Can social and sexual selection explain the bizarre snout of proterosuchid archosauriforms?

Martín D. Ezcurra

Published online: 22 Mar 2016.

Submit your article to this journal ⤤

View related articles ⤤

View Crossmark data ⤤

Taylor & Francis
Taylor & Francis Group

Can social and sexual selection explain the bizarre snout of proterosuchid archosauriforms?

Martín D. Ezcurra[a,b]

[a]Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Sección Paleontología de Vertebrados, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina; [b]School of Geography, Earth and Environmental Sciences, University of Birmingham, Birmingham, UK

ABSTRACT

Proterosuchids are a clade of quadrupedal, carnivorous Permo-Triassic diapsids crucial to understand the successful evolutionary radiation of archosaurs during the Mesozoic. The importance and good fossil record of proterosuchids nourished a renewed interest in recent years, but no function has been proposed for their bizarre snouts. An oversized and downturned premaxilla with up to nine teeth with continuous replacement is present in all proterosuchid species and seems to have represented a physiologically costly phenotype that increased towards adulthood. A non-functional or a species recognition hypothesis are not supported as evolutionary mechanisms that drove this phenotype because features expected for these explanations tend to have a very low or zero physiological cost. There is no evidence favouring – but neither rejecting – that this morphology can be explained by non-sexual and non-social natural selection alone. Mutual social and/or sexual selection is favoured here as the most unambiguously supported explanation for the function and origin of the bizarre snout of proterosuchids based on several lines of evidence, including costliness, positive allometry, positive changes in growth rates and modern analogues. Social and/or sexual selection may have been important evolutionary mechanism in the dawn of the lineage that gave rise to crocodiles and dinosaurs.

Introduction

Proterosuchids are a clade of quadrupedal, sprawling and carnivorous diapsids that inhabited terrestrial ecosystems during the Permo-Triassic (Charig & Reig 1970; Charig & Sues 1976; Ezcurra et al. 2013) (Figure 1). It has been proposed that this group formed the ancestral stock of thecodonts (together with erythrosuchids) from which derived the two extant lineages of Archosauria, namely dinosaurs and pseudosuchians (including birds and crocodiles, respectively) (e.g. Reig 1970; Thulborn 1980). Modern phylogenetic analyses find proterosuchids as the sister-taxon of all other archosauriforms (e.g. erythrosuchids, proterochampsids, euparkeriids, archosaurs) and the oldest evolutionary radiation of this group, which occurred immediately after the Permo-Triassic mass extinction (Ezcurra et al. 2013). Indeed, the proterosuchid *Proterosuchus fergusi* is the first new tetrapod genus to appear in the South African Karroo Basin above the Permo-Triassic boundary (Smith & Botha 2005). *Proterosuchus fergusi* is known from an extensive, highly ontogenetically variable sample of eleven well-preserved three-dimensional skulls that are the result of more than a century of intensive collecting in South Africa (Ezcurra & Butler 2015a). Therefore, this sample represents an exception to extreme scarcity of well-preserved ontogenetic series in the fossil record of early diapsids.

The importance of proterosuchids nourished a renewed interest in the group that shed new light on their anatomy, ontogeny, taxonomy and systematics in recent years (e.g. Ezcurra, et al. 2010; Botha-Brink & Smith 2011; Ezcurra et al. 2013; Ezcurra et al. 2014; Ezcurra 2014, 2015; Ezcurra & Butler 2015a, 2015b; Ezcurra et al. 2015). However, most aspects of their palaeoecology remain enigmatic and poorly explored. Recent analyses found that the unambiguous taxonomic content of Proterosuchidae is restricted to five species collected in beds immediately below and above the Permo-Triassic boundary, namely *Archosaurus rossicus* from Russia, *Proterosuchus fergusi*, *Proterosuchus alexanderi* and *Proterosuchus goweri* from South Africa, and "*Chasmatosaurus*" *yuani* from China (Ezcurra 2015, in press). The largest known proterosuchid specimens reached a total skull length of 50 centimetres and a total body length of 3–3.5 metres (Ezcurra & Butler 2015a) (Figure 1). Palaeohistological and palaeoenvironmental data indicate that they were terrestrial animals (cf. Cruickshank 1972; Botha-Brink & Smith 2011), contrasting with some previous assumptions that proterosuchids were semi-aquatic, with a lifestyle similar to extant crocodiles (Broili & Schröder 1934; Reig 1970). It has been hypothesised that large proterosuchids predated upon fishes and the dicynodont synapsid *Lystrosaurus* (Reig 1970; Tatarinov 1961; Sennikov 1996). However, there is no direct evidence of the trophic habits of proterosuchids and the presence of gut contents in the putative proterosuchid

---
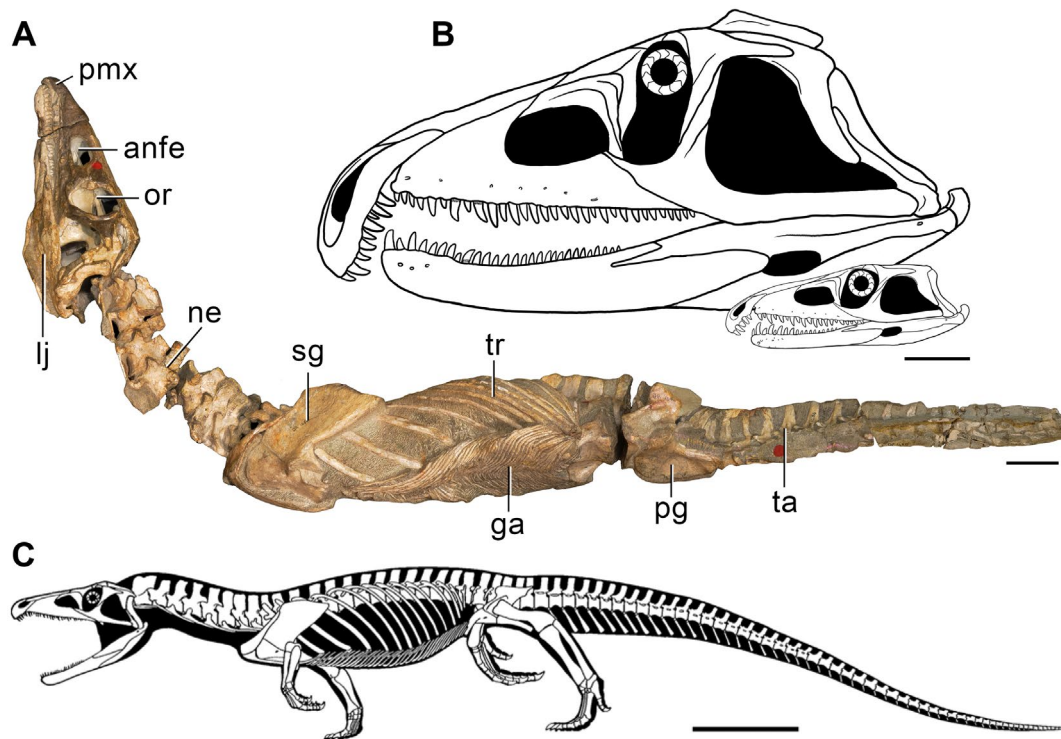
Figure 1. General morphology of proterosuchid archosauriforms. Partial articulated skeleton of the holotype of *Proterosuchus alexanderi* (A: NMQR 1484); skull reconstructions of adult and juvenile of *Proterosuchus fergusi* (B); and skeletal reconstruction of the genus *Proterosuchus* (C). Abbreviations: anfe, antorbital fenestra; ga, gastral basket; lj, lower jaw; ne, neck; or, orbit; pg, pelvic girdle; pmx, premaxilla; sg, scapular girdle; ta, tail; tr, trunk. Scale bars equal 5 cm in (A, B) and 50 cm in (C). B, taken from Ezcurra and Butler (2015b) and C, taken from Ezcurra et al. (2013: courtesy of Gregory Paul).

Table 1. Results of the SMA regressions using total skull length as the independent variable.

Measurement	N	R^2	p-value (regression-test)	Slope	Lower limit (90% CI)	Upper limit (90% CI)	p-value (isometry-test)	Trend
Premaxillary body length	9	0.8955	0.0001	1.2774	1.0155	1.6068	0.0826	(+)
Premaxillary body height	11	0.8774	<0.0001	1.2459	1.0076	1.5407	0.0900	(+)
Number of premaxillary teeth	10	0.6376	0.0056	0.7510	0.5104	1.1049	0.2097	=
Largest premaxillary tooth length at base	9	0.7834	0.0015	1.1711	0.8441	1.6247	0.3973	=
Largest premaxillary tooth height	6	0.6193	0.0635	NA	NA	NA	NA	NA
Largest maxillary tooth length at base	12	0.5989	0.0031	0.6069	0.4254	0.8660	0.0266	−
Largest maxillary tooth height	9	0.6910	0.0055	0.6598	0.4475	0.9727	0.0811	(−)

Abbreviations: (+), marginally significant positive allometry; (−), marginally significant negative allometry; −, negative allometry; =, isometry; CI, confidence interval; N, size of the variable; NA, non-applicable.

Tasmaniosaurus triassicus has been recently dismissed (Ezcurra 2014). Therefore, inferences of the diet of proterosuchids currently rely only on indirect evidence, such as tooth morphology and general skull morphology and body plan (Ezcurra et al. 2013).

Among the obscure issues regarding the palaeoecology of proterosuchids, the origin and function (if present) of the bizarre snout morphology (see below), which has been used as a key feature to diagnose the group (e.g. Charig & Reig 1970; Reig 1970; Charig & Sues 1976; Gower & Sennikov 1997), have not been discussed and remain completely enigmatic. Here the possible evolutionary origin of this bizarre snout architecture is discussed on the light of the relatively very good available sample of well-preserved proterosuchid skulls (mainly in the South African species *Proterosuchus fergusi*) and recent advances on the knowledge of the palaeobiology of the

group. Thus, the objective of this manuscript is to test different, alternative explanations for the presence of this phenotype in proterosuchids and some other early archosauriform species, such as non-functional, species recognition and socio-sexual hypotheses. In order to test these possible explanations, here it is described in detail the morphology of the premaxilla of proterosuchids (using traditional morphological description and a thin-plate spline analysis) and allometric regressions of snout characters are conducted. The morphological description and allometric regressions will allow testing features previously considered supporters of sexual selection, such as costliness, positive allometry, changes in growth rate during ontogeny and sexual dimorphism (see Borkovic & Russell 2014; Hone & Faulkes 2014).

An intense debate about social and sexual selection in the fossil record has been raised in recent years. As a result, the

concept of social and sexual selection is briefly reviewed here. West-Eberhard (1983) defined social selection as a differential reproductive success (ultimately, differential gene replication) due to differential success in social competition whatever the resource at stake. After this definition, Tobias et al. (2012) defined sexual selection as a subset of social competition in which the resource at stake is mates. These authors included social dominance as a particular case of social selection and this interpretation is followed here. This definition of sexual selection agrees with the original proposal of Darwin (1859, 156) that this kind of evolutionary mechanism depends 'not on a struggle for existence, but on a struggle between the males for possession of the females; the result is not death to the unsuccessful competitor, but few or no offspring'. As a result, Tobias et al. (2012) stated that the most accurate approach would be to partition social mechanisms into 'sexual social selection' and 'non-sexual social selection'. Nevertheless, these authors adopted a more simple nomenclature that is used here, in which 'sexual selection' is used for sexual social selection and 'social selection' for non-sexual social selection. It is also followed here the most accepted view that social selection is a subset of natural selection (Darwin 1871; Andersson 1994; Tobias et al. 2012), although some authors consider that sexual selection belongs to a different category distinct from natural selection (Hosken & House 2011). 'Natural selection' is used here for non-social and non-sexual selection in order to simplify nomenclature. In the cases that social and sexual evolutionary mechanisms act in both sexes, the terms mutual social and sexual selection are used here, respectively, as it has been proposed by multiple authors (Kirkpatrick et al. 1990; Jones & Hunter 1993; Kraaijeveld 2003; Hone et al. 2012; Tobias et al. 2012). Padian and Horner (2011a, 2011b, 2013, 2014) considered that a strict sexual dimorphism is a requisite for the Darwinian definition of sexual selection and, as a result, rejected this mechanism as one of the main evolutionary drivers of bizarre cranial structures in dinosaurs. However, multiple authors have provided strong rebuttals for this view and they are followed here in considering that the absence of sexual dimorphism does not invalidate a hypothesis of sexual selection (Knell & Sampson 2011; Hone et al. 2012; Hone & Naish 2013; Knell et al. 2013a, 2013b; Borkovic & Russell 2014; Hone & Faulkes 2014).

Institutional abbreviations

BP, Evolutionary Studies Institute (formerly Bernard Price Institute for Palaeontological Research), University of the Witwatersrand, Johannesburg, South Africa; BSPG, Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; GHG, Geological Survey, Pretoria, South Africa; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; NMQR, National Museum, Bloemfontein, South Africa; PIN, Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia; RC, Rubidge Collection, Wellwood, Graaff-Reinet, South Africa; SAM-PK, Iziko South African Museum, Cape Town, South Africa; TM, Ditsong National Museum of Natural History (formerly Transvaal Museum), Pretoria, South Africa.

Materials and methods

Studied specimens and allometric regressions

The entire hypodigm of the proterosuchids *Proterosuchus fergusi* (see Ezcurra & Butler 2015a: Table 3), *Proterosuchus goweri* (NMQR 880), *Proterosuchus alexanderi* (NMQR 1484), "*Chasmatosaurus*" *yuani* (IVPP V2719, V4067, V36315) and *Archosaurus rossicus* (PIN 1100/55; see Nesbitt 2011; Ezcurra et al. 2014) were studied at first hand by the author. Raw data for the allometric regressions consisted of a subsample of the original linear cranial measurements and tooth counts recorded by Ezcurra and Butler (2015b) for *Proterosuchus fergusi*, with the addition of information gathered from the holotype of *Proterosuchus goweri* (NMQR 880) and a referred specimen of "*Chasmatosaurus*" *yuani* (IVPP V4067). This resulted in a sample of 10 specimens of *Proterosuchus fergusi* (RC 59, 846; BP/3993, 1/4016, SAM-PK-K140, 11,208, K10603; BSPG 1934 VIII 514; TM 201; GHG 231), and one of *Proterosuchus goweri* (NM QR 880) and "*Chasmatosaurus*" *yuani* (IVPP V4067), respectively (see Supplementary Information). Seven measurements of the premaxilla and the premaxillary and maxillary tooth counts are sampled here, taking into account that they were not affected by post-mortem deformation (Table 1, see Supplementary Information). The addition of information from *Proterosuchus goweri* and "*Chasmatosaurus*" *yuani* seeks to increase the sampling of the regressions with respect to those of Ezcurra and Butler (2015b) and increase the statistical power of the analyses (Brown & Vavrek 2015). It should be noted that these regressions test the presence of interspecific allometry, rather than intraspecific allometry (contrasting with Ezcurra & Butler 2015b). Changes in growth timings (e.g. heterochronies) that may occur among the three proterosuchid species can generate differences among their ontogenetic trajectories and result in problems at the time of interpreting the regressions in the context of intraspecific evolutionary mechanisms. However, these cases can be detected if the analyses of these variables result in statistically non-significant regressions and, therefore, if it was the case, they were excluded from further consideration. In addition, the results of the allometric analyses conducted here were compared with the slopes recovered for the same variables in the sample composed only of specimens of *Proterosuchus fergusi* in the analysis of Ezcurra and Butler (2015b). The results of the interspecific regressions were considered for further discussion only if they closely resembled the slope values (i.e. difference < 0.1) found by the intraspecific regressions of *Proterosuchus fergusi*.

Measurements were taken first hand with a digital calliper with a maximum deviation of 0.02 mm, but measurements were rounded to the nearest 0.1 mm. The selected variables were log10-transformed to fit the linear power function before conducting the regression analyses (Gould 1966). The regressions were calculated using the standardised major axis (SMA) regression method implemented in the package SMATR version 3.2.6 for R (Warton et al. 2012; R Development Core Team 2013). SMA regression was employed instead of ordinary least-squared regression because it has been suggested to be the most appropriate method to study allometry in bivariate data (Warton et al. 2006; Smith 2009). Total skull length was used as the independent variable (see Ezcurra & Butler
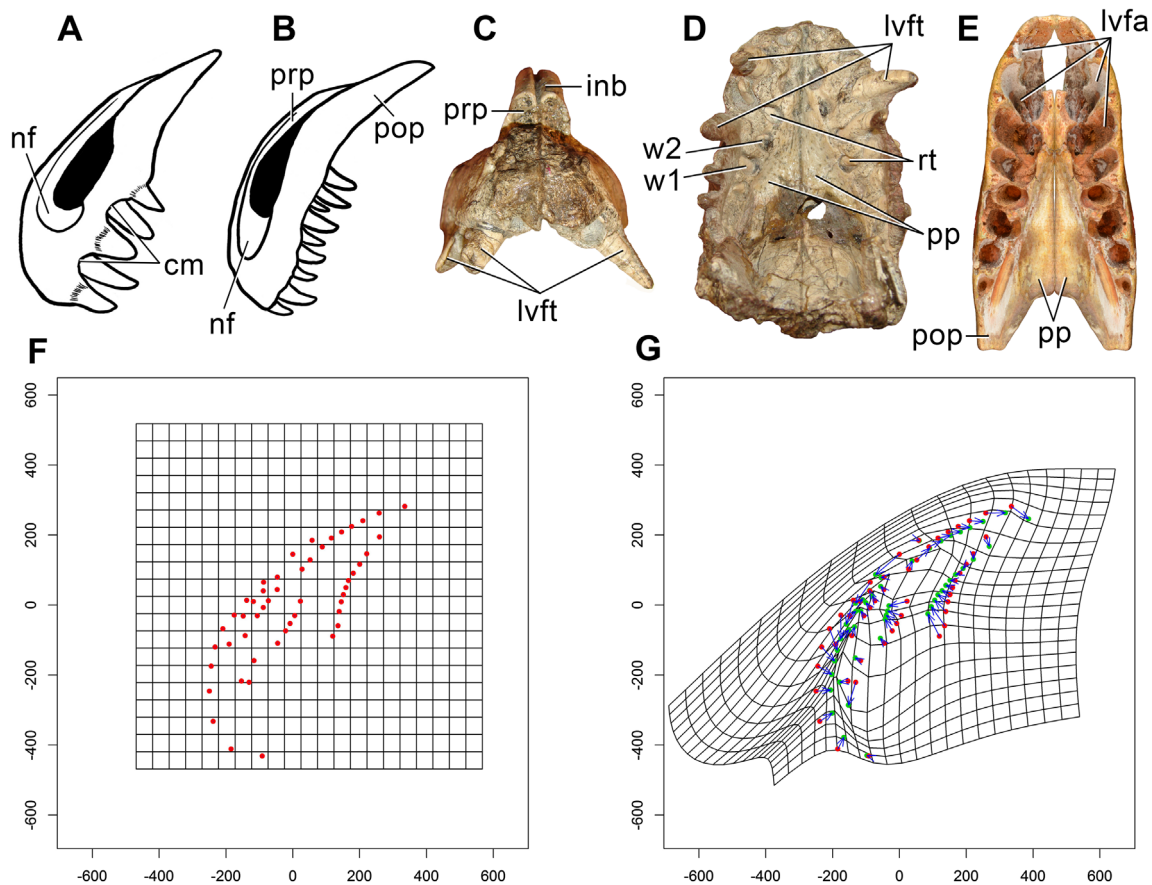
Figure 2. Proterosuchid premaxilla morphology. Reconstruction of the premaxilla of juvenile of *Proterosuchus fergusi* (A: based on RC 59); reconstruction of the premaxilla of adult of *Proterosuchus fergusi* (B: based on BSPG 1934 VIII 514, GHG 231, RC 846); premaxillae and anterior end of the palate of the holotype of *Proterosuchus goweri* (C, D: NMQR 880) in anterior (C) and ventral (D) views; right premaxilla of the holotype of *Archosaurus rossicus* in ventral view (E: PIN 1100/55, left side digitally mirrored); and thin-plate spline results showing the grid in the juvenile (F) and adult (G) of *Proterosuchus fergusi*. Abbreviations: cm, concave margin; inb, internarial bar; lvfa, lateroventrally facing alveoli; lvft, lateroventrally facing teeth; nf, narial fossa; pop, postnarial process; pp, palatal process; prp, prenarial process; rt, replacement tooth; w1–2, wave of tooth replacement 1 and 2. A–E, not to scale.

2015b), and R^2 and *p*-values were obtained from each SMA regression. For variables with a statistically significant fit, the allometric coefficient (*K*) (i.e. the slope of the regression) with its respective 90% confidence intervals (CIs) was calculated and a statistical test (Pitman 1939; Warton et al. 2006) was conducted to determine whether the slope was significantly different from 1 (H_0 = slope not different from 1). Growth was considered isometric if the allometric coefficient was not significantly different from 1. Conversely, the growth was considered allometric if the allometric coefficient was significantly ($p < 0.05$) or marginally significantly ($0.05 < p < 0.10$) different from 1 (i.e. $K > 1$ represents a positive allometry and $K < 1$ a negative allometry).

Thin-plate spline

The cranial fossil record of *Proterosuchus fergusi* is exceptional among early sauropsids, but post-mortem deformation and breakages affected the general morphology of the premaxillae in most specimens. As a result, it was not possible to explore quantitatively the changes in the shape of the premaxilla through ontogeny using geometric morphometrics applied to the actual specimens. However, the reconstructions of the premaxilla of the juvenile and adult stages of this species, generated from multiple specimens by Ezcurra and Butler (2015b), were used to conduct a thin-plate spline (= deformation grid) analysis. Thus, the aim of this analysis is to show changes in the morphology of the premaxilla through the two extremes of the sampled ontogenetic series of *Proterosuchus fergusi*. A total of 50 landmarks were placed in the contours of the premaxillary bone, external naris and narial fossa using their intersections with equidistant radial lines projected from four points: the mid-length of the ventral margin of the postnarial process, and the mid-length of the ventral border, posterior end and anteroventral corner of the external naris (Figures 2(A) and (B); Supplementary Information 2). Thus, these landmarks sample both external contour and internal features (e.g. external naris and narial fossa shapes). The ventral margin of the main body of the premaxilla was not sampled by the landmarks because it was subjected to series of osseous remodelling, as a result of subsequent replacements of teeth with an ankylothecodont implantation, and the homology between the premaxillary teeth is unknown. As a result, tooth morphology was neither sampled by the landmarks. Nevertheless, shape modifications in the main body of the premaxilla were captured by the regression analyses. The thin-plate spline analysis was conducted in R (package Shapes version 1.1-9).

Results

Morphology and ontogenetic variation of the proterosuchid snout

The presence of a premaxilla distinctly more anteriorly extended than the lower jaw and strongly downturned (Figure 1(B)) has been considered one of the most salient features and a diagnostic character-state of Proterosuchidae (Charig & Reig 1970; Charig & Sues 1976; Gower & Sennikov 1997). The premaxilla of the proterosuchids possesses an elongated main body, being 2.4–3.7 times anteroposteriorly longer than tall (Figures 2(A) and (B)). The lateral surface of the main body is convex and mostly smooth, with exception of a pair of foramina placed immediately lateral to the ventral margin of the external naris in some specimens (e.g. *Proterosuchus fergusi*: RC 846; *Proterosuchus goweri*: NMQR 880). The premaxilla possesses three processes: the prenarial, postnarial and palatal processes (Figures 2(B), (C), and (E): pop, pp, prp). The prenarial process forms the anterior and dorsal border of the external naris and articulates posteriorly with the nasal. These two bones form the internarial bar that separates the pair of external nares from each other in the median line of the snout. A moderately deep narial fossa extends anteriorly and dorsally to the external naris on the lateral surface of the prenarial process (Figure 2(B): nf). The narial fossa is proportionally more anteriorly developed in supposed adult proterosuchids (e.g. RC 846, TM 201) than in juveniles (e.g. RC 59) (Figures 2(A) and (B)). The postnarial process is dorsoventrally tall and possesses an extensive diagonal suture with the anterior margin of the maxilla and its distal end articulates with the nasal (Figure 1(B)). As a result, the contact between the premaxilla and nasal excludes the maxilla from participation in the external naris. The main axis of the postnarial process is subparallel to the alveolar margin of the bone in the smallest and supposed youngest specimen of *Proterosuchus fergusi* (RC 59) (Figure 2(A)), whereas in all other and bigger specimens of the species, this process is downturned with respect to the alveolar margin (e.g. BP/1/3993, BSPG 1934 VIII 514, RC 846, SAM-PK-11,208, TM 201) (Ezcurra & Butler 2015b) (Figure 2(B)). The medial surface of the premaxilla possesses a well-developed palatal process that meets its counterpart in the median line of the anterior end of the palate (Figures 2(D) and (E)). The palatal process articulates posteriorly with the vomer and on its dorsal surface lays the septomaxilla (Ezcurra & Butler 2015a). The dentary is very gently dorsally curved in juveniles (RC 59), whereas it becomes more conspicuously curved in larger specimens (e.g. RC 846, TM 201) (Figure 1(B)).

The lateral surface of the main body of the premaxilla is mostly smooth and a few foramina are placed on its anterolateral surface and on the narial fossa (e.g. NMQR 880, RC 846, TM 201). These foramina are interpreted to have transmitted the premaxillary branches of the medial nasal ramus of the ophthalmic branch of the trigeminal cranial nerve (CN V$_1$) (Bubien-Waluszewska 1981; Witmer 1995) and premaxillary branches of the dorsal alveolar, medial nasal and subnarial vessels (Sedlmayr 2002), which may have nourished and innervated the fleshy nostril, as occurs in other amniotes. The foramina placed on the anterolateral surface of the premaxilla are not numerous and concentrated in a distinct array, contrasting with the foramina related to the pressure receptors that detect water movement in modern crocodiles and recently hypothesised to be present in the

theropod dinosaur *Spinosaurus* (Ibrahim et al. 2014). As a result, there is no osteological correlate for the harbouring, nutrition or innervation of an unusual soft tissue structure in the snout of proterosuchids.

The tooth count of the premaxilla varies from five to nine in the sampled ontogenetic sequence of *Proterosuchus fergusi* (Figures 2(A) and (B)), acquiring progressively more teeth during ontogeny (Ezcurra & Butler 2015b). The homology of the premaxillary teeth along the ontogenetic sequence of *Proterosuchus fergusi* is unknown because all the crowns are isodont. All the marginal tooth crowns are recurved distally and serrated on both mesial and distal margins. The teeth are deeply implanted in alveoli (Figure 2(E)), and fused to the bone when fully erupted by apicobasally oriented, densely packed and narrow ridges of bone that completely surround the base of the crown, resulting in an ankylothecodont tooth implantation in all sampled ontogenetic stages (Chatterjee 1974; Modesto & Sues 2004; Nesbitt 2011).

Teeth seem to have been continuously replaced during life (i.e. polyphyodonty, at least in the sampled ontogenetic sequence) as is indicated by the presence of at least two alternate waves of erupting replacement teeth and reabsorption pits in large-bodied, probable adult specimens (e.g. NMQR 880) (Figure 2(D): rt). Details of the tooth replacement mechanism have not been explored for proterosuchids, but available evidence indicates that it should have been similar to that of several sauropsids (e.g. procolophonid pararentiles: Small 1997; agamid lizards: Cooper et al. 1970). Reabsorption pits develop on the lingual surface of the dentigerous bone and the presence of two pit sizes in the premaxilla of NMQR 880 (Figure 2(D): w1, w2), the largest of them connected to the alveolus, indicates that they increased in size during tooth replacement, as occurs in other sauropsids (Edmund 1960; Cooper et al. 1970). In sauropsids (e.g. *Agama agama*: Cooper et al. 1970), reabsorption pits enlarge gradually at the expense of reabsorption of the root of the old tooth, bone and the calcified cementing tissue, until invading the pulp chamber of the old tooth. A small calcified tooth germ develops within the reabsorption pit during this process. Tissue reabsorption continues as the new tooth grows and, ultimately, the old tooth only remains attached by a thin layer of bone on the labial side and eventually breaks off (i.e. shedding) leaving an irregular alveolar edge (Cooper et al. 1970). The erupting tooth continues growing until being fully erupted and cemented to the bone. Subsequently, a new reabsorption pit appears and the cycle stars again. This tooth replacement mechanism is congruent with the morphology observed in different proterosuchid specimens, but the shedding of the old tooth should have also implied the breakage of part of the alveolar margin of the bone (which was fused to the tooth). This breakage is denoted by the usual presence of a ventrally concave and rough alveolar margin of the bone in alveoli that are being replaced (RC 59) or has been lost during taphonomic processes (PIN 1100/55) (Figure 2(A): cm). After the full eruption of the new tooth, the cementing of the tooth to the bone should have been accompanied by the generation of new osseous tissue to fuse the tooth to the bone in an ankylothecodont tooth implantation.

All the premaxillary teeth are ventrally oriented in juvenile and probably sub-adult proterosuchid specimens. However, the first four teeth acquire a distinct lateral orientation in large-sized and probably adult individuals, being strongly divergent from

the sagittal plane of the snout in anterior view (RC 846, NMQR 880, IVPP V4067) (Figures 2(C)–(E): lvfa, lvft). The premaxillary teeth do not occlude with those of the dentary in any of the sampled ontogenetic stages (e.g. RC 59, 846, BP/1/3993, SAM-PK-11,208, IVPP V4067) (Figure 1(B)), contrasting with the condition in the vast majority of amniotes, with the exception of ornithosuchid archosaurs (Baczko & Ezcurra 2013).

Thin-plate spline

The thin-plate spline (= deformation grid) indicates the presence of a considerably large amount of morphological modification in the premaxilla between the extremes of the sampled ontogenetic sequence of *Proterosuchus fergusi* (i.e. reconstructions of the juvenile and adult stages). The grid shows an overall dorsoventral depression and anteroposterior extension of the premaxilla (Figures 2(F) and (G)). The external naris moves slightly dorsally with respect to the rest of the bone and becomes slightly dorsoventrally shorter. The narial fossa becomes more anteriorly extended, finishing close to the anterior margin of the base of the prenarial process. The prenarial and, in a lower degree, the postnarial processes become dorsoventrally shallower. The main ontogenetic change in the premaxilla occurs in the postnarial process (the longest blue arrows), where the base of its ventral margin acquires a distinct ventral inflexion and the process downturns as a whole.

Allometric regressions

Of the seven measurements here considered for the allometric analyses, only the height of the largest premaxillary tooth crown failed the regression test (Table 1). Only specimens of *Proterosuchus fergusi* were sampled for this variable and, as a result, the non-significant regression should be attributed to intraspecific non-ontogenetic variation, rather than to interspecific changes in growth timings within Proterosuchidae. The slope values of the significant regressions closely resemble those of the respective variables of the intraspecific analysis of Ezcurra and Butler (2015b), which used only specimens of *Proterosuchus fergusi*. Indeed, the differences between the respective pairs of slopes ranged between 0 and 0.0527 (mean = 0.0256, SD = 0.0205), showing that the inclusion of the two specimens of the other two proterosuchid species did not affect substantially the slopes of each variable with respect to the intraspecific regression analysis.

The length and height of the premaxillary body show marginally significant positive allometric trends (slopes of 1.24 and 1.27, respectively) (Figures 3(A) and (B)), which are in agreement with the morphological modifications observed in the deformation grid. Ezcurra and Butler (2015b) recovered isometric trends for these two variables, but the different results are very likely a consequence of the increased sample (Brown & Vavrek 2015) because the CIs were larger and the slopes were very similar (slopes of 1.23 and 1.22, respectively) to those found here. The number of premaxillary tooth positions and the length at the base of the crown of the largest premaxillary tooth show isometric trends (Figure 3(C)). The two variables concerning the size of the largest maxillary tooth (i.e. height and length at base of the crown) show negative allometric trends (Figure 3(D)). As a

consequence, the premaxillary teeth maintain a similar relative size through the ontogeny of proterosuchids, but the maxillary teeth become proportionally smaller.

Discussion

The proterosuchid snout in an evolutionary context

The presence of an oversized premaxilla, and five to nine premaxillary teeth with an ankylothecodont implantation and continuous replacement in proterosuchids seems to have been a physiologically costly phenotype because of its cost of growth and maintenance, which increased towards the adulthood of the species. The odontogenesis of up to eighteen teeth in each replacement sequence – that implies the generation of enamel and dentine, and also new osseous tissue to allow the fusion of the teeth to the bone – and the maintenance of a premaxilla that approaches half of the length anterior to the antorbital fenestra should have very likely involved a considerable higher amount of energy than the archosauromorph plesiomorphic phenotype. This phenotype should have been particularly more costly in adult proterosuchids than in juveniles and different ontogenetic stages of closely related archosauromorphs (e.g. *Prolacerta broomi*, *Erythrosuchus africanus*, *Euparkeria capensis*). The presence of a physiologically costly phenotype implies that the bizarre snout of proterosuchids was not a non-functional character because it should have reduced the fitness of the individual and, as a consequence, should have been negatively selected under natural selection. Some authors have stated that species recognition drove the evolution of bizarre or exaggerated cranial structures (ornaments or weapons) in bird-line fossil archosaurs (Padian & Horner 2011a). However, this hypothesis has been widely critiqued in favour of explanations that place social and/or sexual selection as the main evolutionary mechanism to explain these features (Knell & Sampson 2011; Hone et al. 2012; Knell et al. 2013a, 2013b; Hone & Naish 2013; Hone et al. 2016). In the case of proterosuchids, a species recognition hypothesis is not supported as the main evolutionary mechanism that drove their bizarre snouts over other explanations (see below) because features related to this function tend to have a very low or zero physiological cost (e.g. differences in colour of skin, feathers or fur, vocalisations, chemical signals) (Maynard Smith & Harper 2003; Knell & Sampson 2011; Knell et al. 2013a, 2013b; Hone & Naish 2013; Hone et al. 2016). Furthermore, the morphology of the premaxilla of different proterosuchid species is extremely similar between each other (*Proterosuchus fergusi*: RC 59, 846, SAM-PK-11208, BP/1/3993; *Proterosuchus goweri*: NMQR 880; *Archosaurus rossicus*: PIN 1100/55; "*Chasmatosaurus*" *yuani*: IVPP V36315, V4067) and suffers strong intraspecific modifications during ontogeny, resembling the case of the horns of ceratopsian dinosaurs that seems to have been mainly selected under social and/or sexual selection (Hone & Naish 2013). However, it cannot be ruled out that low or zero-cost soft tissue features without a direct osteological correlate in the premaxilla may have been involved in species recognition.

The presence of this bizarre snout in proterosuchids implies that individuals obtained a benefit that increased fitness and exceeded the cost of the structure to prevent it to be negatively selected. In this context, the premaxilla of proterosuchids may
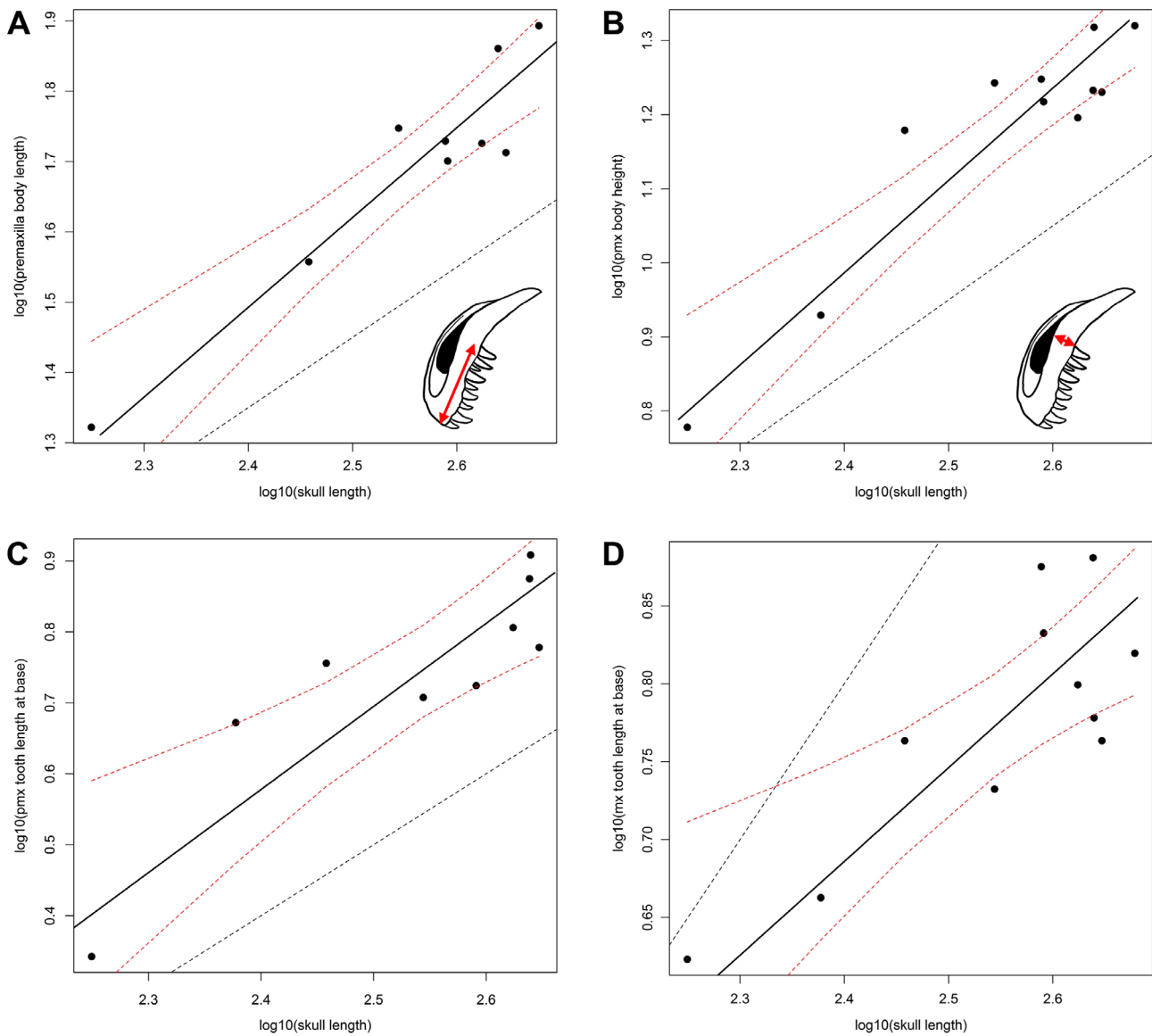
Figure 3. Bivariate plots showing the allometric regression of the length of the main body of the premaxilla (A), height of the main body of the premaxilla (B), length at base of the largest premaxillary tooth (C) and length at base of the largest maxillary tooth (D). Skull length was used as the independent variable in all regressions. Red dotted lines show the limits of the 90% confidence intervals, and the grey dotted line shows a slope equal to 1.

have played a direct functional role in the trophic habits, ethological behaviour or physiology of these animals. However, no mechanical or physiological function has been proposed before for the proterosuchid snouts (or for other diapsids with reminiscent snout morphology, e.g. ornithosuchids, non-averostran neotheropods) and no apparent function can be hypothesised here that may be selected under natural selection. In this regard, none of the teeth of the juvenile and adult proterosuchid specimens show signs of macroscopic wear facets, ruling out the possibility that they were involved in mechanical interactions with hard materials (e.g. digging). In addition, the absence of occlusion of the premaxillary teeth with those of the lower jaw should have prevented them to have participated in prey holding, though the fact that they might have been used in a less common predatory function cannot be ruled out (e.g. prey anchoring or slashing). The polymorphism observed between juvenile–sub-adult and adult specimens (e.g. ventrally vs.

ventrolaterally oriented teeth, more downturned premaxilla) indicates that if premaxillary teeth hypothetically participated in a mechanical function, it may have changed during ontogeny. The situation is additionally obscured by the fact that trophic habits are unknown in proterosuchids. The broad diversity of trophic habits and ethological behaviours in extant animals, sometimes a priori unexpected, force to be cautious at the time of rejecting a trophic functional explanation in extinct animals. We should consider that the absence of evidence supporting an explanation driven by natural selection might be the result of ignorance of the palaeobiology of proterosuchids, as usually occurs at the time of discussing this kind of issues in fossil species. Detailed biomechanial analyses go beyond the scope of this manuscript, but may shed light on the functional capabilities of the proterosuchid snout and contribute to reject alternative explanations based on functional selective pressures. As a result, the current available evidence does not support
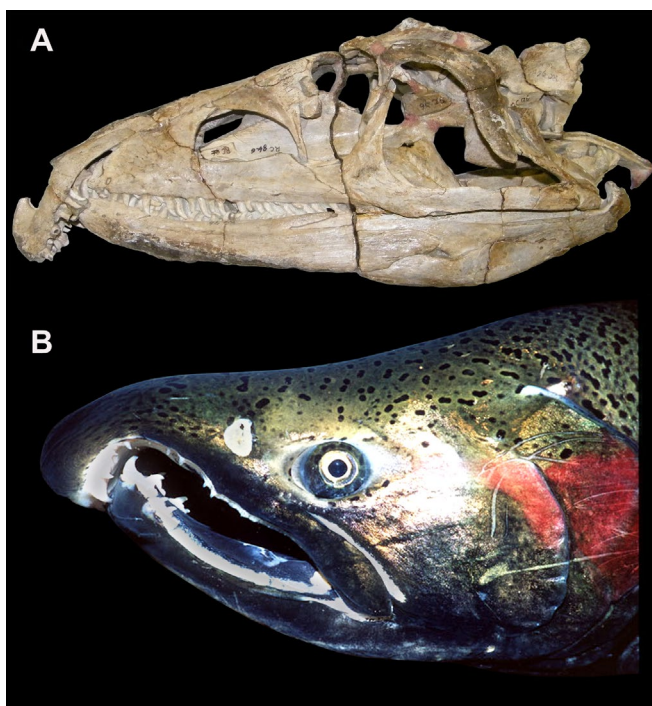
Figure 4. Overall similarity of the snout shape of proterosuchid archosauriforms (A: *Proterosuchus fergusi*, RC 846, neotype) and the hooknose adult male morphotype of *Oncorhynchus kisutch* (coho salmon) (B). B, photograph courtesy of Ernest Keeley and modified from http://sol.zoology.ubc.ca/~keeley/coho.htm. Not to scale.

– but neither reject – the hypothesis that the bizarre snout of proterosuchids can be explained by natural selection.

An alternative explanation for the proterosuchid snout is social and/or sexual selection (e.g. dominance signalling; Hone et al. 2012), in which the exacerbated morphology of the premaxilla played a role as an honest signal of genetic and phenotypic quality, social status and/or, maybe, fighting ability (e.g. peacock's tail; Darwin 1871; Petrie et al. 1991). Honest signalling is an essential component of the handicap principle and is involved in mate choice and/or competition for ecological resources (e.g. establishment of territories or social hierarchies) that may produce apparently non-adaptive features that will reduce fitness under natural selection (Darwin 1871; Zahavi 1975; Zahavi & Zahavi 1999; Andersson 1994). For example, mate choice can produce a ran-away process by sexual selection towards an extreme and costly phenotype, which is usually stabilised in around an optimum by natural selection (Kokko & Brooks 2003). As mentioned above, social and/or sexual selection have been used to explain bizarre structures in many extinct animals (e.g. crests, horns), but the testing of these hypotheses is extremely difficult in the fossil record and should not be viewed as a default explanation (Knell et al. 2013a; Borkovic & Russell 2014; Hone & Faulkes 2014). Knell et al. (2013a) argued that testing of alternative hypotheses (e.g. natural selection, species recognition) and the discussion of a list of features (potentially preserved in the fossil record) that can be used to support the sexual selection hypothesis are strongly necessary to distinguish between possible explanations of bizarre structures. The features listed by these authors as supporters of sexual selection are costliness, positive allometry, changes in growth rate during ontogeny and sexual dimorphism (see also

Borkovic & Russell 2014; Hone & Faulkes 2014). Costliness of the proterosuchid snout has been discussed above and it seems to be congruent with a social or sexual selective mechanism. The positive allometries recovered for the height and length of the main body of the premaxilla with respect to the total length of the skull are also congruent with a sexual selection mechanism. The presence of changes in growth rates during ontogeny cannot be directly determined in the *Proterosuchus fergusi* sample because of the absence of ontogenetic age and well constrained osteochronological information (Ezcurra & Butler 2015b). Nevertheless, estimations can be made using cranial length as a proxy of age following the ontogram reconstructed by Ezcurra and Butler (2015b) for *Proterosuchus fergusi*, which combines several lines of evidence correlated with skeletal somatic maturity (e.g. histology, sequence of neurocentral suture closure, orbit shape). In the case of the increase in the premaxillary tooth count, the ontogram of Ezcurra and Butler (2015b) shows that individuals with a skull length that exceeds 57% of the size range sampled for the species acquires three additional tooth positions, whereas only one tooth position is added in the first 50% of the size range. Indeed, at least two tooth positions were added after individuals probably reached sexual maturity and a complete fusion of the neurocentral sutures in the cervical series – an usually used osteochronological proxy in archosauromorphs (Ezcurra & Butler 2015b: Figure 9). Therefore, the correlation of the sequence of acquisition of premaxillary tooth positions with ontogenetic age proxies indicates acceleration in the addition of teeth towards or during the adulthood of *Proterosuchus fergusi*. The presence of changes in growth rates in the length and height of the main body of the premaxilla are not straightforward to detect because of the limited sample. Nevertheless, at least in the case of the length of the main body of the premaxilla, the non-log transformed values fit better an exponential function ($R^2 = 0.8803$) than a linear function ($R^2 = 0.8037$), indicating possible evidence of a positive change of the growth rate of this variable during ontogeny.

The detection of sexual dimorphism in proterosuchids is problematic because of the absence of sex information in the group, as usually occurs in the vast majority of fossil sauropsids. Ezcurra and Butler (2015a) reported a dimorphism in the transverse width and depth of the supratemporal fossae in large-bodied specimens of *Proterosuchus fergusi* (broad and shallow vs. narrow and deep fossae). This dimorphism can be potentially sexually related and seems to have resulted in different orientations of the origin area of the *M. adductor mandibulae externus profundus*, one of the main adductors of the lower jaw (Holliday & Witmer 2007). However, it is unknown how this dimorphism could have been functionally related to the bizarre snout and, as a result, with social and/or sexual selection. In particular, there is no evidence of dimorphism in the snout of the available sample of *Proterosuchus fergusi*. Furthermore, there is no sympatric early archosauriform species with different snout morphology in the South African record that may represent misidentified dimorphic females (or males). The absence of sexual dimorphism does not result in a rejection of a sexual selection hypothesis and, instead, can be explained by mutual social or sexual selection (see Introduction). Under mutual social and sexual selection, female traits may be under weaker selection from mate choice,

and stronger selection via competition for ecological resources (Tobias et al. 2012). Females maximise their own fecundity rather than their access to matings (Bateman 1948; Trivers 1972), and thus are more likely than males to compete directly or indirectly for the ecological resources needed to leave offspring (Clutton-Brock 2007, 2009).

The discussion of the features that may support a sexual selection hypothesis in the context of the bizarre snouts of proterosuchid archosauriforms indicates that available evidence is congruent with this explanation, in particular mutual selection. In extant animals, it is usually difficult to distinguish clearly between sexual and social selection (Clutton-Brock 2007), and the same traits can function ambiguously in both evolutionary mechanisms (Tobias et al. 2012). Indeed, the proterosuchid snout as an honest signal may have been functional under both sexual and social selection, in which larger and strongly downturned premaxillae were preferred by mates and/or involved in competition for territories (or another kind of social advantage in the population), thus increasing differentiately the fitness of the individuals.

The snout morphology of proterosuchids clearly differs from that of other amniotes, with the exception of ornithosuchid archosaurs. The ornithosuchids are a group of small to medium-sized predatory diapsids, restricted to three species documented in Upper Triassic beds of Argentina and Scotland (Baczko & Ezcurra 2013) and thus post-date proterosuchids in the fossil record. This clade also possesses a large and downturned premaxilla that does not occlude with the lower jaw, but differs from proterosuchids in the presence of a lower tooth count and less downturned premaxilla. The fossil record of ornithosuchids is relatively poor and the best-known species are limited to a couple of articulated skulls of similar size (*Riojasuchus tenuisceps*) and to an articulated skull and partial cranial remains (*Ornithosuchus longidens*) that do not offer too much information about intraspecific ontogenetic variations. As a result, the ornithosuchid record cannot shed light on the evolutionary origin and functionality of the bizarre snouts of proterosuchids. Nevertheless, the conclusions raised here about the snout of proterosuchids may be considered as working hypotheses to be tested in ornithosuchids in future studies, when a broader sample and better cranial anatomical knowledge is available for the clade.

Several mammals also possess an exaggerated, bizarre snout and in some of them they have been proposed to be involved in social and/or sexual selection, but these structures are formed by soft tissue rather than by an osseous overgrown (e.g. the pinniped carnivoran *Mirounga leonina*, elephant seals, Sanvito et al. 2007; the cercopithecid primate *Nasalis larvatus*, proboscis monkey, Dixson et al. 2005). It is possible that the soft tissue of the snout is more evolutionarily plastic than bone in mammals than in sauropsids, and one explanation would be related with morphofunctional constraints imposed by suckling during lactation in early postnatal ontogeny (i.e. strong modifications in the osseous anatomy of the snout would prevent the lactation of the neonate) (Goswami et al. 2012). As a result, mammals do not seem to represent good analogues for the bizarre snouts of sauropsids.

Beyond amniotes, it is interesting to note the striking similarities between the bizarre osseous snouts of proterosuchid diapsids and those of adults of several extant salmonid actinopterygians,

in particular the anadromous species *Oncorhynchus kisutch* (coho salmon). The coho salmon may represent an interesting modern analogous of the condition in proterosuchids, but after keeping in mind the long phylogenetic distance and different mode of life between both species. The native distribution of the coho salmon is the North Pacific Ocean and rivers that disembogue into it (Miller et al. 1996). This species has a freshwater and a marine phase, in which after hatchling the juvenile spends one year growing in the rivers before migrating to the ocean (Gross 1991). Females usually mature after approximately 18 months in the ocean, and males may mature after either around six or 18 months (Gross 1991). The difference in the maturation times of the males is as result of an irreversible life-history decision of the juveniles and produces two different adult morphotypes, the jack (6 months) and hooknose (18 months) (Gross 1987, 1991). The hooknose morphotype develops an elongation of the upper jaw, a strongly downturned snout (kype sensu Gross 1984), large canine-like teeth in the hooked anterior end of the upper jaw, and dorsally curved lower jaw (Fleming & Gross 1994), resembling the condition of large-bodied and probable sexually mature proterosuchids (Figure 4). By contrast, the jack morphotype possesses considerably less-developed secondary sexual traits. After maturation, both males and females return to their river of birth to mate and die (Gross 1987; Quinn & Dittman 1990). Hooknose males usually fight for proximity to a female about to spawn using their modified snout, forming a size-graded hierarchy, with the closest male achieving the greatest fertilisation success (Schroder 1982; Gross 1984, 1985, 1991; Sargent et al. 1986). Jack males are usually forced to the end of the hierarchy and try to sneak close to the females using topographic accidents of the rivers as refuges (Gross 1991). The proterosuchid-like snout of the coho salmon plays a key function in a sexual selection mechanism and, as a result, this also supports the hypothesis that the bizarre snout of proterosuchids may also have played a function in sexual and social selection. It cannot be ruled out that the oversized premaxilla and laterally oriented teeth of proterosuchids took part in intraspecific antagonistic behaviours.

In conclusion, mutual social and/or sexual selection is favoured here as the best supported explanation for the function of the bizarre snout of proterosuchids after discussing several alternative hypotheses and the evidence that support it (e.g. costliness, allometry, changes in growth rates, modern analogue) (Knell et al. 2013a; Borkovic & Russell 2014; Hone & Faulkes 2014). Nevertheless, it cannot be rejected that the bizarre snout of proterosuchids was functional in prey capture/processing and, as a result, explained by natural selection. However, there is no current evidence favouring this explanation. The presence of mutual social and/or sexual selection as drivers of snout morphology was probably widespread among the earliest branching archosauriforms and not restricted to proterosuchids because the late Early Triassic "*Chasmatosuchus*" *vjushkovi* and the early Middle Triassic *Sarmatosuchus otschevi* (both from Russia) also possess a strongly downturned premaxilla (Ochev 1961; Sennikov 1994; Gower & Sennikov 1997). The presence of these probable secondary social and/or sexual traits in non-proterosuchid early archosauriforms implies that social and/or sexual evolutionary mechanisms may be ancestral for the group as a whole or appeared independently at least twice on its early evolutionary history. In any case, these potential case or cases of social and/

or sexual selection are the oldest proposed for diapsids and may have been an important evolutionary mechanism in the dawn of the lineage that gave rise to crocodiles and dinosaurs – and their descendants, the birds – later in the Mesozoic.

Acknowledgements

Disclosure statement

Funding

References

Andersson M. 1994. Sexual selection. Princeton (NJ): Princeton Univeristy Press; p. 599.

Baczko MB von, Ezcurra MD. 2013. Ornithosuchidae. In: Nesbitt SJ, Desojo JB, Irmis RB, editors. Anatomy, phylogeny and palaeobiology of early archosaurs and their kin, vol. 379. London: Geological Society Special Publications; p. 187–202.

Bateman AJ. 1948. Intra-sexual selection in *Drosophila*. Heredity. 2:349–368.

Borkovic B, Russell A. 2014. Sexual selection according to Darwin: a response to Padian and Horner's interpretation. C R Palevol. 13:701–707.

Botha-Brink J, Smith RMH. 2011. Osteohistology of the Triassic archosauromorphs *Prolacerta*, *Proterosuchus*, *Euparkeria*, and *Erythrosuchus* from the Karoo Basin of South Africa. J Vert Paleontol. 31:1238–1254.

Broili F, Schröder J. 1934. Beobachtungen an Wirbeltieren der Karroo Formation. V. Über *Chasmatosaurus vanhoepeni* Haughton [Observations on vertebrates of the Karoo Formation. V. About *Chasmatosaurus* van Hoepen Haughton]. Sitz Bayer Akad Wiss Math-Nat Abt. 3:225–264 (in German).

Brown CM, Vavrek MJ. 2015. Small sample sizes in the study of ontogenetic allometry; implications for palaeobiology. PeerJ. 3:e818.

Bubien-Waluszewska A. 1981. The cranial nerves. In: King AS, McLelland J, editors. Form and function in birds, vol. 2. New York (NY): Academic Press; p. 385–438.

Charig AJ, Reig OA. 1970. The classification of the Proterosuchia. Biol J Linn Soc. 2:125–171.

Charig AJ, Sues H-D. 1976. Proterosuchia. In: Kuhn O, editor. Handbuch der Paläoherpetologie 13 [Handbook of Palaeoherpetology 13]. Stuttgart: Gustav Fischer; p. 11–39.

Chatterjee S. 1974. A rhynchosaur from the Upper Triassic Maleri Formation of India. Philos Trans R Soc Lond B. 267:209–261.

Clutton-Brock TH. 2007. Sexual selection in males and females. Science. 318:1882–1885.

Clutton-Brock TH. 2009. Sexual selection in females. Anim Behav. 77:3–11.

Cooper JS, Poole DFG, Lawson R. 1970. The dentition of agamid lizards with special reference to tooth replacement. J Zool. 162:85–98.

Cruickshank ARI. 1972. The proterosuchian thecodonts. In: Joysey KA, Kemp TS, editors. Studies in vertebrate evolution. Edinburgh: Oliver and Boyd; p. 89–119.

Darwin C. 1859. The origin of species by means of natural selection. London: John Murray; p. 502.

Darwin C. 1871. The descent of man and selection in relation to sex. London: John Murray; p. 828.

Dixson A, Dixson B, Anderson M. 2005. Sexual selection and the evolution of visually conspicuous sexually dimorphic traits in male monkeys, apes, and human beings. Annu Rev Sex Res. 16:1–19.

Edmund AG. 1960. Tooth replacement phenomena in the lower vertebrates. Cont R Ontario Mus Life Sci Div. 52:1–190.

Ezcurra MD. 2014. The osteology of the basal archosauromorph *Tasmaniosaurus triassicus* from the Lower Triassic of Tasmania, Australia. PLoS ONE. 9:e86864.

Ezcurra MD. 2015. Systematics and evolutionary history of proterosuchian archosauriforms [PhD thesis]. Birmingham (AL): University of Birmingham; p. 576.

Ezcurra MD, Butler RJ. 2015a. Taxonomy of the proterosuchid archosauriforms (Diapsida: Archosauromorpha) from the earliest Triassic of South Africa, and implications for the early archosauriform radiation. Palaeontology. 58:141–170.

Ezcurra MD, Butler RJ. 2015b. Post-hatchling cranial ontogeny in the Early Triassic diapsid reptile *Proterosuchus fergusi*. J Anat. 226:387–402.

Ezcurra MD, Butler RJ, Gower DJ. 2013. 'Proterosuchia': the origin and early history of archosauriformes. In: Nesbitt SJ, JB Desojo, RB Irmis, editors. *Anatomy, phylogeny and palaeobiology of early archosaurs and their kin*. London: Geological Society Special Publications. 379; p. 9–33.

Ezcurra MD, Lecuona A, Martinelli AG. 2010. A new basal archosauriform diapsid from the Lower Triassic of Argentina. J Vert Paleontol. 30:1433–1450.

Ezcurra MD, Scheyer TM, Butler RJ. 2014. The Origin and early evolution of Sauria: reassessing the permian saurian fossil record and the timing of the crocodile-lizard divergence. PLoS One. 9:e89165.

Ezcurra MD, Velozo P, Meneghel M, Piñeiro G. 2015. Early archosauromorph remains from the Permo-Triassic Buena Vista Formation of north-eastern Uruguay. PeerJ. 3:e776.

Fleming IA, Gross MR. 1994. Breeding competition in a Pacific Salmon (Coho: *Oncorhynchus kisutch*): measures of natural and sexual selection. Evolution. 48:637–657.

Goswami A, Polly PD, Mock OB, Sánchez-Villagra MR. 2012. Shape, variance and integration during craniogenesis: contrasting marsupial and placental mammals. J Evol Biol. 25:862–872.

Gould SJ. 1966. Allometry and size in ontogeny and phylogeny. Biol Rev. 41:587–638.

Gower DJ, Sennikov AG. 1997. *Sarmatosuchus* and the early history of the archosauria. J Vert Paleontol. 17:60–73.

Gross MR. 1984. Sunfish, salmon, and the evolution of alternative reproductive strategies and tactics in fishes. In: Potts G, Wootton R, editors. Fish reproduction: strategies and tactics. London: Academic Press; p. 55–75.

Gross MR. 1985. Disruptive selection for alternative life histories in salmon. Nature. 313:47–48.

Gross MR. 1987. Evolution of diadromy in fishes. Am Fish Soc Symp. 1:14–25.

Gross MR. 1991. Salmon breeding behavior and life history evolution in changing environments. Ecology. 72:1180–1186.

Holliday CM, Witmer LM. 2007. Archosaur adductor chamber evolution: integration of musculoskeletal and topological criteria in jaw muscle homology. J Morph. 268:457–484.

Hone DWE, Faulkes CG. 2014. A proposed framework for establishing and evaluating hypotheses about the behaviour of extinct organisms. J Zool. 292:260–267.

Hone DWE, Naish D. 2013. The 'species recognition hypothesis' does not explain the presence and evolution of exaggerated structures in non-avialan dinosaurs. J Zool. 290:172–180.

Hone DWE, Naish D, Cuthill IC. 2012. Does mutual sexual selection explain the evolution of head crests in pterosaurs and dinosaurs? Lethaia. 45:139–156.

Hone DWE, Wood D, Knell RJ. 2016. Positive allometry for exaggerated structures in the ceratopsian dinosaur *Protoceratops andrewsi* supports socio-sexual signaling. Palaeontol Electron. 19.1.5A:1–13.

Hosken DJ, House CM. 2011. Sexual selection. Curr Biol. 21:62–65.

Ibrahim N, Sereno PC, Dal Sasso C, Maganuco S, Fabbri M, Martill DM, Zouhri S, Myhrvold N, Iurino DA. 2014. Semiaquatic adaptations in a giant predatory dinosaur. Science. 345:1613–1616.

Jones JL, Hunter FM. 1993. Mutual sexual selection in a monogamous seabird. Nature. 362:238–239.

Kirkpatrick M, Price T, Arnold SJ. 1990. The Darwin–Fisher theory of sexual selection in monogamous birds. Evolution. 44:180–193.

Knell RJ, Sampson S. 2011. Bizarre structures in dinosaurs: species recognition or sexual selection? A response to Padian and Horner. J Zool. 283:18–22.

Knell RJ, Naish D, Tomkins JL, Hone DWE. 2013a. Sexual selection in prehistoric animals: detection and implications. TREE. 28:38–47.

Knell RJ, Naish D, Tomkins JL, Hone DWE. 2013b. Is sexual selection defined by dimorphism alone? A reply to Padian and Horner. TREE. 28:250–251.

Kokko H, Brooks R. 2003. Sexy to die for? Sexual selection and the risk of extinction. Ann Zool Fenn. 40:207–219.

Kraaijeveld K. 2003. Degree of mutual ornamentation in birds is related to divorce rate. Proc R Soc Lond B. 270:1785–1791.

Maynard Smith J, Harper D. 2003. Animal signals. Oxford: Oxford University Press; p. 396.

Miller KM, Withler RE, Beacham TR. 1996. Stock identification of coho salmon (*Oncorhynchus kisutch*) using minisatellite DNA variation. Can J Fish Aquat Sci. 53:181–195.

Modesto SP, Sues H-D. 2004. The skull of the Early Triassic archosauromorph reptile *Prolacerta broomi* and its phylogenetic significance. Zool J Linn Soc. 140:335–351.

Nesbitt SJ. 2011. The early evolution of archosaurs: relationships and the origin of major clades. Bull Am Mus Nat Hist. 352:1–292.

Ochev VG. 1961. New thecodont from the Triassic of the Orenburg region of the Cis-Urals. Paleontol J. 1961:161–162 (in Russian).

Padian K, Horner JR. 2011a. The evolution of 'bizarre structures' in dinosaurs: biomechanics, sexual selection, social selection or species recognition? J Zool. 283:3–17.-

Padian K, Horner JR. 2011b. The definition of sexual selection and its implications for dinosaurian biology. J Zool. 283:23–27.

Padian K, Horner JR. 2013. Misconceptions of sexual selection and species recognition: a response to Knell et al and to Mendelson and Shaw. TREE. 28:249–250.

Padian K, Horner JR. 2014. The species recognition hypothesis explains exaggerated structures in non-avialan dinosaurs better than sexual selection does. C R Palevol. 13:97–107.

Petrie M, Halliday T, Sanders C. 1991. Peahens prefer peacocks with elaborate trains. Anim Behav. 41:323–331.

Pitman ETG. 1939. A note on normal correlation. Biometrika. 31:9–12.

Quinn TP, Dittman AH. 1990. Pacific salmon migrations and homing: mechanisms and adaptive significance. TREE. 5:174–177.

R Development Core Team. 2013. R: a language and environment for statistical computing. Vienna: R Foundation for Statistical Computing. ISBN 3-900051-07-0. Available from: http://www.R-project.org/

Reig OA. 1970. The Proterosuchia and the early evolution of the archosaurs; an essay about the origin of a major taxon. Bull Mus Comp Zool. 139:229–292.

Sanvito S, Galimberti F, Miller EH. 2007. Vocal signalling of male southern elephant seals is honest but imprecise. Anim Behav. 73:287–299.

Sargent RC, Gross MR, van den Berghe EP. 1986. Male mate choice in fishes. Anim Behav. 34:545–550.

Schroder SL. 1982. The influence of intrasexual competition on the distribution of chum salmon in an experimental stream. In: Brannon EL, Salo EO, editors. *Salmon and trout migratory behavior symposium*. Seattle (WA): University of Washington Press; p. 275–285.

Sedlmayr JC. 2002. Anatomy, evolution, and functional significance of cephalic vasculature in archosauria [PhD thesis]. Athens (OH): Ohio University; p. 398.

Sennikov AG. 1994. The first Middle Triassic proterosuchid from eastern Europe. Dokl Akad Nauk. 336:659–661 (in Russian).

Sennikov AG. 1996. Evolution of the Permian and Triassic tetrapod communities of Eastern Europe. Palaeogeogr Palaeoclimatol Palaeoecol. 120:331–351.

Small BJ. 1997. A new procolophonid from the Upper Triassic of Texas, with a description of tooth replacement and implantation. J Vert Paleontol. 17:674–678.

Smith RJ. 2009. Use and misuse of the reduced major axis for line-fitting. Am J Phys Anthropol. 140:476–486.

Smith RMH, Botha J. 2005. The recovery of terrestrial vertebrate diversity in the South African Karoo Basin after the end-Permian extinction. C R Palevol. 4:623–636.

Tatarinov LP. 1961. Pseudosuchians of the USSR. Paleontol J. 1961:117–132 (in Russian).

Thulborn RA. 1980. The ankle joints of archosaurs. Alcheringa. 4:241–261.

Tobias JA, Montgomerie R, Lyon BE. 2012. The evolution of female ornaments and weaponry: social selection, sexual selection and ecological competition. Phil Trans R Soc B. 367:2274–2293.

Trivers RL. 1972. Parental investment and sexual selection. In: Campbell B, editor. Sexual selection and the descent of man. Chicago (IL): Aldine; p. 136–179.

Warton DI, Wright IJ, Falster DS, Westoby M. 2006. Bivariate line-fitting methods for allometry. Biol Rev. 81:259–291.

Warton DI, Duursma RA, Falster DS, Taskinen S. 2012. SMATR 3 – an R package for estimation and inference about allometric lines. Methods Ecol Evol. 3:257–259.

West-Eberhard MJ. 1983. Sexual selection, social competition, and speciation. Q Rev Biol. 58:155–183.

Witmer LM. 1995. Homology of facial structures in extant archosaurs (birds and crocodilians), with special reference to paranasal pneumaticity and nasal conchae. J Morphol. 225:269–327.

Zahavi A. 1975. Mate selection – a selection for a handicap. J Theor Biol. 53:205–214.

Zahavi A, Zahavi A. 1999. The handicap principle: a missing piece of Darwins puzzle. Oxford: Oxford University Press; p. 304.