaw, noting that it closely resembled *Jonkeria* (with similarities in the splenial and articular bones) and recombining it as *J. cloetei*. He did not transfer it to an existing *Jonkeria* species, because *J. vanderbyli* did not have a lower jaw for comparison and the jaw of *J. truculenta* was of an immature specimen. Boonstra (1969) considered *J. cloetei* as identifiable only to family level.

Broom (1936) described *Dinopolus atrox* based on a

partial snout (TM 274) from Abrahamskraal. Boonstra (1969) considered the features of this snout to be indistinguishable from those of *Jonkeria*, suggesting that *Dinopolus atrox* is an indeterminable species of that genus.

Boonstra (1955) described a number of new titanosuchids in his review of dinocephalian appendicular materials, including three new species of *Jonkeria*: *J. koupensis*, *J. parva*, and *J. rossouwi*. The holotype of *Jonkeria koupensis* is a pelvis lacking ischia and the distal two-thirds of an ulna (SAM-PK-9004) from Klein Koedoeskop, Beaufort West. There is also a referred specimen of this species comprising only an ilium (SAM-PK-11983) from Abrahamskraal, Prince Albert. *Jonkeria parva* was based on a well-preserved right humerus (SAM-PK-9149) from Saairivier (Jan Willemsfontein 32), Prince Albert, whereas *J. rossouwi* was based on a pectoral girdle, deformed left humerus, ulna, radius, pelvis, left femur, left tibia, and left fibula (SAM-PK-5014) from Abrahamskraal. In addition to the *Jonkeria* specimens, Boonstra (1955) described several additional titanosuchid specimens from the Beaufort West and Prince Albert districts, which he assigned to *Scapanodon duplessisi* and the new species *Scapanodon septemfontis* (holotype SAM-PK-5001 from Sewefontein) and *Parascapanodon avifontis* (holotype SAM-PK-9127 from Vogelfontein). However, he later (Boonstra 1969) synonymized all the *Scapanodon* and *Parascapanodon* species with *Titanosuchus ferox*.

The final titanosuchid species to be named, *Jonkeria boonstrai*, was described by Janensch (1959) on the basis of a skull and partial lower jaw (MB.R.983) from Springfontein near Letjiesbosch, Beaufort West.

Between 1879 and 1959, a total of 13 genera and 23 species had been described in what would today be considered Titanosuchidae. Boonstra (1962) studied the dentition of titanosuchid dinocephalians based on 37 specimens housed at the Iziko South African Museum. His descriptions focused on dental formulae, crown morphology, and tooth replacement patterns, and he pointed out the importance of the intermeshing incisors as a uniquely dinocephalian character. In examining variation within the group, he noted that the characters 'used by previous authors for the establishment of genera and species do not at present appear to be sufficiently distinctive or constant and such classification must at the present stage be considered of doubtful validity' (Boonstra 1962, p. 59). In his later review of the *Tapinocephalus* Zone fauna, Boonstra (1969) substantially reduced the number of valid titanosuchid taxa, recognizing only two genera (*Titanosuchus* and *Jonkeria*) and nine species (*Titanosuchus ferox*, *Jonkeria boonstrai*, *J. haughtoni*, *J. ingens*, *J. koupensis*, *J. parva*, *J. rossouwi*, *J. truculenta*, and *J. vanderbyli*). Boonstra (1969) separated *Titanosuchus* and *Jonkeria* on the basis of humerus proportions, with the former having a relatively more elongate humerus than the latter. This taxonomic arrangement was largely accepted by subsequent authors, appearing in standard references such as that of King (1988).

In an unpublished Ph.D. thesis, Kammerer (2009) stated that the cranial proportions used by earlier authors (e.g. Boonstra 1953) to differentiate titanosuchid species were unreliable. He argued that these characters vary continuously between specimens and more likely reflect individual variation, and considered *Jonkeria* to include a single valid species (the type, *J. truculenta*). He supported Boonstra's (1969) observation that *Titanosuchus* and *Jonkeria* could be distinguished based on appendicular morphology, but considered species known only from skulls to be indeterminable, as no cranial material associated with *Titanosuchus*-morph postcrania is complete enough to tell if and how it differs from that of *Jonkeria*. Morphometric analyses in this thesis treated all titanosuchid crania as representing a single taxon, labelled '*Jonkeria truculenta*', but with the caveat that these could pertain to different postcranial morphotypes (i.e. the sample of titanosuchid crania could conceivably include both *Jonkeria truculenta* and *Titanosuchus ferox*). He noted that comprehensive revision of Titanosuchidae was needed, with the hope that future discoveries of associated *Titanosuchus* crania and postcrania would allow the former to be properly identified.

In this contribution, the problem of titanosuchid taxonomy is revisited, and a detailed description of titanosuchid cranial morphology is presented based on first-hand examination of all available material of these remarkable South African dinocephalians. We provide a new diagnosis for the family Titanosuchidae and for *Jonkeria truculenta*, the only species recognized as valid in the genus, offering justifications for the synonymy of the previously-recognized species. We also propose a growth model for the skull of *J. truculenta* incorporating information from the broad size range now available for this species.

MATERIALS AND METHODS

Material

All Karoo titanosuchid specimens housed in museum collections around the world were personally examined by the lead author (with the exceptions of the type specimens of *Dinartamus vanderbyli* and *Scullya gigas*, whose current whereabouts are unknown). The study concentrated on holotype and referred specimens, but also included other published and undescribed materials. All specimens used for this study are presented in Appendix A and come from the Guadalupian (middle Permian) *Tapinocephalus* Assemblage Zone in the Moordenaars Member of the Abrahamskraal Formation, Beaufort Group of the South African Karoo Basin, except for BP/1/7168, which is from the Poortjie Member of the overlying Teekloof Formation (Beaufort Group).

Preparation

Mechanical repreparation of the specimens SAM-PK-11884 and SAM-PK-12030 was undertaken using a Desoutter VP2-X air scribe fitted with tips of tungsten carbide under a stereoscopic microscope (magnification from ×4 to ×40) at the Evolutionary Studies Institute (University of the Witwatersrand, Johannesburg). Specimen TM 212 (the holotype of *Jonkeria truculenta*) was prepared at the Ditsong National Museum of Natural

History (Pretoria), with the plaster that previously held the cranium and lower jaw together (as well as the lower jaw pieces together) being removed.

Quantitative analyses

A series of cranial and mandibular measurements (Fig. 1) are provided in Table 1. A digital Vernier caliper and a tailor's tape measure were used, with measurements recorded to the nearest millimetre. The main intention was to use these variables to evaluate allometric trends quantitatively. Unfortunately, the paucity of well-preserved, complete titanosuchid skulls and deformation of available specimens resulted in a lack of statistically significant results. In some instances, this was because of a lack of correlation, and in others because the obtained values were not statistically different from isometry. Proportional ratios between variables of different specimens (usually measurements in the smallest *versus* the largest) were used instead to propose potential ontogenetic trends.

SYSTEMATIC PALAEONTOLOGY

Synapsida Osborn, 1903
Therapsida Broom, 1905
Dinocephalia Seeley, 1894
Titanosuchidae Broom, 1903b

Diagnosis. Large (maximum skull length of 680 mm), long-snouted dinocephalians with incisors exhibiting a very well-developed 'talon and heel' morphology, lingual edge of the heel forming a sharp ridge with coarse serrations in unworn teeth; numerous leaf-shaped, roughly denticulated postcanines, with the anteriormost being larger and positioned medial to the canine on the mandible; skull is less pachyostosed than in tapinocephalids and anteosaurines, but does exhibit pachyostosis on the prefrontals, postfrontals, postorbitals, and especially the parietals; parietal laterally bayed; round pineal foramen present on the raised parietals; mandible with a sloping mentum, with the angle of slope varying from 45° to 80°.

Titanosuchidae *incertae sedis*

Titanosuchus cloetei Broom, 1903a
Lamiasaurus newtoni Watson, 1914
Titanosuchus dubius Haughton, 1915
Dinartamus vanderbyli Broom, 1923
Enobius strubeni Broom, 1923
Dinopolus atrox Broom, 1936
Jonkeria koupensis Boonstra, 1955

Remarks. These taxa are all represented by type material so poor that identification beyond Titanosuchidae is not possible based on current data. Broom's (1923) reconstruction of the skull of *Dinartamus vanderbyli* is very unlike that of other titanosuchids, but the accuracy of this reconstruction is highly questionable, and the currently unlocated holotype makes it impossible to verify. For the most part, consideration of these taxa as indeterminable follows Boonstra (1969), except for *Jonkeria koupensis*. This species is based on a partial pelvis and ulnar fragment

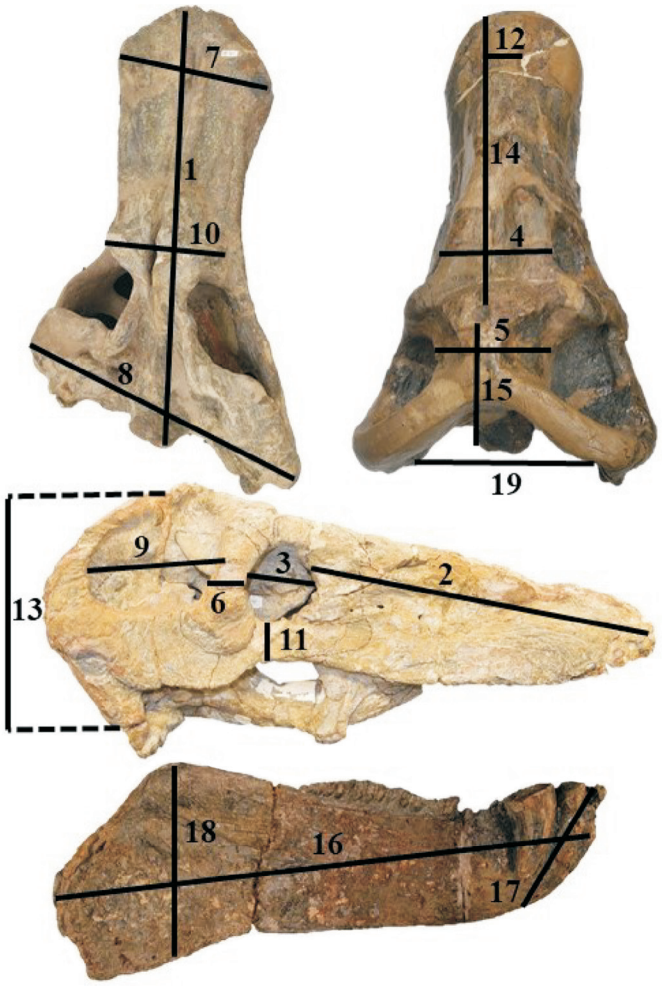


Figure 1. Photographs of specimens of *Jonkeria*, illustrating the cranial measurements taken for comparison between different skulls. 1, Total skull length (snout tip to occipital condyle); 2, snout length (tip of snout to orbit); 3, orbital length (anteroposterior); 4, interorbital width; 5, intertemporal width (at level of pineal foramen); 6, width of postorbital bar (anteroposterior); 7, width of snout (at level of canine eminence); 8, greatest width of skull (across squamosals); 9, length of temporal fenestra (anteroposterior); 10, width of pterygoid transverse process; 11, height of jugal below orbit; 12, internarial width; 13, occipital height; 14, length from snout tip to anterior margin of pineal foramen; 15, length from posterior margin of pineal foramen to occipital condyle; 16, lower jaw length (tip of jaw to articular process); 17, lower jaw height at symphysis; 18, lower jaw height at coronoid process; 19, occipital width (across squamosals).

(SAM-PK-9004), and as we have been unable to find any consistent variation in pelvic morphology among titanosuchids (Jirah, unpubl. data), we consider this specimen unidentifiable to lower taxonomic levels. The same is true of a referred specimen (SAM-PK-11983) consisting of an isolated ilium from Abrahamskraal.

Titanosuchus ferox Owen, 1879
Figures 2, 3

1904 *Scapanodon duplessisi* Broom, p. 182
1953 *Titanosuchus duplessisi* Boonstra, p. 28
1955 *Scapanodon septemfontis* Boonstra, p. 271
1955 *Parascapanodon avifontis* Boonstra, p. 278

Type series. NHMUK PV OR 49370: a set of jaw fragments, most of them sectioned and polished to show the tooth roots, including the left dentary symphysis and representative portions of the incisor, canine, and postcanine-

Table 1. Craniomandibular measurements of *Jonkeria truculenta* specimens. All measurements in millimetres. Measurements marked with asterisks represent closest estimates based on incomplete or distorted materials. 1, Total skull length (snout tip to occipital condyle); 2, snout length (tip of snout to orbit); 3, orbital length (anteroposterior); 4, interorbital width; 5, Intertemporal width (at level of pineal foramen); 6, width of postorbital bar (anteroposterior); 7, width of snout (at level of canine eminence); 8, greatest width of skull (across squamosals); 9, length of temporal fenestra (anteroposterior); 10, width of pterygoid transverse process; 11, height of jugal below orbit; 12, internarial width; 13, occipital height; 14, length from snout tip to anterior margin of pineal foramen; 15, length from posterior margin of pineal foramen to occipital condyle; 16, lower jaw length (tip of jaw to articular process); 17, lower jaw height at symphysis; 18, lower jaw height at coronoid process; 19, occipital width (across squamosals).

Specimen	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
AMNH FARB 5608	610*	390*	–	130*	83	70	–	–	–	140*	63	–	–	–	–	–	63	–	300
AMNH FARB 5620	650*	400*	86	113*	83	42	210	310*	–	130*	47	54	195	540	120*	–	–	–	240
AMNH FARB 5633	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	565*	110	–	–
AMNH FARB 5634	520*	–	–	–	–	–	–	–	–	140	–	–	–	–	–	–	–	–	280
FMNH UC 1511	680	390	95	125	103	38	248	–	140	140	55	48	225	610	105	560	100	183	310
MB.R.983	660	400	75*	–	138	73	250	420*	160	–	–	53	–	515	90	–	109	–	–
SAM-PK-11884	640	431	95	158	80	35	217	244*	138	124	44	48	224	530	94	590	78	151*	171*
SAM-PK-12030	–	315	–	–	–	–	240*	–	–	–	–	–	–	–	–	520	91	–	–
SAM-PK-4343	590	420	75	114	92*	40	235	480	140	133	–	–	–	–	–	–	–	–	197
TM 212	525	330	58	100	151	34	161	280	75	119*	55	43	167	440	90	410	55	43	222

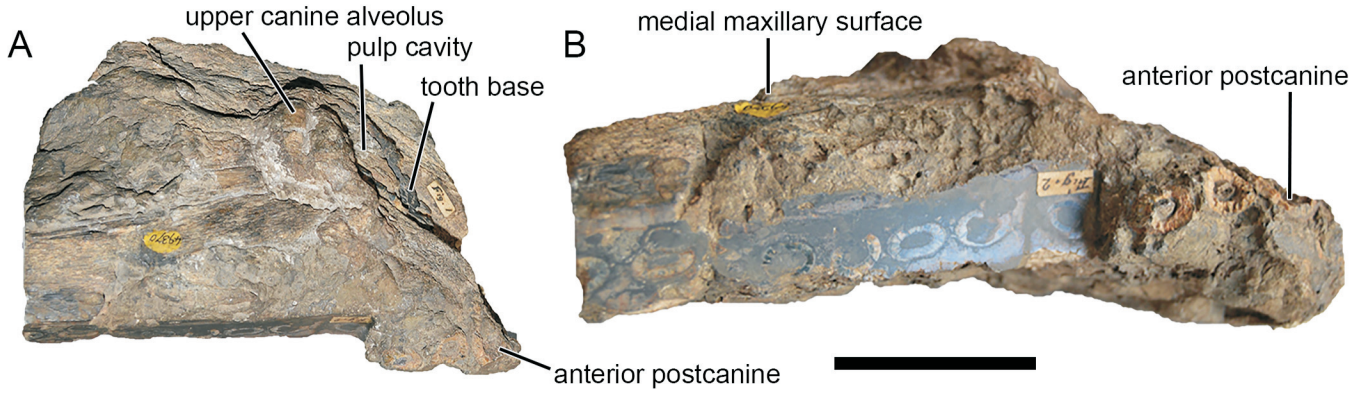


Figure 2. Holotype of *Titanosuchus ferox* (NHMUK PV OR 49370), maxillary fragment. Medial view (**A**) and longitudinal section (**B**) of the alveolar border and implanted roots of the postcanine teeth of a portion of the left maxilla. Scale bar represents 10 cm.

bearing regions of the upper and lower jaws (holotype); NHMUK PV OR 49367: numerous skull fragments, vertebrae, ribs, and appendicular elements, of which the most complete are a partial left humerus, left coracoid, right fibula, and three phalanges; NHMUK PV OR 49368, right femur; NHMUK PV OR 49369, left humerus (topotypes).

Referred specimens. SAM-PK-739: femur; SAM-PK-772 and 773: humeri (syntypes of *Scapanodon duplessisi*); SAM-PK-5001: pelvic girdle, humerus, and femur (holotype of *Scapanodon septemfontis*); SAM-PK-9127: procoracoid, clavicle, femur, and fibula associated with craniomandibular fragments, most notably the anterior half of a right lower jaw (holotype of *Parascapanodon avifontis*); SAM-PK-11491: femur; SAM-PK-11578: part of scapula and part of humerus; SAM-PK-11881: humerus.

Remarks. Owen (1879) diagnosed *Titanosuchus ferox* (Figs 2, 3) as having a strong, massive dentary with a fairly upright symphysis that is thick in proportion to its depth; cross-section through incisors nearly elliptical; canine in cross-section with a less regular oblong shape; anterior postcanines largest in size, decreasing posteriorly, with the roots of the anterior postcanines elliptical in cross-section, with long axes parallel to that of the jaw, and those of the posterior postcanines circular in cross-section. He listed the dental formula as i5/4, c1/1, pc11/10–11, but Boonstra (1953) provided an emended dental formula for this taxon: i4–5/4, c1/1, pc11–15/7–12. Haughton & Brink (1954, p. 45) characterized this taxon as follows, and their diagnosis was largely repeated by King (1988): 'Skull possibly large and massive, bosses probably present, no evidence of pachyostosis, dentigerous border of the premaxilla curves anterodorsally with an associated step-up of the anterior part of the alveolar border of the dentary, incisors long with no lingual crushing surface and strong and massive dentary with a slanted and upright mentum.'

The suite of cranial characters above are non-diagnostic within Titanosuchidae, and in some cases likely erroneous (e.g. the stated absence of pachyostosis and inferred presence of cranial bosses). They do not enable a distinction of *Titanosuchus* from *Jonkeria*, and the fragmentary nature of the *T. ferox* holotype is problematic for differentiating this species. However, Seeley (1889) considered the topotypic postcranial material (NHMUK PV OR 49367–49369) and the holotype to form a coherent hypodigm, a stance accepted by Boonstra (1953). Whether the differences between the *T. ferox* topotype postcrania and those of *Jonkeria*, previously commented on by Boonstra (1969) and Kammerer (2009), are consistent and indicative of



Figure 3. Holotype of *Titanosuchus ferox* holotype (NHMUK PV OR 49370), maxillary and dentary fragments. **A**, Left dentary, sectioned and polished surface in dorsal view; **B**, vertical section of the implanted root of the dentary canine; **C**, polished surface of left maxilla showing the cross-sections of postcanine teeth. *Abbreviations*: c, lower canine; i, lower incisor; pc, lower postcanine; PC, upper postcanine. Scale bar represents 5 cm.

taxonomic distinction will be addressed in a future paper on titanosuchid postcranial morphology.

The medial side of the left maxilla of the *Titanosuchus ferox* holotype (NHMUK PV OR 49370) (Fig. 2A) show the trace of the socket of the canine, with part of the base or root of that canine tooth and of its pulp cavity. The first postcanine is implanted close to the canine. The bases of three of the postcanines are visible in what remains of their sockets, and a section along the rest of the alveolar border (Figs 2B, 3C) shows eight additional postcanine teeth of similar size and shape.

Anteriorly, the mandible fragment is fairly massive, to support the powerful incisors and canine (Fig. 3), and has a tall, sloping mentum. The anterior lower postcanines are positioned medial to the canine, whereas the posterior ones are almost in line with the canine (Fig. 3A). No crowns are preserved; in cross-section, i2 and i3 are strongly ellipsoid while i4 is closer to circular with no diastema between it and the canine.

The dentary bears a single canine, which has a long, thick root (Fig. 3B) causing the dentary to bulge laterally and medially. The canine cross-section is antero-posteriorly longer than laterally wide. The maxilla and dentary present cross-sections of 11 postcanines (Fig. 3A,C). The roots of the anterior four postcanines are elliptical, with an anteroposterior long axis, and the posterior roots are almost circular. The dentary postcanine teeth are close to the midline of the jaw, whereas the maxillary teeth are more laterally positioned. The first postcanine of both the maxilla and dentary is the largest and the rest of the postcanines decrease in size posteriorly.

Jonkeria truculenta van Hoepen, 1916
Figures 4–19

1923 *Dinophoneus ingens* Broom, p. 666
1929 *Dinosphageus haughtoni* Broom, p. 31
1929 *Jonkeria crassus* Broom, p. 26
1929 *Jonkeria pugnax* Broom, p. 33
1929 *Jonkeria vanderbyli* Broom, p. 23
1929 *Phoneosuchus angusticeps* Broom, p. 31
1935 *Jonkeria ingens* Boonstra, p. 331
1953 *Jonkeria angusticeps* Boonstra, p. 27
1953 *Jonkeria haughtoni* Boonstra, p. 27
1955 *Jonkeria parva* Boonstra, p. 303
1955 *Jonkeria rossouwi* Boonstra, p. 303
1959 *Jonkeria boonstrai* Janensch, p. 23

Holotype. TM 212: skull with an incomplete right mandible (Fig. 4); 26 vertebrae (cervical-dorsal series); right shoulder girdle, with top of scapular blade broken; complete right and partial left clavicles; partial interclavicle; femoral fragments; right tibia, fibula, astragalus, and calcaneum; incomplete ribs.

Referred specimens. AMNH FARB 5577: scapula, humerus, part of ulna and ilium, associated dentaries (holotype of *Jonkeria crassus*); AMNH FARB 5608: partial skull and right mandibular ramus (holotype of *Jonkeria pugnax*); AMNH FARB 5620: partial skull (holotype of *Jonkeria vanderbyli*; Fig. 5A); AMNH FARB 5633: ischium and lower jaw (holotype of *Phoneosuchus angusticeps*); AMNH FARB

5634: incomplete skull (holotype of *Dinophoneus ingens*; Fig. 5B); FMNH UC 1511: skull, lower jaw, and fragmentary postcranial elements; MB.R.983: partial skull and lower jaw (holotype of *Jonkeria boonstrai*; Fig. 5C); ROZ.B96: partial skull and lower jaw; SAM-PK-738: isolated humerus; SAM-PK-3433 isolated humerus; SAM-PK-4343: partial skull, humeri, ilia, scapula, cleithrum, ulna, ischium, incomplete femur, fibula, coracoids, and vertebrae (holotype of *Dinosphageus haughtoni*; Fig. 5D); SAM-PK-5014: left scapula, incomplete procoracoid and coracoid, incomplete interclavicle, left humerus, left ulna, left radius, right ilium, left femur, left tibia, and left fibula (holotype of *Jonkeria roussowi*); SAM-PK-9149: right humerus (holotype of *Jonkeria parva*); SAM-PK-11884: skull and lower jaw; SAM-PK-12005: isolated humerus; SAM-PK-12030: incomplete skull with right mandibular ramus.

Revised diagnosis. *Jonkeria truculenta* crania exhibit the following consistent set of characters: large skulls (adult length ranging from 500 to 680 mm) with a long, narrow snout (length of snout on average about 60% of total skull length); skull broadens considerably behind the orbit; no pronounced thickening of the dorsal and hind rim of the orbit; external nares situated far anteriorly and laterally; swelling around the pineal foramen due to pachyostosis of the parietal, with this thickened parietal mound pierced by a prominent, circular pineal foramen, situated on a chimney; intertemporal width slightly wider than the interorbital width; temporal opening is relatively large and its anteroposterior diameter is not reduced to a transverse slit as in tapinocephalids; lateral surface of the snout has a moderate concavity between the orbit and posterior margin of the septomaxilla; in lateral view, the jaw articulation is positioned far anteriorly, almost ventral to the postorbital bar; dental formula: i5/4, c1/1, pc19/18–21, large incisors with a high, sharp-edged anterior 'talon' and a broad, flat posterior 'heel'; robust canines, with the upper ones having a large conical crown lacking serrations and curving backwards, moderately flattened from side to side; lower canine is smaller, shorter, less pointed and less curved than the upper canine, and with its blunt point directed outwards; canine has a thick, long root, which causes the maxilla to bulge both internally and externally; presence of a diastema between the last upper incisor and the canine to enable the lower canine to pass between these two teeth in occlusion; posterior to the canine is a row of small postcanines on the maxilla, the crowns of which are flattened and roughly serrated on the anterior and posterior surfaces; palatines without any prominent bosses or teeth, but slightly raised towards their posterior extremity where they contact the vomers; flat, elongate, strap-like vomers extending nearly two-thirds of the length of the palate, with a shallow midline trough and bifurcated anterior end. It is at present uncertain which of these characters are also present in *Titanosuchus ferox*; a number of them may be apomorphies of Titanosuchidae rather than diagnostic for *J. truculenta*.

Taxonomic comparisons

Comparisons provided below are restricted to those specimens including crania; taxonomic comparisons with nominal *Jonkeria* species based primarily on postcrania

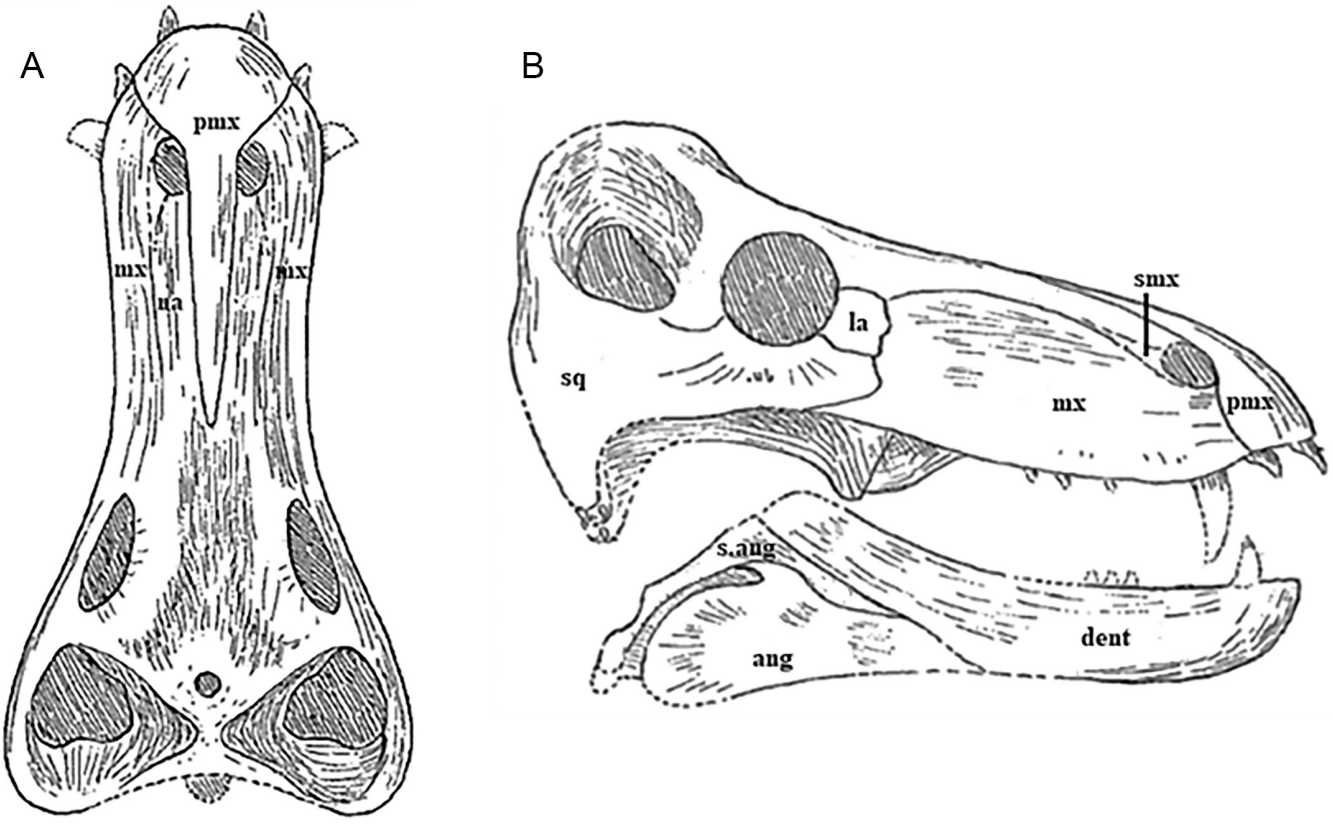


Figure 4. Illustrations of the dorsal (**A**) and right lateral (**B**) views of the *Jonkeria truculenta* holotype (TM 212), adapted from Broom (1929: pages 12–13: fig.1 & fig. 2). Broom managed to trace only a few sutures owing to the similarity between bone and matrix. *Abbreviations*: ang, angular; la, lacrimal; mx, maxilla; na, nasal; pmx, premaxilla; s.ang, surangualr; smx, septomaxilla; sq, squamosal.

(i.e. *J. angusticeps*, *J. crassus*, *J. parva*, and *J. rossouwi*) will be provided in a future contribution.

Jonkeria vanderbyli

Broom (1929) noted that the skull of *Jonkeria vanderbyli* (Figs 5A, 6D, 8D, 11D) agreed morphologically with that of *Jonkeria truculenta*, with only minor dissimilarities, namely a larger, flatter premaxilla that is more downturned anteriorly, a dorsal (internasal) process of the premaxillae, presence of a groove towards the middle of the frontal region, and a more anterior position of the quadrate. Broom (1929, p. 24) seemed somewhat uncertain of these distinctions, however, stating that 'the skull agrees closely with that of *Jonkeria truculenta*; so much so that it has only been after some hesitation that I have decided that it is a new species and not the adult of the species described by van Hoepen'.

Examination of the holotype of *J. vanderbyli* (AMNH FARB 5620) demonstrates that Broom's (1929) supposed diagnostic characters for the species are problematic. The dorsal and anterior skull profiles of this specimen are distorted, and the anterior snout tip is largely reconstructed in plaster, making features of the frontals and premaxillae questionable. The dorsal process of the premaxillae extends posteriorly as far as the anterior edge of the frontals in both TM 212 and AMNH FARB 5620. Finally, the relative position of the quadrate is easily altered by taphonomic factors, with its somewhat more anterior angle in AMNH FARB 5620 likely attributable to dorsoventral crushing.

Jonkeria ingens

Broom (1923) described two skulls, AMNH FARB 5608 and AMNH FARB 5634 (Fig. 5B), as belonging to *Dinophoneus ingens*, but later removed the topotype specimen (AMNH FARB 5608) and placed it in the new species *Jonkeria pugnax*. Broom (1923) presented a cursory description of *Dinophoneus ingens* with no diagnosis or comparison with *Jonkeria truculenta*. Broom (1932, p. 27) compared *D. ingens* with *J. truculenta* and *J. vanderbyli*, pointing out that 'the parietals in *Dinophoneus ingens* are much wider than in *J. truculenta* or *J. vanderbyli* and though the postorbitals are large they do not meet the squamosals'.

Boonstra (1935) synonymized *Dinophoneus* with *Jonkeria* and *J. pugnax* with *J. ingens* and a year later (Boonstra, 1936) provided a detailed description of *J. ingens*, but he compared this species with gorgonopsians, therocephalians, and cynodonts, rather than specifically with *Jonkeria truculenta*. Boonstra (1936, p. 111) mentioned that 'in palatal view, the morphological details in *J. vanderbyli* are as described for *J. ingens*, but differing in proportions, such as the quadrate rami of the pterygoids being not so divergent in posterior direction, slender vomers, the median pterygoid keel posterior to the interpterygoid vacuity being much deeper and the basioccipital being situated relatively farther posteriorly in *J. vanderbyli* compared to *J. ingens*'.

Contra Broom (1932), the parietals are of similar size in the holotypes of *J. ingens* and *J. vanderbyli* (~83 mm) and both are wider than those of *J. truculenta* (represented by a juvenile or subadult skull; see below). The postorbitals in the holotype of *J. ingens*, as in all *Jonkeria* specimens, do not meet the squamosals. Differences in the divergence of the quadrate rami of the pterygoids are interpreted here as taphonomic distortion and/or a consequence of ontogenetic stage. Boonstra's (1935) arguments for considering the species *ingens* and *pugnax* conspecific are sound, and the latter species is also included in the synonymy of *J. truculenta* here.



Figure 5. *Jonkeria* skulls in lateral view. **A**, Holotype of *Jonkeria vanderbyli* (AMNH FARB 5620); **B**, holotype of *Jonkeria ingens* (AMNH FARB 5634); less than 50% of the skull is preserved; the remainder is reconstructed with plaster of Paris; **C**, holotype of *Jonkeria boonstrai* (MB.R.983); the skull is distorted, with two-thirds of the ventral surface and the teeth missing (reconstructed in plaster of Paris); **D**, holotype of *Jonkeria haughtoni* (SAM-PK-4343). Specimen in **D** in right lateral view; specimens in **A**– **C** in left lateral view but mirrored for comparison. Scale bars represent 10 cm.

Jonkeria haughtoni

According to Broom (1929, p. 31), in *Jonkeria haughtoni*, 'vomers form a marked median ridge on their posterior two-thirds and the pterygoids project much less downwards than in other species of *Jonkeria*'.

This species was described based on a well-preserved skull (Fig. 5D) with an associated humerus and numerous other postcranial elements (SAM-PK-4343). There are no diagnostic features of the skull to separate it from the other *Jonkeria* species; the downward projection of pterygoids is the result of dorsoventral crushing of this skull and the vomerine morphology accords with that of other *Jonkeria* specimens.

Jonkeria boonstrai

According to Janensch (1959), in the *Jonkeria boonstrai* holotype (MB.R.983; Fig. 5C) the ratio of the occiput height to the total skull length is approximately 57%, compared to 50% for *J. truculenta*, *J. vanderbyli*, and *J. haughtoni*, and slightly more for *J. ingens*. He also stated that the difference in the ratio of the width of the snout to the total skull length is about 41% for *J. boonstrai*, compared to only 30% in the other species of *Jonkeria*, and the angled skull profile and steep symphyseal mentum of MB.R.983 is not seen in other species of *Jonkeria*.

MB.R.983 is compressed in the posterior region, distorting the proportions of the occiput. The ratio of the snout width to the total skull length is, as stated by Janensch (1959), higher for MB.R.983 than other *Jonkeria* specimens. However, this specimen appears to have suffered both compression and shear, and this, together with ontogenetic factors, is likely responsible for the differences between it and other *Jonkeria* crania. It is noteworthy that the symphysis of the mandible of MB.R.983 is much more inclined (with the slope of its anterior margin almost 60°) compared to that of other *Jonkeria* mandibles (where this slope is usually ~30°), but this may be due to the anteroposterior compression of the lower jaw. The unusual proportions of MB.R.983 could potentially indicate taxonomic distinction, but additional specimens showing that this is a consistent morphotype rather than simply the result of taphonomic distortion are required to demonstrate this.

Craniomandibular description

Van Hoepen (1916) provided a preliminary description of the skull of the *Jonkeria truculenta* holotype, which was later described in detail by Broom (1929) (Fig. 4). Boonstra (1936) provided a comprehensive description of the cranial morphology of some *Jonkeria* skulls and lower jaws housed in American Museum of Natural History, but this description was operating under the assumption that these specimens represented different taxa rather than growth stages or taphomorphs. Here is presented the first detailed craniomandibular description of *Jonkeria* incorporating data from all available material referable to this genus, under our revised taxonomic concept.

Skull roof

The following description is based largely on specimen SAM-PK-11884, as it is the best-preserved and one of very few complete *Jonkeria* skulls, but additional information is included from other specimens.

Jonkeria skulls have an almost horizontal dorsal profile. The snout is fairly large, representing about 60% of the skull length, the rounded orbit is dorsoposteriorly rimmed mostly by pachyostotic bone, and the temporal opening is quadrangular, clearly larger than the orbit (Fig. 6A). The centre of the temporal region, formed by the parietal, is the highest point of the skull.

Premaxilla

The premaxilla is a fairly large bone located at the anterior tip of the snout, with a midline sutural contact with its contralateral element, forming part of the anterior and dorsal margin of the external naris (Figs 6–9). In dorsal view, the anterior part of the roughly triangular premaxilla makes up a large portion of the snout anterior to the external nares, and from this anterior portion a long and broad dorsal (internasal) process tapers posteriorly to form a pointed posterior contact with the frontals, flanked by the nasals on either side (Figs 8, 9).

Laterally, the premaxilla is longer than is visible externally, as it is overlapped by the maxilla (Broom 1929). In SAM-PK-11884, SAM-PK-4343, and FMNH UC 1511 (Figs 6A,C, 7B), the premaxilla is less abruptly downturned anteriorly, unlike in specimens TM 212, AMNH FARB 5620, and MB.R.983 (Figs 6B,D, 7A).

In ventral view, the premaxilla has an oblique sutural contact with the maxilla laterally and meets the vomer posteromedially, where the anterior bifurcated end of the paired vomers forms a V-shaped contact (Figs 10, 11). The premaxilla bears five incisor teeth. Ventrally, the premaxilla overlies the anteromedial surface of the maxilla and extends posteriorly beyond the canine, but does not contact the palatine. However, in SAM-PK-4343, the premaxilla shows a suture with the palatine and extends into the trough formed at the palatine–vomer junction, thereby forming the lateral border of the internal naris to the exclusion of the maxilla (Fig. 10C).

Septomaxilla

Facial expression of the septomaxilla is relatively small and triangular, producing a tapering posterior projection on the skull roof behind the external naris. In a few specimens (Fig. 6C, 7A,B,E), this bone extends ventrally to the anterior rim of the external naris, while for specimen SAM-PK-11884 (Fig. 6A) the septomaxilla is close to the posterior rim of the external naris. SAM-PK-12030 has an especially well-preserved septomaxilla, which extends into and forms the floor of the external naris (Fig. 7E).

Maxilla

In lateral view, the maxilla is a long and rather flat bone, which covers most of the lateral side of the snout. It bears a single canine anteriorly and behind it are small postcanines varying in number from 19 to 21, with smaller skulls having fewer postcanines than larger skulls. The maxilla (in lateral view) is a vertically oriented bone with an oblique to slightly crescent-shaped sutural contact

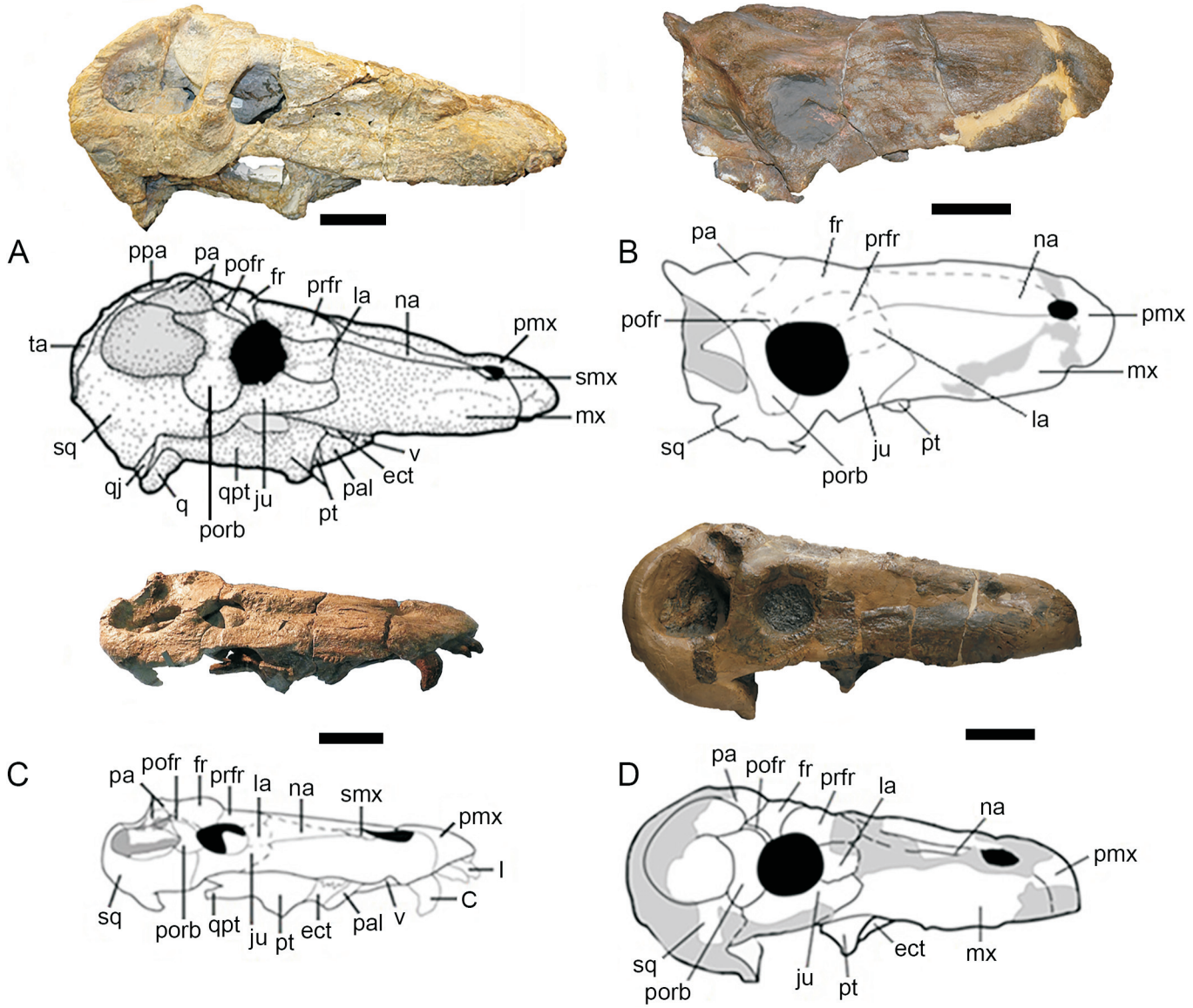


Figure 6. *Jonkeria* skulls in lateral view with interpretive drawings. **A**, SAM-PK-11884; **B**, TM 212; **C**, SAM-PK-4343; **D**, AMNH FARB 5620. Specimens in **A** and **C** in right lateral view; specimens in **B** and **D** in left lateral view but mirrored for comparison. *Abbreviations*: C, upper canine; ect, ectopterygoid; fr, frontal; I, upper incisor; ju, jugal; la, lacrimal; mx, maxilla; na, nasal; pa, parietal; pal, palatine; pmx, premaxilla; pofr, postfrontal; porb, postorbital; ppa, postparietal; prfr, prefrontal; pt, pterygoid; q, quadrate; qj, quadratojugal; qpt, quadrate ramus of pterygoid; smx, septomaxilla; sq, squamosal; ta, tabular; v, vomer. Scale bars represent 10 cm.

with the premaxilla, anterior to the external naris. Below and slightly posterior to the external naris it contacts the septomaxilla, and posterior to the septomaxilla has a long horizontal dorsal sutural contact with the nasal (Figs 6, 7). In FMNH UC 1511, the dorsal maxilla–nasal suture is slightly oblique posteriorly (Fig. 7B). Posteriorly, the maxilla is in sutural contact with the prefrontal, has an almost vertical contact with the lacrimal, and a posterior oblique sutural contact with the jugal. There is a notable lateral expansion (bulge) in the anterior portion of the maxilla to accommodate the root of the large canine. The right maxilla of SAM-PK-11884 is well preserved compared to the left maxilla, but appears to be slightly displaced dorsally. In this skull, a posteroventral spur of the maxilla extends along the ventral border of the skull up to a point halfway along the orbit, a condition also seen in AMNH FARB 5620 (Fig. 6A,D). However, in TM 212 and AMNH FARB 5608, this posterior extension of the maxilla ends anterior to the orbit (Figs 6B, 7C).

In ventral view, the maxilla has a curved anteromedial sutural contact with the premaxilla and is ventrally overlain by the palatine posteriorly (Fig. 10). On the medial side, it contacts the lateral margin of the vomers (Figs 10A,B,D, 11A), but in SAM-PK-4343, the maxilla does not make any contact with the vomers, being interposed with the palatines (Fig. 10C). The anterior maxilla–palatine contact is posterior to the canine and almost in line with the second postcanine in SAM-PK-11884 (Fig. 10A), but at the level of the first postcanine in SAM-PK-4343 (Fig. 10C).

Nasals

These are long, narrow, and anteriorly tapering bones positioned between the posterior end of the external nares and the frontal. For their entire length, the dorsal process of the premaxillae separates them medially. Anteriorly and laterally, the nasal has sutural contact with the maxilla, a short posteroventral contact with

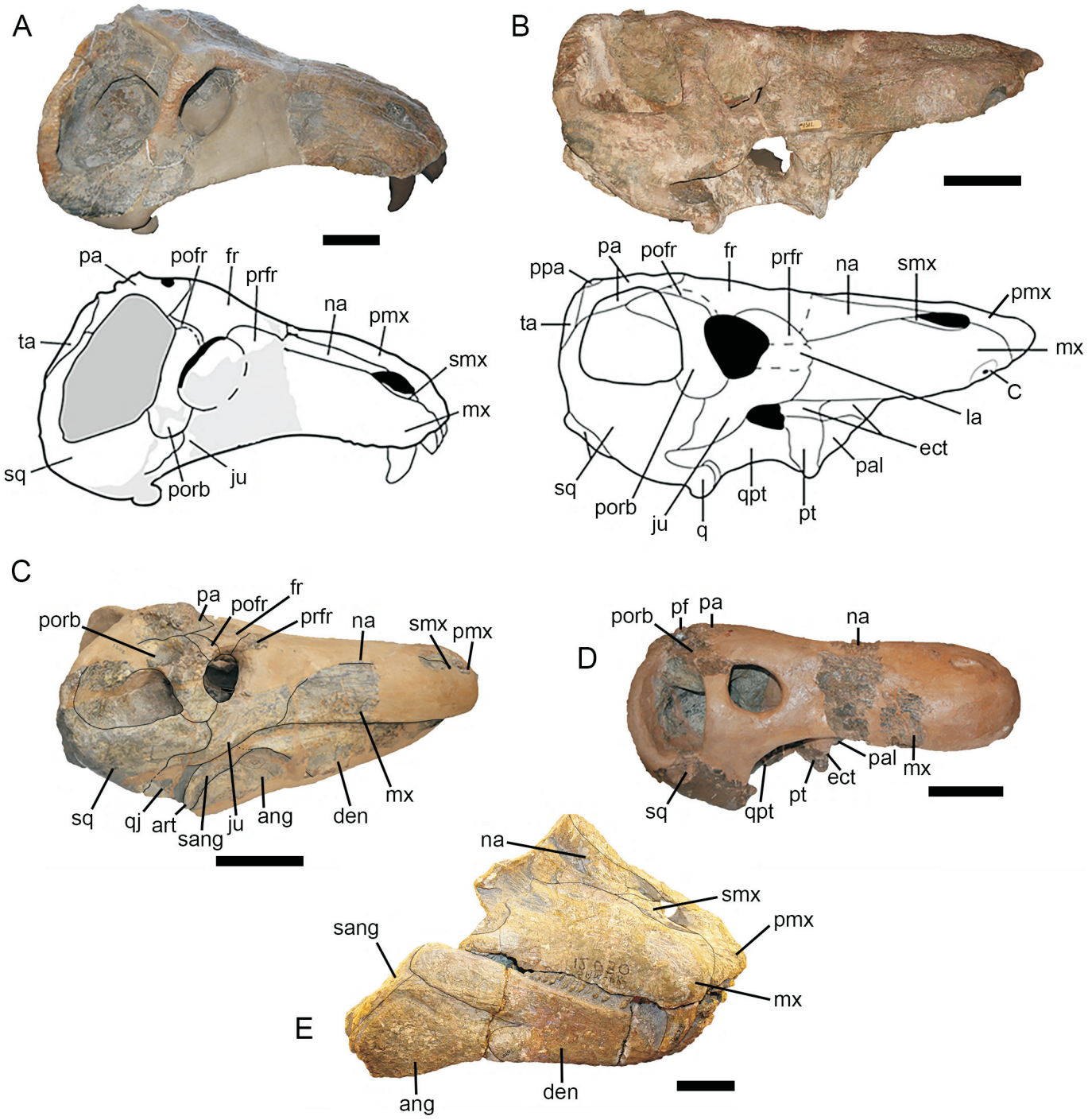


Figure 7. *Jonkeria* skulls in lateral view with interpretive drawings. **A**, MB.R.983; **B**, FMNH UC 1511; **C**, AMNH FARB 5608; **D**, AMNH FARB 5634; **E**, SAM-PK-12030. Specimens in **B** and **C** in right lateral view; specimens in **A**, **D**, and **E** in left lateral view but mirrored for comparison. *Abbreviations*: ang, angular; art, articular; C, upper canine; den, dentary; ect, ectopterygoid; fr, frontal; ju, jugal; la, lacrimal; mx, maxilla; na, nasal; pa, parietal; pal, palatine; pmx, premaxilla; pofr, postfrontal; porb, postorbital; ppa, postparietal; prfr, prefrontal; pt, pterygoid; q, quadrate; qj, quadratojugal; qpt, quadrate ramus of pterygoid; sang, surangular; smx, septomaxilla; sq, squamosal; ta, tabular. Scale bars represent 10 cm.

the prefrontal, and transverse posterior contact with the frontal (Figs 8, 9).

Lacrimal

The lacrimal is a relatively small, quadrangular bone in lateral view, forming the anterior margin of the orbit (Figs 6, 7B). It contacts the jugal ventrally, the maxilla anteriorly, and the prefrontal dorsally. The lacrimal has an almost horizontal ventral contact with the jugal and a horizontal to slightly oblique contact with the prefrontal, which occurs along a small ridge. The lacrimal has a slightly vertical anterior contact with the maxilla and forms the antorbital depression in lateral view.

Jugal

This is a large bone, which forms most of the suborbital arch, part of the temporal arch, and a considerable part of the pre-orbital portion of the face (Fig. 6A). The jugal makes up the entire ventral border of the orbit and extends anteriorly as far as the anterior end of the lacrimal to form an anterior and anteroventral contact with the maxilla. Posteriorly, it forms a curved suture with the

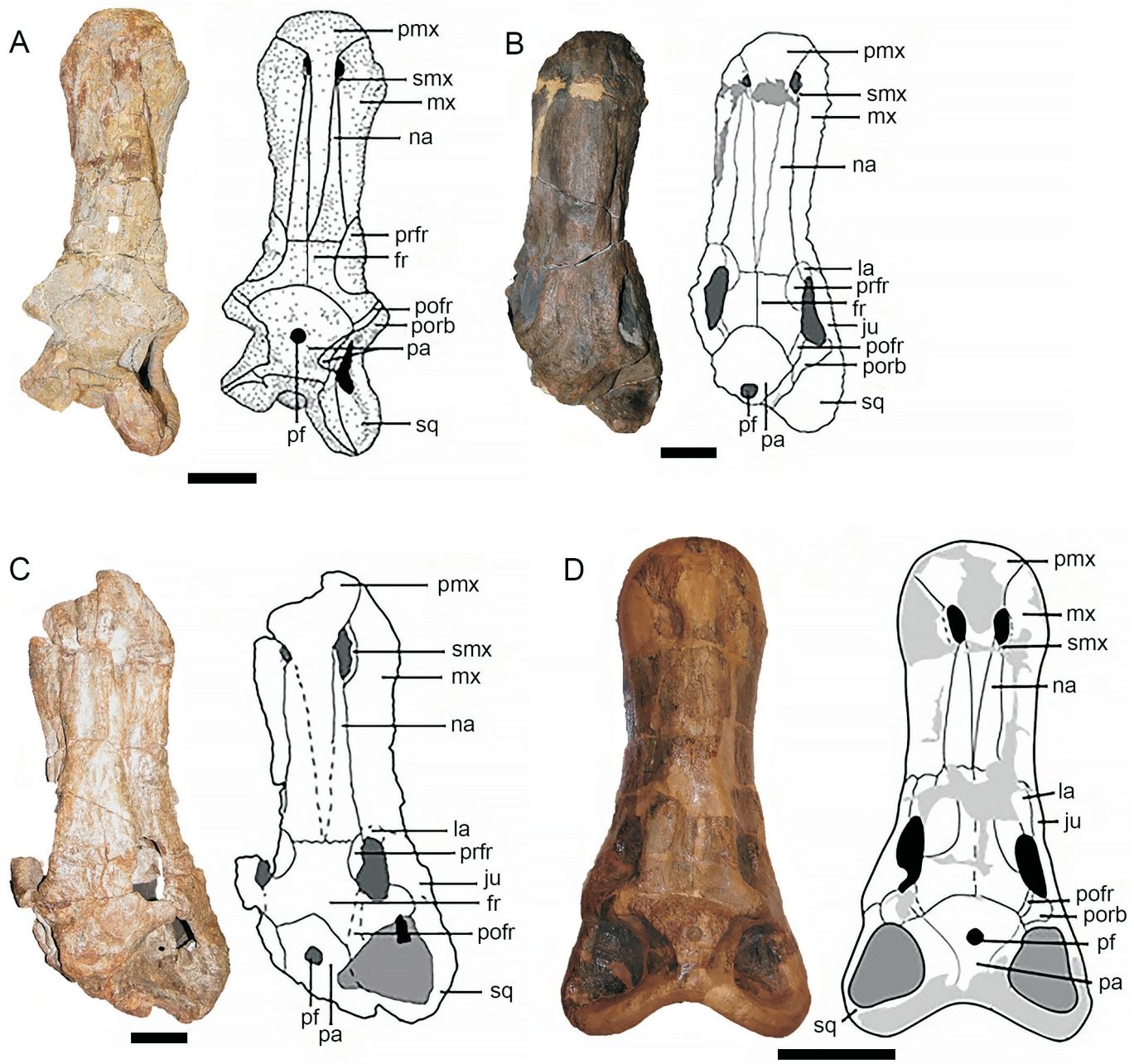


Figure 8. *Jonkeria* skulls in dorsal view with interpretive drawings. **A**, SAM-PK-11884; **B**, TM 212; **C**, SAM-PK-4343; **D**, AMNH FARB 5620. *Abbreviations*: fr, frontal; ju, jugal; la, lacrimal; mx, maxilla; na, nasal; pa, parietal; pf, pineal foramen; pmx, premaxilla; pofr, postfrontal; porb, postorbital; prfr, prefrontal; smx, septomaxilla; sq, squamosal. Scale bars represent 10 cm.

ventral part of the postorbital bar. The posterior extension of the jugal and its contact with the squamosal is preserved only in SAM-PK-11884 and FMNH UC 1511 (Figs 6A, 7B). In these specimens, the anterior projection of the squamosal forms a notch where the posterior end of the jugal and the quadratojugal meet. This notch is lost or absent in all the other specimens. In SAM-PK-11884, the ventral part of the jugal is weathered more in the posterior end (Fig. 6A), such that the jugal and quadratojugal appear as if they are separated.

Prefrontal

The ovoid prefrontal, which is slightly pachyostosed on the dorsal surface, has both dorsal and lateral exposures on the skull roof (Figs 6–9). It is twice as long as it is wide, forming the anterior and dorsal borders of the orbit, and articulates with the maxilla anteriorly, lacrimal ventrally, nasal anteromedially, and frontal medially.

Frontal

This paired bone comprises most of the interorbital region on the dorsal surface of the skull and is relatively short and posteriorly broad. On its dorsal surface, the frontal is flat anteriorly but bends upwards posteriorly to articulate with the elevated parietal (Figs 6–9). Anteriorly, the frontal has a straight, transverse suture with the nasals and anterolaterally a curved suture with the prefrontal. Between the prefrontal and postfrontal, the frontal forms a small part of the supraorbital border, and posterolaterally has a short, almost straight suture with the postfrontal. Posterolaterally, it forms a small part of the anteromedial border of the temporal fenestra (Figs 8, 9) and has a

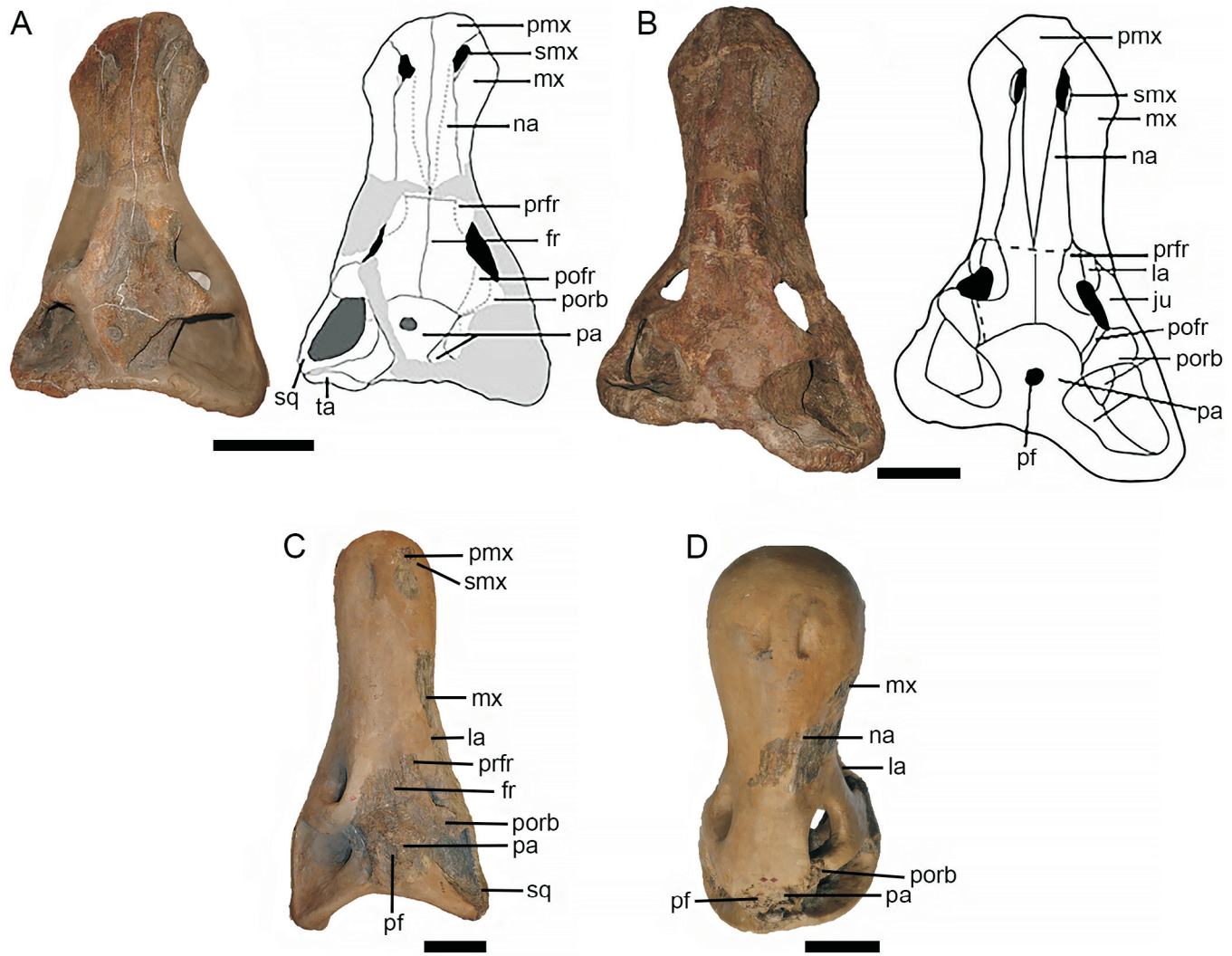


Figure 9. *Jonkeria* skulls in dorsal view with interpretive drawings. **A**, MB.R.983; **B**, FMNH UC 1511; **C**, AMNH FARB 5608; **D**, AMNH FARB 5634. *Abbreviations*: fr, frontal; ju, jugal; la, lacrimal; mx, maxilla; na, nasal; pa, parietal; pf, pineal foramen; pmx, premaxilla; pofr, postfrontal; porb, postorbital; prfr, prefrontal; smx, septomaxilla; sq, squamosal; ta, tabular. Scale bars represent 10 cm.

curved sutural contact posteriorly with the parietal. There is no visible pachyostosis on the dorsal surface of the frontals except a slight thickening at its contact with the postfrontal as well as at its contribution to the dorsal orbital rim. There is a dorsal ridge that runs on the frontal midline from the frontal–parietal suture and terminates almost in line with the anterior border of the orbits. This is more prominent on TM 212 and MB.R.983 (Figs 8B, 9A) and to a lesser extent on AMNH FARB 5620 (Fig. 8D).

Postfrontal

The postfrontal is a small, almost rectangular bone in dorsal view, and is positioned between the frontal and the postorbital, where it forms the dorsal part of the postorbital bar and has a small contribution to the posterodorsal orbital border, and the anterodorsal border of the temporal opening (Figs 6–9).

Postorbital

This is a large bone, which forms nearly all of the postorbital bar, delimiting the temporal fenestra anteriorly and the orbit posteriorly. Dorsally it meets the postfrontal and posteromedially it has a long sutural contact with the parietal, also meeting the squamosal above the temporal fenestra. Its ventral margin contacts the jugal anteroventrally (Figs 8, 9) and posteroventrally has an extensive rounded contact with the squamosal. In the middle of the orbit, this bone is 34 mm wide in the smallest specimen TM 212 and 42 mm in the larger skull AMNH FARB 5620.

Parietal

This bone is laterally bayed, but because it is pachyostosed, the midline suture is not visible in any specimens. Posteriorly it forms a high and fairly narrow sagittal crest. The anterior end of the parietal forms a transverse sutural contact with the frontal and laterally it is in contact with both the postorbital and the squamosal within the temporal fenestra. Posteriorly, it contacts both the postparietal and tabular bones. A circular pineal foramen is located centrally or slightly posteriorly on the parietal (Figs 8, 9).

Squamosal

The squamosal is a large element forming the subtemporal bar and making up the entire ventral and posterior borders of the temporal fenestra. At the posterior end of the temporal fenestra, the squamosal is very large and consists of an ascending, descending, and anterior

process, which form much of the sub-temporal arch. The ascending process of the squamosal forms the back of the temporal fenestra and sutures with the parietal dorsally and the tabular posteriorly. The descending process passes ventrally and curves slightly forwards as the anterior process, which meets the jugal anteroventrally (Fig. 9a). Anterodorsally, the squamosal has a sutural contact with the postorbital. The squamosal is in contact with the quadratojugal on the ventrolateral side of the external auditory meatus, and on the ventral side it contacts the ascending quadrate ramus of the pterygoid. The squamosal forms the lateral side of the occiput, where it contacts the tabular, supraoccipital, and paroccipital process of the opisthotic.

Quadratojugal

The quadratojugal (Figs 6A, 7C) is wedge-shaped and is partially obscured from lateral view by the squamosal. It is situated on the posteroventral corner of the zygoma, having a laterally exposed portion positioned under the posteroventral portion of the squamosal while medially it contacts the lateral condyle of the quadrate.

Quadrate

This is a fairly large bone extending dorsally on the anterior side of the squamosal (Figs 6A, 7B) and comprises a flattened dorsal process and two large ventral condyles with a sulcus between them. The medial condyle contacts the posterior end of the quadrate ramus of the pterygoid. The anterior-facing surface of the dorsal process of the quadrate is smooth, and is positioned anterior to the ventral process of the squamosal. A stapedial groove is situated between the dorsal process and the medial condyle of the quadrate to receive the distal end of the stapes.

Palate

The palate comprises the vomer, palatine, ectopterygoid, pterygoid (consisting of anterior, transverse, and posterior/quadrate processes), as well as the palatal sections of the premaxilla and maxilla. The titanosuchid palate forms a flat, edentulous, mostly horizontally oriented shelf.

Vomer

The paired vomers are flat, elongate, strap-like bones extending as stout rods nearly half of the length of the skull. The vomers are separated by a shallow midline trough. In well-preserved specimens, the anterior end of the paired vomers is bifurcated (Figs 10, 11A). Posteriorly, the vomers are slightly projected dorsally where they meet the pterygoids and posterolaterally they are overlain by the palatines. They form the medial border of the elongated internal naris.

Palatine

The palatine (Figs 10, 11) is a complex bone with a broad posterior portion with sutural contacts with the vomers anteromedially, the ectopterygoid laterally, and the pterygoids posteriorly and posterolaterally. The anterolateral process overlies the maxilla on the ventral side and extends anteriorly almost as far as the canine tooth, forming most of the posterior and lateral borders of the internal nares. There are no discrete palatine bosses in *Jonkeria*, but the palatines are ventrally projected near the contact with the vomers.

Ectopterygoid

The ectopterygoid is a small, triangular bone positioned between the palatine anteriorly, the jugal posterolaterally, and the lateral process of the pterygoid on the posterior side. It descends halfway down the anterior face of the lateral pterygoid ramus and abuts against the posterior end of the maxilla. Just like the palatine, the ectopterygoid is also exposed in lateral view in some specimens (Figs 6A,C,D, 7B,D) and is morphologically similar in all specimens (Figs 10, 11).

Pterygoid

The pterygoid is one of the largest bones of the palate and accounts for about a third of the total palatal length. This bone comprises three rami: anterior, transverse, and posterior. The anterior ramus is very short anteromedially, with a curved sutural contact with the palatine and a transverse sutural contact with the vomers. The transverse ramus comprises the prominent lateral flange of the pterygoid, which is weathered in all specimens. Its ventral surface is a broad, rugose ridge, which narrows as it curves posteromedially toward the interpterygoid vacuity. The slit-shaped interpterygoid vacuity extends posteriorly from behind the level of the vomer–pterygoid contact to the posterior side of the lateral flanges of the pterygoid (Figs 10, 11). The posterior ramus of the pterygoid extends posteromedially to meet the basisphenoid and posterolaterally to contact the medial condyle of the quadrate; this portion is also known as the quadrate ramus of the pterygoid (Figs 10, 11). The quadrate ramus of the pterygoid sweeps backwards as a thin sheet of bone in ventral view but is broader in lateral view (Fig. 6A, 7B).

Occiput and basicranium

The occiput is best preserved in FMNH UC 1511, but is also partially complete in AMNH FARB 5620, SAM-PK-4343, SAM-PK-11884, and TM 212. In occipital view, the skull is broadly ovoid and vertically oriented, with a slight anteroventral inclination.

Postparietal

The postparietal is positioned dorsally on the occipital plate (Fig. 12) and enters the dorsal surface of the skull, where it has a slightly curved sutural contact with the parietal. Laterally, the postparietal contacts the tabular and ventrally, it has a long horizontal sutural contact with the supraoccipital. It is wider dorsally where it contacts the parietal and tapers ventrally where it contacts the supraoccipital.

Tabular

The tabular is a relatively large, paired, semilunate bone with a long ventral projection extending between the squamosal and the supraoccipital (Fig. 12) and forming

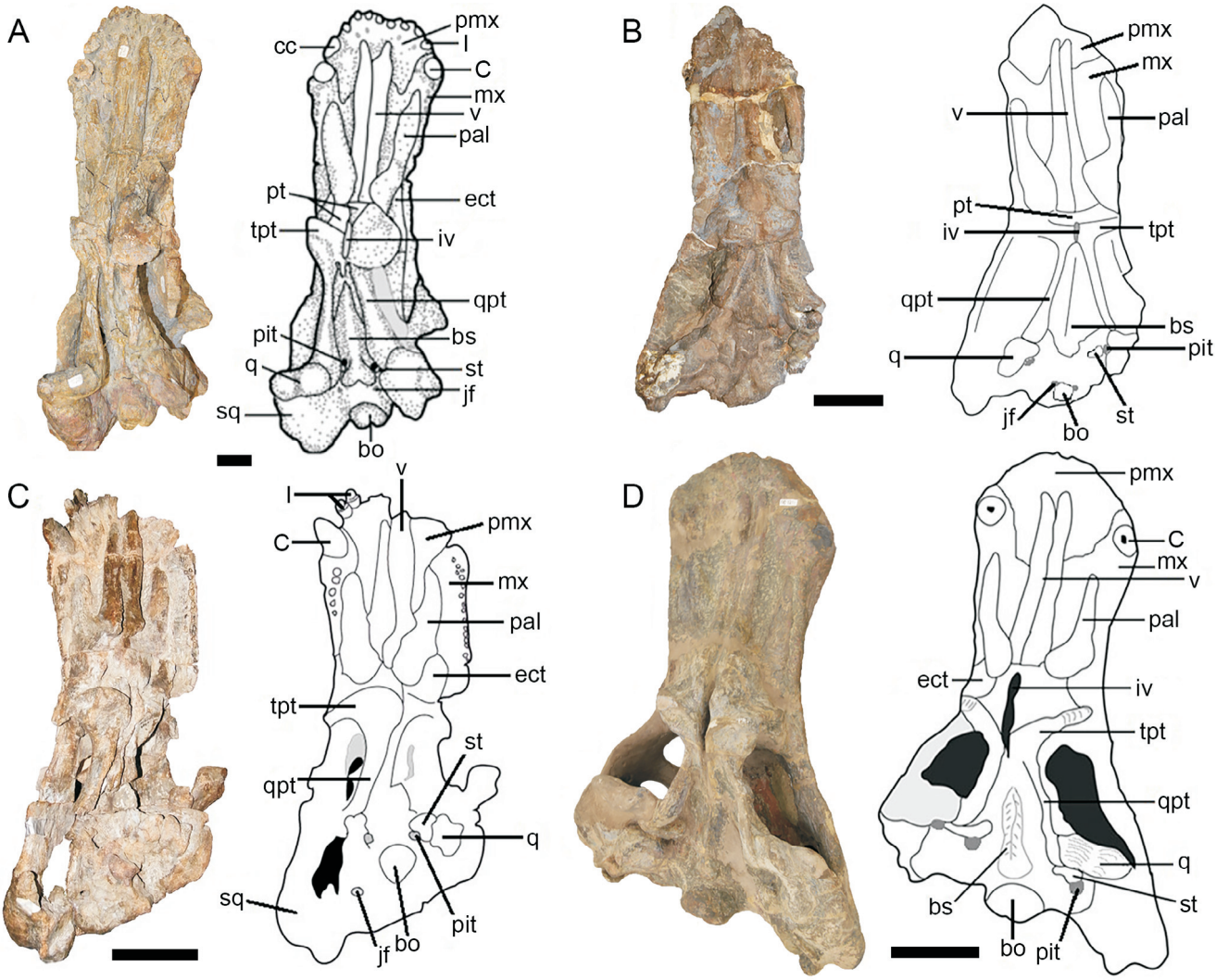


Figure 10. *Jonkeria* skulls in ventral view with interpretive drawings. **A**, SAM-PK-11884; **B**, TM 212; **C**, SAM-PK-4343; **D**, FMNH UC 1511. *Abbreviations*: bs, basisphenoid; bo, basioccipital; C, upper canine; cc, cross-section through lower canine; ect, ectopterygoid; I, upper incisor; iv, interpterygoid vacuity; jf, jugular foramen; mx, maxilla; pal, palatine; pit, opening of the pituitary fossa; pmx, premaxilla; pt, pterygoid; q, quadrate; qpt, quadrate ramus of pterygoid; sq, squamosal; st, stapes; tpt, transverse process of pterygoid; v, vomer. Scale bars represent 10 cm.

the posterodorsal margin of the temporal fenestra (Figs 6A, 7A,B). Laterally, the tabular has extensive contact with the squamosal, dorsomedially with the postparietal where the suture is on a ridge, and ventrally meets the supraoccipital and paraoccipital process of the opisthotic (Fig. 12A).

Supraoccipital

This relatively large, transversely positioned, unpaired bone occupies most of the central part of the occiput. Dorsally it is in sutural contact with the postparietal, laterally with the tabulars, and ventrally it forms the dorsal border of the foramen magnum and is in contact with the exoccipital and the paroccipital process of the opisthotic (Fig. 12A).

Basioccipital

This bone is part of a tripartite structure that forms a large occipital condyle (Fig. 12), and in ventral view, it contacts the parabasisphenoid anteriorly. The occipital condyle is well preserved in most specimens and protrudes relatively far posteriorly.

Opisthotic

This bone makes up a large part of the occiput in the form of the robust paraoccipital process, which is preserved in FMNH UC 1511, SAM-PK-4343, and SAM-PK-11884 (Fig. 12A,B,C). In occipital view, the paroccipital process is medially narrow where it borders the ventral side of the jugular foramen and expands laterally where it has a sutural contact with the squamosal and ventrally with the dorsal process of the quadrate. Dorsally, the opisthotic is in contact with the supraoccipital and the tabular. Ventromedially, the opisthotic meets the basioccipital.

Exoccipital

The paired exoccipitals (Fig. 12) are small, sub-triangular bones positioned lateroventrally relative to the foramen magnum, and ventromedially to the basioccipital. Exoccipitals overlie the paroccipital process of the opisthotic and abut against the basioccipital.

Parabasisphenoid

This is a relatively small, triangular bone, at least as exposed ventrally, which forms a pointed contact anteriorly with the posteromedial portion of the pterygoid and

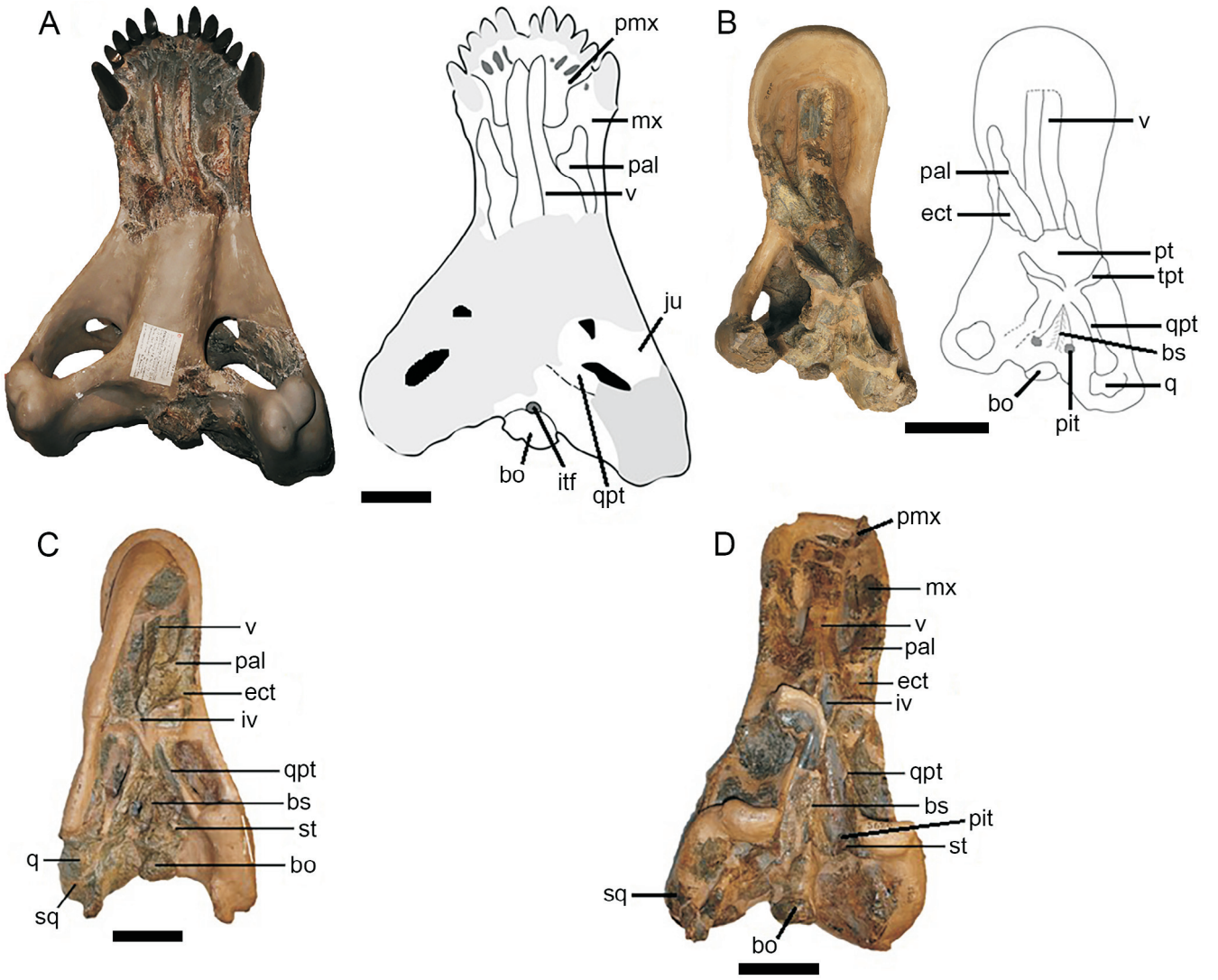


Figure 11. *Jonkeria* skulls in ventral view with interpretive drawings. **A**, MB.R.983; **B**, AMNH FARB 5634; **C**, AMNH FARB 5608; **D**, AMNH FARB 5620. *Abbreviations*: bs, basisphenoid; bo, basioccipital; ect, ectopterygoid; itf, intertuberal fossa; iv, interpterygoid vacuity; mx, maxilla; pal, palatine; pit, opening of the pituitary fossa; pmx, premaxilla; pt, pterygoid; q, quadrate; qpt, quadrate ramus of pterygoid; sq, squamosal; st, stapes; tpt, transverse process of pterygoid; v, vomer. Scale bars represent 10 cm.

widens posteriorly where it meets the basioccipital. The parabasisphenoid has a low midline ridge, which bifurcates posteriorly (Fig. 10A). Laterally, towards its posterior end, the parabasisphenoid has two notches, the anterior one is the lateral opening leading into the pituitary fossa and the posterior one is the large fenestra ovalis. Posteriorly, the parabasisphenoid and basioccipital are indistinguishably fused.

Stapes

In AMNH FARB 5620, SAM-PK-11884, and FMNH UC 1511, the stapedes are preserved *in situ*, whereas in SAM-PK-4343, the left stapes is oriented anteroposteriorly instead of mediolaterally (Fig. 10C). The stapes is a rod-like structure with expanded ends. It extends medially from the medial face of the quadrate, immediately posterior to the quadrate ramus of the pterygoid, to the fenestra ovalis. The rounded proximal end of the stapes is positioned in the fenestra ovalis with the slender posterodorsal projection lacking a stapedial foramen. The distal end articulates with the medial condyle of the quadrate.

Lower jaw

The lower jaw of *Jonkeria* comprises the dentary, coronoid, splenial, angular, surangular, prearticular, and articular bones (Figs 13, 14). Seven skulls (AMNH FARB 5608, FMNH UC 1511, MB.R.983, ROZ.B96, SAM-PK-11884, SAM-PK-12030, and TM 212) have an associated lower jaw preserved. The lower jaw of FMNH UC 1511 is well preserved, but is mostly covered in matrix. Partial lower jaws are preserved in AMNH FARB 5577 and AMNH FARB 5633, but they have no accompanying cranial material.

Dentary

The dentary (Figs 13, 14) forms more than half of the lateral surface of the jaw, but only about a third of the medial side. Anteriorly, the bone is fairly massive to support the four large incisors and canine, and in the symphysial region forms a large, posteriorly sloping mentum.

On the lateral surface, the dentary is in contact with the angular posteriorly and with the surangular posterodorsally by means of an inclined suture extending anteroventrally from the coronoid eminence (Fig. 13A). The

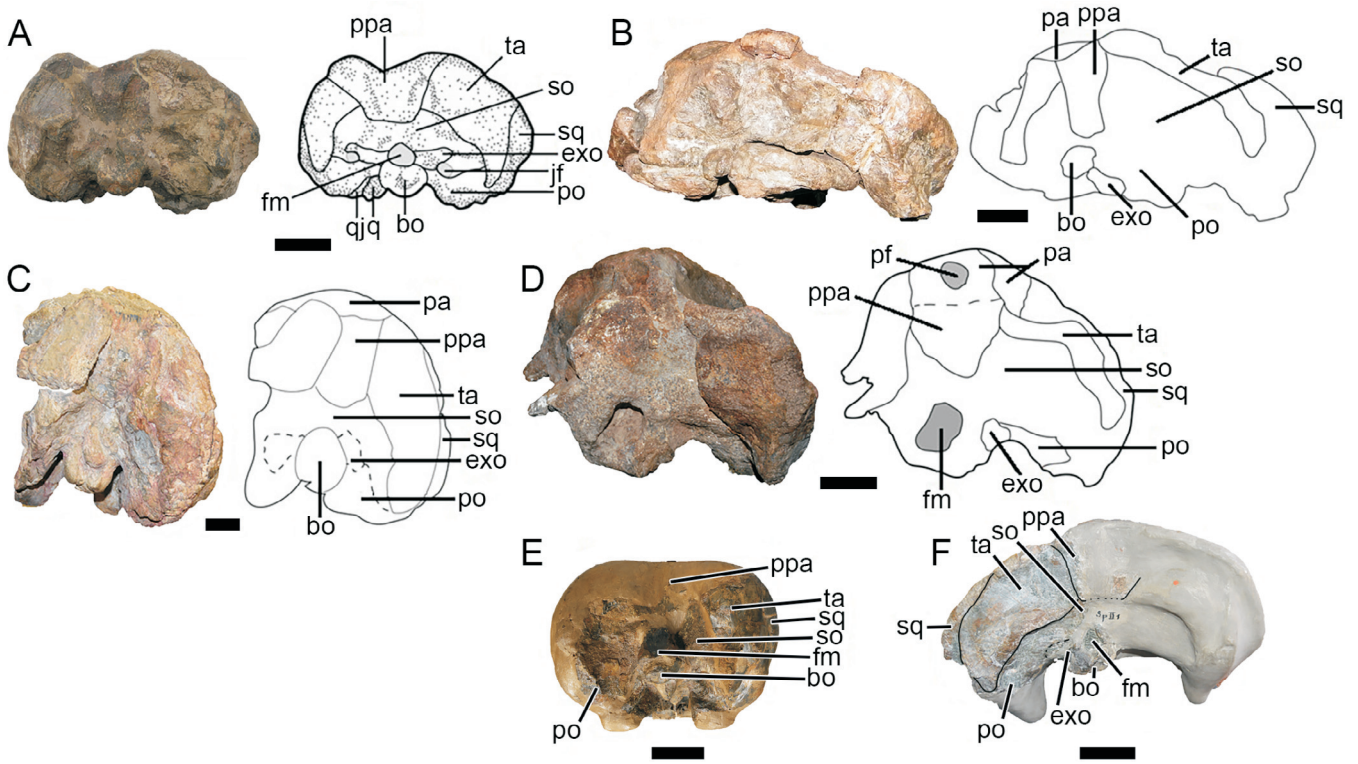


Figure 12. *Jonkeria* skulls in occipital view. **A**, FMNH UC 1511; **B**, SAM-PK- 4343; **C**, SAM-PK-11884; **D**, TM 212; **E**, AMNH FARB 5620; **F**, MB.R.983. *Abbreviations*: bo, basioccipital; exo, exoccipital; fm, foramen magnum; jf, jugular foramen; pa, parietal; pf, pineal foramen; po, paroccipital process of opisthotic; ppa, postparietal; q, quadrate; qj, quadratojugal; so, supraoccipital; sq, squamosal; ta, tabular. Scale bars represent 10 cm.

ventral margin of the dentary, behind the symphysial region, is mostly sub-horizontal. The posterior margin of the dentary curves posterodorsally at the contact with the angular and has a posterior-facing, inverted, sigmoid-shaped sutural contact with the angular. Posterolateral to the symphysis, the dentary has a slight convexity, which extends from the canine for about a third of the length of the mandible. A concavity extends from this point up to the coronoid eminence and the anterior portion of the reflected lamina of the angular. The ventral margin of the dentary is straight.

In medial view (Fig. 13B,D), the dentary is exposed over a shorter distance than in lateral view and makes up a little more than half of the length of the jaw. It tapers posterodorsally and in this region, it contacts the anterior portion of the surangular. Dorsomedially, the dentary is overlain by the coronoid (Grine 1997). Anteromedially, the dentary widens on either side of the symphysis to form a dorsal shelf and a ventral depression, which accommodates the symphyseal portion of the splenial. On the medial side, the dentary has a long, horizontal, ventral sutural contact with the splenial and is overlain by the prearticular posteromedially.

Surangular

The surangular is a relatively large bone forming the posterodorsal part of the mandible in lateral view (Fig. 13A,C) and contacting the dentary, coronoid, prearticular, and angular (Fig. 13B,D). In lateral view, the surangular forms a laterally projecting ridge on the dorsolateral face of the mandible that separates it from the angular. In medial view, the surangular forms the posterior end of the lower jaw from the coronoid eminence to the posterior end of the jaw positioned dorsally to the prearticular. Here, it is in contact with the posterior portion of the prearticular anteroventrally and meets the articular posteroventrally (Fig. 14). On the medial side, the anterodorsal surface of the surangular forms a slight trough, which accommodates the posterior end of the coronoid.

Prearticular

The prearticular, which extends more than half the length of the mandible, is exposed only on the medial side of the jaw and has an open inverted 'V' shape (Figs 13B, 14). It is triangular and higher in the middle region and ventrally directed in both the anterior and posterior directions. It contacts the dentary anterodorsally, the splenial anteroventrally, the angular posteroventrally, the surangular posterodorsally, and the coronoid dorsally.

Articular

The articular is positioned on the posteromedial side of the surangular and angular bones and contacts the prearticular anteriorly. The articular is mediolaterally robust. The dorsally positioned articulation surface comprises a small, anteriorly positioned elliptical cavity with the long axis oriented dorsoventrally, and a larger, posteriorly positioned outer cavity with its long axis oriented mediolaterally, which extends dorsally (Figs 13B, 14).

Angular

The angular bone (Figs 13, 14) forms most of the posterior external portion of the lower jaw. The anterior thinner end of the angular is wedged between the splenial and

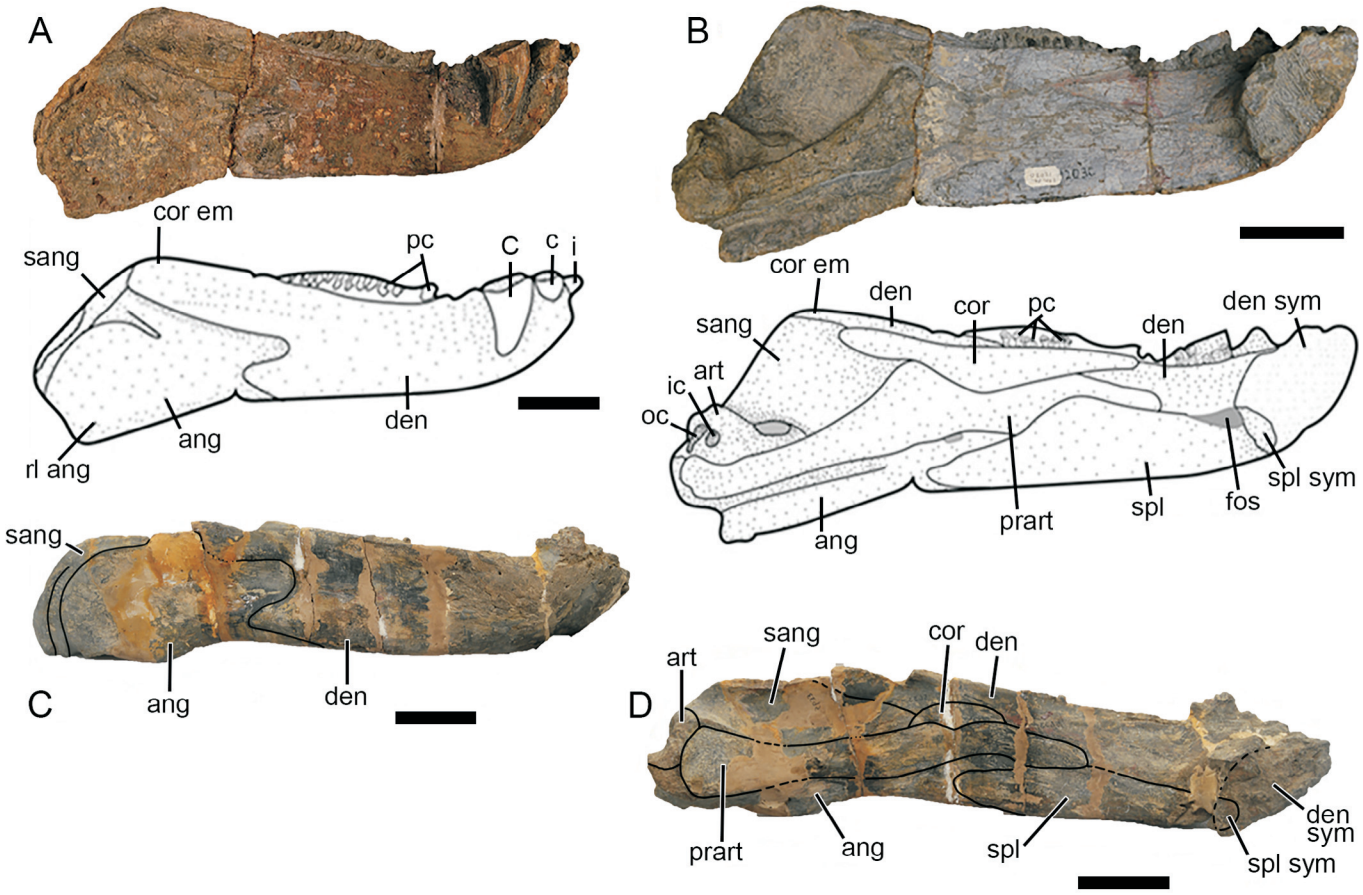


Figure 13. *Jonkeria* mandibles. SAM-PK-12030 in(**A**) left lateral view (mirrored for comparative purposes) and SAM-PK-12030 in (**B**) right medial view. AMNH FARB 5633 in (**C**) right lateral view and (**D**) left medial view (mirrored for comparative purposes). *Abbreviations*: ang, angular; art, articular; C, upper canine; c, lower canine; cor, coronoid bone; cor em, coronoid eminence of dentary; den, dentary; den sym, dentary symphysis; fos, Meckelian fossa; i, lower incisor; ic, inner cavity of articular; oc, outer cavity of articular; pc, lower postcanine; prart; prearticular; rl ang, reflected lamina of angular; sang, surangular; spl, splenial; spl sym, splenial symphysis. Scale bars represent 10 cm.

the dentary. In lateral view, the angular becomes taller towards the back. Laterally, a prominent reflected lamina is present below the coronoid eminence, which extends to the ventral margin of the lower jaw. The reflected lamina has a flat lateral surface with no ridges (Fig. 13A). There is a groove that runs from the posterior end of the angular in a dorsoventral direction, then downturns into the angular just below the coronoid eminence. On the medial side, exposure of the angular is relatively small and is largely obscured by the prearticular (Fig. 13B).

Splenial

This bone is exposed only on the medial side of the jaw and attains its greatest height halfway along its length, where it contacts the prearticular posterodorsally and the angular posteroventrally (Fig. 13B). The splenial is an exceptionally long splint of bone, forming the lower half of the medial surface of the jaw and a small part of the mandibular. A fossa on the dorsomedial surface of the splenial, close to the symphysis, was possibly for insertion of the anterior end of the genioglossus muscle (Smith 1992).

Coronoid

The coronoid is a long bone positioned posterodorsally on the medial side of the dentary. It extends from the first third of the postcanine series to halfway along the coronoid eminence (Fig. 13B). In SAM-PK-12030, the coronoid is positioned at the base of the postcanine tooth series, while in SAM-PK-11884, the position of this bone differs between the right and left sides of the jaw (Fig. 14). According to Grine (1997), the position of the right coronoid bone on SAM-PK-11884, along the superior aspect of the dentary adjacent to the tooth row, is the correct anatomical position, indicating the other side is distorted. In TM 212 and NHMUK PV OR 49730, the coronoid is not visible, as this part of the mandible is weathered, and in AMNH FARB 5633, the dorsal extent of the coronoid is not clear.

Dentition

Like most therapsids, *Jonkeria* is characterized by a heterodont dentition comprising incisors, canines, and postcanines. It is characterized by a dental formula of i5/4, c1/1, pc19–21/18–21 (Boonstra 1962). The dentition is poorly preserved in most specimens of *Jonkeria*, but within the available sample intact crowns of each of the three major tooth types are represented.

Incisors

Incisor morphology. SAM-PK-4343 has two complete upper incisors preserved, whereas only cross-sections through the roots remain in SAM-PK-11884 and SAM-PK-12030 (Figs 15, 16D). ROZ.B96 has well-preserved incisors in the

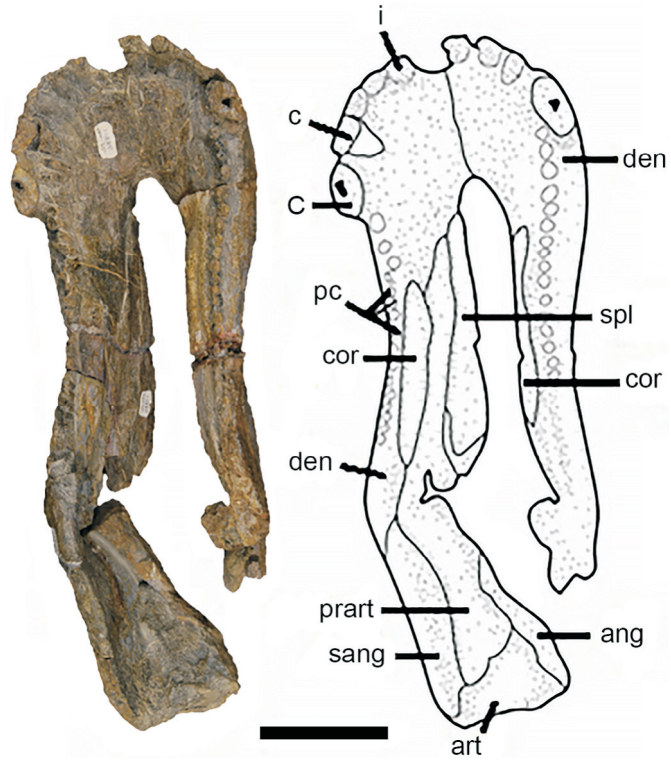


Figure 14. *Jonkeria* mandible SAM-PK-11884 in dorsal view. *Abbreviations*: ang, angular; art, articular; C, upper canine; c, lower canine; cor, coronoid bone; den, dentary; i, lower incisor; pc, low postcanine; prart; prearticular; sang, surangular; spl, splenial. Scale bar represents 10 cm.

dentary (Fig. 16A). These teeth have a convex labial face and a more flattened lingual face, with a prominent heel on the lingual side at the junction of the crown and root (Boonstra 1962). In SAM-PK-4343, the well-preserved crowns of I4 and I5 are directed far anteriorly, whereas the other three are broken off at the alveolar border (Fig. 15). The inner face of the talon in I4 runs obliquely from the heel to the tip, without the usual distinctive face on the heel itself. The sloping inner face in I5 is also evident, but in this tooth, it is bipartite — the outer and greater part is for the reception of the lower canine. The morphology of these crowns seems to be similar and the cross-sections though the maxillary incisors of ROZ.B96 and SAM-PK-12030 (Fig. 16C,D) show that I1 is smaller than the rest of the incisors and I2–I5 are almost of the same size. The upper incisor heel forms an oblique ledge where the inner (lingual) side of the incisor heel is lower than the outer (labial side) and the opposite is true for the lower incisors. The dentary incisors of ROZ.B96 seem to be of the same size from I1–I4 (Fig. 16A). In unworn teeth, the lingual portion of the heel forms a sharp ridge with coarse serrations, as is the case for the well-preserved dentary incisor teeth in ROZ.B96. In worn teeth, the edge loses the serrations and the sharp edge becomes rounded. The crown of the first incisor is wider than long and this width increases towards the fourth.

Incisor replacement

In the premaxilla of ROZ.B96, SAM-PK-4343, and SAM-PK-12030, a cavity develops in the bone lingual to the alveolus housing the functional incisor (Figs 15, 16A,C,D), in which the replacing incisor develops. The talon of the emerging replacement tooth is flattened anteroposteriorly and is roughly triangular in outline (Fig. 16A,C).

ROZ.B96 (Fig. 16C) and SAM-PK-12030 (Fig. 16D) show cross-sections through five upper incisors. The locus of replacement incisor $I2^1$ is still an empty pit, whereas the remaining incisor loci show crowns in replacement pits. The emerging cusps of replacing teeth can be seen, each lying lingual to a functional tooth. The replacement order for upper incisors in both specimens (Fig. 16C,D) seems to be 1, 4, 3, 5, 2, in agreement with Boonstra (1962).

Canines

Canine morphology. The upper canine is preserved intact in SAM-PK-4343, SAM-PK-11884, SAM-PK-12030, and ROZ.B96 and the lower canine is intact in ROZ.B96. In SAM-PK-4343, the right upper canine has its crown very well preserved. This is greatly recurved and directed outwards (Fig. 15), though this outward projection may be due in part to taphonomic alteration. The upper canine

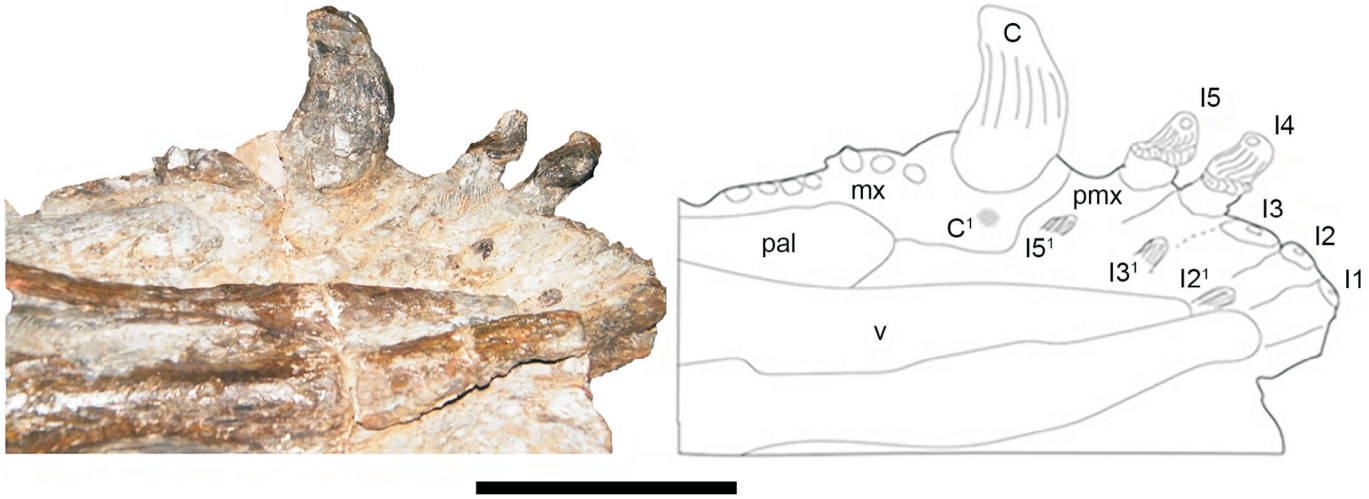


Figure 15. Close-up of the anterior snout of SAM-PK-4343 in semi-ventral view, showing the morphology of the canine, incisor crowns I4 and I5, and tooth replacement in the right maxilla and premaxilla. Developing replacement teeth designated with superscripts for the involved tooth positions (e.g. C^1). *Abbreviations*: C, upper canine; I, upper incisor; mx, maxilla; pal, palatine; v, vomer. Scale bar represents 10 cm.

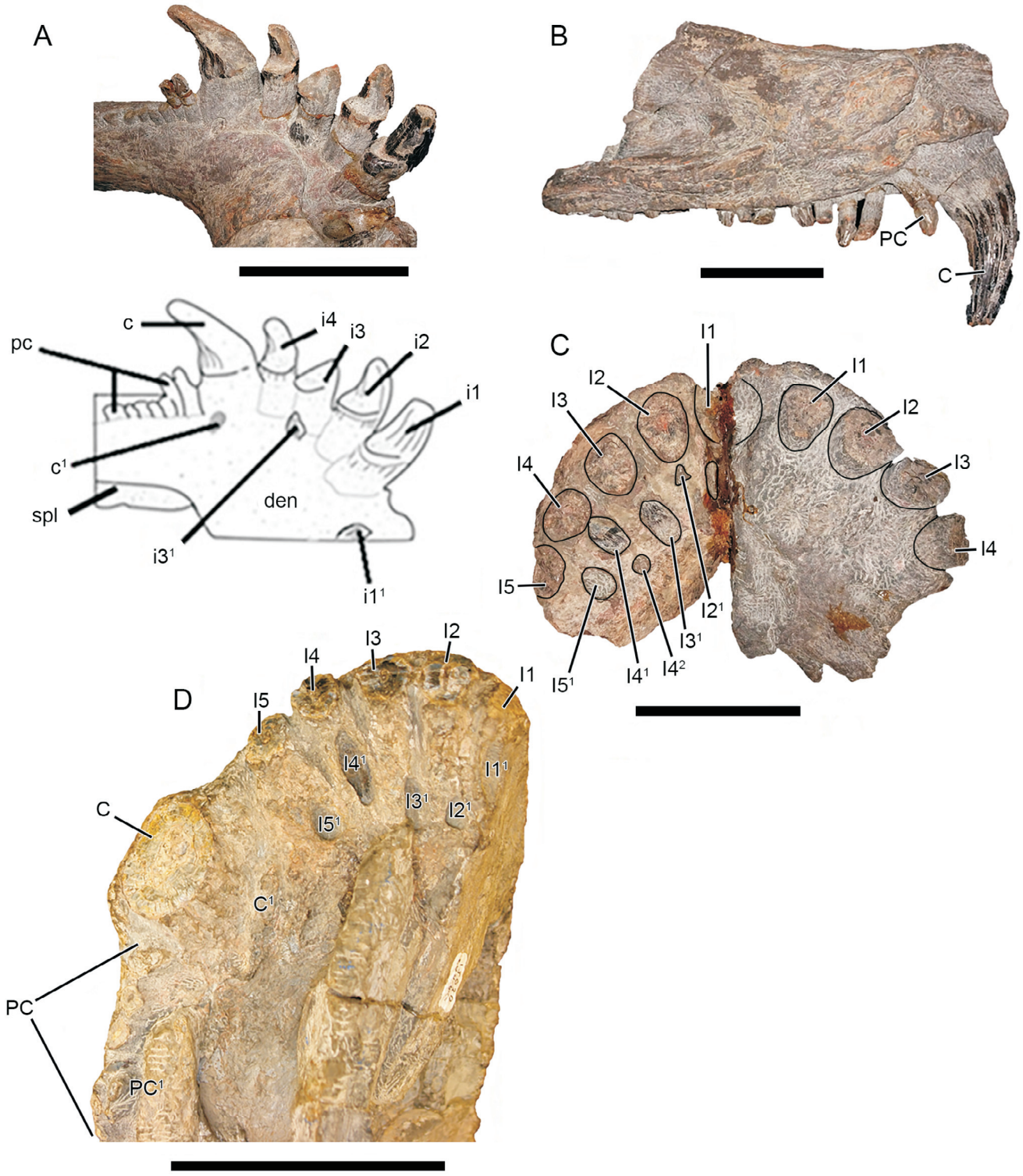


Figure 16. *Jonkeria* anterior dentition. ROZ.B96. **A**, Left mandible in mediodorsal view; **B**, left maxilla in medial view; **C**, premaxillae in ventral view; **D**, right anterior snout of SAM-PK-12030 in ventral view. Developing replacement teeth designated with superscripts for the involved tooth positions (e.g. C^1). *Abbreviations*: C, upper canine; c, lower canine; den, dentary I, upper incisor; i, lower incisor; PC, upper postcanine; pc, lower postcanine; spl, splenial. Scale bars represent 10 cm.

has a large, conical crown, which curves backwards and is slightly laterally flattened (Figs 15, 16B). The lower canine is smaller, less curved than the upper, and is more outwardly directed.

The upper canine has a long, robust root, which causes the maxilla to swell around it. In cross-section, the canine roots are longer anteroposteriorly than wide (Fig. 16D). A diastema (Figs 15, 16D, 17) is present between the upper canine and the last upper incisor to allow the lower canine to fit between these two teeth in occlusion, and the upper canine passes behind the lower canine to fit in a hollow in the outer face of the dentary (Fig. 17). In all specimens where the crown is preserved, the canine is rounded in cross-section.

In SAM-PK-11884, the upper canines are large, pointed, and curve backwards. The height of the crown is 90 mm and the basal diameters (anteroposterior length × labiolingual width) are 49 × 36 mm for the right and 45 ×



Figure 17. SAM-PK-12030, referred partial skull of *Jonkeria truculenta* in left lateral view, showing arrangement of the teeth in occlusion. The upper postcanines are situated at the edge of the maxilla and their crowns rest on the dorsal ledge on the dentary, with the lower postcanines situated lingual to them. The upper canine rests on a hollow in the outer face of the dentary. There is a diastema between the fifth upper incisor and the upper canine to accommodate the outward-pointing lower canine when in occlusion. *Abbreviations*: C, upper canine; c, lower canine; I, upper incisor. Scale bar represents 10 cm.

34 mm for the left. ROZ.B96 has both the lower and upper canine crowns preserved and the lower canine is smaller, shorter, and less pointed than the upper (Fig. 16A,B).

Canine replacement. In both the maxilla (SAM-PK-4343, SAM-PK-12030) and dentary (ROZ.B96) there is a small pit in the lingual wall just above the inner alveolar edge of the functional canine (Figs 15, 16A,D), indicating the development of the replacing canine.

Postcanines

Postcanine morphology. In specimen SAM-PK-11884, the upper postcanines are very poorly preserved, most have fallen out (possibly after death), and their alveoli are difficult to distinguish. However, on both sides the first postcanine is much larger than those further back. In the dentaries of this specimen, the postcanines are well preserved. On the right side, 18 postcanine teeth are preserved, while the left side has 19 teeth with the last two loci represented by empty alveoli.

In the left dentary of MB.R.983 (Fig. 18A), a good set of crowns has been exposed from the lingual side. The functional lower postcanines show, on their lingual faces, a moderately developed heel forming a cingulum at the junction of crown and root and above this, the inner face of the crown is concave. The spatulate crowns are roughly triangular in outline with the outer face moderately convex and the inner face slightly concave.

Unlike the incisors and canines, the postcanine teeth of the lower and upper jaws do not intermesh and the lower set lies lingual to the upper set. The upper postcanines are implanted closer to the lateral edge of the maxilla, while those of the lower jaw are closer to the medial edge, almost 20 mm away from the edge of the dentary. The resulting dentary ledge receives the maxillary teeth in occlusion. In both the upper and lower jaws, the crowns lie obliquely to the long axis (almost 40°), with the anterior edge directed inwards and the posterior edge directed outwards (Boonstra 1962) (Fig. 18A).

The first postcanine is the largest and their size decreases posteriorly. Each postcanine tooth is oval in section (Fig. 18B,C) and has a spatulate crown that is almost triangular in outline. Unworn postcanine teeth are flattened and serrated on both the mesial and distal margins as well as the anterior and posterior sides. The number of postcanines in fully-grown individuals is 19 uppers and varies from 18 to 21 for the lowers (smaller skulls with 18 and the largest skulls with 21).

Because of the paucity of preservation, it is not possible to fully describe tooth replacement of the postcanines, but there is evidence of replacement pits lingual to some postcanine teeth on the left maxillae of SAM-PK-4343 and SAM-PK-12030 (Fig. 18B,C).

DISCUSSION

As is evident from the description of the holotype of *Titanosuchus ferox* presented above, the cranial material of this species is very incomplete, comprising only maxillary and mandibular fragments. Because these fragments are undiagnostic to genus, it is not possible to determine the cranial morphology of *Titanosuchus* and to differentiate it from *Jonkeria* on the basis of craniodental characters, as was previously noted by Boonstra (1969).

Jonkeria has been considered to include five species in the most recent treatments of titanosuchid taxonomy using cranial characters (e.g. King 1988). The current study, however, recognizes *Jonkeria truculenta* as the only valid species.

The skull roofing bones (prefrontal, frontal, postfrontal, parietal, and squamosal) are well preserved in the specimens TM 212 (holotype of *J. truculenta*), MB.R.983, AMNH

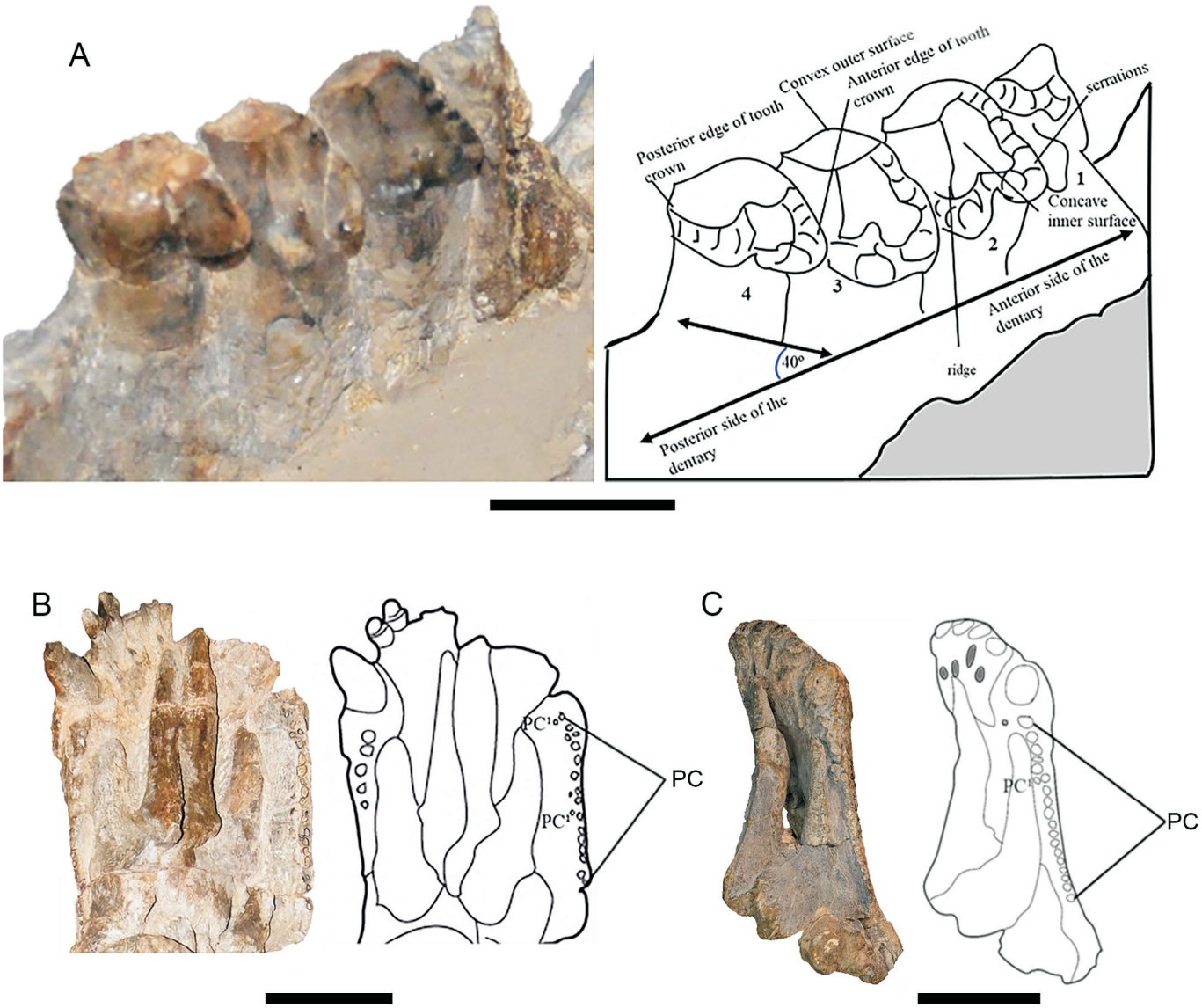


Figure 18. *Jonkeria* postcanine dentition. **A**, Close-up of the dentary in specimen MB. R. 983 in posteromedial view, showing the anterior four postcanine tooth crowns; **B**, snout of SAM-PK-4343 in ventral view, showing replacement teeth (PC^1) for the first and 13th postcanines; **C**, left side of the snout of specimen SAM-PK-12030 in ventral view, showing the row of postcanine teeth with tooth size decreasing in an anterior–posterior direction. Lingual to the 6th postcanine is a pit for a replacement tooth (PC^1). *Abbreviation*: PC, upper postcanine. Scale bar for **A** represents 1 cm and for **B** and **C** represents 10 cm.

FARB 5620, SAM-PK-4343, and SAM-PK-11884, and have the same morphology in all specimens. The prefrontal, frontal, and postfrontal are slightly pachyostosed and the parietal is the most pachyostosed cranial bone (less pachyostosed in TM 212 and more pachyostosed in the rest of the specimens). There is a gentle transition from the skull roof to the snout on the top of the skull, giving all the skulls an almost horizontal dorsal profile. All the skulls have a narrow interorbital region, which ranges in width from 100 mm for the smallest specimen (TM 212) to 125 mm for the largest specimen (FMNH UC 1511). Some cranial characters previously judged as being of taxonomic relevance, such as dorsal profile of the skull and divergence of the quadrate rami of pterygoids, vary between skulls largely because of deformation.

Ontogenetic variation in *Jonkeria*

As mentioned above, the bivariate allometric analyses did not yield statistically significant results . Accordingly, we here compare measurements between larger and smaller specimens to provide some clues about the growth model of *Jonkeria truculenta*. Considering cranial length, the holotype of *J. truculenta* (525 mm) is interpreted as a juvenile, whereas SAM-PK-4343 and AMNH FARB 5608 are intermediate, with estimated skull lengths of 590 and 610 mm, respectively. This is a skull length difference of 11 to 14% between the juvenile and intermediate size. SAM-PK-11884, MB.R.983, AMNH FARB 5620, and FMNH UC 1511, with skull lengths ranging from 640 mm to 680 mm, are the largest and are interpreted as fully adult (Fig. 19). There is a 23% skull length difference between the smallest and largest specimens of the series.

The ratio of length of the snout relative to the total skull length is 63% for the juvenile and 57% for the largest skull. In comparison, variation in this ratio for individuals of the adult sample is greater (from 61% to 71%). There is thus no discernible difference in the length of the snout during



Figure 19. Ontogenetic variation within *Jonkeria truculenta* skulls. The arrow indicates size increase of the different skulls. As this species grows larger, it acquires a relatively wider snout and more cranial pachyostosis around the prefrontal, frontal, postorbital, and parietal bones. Total skull length of each skull is provided. Scale bar represents 10 cm.

ontogeny. There is a slight difference in the width of the snout at the level of the canine, which is proportionally wider in adults (33% in the juvenile to 40% for the adult). This variation in the width of the snout seems to be related to an increase in the size of canines as the snout expands to accommodate the enlarged canine roots.

Juvenile TM 212 has proportionally larger orbits relative to the size of the temporal fenestra (77% of the fenestra length) in comparison with the other skulls (68% in the largest) in which the temporal opening is proportionally longer. The combination of a proportionally large orbit and small temporal opening is generally considered a feature of juvenile therapsids (e.g. Ivakhnenko 1999, 2008; Abdala & Giannini 2000; Abdala *et al*. 2001; Giannini *et al*. 2010; Jasinoski & Chinsamy-Turan 2012; Kruger *et al*. 2015, 2017). The temporal fenestra also enlarges diagonally (anterodorsal–posteroventral direction) in adults. Associated with this is the height of the lower jaw at the level of the coronoid process relative to the skull length. This ratio is 8 % in the juvenile and 27% for the largest adult. Both the increase of the temporal fenestra size and the height of the coronoid process are linked to an increase in the volume of the adductor musculature in adults.

In the smallest specimen (TM 212) the anteroventral slant of the occiput is only slight and the angle of inclination increases in larger skulls, with the occiput of the largest specimen (FMNH UC 1511) having the greatest angle of inclination. This anteroventral inclination of the occiput means that the jaw joint of the smallest specimen (TM 212) is located below the temporal fenestra, while that of larger adults is positioned further forward, almost below the postorbital bar (Fig. 19).

In the neurocranial region of the skull, intertemporal width at the level of the pineal foramen relative to skull length is proportionally larger in the juvenile (29%) than in the largest specimen (15%). This suggests that the juveniles had proportionally wider skulls and brains in comparison with adults.

Other important cranial modifications related to growth are the thickening (pachyostosis) of the prefrontal, postfrontal, and parietal and the postorbital bar. Similar changes in the skull roofing bones have been noted in the ontogeny of the predatory dinocephalian *Anteosaurus* (Kruger *et al*. 2017). A low degree of development of cranial ornamentation and pachyostosis has been linked to an early ontogenetic stage in various groups of therapsids (Estes 1961; van Heerden 1972; Ivakhnenko 2008; Kammerer 2011; Liu 2013; Cassini *et al*. 2015; Kruger *et al*. 2017; Kulik & Sidor 2019). Ivakhnenko (2008) and Kruger *et al*. (2017) showed that in the anteosaurid dinocephalians *Titanophoneus potens* and *Anteosaurus magnificus*, the fronto-nasal ridge, supraorbital bosses, and pachyostosis developed between the juvenile and the adult conditions. The formation of cranial bosses in the anteosaurian genus *Sinophoneus yumenensis* was also noted as a postnatal development (Liu 2013) and a similar ontogenetic change has been observed for the bosses of *Estemmenosuchus uralensis* (Ivakhnenko 2008). In tapinocephalids, the extent of cranial pachyostosis increases while the relative size of the orbit and temporal fenestra shrinks during ontogenetic growth (Gregory & Broom 1926; Broom 1936; Boos *et al*. 2015; Neumann 2020). In burnetiamorphs, a low degree of pachyostosis has also been linked to juvenility, with greater pachyostosis occurring in more mature

individuals (Duhamel *et al*. 2021). However, the degree of pachyostosis and cranial boss development also seems to have a phylogenetic component in biarmosuchians, with basal forms displaying a lower degree of cranial pachyostosis and smaller cranial bosses than derived burnetiamorphs (Sidor & Rubidge 2006; Day *et al*. 2018). Sexual dimorphism may also result in differences in pachyostotic development, in which males are interpreted as having stronger pachyostotic skulls for intraspecific combat (Barghusen, 1975; Lande 1980; Kraaijeveld *et al*. 2007; Benoit *et al*. 2016; Gates *et al*. 2016), but this has yet to be demonstrated in titanosuchid dinocephalians, and would require a larger sample of well-preserved specimens than is currently available.

CONCLUSIONS

The results of this study do not permit distinction of *Titanosuchus* from *Jonkeria* solely on cranial characters, largely because the preserved cranial remains of *Titanosuchus* are too poorly preserved for comparison. However, there are differences in the postcranium supporting the separation of these genera, as will be detailed in a future paper.

The cranial description and the growth model inferred in this study indicates that all cranial specimens of *Jonkeria* can be included within the type species *J. truculenta*. The morphology of the cranial bones is similar in all the *Jonkeria* specimens, and the characters previously used to differentiate between species have been shown to be manifestations of taphonomic deformation or, in some cases, ontogenetic variation. The potential of sexual dimorphism in these large-bodied herbivores must also be considered, although clear evidence of dimorphism is wanting in the available sample. It is thus concluded that *Jonkeria* comprises a single species, *Jonkeria truculenta* van Hoepen, 1916, and that the species *J. ingens*, *J. vanderbyli*, *J. haughtoni*, and *J. boonstrai*, considered valid by Boonstra (1969) and King (1988), are junior synonyms of it.

Considering the growth model, the smallest specimen, TM 212, is interpreted as an earlier ontogenetic stage of *Jonkeria truculenta*, representing 77% of the skull length of the largest specimen. This inferred juvenile has larger orbits relative to the size of the temporal fenestra, a lesser angle of the frontal, and a more posterior position of the jaw joint. Larger, presumed more mature, *J. truculenta* specimens show a higher degree of cranial pachyostosis.

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Author contributions. S. Jirah examined the specimens wrote the text and did the illustrations. B.S. Rubidge and F. Abdala supervised the research and enhanced the manuscript.

ABBREVIATIONS

Institutional

AMNH: American Museum of Natural History, New York, U.S.A.
BP (ESI): Evolutionary Studies Institute (formerly Bernard Price Institute for Palaeontological Research), University of the Witwatersrand, Johannesburg, South Africa
FMNH: Field Museum of Natural History, Chicago, U.S.A.
MB (MfN): Museum für Naturkunde, Berlin, Germany
NHMUK: Natural History Museum, London, U.K.
ROZ: Roy Oosthuizen collection, Prince Albert Museum (specimens currently curated at the Iziko South African Museum).
SAM: Iziko South African Museum, Cape Town, South Africa
TM (DMNH): Ditsong National Museum of Natural History (formerly Transvaal Museum), Pretoria, South Africa

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Appendix A. Fossils examined for this study. Holotypes of species considered valid by King (1988) are marked in bold.

Specimens	Material	Locality	Previous ID, as per King (1988)	Current ID
TM 212	Skull, right mandible, right tibia	Abrahamskraal, Prince Albert, South Africa	***Jonkeria truculenta***	***Jonkeria truculenta***
AMNH FARB 5620	Skull without lower jaw	Jan Willemsfontein, Prince Albert, South Africa	***Jonkeria vanderbyli***	***Jonkeria truculenta***
FMNH UC 1511	Skull, lower jaw, and fragmentary postcranial elements	Stinkfontein 7, Beaufort West, South Africa	*Jonkeria* sp. (FMNH database; not listed by King)	*Jonkeria truculenta*
MB.R.983	Imperfect skull and partial lower jaw	Springfontein, Beaufort West, South Africa	***Jonkeria boonstrai***	***Jonkeria truculenta***
SAM-PK-12030	Incomplete skull with right mandibular ramus	Bosluiskraal, Dikbome 53, Laingsburg, South Africa	*Jonkeria truculenta*	*Jonkeria truculenta*
SAM-PK-11884	Skull and lower jaw	Skroefpaal, Prince Albert, South Africa	*Jonkeria vanderbyli*	*Jonkeria truculenta*
SAM-PK-4343	Skull without lower jaw, humeri, ulna, femur, fibula	Welgemoed, Leeu-Gamka, Prince Albert, South Africa	***Jonkeria haughtoni***	***Jonkeria truculenta***
AMNH FARB 5608	Imperfect skull	Kookfontein, Prince Albert, South Africa	*Jonkeria ingens*	*Jonkeria truculenta*
AMNH FARB 5634	Imperfect skull	Kookfontein, Prince Albert, South Africa	***Jonkeria ingens***	***Jonkeria truculenta***
AMNH FARB 5633	Right mandibular ramus	Abrahamskraal, Prince Albert, South Africa	*Jonkeria truculenta*	*Jonkeria truculenta*
ROZ.B96	Imperfect skull and lower jaw	Zwartskraal, Prince Albert, South Africa	*Jonkeria haughtoni* (Roy Oosthuizen catalogue; not listed by King)	*Jonkeria truculenta*
NHMUK 49367a,b,c: NHMUK 4986–70	Fragmentary jaw and some 'associated post-crania'	Klein Koedoeskop 310, Beaufort West, South Africa	***Titanosuchus ferox***	***Titanosuchus ferox***
BP/1/7380	Cranial fragments, humerus, distal femur	Puntkraal, Sutherland, South Africa	*Titanosuchus ferox* (ESI catalogue; not listed by King)	*Titanosuchus ferox*
SAM-PK-9004	Pelvis lacking ischia, distal two-thirds of ulna	Klein Koedoeskop, Beaufort West, South Africa	***Jonkeria koupensis***	**Titanosuchidae *incertae sedis***
SAM-PK-3433	Humerus	Jan Willemsfontein, Prince Albert, South Africa	*Jonkeria ingens*	*Jonkeria truculenta*
SAM-PK-5014	Deformed left humerus, deformed left ulna, left radius, left femur, left tibia and left fibula	Abrahamskraal, Prince Albert, South Africa	***Jonkeria rossouwi***	***Jonkeria truculenta***
SAM-PK-9002	Ulna	Klein Koedoeskop,Beaufort West, South Africa	*Jonkeria haughtoni*	*Jonkeria truculenta*
SAM-PK-9006	Proximal humerus	Klein Koedoeskop, Beaufort West, South Africa	*Jonkeria ingens*	*Jonkeria truculenta*
SAM-PK-9145	Radius	Zeekoeivlei, Beaufort West, South Africa	*Jonkeria haughtoni*	*Jonkeria truculenta*
SAM-PK-9147	Ulna	Zeekoeivlei, Beaufort West, South Africa	*Jonkeria haughtoni*	*Jonkeria trucuclenta*
SAM-PK-9149	Right humerus	Saairivier, Prince Albert, South Africa	***Jonkeria parvus***	***Jonkeria truculenta***
SAM-PK-9348	Incomplete and distorted humerus	Mierfontein 318, Beaufort West, South Africa	*Jonkeria ingens*	*Jonkeria truculenta*
SAM-PK-11463	Ulna	Koedoeskop, Beaufort West, South Africa	*Jonkeria haughtoni*	*Jonkeria truculenta*
SAM-PK-11994	Humerus with good distal end	Welgemoed, Prince Albert, South Africa	*Jonkeria ingens*	*Jonkeria truculenta*
SAM-PK-12005	Humerus	Wolwefontein, Prince Albert, South Africa	*Jonkeria parva*	*Jonkeria truculenta*
SAM-PK-738	Humerus	Jan Willemsfontein, Prince Albert, South Africa	*Titanosuchus ferox*	*Titanosuchus ferox*
SAM-PK-739	Femur	Beaufort West district, South Africa	*Titanosuchus ferox*	*Titanosuchus ferox*
SAM-PK-772	Humerus	Seekoegat, Prince Albert, South Africa	*Titanosuchus ferox*	*Titanosuchus ferox*
SAM-PK-773	Humerus	Seekoegat, Prince Albert, South Africa	*Titanosuchus ferox*	*Titanosuchus ferox*
SAM-PK-5001	Humerus, femur	Sewefontein, Prince Albert, South Africa	*Titanosuchus ferox*	*Titanosuchus ferox*
SAM-PK-9127	Lower jaw fragment, femur and fibula	Voëlfontein, Prince Albert, South Africa	*Titanosuchus ferox*	*Titanosuchus ferox*
SAM-PK-9163	Ulna, fibula	Wakkerstroom, Prince Albert, South Africa	*Titanosuchus ferox*	*Titanosuchus ferox*
SAM-PK-11299	Radius, tibia	Boesmansrivier, Beaufort West, South Africa	*Titanosuchus ferox*	*Titanosuchus ferox*
SAM-PK-11881	Humerus	Blaauwkranz, Prince Albert, South Africa	*Titanosuchus ferox*	*Titanosuchus ferox*
SAM-PK-11488	Fibula, tibia	Mynhardtskraal, Beaufort West, South Africa	*Titanosuchus ferox*	*Titanosuchus ferox*

Continued on p. 27

Appendix A (continued)

Specimens	Material	Locality	Previous ID, as per King (1988)	Current ID
SAM-PK-11938	Tibia	Steenboksfontein, Laingsburg, South Africa	*Titanosuchus ferox*	*Titanosuchus ferox*
SAM-PK-11491	Femur	Mynhardtskraal, Beaufort West, South Africa	*Titanosuchus ferox*	*Titanosuchus ferox*
SAM-PK-11578	Humerus	Aasvoëlbos, Beaufort West, South Africa	*Titanosuchus ferox*	*Titanosuchus ferox*
SAM-PK-11881	Humerus	Blaauwkranz, Prince Albert, South Africa	*Titanosuchus ferox*	*Titanosuchus ferox*
SAM-PK-11989	Fibula	Koedoeskop, Beaufort West, South Africa	*Titanosuchus ferox*	*Titanosuchus ferox*
BP/1/7168	Imperfect skull and postcranial fragments	Puntkraal portion of Uitvlug 90, Sutherland, South Africa	Titanosuchid indet. (ESI catalogue)	Titanosuchidae *incertae sedis*