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A NEW SPECIES OF THE LATE TRIASSIC PHYTOSAUR *PSEUDOPALATUS* (ARCHOSAURIA: PSEUDOSUCHIA) FROM PETRIFIED FOREST NATIONAL PARK, ARIZONA

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ABSTRACT—We describe a partial phytosaur skull (PEFO 31207) from the Sonsela Member of the Upper Triassic Chinle Formation of Petrified Forest National Park, Arizona as a new species of *Pseudopalatus*, *P. jablonskiae* sp. nov. Although the holotype specimen is incomplete, the new taxon is diagnosed by at least one autapomorphy and a unique suite of character-states. A phylogenetic analysis of pseudopalatine phytosaurs recovers *P. jablonskiae* as the most basal species of *Pseudopalatus*. The holotype of *P. jablonskiae* is especially important because it includes a well-preserved braincase; this portion of the skull is not preserved or described in detail for most phytosaur specimens. Additionally, *P. jablonskiae* is of biochronological significance because it is the stratigraphically lowest occurrence of *Pseudopalatus* within the Chinle Formation of Petrified Forest National Park, and provides strong evidence for the overlap of the Adamanian and Revueltian land-vertebrate faunachrons.

Keywords: Triassic, Petrified Forest, Chinle Formation, Sonsela Member, Archosauria, Phytosauridae, *Pseudopalatus*

INTRODUCTION

THE PARASUCHIA (=Phytosauria) form a basal clade of pseudosuchian archosaurs known as phytosaurs that are common in Laurasian deposits of Late Triassic age. Phytosaurs bear superficial resemblance to extant crocodylians and have been interpreted as possessing a similar semi-aquatic lifestyle (Gregory, 1962). Phytosaur taxonomy has a confused history; however, recent studies by Doyle and Sues (1995), Long and Murry (1995), and Hungerbühler (2002) have attempted to clarify ingroup relationships and taxonomy. Phytosaur alpha taxonomy has been plagued by descriptions of non-diagnostic fragmentary material, incorrect referral of material, misinterpretation of crushed and deformed specimens, inclusion of non-phytosaur specimens (aetosaurs), lost holotypes, stratophenetic assignment of specimens, and speculations about sexual dimorphism based on rostral characters. Phytosaur taxonomy is based almost exclusively on skull characteristics and early workers have been inconsistent regarding which characters are phylogenetically informative. Furthermore, character variance in the skull due to ontogeny, sexual dimorphism, and individual variation is poorly understood.

Despite the ambiguity surrounding phytosaur systematics, it is clear that this clade, although temporally restricted, was taxonomically diverse. Recent workers (e.g., Hungerbühler, 2002: table 1) recognize at least 14-17 valid species, all found in the Upper Triassic sediments of North America, Europe, and north Africa. Fragmentary material is also known from Madagascar (Gregory, 1969; Burmeister, 2000), Brazil (Kischlat and Lucas, 2003), Turkey (Buffetaut et al., 1988), and Thailand (Buffetaut and Ingavat, 1982).

In nearly all cases where relatively complete cranial material is preserved, co-occurring taxa include both robust and gracile morphs that have been interpreted as separate species. Recently, Zeigler et al. (2002, 2003) have suggested that these two forms in *Pseudopalatus* (*P. pristinus* and *P. buceros*) represent conspecific sexual dimorphs. This idea is not new (e.g., Camp, 1930; Colbert, 1947; Lawler, 1979), and though intriguing, it rests on a number of assumptions that have yet to be tested. We tentatively reject the sexual dimorphism hypothesis until further testing for the reasons outlined by Irmis (2005). In particular, it is difficult to hypothesize dimorphism in *Pseudopalatus* when similar "dimorphic" features have evolved separately several times in phytosaurs (e.g., *Rutiodon*/*Angistorhinus*, *Leptosuchus*, *Nicrosaurus*, *Mystriosuchus*, and *Redondasaurus*). It is impossible to determine with the current evidence if *P. buceros* and *P. pristinus* are sympatric but separate species, ecological dimorphs, or true sexual dimorphs. We also consider *Pseudopalatus mccauleyi* to represent a valid taxon following Ballew (1989) and Hungerbühler (2002), *contra* Long and Murry (1995) and Zeigler et al. (2002, 2003); this is supported by previous phylogenetic analyses as well as the phylogeny presented in this paper.

In September 2002, a partial phytosaur skull was discovered near Mountain Lion Mesa in Petrified Forest National Park, Arizona at locality PFV 295 (Fig. 1). Parker and Irmis (2004) tentatively referred this specimen to *Pseudopalatus* cf. *mccauleyi* based on the morphology of the squamosals and the opisthotic. Although less than complete, further examination and comparison makes it clear that PEFO 31207 is a unique specimen that represents a new spe-

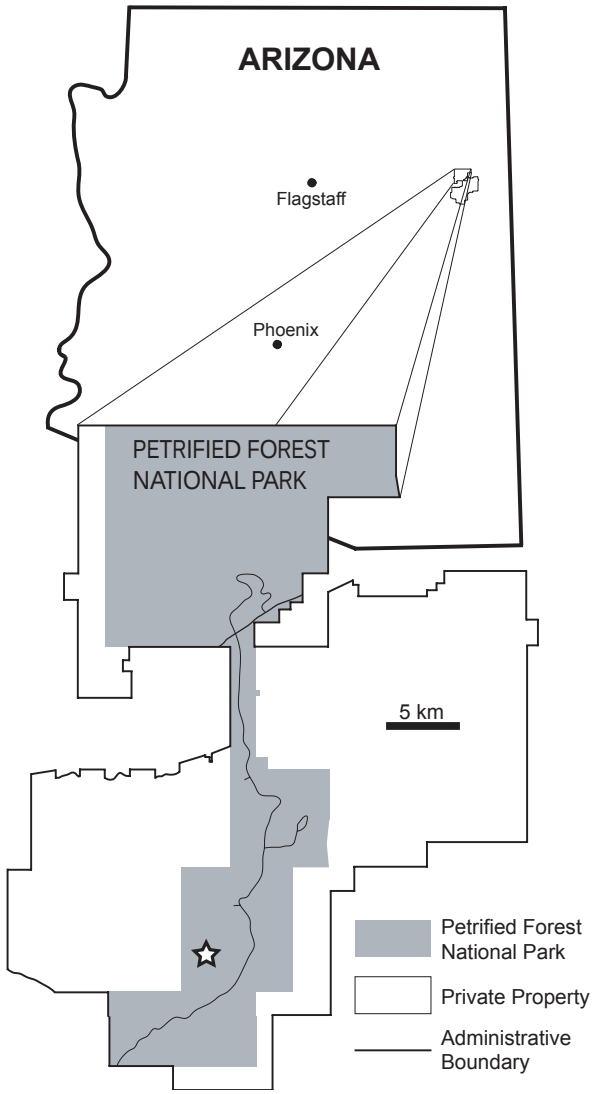

Figure *1*. Map of Petrified Forest National Park and surrounding vicinity. The type locality of *Pseudopalatus jablonskiae* n. sp. is indicated by a star.

cies with important implications for phytosaur systematics and biostratigraphy.

Institutional Abbreviations.—PEFO, Petrified Forest National Park, Arizona; UCMP, University of California Museum of Paleontology, Berkeley, California.

GEOLOGICAL SETTING

Petrified Forest National Park Vertebrate locality (PFV) 295 is in the basal Jim Camp Wash beds of the Sonsela Member of the Chinle Formation (Fig. 2; Heckert and Lucas, 2002; Woody, 2003, this volume). The Chinle Formation in Petrified Forest National Park is divisible into five members: the Mesa Redondo, Blue Mesa, Sonsela, Petrified Forest, and the Owl Rock Members. The Sonsela Member consists of a lithologically distinct package of sandstones and mudrocks that are bounded by upper and lower sandstone beds (Woody, this volume). The upper sandstone bed was historically assigned to the "Sonsela Sandstone Bed" (Akers et al., 1958; Deacon, 1990) and has recently been correlated to a local bed in PEFO called the Flattops Sandstone #1 of Billingsley (1985) (Heckert and Lucas, 2002; Woody, 2003, this volume). The lower sandstone bed was historically called the Rainbow Forest sandstone (Billingsley, 1985), now the Rainbow Forest beds (Woody, this volume). Sandstone and mudstone beds between these units display characteristic cut and fill architecture and the unit as a whole possesses a high sand content (Woody, 2003, this volume). The medial unit is called the Jim Camp Wash beds (Heckert and Lucas, 2002) and consists of strata that in the southern portion of the park had previously been assigned to the upper Petrified Forest Member (Billingsley, 1985; Long and Murry, 1995) and in the central portion of the park, to the lower Petrified Forest Member (Billingsley, 1985; Long and Murry, 1995). Historically, PFV 295 would have been considered to be low in the upper Petrified Forest Member (Long and Murry, 1995); however, the work of Heckert and Lucas (2002) and Woody (2003) suggests instead that it is low in the Sonsela Member, a few meters above the Rainbow Forest beds. This represents the stratigraphically lowest occurrence of *Pseudopalatus* in PEFO (Parker and Irmis, 2005; Parker, this volume).

The specimen was recovered from a sandy brown-gray mudstone containing pebble-sized mud rip-up clasts 10.75 meters below a thick, cross-bedded brown sandstone that represents the Flattops One bed of Woody (2003) (Fig. 2). The skull is several meters above a whitish-gray cross-bedded sandstone that is correlative with the Rainbow Forest beds (Woody, 2003). Although this sandstone is not directly visible at PFV 295, it floors the valley in this area and is exposed in a large wash to the north (Fig. 2). The conglomeratic nature of the encasing deposits suggests that the specimen was transported before burial.

TAPHONOMY

The skull was discovered palate side up, a common position for recovered phytosaur skulls. The rostrum anterior to the external nares and the ventral portion of the skull are missing. Bone fragments collected as float allowed reconstruction of a portion of the right jugal as well as much of the braincase. The skull was located in a path used by cultural researchers to access sites on the mesa top above the specimen locality and apparently the skull sustained damage from repeated human foot travel. The discoverer, Pat Jablonsky, brought the specimen to the attention of park staff who subsequently excavated it. The specimen displays very little distortion. The skull roof and the external nares has been slightly twisted left laterally and downwards causing some separation along the midline suture. The parietals are slightly depressed

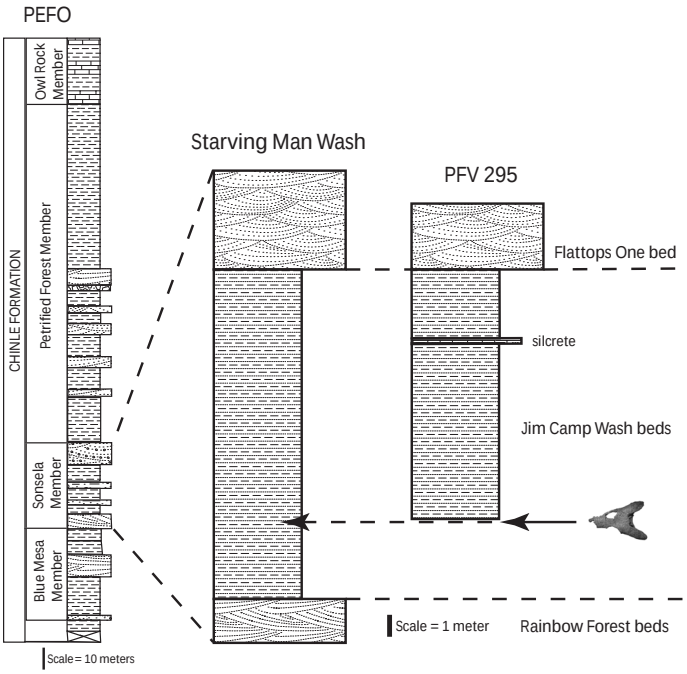

Figure 2. Measured stratigraphic sections showing the level where the holotype of *Pseudopalatus jablonskiae* n. sp. was recovered. These sections are correlated to the regional stratigraphy of the Upper Triassic Chinle Formation in the Petrified Forest National Park area.

relative to the frontals and postorbitals, although this appears to be uniform and may be natural.

SYSTEMATIC PALEONTOLOGY

ARCHOSAURIA Cope, 1869-71 sensu Gauthier, 1986
PSEUDOSUCHIA Zittel, 1887-90 sensu Gauthier, 1986
PARASUCHIA Huxley, 1875 sensu Sereno, 1991
PHYTOSAURIDAE Jaeger, 1828 sensu Doyle and Sues, 1995
PSEUDOPALATINAE Long and Murry, 1995 sensu Hungerbühler, 2002
PSEUDOPALATUS Mehl, 1928

Definition.—All phytosaurs closer to *P. pristinus* Mehl, 1928 and *P. buceros* Cope, 1881 than to *Redondasaurus gregorii* Hunt and Lucas, 1993; *Mystriosuchus planirostris* (von Meyer, 1863); and *Nicrosaurus kapffi* (von Meyer, 1860).

Revised Diagnosis.— Differs from all other phytosaurs in possessing the following synapomorphies: strongly developed medial lamella of postorbito-squamosal bar with the supratemporal fenestra reduced to slit (Hungerbühler, 2002: character 19) and visible in dorsal view; rounded top of the parieto-supraoccipital complex (Hungerbühler, 2002: character 24); dorsal portion of squamosals mediolaterally expanded forming a shelf level with the parietal and postorbital; lamina of the squamosal extends onto the paroccipital process forming the ventrolateral border of the posttemporal fenestra (unknown in *Pseudopalatus jablonskiae* n. sp.) (Hungerbühler, 2002: character 38). Differs from *Redondasaurus* and *Mystriosuchus* in possessing a posttemporal fenestra less than three times wider than high (Hungerbühler, 2002: character 41). Differs from *Redondasaurus* in having a supratemporal fenestra that is visible in dorsal view.

Comments.—There is a long history of alternating names for the clade of archosaurs known as phytosaurs. The earliest available name, Phytosauridae (also Phytosauria), was proposed by Jaeger (1828) (see Hungerbühler, 2002), although Huxley's (1875) name Parasuchia has also been widely used. Sereno (1991) was the first to explicitly phylogenetically define and diagnose this clade. He considered the clade Parasuchia to include the common ancestor and all the descendents of *Angistorhinus*, *Francosuchus*, *Mystriosuchus*, *Nicrosaurus*, *Parasuchus*, and *Rutiodon*. Doyle and Sues (1995) defined the Phytosauria as the closest common ancestor and all its descendents of *Paleorhinus* and Phytosauridae. They defined the Phytosauridae as the last common ancestor of *Angistorhinus*, *Mystriosuchus*, *Nicrosaurus*, *Pseudopalatus,* and *Rutiodon* and all descendents of their closest common ancestor. With our current understanding of phytosaur phylogenetics, Sereno's Parasuchia has the same content as Doyle and Sues' Phytosauria. Thus, under the rules of phylogenetic taxonomy (de Queiroz and Gauthier, 1992) we use the first phylogenetically defined name, Parasuchia. We recognize that *Parasuchus* (="*Paleorhinus*") may represent a paraphyletic grade (see Irmis, 2005), in which case Parasuchia and Phytosauria might not have synonymous content.

Hungerbühler (2002) did not explicitly define Pseudopalatinae phylogenetically, but he clearly used it to mean a clade that included *Nicrosaurus*, *Mystriosuchus*, *Pseudopalatus*, and *Redondasaurus* (e.g., Hungerbühler, 2002: fig. 11). Therefore, we follow Hungerbühler and define the node-based clade Pseudopalatinae as *Nicrosaurus*, *Mystriosuchus*, *Pseudopalatus*, *Redondasaurus,* and all descendents of their closest common ancestor.

Historically, phytosaur taxonomists have often chosen particular characters they found phylogenetically informative (e. g., rostral morphology) to the exclusion of other characters. This "cherrypicking" of characters based on personal preference has lead to much of the confusion in phytosaur systematics and instability in the alpha taxonomy of the group. Because of this, and also because genus-level clades have no more natural meaning than higher-level clades, we provide a phylogenetic definition for the clade *Pseudopalatus* based onour concept and that of Ballew (1989) and Hungerbühler (2002).

PSEUDOPALATUS JABLONSKIAE new species
(Figs. 3-8, 11)

Pseudopalatus cf. *mccauleyi* Parker and Irmis (2004: p.100A)
Pseudopalatus sp. Parker and Irmis (2005: p.47, fig. 3)

Diagnosis.—*Pseudopalatus jablonskiae* differs from all other phytosaurs in possessing the autapomorphy of a distinct, smooth beveled edge on the antero-medial edge of the postorbital-squamosal bar that forms a supratemporal fossa lateral to the supratemporal fenestra and a unique combination of the following characters: apomorphic characters for the *Pseudopalatus*-clade such as supratemporal fenestra that are slit-like and visible in dorsal view (hidden from dorsal view in *Redondasaurus*), and a transversely broad postorbito-squamosal bar that is heavily sculptured; squamosal tips that are not knob-like as in *P. buceros* and *P. pristinus*; thin, oar-like paroccipital process of the opisthotic that is fused to the internal squamosal process as in *P. buceros* and *P. mccauleyi*; anterior process of the squamosal enters the lateral wall of the braincase as in *M. westphali* and *L. gregorii* (unknown in *Redondasaurus*); differs from all other *Pseudopalatus* species in the lack of a lateral groove or ridge on the squamosal and in possessing squamosals that are strongly anteroposteriorly shortened.

Etymology.—For Pat Jablonsky, discoverer of the type and only known specimen.

Holotype.—PEFO 31207, posterior skull roof and braincase missing the rostrum and palate.

Type Horizon and Locality.— Basal Jim Camp Wash beds, Sonsela Member (*sensu* Woody, this volume), Upper Triassic Chinle Formation. PFV 295, near Mountain Lion Mesa, Petrified Forest National Park, Arizona (Figs. 1-2).

DESCRIPTION

The dorsal surface of the skull is heavily sculptured as in other pseudopalatines making determination of sutures other than the midline extremely difficult. The entire rostrum anterior to the posterior margin of the external nares is missing. Also missing are both quadrates, quadradojugals, maxillae, the left lacrimal, both jugals, and the entire palate. No teeth are preserved. The upper portion of the braincase and the rear of the skull were pieced together from float and are mostly complete and well-preserved. The skull has postnarial lengths of 162 mm (posterior border of external nares to the back of the parietal) and 236 mm (from the posterior border of the nares to the squamosal tips).

Nasal.—The nasals are incomplete, only the portions posterior to the external nares are well-preserved. Despite the heavily ornamented external surface, sutures with the frontals and the prefrontals are discernable (Fig. 3), demonstrating that the nasals rapidly taper medially upon contact with the prefrontal as is typical for phytosaurs. What appears to be the suture with the dorsal surface of the lacrimal is also apparent where these two bones form a tri-radiate suture with the prefrontal (Fig. 3). The posterior margin of the external nares is damaged; however, it is apparent that they were situated above the level of the skull roof as is typical for *Pseudopalatus*. The lateral surface below the external nares is preserved but badly damaged and offers no information.

Ventrally, the nasals meet the frontals posteriorly in a broad "U"-shaped suture (Fig. 4). Here, each nasal forms a distinct crescent-shaped platform with the posterior-most projection nestled between the frontal and the prefrontal. The margin with the prefrontal is thickened as is the symphysial area between the nasals, causing the crescent-shaped platform to be noticeably concave dorsally. This platform extends anteriorly to approximately midway between the nasal-frontal suture and the opening for the external nares. A sharp anteromedially directed ridge separates the crescent-shaped platform from a thinner smooth, depressed region of bone that appears to be a posteriorly expanded ventral expression of the external nares. In this region, just anterior to the anteromedial corner of the crescent-shaped platform and the nasal symphysis are two deep pits, the anteriormost being largest (Fig. 4).

Prefrontal.—Both the left and right prefrontals are present. Dorsally, they are heavily ornamented and form the anteromedial margin of the orbits. This margin is slightly raised and forms a distinct "bar" that rims that portion of the orbit (Fig. 3). The ventral prefrontal-lacrimal suture is not clear; thus the ventral extension of this element cannot be determined. As previously mentioned this element is thickened in comparison to the nasals, and thins laterally and ventrally. The ventral surface of the prefrontals is exposed but unremarkable.

Lacrimal.— The right lacrimal is preserved but badly damaged and too incomplete to provide much information, and the left lacrimal is missing. The lacrimal forms the antero-ventral border of the orbit. The orbital 'bar' of the prefrontal extends ventrally onto the lacrimal so that the posterior portion of the element is slightly raised compared to the more anterior portions (Fig. 5a, b). The suture with the postorbital is not discernible; in other phytosaurs it excludes the jugal from the ventral margin of the orbit. The anterior portion of the lacrimal is badly damaged and incomplete; the margin of the antorbital fenestra is not preserved, nor is the suture with the more ventrally situated jugal. There is a round area of missing bone in the area where the lacrimal/nasal suture was probably located (Fig. 5a).

Frontals.—The frontals are heavily sculptured and form the medial margins of the orbits (Fig. 3). The symphysial region is slightly depressed in comparison to the orbit margins, providing a slightly concave surface for this portion of the skull roof. The anterior portion of the dorsal surface slopes ventrally very slightly anteriorly to where the frontals contact the

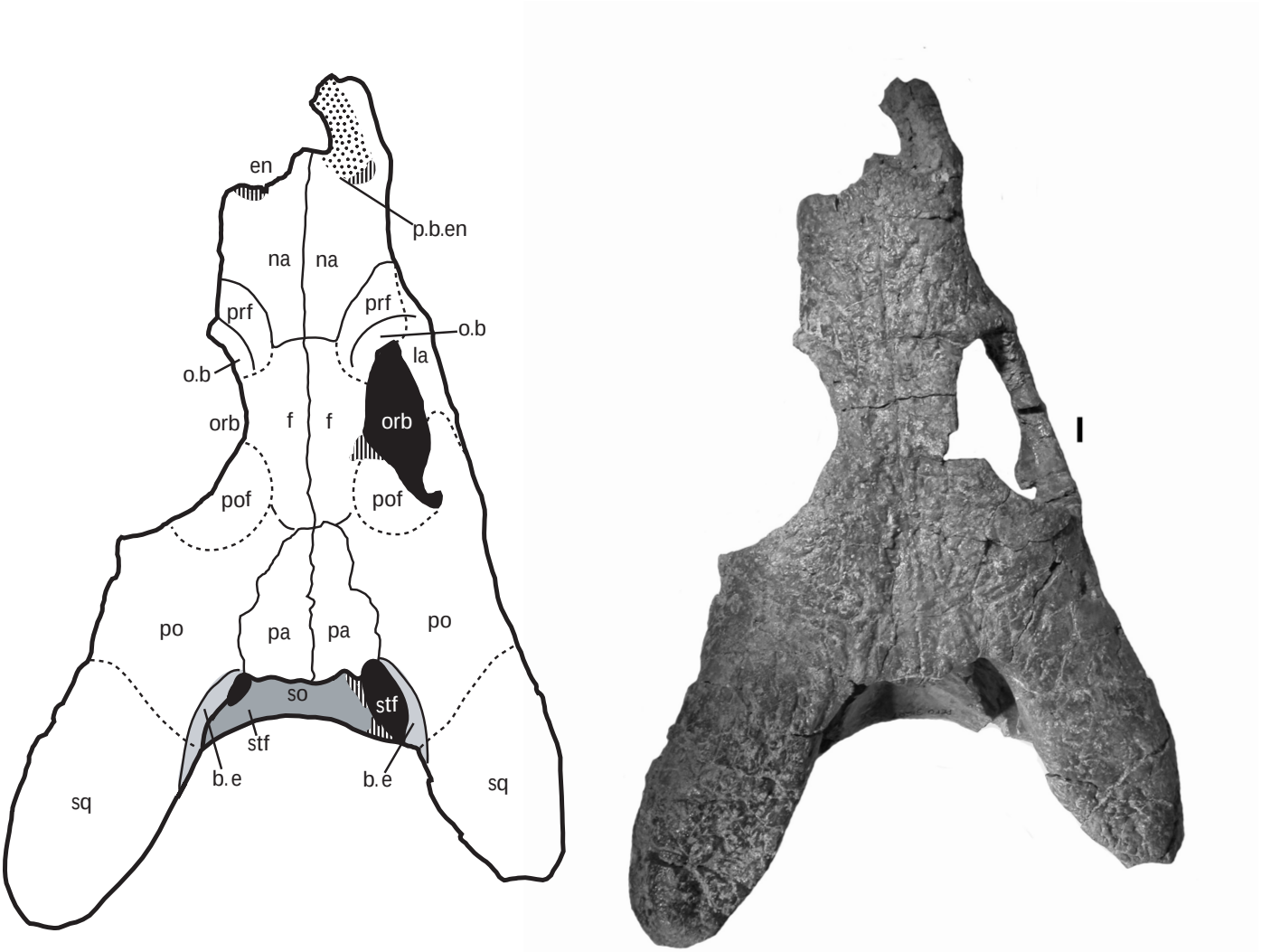

Figure *3*. PEFO 31207, skull of *Pseudopalatus jablonskiae* n. sp. in dorsal view. b.e, beveled edge; en, external nares; f, frontal; la, lacrimal; na, nasals; o.b, orbital bar; orb, orbit; p.b., posterior border of…; pa, parietal; po, postorbital; pof, postfrontal; prf, prefrontal; so, supraoccipital; sq, squamosal; stf, supratemporal fenestra. In all figures, dotting pattern represents matrix and cross-hatching pattern represents broken ares. Scale bar = 1cm.

nasals. Consequently, the orbital bar described for the prefrontals does not continue posteriorly onto the frontals.

The ventral surface of the frontals is 'hour-glass' shaped with an anterior projection that meets the nasals in a broad "U"-shaped suture (Fig. 4). Just posterior to this is an elongate depression that fits the dorsal surface of the laterosphenoid. Lateral to this depression are thin sharp ridges that form the ventromedial margin of a large ventral orbital fossa (Fig. 4). This fossa is fairly deep with medial margins that slope ventromedially at approximately 45° and delineate the ventral and dorsal expressions of the orbits.

Postfrontals.—The postfrontals cannot be discerned on the dorsal surface but are presumably similar to those of other phytosaurs in forming the posterodorsal rim of the orbits (Fig. 3). There is no raised orbital 'bar' on the postfrontals. Ventrally, they must form the posteroventral surface of the orbital fossa but the sutures are not visible (Fig. 4).

Postorbital.—The only clear sutures delineating the postorbitals are those meeting the medial border of the parietals (Fig. 3). In most phytosaurs, the postorbital forms much of the posterior and ventral margins of the orbit, and contacts the lacrimal excluding the jugal from participation in the orbital rim (Camp, 1930). Therefore, all of the right postorbital appears to be present, whereas the anterior sub-orbital process is missing from the left postorbital. The dorsal surface is heavily ornamented and the anterior portion of the postorbito-squamosal bar is thickened transversely as is typical for pseudopalatine phytosaurs (Ballew, 1989). The medial expansion of the posterior process of the postorbital results in the narrowing of the dorsal expression of supratemporal fenestra (Fig. 3). Laterally, the postorbital forms the dorsal and anterodorsal margins of the lateral temporal fenestra (Figs. 5a, b).

The contact of the posterior process of the postorbital with the squamosal is unknown because no clear suture can be discerned on the dorsal surface. Camp (1930: fig. 2b) placed the suture between the posterior portion of the supratemporal fenestra and the posterior margin of the lateral temporal fenestra in his reconstruction of "*Machaeroprosopus*

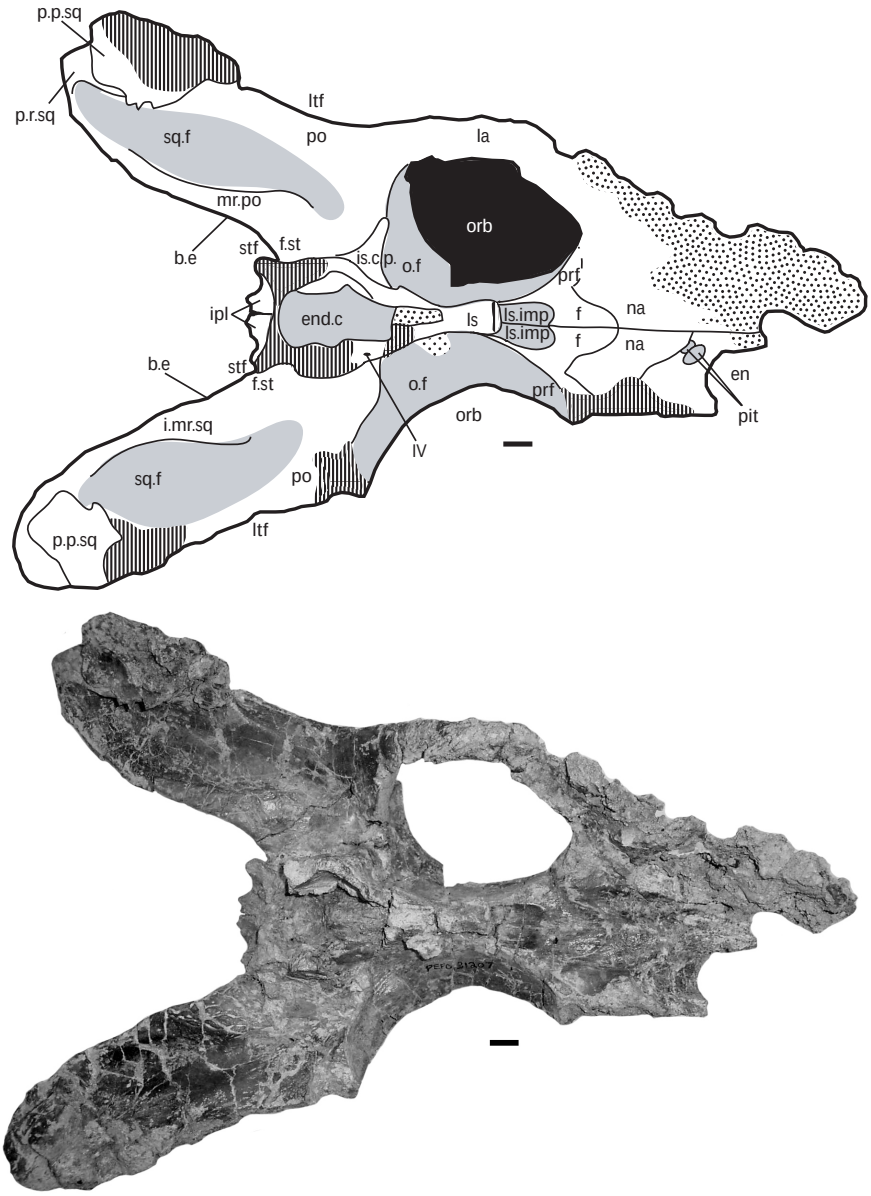

Figure *4*. PEFO 31207, skull of *Pseudopalatus jablonskiae* n. sp. in ventral view with a portion of the braincase removed. b.e, beveled edge; en, external nares; end.c, endocranial cavity; f, frontal; f.st, supratemporal fossa; ipl, incipient parietal ledge; la, lacrimal; ls, laterosphenoid; ls.c.p., capitate process of laterosphenoid ; ls.imp, impression of the laterosphenoid; mr.po, medial ridge of the postorbital; na, nasals; o.f, orbital fossa; orb, orbit; p.p., parietal process of…; pa, parietal; po, postorbital; pr.sq, posterior squamosal ridge; prf, prefrontal; sq, squamosal; sq.f, squamosal fossa; stf, supratemporal fenestra. Scale bar = 1cm.

tenuis" (*Pseudopalatus pristinus* of subsequent authors), in agreement with the Mehl's (1928: fig. 1) reconstruction of the holotype of *P. pristinus*. This is also the case for *Mystriosuchus westphali* (Hungerbühler, 2002: fig. 2) and for *Leptosuchus zunii* (= *L. adamanensis*) (Camp, 1930: fig. 9; Long and Murry, 1995). From these reconstructions, it appears that the length of the posterior process of the postorbital is equal to the length of the supratemporal fenestra in dorsal view. Accordingly, phytosaurs with slit-like supratemporal fenestrae have shorter posterior postorbital processes that shorten the total length of the postorbital-squamosal processes.

Ventrally, just lateral to the supratemporal fenestra, there is a thickened, rugose, and ornamented medial ridge that extends anteriorly to form the lateral border of a shallow fossa that is a ventral expression of the supratemporal fenestra (Fig. 4). This ridge is also expressed in the lateral edge of the supratemporal fenestra as a beveled edge partially incised into the dorsal surface of what is presumably the posteromedial portion of the postorbital (Figs. 3, 4, 6). This beveling forms what is essentially a supratemporal fossa on the lateral margin of the supratemporal fenestra. We have not noted this characteristic beveled edge in any other phytosaur and consider it an autapomorphy of *P. jablonskiae*.

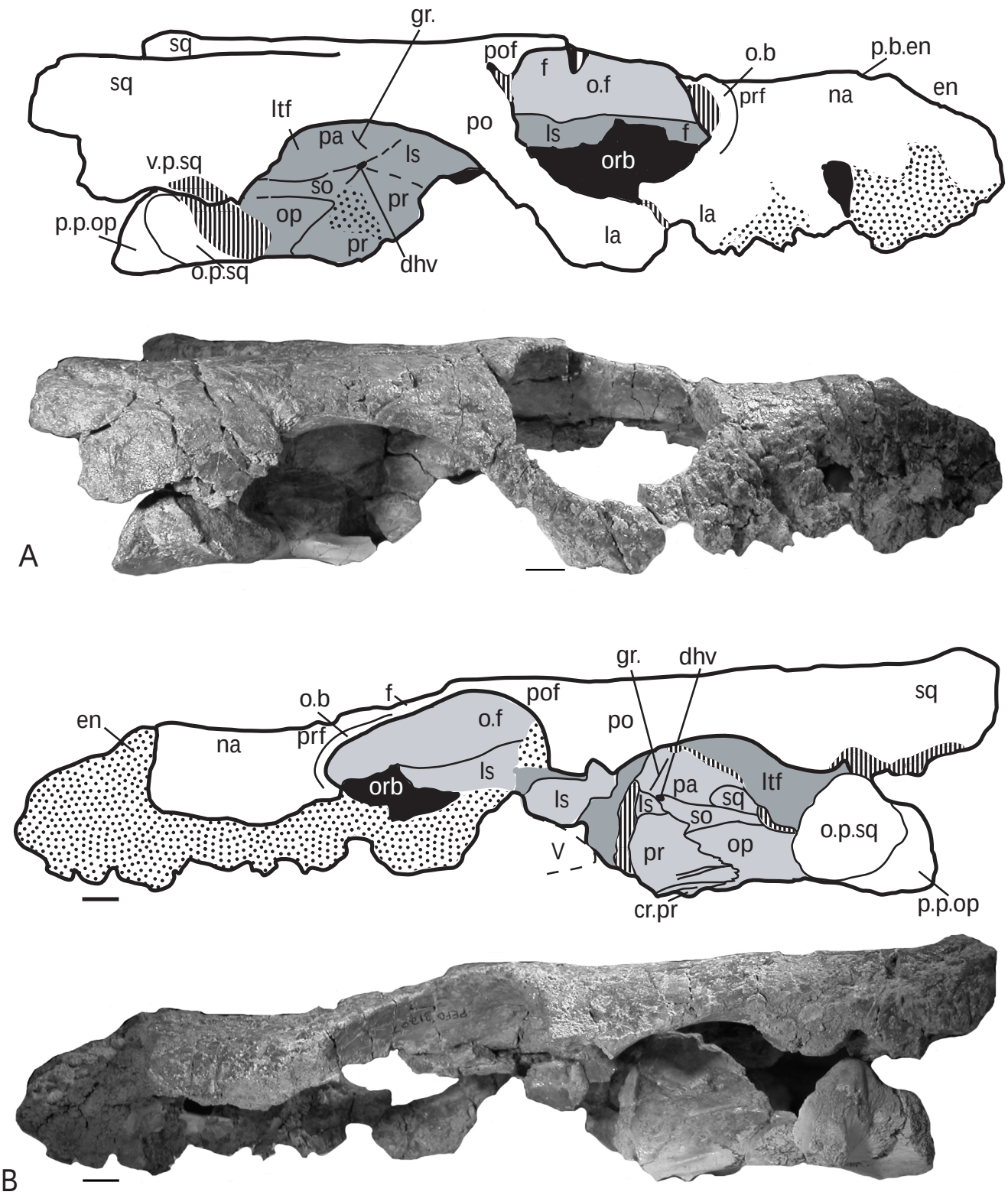

Figure *5*. PEFO 31207, skull of *Pseudopalatus jablonskiae* n. sp. *A*. right lateral view and *B*. left lateral view. cr.pr, crista prootica; dhv, dorsal head vein; en, external nares; f, frontal; gr., groove; la, lacrimal; ls, laterosphenoid; ltf, lateral temporal fenestra; na, nasals; o.b, orbital bar; o.f, orbital fossa; o.p., ophisthotic process of…; op, opisthotic; orb, orbit; pa, parietal; p.b., posterior border of…; po, postorbital; pof, postfrontal; prf, prefrontal; pr, prootic; so, supraoccipital; sq, squamosal; v.p., ventral process of....; V, notch for passage of cranial nerve V. Scale bar = 1cm.

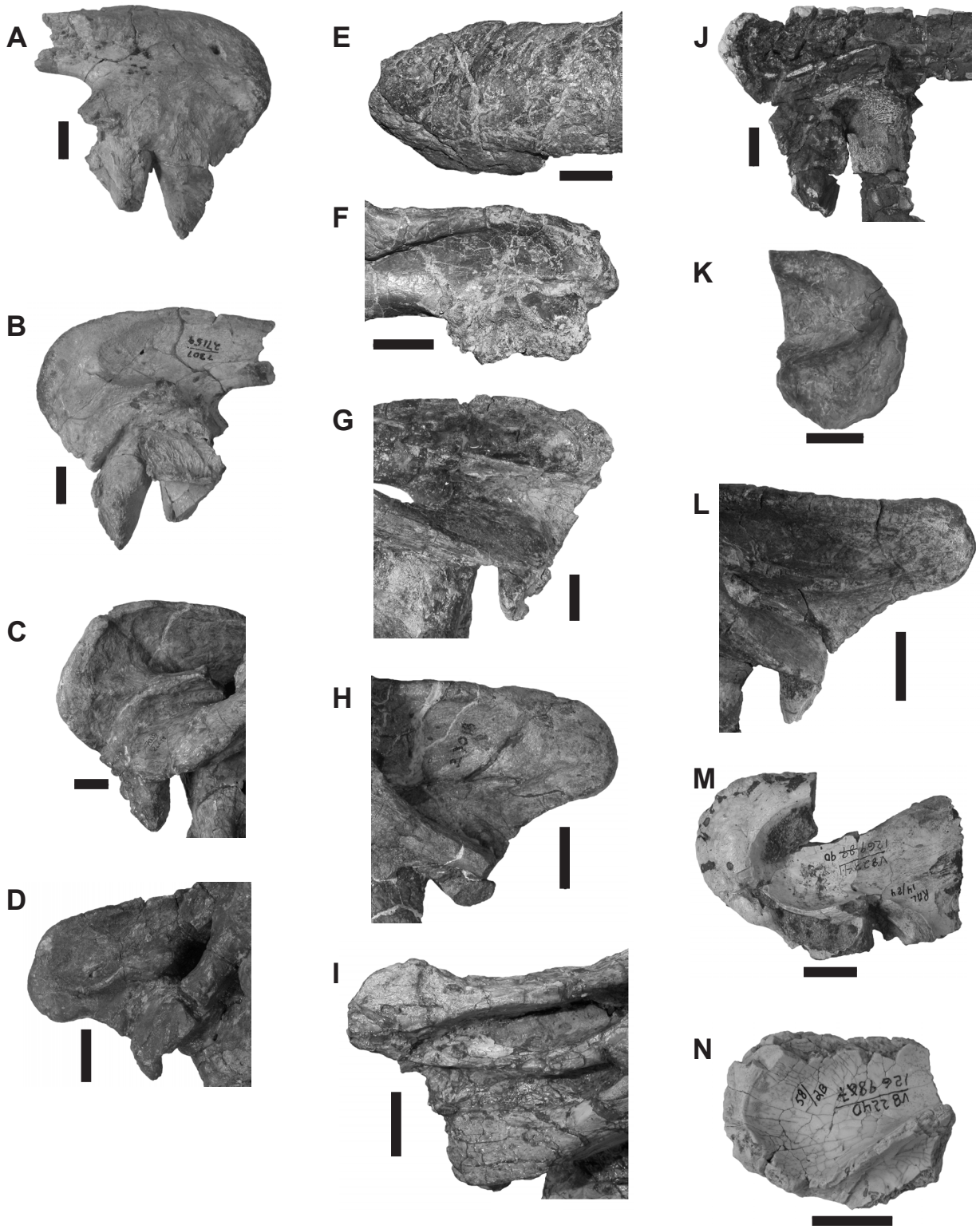

Figure *6*. Comparison of squamosals from *Leptosuchus* and *Pseudopalatus* displaying the range of morphological variation. *A*. left squamosal of *Leptosuchus adamanensis* (UCMP 27159) in lateral view; *B*. left squamosal of *Leptosuchus adamanensis* (UCMP 27159) in medial view; *C*. left squamosal of the holotype of *Leptosuchus adamanensis* (UCMP 26699) in medial view; *D*. left squamosal of *Leptosuchus crosbiensis* (UCMP 27181) in medial view; *E*. right squamosal of *Pseudopalatus jablonskiae* n. sp. (PEFO 31207) in dorsal view; *F*. right squamosal of *Pseudopalatus jablonskiae* n. sp. (PEFO 31207) in ventral view; *G*. right squamosal of the holotype of *Pseudopalatus mccauleyi* (UCMP 126999) in ventral view; *H*. right squamosal of *Pseudopalatus pristinus* (holotype of "*Machaeroprosopus*" *tenuis*, UCMP 27018) in ventral view; *I*. left squamosal of *Pseudopalatus buceros* (UCMP 34250) in ventro-medial view; *J*. left squamosal of *Leptosuchus crosbiensis* (UCMP 27182) in medial view; *K*. right squamosal of *Leptosuchus* sp. (UCMP 126737) in medial view; *L*. right squamosal of *Pseudopalatus pristinus* (UCMP 137319) in ventral view; *M*. left squamosal of *Pseudopalatus* sp. (UCMP 126990) in ventral view; *N*. left squamosal of *Pseudopalatus* sp. (UCMP 126987) in ventral view. All scale bars = 2 cm.

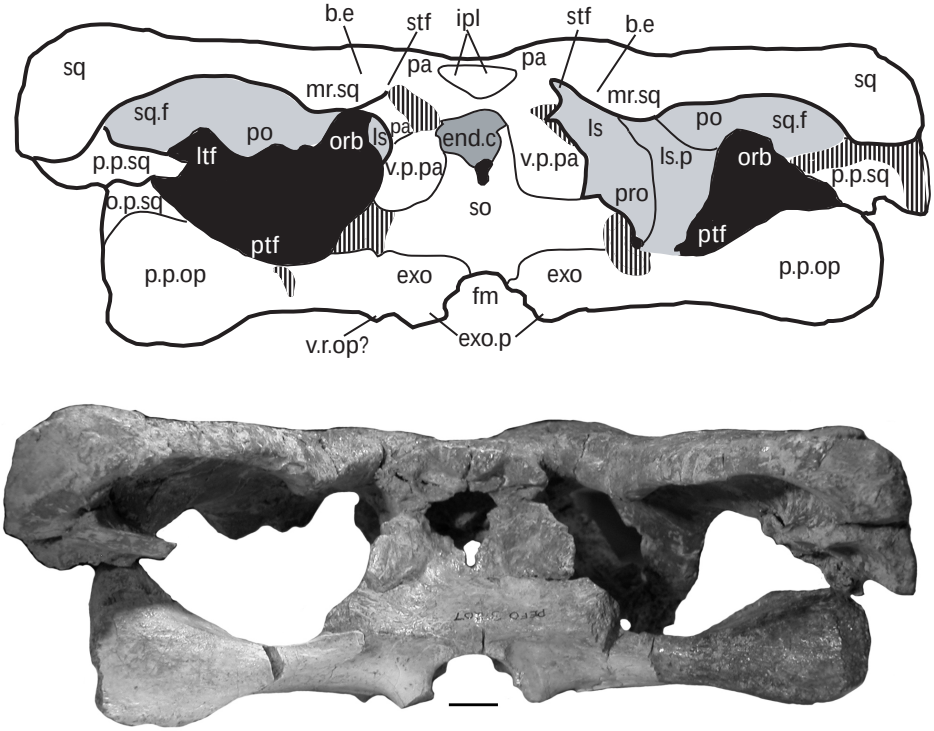

Figure 7. PEFO 31207, skull of *Pseudopalatus jablonskiae* n. sp. in posterior view. b.e, beveled edge; end.c, endocranial cavity; ex.p, exocipital pillar; exo, exoccipital; fm, foramen magnum; ipl, incipient parietal wings; ls, laterosphenoid; ls.c.p., capitate process of laterosphenoid ; m.r.sq, medial ridge of the squamosal; o.p., ophisthotic process of…; orb, orbit; p.p., parietal process of…; pa, parietal; po, postorbital; pr, prootic; ptf, post temporal fenestra; so, supraoccipital; sq, squamosal; sq.f, squamosal fossa; stf, supratemporal fenestra; v.p. ventral process of…; v.r., ventral ramus of… Scale bar = 1cm.

Parietals.—Both parietals are preserved. They have a sculptured dorsal surface, and are slightly depressed relative to the rest of the skull roof, allowing clear identification of their sutures. The supratemporal fenestrae are strongly incised into the posterolateral corner of the parietal, a character found in all pseudopalatines except *Redondasaurus* (Fig. 3; Hunt and Lucas, 1993). Two small posterior projections (incipient parietal ledge) occur along the symphysial surface and the posterior projections of the parietals 'roof' the supraoccipital like in other pseudopalatine phytosaurs (Fig. 4; Ballew, 1989).

Posteriorly, two wedge-shaped processes sharply downturn ventrally to laterally contact the external surface of the supraoccipital (Fig. 7). Internally, these processes form the dorsolateral wall of the braincase contacting the laterosphenoid anteroventrally and an anterior process of the supraoccipital ventrally (Figs. 5a, b). The contact between this process of the supraoccipital and the laterosphenoid prohibits contact between the parietal and the prootic and opisthotic. In *Mystriosuchus westphali*, these wedge-shaped processes are a separate ossification, which Hungerbühler (2002) called a 'supernumerary occipital' bone. Camp (1930) considered these processes to represent tabulars in *Leptosuchus gregorii*, but in *P. jablonskiae* no suture is visible and therefore these elements are most likely part of the parietal as in *Nicrosaurus kapffi* (McGregor, 1906), *Pseudopalatus pristinus* (Mehl, 1928; Ballew, 1989), and *Pseudopalatus mccauleyi* (Ballew, 1989).

Squamosals.—Both squamosals are present and almost complete except for the internal squamosal processes (portions of which are fused to the paroccipital processes of the opisthotics) and the parietal processes of the squamosal (the parieto-squamosal arcade of McGregor (1906) and earlier authors). The squamosals have an approximate length of 70 mm and are transversely broad with a flat medial dorsal surface and rounding laterally to form an almost vertical lateral surface roofing the lateral temporal fenestrae (Fig. 3). The squamosals lack a prominent lateral 'groove' or ridge found in many pseudopalatine squamosals (Figs. 6, 8; Murry and Long, 1989). The squamosal tips are rounded, not pointed as in *P. pristinus* and *P. buceros*, and do not possess the thickened "pinched" knob-like process that is always found in *P. pristinus* and *P. buceros* (Fig. 6; Ballew, 1989). Although the squamosals of *P. jablonskiae* show some similarities to *Leptosuchus*, the broad dorsal surface of the squamosal and the dorsoventrally shortened nature of the squamosal are different from any known specimens of *Leptosuchus*. The squamosals of *P. jablonskiae* are similar to those of *Redondasaurus gregorii* in lacking the knob-like posterior process and a lateral ridge; however, the postorbital/squamosal bar is much wider mediolaterally (52% length to width ratio of process in *R. gregorii* compared to 32% in *P. jablonskiae*) in *Redondasaurus* effectively hiding the supratemporal fenestra in dorsal view (Hunt and Lucas, 1993).

Ballew (1989) described the squamosals of *Pseudopalatus* (especially those of the *P. mccauleyi*) as being anteroposteriorly short in comparison to *Leptosuchus*. The squamosals of *P. jablonskiae* are proportionally even more shortened. The distance from the posterior rim of the external nares to the back of the parietals makes up 68% of the total postnarial length (external nares to the squamosal tips) in *P. jablonskiae* compared to 61% in UCMP 126999 (holotype of *P. mccauleyi*), and 62% in UCMP 34250 (referred to *P. buceros*) and UCMP 27018 (holotype of *M. tenuis*, referred to *P. pristinus*). A referred specimen of *Redondasaurus* (YPM 3300) has a ratio close to 65%. The higher percentages in these taxa is due to a greater length of the squamosal.

The internal squamosal process is preserved and fused to the paroccipital processes of the opisthotics (Figs. 5b, 7). Ballew (1989) considered fusion of the opisthotic to the squamosal to be a synapomorphy of *P. buceros* and *P. mccauleyi*, exclusive of *P. pristinus*, although this character is often difficult to evaluate in articulated skulls.

BRAINCASE

Much of the dorsal and posterodorsal portions of the braincase are preserved, including much of the otic capsule. Only an isolated basipterygoid process was recovered from the ventral portion of the braincase. An isolated partial braincase of *Pseudopalatus* cf. *pristinus* (PEFO 34042) was used to help determine sutures within the endocranial cavity and in the lateral braincase wall. Because very few descriptions of pseudopalatine braincases exist, both specimens will be described here. When a description specifically refers to PEFO 34042, the specimen will be explicitly mentioned, otherwise all of the following description pertains solely to PEFO 31207 or to both specimens.

Parietal.—The ventral process of the parietal forms the dorsolateral wall of the braincase (Figs. 5b, 9). Both Camp (1930) and Hungerbühler (2002) considered this process to represent a separate ossification; a "tabular" bone in *Leptosuchus gregorii* and a supernumerary bone in *Mystriosuchus westphali*. In *M. westphali* there is a distinct suture that demonstrates that this process does indeed represent an element separate from the parietal. Such a suture is not clear in the holotype of *L. gregorii*. There is no evidence in PEFO 34042 or *P. jablonskiae* to suggest that they have this separate ossification. In *P. jablonskiae*, the posterior portion of the parietal process meets a process of the squamosal that invades the lateral braincase wall (Fig. 5b).

The dorsolateral surface of the ventral projection of the parietal in *P. jablonskiae* is marked by a distinct groove that originates just below the level of the skull roof and continues antero-ventrally to contact the suture with the laterosphenoid, anterior of the opening for the dorsal head vein

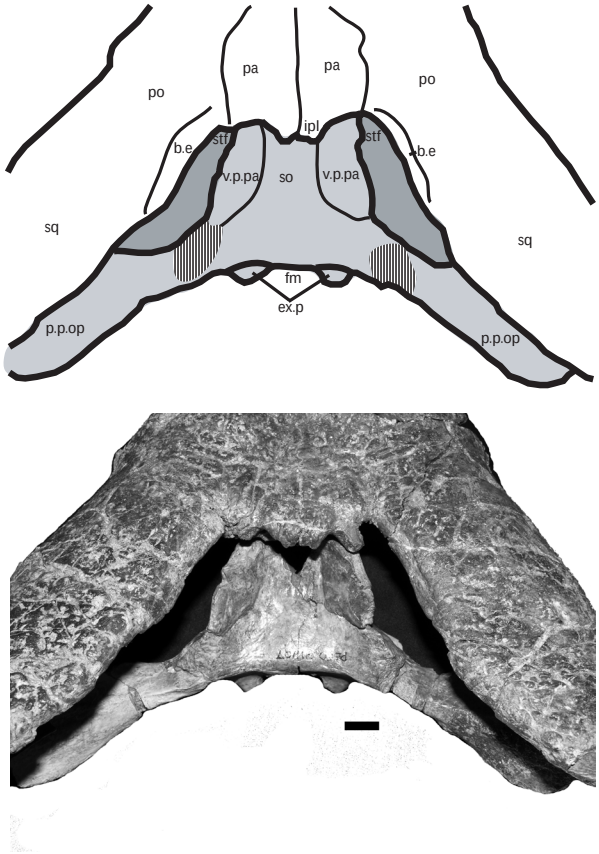

Figure 8. PEFO 31207, skull of *Pseudopalatus jablonskiae* n. sp. in posterodorsal view. b.e, beveled edge; ex.p, exoccipital pillar; fm, foramen magnum; ipl, incipient parietal ledge; p.p., parietal process of…; pa, parietal; po, postorbital; so, supraoccipital; sq, squamosal; stf, supratemporal fenestra; v.p. ventral process of…Scale bar = 1cm.

(Figs. 5a, b). The purpose of this groove is a mystery. It is not an artifact of preparation because the groove is present in the same position on both sides of the skull. It does not represent a suture and is most likely a path for a blood vessel. This structure is not present in PEFO 34042.

Squamosal.—A U-shaped medial process of the squamosal enters the lateral braincase wall dorsal to the anterior supraoccipital process, where it meets the posterior portion of the parietal process (Fig. 5b). As mentioned above, this process also occurs in *L. gregorii* (Camp, 1930) but not in PEFO 34042. Hungerbühler (2002) figures a "squamosal lamella" in the braincase of *M. westphali*; however, it divides the anterior portion of the opisthotic (exoccipital) and does not contact the supernumerary bone (ventral process of the parietal in other forms). The contribution of the squamosal in the lateral wall of the braincase may have systematic value. According to Hungerbühler (2002) this contribution occurs in *Pseudopalatus buceros* and *P. mccauleyi*, but not in *P. pristinus*. It also occurs in *Redondasaurus bermani* but is absent in *R. gregorii*. Thus, the lack of this medial extension of the squamosal in PEFO 34042 along with the presence of a knob-like squamosal suggests that this specimen is referable to *P. pristinus* even though it consists of only a few isolated elements.

Supraoccipital.—In posterodorsal view the supraoccipital is a triangular-shaped element that slopes posteroventrally roofing the foramen magnum (Fig. 8). Dorsally and dorsolaterally the supraoccipital meets the parietals (Fig. 7). There is no evidence for a separate supernumerary bone ("tabular") as described for *Mystriosuchus westphali* and *Leptosuchus gregorii* by Hungerbuhler (2002) and Camp (1930) respectively. Camp (1930) also restricted the supraoccipital to the region just dorsal to the foramen magnum and considered two separate elements, interparietals, to contact the parietals in *L. gregorii*. There is no evidence for these elements in *Pseudopalatus*. Ventrolaterally, the supraoccipital contacts the exoccipitals and forms the dorsal margin of the foramen magnum.

Dorsal and lateral to the ventrolateral corners of the supraoccipital, an anteromedially directed flange is sandwiched between the parietal and squamosal dorsally and the opisthotic and prootic ventrally (Figs. 5b, 9). At its anteriormost extent it meets the laterosphenoid just below the parietal. At this junction is a foramen that probably represents the exit for the vena capitis dorsalis (dorsal head vein). Hungerbühler (2002) identified a similar flange in *Mystriosuchus westphali* as an anterior projection of the squamosal; however, reference to PEFO 34042 demonstrates that in *Pseudopalatus* this flange is a continuation of the supraoccipital (Fig. 11). An autapomorphy of *Mystriosuchus* is a squamosal/prootic contact (Hungerbühler, 2002), a character state that is absent in *Pseudopalatus* and *Leptosuchus* (Camp, 1930).

Internally, the supraoccipital forms almost the entire roof and a portion of the lateral walls of the posterior endocranial cavity. At its anteriormost extent, just posteroventral to the suture with the laterosphenoid, a prominent foramen is present that represents the internal path of the dorsal head vein (Fig. 5b).

Exoccipitals.—The sutures between the exoccipitals and the opisthotics are indistinguishable as in most archosaurs. The exoccipitals form the lateral margins of the foramen magnum and are prevented from meeting dorsally by the supraoccipital (Fig. 7). The ventral portions are not preserved. The preserved dorsal portion, which borders the proximal end of the paroccipital process, is roughly trapezoidal-shaped in ventral view with the medial edge and posteromedial corner meeting the supraoccipital and forming a portion of the lateral wall of the posterior portion of the endocranial cavity just inside the foramen magnum (Figure 12). The anteriormost corner is dorsally excavated, forming the posterodorsal portion of the vestibule of the inner ear. Here, the exoccipital meets the prootic anteriorly and laterally (Fig. 12). In PEFO 31207 the anterior portion of the right vestibule is free of matrix and although the lateral wall is missing, some internal details can be made out. The medial wall is damaged but appears to have not been closed. A similar condition is present

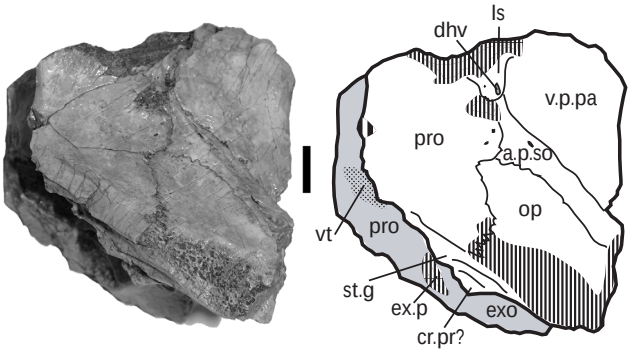

Figure 9. PEFO 34042, partial braincase of *Pseudopalatus* cf. *pristinus* in left lateral view. a.p. anterior process of…; cr.pr, crista prootica; dhv, dorsal head vein; ex.p, exoccipital pillar; exo, exoccipital; ls, laterosphenoid; op, opisthotic; pa, parietal; pr, prootic; so, supraoccipital; st.g, stapedial groove; v.p. ventral process of…; vt, vestibule of the inner ear. Scale bar = 1cm.

in PEFO 34042 (Fig. 12). This lack of closure results in an opening at the junction between the prootic, supraoccipital and the exoccipital in the dorsomedial corner of the vestibule (Figs. 11, 12). This resulting foramen would most likely represent the opening for the endolymphatic sac (Camp, 1930). Just dorsal to this foramen is a second opening in the roof of the vestibule, which Camp (1930) labeled as a superior sinus. The posterodorsal corner of the vestibule (part of the exoccipitals) is marked by a pronounced foramen that Camp (1930) identified as the entrance of the posterior semicircular canal (Figs. 11, 12).

Only the dorsal-most portions of the exoccipital pillars are preserved. Just anterior to these within the foramen magnum are two prominent fenestrae that may represent a path for the hypoglosseal nerve (XII) (Figs. 11, 12). Alternatively, it could represent the interior expression of the metotic foramen and the opening for cranial nerves IX, X, and XI. Unfortunately, the ventral portion of the exoccipitals is missing, obfuscating other possible locations for these structures. A perusal of the available literature on pseudosuchian braincases turned up no other taxa with foramina in this position, yet they are present in both *P. jablonskiae* and PEFO 34042.

Because the ventral portion of the exoccipitals is not preserved in both specimens, determination of the morphology and locations of the metotic fissures, the fenestra ovalis is difficult, and a determination of the make-up of the floor of the endocranial canal is not possible. Anterolateral to the exoccipital pillar, the stapedial groove is present. This groove extends posterolaterally from the vestibular wall back to an area approximately halfway along the paroccipital process (Fig. 11). The groove is demarcated by two elongate ridges that are parallel to the orientation of the paroccipital process. The anterior ridge is situated along the suture between the exoccipitals and the prootic. Posterior to the stapedial

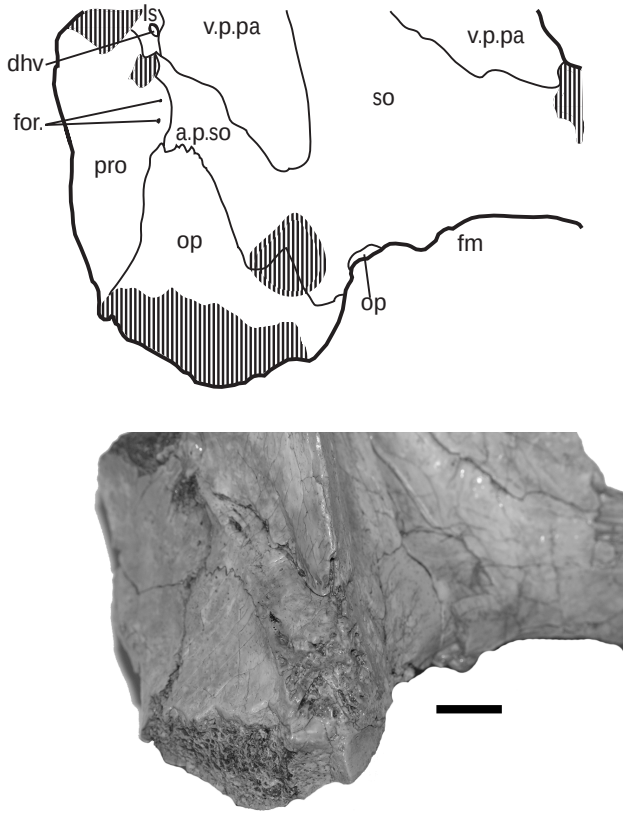

Figure *10*. PEFO 34042, partial braincase of *Pseudopalatus* cf. *pristinus* in left posterolateral view. a.p. anterior process of…; dhv, dorsal head vein; fm, foramen magnum; for., foramina; ls, laterosphenoid; op, opisthotic; pa, parietal; pr, prootic; so, supraoccipital; v.p. ventral process of…. Scale bar = 1cm.

groove is another parallel trough that is directed sharply medially at its distal end where it occurs between the posterior corner of the vestibule and the anterior margin of the exoccipital pillar. This groove intersects the foramen mentioned above that is just within the foramen magnum and likely represents the dorsal-most expression of the metotic fissure (i.e., the jugular groove).

Opisthotics.—In ventral view, the suture between the opisthotic and the supraoccipital is indistinguishable. The opisthotic has an anteriorly directed, triangular shaped process that is bounded by the prootic ventrally and the anterior process of the supraoccipital dorsally (Fig. 5b, 9). The ventral ramus of the opisthotic is not preserved. The majority of the opisthotic consists of the paroccipital process which is directed posterolaterally. The process is "twisted" posteroventrally, thinning medially before expanding into a broad head that articulates with the squamosal anteriorly and laterally (Figs. 7, 11). Ballew (1989) described this morphology as "oar-shaped". The opisthotic process forms the entire ventral margin of the supratemporal fenestra.

The internal process of the squamosal is still firmly fused to the anterolateral face of the distal end of the paroccipital process. In phytosaurs, Ballew (1989) considered this fusion to be a synapomorphy of *Pseudopalatus mccauleyi and P. buceros*. *P. jablonskiae* shares with *P. mccauleyi* this fusion of the paroccipital process with the squamosal, an oar-shaped paroccipital process, and a squamosal tip that is not knob-like (Ballew, 1989). These similarities led Parker and Irmis (2004) to originally refer PEFO 31207 to *P. mccauleyi*.

Epiotics.—In most reptiles the epiotic fuses indistinguishably with the supraoccipital (Currie, 1997). In PEFO 34042 and *P. jablonskiae*, an anterior process of the supraoccipital that is present in the lateral wall of the braincase may represent the epiotic (Figs. 5, 9; Hungerbühler, 2002); however, because there is no clear suture between this process and the main body of the supraoccipital (Fig. 10) we consider it to be an anterior process of the supraoccipital.

Hungerbühler (2002) described a ventrally open, crescent-shaped crest that forms the posterodorsal border of the epiotic in *Mystriosuchus westphali*. Ventral to this crest is the foramen for the vena capitis dorsalis. Whereas this crest and associated foramen is clearly visible in PEFO 34042, in *P. jablonskiae* the vena capitis dorsalis is ventral to a slightly developed ridge that is straight rather than crescentic. In both PEFO 34042 and *P. jablonskiae* this ridge is part of the posterior margin of the wedge-shaped process of the parietal (the supernumerary bone in *M. westphali*) (Figs. 5a, 9). Unfortunately, the area anterior to the vena capitis dorsalis is not well-preserved in either of the PEFO specimens; however, what is preserved appears to represent the posterior portion of the laterosphenoid (Fig. 9). Camp (1930) described this foramen for *Leptosuchus gregorii* piercing the anterodorsolateral surface of the anterior portion of the supraoccipital (= epiotic of other authors) where it meets the "tabular" bone; however, in both of the Petrified Forest specimens there is a clear suture separating the anterior supraoccipital process from the foramen (Figs. 5a, 9).

Prootics.—PEFO 31207 preserves much of both prootics. The anterior portions are damaged and incomplete in places, whereas the posterior portions are preserved in both specimens. A posteriorly tapering process overlaps the anteroventral surface of the opisthotic at the base of the paroccipital process (Fig. 12). Behind this, the prootic forms much of the lateral wall of the braincase (Figs. 5b, 9). The lateral sutures with the opisthotic and anterior portion of the supraoccipital are clear. This suture starts ventral to the opisthotic, just dorsal to the tympanic fossa of the paroccipital process, and continues posterodorsally to an area just ventral to the vena capitis dorsalis. The prootic is separated from the parietal by the union of the anterior supraoccipital process with the laterosphenoid. Ventrally, the prootic includes the medial extent of the stapedial fossa at the base of the paroccipital process, with a straight suture parallel to the paroccipital process that meets the exoccipital posteriorly (Fig. 12). Medially, the prootic forms a

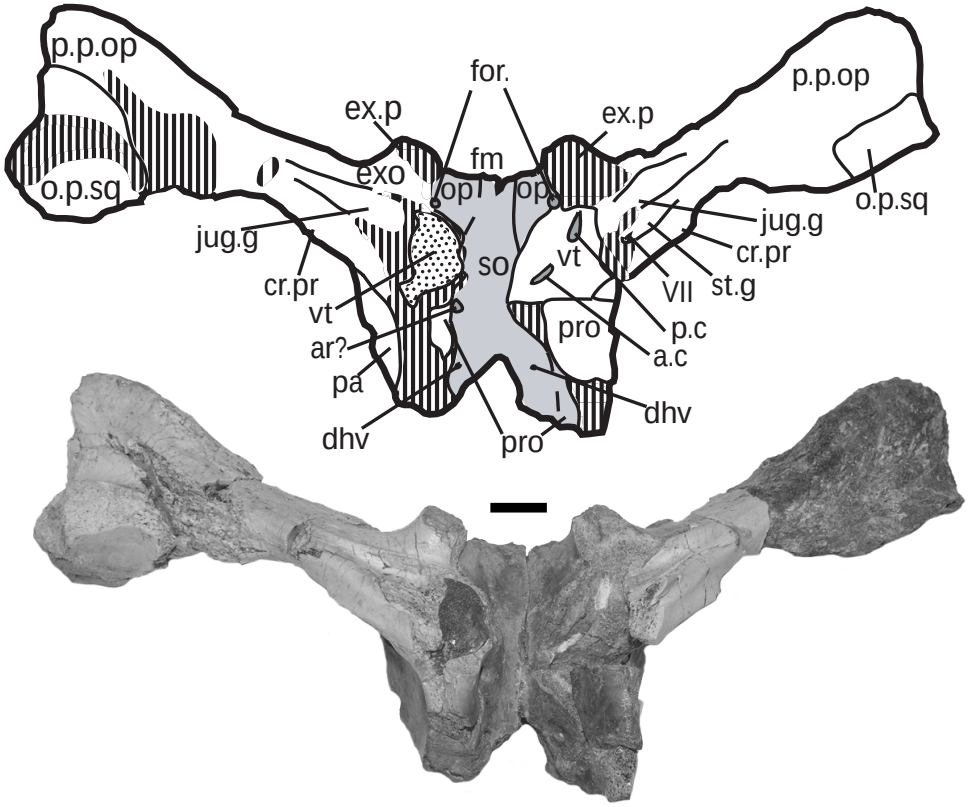

Figure *11*. PEFO 31207, partial braincase of *Pseudopalatus jablonskiae* n. sp. in ventral view. ar, auricular recess; cr.pr, crista prootica; dhv, dorsal head vein; e.s., endolymphatic sac; ex.p, exoccipital pillar; exo, exoccipital; fm, foramen magnum; for., foramina; jug.g., jugular groove; ls, laterosphenoid; o.p., ophisthotic process of…; op, opisthotic; p.c, posterior canal; p.p., parietal process of…; pa, parietal; pr, prootic; s.sin, superior sinus; so, supraoccipital; sq, squamosal, st.g, stapedial groove; vt, vestibule of the inner ear. Scale bar = 1cm.

longitudinal suture with the supraoccipital; the dorsalmost extent of this suture is unclear due to missing bone.

Posteroventrally, the prootic forms the anterolateral and anteromedial margins of the vestibule of the inner ear. Lateral to the anterolateral margin of the vestibule, the prootic forms the anterior portion of the base of the paroccipital process (Fig. 12). Two grooves are present that are parallel with the paroccipital process and are separated by a sharp ridge that although broken proximally appears to have curved to project ventromedially. The posteriormost groove is part of the stapedial groove which meets the vestibule wall laterally. The anteriormost groove ends in a small foramen that probably represents an opening for the facial nerve (VII) (Fig. 11; Camp, 1930). Anterolateral to this is another sharp ridge with an anterolaterally facing crest (Figure 12). This crest originates a short distance from the posteriormost extent of the prootic tongue that overlaps the opisthotic, and progresses anteromedially where it then curves anteriorly before flattening on the lateral prootic wall just dorsal to the point where the prootic divides into dorsal and ventral rami (the prootic foramen or trigeminal notch) (Hungerbühler, 2002). This ridge most likely represents the crista prootica; however, none of the existing phytosaur braincase descriptions (e.g., Camp, 1930; Chatterjee, 1978; or Hungerbühler, 2002) have labeled this structure or noted the presence of the crista prootica.

The interior surface of the prootic just anterior to the vestibule and along the supraoccipital/prootic suture is a pronounced foramen (Fig. 11). Chatterjee (1978) labeled an opening in a similar position in *Parasuchus* as the endolymphatic sac; however Gower and Nesbitt (in press) considered this opening in the archosaur *Arizonasaurus babbitti* to represent an opening for the auricular recess.

The anterior portions of the prootics are incompletely preserved and damaged in PEFO 31207. Hungerbühler (2002) described a thin, sinuous slit that divided the anterior portion of the braincase into dorsal and ventral portions. In *Mystriosuchus westphali* the slit originates in the prootic, effectively dividing that bone as well. This is similar to the condition found in *Parasuchus* (Chatterjee, 1978) and *Leptosuchus* (Camp, 1930). The posterior portion of this slit is the opening for the trigeminal nerve (V); however, this area can only be inferred for *P. jablonskiae* as it is missing, although the prootics are divided into dorsal and ventral rami suggesting that this slit was present (Fig. 5b). Only the proximal portion of the ventral margin of the dorsal branch is preserved on the right side, whereas on the left side a more medial portion is preserved that is probably part of the laterosphenoid and will be described as part of that bone. Thus, the anterior extent of the prootic

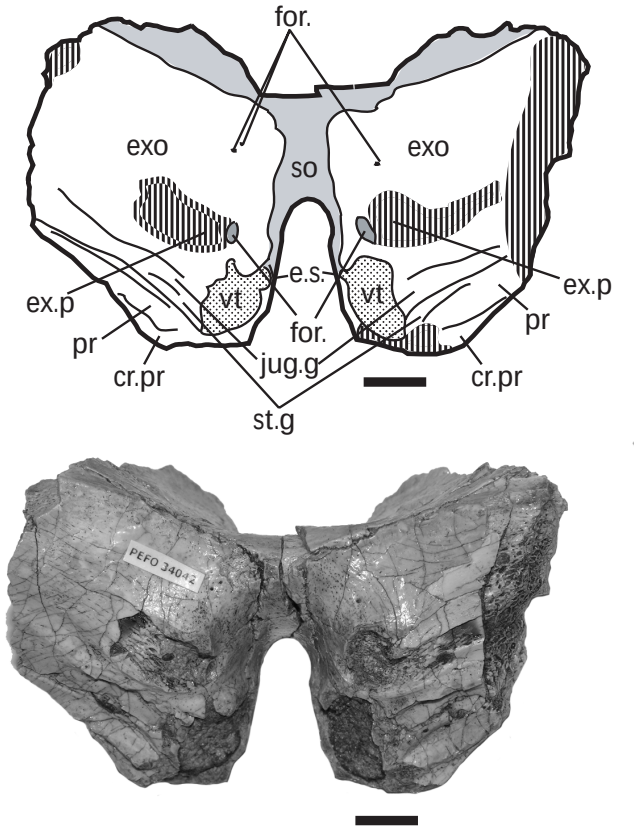

Figure *12*. PEFO 34042, partial braincase of *Pseudopalatus* cf. *pristinus* in ventral view. cr.pr, crista prootica; e.s., endolymphatic sac; ex.p, exoccipital pillar; exo, exoccipital; for., foramen; ls, laterosphenoid; p.c, posterior canal; p.p., parietal process of…; pa, parietal; pr, prootic; s.sin, superior sinus; so, supraoccipital; sq, squamosal, st.g, stapedial groove; typ.g, tympanic groove; vt, vestibule of the inner ear. Scale bar = 1cm.

cannot clearly be determined, but it most likely did not extend much farther anteriorly than the base of the paroccipital process.

Laterosphenoids.—The posterior portion of the laterosphenoid is triangular in shape and points posteriorly, meeting the prootic ventrally, the parietal dorsally and the anterior process of the supraoccipital posteriorly (Figs. 5a, 9). The anteriormost portions are badly damaged, with much of the prootic/laterospenoid suture missing and the laterosphenoid/parietal suture being indeterminable along much of its length. The walls are thin and deep in the otic region, shallowing anteriorly in the sphenoid region where the laterosphenoids meet medially to form a pronounced hour-glass-shaped ridge between the orbits (Fig. 4). A vertically oriented thickened bar (the capitate process of the laterosphenoid) is formed along the lateral wall of the laterosphenoid from the dorsal margin of the trigeminal notch to a portion of the skull roof where the postorbital is located (Fig. 4). On the left side of the braincase where this process meets the forward portion of the trigeminal notch is a small foramen that according to Chatterjee (1978) is the opening for the trochlear nerve (IV) (Fig. 4).

A portion of the interorbital septum is present; it is unclear whether this represents a separate orbitosphenoid bone as in *Mystriosuchus westphali* or just an anterior projection of the laterosphenoid as in *Leptosuchus gregorii*. The anteriormost portion of this bone (medial to the anterior margins of the orbits) is missing; a shallow depression in the skull roof shows that the bone extended to the anterior border of the orbits, was lobate, and transversely expanded (Fig. 4).

Basisphenoid.—As mentioned previously, the ventral portion of the occiput and the entire sphenoid region are missing with the exception of a single right basal tuber of the basisphenoid/basioccipital complex that was collected as float. The process is short, blunt and roughly horn-shaped, being slightly recurved posteriorly. It is indistinguishable from the basal tubera of other phytosaurs.

PHYLOGENETIC ANALYSIS

The phylogenetic relationships of PEFO 31207 were determined using Hungerbühler's (2002) matrix, adding *Pseudopalatus jablonskiae* as an OTU (Appendix 1), and rescoring character 5 (state 2) for *Pseudopalatus buceros*, and characters 32 (state 1) and 42 (state 0) for *Pseudopalatus mccauleyi* after re-examining material from the UCMP collections. The matrix was analyzed using PAUP* version 4.0b10 for Windows. All characters were equally weighted and treated as unordered. A heuristic search resulted in a single most parsimonious tree (Fig. 13) with a length of 108, a consistency index (CI) of .6667, a retention index (RI) of .7000, and a rescaled consistency index (RC) of .4667. Bootstrap values for 1000 replicates were determined for nodes (Fig. 13).

The recovered tree is almost identical to the one figured by Hungerbühler (2002) with five fewer steps. *Pseudopalatus jablonskiae* is the basal sister taxon to the other three species of *Pseudopalatus*. It is important to note that Hungerbühler (2002) did not include *Angistorhinus* or *Leptosuchus* in his analysis. Their inclusion is beyond the scope of this study; based on the analysis presented by Ballew (1989), these taxa would most likely fall out as successive sister taxa to Pseudopalatinae. Although the bootstrap value for the clade containing *P. jablonskiae* plus the other species of *Pseudopalatus* is low (34%), this is most likely a result of missing data in *P. jablonskiae* because the placement of this taxon in *Pseudopalatus* is supported by several synapomorphies (see diagnosis).

DISCUSSION

Although the holotype and only known specimen of *Pseudopalatus jablonskiae* is incomplete, the unique suite of preserved character-states provides a strong case for establishing a new taxon. These include: a squamosal posterior terminus that is not mediolaterally 'pinched' and knob-like (Ballew, 1989); the lack of a lateral ridge of the squamosal; a

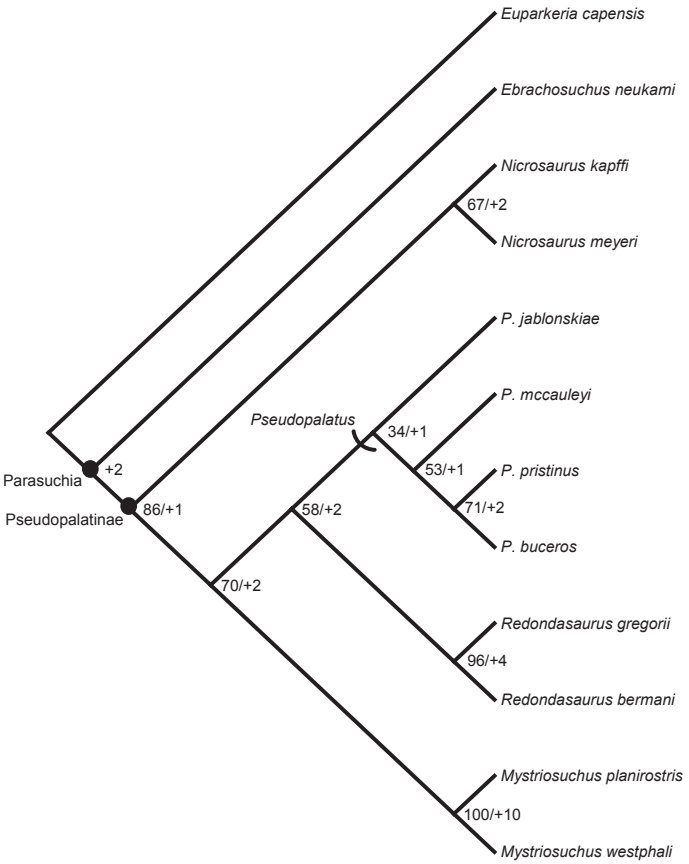

Figure *13*. Single most parsimonious tree showing phylogenetic relationships of *Pseudopalatus jablonskiae*.

post-temporal arcade that is ventrally depressed; supratemporal fenestra that are slit-like but still exposed in dorsal view; a mediolaterally broad postorbito-squamosal bar; a heavily sculptured skull roof; anteroposteriorly foreshortened postorbito-squamosal processes; and the contribution of a medial process of the squamosal to the lateral braincase wall, sandwiched between the anterior projection of the supraoccipital and the ventral flange of the parietal. In addition, the presence of a beveled medial margin of the postorbital forming a distinct supratemporal fossa lateral to the supratemporal fenestra has not been described for any other phytosaur and is an autapomorphy of *P. jablonskiae*. The combination of character-states not only differentiates *P. jablonskiae* from phytosaur taxa such as "*Paleorhinus*", *Parasuchus*, *Angistorhinus* (= *Rutiodon*), and *Leptosuchus*, they also distinguish this taxon from all other pseudopalatine phytosaurs.

The morphology of the posterior process of the squamosal has been repeatedly utilized in studies by phytosaur systematists and biostratigraphers. This is at least in part because the squamosal is one of the most robust cranial elements that preserves well and is easily identifiable; therefore it is a commonly collected isolated cranial element. Camp (1930) was the first to propose that characteristics of the squamosal are taxonomically relevant for phytosaurs, using them to partially diagnose his proposed new species of "*Machaeroprosopus*." Camp argued that a clear progression of change could be seen in phytosaurs from stratigraphically older to stratigraphically younger forms. Unfortunately, because of this hypothesis, Camp (1930) assigned much of his material to taxa based on stratigraphic position rather than possession of discrete character-states. Gregory (1962) also noted variation in squamosal morphology between phytosaur taxa; however, he placed more emphasis on rostral morphology for distinguishing genera, downplaying characters of the squamosal and temporal regions. Long and Ballew (1985) divided the phytosaurs of the Chinle Formation into those with 'primitive' ("*Rutiodon* Group A") and 'advanced' ("*Rutiodon* Group B") temporal regions. Phytosaurs with depressed post-temporal arcades and reduced supratemporal fenestra were considered more derived than those with depressed arcades but with supratemporal fenestrae still fully open dorsally. Ballew (1989) was the first worker to emphasize the usefulness of explicit squamosal characters (e.g., presence of a knob-like squamosal; squamosals vertical) in differentiating taxa, especially in a cladistic framework. She recognized that most of the specimens grouped in "*Rutiodon* Group B" actually belonged to a separate genus, *Pseudopalatus*. Long and Ballew (1985) and Ballew (1989), followed by Long and Murry (1995), demonstrated that isolated squamosals had taxonomic utility. Nevertheless, there has been little published on the potential variation within and among taxa.

To understand the variation in squamosal morphology and their utility in phytosaur taxonomy, we examined collections of North American phytosaur squamosals, both those associated with skulls and isolated specimens. We focus on specimens of *Leptosuchus* and *Pseudopalatus*, because they represent the vast majority of phytosaur specimens from Arizona, and isolated squamosals assigned to these two taxa are commonly used for biostratigraphic correlation in the Upper Triassic strata of the American southwest. Squamosals of *Parasuchus* (="*Paleorhinus*") would be difficult to confuse with those of *Pseudopalatus* because they enclose completely dorsally exposed supratemporal fenestrae, and have not been found in the Chinle Formation to date.

In both *Leptosuchus* and *Pseudopalatus*, the posterior process of the squamosal extends past the posterior margin of the braincase and quadrate. It is dorso-ventrally expanded, with a triangular process that extends ventrally and articulates with the paroccipital process of the opisthotic (Fig. 6). A thin ridge originates medially on the posterior-most portion of the squamosal, and enlarges antero-medially to become the parietal process of the squamosal (Figs. 6b-d). This process forms the dorsal margin of the posttemporal fenestra and the postero-ventral margin of the supratemporal fenestra. Just above this ridge on the ventro-medial

face of the squamosal is a well developed fossa that borders the supratemporal fenestra (Figs. 6b-d) and probably accommodated the jaw musculature that originates from this area. Both the ridge and fossa vary widely among specimens of phytosaur squamosals. In particular, the posterior extent of these two features is subject to extensive variation in the sample of specimens examined, and does not appear to have any taxonomic utility. For example, in some specimens of *Pseudopalatus*, the ridge and/or the fossa extend to the posterior tip of the squamosal (Fig. 6n), whereas in other specimens they stop well short of the posterior extremities (Fig. 6h, l-m).

The posterior squamosals of *Leptosuchus* species are expanded dorsoventrally to form a broad plate-like process (Figs. 6a-b). Mediolaterally, they are not very thick relative to their height. In all specimens examined, the posterior margin is broadly rounded. In the species *L. adamanensis* and *L. gregorii*, this margin is nearly semicircular and does not extend much beyond the posterior edge of the opisthotic process, whereas it is more angular and extends significantly beyond the opisthotic process in *L. crosbiensis* (Figs. 6d, j), although these characters can vary somewhat with size. In contrast, the dorsal portion of all *Pseudopalatus* squamosals is mediolaterally expanded to form a shelf level with the parietal and postorbital (Fig 6e). This dorsal portion of the squamosal is often moderately to heavily sculptured (Fig 6e). In all *Pseudopalatus* species except *P. jablonskiae* (i.e., *P. pristinus*, *P. buceros*, and *P. mccauleyi*), the medio-lateral expansion of the dorsal portion of the squamosal results in the development of a strong ridge along the dorso-lateral margin of the squamosal, with a corresponding shallow trough ventrally adjacent to it. In *Pseudopalatus pristinus* and *P. buceros*, the dorsal portion of the squamosal extends well beyond the posterior margin of the opisthotic process and is extremely thickened (Fig 6h ,i ,l), resulting in a morphology that Ballew (1989) described as "knob-like". This contrasts with the condition in *P. jablonskiae* (Figs. 4, 6e) and *P. mccauleyi* (Fig. 6g), where the squamosal tips only extend slightly beyond the opisthotic process.

Our examination of phytosaur squamosal morphology reaffirms the utility of the squamosal for taxonomic discrimination. Although some characters display significant individual variation (e.g., posterior extent of the ridge and fossa on the medial squamosal), most characters previously used to differentiate *Leptosuchus* and *Pseudopalatus* squamosals are still valuable in phytosaur systematics. This suggests that when more complete specimens are also known and taxon ranges are well-refined, isolated phytosaur squamosals are useful as biostratigraphic markers, at least at a local to regional level.

CONCLUSIONS

Although the specimen is incomplete, a new partial phytosaur skull (PEFO 31207) from the Sonsela Member of the Upper Triassic Chinle Formation of Petrified Forest National Park, Arizona clearly represents a new taxon, *Pseudopalatus jablonskiae*. This new species is diagnosed by the autapomorphy of a beveled medial edge on the postorbito-squamosal bar as well as a suite of other character-states not observed in phytosaurs. The braincase of *P. jablonskiae* is well preserved; clarifying and augmenting our understanding of pseudopalatine braincase morphology. Including *P. jablonskiae* in a phylogenetic analysis of pseudopalatine phytosaurs recovers it as the basal-most species of *Pseudopalatus*. To clarify future systematic studies, we provide phylogenetic definitions for the clades Pseudopalatinae and *Pseudopalatus*.

This new species of *Pseudopalatus* is not only important because it increases the diversity of known phytosaur taxa from the Chinle Formation. The holotype and only known specimen of *P. jablonskiae* is equally important because it is the stratigraphically lowest occurrence of *Pseudopalatus* within Petrified Forest National Park. The First Appearance Datum of *Pseudopalatus* defines the beginning of the Revueltian land-vertebrate faunachron (Lucas, 1998) and this specimen provides strong evidence for the overlap of the end of the Adamanian lvf and the beginning of the Revueltian lvf in Petrified Forest National Park (Parker and Irmis, 2005). This suggests that at least a portion of the Sonsela Member in Petrified Forest National Park preserves a transitional fauna between the two biostratigraphic units (Woody and Parker, 2004).

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APPENDIX 1-Character codings for *Pseudopalatus jablonskiae* using the matrix of Hungerbühler (2002).

P. jablonskiae: ????? ???0? ???10 ?1?30 20211 20021 100?1 1??1? ????? ??