

# TOOTH IMPLANTATION AND DENTAL MORPHOLOGY OF PALACRODON

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## ABSTRACT

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*Palacrodon browni*, a reptile known from the Early Triassic strata of South Africa, is of uncertain phylogenetic affinities, and its relationships have been argued for over a century. Additionally, its presumed diet is also uncertain. Using computed tomography and the literature, features of the dentition are revealed that indicate *Palacrodon* is a procolophonid. Furthermore, computed tomography reveals two parallel ridged beneath the teeth of *Palacrodon*, a unique feature unknown in any other tetrapod. Comparison to the dentition of other taxa and the severe wear seen on the teeth of *Palacrodon* also indicate that *Palacrodon* was likely either an herbivore or an omnivore.

KEY WORDS: Triassic, Karoo, South Africa, paleontology, procolophonids, Rhynchocephalia

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## CHAPTER I

### Literature Review

For over a century the taxonomic standing of *Palacrodon* has been questioned due to the limited amount of material available and the unusual morphology of its teeth. *Palacrodon* has acrodont dentition, which leads paleontologists to group it with other acrodont organisms such as rhynchocephalians and procolophonids (Broom, 1906a; Malan, 1963), although the material is not substantial enough to classify it further than diapsid (Gow, 1992, 1999). Additionally, the unique dental morphology led to multiple conflicting diet reconstructions (Gow, 1999; Nicolas and Rubidge, 2010; Smith et al., 2012). In the last few decades numerous dentaries and maxillae belonging to *Palacrodon* were recovered from Early Triassic sediments at Driefontein, near Paul Roux in the Free State Province of South Africa. With this larger sample I will use computed tomography (CT) and comparative and statistical methods to address two questions: 1) What taxonomic group shares more morphological similarities with *Palacrodon*? and 2) what was the most likely principle food source for *Palacrodon*?

The dentition and small body size of *Palacrodon*, and its restriction to the Early Triassic makes it an intriguing study organism. *Palacrodon* is part of the recovery fauna which existed after the Permian mass extinction (Hancox and Rubidge, 2001; Neveling et al., 2005; Rubidge, 2005; Nicolas and Rubidge, 2010). Extant groups of tetrapods such as Anura, Mammalia, Archosauria, and Lepidosauria have origins in the Triassic (Romer, 1956; Carroll, 1969; Pyron, 2010). The origins of these groups are uncertain because they are missing many early taxa, which are presumed to be small, often poorly preserved, and understudied in comparison to the larger-bodied fauna which evolve later in these

lineages (Carroll, 1969). There is the potential that *Palacrodon* is a stem member of one of these lineages because it has similar dental morphology to other early Triassic tetrapods (e.g. rhynchocephalians, trilophosaurs) making this research crucial for the study of Early Triassic tetrapod relationships.

## BACKGROUND

**Geologic Setting.** The Triassic dated from 251.9 to 201.4 million years ago, and is subdivided into the Early (251.9-246.8 mya), Middle (246.8-237.0 mya), and Late Triassic (237.0-201.4 mya; Ogg et al., 2016). During the Triassic the continents were positioned together as a single landmass called Pangaea (Wegener, 1920; Fraser, 2006; Fig. 1) surrounded by an ocean termed Panthalassa (Suess, 1885; Wegener, 1920). The large singular landmass and the high carbon-content of the atmosphere allowed for extreme conditions marked by increased climatic instability (Holser and Magaritz, 1987; Fraser, 2006). As such, the Triassic was much hotter and more arid than the present-day, with some areas characterized by intense monsoon seasons (Fraser, 2006; Benton, 2016).

**Mass Extinction.** The Triassic follows the end-Permian mass extinction. That extinction is considered the most devastating extinction event in the history of the planet, accounting for the extinction of over 50% of all marine families and 80% of marine genera, and 77% for all land animals (Raup and Sepkoski, 1982; Benton, 2003; MacLeod, 2013). As such, the animals that survived into the Triassic act as a recovery fauna that diversifies and characterizes the period and much the Mesozoic (R. Smith and Botha, 2005; Sahney and Benton, 2008; Sues and Fraser, 2010).

The groups that survived the Triassic act as the stems from which many extant tetrapod lineages develop, including archosaurs, squamates, mammals, and turtles

(Sahney and Benton, 2008; Sues and Fraser, 2010; Chen and Benton, 2012). Throughout the Triassic insects such as beetles, flies, and giant insects like titanopterans proliferate, and the first representatives of conifers and ferns evolve (Sues and Fraser, 2010). In the marine realm calcareous nannoplankton, scleractinian corals, and teleost fish make their first appearances in the Triassic (Arratia, 2001; Stanley, 2003; Erba, 2006; Hurley et al., 2007; Sues and Fraser, 2010). With the appearance of these organisms in the Triassic, the designation “Dawn of the Modern Ecosystems” is appropriate for that period (Sues and Fraser, 2010:1).

**The Karoo Basin.** The Karoo basin spans the majority of South Africa (du Toit, 1918), and is one of the most thoroughly investigated strata in terms of its vertebrate faunal record (e.g., Lucas, 1998; Ward et al., 2000; Rubidge, 2005), providing a unique and detailed record of terrestrial extinction at the end of the Permian and faunal recovery in the Triassic (Hancox and Rubidge, 2001; Damiani, 2004; Neveling et al., 2005; Ward et al., 2005; Nicolas and Rubidge, 2010). The deposits of the Karoo basin span from the Late Carboniferous to the Middle Jurassic and are nearly 12 km thick in some areas (R. Smith, 1995; Catuneanu et al., 1998). The Karoo basin is categorized as a retroarc foreland basin (Catuneanu et al., 1998), meaning the basin is a geologic structure adjacent to a mountain belt and occurs on the overriding plate where two tectonic plates converge, resulting in a depression of rock (Dickinson, 1978).

The strata which mark the Permo-Triassic transition are known as the Beaufort group (du Toit, 1918; Keyser, 1979; R. Smith, 1995; Hancox, 2000). These strata are predominantly fluvio-lacustrine rocks, meaning the area is predominantly composed of sediments indicative of a deltaic system with many rivers, lakes, and floodplains (du Toit,

1918; Theron, 1975; Van Dijk et al., 1978; R. Smith, 1990). The Beaufort group is further divided into formations which are characterized by biostratigraphic assemblages when fossils are abundant (Fig. 2; Seeley, 1892; Broom, 1909; Hotton and Kitching, 1963; Kitching, 1977; Keyser, 1979; Rubidge, 1990, 1995). The Permo-Triassic transition is marked by the Katberg Formation and the *Lystrosaurus* assemblage zone (LAZ), and the rest of the Early Triassic is marked by the Burgersdorp Formation and the *Cynognathus* assemblage zone (CAZ; Rubidge, 1990, 1995; Hancox, 2000; Hancox and Rubidge, 2001). These formations are defined by changes in lithostratigraphy of the rocks and the assemblage zones are determined using biostratigraphy, or changes in the faunal composition, particularly the change from the therapsid *Lystrosaurus* to the therapsid *Cynognathus*. As the term biostratigraphy implies, the discovery of certain taxa within a sedimentary sequence may help identify the age of the strata in which those taxa are found. As such, the LAZ and CAZ are characterized by different sets of tetrapods.

The LAZ is associated with an abundance of the synapsid *Lystrosaurus*, a dicynodont therapsid, and a low diversity of reptiles (Broom, 1906b; Rubidge, 1995; Hancox, 2000). A number of tetrapods are found in these sediments including amphibians, captorhinids, younginiformes, squamates, rhynchosaurs, protosaurs, archosauriforms, dicynodonts, therocephalians, and cynodonts (see Appendix A for full list of species; Rubidge, 1995, Hancox, 2000; Neveling, 2004). Aside from tetrapods, fossil millipedes, ferns, woody plants, and vertebrate burrow complexes also are found within the LAZ (Rubidge, 1995). Although *Lystrosaurus* is the predominant tetrapod found in this assemblage zone, it is often found in association with the procolophonid *Procolophon* (Rubidge, 1995, Neveling, 2004).

The CAZ is defined by the therapsids *Cynognathus*, *Diademodon*, and *Kannemeyeria* (Broom, 1906b; Kitching, 1977; Rubidge, 1995; Neveling, 2004).

Tetrapods associated with the CAZ include amphibians, captorhinids, rhynchosauroids, archosaurs, dicynodonts, therocephalians, and cynodonts (see Appendix A for list of species; Rubidge, 1995; Neveling, 2004). *Palaeocradon* is only found within the CAZ. Fish, mollusks, ferns, woody plants, arthropod trails, vertebrate burrows, and worm burrows also are found within the CAZ (see Appendix A; Rubidge, 1995; Hancox, 2000).

**Driefontein Locality.** Driefontein is located on a farm in the Nketoana Local Municipality near the town of Paul Roux in the northeastern Free State Province of South Africa (Fig. 3; Gow, 1999; Damiani and Jeannot, 2002; Bender and Hancox, 2003; Yates et al., 2012). The strata of Driefontein are assigned to the *Kestrosaurus* assemblage zone, which is of the CAZ, subzone A (Hancox and Rubidge, 2001; Yates et al., 2012).

Subzone A correlates with the Olenekian stage of the Early Triassic which began 249.7 million years ago and ended 245.0 million years ago (Damiani and Jeannot, 2002; Gradstein et al., 2004). Though the stratigraphy of the site was not thoroughly investigated until more recently (Gaetano et al., 2012; Yates et al., 2012), fossils were found from this area starting in 1989 (Gow, 1999; Damiani and Jeannot, 2002; Hancox et al., 2010). The strata are composed of finely laminated lacustrine muds and channelized sandstones that incorporate lag layers, deposits left by fluvial processes (Bender and Hancox, 2004; Hancox et al., 2010; Gaetano et al., 2012; Yates et al., 2012).

Environmental reconstruction of the strata from Driefontein is interpreted to have been a dried lake bed and those sediments were soured and redeposited, depositing fossils in those strata (Yates et al., 2012). The deposits at Driefontein incorporate blue-grey

sandstones and red-green mudstones, typical of the fluvial systems that characterize Beaufort group and the CAZ (Damiani and Jeannot, 2002; Gaetano et al., 2012).

The lag deposits at Driefontein preserve mostly disarticulated fossils. This includes the temnospondyls *Parotosuchus* sp. (Damiani, 1999), *Parotosuchus haughtoni* (Damiani, 2002), *Kestrosaurus kitchingi* (Shishkin et al., 2004), and *Bathignathus poikilops* (Damiani and Jeannot, 2002). Fish fossils from this locality include actinopterygian jaw fragments, chondrichthyan fin spines, and lungfish tooth plates (Bender and Hancox, 2003; Ortiz et al., 2010). The only synapsid material found includes two incisors and five post canine teeth from an unnamed cynodont and two more postcanines from the cynodont *Langbergia modisei* (Abdala et al., 2006, 2007; Gaetano et al., 2012). In 1996 a partial dentary and maxilla belonging to *Palacrodon* were found at Driefontein, leading to the synonymy of *Palacrodon* and *Fremouwosaurus* (Gow, 1999). Since then nearly one hundred specimens of *Palacrodon* have been found, with 39 available for research at the Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg. All the specimens of *Palacrodon* are partial tooth-bearing elements. Much of the material from Driefontein is not yet described, but includes remains of numerous fish, procolophonids, archosaurs, and therocephalians (Hancox et al., 2010; Gaetano et al., 2012). Thousands of coprolites are found at the site with some containing freshwater bivalves (Yates et al., 2012), and an arthropod trackway was recovered in 2011. Fossils are still collected from Driefontein on a nearly yearly basis.

### *PALACRODON*

**Taxonomy.** The systematic position of *Palacrodon* has been uncertain since its initial description in 1906. *Palacrodon browni* was originally described as a

rhynchocephalian, due to a resemblance to *Homoeosaurus* (Broom, 1906a). Following that publication, it was thought to be a close relative of *Acrosaurus* (a basal lizard; Nopsca, 1907), a pleurosauro (Hoffstetter, 1955), a sphenodontid (Huene, 1956; Benton, 1985; Whiteside, 1986), an eosuchian (Kuhn, 1969), or possible procolophonid (Weishampel and Kerscher, 2013). The holotype dentary that was used as the basis for those classifications is so fragmentary, however, that one could just as easily classify *Palacrodon* as a procolophonid, lizard, or rhynchocephalian (Malan, 1963; Benton, 1985; Whiteside, 1986).

Since its initial description, *Palacrodon* was formally described twice more based upon the Antarctic specimen known as *Fremouwosaurus geludens* (Gow, 1992), which later was synonymized with *Palacrodon* based on the specimens found at Driefontein (Gow, 1999). Both descriptions place *Palacrodon* in *Diapsida incertae sedis*, and Gow stated that *Palacrodon* cannot possibly be a sphenodontid due to the placement of the quadrate foramen (Gow, 1999) and the presence of a lacrimal bone (Gow, 1992). Though *Palacrodon* shares similar overall morphology to procolophonids, it is distinguished by mesiodistal contact between the cheek teeth and inferiorly concave mesial and distal crown surfaces (Gow, 1999). The specimens uncovered thus far led some to believe it could possibly represent an early archosauromorph, trilophosaur (Hancox and Rubidge, 2001; Rubidge, 2005), although it was also recently placed with eosuchians (Nicolas and Rubidge, 2010; R. Smith et al. 2012). Most recently, it was said to be a putative rhynchocephalian (Benton et al., 2015), despite the widespread disagreement and uncertainty that surrounded *Palacrodon* in the past century.

Despite the taxonomic disagreement, *Palacrodon* was compared to several taxa (namely rhynchocephalians and early lepidosaurs) and was listed as a possible, although perhaps doubtful, rhynchocephalian in many publications from the last century (Robinson, 1973; Benton, 1985; Whiteside, 1986; Chaline, 1990; Borsuk-Bialynicka et al., 1999; Benton et al., 2015). *Palacrodon* was used to show that sphenodontid marginal dentition evolved by the Early Triassic in a study of *Clevosaurus hudsoni* (Robinson, 1973) and to establish sphenodontids in the Early Triassic (Romer 1956; Chaline, 1990). *Palacrodon* was used to support a Permo-Triassic origin of Lepidosauria (Borsuk-Bialynicka et al., 1999), and was used to justify the soft maximum age (252.7 Ma) of the Triassic to accommodate it (Benton et al., 2015). It was brought up in taxonomic reviews of Triassic and/or diapsid organisms but was sometimes only noted as being of uncertain origin (Murry, 1987; Dilkes, 1998). In one of the first modern phylogenetic studies of lizards, *Palacrodon* is noted as being poorly known and omitted from phylogenetic analysis due to difficulty in determining character states (Gauthier et al., 1988a). No authors make an attempt to classify *Palacrodon* following this, and its taxonomy is still uncertain.

**Biostratigraphy.** Although there is no consensus on its phylogenetic affinity, *Palacrodon* is frequently used as a taxonomic descriptor for the CAZ (Watson, 1957; Benton, 1983; Neveling, 2004; Neveling et al., 2005; Cisneros, 2007; Gower et al. 2014) and is considered an important taxonomic indicator for strata of the Burgersdorp Formation (Haughton, 1963; Hancox and Rubidge, 2001; Damiani and Jeannot, 2002; Bender and Hancox, 2003; Gaetano et al., 2012). CAZ (and potentially LAZ) equivalent rocks in the Antarctic Fremouw Formation were also described using *Palacrodon* and its



synonymy *Fremouwssaurus* (Gow, 1992, 1999; Sidor et al., 2008; Fröbisch et al., 2010; N. Smith et al., 2011; Huttenlocker and Sidor, 2012). Aside from Driefontein, *Palacrodon* fossils are known from Odendallstroom farm near the Orange River in the Eastern Cape Province, and from Antarctica (Gow, 1992; Neveling, 2004). The holotype is from an unknown locality in South Africa (Broom, 1906a).

**Diet.** In addition to its uncertain phylogenetic placement, the diet of *Palacrodon* is also uncertain. *Palacrodon* possibly was herbivorous (Gow, 1992). In studies of trophic analyses of Early Triassic tetrapods, it was listed as a carnivore (Nicolas and Rubidge, 2010) and then as an omnivore (R. Smith et al., 2012). How those diets were determined was not explained in any previous research.

Dentition is often used by paleontologists to determine diet, because diet and tooth morphology often are strongly correlated (Kingsley, 1899; Shimer, 1914; Todd, 1918). Occasionally other traits such as cranial morphology and body size are used to support certain dietary tolerances (Weishampel and Norman, 1989; MacFadden, 2000). Research involving enamel thickness, enamel striae, and microwear patterns also were used in previous diet studies (Walker et al., 1978; Kay, 1981; Ciochon et al., 1990; Dumont, 1995). Aside from morphology, analyses of material such as coprolites (fossilized feces; Shimer, 1914; Chin, 2002), phytoliths (microscopic silica-based plant material; Walker et al., 1978; Ciochon et al., 1990), and isotopes (Sullivan and Krueger, 1981; Lee-Thorp and Sponheimer, 2003; Reynard and Balter, 2014) can be used to determine the diet of extinct animals.

## TOOTH IMPLANTATIONS

Tooth implantation is a character frequently used to describe and classify taxa (Owen, 1840; Camp, 1923; Romer, 1956; Gauthier et al., 1988a, 2012). Pedicellate, pleurodonty, subthecodonty, thecodonty, and acrodonity are the five major implantation categories (Fig. 4; Owen, 1840; Romer, 1956; H. Smith, 1958; Edmund, 1969; Zaher and Rieppel, 1999; Jenkins et al., 2017). Variation exists within each category, and although those classifications provide good initial descriptors, not all animals have teeth that fit discretely in each category, thus those terms do not always suffice in describing tooth implantation (Jenkins et al., 2017).

**Pedicellate.** This mode of implantation has teeth that are attached with fibrous tissue or are ankylosed to a bone-like pedicle (Hughes et al., 1994; Kozawa et al., 2005). The pedicle, also known as the pedestal bone, cementum, or bone of attachment, unites the teeth to the tooth-bearing bone (Tomes, 1874; Kozawa et al., 2005). When this mode is exhibited in fish is it typically connected by fibrous tissue, and when this is seen in reptiles is it typically through ankylosis (Shellis, 1982; Hughes et al., 1994; Kozawa et al., 2005). Some amphibians also have pedicellate dentition, with the genus *Xenopus* forming a pedical from periodontal tissue (Kozawa et al., 2005). Pedicellate describes the relationship of tooth attachment to bone, while pleurodonty, subthecodonty, thecodonty, and acrodonity describes the position of the tooth in relation to the bone.

**Pleurodonty.** Taxa exhibiting this mode of implantation have teeth that are fused to the lingual shelf of the marginal bones (Owen, 1840; Romer, 1956; Edmund, 1969). This mode of implantation is typically only seen in lepidosaurs, and teeth are typically replaced continuously throughout the life of an animal (Camp, 1923; Romer, 1956;

Edmund, 1969; Rieppel, 2001). Variations found in pleurodont implantation are subdivided into three different types of pleurodonty, iguanian mode, agamid mode, and varanid mode (McDowell and Bogert, 1954; Edmund, 1960; Cooper et al., 1970; Jenkins et al., 2017).

In the iguanian mode all the teeth have long roots with extensive attachment to the marginal bones (Lessmann, 1952; Edmund, 1960; Kline and Cullum, 1985; Rieppel, 2001). That category accommodates most lizards and also describes the rhynchocephalian *Gephyrosaurus* (Romer, 1956; Evans, 1980; Motani, 1997; Zaher and Rieppel, 1999; Jenkins et al., 2017).

In the agamid mode, only the mesialmost teeth exhibit pleurodont implantation while the other teeth are fused to the crest of the jaw bone (i.e., they are partially acrodont and partially pleurodont; Cooper, 1970; Cooper and Poole, 1973; Zaher and Rieppel, 1999; Smirina and Ananjeva, 2007). This is seen in agamid lizards and a possible version of this is seen in several rhynchocephalians (Cooper et al., 1970; Whiteside, 1986; Fraser and Shelton, 1988; Renesto, 1995; Heckert et al., 2008; Whiteside et al., 2016).

In the varanid mode, the teeth are attached to the inside of the jaw bone and possess plicidentine, a condition characterized by dentine folds around the base of the tooth that aid in tooth attachment (Edmund, 1969; Cooper et al., 1970; Zaher and Rieppel, 1999). The dentine folds inwards, forms lamellae, and creates a honeycomb-like structure which ankyloses the tooth to the bone (Estes et al., 1988; Kearney and Rieppel, 2006; Maxwell et al., 2011). When the tooth is replaced, this dentine structure may not be completely resorbed, leaving evidence of previously embedded teeth on the bone

(Bullet, 1942; Edmund, 1969; Borsuk-Bialynicka, 1996; Kearney and Rieppel, 2006).

This mode is restricted to a few groups within Squamata, although plicidentine is found in other tetrapods (Estes et al., 1988; Zaher and Rieppel, 1999; Kearney and Rieppel, 2006; Maxwell et al., 2011).

**Subthecodonty.** Teeth exhibiting this mode of implantation are implanted in a shallow socket (Romer, 1956; Peyer, 1968; Edmund, 1969; Wild, 1973). This is thought to be the ancestral state in amniotes (Romer, 1956; H. Smith, 1958). A number of reptiles show this implantation, including stem-lepidosaurs, stem turtles, ichthyopterygians, choristoderes, and some early amphibians (Romer, 1956; Evans, 2009; Schoch and Sues, 2015; Skutschas and Vitenko, 2015; Kelley et al., 2016).

**Thecodonty.** Teeth exhibiting this mode of implantation are set within a bony socket (Owen, 1840; Romer, 1956; Edmund, 1969; Osborn, 1984; Zaher and Rieppel, 1999). This is seen in all mammals and archosaurs, including birds (Saint-Hilaire, 1821; Romer, 1956; Osborn, 1984; Zaher and Rieppel, 1999; Harris et al., 2006). This mode of implantation also is exhibited in the extinct snake *Dinilysia patagonica* (Budney et al., 2006) and mosasaurids (Caldwell, 2007; LeBlanc and Reisz, 2013). Mosasaurs may not be truly thecodont because there is argument if they possess a true socket (Zaher and Rieppel, 1999; Caldwell, 2007; Liu et al., 2016). Another term, aulacodonty, is used to describe ichthyosaurs, marine reptiles that possess a longitudinal groove instead of a bony socket (Mazin, 1983; Motani, 1997).

A subset of thecodonty is called ankylothecodonty (Edmund, 1969; Motani, 1997; Zaher and Rieppel, 1999). Teeth exhibiting this mode of implantation have roots that are firmly ankylosed to the bone and set within well-developed sockets (Edmund, 1969;

Chatterjee, 1974). This is exhibited by a procolophonid (Sues and Olsen, 1993), thalattosaurs (Nicholls and Brinkman, 1993; Müller, 2007; Liu et al., 2013), rhynchosaurs (Chatterjee, 1974; Benton, 1984), trilophosaurs (Robinson, 1956; Murry, 1987), an ichthyosaur (Motani, 1997), and a rhynchocephalian (Reynoso, 2000).

**Acrodonty.** Several definitions are associated with this term, and variably include traits such as location of teeth in relation to the bone, degree of fusion, and lack of replacement (Owen, 1840; Romer, 1956; Edmund, 1969; Osborn, 1984; Luan et al., 2009). Authors defined acrodonty several ways. It is defined as a suppression of the walls of the dental groove with teeth that are ankylosed to the crest of the bone (Edmund, 1969; Luan et al., 2009). Acrodonty is used to describe tooth fusion to the horizontal surface or summit of the bone (Romer, 1956; Osborn, 1984), and a lack of replacement or extensive ankyloses (MacDougall and Modesto, 2011). Some see it as a conversion between pleurodonty and thecodonty (Estes et al., 1988; Gauthier et al., 1988a). A three-part definition of acrodonty is given by Augé (1997) where the tooth is not fused to subdental shelf or subdental shelf absent, there is occlusal wear on the labial surface of bone and teeth, and no tooth replacement. For the purpose of this study, I restrict acrodont to a positional definition, by which the tooth is on the crest of the bone, without reference to the degree of fusion or replacement of teeth (Jenkins et al., 2017). Many authors do not state which definition of acrodont they are using even though many animals are described as acrodont, particularly most rhynchocephalians (Günther, 1867; Simpson, 1926; Romer, 1956; Edmund, 1969; Rasmussen and Callison, 1981; Evans, 1994; Reynoso, 1997, 2000; Jones et al., 2009; Jenkins et al., 2017), a few squamates such as chameleons and trogonophid amphisbaenians (Romer, 1956; Gans, 1960; Edmund, 1969; Augé, 1997;

Zaher and Rieppel, 1999), and some procolophonids (Sun, 1980; Gow, 2000; Cabreira and Cisneros, 2009; MacDougall and Modesto, 2011; Schoch, 2011).

## REPTILE ANATOMY

Three reptile groups are most often suggested for *Palacrodon*, those being rhynchocephalians, trilophosaurs, and procolophonids (Broom, 1906a; Malan, 1963; Hancox and Rubidge, 2001; Rubidge, 2005). Though *Palacrodon* shows some morphological similarities with each of these groups, the three taxa are quite different from each other morphologically, and each has a distinct evolutionary history. Rhynchocephalians and trilophosaurs both belong to the crown group Diapsida, reptiles with two temporal fenestra located posterior to the orbits (Fig. 5; Williston, 1917; Gauthier, 1984; Modesto and Anderson, 2004; Lee, 2013). This classification is divided into two groups, the archosauromorphs, to which trilophosaurs belong with other thecodont taxa such as crocodilians, dinosaurs, and birds, and the lepidosauromorphs, to which both rhynchocephalians and squamate reptiles (lizards, snakes, amphisbaenians) belong (Benton and Clark, 1988; Gauthier et al., 1988a; Gower and Wilkinson, 1996; Lee, 2013). Given that archosaurs and lepidosaurs lie within the crown group reptiles, they do share more morphological similarities with each other (e.g., diapsid temporal state) than with procolophonids, which are from a larger clade of parareptiles, a group which lies outside of “true reptiles” and includes several basal reptile groups from the Permian and Triassic (Gauthier et al., 1988b; Laurin and Reisz, 1995; Modesto and Anderson, 2004; Tsuji and Müller, 2009).

**Rhynchocephalia.** Though *Sphenodon* is only one living representative, rhynchocephalians were a diverse group with a broad geographic range in the Mesozoic

(Jones, 2008; Evans and Jones, 2010). The architecture of the skull is similar among members of this group, but rhynchocephalians display a wide range of body proportions, and skull and teeth morphology can vary greatly between species (Romer, 1956; Gauthier et al., 1988a; Jones, 2008; Evans and Jones, 2010). Basal forms, such as *Gephyrosaurus bridensis*, possess conical teeth (Fig. 6; Evans, 1980; Fraser, 1982; Whiteside 1986; Fraser and Shelton 1988; Heckert, 2004; Jones, 2008), but more derived forms have stouter, flanged teeth that possess more efficient shearing mechanics to aid in chewing (Fig. 7; Fraser, 1988; Carroll, 1985; Dupret, 2004; Jones, 2008). These shearing mechanics can lead to tooth wear which maintains a sharp cutting edge and increased surface area (Throckmorton et al., 1981; Fraser, 1988; Jones 2006, 2008). Many rhynchocephalians have acrodont tooth implantation with no evidence of tooth replacement (Simpson, 1926; Rasmussen and Callison; 1981; Throckmorton et al., 1981; Evans, 1994; Reynoso, 1996; Ross et al., 1999; Rauhut et al., 2012), although the most basal species *Gephyrosaurus* is pleurodont (Evans, 1980, 1985). Several basal species show a combination of acrodonty and pleurodonty (Whiteside, 1986; Fraser and Shelton, 1988; Renesto; 1995; Heckert et al., 2008). Those species that do not show tooth replacement often have additional teeth to the posterior end of the jaw ontogenetically (Reynoso, 2003; Apesteguía et al., 2014; Klein et al., 2015). The teeth all possess the same morphology (i.e. homodont) and do not exhibit regionalization (i.e. heterodont), although some possess an enlarged caniniform tooth (Reynoso, 1996, 2003, 2005; Jones, 2006).

Other anatomical features worth noting are the absence of the splenial and lacrimals in rhynchocephalians (Romer, 1956; Jones, 2006; Gauthier et al., 2012), apart

from *Gephyrosaurus* which possesses a reduced lacrimal, similar to other early lepidosauromorph taxa (Evans, 1980, 1991; Gauthier et al., 1988a; Molero and Jones, 2012). Rhynchocephalians range in their diets, and are thought include carnivores, herbivores, and insectivores based upon tooth morphology of fossil material (e.g., Newman, 1977; Walls, 1978; Evans, 1980; Rassmussen and Callison, 1981; Fraser, 1988; Reynoso, 2000; Jones, 2008).

**Trilophosauria.** Trilophosaurs are closely related to archosaurs and are known from the Late Triassic of the U.S.A., Canada, U.K., and Russia (Fig. 8; Case, 1928a; Gregory, 1945; Robinson, 1956; Sues, 2003; Heckert et al., 2006; Mueller and Parker, 2006; Arkhangel'skii and Sennikov, 2008). They possess heterodont dentition with subconical teeth mesially and cusped teeth distally (Case, 1928a; Robinson, 1956). The premaxillae form a rounded, edentulous beak (Gregory, 1945). Many species possess transversely expanded, tricuspid teeth that are connected by a ridge (Heckert et al., 2006; Mueller and Parker, 2006). Teeth are smallest at the mesial and distal ends of the tooth-bearing element and widest at the middle (Gregory, 1945). Teeth have an ankylotheodont implantation with substantial roots, although this implantation is not always clear (Sues, 2003; Heckert et al., 2006). The teeth are so firmly implanted that it was once considered to be pseudo-acrodont, because it is difficult to determine the border between tooth and bone (Gregory, 1945; Robinson, 1956). Striations appear at the edges of the alveoli, and the teeth merge with the bone in that area, creating what appears to be a combination of thecodont and acrodont implantation types (Gregory, 1945; Robinson, 1956). Teeth are replaced throughout the animal's lifetime, and wear patterns on the occlusal surface vary ontogenetically (Demar and Bolt, 1981).



Though trilophosaurs are considered diapsids, there is only one post-orbital fenestra (Gregory, 1945). This is called the euryapsid condition, in which the single fenestra is a result of the loss of the lower temporal bar which forms the lower temporal fenestra, and it is seen in several groups of reptiles (Williston, 1904; Frazzetta, 1968, Romer, 1971). By this definition, this temporal state is a derivative of the diapsid condition and is not to be confused with the synapsid condition that is also defined by a single temporal fenestra (Osborn, 1903; Williston, 1904). In the euryapsid condition the postorbitals and squamosals at the site of the lower temporal opening, unlike the modified diapsid skull seen in lepidosaurs where the lower temporal bar is lost due to the reduction of the quadratojugal and results in a single temporal fenestra (Romer, 1956). The skull material of *Trilophosaurus* is poorly preserved, and many sutures cannot be determined (Gregory, 1945). Trilophosaurs were thought to be herbivorous by Gregory (1945), although there is evidence that juveniles were carnivorous (Demar and Bolt, 1981).

**Procolophonomorpha.** Procolophonids originated in the Permian and survived into the Triassic, when they experienced great dispersal and diversification until their extinction at the Triassic-Jurassic boundary (Romer, 1956; Daly 1969; Anderson and Anderson, 1970; Sues et al., 2000; Modesto et al., 2003; Cisneros, 2008; Tsuji and Müller, 2009). Typically, procolophonids are small, have elongated orbits, are heterodont, and have bulbous, sometimes cuspid molariform teeth (Romer, 1956; Ivakhnenko, 1973; de Braga, 2003; Sues and Baird, 1998; Cisneros, 2008). Bulbous molariform teeth are acquired independently in several clades of procolophonids, such as the more basal group Bolosauridae, including *Bolosaurus* (Fig. 9; Case 1907; Watson, 1954; Romer, 1956; Reisz et al., 2002; Cisneros, 2008). Several procolophonids, such as

*Procolophon* (Fig. 10), have pointed or incisiform teeth anteriorly, and transversely broad molariform teeth posteriorly with concave wear patterns on the occlusal surface (Fig. 12; Romer, 1956; Ivakhnenko, 1973; Colbert and Kitching, 1975; Gow, 1977; Small, 1997; Cisneros, 2007). Tooth implantation in this group varies and is debated (Case, 1928b; Small, 1997; Cabreira and Cisneros, 2009; MacDougall and Modesto, 2011). Acrodonty, subthecodonty, and ankylothecodonty were proposed previously for this group (Case, 1928b; Broom, 1905; Broili and Schröder, 1936; Edmund, 1969; Sues and Olsen, 1993; Small, 1997; Cabreira and Cisneros, 2009). Several species show evidence of tooth replacement, and acrodonty is not usually associated with replacement (Small, 1997; Cabreira and Cisneros, 2009; MacDougall and Modesto, 2011). Because there is rare replacement in some species, this may support a protothecodont implantation. However, these teeth do not have sockets or roots, which supports an acrodont implantation, depending on the definition of acrodont used (MacDougall and Modesto, 2011). Procolophonids are also thought to range in their diets, and included carnivores, insectivores, and herbivores based on dental morphology of fossil material (Anderson and Anderson, 1970; Cisneros, 2007; Modesto et al., 2010).

Originally, procolophonids were thought to be anapsid, possessing no temporal fenestra (Williston, 1917; Frazzetta, 1968; Daly, 1969). However, later findings show that some procolophonids have lower temporal fenestration (Hamley and Thulborn, 1993; Cisneros et al., 2004; Tsuji et al., 2010; MacDougall and Reisz, 2012, 2014). Fenestration in procolophonids may possibly be a juvenile characteristic that is lost or changes ontogenetically (MacDougall and Reisz, 2014; Reisz et al., 2014). Lower temporal fenestration may have originated once or several times in procolophonids, but many of

the procolophonid interrelationships remain obscure making this difficult to determine (Hamley and Thulborn, 1993; de Braga, 2003; Cisneros et al., 2004; Tsuji and Müller, 2009).

## REPTILIAN DENTITION AND DIET

Diet often is reflected in the morphology of an animal's teeth (Kingsley, 1899; Parker and Haswell, 1899; Hotton, 1955). For example, a carnivore will display dentition that is more efficient at tearing flesh than an herbivore, and an herbivore will display dentition that is more efficient at orally processing plant material than a carnivore (Kingsley, 1899; Parker and Haswell, 1899). Tooth morphology may also change as the animal ages, often through replacement, and this may or may not reflect an ontogenetic change in diet (Peyer, 1929; Edmund, 1969; Gow, 1978; Dessem, 1985). Ontogenetic changes in tooth morphology can also be a result of wear (Gow, 1977, 1978; Demar and Bolt, 1981; Cabreira and Cisneros, 2009).

**Carnivory.** The earliest reptiles possessed conical or cylindrical teeth which are thought to indicate a carnivorous diet, one where an animal feeds on another (Edmund, 1969; Gow, 1978). Many carnivores may exhibit similar tooth morphology, but there is a range of tooth morphology exhibited by carnivorous reptiles (Fig. 12; Owen, 1840; Edmund, 1969; Vaeth et al., 1985; Massare, 1987; Britt et al., 2009). Reptiles may exhibit one or more different tooth morphology including conical teeth with pointed apices; laterally compressed teeth with a sharp, serrated cutting edge; conical teeth with a rounded apex; robust and blunt teeth; sharp, recurved teeth; fluted teeth, and even round, bulbous teeth (Owen, 1840; Romer, 1956; Edmund, 1969; Vaeth et al., 1985; Massare, 1987; Britt et al., 2009). The morphology exhibited by those teeth have different

functions such as piercing, cutting, grasping, and crushing (Vaeth et al., 1985; Massare, 1987).

Molluscivores, carnivores which feed on molluscs, may have a more specialized dentition (Russell, 1975; Massare, 1987; Sues, 1987; Neenan et al., 2013). Some, such as the mosasaur genus *Globidens*, may exhibit rounded, bulbous, and even “acorn-shaped” teeth (Gilmore, 1912; Russell, 1975; Massare, 1987). Other molluscivores may exhibit broad plate-like teeth for crushing, such as placodonts (Edmund, 1969; Sues, 1987; Neenan et al., 2013). Molluscivores may not have overly-specialized tooth morphology however, as demonstrated by some snakes which have long, recurved teeth and feed on snails (Zweifel, 1954; Vaeth et al., 1985; do Amaral, 1999; Britt et al., 2009).

Insectivores, another subset of carnivores which feed on insects, may sometimes exhibit a cusate appearance (Hotton, 1955; Dessem, 1985; Sumida and Murphy, 1987). They may also exhibit small, peg-like teeth (Gow, 1978). Teeth in this group are typically slender, cylindrical, and possess a sharp point for piercing, but may also reflect the typical carnivorous morphologies previously listed (Hotton, 1955, Dessem, 1985).

**Herbivory.** There are a variety of tooth morphology possessed by herbivorous reptiles, those reptiles which feed on plant material (Fig. 13; Edmund, 1969; Gow, 1978; Sues and Reisz, 1998). To efficiently process plant material, teeth often exhibit morphology for crushing, grinding, and shearing (Gow, 1978; Sues and Reisz, 1998). Some reptiles have grinding, cuspid, and transversely-wide teeth, although this is a morphology also associated with molluscivores and omnivores (Colbert, 1946; Edmund, 1969; Gow, 1978; Weishampel and Norman, 1989; Sues and Reisz, 2008). Others have cusate or serrated leaf-like teeth and/or anteriorly-posteriorly expanded crowns (Hotton,

1955; Edmund, 1969; Gow, 1978; Weishampel and Norman, 1989; Sues and Reisz, 1998; Lee, 1997). Others, like iguanodontid and ceratopsian dinosaurs, possessed dental batteries of numerous, closely packed teeth to grind plant material (Case, 1898; Sander, 1997).

Herbivore teeth may also exhibit higher levels of wear over time than carnivore teeth due to the fibrous content of plants, particularly if tooth replacement is absent or infrequent (Gow, 1977, 1978; Cabreira and Cisneros, 2009). This wear is often more pronounced in the posterior portion of the tooth row (Colbert, 1946; Gow, 1977, 1978). The amount of wear also can be indicative of what plant material is being eaten, i.e. a high-fiber diet vs. a low-fiber diet (Gow, 1978; Cisneros, 2008; Cabreira and Cisneros, 2009).

## HYPOTHESES

Based upon the literature, I define the following hypotheses concerning the anatomy, morphology, and evolutionary relationships of *Palacrodon*.

1. H<sub>0</sub>: *Palacrodon* possesses no tooth roots or sockets, and teeth are located on the apical surface of the tooth-bearing element.

H<sub>A</sub>: The teeth of *Palacrodon* are thecodont, possessing roots and sockets in the tooth-bearing element.

2. H<sub>0</sub>: *Palacrodon* does not share more or fewer synapomorphies with any particular group, and taxonomic status cannot be determined.

H<sub>A1</sub>: *Palacrodon* shares more characters with rhynchocephalians.

H<sub>A2</sub>: *Palacrodon* shares more characters with procolophonids.

H<sub>A3</sub>: *Palacrodon* shares more characters with trilophosaurs.

H<sub>A4</sub>: *Palacrodon* shares more characters with a group which was not previously suggested.

3. H<sub>0</sub>: Based on tooth morphology and wear patterns, *Palacrodon* was a carnivore.

H<sub>A1</sub>: Based on tooth morphology and wear patterns, *Palacrodon* was an herbivore.

H<sub>A3</sub>: Based on tooth morphology and wear patterns, *Palacrodon* was an omnivore.

H<sub>A4</sub>: Based on tooth morphology and wear patterns, *Palacrodon* had a diet not yet suggested in the literature.

4. H<sub>0</sub>: *Palacrodon* does not display dental regionalization.

H<sub>A</sub>: *Palacrodon* does displays dental regionalization.

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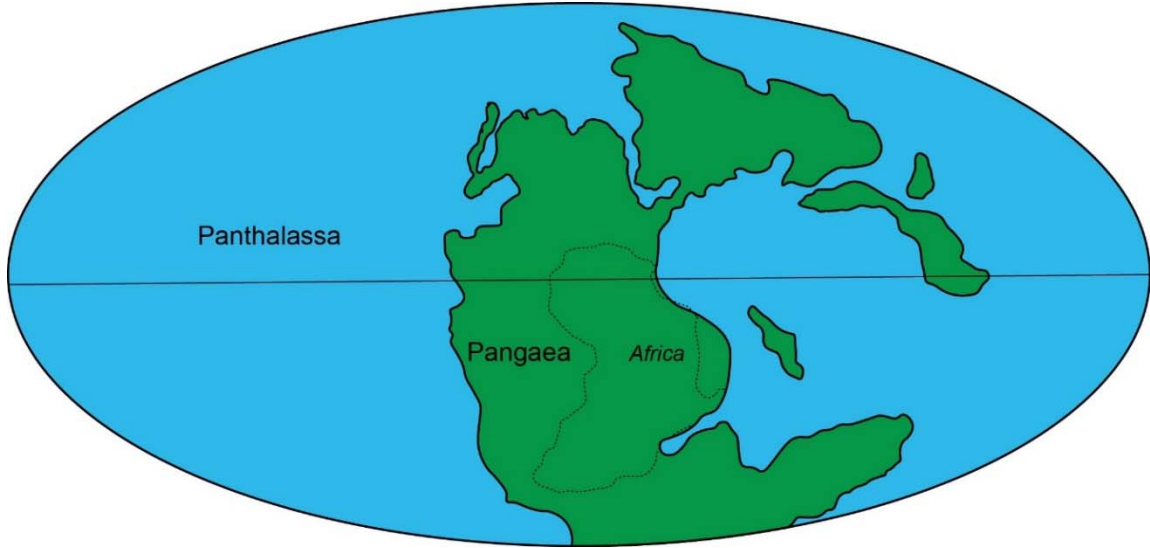


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*FIGURE 1.* Pangaea. Laurasia is the northern landmass and Gondwana is the southern landmass, divided by the equator. The majority of the modern African continent is in Gondwana.

Stratigraphy				
		Subunit	Age	Assemblage Zone
Triassic	Beaufort Group	Molteno Formation	Carnian	
		Burgerdorp Formation	Anisian	<i>Cynognathus</i>
			Olenekian	
Katberg Formation		Induan	<i>Lystrosaurus</i>	
Permian		Balfour Formation	Tatarian	<i>Dicynodon</i>
				<i>Cistecephalus</i>
		Middleton Formation		<i>Tropidostoma</i>
	<i>Pristerognathus</i>			
	Koonap Formation	<i>Tapinocephalus</i>		
Ecca Group		Kazanian	<i>Eodicynodon</i>	
	Waterford Formation			

FIGURE 2. Litho- and biostratigraphic subdivision of the Permo-Triassic of South Africa edited from Hancox and Rubidge (2001) with permission from Pergamon Press.

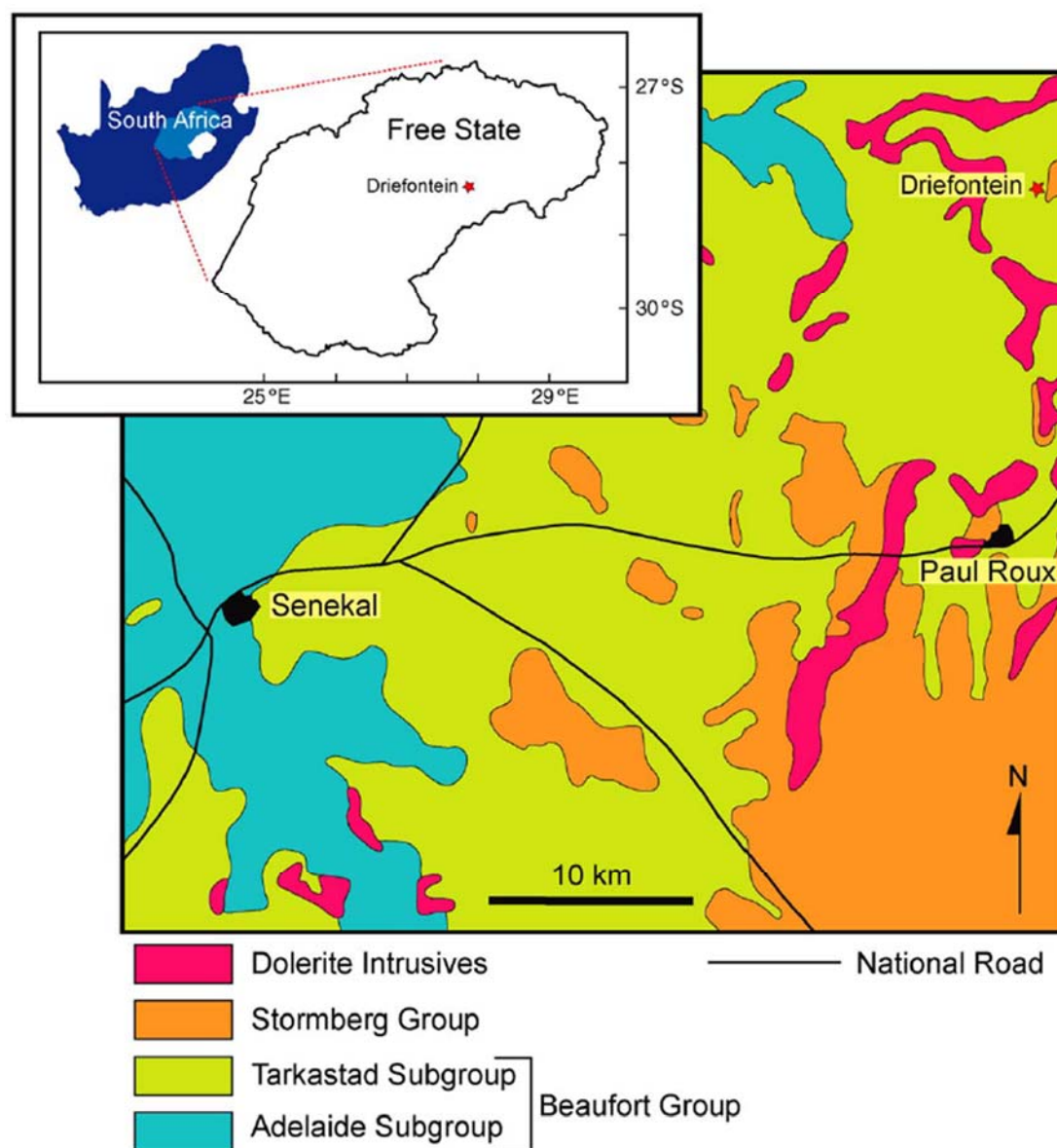


FIGURE 3. Map of Driefontein. Simplified geologic map of Driefontein take from Yates et al. (2012) and is publicly available to reuse.

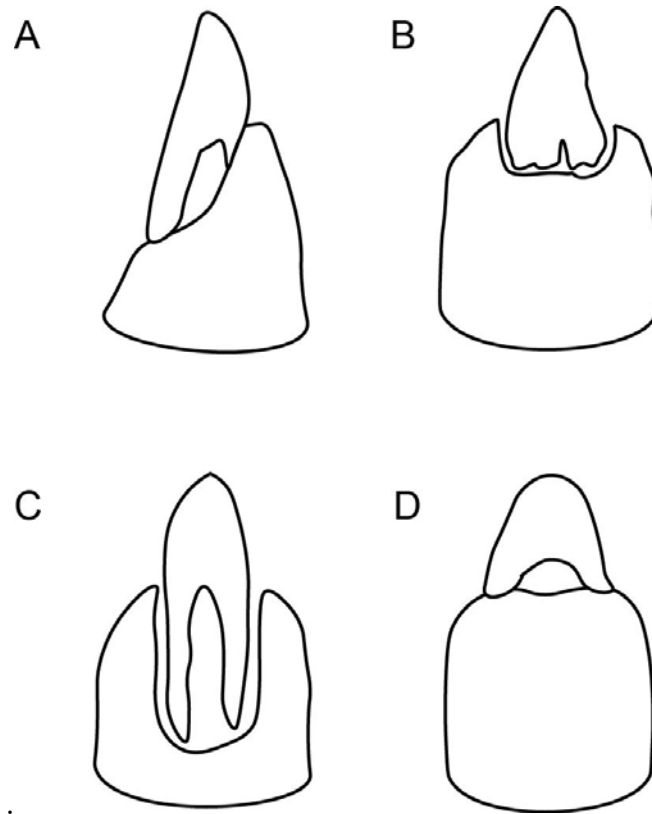


FIGURE 4. Illustration of the positional terms regarding tooth implantation. A) pleurodonty, B) subthecodonty, C) thecodonty, D) acrodonity from Edmund (1969) with permission from University of Chicago Press.



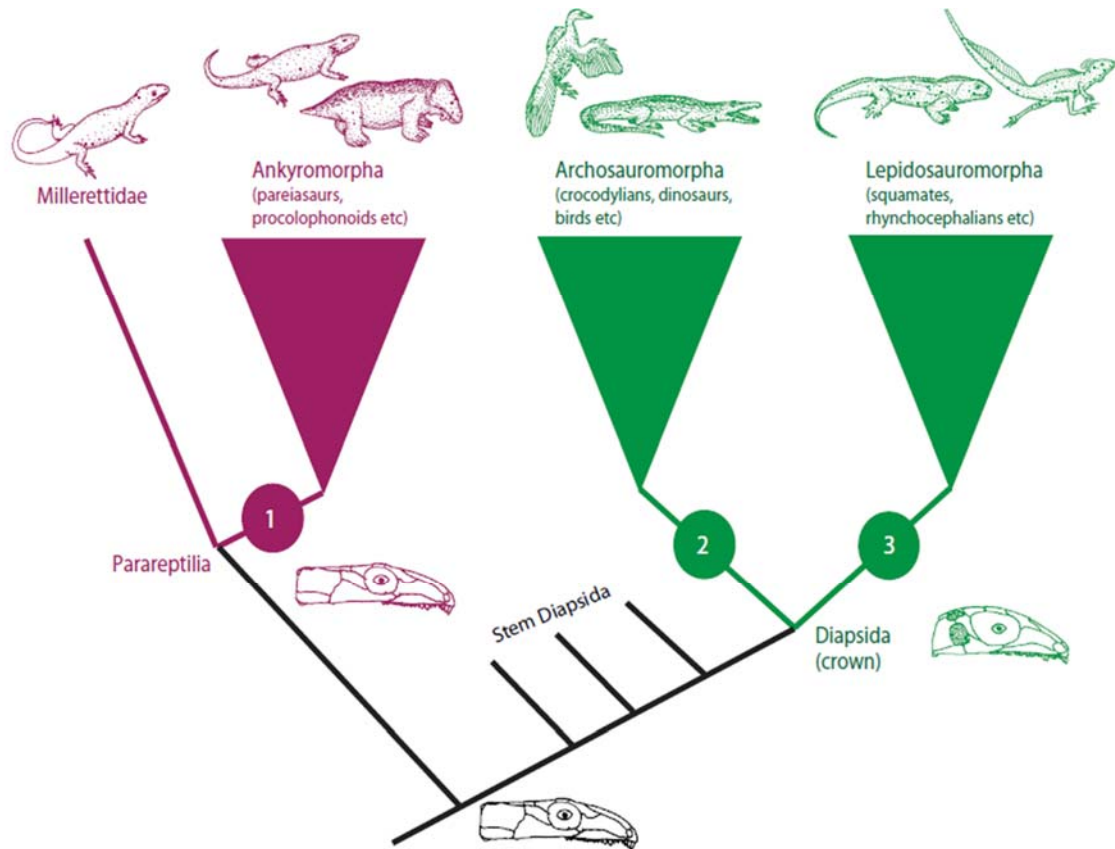


FIGURE 5. Simplified phylogeny including Parareptilia and Diapsida. Taken from Lee (2013) with permission from John Wiley and Sons Inc.

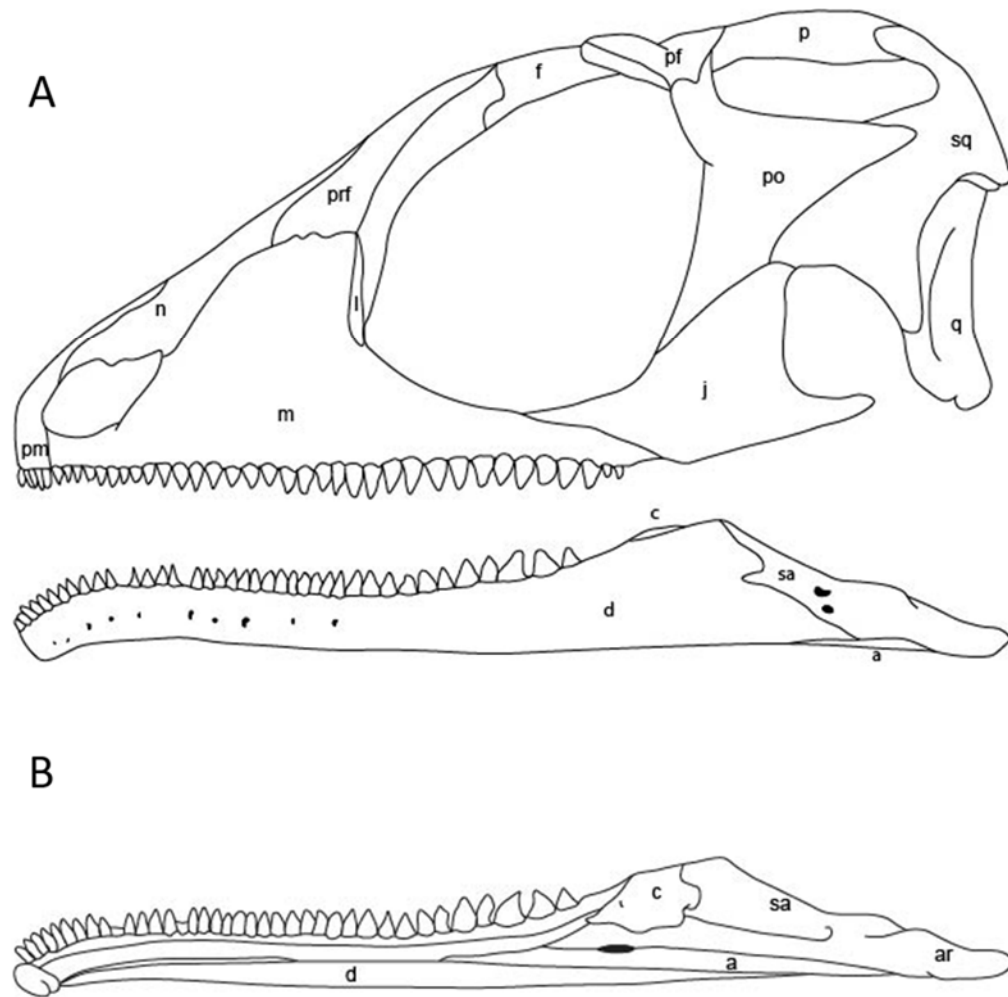


FIGURE 6. Skull and jaw of *Gephyrosaurus*. Redrawn from Evans (1980) with permission from Blackwell Publishing LTD. Jaw shown in both labial (A) and lingual (B) view. Abbreviations listed in Appendix B.

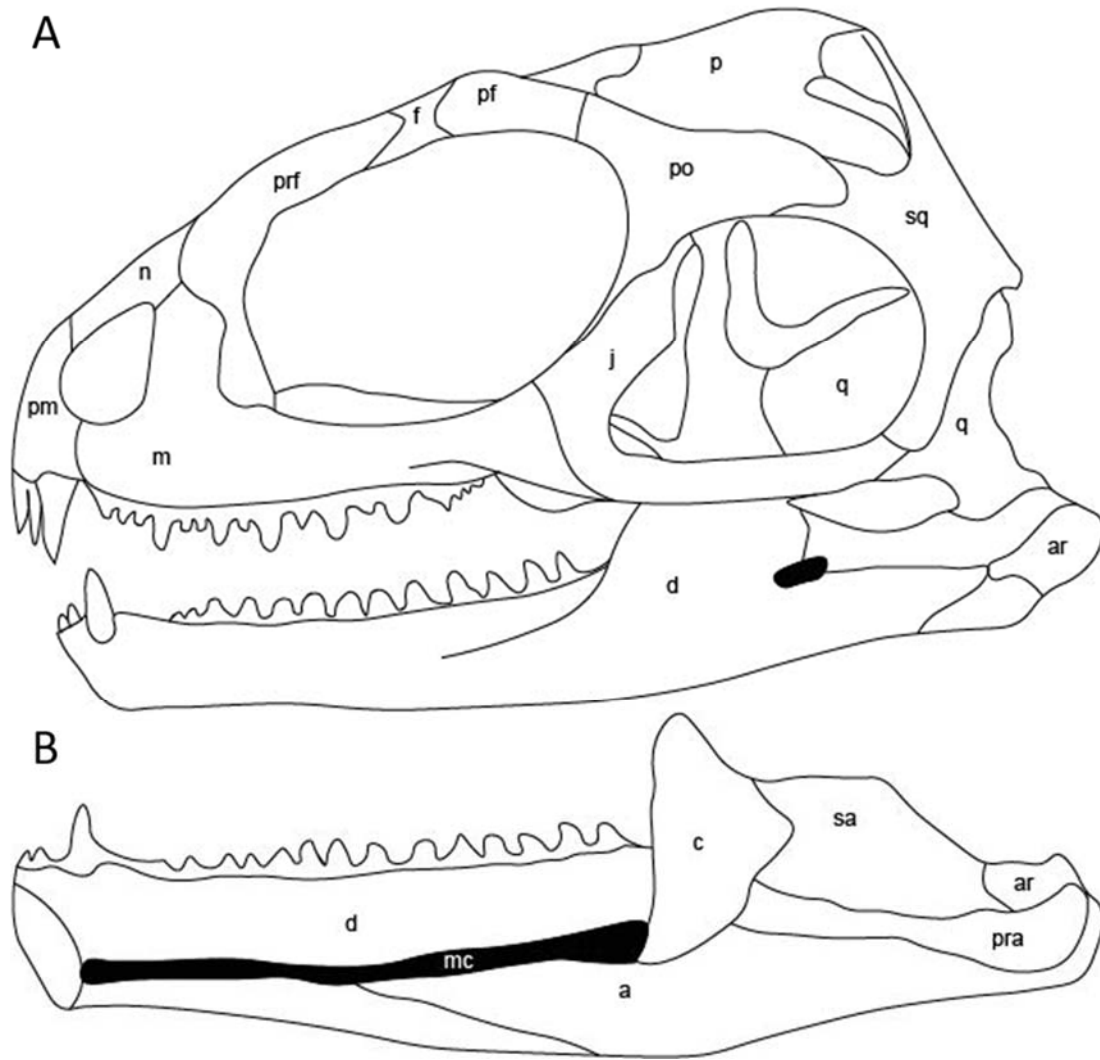


FIGURE 7. Skull and jaw of *Sphenodon*. Redrawn from Romer (1956) with permission from the University of Chicago Press. Jaw shown in both labial (A) and lingual (B) view. Abbreviations listed in Appendix B.

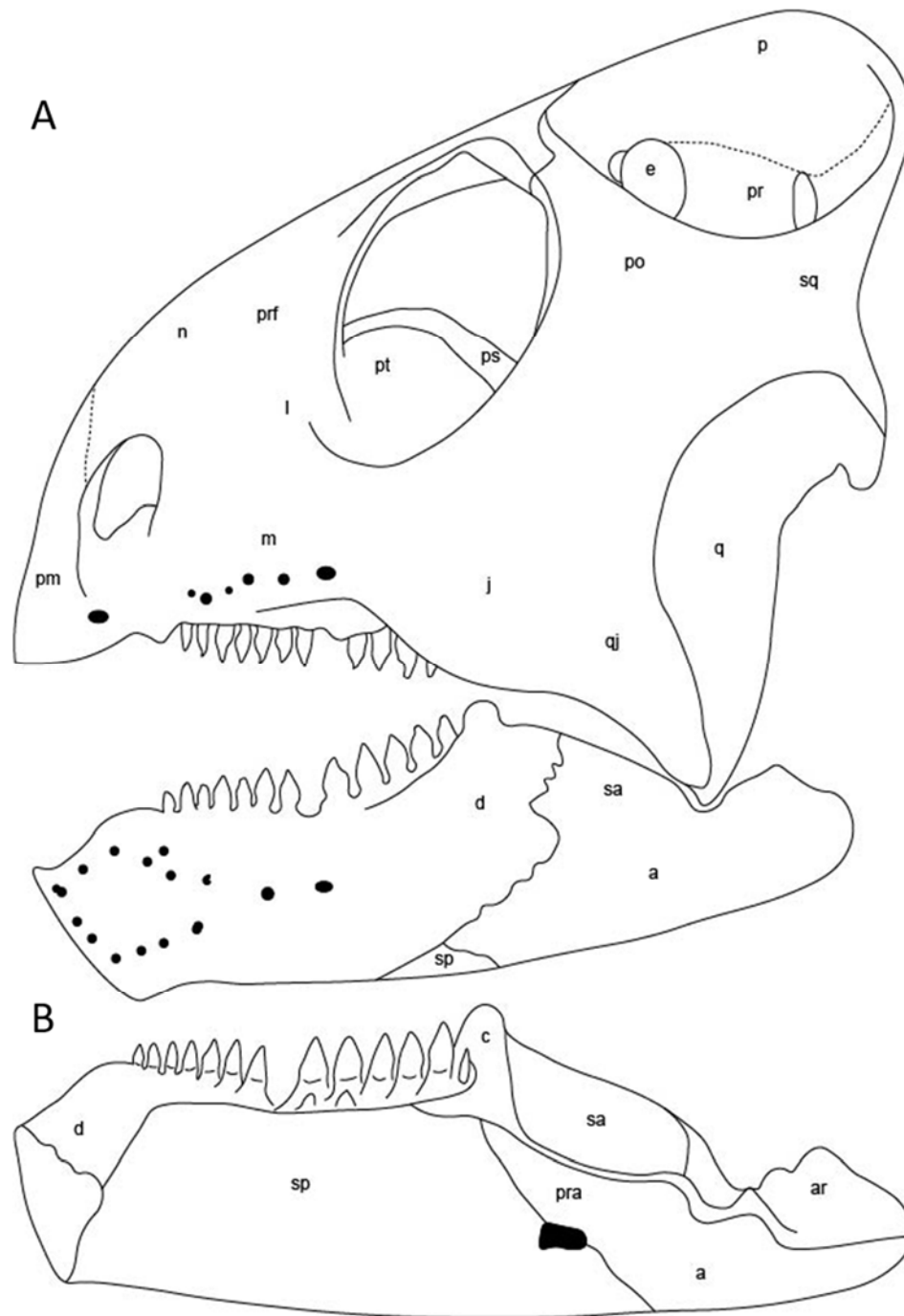


FIGURE 8. Skull and jaw of *Trilophosaurus*. Redrawn from Romer (1956) with permission from the University of Chicago Press. Jaw shown in both labial (A) and lingual (B) view. Abbreviations listed in Appendix B.

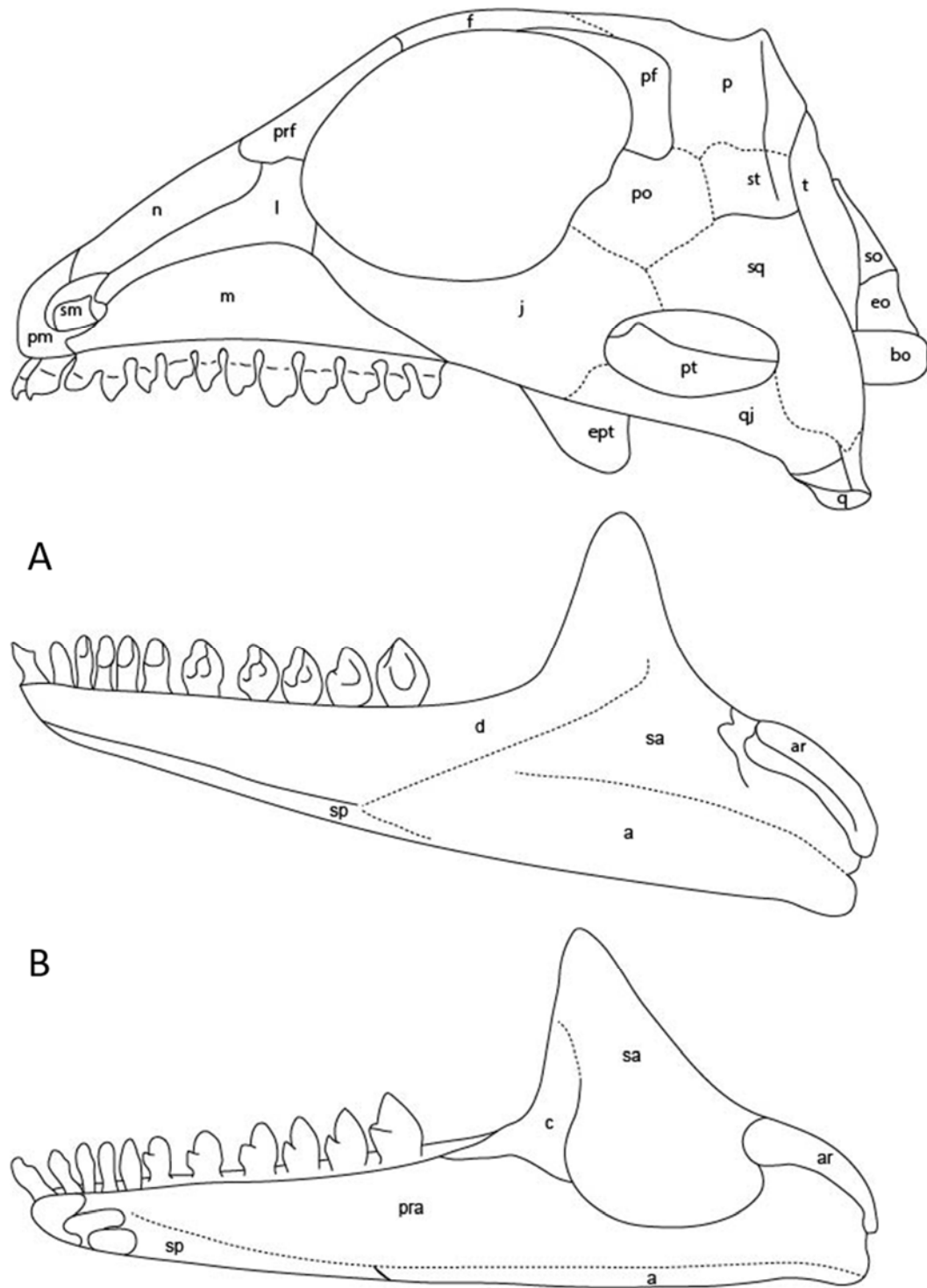


FIGURE 9. Skull and jaw of *Bolosaurus*. Redrawn from Watson (1954). Jaw shown in both labial (A) and lingual (B) view. Abbreviations listed in Appendix B. Reprinted with permission from Museum of Comparative Zoology, Harvard University.

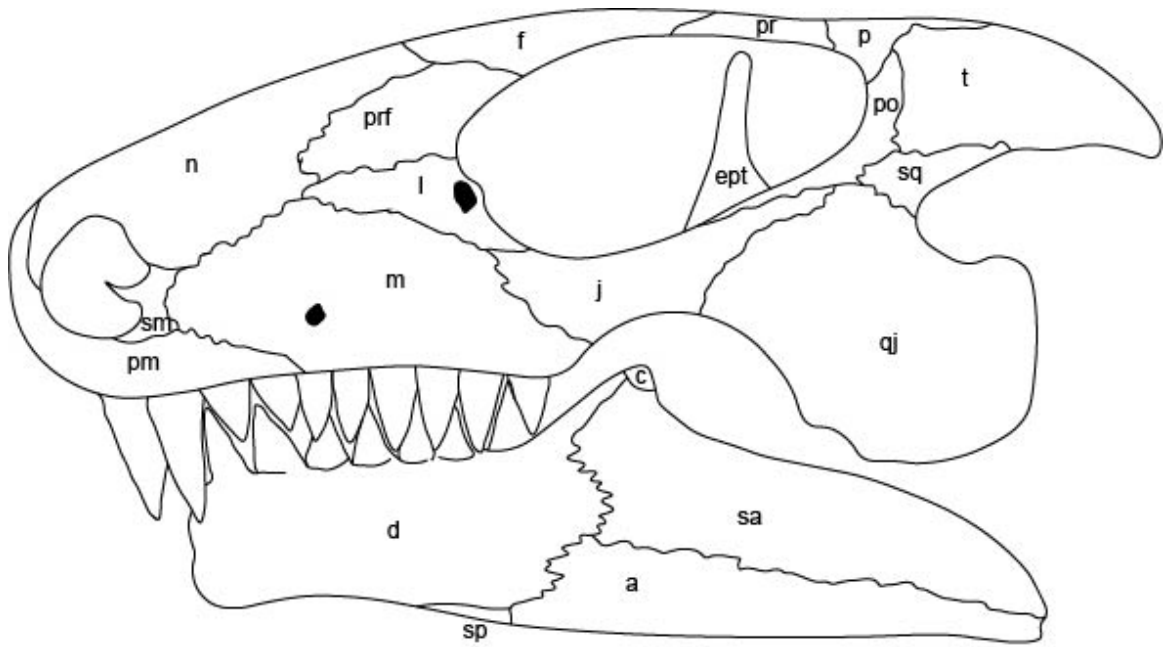


FIGURE 10. Skull and jaw of *Procolophon*. Redrawn from Romer (1956) with permission from the University of Chicago Press. Abbreviations listed in Appendix B.

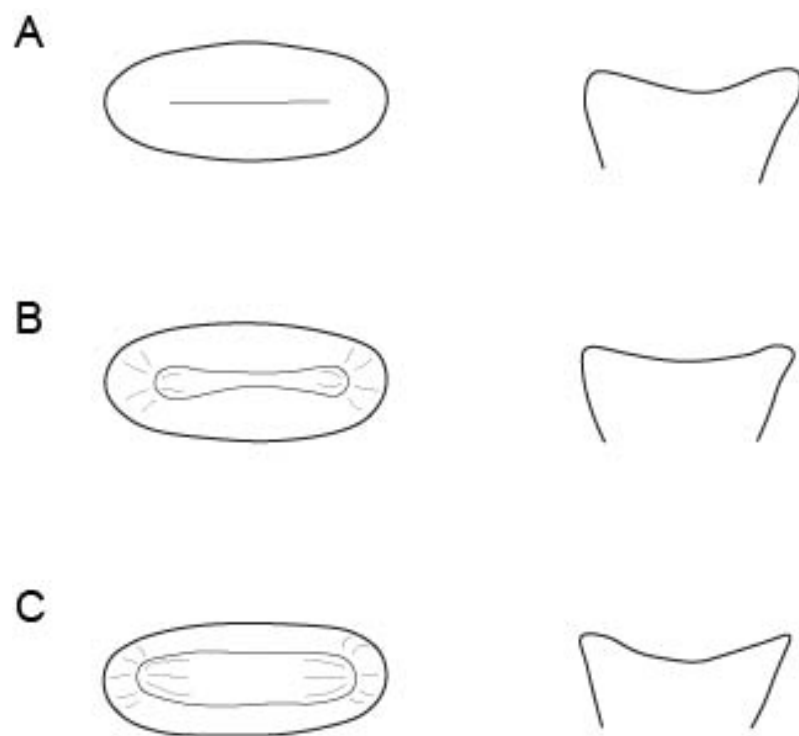


FIGURE 11. Stages of dental wear in *Procolophon*. A) cusps are connected by a sharp ridge, B) wear begins to appear, dulling the ridge, C) uniform wear. Redrawn from Gow (1977) with permission from John Wiley and Sons Inc.

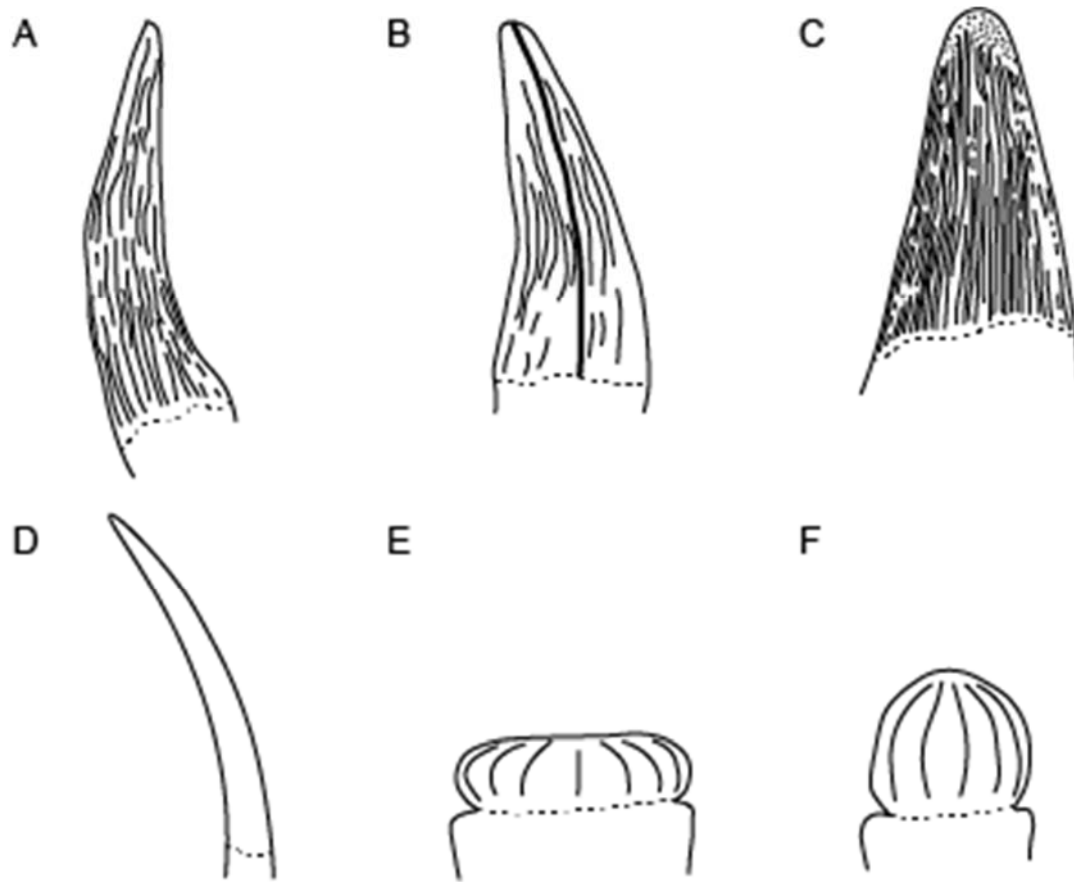


FIGURE 12. Example carnivore tooth morphology. Forms include A) pointed teeth, B) serrated teeth, C) robust teeth, D) piercing teeth, and E and F) crushing teeth. Redrawn from Massare (1987) with permission from Taylor and Francis LTD and Neenan et al. (2013) with permission from Nature Publishing Group.



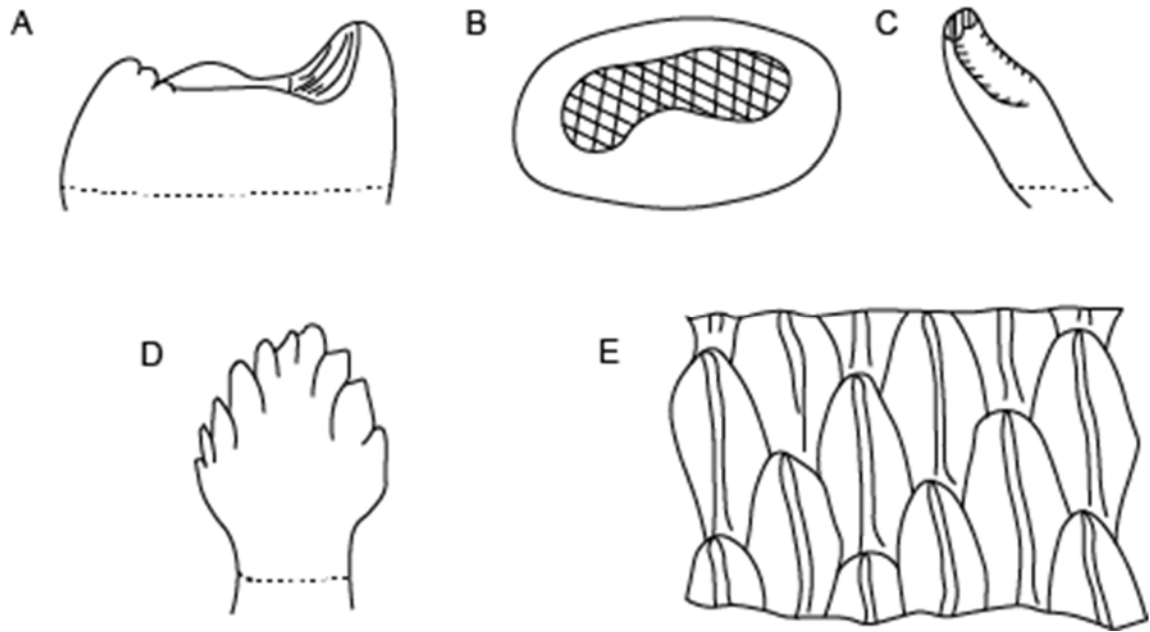


FIGURE 13. Example herbivore tooth morphology. Forms include A) wide, cuspid teeth, B) wide, cuspid teeth (occlusal view), C) grasping teeth, D) serrated leaf-like teeth, and E) grinding dental batteries. Redrawn from Gow (1977) with permission from John Wiley and Sons Inc. and Romer (1956) with permission from the University of Chicago Press.

## CHAPTER II

### **Phylogenetic Placement of *Palacrodon*, an Early Triassic Reptile from Southern Gondwana**

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This thesis follows the style and format of *Journal of Vertebrate Paleontology*.

## ABSTRACT

The taxonomy of *Palacrodon* is not agreed upon despite decades of research, with suggestions that it may be a rhynchocephalian, a trilophosaur, or a procolophonid. This uncertainty is due in part to the incompleteness of the holotype. Specimens of *Palacrodon* collected from the Free State Province of South Africa during the last two decades provide more information about the morphology of *Palacrodon*. CT scans of *Palacrodon* reveal aspects of tooth attachment that suggest *Palacrodon* may be a procolophonid. Phylogenetic analysis places *Palacrodon* within Procolophonidae.

**Keywords:** procolophonid, Rhynchocephalia, trilophosaur, Karoo

# Phylogenetic Placement of *Palacrodon*, an Early Triassic Reptile from Southern Gondwana

## INTRODUCTION

*Palacrodon browni* is an early Triassic reptile found in South Africa and Antarctica (Broom, 1906; Gow, 1992, 1999; Neveling, 2004). Since the discovery of the South African holotype, another 75 specimens of *P. browni* have been recovered, with the majority being fragmented jaws and maxillae found at the Driefontein locality in the Free State Province of South Africa. The phylogenetic placement of *P. browni* has been debated for over a century, with suggestions that it could be a rhynchocephalian, a trilophosaur, or a procolophonid (Broom, 1906; Malan, 1963; Rubidge, 2005). This debate is in part due to the uninformative nature of the dentition, but also due to its acrodont tooth implantation and labio-lingually aligned tricuspid tooth morphology (Broom, 1906; Gow, 1992, 1999). Acrodonty is a feature that evolved several times (Romer, 1956; Edmund, 1969), but is not known in combination with the labio-lingually aligned tricuspid tooth morphology like what is seen in *P. browni*. Here, I will test the phylogenetic placement of *P. browni* by first comparing internal and external features of the dentition of *P. browni* to the taxa that were previously suggested, and then placing *Palacrodon* in a phylogenetic analysis.

Tooth implantation is a useful character for understanding relationships among tetrapods because the mode of dental implantation (i.e., acrodont, pleurodont, thecodont) can be characteristic of entire lineages (Romer, 1956; Edmund, 1969). As such, comparing dental implantation in *P. browni* to groups that are historically labeled as “acrodont” (rhynchocephalians and procolophonids) and to groups that have the labio-lingually

aligned tricuspid tooth morphology (trilophosaurs) can provide a better understanding of the phylogenetic standing of *P. browni*. Terms used to describe implantation are often conflated with tooth replacement (Edmund, 1969; Osborn, 1984; Estes et al., 1988; Gauthier et al., 1988; Augé, 1997; Luan et al., 2009), so my use of these words are outlined below.

For this study, acrodont dentition is defined as tooth ankylosis to the crest of the marginal bones (i.e., premaxilla, maxilla, dentary; Edmund, 1969; Osborn, 1984; Jenkins et al., 2017). Acrodont implantation is seen in rhynchocephalians, chameleons, trogonophid amphisbaenians, agamids, and procolophonids (Gans, 1960; Edmund, 1969; Jones, 2008; Cabreira and Cisneros, 2009; MacDougall and Modesto, 2011; Falconnet et al., 2012). With pleurodont implantation the tooth is ankylosed to the lingual portion of the marginal bone (Edmund, 1969). Pleurodont dentition is seen in most lizards and several basal rhynchocephalians (Romer, 1956; Edmund, 1969). Thecodont implantation is present in archosaurs and mammals and is characterized by a tooth that sits within a socket. In some cases, thecodont teeth are ankylosed within the socket, a condition called ankylotheodont (Edmund, 1969; Chatterjee, 1974). Prototheodont implantation is present in many early reptiles and refers to a tooth ankylosed within a shallow pit (Edmund, 1969).

## GEOLOGIC SETTING

Specimens used in this study were collected at the farm Driefontein 11, Paul Roux District, Free State Province, South Africa. The strata at Driefontein belong to the Early Triassic Burgersdorp Formation, *Cynognathus* Assemblage Zone, subzone A (also called the '*Kestrosaurus*' assemblage zone), which is Olenekian in age (Hancox and Rubidge,

2001; Neveling, 2004). Vertebrate fossils from those strata are dominated by mastodonsaurid, brachyopid, and trematosuchid amphibians, erythrosuchids, and actinopterygian, chondrichthyan, and lungfish taxa (Bender and Hancox, 2003, 2004). Rare synapsid material, including cynodont and bauriid specimens, also are found (Bender and Hancox, 2003; Abdala et al., 2006, 2007).

Driefontein incorporates laminated lacustrine muds overlain by channelized sandstones, and at the base of these sandstones are occasional lag deposits (Yates et al., 2012). One particularly fossiliferous lag contains numerous fish remains, coprolites, and fragmented tooth-bearing specimens attributed to *Palacrodon* (Gow, 1999; Bender and Hancox, 2003, 2004; Yates et al., 2012).

## MATERIALS AND METHODS

Thirty-nine specimens of *P. browni* housed at the Evolutionary Studies Institute (ESI) at the University of the Witwatersrand, Johannesburg, South Africa were examined. Eight specimens of *P. browni* were CT scanned at the ESI (sp. no. BP/1/5672 A, BP/1/7819, BP/1/7824, BP/1/7830, BP/1/7840, BP/1/7898, BP/1/7899, BP/1/7904). One specimen (BP/1/5672) was previously described by Gow (1999). CT scans were set at the following parameters (voltage: 90 kV, intensity: 110  $\mu$ A) using a Nikon Metrology micro-CT scanner with a voxel size of 10  $\mu$ m. Segmentation and 3D reconstruction of the material was performed using Amira 5.6 (Mercury Computer Systems, Inc.) at Sam Houston State University, Huntsville, Texas. Using Amira, specimens were digitally cleaned of debris and cement if necessary. Two of the specimens to be CT scanned (BP/1/5672 A and BP/1/7819) are described because they are the most complete, and an

isolated tooth (BP/1/7904) is described because it shows apomorphic features unique to *P. browni*.

Using published literature, the taxa previously suggested to be related to *Palacrodon* (rhynchocephalians, trilophosaurs, procolophonids) were examined for synapomorphies. The features discussed in the following sections are deemed relevant for the purpose of comparing the anatomy of *P. browni* to the suggested taxa. The similarities in anatomy can then be used to perform a phylogenetic analysis that includes *P. browni*.

For the phylogenetic analysis, the character matrix from MacDougall et al. (2013) was used, and I used their characters and added *P. browni* to their matrix (Appendix C). That matrix includes 26 taxa and 59 characters (MacDougall et al., 2013). Two changes were made to the previous character matrix to reflect autapomorphies seen in *Palacrodon*. For character 30 (the number of maxillary cusps), character state (3) was added for three maxillary cusps, so that now the character states are: maxillary teeth cusps: (0) one, (1) two, (2) two and anterior monocuspid teeth absent, (3) three. For character 40 (the number of molariform cusps), character state (3) was added for three molariform teeth cusps, so that now the character states are: dentary molariform teeth cusps: (0) one, (1) two adjacent cusps, (2) two widely separated cusps, (3) three.

The revised data matrix was imported in the phylogenetic program TNT which runs phylogenetic analyses using parsimony (Goloboff and Catalano, 2016). A parsimony analysis is performed because it is considered an appropriate analysis for a morphological data set (Baum and Smith, 2013) and because I want to compare the results of my analysis to a previous analysis that also utilized parsimony (MacDougall et al., 2013). In

the parsimony analysis, the data set was subjected to a Traditional Search, which utilizes traditional computer algorithms for tree building using Tree Bisection and Reconnection (TBR) (Giribet, 2007). TBR is a standard branch-swapping technique in which all possible connections are made to the various branches of a tree to determine which connections are the most parsimonious (Felsenstein, 2004). Characters were considered unordered and equally weighted, meaning that all character changes are counted equally when calculating the most parsimonious trees, and no characters were considered more important (or weighted) than others (Baum and Smith, 2013).

Bootstrap support values were calculated using 100 replicates in order to place confidence intervals on the phylogeny, and if a clade had a bootstrap value of 95% then it is considered to be statistically significant (Felsenstein, 1985). Each node found by the phylogenetic analysis reports bootstrap values. Consistency index (CI) was calculated to show the amount of homoplasy on the tree and was calculated as  $CI = 100 \times \text{minimum number of changes} / \text{tree length}$  (Kluge and Farris, 1969; Baum and Smith, 2013). CI ranges from 0.0 to 1.0, with values closer to 1.0 representing less homoplasy (Kluge and Farris, 1969; Baum and Smith, 2013). Retention index (RI) reports the proportion of taxa without homoplastic character states and is calculated as  $RI = 100 \times (\text{max changes} - \text{tree length}) / (\text{max changes} - \text{min changes})$  (Farris, 1989; Baum and Smith, 2013). RI is also ranges from 0.0 to 1.0, with values closer to 1.0 signifying that a greater proportion of the taxa do not have homoplastic character states (Farris, 1989; Baum and Smith, 2013). CI and RI are similar in that they report homoplasy, but RI is often preferred because it uses the full range from 0.0-1.0, whereas minimum CI values vary but are always above 0.0



(Archie, 1989; Baum and Smith, 2013). Bootstrap values, CI, and RI all were calculated using TNT.

An additional parsimony analysis using the TNT macro “aquickie.run” was performed. This macro finds the most parsimonious tree for the data set and then calculates support values for a strict consensus tree. While aquickie.run can be used for several kinds of parsimony analyses, for this study Bremer support values and Jackknife values were calculated. Bremer support values are considered to be more popular and less ambiguous of the support value calculations (Bremer, 1988). Bremer support values are calculated as the number of additional steps required to deresolve a clade in a tree (Bremer, 1988). Jackknifing is used to assess the stability of clades by removing each character in succession and then replacing the removed taxa before removing the next one in the succession (Lanyon, 1985).

## RESULTS

### **Description**

BP/1/5672 A is a partial right dentary previously described by Gow (1999). The bone has multiple nutrient foramina visible from the labial side (Fig. 14 A). Large nutrient foramina are visible beneath the four largest, distal-most teeth. A pronounced Meckelian canal is visible from the lingual and inferior views and possess nutrient foramina (Fig. 14 B and D). There are five acrodont teeth, the mesial-most being the smallest, and the teeth increase in height, length, and width moving distally. The teeth are broadened labio-lingually and expand past the margins of the dentary. Almost the entire mesial-distal margin of each tooth comes in contact with the mesial-distal margin of the adjacent teeth (Fig. 14 C). All teeth are heavily worn on the occlusal surface. The three

mesial-most teeth show a tricuspid appearance where the three cusps are labiolingually aligned. The two distalmost teeth are too heavily worn to determine the number of cusps.

BP/1/7819 is a partial left maxilla bearing five acrodont teeth (Fig. 15). The first four teeth increase in labial-lingual length and height moving distally, and the fifth, distal-most tooth is the smallest. The maxillary teeth have a tricuspid appearance except for the distal-most tooth which is bicuspid. The teeth are labio-lingually expanded and the two mesial-most teeth expand past the margins of the maxilla.

Many teeth for some specimens of *P. browni* show that the central portions of each tooth are more heavily worn than the two cusps on the labio-lingual margins. The underside portion of each tooth has two parallel ridges which run labio-lingually and may assist in tooth attachment (Fig. 16).

CT scans reveal numerous channels for blood vessels and nerves which run the length of the bone (Fig. 17 and 18). Depending on the portion of the bone, two to four large channels, including the alveolar canal, are visible with smaller vessels branching from those larger vessels. From the alveolar canal those smaller vessels feed the pulp cavity beneath the tooth. The pulp cavity is large, transversely wide, and nearly flat, excepting for the ridges located on the under portion of each tooth (Fig. 16).

The tooth is firmly ankylosed to the surface of the bone. Though the tooth and bone are distinct in composition (dentine vs. bone), at the point of ankylosis there is no distinction between the two indicated by CT scans, showing that the material is all the same density. The two parallel ridges seen on the ventral portion of each tooth are also seen in sagittal slices of the dentary teeth (Fig. 17).

## Anatomical Features in Suggested Taxa

Previous workers suggested rhynchocephalians, trilophosaurs, and procolophonids as potential relatives of *Palacrodon* (Broom, 1906; Malan, 1963; Rubidge, 2005). However, from specimens collected thus far, those groups are restricted temporally and in some cases geographically, and those restrictions must be considered in determining the phylogenetic position of *Palacrodon*. Those restrictions, as well as basic morphological descriptions of each group are detailed below.

**Rhynchocephalians**— The basal-most rhynchocephalians have fully or partially pleurodont, conical dentition (Evans, 1980; Whiteside, 1986; Fraser and Shelton, 1988; Jenkins et al., 2017). One species, *Ankylophenodon pachyostosis* from the Early Cretaceous, shows ankylotheodont dental implantation (Reynoso, 2000). All others are described as having acrodont dentition with no evidence of replacement, but successional teeth may be added to the posterior end of the jaw (Romer, 1956; Edmund, 1969; Jones, 2008; Jenkins et al., 2017).

The earliest rhynchocephalians appear in the Middle Triassic with fully or partially pleurodont, conical dentition (Evans, 1980; Whiteside, 1986; Fraser and Shelton, 1988; Jenkins et al., 2017). Early rhynchocephalians are only known from sites in the northern hemisphere (Evans, 1980; Whiteside, 1986; Renesto, 1995; Heckert et al., 2008; Whiteside and Duffin, 2017). The first known appearance of a rhynchocephalian in the southern hemisphere is a species of *Clevosaurus* from the Early Jurassic of South Africa (Sues and Reisz, 1995). Fully acrodont dentition appears by the late Triassic, first seen in *Clevosaurus*, and teeth are not replaced (Fraser, 1988). A few rhynchocephalians show transversely broad dentition, and those taxa appear in the Late Jurassic and the

Cretaceous (Rasmussen and Callison, 1981; Throckmorton et al., 1981; Apesteguía and Novas, 2003; Martínez et al., 2013).

**Trilophosaurs**— Dental implantation in trilophosaurs is ankylothecondont (Gregory, 1945; Parks, 1969; Murry, 1987; Sues, 2003; Heckert et al., 2006).

Trilophosaurs possess transversely wide molariform teeth, and some species such as *Trilophosaurus*, possess three labio-lingually aligned cusps (Case, 1928a, 1928b; Gregory, 1945; Parks, 1969; Demar and Bolt, 1981). Trilophosaur fossils are only known from the American southwest, with questionable trilophosaur material from Canada, and they are temporally restricted to the Upper Triassic (Sues, 2003; Heckert et al., 2006; Spielmann et al., 2008, 2009).

**Procolophonids**— Tooth implantation in procolophonids is disputed, with some arguing that implantation is protothecondont (Gow, 1977; Li, 1983; Small, 1997; MacDougall and Modesto, 2011), ankylothecondont (Sues and Olsen, 1993), or acrodont (Li, 1983; Cabreira and Cisneros, 2009) because some procolophonids show tooth replacement. Some uses of the term “acrodont” include a lack of replacement in addition to the apical position of the tooth to the marginal bones (Augé, 1997), and because some procolophonids show evidence of replacement, some conclude that procolophonids are not acrodont (MacDougall and Modesto, 2011). However, not all definitions of acrodont include replacement, and acrodont can be used to describe the position of the tooth in relation to the marginal bone (Edmund, 1969; Osborn, 1984; Luan et al., 2009; Jenkins et al., 2017). In this thesis, acrodont will only be used as a positional term in which the tooth sits atop the marginal bones, not it does not refer to tooth replacement. As such, if a

procolophonid shows replacement, it may still possess acrodont tooth implantation if the tooth sits at the crest of the marginal bones.

Some procolophonids and other parareptiles show extreme ankylosis between tooth and bone (Cabreira and Cisneros, 2009; MacDougall et al., 2014). Many procolophonids also have differentiated incisiform and molariform teeth (Small, 1997; Sues et al., 2000; Säilä, 2010a). *Procolophon* and other Triassic procolophonids possesses transversely wide molariform teeth, often with two cusps on the occlusal surface which are connected by a loph, and that loph wears down ontogenetically to create a flat and smooth grinding surface (Gow, 1978; Fraser et al., 2005; Cisneros, 2008a; Säilä, 2010a). Additionally, a few procolophonids (*Xenodiphydon*, *Tricuspisaurus*, and *Scoloparia*) are noted to have labio-lingually aligned tricuspid teeth (Fraser, 1986; Sues and Olsen, 1993; Sues and Baird, 1998).

Procolophonids span the Late Permian to the Late Triassic, and they are the only known lineage within Parareptilia to survive the Permian mass extinction and then go extinct at the end of the Triassic (Piñero et al., 2004; Tsuji and Müller, 2009; Säilä, 2010a; Botha-Brink and Smith, 2012). In the Early Triassic, the dentition of procolophonids exhibited dental regionalization which included both incisiform and molariform morphologies, and replacement is not frequently seen in procolophonids (Ivakhnenko, 1974; Gow, 1978; Small, 1997; MacDougall and Modesto, 2011). Procolophonids were a cosmopolitan group, and several members were found in South Africa (e.g., Colbert and Kitching, 1975; Gow, 2000; Modesto et al., 2001; Cisneros, 2008a; MacDougall et al., 2013).

## Phylogenetic Analysis

### SYSTEMATIC PALEONTOLOGY

PARAREPTILIA Olson, 1947 sensu Laurin and Reisz, 1995

PROCOLOPHONOMORPHA Romer, 1964

PROCOLOPHONIDAE Seeley 1888

*PALACRODON BROWNI* Broom 1906

**Institutional Abbreviations**—**BP**, Evolutionary Studies Institute, Johannesburg, South Africa (formerly the Bernard Price Institute); **SAM**, South African Museum, Cape Town, South Africa.

**Holotype**—SAM-PK-5871, partial dentary, unknown locality in South Africa.

**Referred Specimens**—BP/1/5672 A, BP/1/5672 B, BP/1/6724, BP/1/7819, BP/1/7824, BP/1/7825, BP/1/7826, BP/1/7827, BP/1/7828, BP/1/7829, BP/1/7830, BP/1/7831, BP/1/7832, BP/1/7833, BP/1/7834, BP/1/7835, BP/1/7836, BP/1/7837, BP/1/7838, BP/1/7839, BP/1/7840, BP/1/7841, BP/1/7892, BP/1/7893, BP/1/7894, BP/1/7895, BP/1/7896, BP/1/7897, BP/1/7898, BP/1/7899, BP/1/7900, BP/1/7901, BP/1/7902, BP/1/7903. BP/1/7904, BP/1/7905, BP/1/7906, BP/1/7930; all are fragmented tooth-bearing elements; Olenekian (Early Triassic), Burgersdorp Formation, *Cynognathus* Assemblage Zone, subzone A, Farm Driefontein 11, Paul Roux district, Free State Province, South Africa (Gow, 1999). BP/1/5296; partial skull belonging to *Fremouwsaurus*; Lower Fremouw Formation, equivalent to the *Lystrosaurus* Assemblage zone, unknown locality at Kitching Ridge, Antarctica (Gow, 1992; Sidor et al., 2008).

The similarities between *Palacrodon* and procolophonids justifies placing *Palacrodon* in a phylogenetic analysis with other procolophonids (MacDougall et al.,

2013). The first parsimony analysis produced six equally parsimonious trees, with a tree length of 160 steps, which is the number of character changes on the tree (Baum and Smith, 2013). Those six trees were combined in a strict consensus tree (Fig. 19). Bootstrap support is below 50% for most clades. However, low bootstrap support is common in analyses of procolophonids and other parareptiles owing to missing data (Cisneros, 2008b; Säilä, 2008; MacDougall and Modesto, 2011; MacDougall et al., 2013). CI is calculated as 0.602 and RI is calculated as 0.689, showing that most character states are not homoplastic, although there is some homoplasy on the tree. The results of the phylogenetic analysis suggest that *P. browni* belongs in the family Procolophonidae and is sister to *Hypsognathus*, although with a low bootstrap support of seven.

The overall topology of the consensus tree resulting from my analysis is similar to that recovered by MacDougall et al. (2013). My analysis shows a sister relationship between '*Eumetabolodon*' *dongshengensis* and *Theledectes* that was not previously recovered. The polytomy in my analysis consisting of *Pentaedrusaurus*, *Neoprocolophon*, and *Phonodus* also included *Phaanthosaurus*, '*Eumetabolodon*,' *Theledectes*, *Tichvinskia*, *Timanophon*, and *Kitchingnathus* in MacDougall et al.'s analysis (2013). The additional analysis performed (Fig. 20) also resolved the large polytomy seen in MacDougall et al.'s. However, this analysis shows *Palacrodon* within a polytomy that also includes *Sclerosaurus*, *Scoloparia*, *Leptopleuron*, *Soturnia*, and *Hypsognathus*.

For my analysis, the presence of labio-lingually aligned tricuspid teeth in *P. browni* is autapomorphic. However, a phylogenetic analysis that includes other tricuspid

taxa (*Xenodiphyodon*, *Tricuspisaurus*, and *Scoloparia*) has not been performed by the authors who described those taxa. Those three taxa and *P. browni* may potentially represent a tricuspid clade within Procolophonidae; the alternative is that the trait is homoplastic.

## DISCUSSION

As seen in the literature, there are several important features in rhynchocephalians, trilophosaurs, and procolophonids that are similar to *P. browni*. Comparisons between *P. browni* and those taxa, are outlined below.

**Rhynchocephalians**— Fusion between the tooth and bone in acrodont rhynchocephalians, such as *Clevosaurus*, is extensive, obscuring the boundary between the two, similar to *P. browni* (Jenkins et al., 2017:230). However, *Gephyrosaurus* (which is pleurodont), *Clevosaurus*, and *Sphenodon* have a more conical pulp cavity (Harrison, 1901:214–216; Kieser et al., 2011:46; Jenkins et al., 2017:303), whereas the pulp cavity of *Palacrodon* is transversely wide. Because basal rhynchocephalians do not possess fully acrodont dentition and their dentition is conical, *Palacrodon* is not a basal rhynchocephalian. Additionally, those rhynchocephalians with transversely broad dentition do not possess cusps similar to those seen in *Palacrodon* and do not appear until the Early Jurassic. The most parsimonious explanation is that the acrodont implantation seen in rhynchocephalians and *Palacrodon* evolved independently.

**Trilophosaurs**— Physical slices through the maxillary of *Trilophosaurus* shows that it possesses a large, tear-shaped pulp cavity in sagittal sections (Gregory, 1945:337), unlike what is seen in *Palacrodon*. Both *Palacrodon* and trilophosaurs show ankylosing between tooth and bone, but unlike *Palacrodon*, trilophosaurs possess extensive roots



that extend into the jaw and replaces its teeth (Case, 1928b; Demar and Bolt, 1981; Heckert et al., 2006). The temporal fenestration in *Palacrodon* (seen in a specimen in Antarctica) also does not correspond with the temporal fenestration in trilophosaurs (Gregory, 1945; Parks, 1969; Heckert et al., 2006). Considering those morphological differences between *Palacrodon* and trilophosaurs and the restricted geography and temporal distribution of trilophosaurs, *Palacrodon* is not a South African, Early Triassic trilophosaur. The tricuspid appearance seen in *Palacrodon* and trilophosaurs is better explained by convergence.

**Procolophonids**— *Palacrodon* shares three apomorphies with procolophonids described below. The extensive dental ankylosis and acrodont dental implantation of *Palacrodon* resembles several procolophonids. Anatomical research shows that procolophonids and other parareptiles have a relatively large pulp cavity that is conical or rounded (Cabreira and Cisneros, 2009; MacDougall and Reisz, 2012:1022; MacDougall et al., 2014). *Palacrodon* also possesses a large pulp cavity, although not it is not morphologically similar to the cavities of parareptiles studied thus far. The tricuspid, transversely wide, molariform-like teeth associated with *Palacrodon* are similar to the procolophonids *Xenodiphyodon*, *Tricuspisaurus*, and *Scoloparia*.

The most complete specimen of *Palacrodon* was found in Antarctica (Gow, 1992). The presence of partial lower temporal fenestration indicates that it is likely a diapsid, and this specimen is currently classified as *Diapsida incerte sedis* (Gow, 1992, 1999). Procolophonids and other parareptiles possessing lower temporal fenestration were discovered since those descriptions of *Palacrodon* (e.g., Hamley and Thulborn, 1993; Cisneros et al., 2004; MacDougall and Reisz, 2014). With this evidence, it is

reasonable to infer that *Palacrodon* could be a procolophonid, and this is congruent with its placement in the phylogenetic analysis as part of procolophonids.

## CONCLUSIONS

Based on the temporal and geographic ranges of rhynchocephalians, trilophosaurs, and procolophonids as well as the similarities of the dentition, *Palacrodon* is likely a procolophonid. The results of the phylogenetic analysis show that *Palacrodon* most likely lies within Procolophonidae. The labiolingually aligned tricuspid tooth morphology may be a synapomorphy for a clade of tricuspid procolophonids including *Palacrodon*, but more phylogenetic and descriptive work is needed to corroborate this hypothesis.

Furthermore, additional anatomical work on procolophonids with transversely wide dentition, rather than on those with more conical teeth (the focus of prior research), may reveal similarities in the pulp cavities between *Palacrodon* and other procolophonids. Anatomical research on other procolophonids with expanded molariform dentition may reveal transverse parallel ridges beneath the crowns like those of *Palacrodon*, further supporting the hypothesis that it is a procolophonid. It could also reveal the opposite, revealing a unique morphological feature in *Palacrodon* related to tooth attachment. This feature has not yet been reported in any tetrapod.

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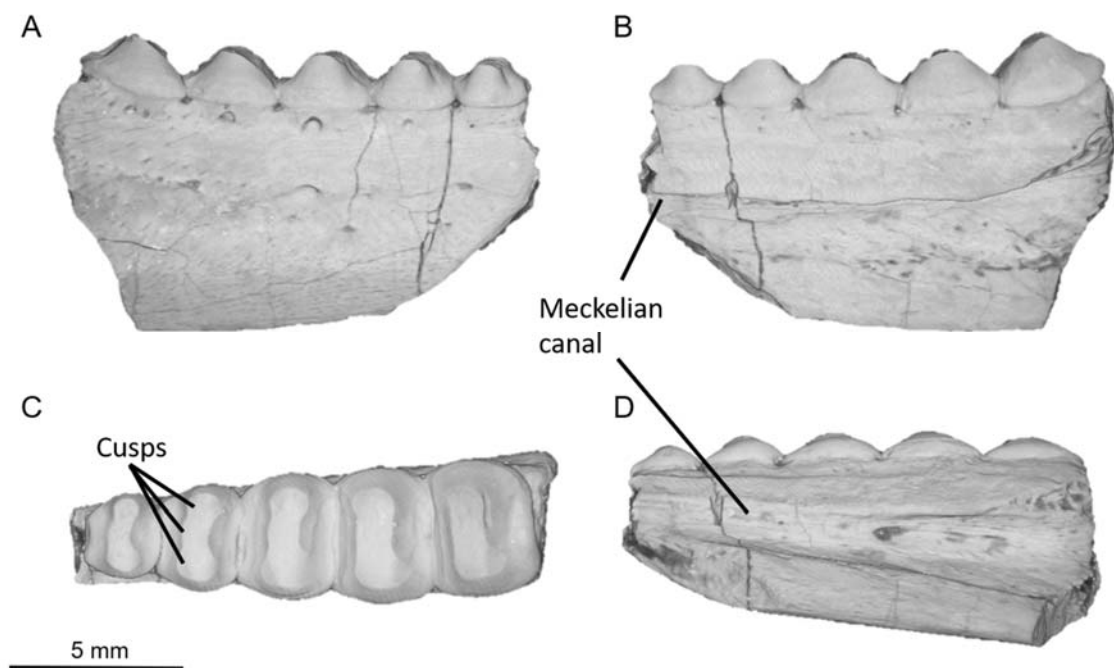


FIGURE 14. *Palacrodon* specimen BP/1/5672 A external views. Partial right dentary in A) labial view, B) lingual view, C) occlusal view, and D) inferior view.

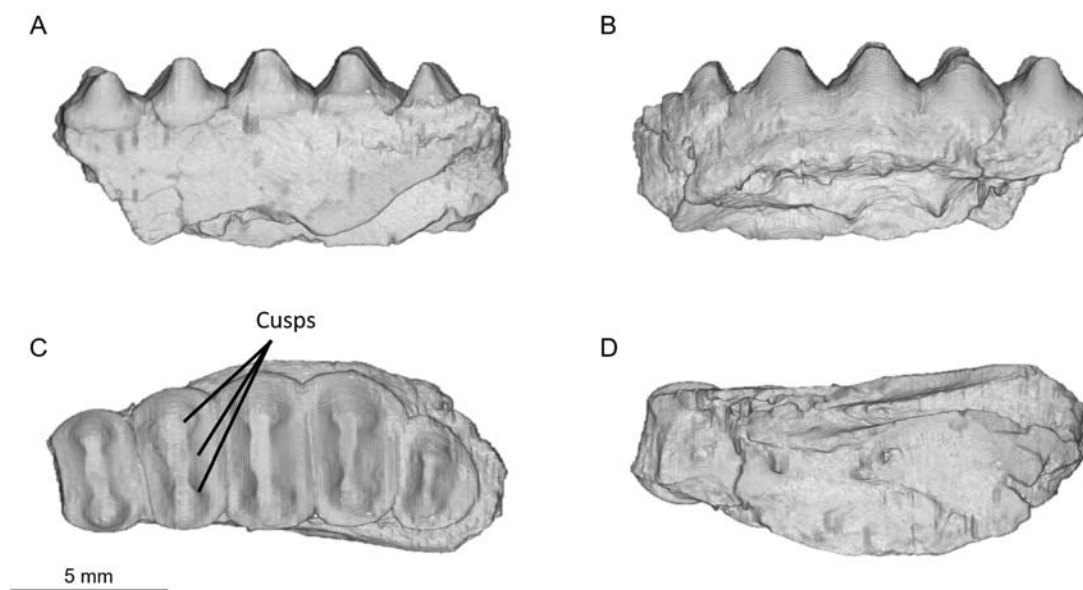


FIGURE 15. *Palacrodon* specimen BP/1/7819 A external views. Partial left maxilla in A) lingual view, B) labial view, C) occlusal view, and D) superior view



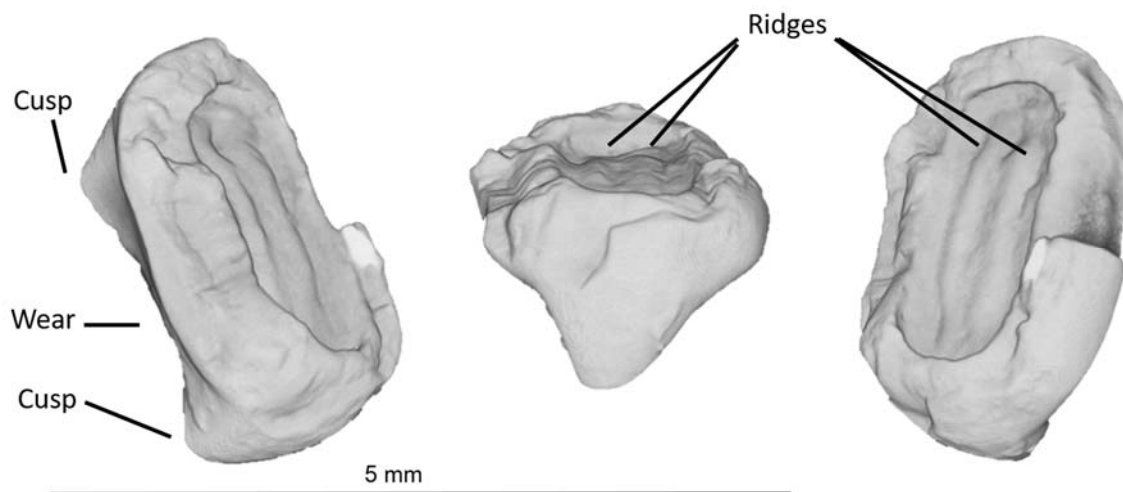


FIGURE 16. *Palacrodon* specimen BP/1/7904 external views. Longitudinal ridges are visible on the underside of the tooth. Tooth exhibits concave wear in the central portion towards the base of the tooth. Two cusps are visible.

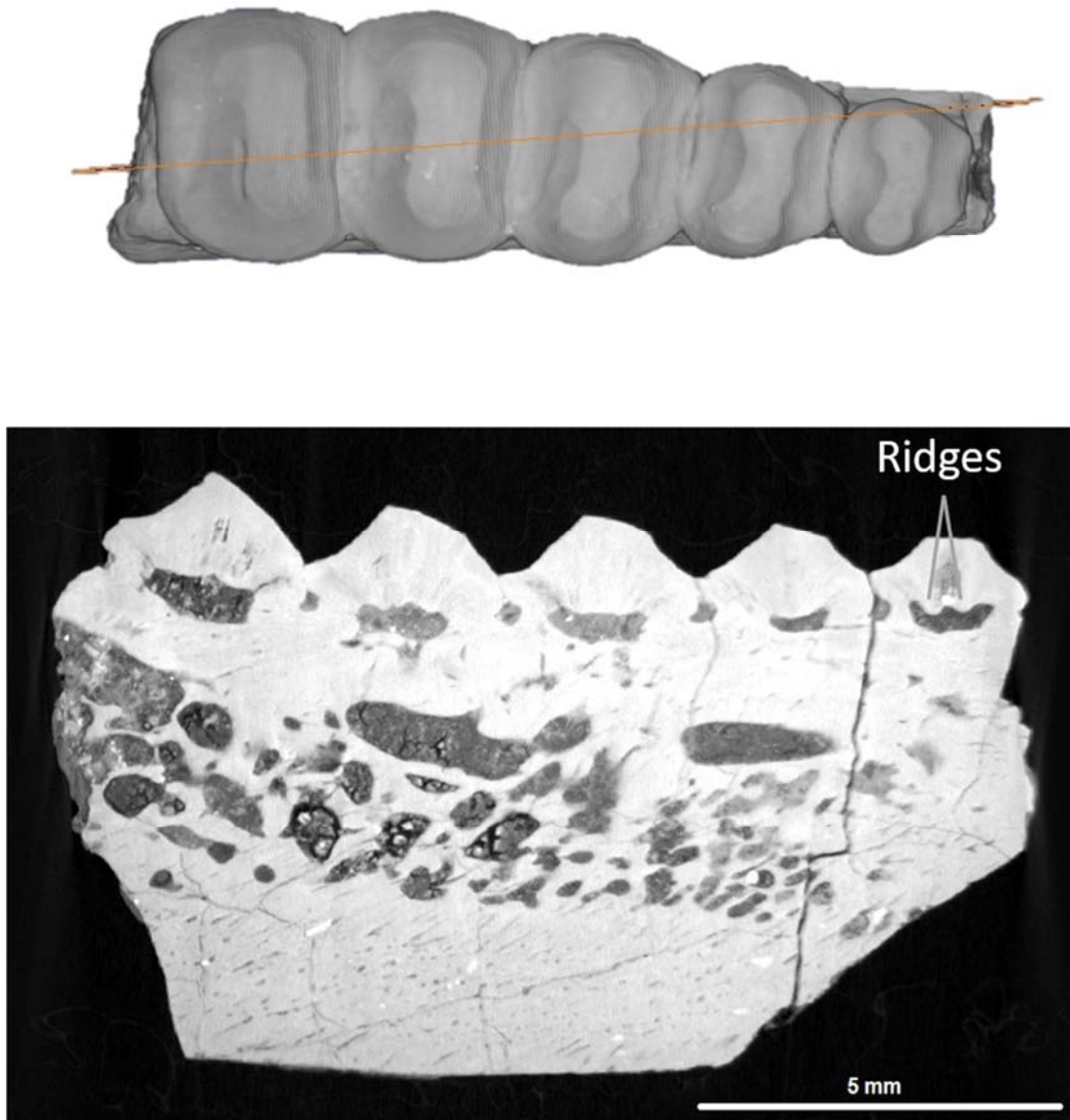


FIGURE 17. *Palacrodon* specimen BP/1/5672 A sagittal view of right dentary. Location of the slice is indicated by the orange line. The two longitudinal ridges beneath the mesialmost tooth are indicated.

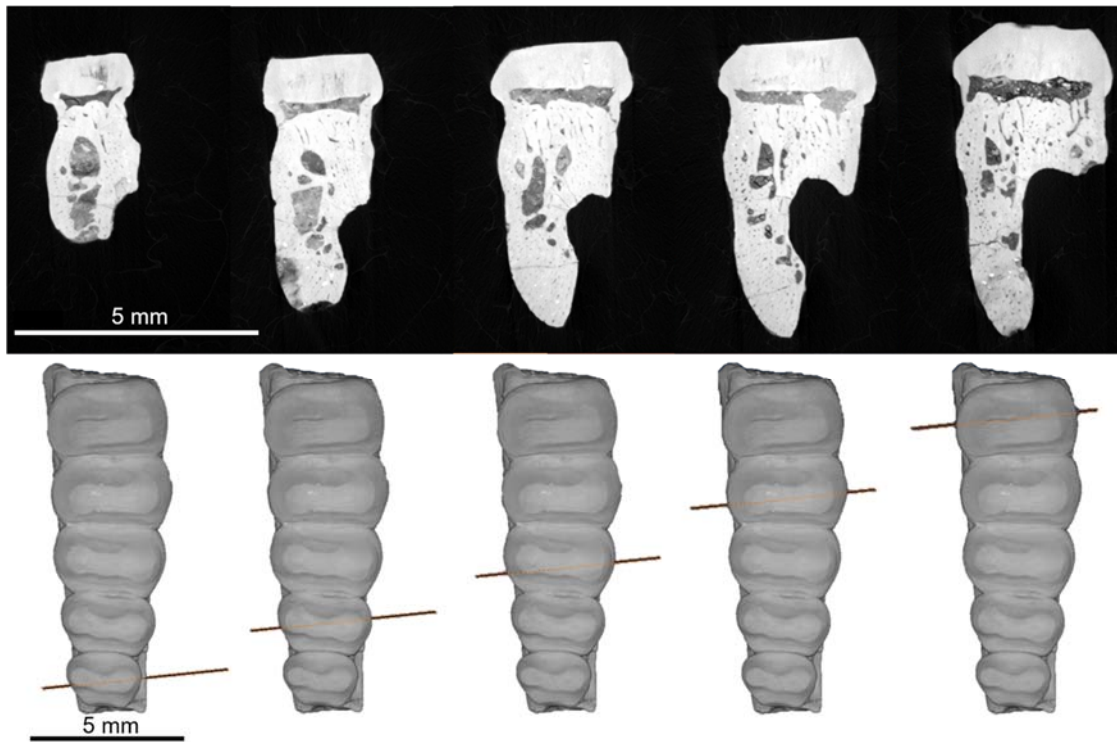


FIGURE 18. *Palacrodon* specimen BP/1/5672 A coronal views of right dentary. Location of the slices are indicated by the orange lines.

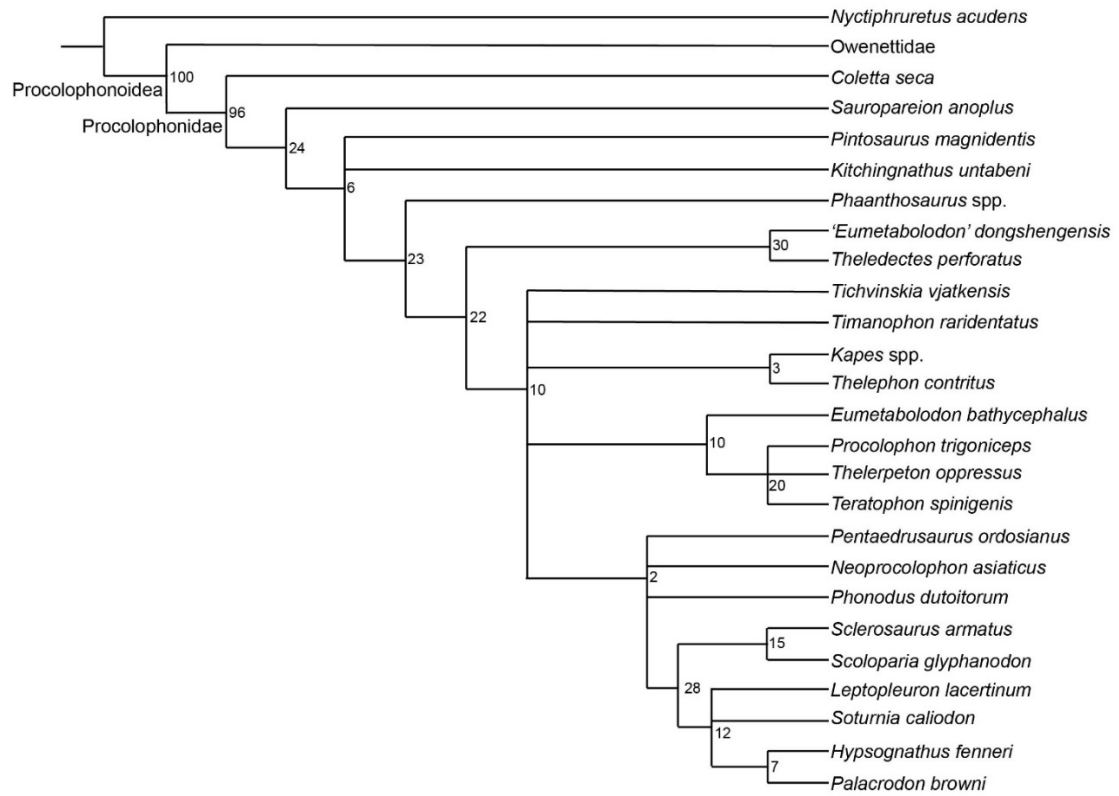


FIGURE 19. Strict consensus of six trees discovered in TNT including character data for *Palacrodon*. Bootstrap values are indicated at the branch nodes.

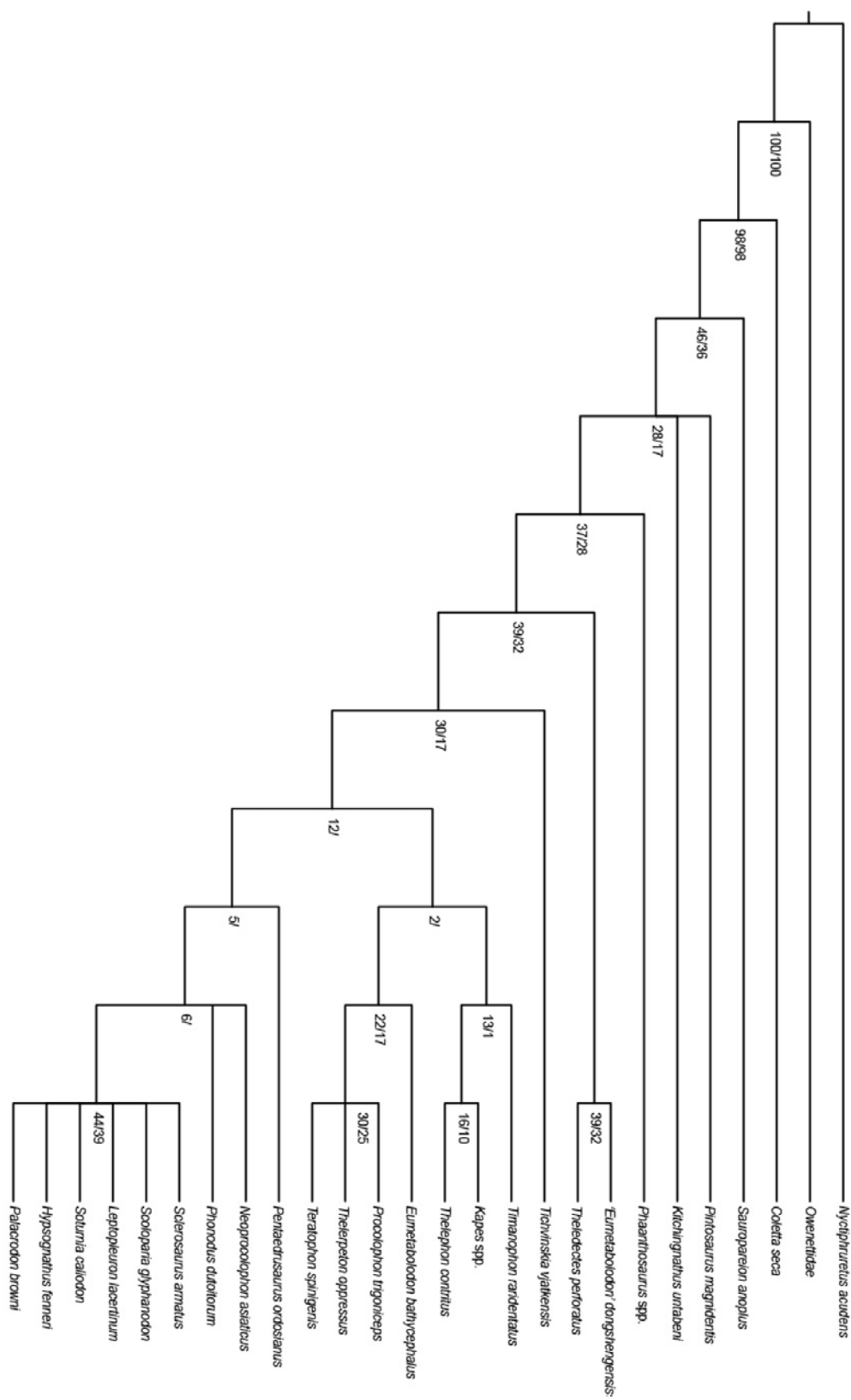


FIGURE 20. Consensus tree recovered with Bremer and Jackknife support values.

### CHAPTER III

#### Inferring the Diet of *Palacrodon* from its Dentition

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This thesis follows the style and format of *Palaeontologia africana*.

## ABSTRACT

The diet of the Early Triassic reptile *Palacrodon* is uncertain. New specimens of *Palacrodon* discovered in the Free State Province, South Africa reveal aspects of the dental morphology and wear patterns from which diet can be inferred. Labiolingually elongated, cusped, molariform dentition paired with severe wear on the occlusal surfaces of the teeth is indicative of an herbivorous or omnivorous diet. Three distinct wear patterns are identified that indicate shearing and grinding movements. Similar dental morphologies are also present in the teiid *Teius teyou* and multiple extinct lineages.

**Keywords:** dentition, herbivory, wear patterns, Karoo, Triassic

## Inferring the Diet of *Palacrodon* from its Dentition

### INTRODUCTION

There is no consensus on the diet of *Palacrodon*. One author classified it as an herbivore (Gow 1992), but it has since been classified as a carnivore and an omnivore (Nicolas & Rubidge 2010; Smith et al. 2012). In 1996 a partial dentary and maxilla associated to *Palacrodon* were discovered at the Driefontein locality in the Free State Province of South Africa (Gow 1999). Now a total of 76 specimens have been discovered, allowing the dental morphology of *Palacrodon* to be examined with a large sample size. Morphology, dental regionalization, and wear are features from which diet can be inferred (e.g., Edmund 1969; Gow 1978; Weishampel & Norman 1989; Ungar 1998). Here I will test the initial hypothesis set forth by Gow (1992) that *Palacrodon* is an herbivore using those aspects of tooth morphology.

Diet can be estimated by dental morphology (Kingsley 1899; Parker & Haswell 1899; Hotton 1955; Edmund 1969; Hillson 2005). In reptiles, a carnivore's tooth typically is adapted for piercing and/or mastication, compared to an herbivorous reptile's tooth which is often adapted for more sophisticated oral processing such as shearing and grinding (Chapter 1, Figure 12; Kingsley 1899; Parker and Haswell 1899). Highly specialized clades within Reptilia (e.g., turtles and birds) lack teeth entirely but are adapted for many forms of herbivory, carnivory, and omnivory (Lack 1947; Edmund 1969). Additionally, some features like dentition are constant phylogenetically, as in the case of anoles and iguanians which retain multicuspid teeth even though some species are insectivorous while others are herbivorous (Melstrom 2017).



Cylindrical teeth in reptiles often correlate with a carnivorous or insectivorous diet (Edmund 1969). Those teeth are sometimes modified by serrations, lateral compression, pointed apices, and/or blunt surfaces which aid in grasping, piercing, or crushing (Romer 1956; Edmund 1969). Some insectivorous reptiles, like many iguanians, geckos, and teiids, may also have cusps (Hotton 1955; Sumida & Murphy 1987; Berkovitz & Shellis 2016; Zahradnicek et al. 2014). Some reptiles, like snakes, possess recurved teeth that are either smooth or that have lateral ridges to accommodate different prey items (Vaeth et al. 1985). Specialized carnivores with a durophagous diet, a diet consisting of conchiferan mollusks, corals, and other hard-shelled organisms, have teeth adapted for crushing those hard materials; and the teeth may be more rounded, as in the mosasaur genus *Globidens*, or may possess flat tooth plates that cover large portions of the palate, as seen in most placodonts (Romer 1956; Massare 1987; Neenan et al. 2013; Berkovitz & Shellis 2016). In carnivorous mammals, teeth are often modified from the conical or triangular shape seen in reptiles and exhibit features like cusps and ridges (Osborn 1907; Crompton 1971; Hillson 2005; Jernvall & Thesleff 2012).

An herbivorous reptile's tooth also often strays from the typical conical shape seen in carnivorous forms, and they may also possess larger grinding surfaces in some cases to chew food more thoroughly (Chapter 1 Figure 13; Gow 1978; Weishampel & Norman 1989; Hillson 2005). For herbivorous reptiles, dental morphology varies, but may include features like cusps and leaf-like serrations, as seen in iguanids and some dinosaurs (Hotton 1955; Edmund 1969; Sander 1997; Melstrom 2017). Other herbivorous dental characters are more suited for grinding, such as reptilian molariform teeth seen in extinct groups such as procolophonids and trilophosaurs that possess labiolingually-wide

dentition, and the molariform teeth seen in some extant skinks, chameleons, and teiids (Romer 1956; Gow 1977; Demar & Bolt 1981; Estes & Williams 1984; S  il   2010).

Dental batteries (i.e., numerous interlocked teeth) seen in ornithomimid dinosaurs are also suitable for grinding plant material (Edmund 1969; Sander 1997; Sereno & Wilson 2005; Barrett 2014).

Tooth morphology in many herbivorous reptiles is also characterized by isognathia, defined as the upper and lower dental arch being equally wide, and occurs with dental occlusion, particularly in early herbivores that diversified in the Middle Permian through the Triassic (Weishampel & Norman 1989; King 1996). Herbivory in reptiles can also be inferred by dental organization (i.e., heterodonty), with teeth being separated into mesial incisiform teeth suited for chopping or slicing and distal molariform teeth suited for grinding (Romer 1956; Edmund 1969). Although heterodonty is a feature often associated with herbivory in the fossil record, extant carnivorous taxa may also possess heterodont dentition, like *Crocodylus niloticus* which is a carnivore with incisor, canine, and molar regions and *Anolis allisoni* which is an insectivore with unicuspid and tricuspid teeth (Kieser et al. 1993; Zahradnicek et al. 2014). Omnivorous lizards also may have heterodont dentition with enlarged molariform teeth, like some members of the genus *Tiliqua* (Estes & Williams 1984).

Tooth wear can be indicative of herbivory as the teeth are worn down by fibrous plant materials, nuts, and/or seeds, and those wear patterns also can indicate masticatory movement (e.g., orthal, propalinal, transverse; Crompton & Attridge 1986; Weishampel & Norman 1989; Reisz 2006). Yet, carnivorous and insectivorous animals may also experience tooth wear, particularly if the teeth are not replaced or if they are replaced

slowly as the animal ages, as in *Sphenodon* or agamid lizards (Harrison 1901; Throckmorton 1979; Smirina & Ananjeva 2007; Kieser et al. 2011), if the animal eats material that is harder than flesh like shells and bone (Estes & Williams 1984; Neenan et al. 2014), or if interlocking teeth abrade against each other (Massare 1987).

It was previously hypothesized that smaller animals lack the elongated gut necessary for digesting plant material (Pough 1973; Wilson & Lee 1974), in addition it was estimated that herbivorous reptiles needed to weigh at least 300 g in order to effectively ferment plant material in the gut (Pough 1973). Carnivores typically range between 50-100 g, and juveniles of herbivorous species generally are carnivorous or insectivorous until reaching an adult body size (Pough 1973). However, there are extant small-bodied herbivorous and omnivorous reptiles like the lizards *Sceloporus torquatus torquatus*, *Angolosaurus skoogi*, and many liolaemids (Búrquez et al. 1986; Pietruszka et al. 1986; Espinoza et al. 2004). Additionally, tooth morphology can also differ ontogenetically to accommodate changes in diet, as seen in the teiids *Ameiva exsul alboguttata*, *Tupinambis rufescens*, and *T. teguixin*, and the anguid *Diploglossus cruscus* (Presche 1974; Estes & Williams 1984). Some extinct small-bodied reptiles, including many procolophonids and bolosaurs, are thought to have been herbivorous based on tooth morphology (Romer 1956; Berman et al. 2000; Reisz 2006). As such, body size is not always the most useful indicator of diet, but it can support other morphological features that suggest diet (e.g., teeth).

## GEOLOGIC SETTING

Because environmental setting may also help predict the diet of an animal, here I provide a brief description of the environment associated with the specimens I examined.

Specimens for this study (with the exception of one from Antarctica) were collected at the farm Driefontein 11, Paul Roux District, Free State Province, South Africa. The strata at Driefontein belong to the Early Triassic (Olenekian) Burgersdorp Formation, *Cynognathus* Assemblage Zone, subzone A (also called the ‘*Kestrosaurus*’ assemblage zone) (Hancox & Rubidge 2001; Neveling 2004). The Burgersdorp Formation is dominated by fluvio-lacustrine siliciclastic rocks (Johnson 1976; Hancox & Rubidge 2001). Driefontein incorporates laminated lacustrine muds overlain by channelized sandstones, and at the base of these sandstones are occasional lag deposits containing fossils (Yates et al. 2012).

The strata at Driefontein are dominated by mastodonsaurid, brachyopid, and trematosuchid amphibians, erythrosuchids, and rare cynodont and bauriid specimens (Bender and Hancox 2003, 2004; Abdala et al. 2006, 2007). One particularly fossiliferous lag deposit contains numerous actinopterygian, chondrichthyan, and dipnoian elements, fish coprolites, and fragmented tooth-bearing specimens attributed to *Palacrodon* (Ortiz et al. 2010; Gow 1999; Bender and Hancox 2003, 2004; Yates et al. 2012). Coprolites from this lag contain shellfish (Yates et al. 2012). The high percentage of fish remains found in this lag indicates that the assemblage is predominantly aquatic (Yates et al. 2012).

## MATERIALS AND METHODS

Thirty-nine specimens of *Palacrodon* were available to study at the Evolutionary Studies Institute at the University of the Witwatersrand, Johannesburg, South Africa. Referred specimens are BP/1/5672 A, BP/1/5672 B, BP/1/6724, BP/1/7819, BP/1/7824, BP/1/7825, BP/1/7826, BP/1/7827, BP/1/7828, BP/1/7829, BP/1/7830, BP/1/7831,

BP/1/7832, BP/1/7833, BP/1/7834, BP/1/7835, BP/1/7836, BP/1/7837, BP/1/7838, BP/1/7839, BP/1/7840, BP/1/7841, BP/1/7892, BP/1/7893, BP/1/7894, BP/1/7895, BP/1/7896, BP/1/7897, BP/1/7898, BP/1/7899, BP/1/7900, BP/1/7901, BP/1/7902, BP/1/7903. BP/1/7904, BP/1/7905, BP/1/7906, BP/1/7930.

Height, width, and length were measured for teeth not broken or obscured by matrix using Mitutoyo Absolute Digimatic calipers. Height, width, and length are normally distributed (Shapiro-Wilk test;  $p=0.29$ ,  $p=0.83$ ,  $p=0.65$ , respectively). Measurements for the specimen from Antarctica (*Fremouwosaurus*, BP/1/5296) were not taken because the specimen is encased in resin. In many cases an analysis of covariance (ANCOVA) can be used to compare morphology between populations and/or species while using body size as a covariate (McCoy et al. 2006). Since no complete elements of *Palacrodon* have been found, precise body size cannot be calculated in order to make direct statistical comparisons to other taxa. A qualitative assessment plotting the averages and standard deviations of height, width, and length (Figure 21) and bivariate plots (Figure 22 & 26) are used to view the general shape and assess size differences of the teeth of *Palacrodon*.

## RESULTS

### Tooth Size

The average tooth measurements for height, width, and length are 1.27 mm (SD = 0.45), 2.82 mm (SD = 0.80), and 1.71 (SD = 0.45), respectively, and raw tooth measurements are reported in Appendix D. These values are reported on Figure 21. These data show that the teeth are wider than they are long or tall. The dimensions of the teeth

reported on Figure 22 plot near the grinding/shredding morphotypes reported by Jones (2009) in Figure 23.

### **Tooth Morphology**

The morphology of the teeth is best described as molariform, because they are cusate, rectangular, and have increasing surface area distally. The molariform teeth of *Palacrodon* are wider along the labiolingual plane than the mesiodistal plane, and the teeth are either bicusate or tricusate. All specimens from Driefontein only possess molariform teeth. However, the specimen from Antarctica shows regionalization possessing both incisiform and molariform teeth (Fig. 24). Because *Fremouwssaurus* and *Palacrodon* are regarded as being the same genera (Gow 1992, 1999), we may infer that *Palacrodon* specimens from Driefontein also possesses regionalization.

Isognathly cannot be inferred from the specimens collected at Driefontein because all specimens recovered are isolated dentary and maxillary fragments. The Antarctic specimen preserves a larger portion of the skull, but is imbedded in resin, so it is not possible to determine isognathly.

### **Tooth Wear**

In all cases where wear is present, it appears along the labiolingual plane of the teeth. The degree of wear differs between specimens and sometimes between teeth located on the same specimen. Here I define three distinct wear patterns on the teeth of *Palacrodon*.

Type I wear is exhibited evenly across labiolingual plane of the tooth and is located on the anterior or posterior slope of the tooth. This wear only appears on either the mesial or distal portion of the tooth, but never appears on both slopes on the same

specimen (Fig. 25 A & B). For some teeth this creates a sharp ridge at the apex of the tooth (Fig. 25 B).

Type II is a flat wear pattern that is centered on the apex of the tooth (Fig. 25 C & D). This wear pattern is not always centered on the labiolingual plane of the tooth, and some teeth show more wear near one cusp than the other.

Type III wear is also centered on the apex of the tooth, but the wear is heavier along the mesial portion of the tooth, and the distal portions of the tooth slope upwards to create a concave wear pattern towards the base of the tooth (Fig. 25 E). This type of wear usually preserves cusps. Types I and II rarely preserve cusps.

As teeth increase in height they also increase in width (Fig. 26). However, the widest teeth are not the tallest teeth. Those teeth that are wider are also more heavily worn than those teeth that are narrower.

## DISCUSSION

The specific dimensions of the teeth show that they align with the teeth of rhynchocephalians that are presumed to be herbivorous (Jones 2009). The similarity of the dimensions of *Palacrodon* to those herbivorous rhynchocephalians supports the hypothesis that *Palacrodon* incorporated plants into its diet. The teeth of *Palacrodon* are wider than they are long and cusped as seen in procolophonids, trilophosaurs, diadectids, and perrinites which are also thought to be herbivorous (J. Gregory 1945; W. Gregory 1946; Edmund 1969; Gow 1977, 1978; Demar & Bolt 1981; Li 1983). Because of its resemblance to extinct rhynchocephalians that are presumed to be herbivorous, herbivory is supported for *Palacrodon*. However, given that all but one species of rhynchocephalian is extinct, this support is weak.

Similar to *Palacrodon*, the insectivorous Teiid *Teius tegu* has bicuspid and occasional tricuspid teeth with labiolingually aligned cusps (Brizuela & Albino 2009; Zahradnicek et al. 2014). In other lizards, like iguanians, tricuspid teeth are utilized in insectivorous, herbivorous, and even durophageous diets, although their teeth are labiolingually compressed (Zahradnicek et al. 2014). Comparing the teeth of *Palacrodon* to the teeth of extant reptiles does support an herbivorous diet, but no more than it does an insectivorous or durophageous diet.

*Palacrodon* possessed both incisiform and molariform teeth, a condition that is frequently associated with herbivory and omnivory in reptiles. Because heterodonty is a feature associated with various diets, that feature cannot be used to solely support an herbivorous diet for *Palacrodon*, and an omnivorous diet may also be supported.

The shearing ridge seen in the Type I wear pattern would be useful in chopping plant material as well as puncturing hard exoskeletons of arthropods. The Type II wear that appears on the apex of the tooth indicates a grinding surface for grinding plants or even crushing hard material like arthropods or shells. It is difficult to determine what caused the Type III wear pattern, but the heavy amount of the wear is indicative of hard objects, although all cases of wear could be a symptom of aging as well. Durophagy is also a possibility, because the broad teeth flattened by wear would be useful in crushing hard-shelled organisms, and previous research at Driefontein shows there were mollusks present (Yates et al. 2012). Wear patterns along support an herbivorous, omnivorous, insectivorous, or even durophageous diet.

As seen in Figure 26, teeth are taller as they become wider to an extent. However, teeth that are wider than three millimeters appear to drop off in height. Teeth wider that



three millimeters are also more heavily worn than teeth less than three millimeters wide.

Those data show that teeth grow taller and wider ontogenetically, but at approximately three millimeters teeth continue to grow wider but shorten in height due to wear.

Although the heavy wear supports an herbivorous diet, it may also support an omnivorous or durophagous diet or ontogenetic stages of wear. Additionally, these data can be interpreted as a possible ontogenetic shift in diet, sexual dimorphism, ecophenotypic plasticity over time, or may represent different portions of the dentary and maxilla.

Even though body size of *Palacrodon* cannot be determined, the mesiodistal length of the teeth indicate it is a smaller animal, similar in size to median sized lizards (e.g., *Chamaeleolis porcus*, *C. chamaeleonides*, *Diplolaemus bibroni*, *Tiliqua scincoides*; Estes & Williams 1984). Although there are instances of small herbivorous reptiles, those instances are less common. The cuspatation and sharp ridges of some specimens suggest that *Palacrodon* may have incorporated arthropods into its diet because its small size may not have been conducive to digesting plants, and arthropods are a more calorically dense food. Another possibility is that *Palacrodon* switched from insectivory to herbivory ontogenetically, as seen in several extant reptiles like the iguanids *Sceloporus poinsetti* and the *Liolaemus lutzae* (Pough 1973; Ballinger et al. 1977; Werner & Gilliam 1984; Rocha 1998) and as suggested for several other small-bodied extinct reptiles, like procolophonids and trilophosaurs (Gow 1977; Demar & Bolt 1981; Li 1983). Although body size is not always a reliable indicator of diet, body size suggests that *Palacrodon* was most likely herbivorous or omnivorous.

The teeth of *Palacrodon* suggest that it was an herbivore or omnivore with a diet consisting of plant material and possibly arthropods and/or hard-shelled organisms as indicated by the aquatic assemblage from which *Palacrodon* is found. Strict carnivory is not supported by the morphology of the teeth.

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Figure 21. Average height, width, and length of the teeth of *Palacrodon*. Height, width, and length were measured for teeth not broken or obscured by matrix. Height, width, and length are normally distributed (Shapiro-Wilk test;  $p=0.29$ ,  $p=0.83$ ,  $p=0.65$ , respectively).

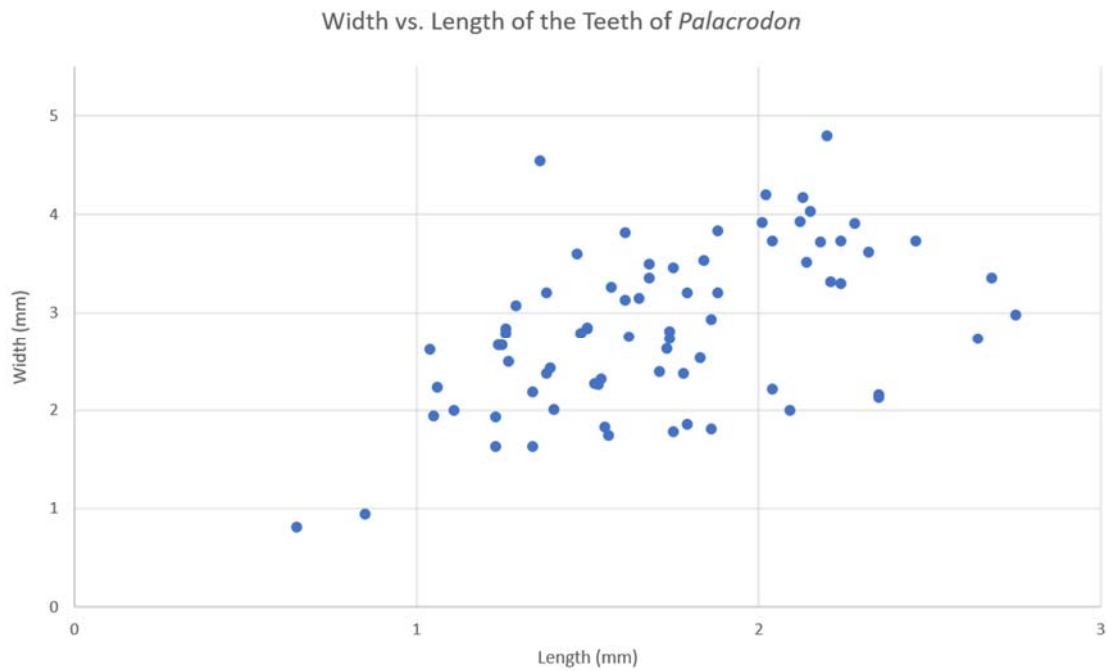


Figure 22. Width vs. length of the tooth base of *Palacrodon*. All measurements are in millimeters.

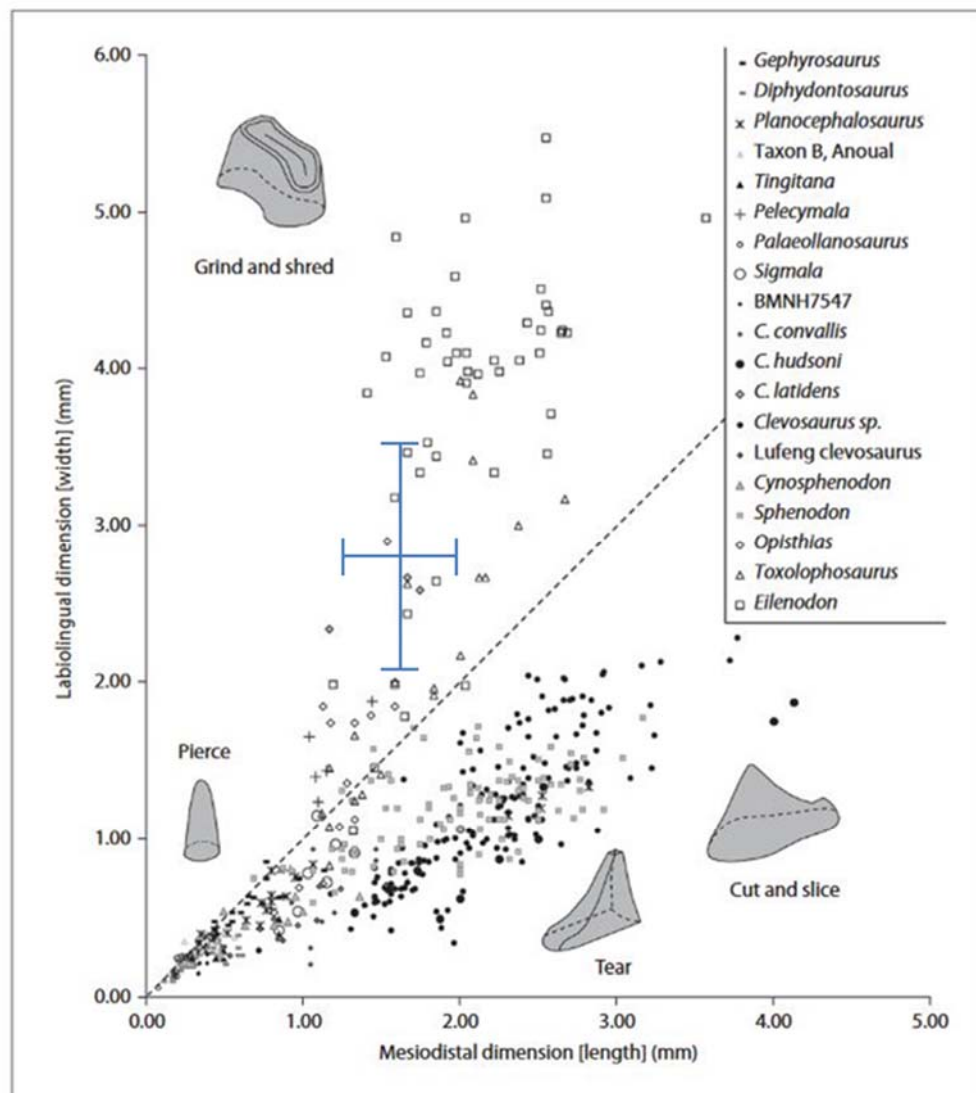


Figure 23. Dimensions of the dentary tooth base in Rhynchocephalia (modified from Jones [2009] with permission from Karger Publishers). The dimensions for *Palacrodon* are indicated by error bars, and they show that the teeth of *Palacrodon* fall near the grinding/shredding morphotypes.

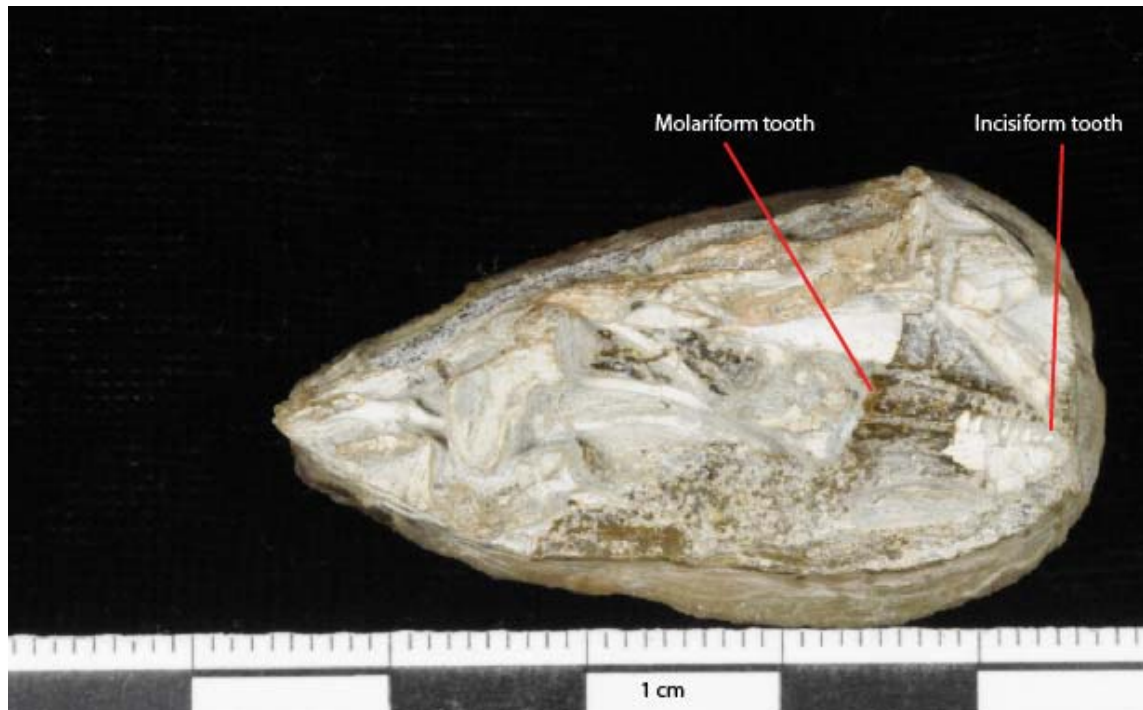


Figure 24. *Palacrodon* (specimen from Antarctica). Labels indicate regionalization by the presence of molariform and incisiform teeth.

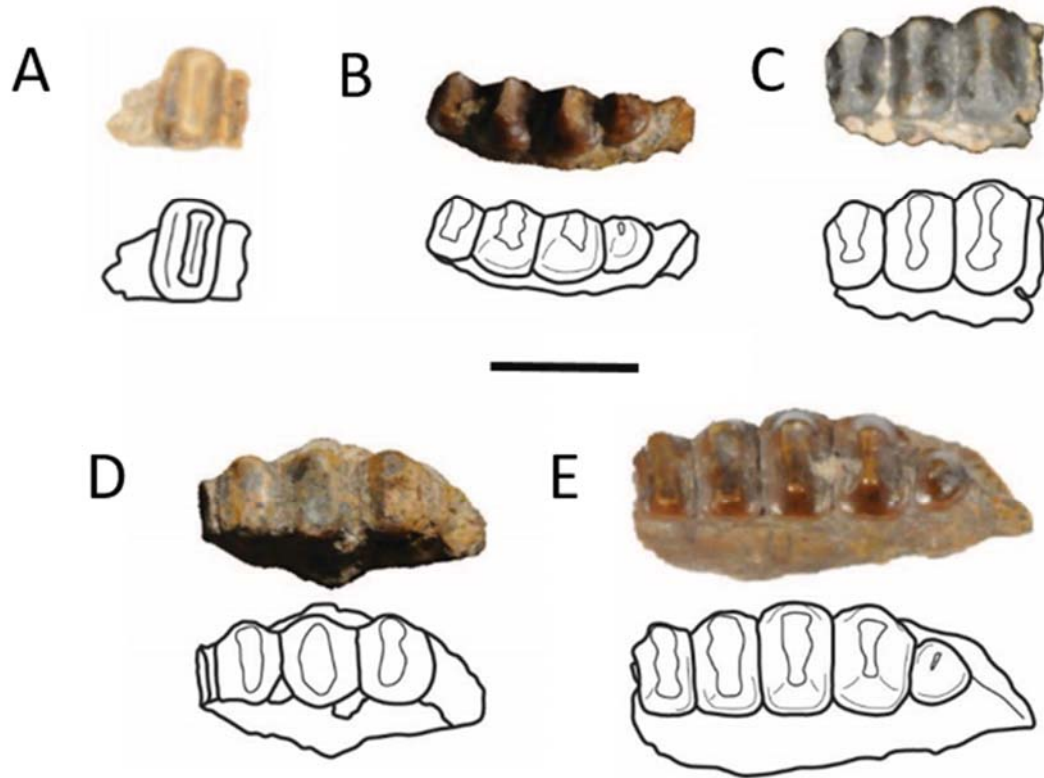


Figure 25. Wear patterns seen in *Palaeocrodon*. A) BP/1/7901 – tooth-bearing fragment with Type I wear; B) BP/1/7826 – tooth-bearing fragment with Type I; C) BP/1/7827 – tooth-bearing fragment with Type II wear; D) BP/1/7841 – partial maxilla with Type II wear; E) BP/1/6724 – partial maxilla with Type III wear. Scale bar equals five millimeters.

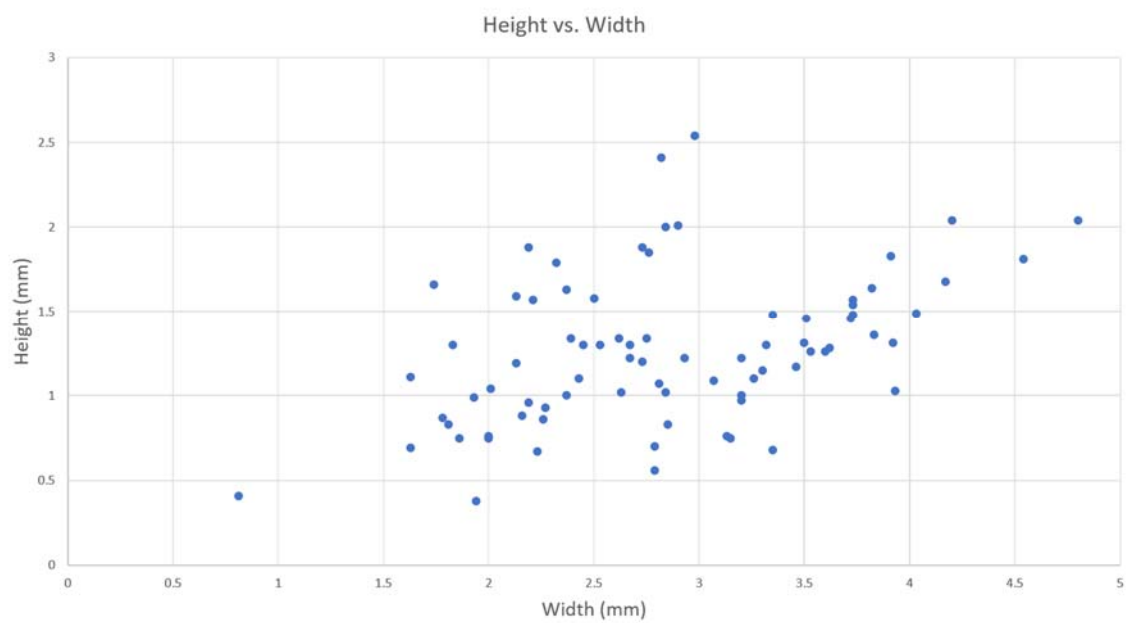


Figure 26. Height vs. width of the teeth of *Palacrodon*. All measurements are in millimeters.



## CHAPTER IV

### Conclusions

The analyses performed for this research supported several hypotheses about *Palacrodon* initially set forth. Of the four hypotheses originally tested, two address the phylogenetic relationships of *Palacrodon* and two address its diet.

My first hypothesis concerning dental implantation was evaluated using computed tomography, which revealed *Palacrodon* possesses acrodont dentition where the tooth is set on the apical crest of the tooth-bearing bone. This finding, along with other anatomical features, supports the hypothesis that *Palacrodon* is a procolophonid.

My second hypothesis concerning synapomorphies was evaluated using computed tomography, museum specimens, and literature. Although *Palacrodon* shares some features with all suggested taxa (rhynchocephlians, trilophosaurs, procolophonids), it shares the most features with procolophonids, with those features being labiolingually wide teeth, cusped molariform teeth, acrodont tooth implantation, and temporal fenestration. Phylogenetic analyses performed suggest that *Palacrodon* is closely related to procolophonids with similar tooth morphologies, such as *Hypsognathus*, *Soturnia*, *Leptopleuron*, *Scoloparia*, and *Sclerosaurus*.

My third hypothesis concerning wear patterns support *Palacrodon* having an herbivorous, insectivorous, durophagous, or insectivorous diet. Three distinct wear patterns were identified on the teeth of *Palacrodon*. Although several hypotheses pertaining to diet were supported by wear patterns, other characters regarding dental morphology were identified to possibly support an herbivorous or omnivorous diet.

My fourth hypothesis concerning regionalization was evaluated by studying the external features of museum specimens. While specimens of *Palacrodon* uncovered at the site Driefontein were not informative on this matter, the Antarctica specimen does show both incisiform and molariform teeth that characterize dental regionalization. This character supports *Palacrodon* having either an herbivorous or omnivorous diet.

In addition to these conclusions, I identified a feature, two parallel ridges beneath the tooth crowns of *Palacrodon*, which has not been identified in any known tetrapod. This feature may be unique to *Palacrodon*, and I hypothesize it aids in tooth attachment. *Palacrodon* warrants further study because its phylogenetic relationship to procolophonid parareptiles is only lowly supported by the analyses performed for this study. However, the discovery of the parallel ridges may be a feature that aligns *Palacrodon* with the proper clade. Future anatomical work on procolophonids needs to be performed to confirm if any taxa also have those two parallel ridges beneath the tooth crowns.

Aside from the identification of the parallel ridges in other taxa, continued work and excavation at Driefontein would also help in determining the phylogenetic relationship of *Palacrodon*. Since collection began at Driefontein, there have been few systematic excavations and most finds are a result of surface collection. As a result, findings are predominantly limited to isolated elements. However, systematic excavations may reveal more articulated elements of *Palacrodon* which would provide more characters to support a phylogenetic hypothesis.

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## APPENDIX A

Species found in the *Lystrosaurus* Assemblage Zone, compiled from Rubidge (1995)

### Vertebrates

#### Amphibia

*Broomulus dutoiti*, *Kestrosaurus dreyeri*, *Limnoiketes paludinas*, *Lydekkerina huxleyi*, *Micropholis stowi*, *Putterillia platyceps*, *Rhytidosteus capensis*,  
*Uranocentron senekalensis*

#### Reptilia

**Captorhinida** *Owenetta* sp., *Procolophon trigoniceps*

**Younginiformes** *Heleosuchus griesbachi*

**Squamata** *Paliguana whitei*

**Rhynchosauria** *Noteosuchus colletti*

**Protosauria** *Aenigmatasaurus grallator*, *Prolacerta broomi*

**Archosauriformes** *Proterosuchus fergusi*, *Proterosaurus vanhoepeni*

#### Synapsida

**Dicynodontia** *Lystrosaurus oviceps*, *L. curvatus*, *L. declivis*, *L. murrayi*, *L. maccaigi*, *Myosaurus gracilis*

**Terocephalia** *Erciolacerta parva*, *Moschorhinus kitchingi*, *Oliviera parringtoni*, *Regisaurus jacobi*, *Scaloposaurus constrictus*, *Tetracynodon darti*,  
*Zorillodontops gracilis*

**Cynodontia** *Galesaurus planiceps*, *Platycranellus elegans*, *Thrinaxodon liorhinus*



**Invertebrates**

## Arthropoda

Fossil millipedes – cf. *Gymnostreptus*

**Plant Fossils**

*Dadoxylon, Glossopteris, Schizoneura*

**Trace Fossils**

*Gyrolithes, Histioderma, Planolites, Scolithos, Scoyenia, Thalassinoides,*

Vertebrate burrows

Species found in the *Cynognathus* Assemblage Zone, compiled from Rubidge (1995).

**Vertebrates**

## Pices

*Atopocephala watsoni, Certatodus capensis, C. omatus, Cleithrolepedina extoni,*

*Coelocanthus africanus, Elonichthys browni, Helichthys browni, H. elegans,*

*Meidichthys browni*

## Amphibia

*Batrachosuchus watsoni, B. browni, Laideria gracilis, Paratosuchus dirus, P.*

*albertyni, P. africanus, P. haughtoni, Trematosuchus kannemeyeria, T. sobeyi*

## Reptilia

**Captihinida** *Microthelodon parvus, Myocephalus crassiden, Thelegnathus*

*browni, T. oppressus, T. spinigenus*

**Rhynchosauria** *Howesia browni, Mesosuchus browni*

**Archosauriformes** *Erythrosuchus africanus, Euparkeria capensis*

**Diapsida *incerte sedis* *Palacrodon browni***

Synapsida

**Dicynodontia** *Kannemeyeria simocephalus*, *Kombuisia frerensia*

**Therocephalia** *Bauria cynops*, *Melinodon simus*, *Sesamodon browni*, *Watsoniella breviceps*

**Cynodontia** *Bolotridon frerensis*, *Cynognathus crateronotus*, *Diademodon tetragonus*, *Trirachodon berryi*, *T. kannemeyeria*

**Invertebrates**

Mollusca

*Unio karooensis*

**Plant Fossils**

*Dadoxylon*, *Dicrodium*, *Schizoneura*

**Trace Fossils**

Arthropod trails, vertebrate burrows, worm burrows

**APPENDIX B**

## List of anatomical abbreviations

a – angular

ar – articular

bo - basioccipital

c – coronoid

d – dentary

e – epipterygoid

eo – exoccipital

ept – ectopterygoid

f – frontal

l – lacrimal

j – jugal

m – maxilla

mc – Meckel’s canal

n – nasal

p – parietal

pf – post frontal

pm – premaxilla

po – post orbital

pra – preaticular

pr – prootic

prf – prefrontal

ps – parasphenoid

pt – pterygoid

q – quadrate

qj – quadratojugal

sa – surangular

sm – septomaxilla

so – supraoccipital

sp – splenial

sq – squamosal

st – supratemporal

t – tabular



	01001 2???? ????? ????? ????
<i>Kapes spp.</i>	1111? 11201 30201 1111? ???00 211B0 13101
	0100C 1???? ????? ????? ???1
<i>Thelephon contritus</i>	????? ?1201 2020? 111?? ???0? ??B10 1D101
	?10?? ????? ????? ????? ????
<i>Eumetabolodon bathycephalus</i>	21111 10210 20211 ??21? ?1000 21110 13101
	01001 2?1?? ????? ????? ????
<i>Procolophon trigoniceps</i>	21111 10110 20211 11210 01000 21B00 B3101
	A1001 21010 10111 10110 1101
<i>Thelerpeton oppressus</i>	2?111 ?0110 20211 1121? ?1?00 21110 1D101
	01001 ????? ?011? ??11? ????
<i>Teratophon spinigenis</i>	21111 1A110 E0211 1121? 01000 21110 13101
	0100? ?1??? 10111 10??? ??01
<i>Pentaedrusaurus ordosianus</i>	B1111 10212 30211 1111? ???11 21110 131?1
	11001 B11?0 ?1111 1010? 110?
<i>Neoprocolophon asiaticus</i>	??111 1?21C ?021? 21B1? ?????1 ??B?? 1D1?1
	1?0?? ????? ????? ????? ????
<i>Sclerosaurus armatus</i>	????? ??310 ??32? 2???? ????? 3?B1? B31??
	????? ??110 10??1 1?101 111?
<i>Scoloparia glyphanodon</i>	????? 0031? 3232? ??1?? ???1? 31100 2D10?
	???01 2???? ????? ????? ??1?
<i>Leptopleuron lacertinum</i>	?1100 02210 3132? 21211 1?111 3?111 B41?1
	1201? 1??0? 1???? ????? ??0?

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<i>Hypsognathus fenneri</i>	?01A0 02310 32320 B1211 11111 31111 14112 1211? ??1?1 1???? ?0??? ??0?
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<i>Kitchingnathus untabeni</i>	B0??0 10?00 C020? 110?? ??00 B0100 1200? ????1 2???? ????? ????? ????
<i>Palacrodon browni</i>	????? ????? ????? ????? ????? ??113 1?11? ????3 2???? ????? ????? ????

Character state descriptions originally from Cisneros (2008b). Character 59 added by MacDougall and Modesto (2011).

0. Maxilla premaxillary subnarial process: (0) present, (1) absent, (2) premaxilla posterodorsally expanded.
1. External naris: (0) posterior or at level of first premaxillary tooth, (1) anterior to first premaxillary tooth.
2. External naris: (0) anteroposteriorly elongated, (1) subcircular or dorsoventrally expanded.
3. Wide internarial bar: (0) absent, (1) present.
4. Snout: (0) long and flat, (1) deep and short.
5. Maxillary depression: (0) absent, (1) present.
6. Prefrontal: (0) medial border straight, (1) medial border with a medial process, (2) confined to the orbital rim.
7. Posterior margin of orbitotemporal fenestra: (0) anterior to posterior margin of pineal foramen, (1) at level of posterior-most point of the pineal foramen, (2) beyond the posterior border of the pineal foramen, (3) considerably beyond the posterior border of the pineal foramen.
8. Pineal opening insertion: (0) in a shallow fossa, (1) flush with dorsal surface.
9. Contour of the pineal opening: (0) rounded, (1) 'teardrop shaped', (2) straight posterior border.
10. Postfrontal: (0) contacts frontal, parietal and postorbital, (1) contacts frontal, parietal, postorbital and supratemporal, (2) contacts frontal and parietal only, (3) absent and area occupied by parietal or fused to parietal.



11. Jugal lateral processes: (0) absent, (1) one, (2) two.
12. Temporal ventral margin: (0) roughly straight, (1) acutely emarginated, (2) broadly excavated, (3) convex.
13. Quadratojugal lateral surface: (0) spineless, (1) one spine, (2) two or more spines.
14. Squamosal ventral margin terminates: (0) at least as far ventrally as quadratojugal, (1) dorsal to quadratojugal in the tympanic notch.
15. Posterior margin of the skull roof: (0) concave, (1) acute posterior process, (2) broad posterior emargination.
16. Postparietals: (0) present, (1) absent/fused.
17. Supratemporal posterolateral margin: (0) rounded, (1) acute, (2) prominent spine.
18. Vomer width: (0) broader than choana, (1) roughly equal or narrower.
19. Epipterygoid columella: (0) ends freely, (1) contacts dorsally prootic and supraoccipital.
20. Parasphenoid cultriform process: (0) directed anteriorly and tapers to sharp tip, (1) projects vertically as robust pillar.
21. Relation of basioccipital tuber and quadrate condyle: (0) approximately at the level, (1) basioccipital projected far posteriorly.
22. Occipital condyle: (0) uniform, (1) tripartite.
23. Dentary ventral and dorsal surfaces: (0) nearly parallel, (1) oblique.
24. Relation of articular bone to marginal dentary teeth: (0) roughly in line, (1) well below.
25. Premaxillary teeth number: (0) five or more, (1) four, (2) three, (3) two.
26. Premaxillary teeth: (0) sub-equal in size, (1) enlarged mesial-most teeth.

27. Maxillary teeth with labiolingually expanded bases: (0) absent, (1) present.
28. Presence of prominently bulbous teeth in the maxilla: (0) absent, (1) present.
29. Maxillary teeth cervices: (0) not constricted, (1) constricted.
30. Maxillary teeth cusps: (0) one, (1) two, (2) two and anterior monocuspid teeth absent, (3) three.
31. Maxillary tooth number: (0) 40 or more, (1) 35 to 15, (2) 12 to 10, (3) eight to six, (4) five or less.
32. Maxillary cheek teeth: (0) not inset, (1) inset.
33. Deep occlusal depression in maxillary teeth: (0) absent, (1) present.
34. Anterior vomerine dentition: (0) several denticles, (1) true teeth, (2) entirely absent.
35. Vomerine denticles or teeth along posterior medial suture: (0) present, (1) absent.
36. Palatine dentition: (0) denticles, (1) true teeth, (2) absent.
37. Pterygoid dentition: (0) present; (1) absent.
38. Dentary incisors: (0) two or more, (1) one.
39. Dentary teeth in basal cross-section: (0) circular, (1) labiolingually expanded, (2) mesodistally elongated.
40. Dentary molariform teeth cusps: (0) one, (1) two adjacent cusps, (2) two widely separated cusps, (3) three.
41. Posterior dorsal zygapophyses: (0) gracile, (1) robust.
42. Presacral pleurocentral ridge: (0) bearing a longitudinal sulcus, (1) longitudinal sulcus absent.
43. Number of caudal vertebrae: (0) 20 or more, (1) 17 or less.
44. Ossified presacral intercentra: (0) present, (1) absent.

- 45. Rib cage: (0) narrow, (1) broad.
- 46. Posteromedial margin of lateral processes of the interclavicle: (0) concave, (1) straight.
- 47. Interclavicle medial ridge: (0) smooth, (1) prominent.
- 48. Distal ends of interclavicular lateral processes: (0) straight, (1) posteriorly recurved.
- 49. Ectepicondylar foramen or groove on humerus: (0) present, (1) absent.
- 50. Entepicondylar process: (0) reduced, (1) prominent.
- 51. Entepicondylar foramen on humerus: (0) present, (1) absent.
- 52. Non-terminal manual phalanges on digits ii, iii and iv: (0) long–slender, (1) short–robust.
- 53. Length ratio of unguals/penultimate phalanges on manus: (0) unguals short, (1) unguals long.
- 54. Iliac anterior margin: (0) convex, (1) straight.
- 55. Femur–humerus length ratio: (0) femur longer than humerus, (1) femur length equal to humerus.
- 56. Femur: (0) slender, (1) robust.
- 57. Osteoderms: (0) absent, (1) present.
- 58. Lacrimal-ectopterygoid contact absent (0) or present (1).

## APPENDIX D

*Specimen teeth measurements in millimeters.*

Specimen No.	Tooth 1	Tooth 2	Tooth 3	Tooth 4	Tooth 5
Example	Height Labiolingual width Mesial-distal length	Height Labiolingual width Mesial-distal length	Height Labiolingual width Mesial-distal length	Height Labiolingual width Mesial-distal length	Height Labiolingual width Mesial-distal length
BP/1/5672 A	0.93	1.07	1.30	1.46	1.48
	2.27	2.81	3.32	3.72	3.73
	1.52	1.74	2.21	2.18	2.46
BP/1/5672 B	1.02	1.17	1.36	1.57	-
	2.84	3.46	3.83	3.73	-
	1.50	1.75	1.88	2.24	-
BP/1/6724	1.34	1.54	1.64	1.26	1.09
	2.39	3.73	3.82	3.60	3.07
	1.71	2.04	1.61	1.47	1.29
BP/1/7819	1.59	1.81	2.04	2.04	1.28
	2.13	4.54	4.80	4.20	3.62
	?	1.36	2.20	2.02	2.32
BP/1/7824	2.09	-	-	-	-
	?	-	-	-	-
	1.34	-	-	-	-
BP/1/7826	1.11	1.30	1.22	0.96	-
	1.63	2.67	2.69	2.19	-
	1.23	1.24	1.25	1.34	-
BP/1/7827	1.00	1.31	1.68	-	-
	3.20	3.92	4.17	-	-
	1.38	2.01	2.13	-	-
BP/1/7828	0.67	1.31	1.83	1.26	-
	2.23	3.50	3.91	3.53	-
	1.06	1.68	2.28	1.84	-
BP/1/7829	0.99	1.48	1.22	1.34	-
	1.93	3.35	3.20	2.62	-
	1.23	2.68	1.79	1.04	-

Specimen No.	Tooth 1	Tooth 2	Tooth 3	Tooth 4	Tooth 5
BP/1/7830	1.88	2.41	2.01	1.85	-
	2.19	2.82	2.90	2.76	-
	?	?	?	?	-
BP/1/7831	1.20	1.34	-	-	-
	2.73	2.75	-	-	-
	1.74	1.62	-	-	-
BP/1/7832	1.04	1.00	-	-	-
	2.01	2.37	-	-	-
	1.40	1.38	-	-	-
BP/1/7833	0.86	1.30	-	-	-
	2.26	2.53	-	-	-
	1.53	1.83	-	-	-
BP/1/7834	0.41	-	-	-	-
	0.81	-	-	-	-
	0.65	-	-	-	-
BP/1/7835	1.30	1.66	-	-	-
	1.83	1.74	-	-	-
	1.55	1.56	-	-	-
BP/1/7836	1.88	-	-	-	-
	2.73	-	-	-	-
	2.64	-	-	-	-
BP/1/7837	2.54/1.68*	-	-	-	-
	2.98	-	-	-	-
	2.75	-	-	-	-
BP/1/7839	0.75	0.69	-	-	-
	1.86	1.63	-	-	-
	1.79	1.34	-	-	-
BP/1/7840	1.22	1.03	1.49	-	-
	2.93	3.93	4.03	-	-
	1.86	2.12	2.15	-	-
BP/1/7841	0.56	0.68	0.83	-	-
	2.79	3.35	2.85	-	-
	1.26	1.68	1.50	-	-


Specimen No.	Tooth 1	Tooth 2	Tooth 3	Tooth 4	Tooth 5
BP/1/7892	0.52	1.58	2.00	-	-
	?	2.50	2.84	-	-
	1.07	1.27	1.26	-	-
BP/1/7893	0.70	0.97	-	-	-
	2.79	3.20	-	-	-
	1.48	1.88	-	-	-
BP/1/7894	0.75	A	0.75	0.76	-
	2.00	A	3.15	3.13	-
	2.09	A	1.65	1.61	-
BP/1/7895	?	0.38	1.10	-	-
	0.94	1.94	3.26	-	-
	0.85	1.05	1.57	-	-
BP/1/7896	1.57	1.10	-	-	-
	2.21	2.43	-	-	-
	2.04	1.39	-	-	-
BP/1/7897	1.63	1.79	-	-	-
	2.37	2.32	-	-	-
	1.78	1.54	-	-	-
BP/1/7898	?	0.83	-	-	-
	?	1.81	-	-	-
	?	1.86	-	-	-
BP/1/7899	1.19	-	-	-	-
	2.13	-	-	-	-
	2.35	-	-	-	-
BP/1/7900	0.76	0.88	-	-	-
	2.00	2.16	-	-	-
	1.11	2.35	-	-	-
BP/1/7901	1.46	-	-	-	-
	3.51	-	-	-	-
	2.14	-	-	-	-
BP/1/7903	1.15	-	-	-	-
	3.30	-	-	-	-
	2.24	-	-	-	-

Specimen No.	Tooth 1	Tooth 2	Tooth 3	Tooth 4	Tooth 5
BP/1/7904	1.02/0.88*	-	-	-	-
	2.63	-	-	-	-
	1.73	-	-	-	-
BP/1/7905	1.03	-	-	-	-
	2.45	-	-	-	-
	?	-	-	-	-
BP/1/7906	1.27	-	-	-	-
	?	-	-	-	-
	2.40	-	-	-	-
BP/1/7930	0.87	-	-	-	-
	1.78	-	-	-	-
	1.75	-	-	-	-

*Note. Each specimen includes three measurements per tooth when possible: tooth height, labiolingual width, and mesial-distal length. For specimens with multiple teeth preserved, Tooth 1 refers to the mesial-most tooth present on the specimen, not a dedicated tooth number. Dashes (-) indicate no teeth present, question marks (?) indicate that tooth is present, but measurement is not possible, the letter "A" represents a tooth gap. \*BP/1/7837 and BP/1/7904 exhibits such extreme wear in the center of the tooth that a maximum height of the cusps and a minimum height of the center is reported. Tooth measurements could not be taken for BP/1/7825, BP/1/7838, and BP/1/7902 due to poor preservation. BP/1/5296 could not be measured as it is preserved within resin.*

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## VITA

### EDUCATION

Sam Houston State University

Master of Science, *in progress* (Department of Biological Sciences)

Advisor: Dr. Patrick J. Lewis

Committee Members: Dr. Juan D. Daza and Dr. Jeffrey Wozniak

External Committee Member: Dr. Christopher J. Bell (University of Texas)

Louisiana State University and Agricultural and Mechanical College

Bachelor of Science, conferred May 2015 (Department of Geology and Geophysics)

Advisors: Dr. Judith Schiebout and Dr. Suyin Ting

### PROFESSIONAL EXPERIENCE

Sam Houston State University Department of Biological Sciences

Teaching Assistant

August 2015 – present

Louisiana State University Museum of Natural History

Student worker assisting in collections management

September 2013 – May 2015

Law Enforcement Online – Federal Bureau of Investigation

Senior technical support operator and team manager

January 2012 – June 2013

### COURSES TAUGHT

BIOL 1436 – Foundations of Science Lab, Fall 2015-Fall 2017, head TA Fall 2016-Fall 2017

BIOL 1436 – Foundations of Science Lab Online Spring 2017-Fall 2017

BIOL 4362 – Paleobiology lab, Spring 2017

BIOL 1413 – Zoology Lab, Fall 2016

### FIELD WORK

Driefontein Fossil Collection, Bethlehem, South Africa

Directors: Dr. John Hancox, Dr. Patrick Lewis, myself

Early Triassic terrestrial fauna surface collection and excavation

May 2017

Whiskey River Bridge Fossil Collection, College Station, Texas

Director: Dr. Patrick Lewis

Middle Eocene marine fauna collection/excavation, prep, and identification

February 2017

Earthwatch Ignite, Aransas National Wildlife Refuge, Port Aransas, Texas

Director: Dr. Jeffrey Wozniak

Staff member and instructor for high school science fellowship concerning Gulf Coast ecosystems

June 2016

Lubbock Lake National Historical Landmark. Lubbock and Post, Texas

Director: Dr. Eileen Johnson

Excavation of Pleistocene fossils, bone and matrix sorting

July-August 2015

Course: Geoarchaeological Survey of Fort Pike, New Orleans, Louisiana

Director and course instructor: Dr. Brooks Ellwood

Magnetic survey and mapping, electrical survey, stratigraphy for geoarchaeology course

October 2014

Course: Environmental Reconstruction of Gulf Coast, Cocodrie, Louisiana

Director and course instructor: Dr. Sophie Warny

Collection and identification of pollen and microfauna for micropaleontology course

October 2014

Course: Louisiana State University Geological Field School, Colorado Springs, Colorado

Director and course Instructor: Dr. Amy Luther

Geologic mapping, biostratigraphy, depositional environment

June-July 2014

## **LAB EXPERIENCE**

SHSU Paleobiology Lab

Lab Coordinator - Organizing lab meetings and events, undergraduate lab training

September 2015 – present

University of the Witwatersrand, Johannesburg, South Africa

Director: Dr. Bernard Zipfel

Analysis of Triassic vertebrates

August 2016

## MUSEUM EXPERIENCE

Louisiana State University Museum of Natural History  
 Director: Dr. Judith Schiebout and Dr. Suyin Ting  
 Fossil prep, cataloging, and excel databasing  
 September 2013 – May 2015

## AWARDS AND ACHIEVEMENTS

Sam Houston State University Outstanding Graduate Student Award, 2017  
 SHSU Department of Biological Sciences Outstanding Graduate Student Award, 2017

## GRANTS AND SCHOLARSHIPS

Sam Houston State University COSET Special Graduate Scholarship, 2017 **\$1500**  
 Sigma Xi Grants-in-Aid-of-Research, 2017 **\$720**  
 Sam Houston State University Student Organization Leadership Scholarship, 2016, 2017  
**\$1000**  
 Louisiana State University Tiger Excellence Award, 2011, 2012, 2013, 2014, 2015 **\$4000**  
 TOPS Award, 2011, 2012, 2013, 2014, 2015 **\$28,496**  
 Candace Hays and Ronnie D. Johnson Scholarship, 2014 **\$3000**  
 Baton Rouge Gem and Mineral Society Scholarship, 2014 **\$500**

## SOCIETIES

Sigma Xi, joined 2017  
 Society for the Study of Amphibians and Reptiles, joined 2017  
 Association of Women Geoscientists, joined 2016  
 Society of Vertebrate Paleontology, joined 2015  
 Paleontological Society, joined 2015  
 Biological Sciences Graduate Student Organization, joined 2015  
 Treasurer, Fall 2016-Spring 2017  
 Louisiana State University Geology Club, Fall 2012- Spring 2015  
 Volunteer Coordinator and Outreach Commissioner, Fall 2014-Spring 2015

## OUTREACH

Home school co-op “How to be a paleontologist” lesson, Huntsville Home School Co-op,  
 Huntsville, TX (18 April 2017)  
 Girls Exploring Math and Science (GEMS), Houston Museum of Natural Sciences,  
 Houston, TX. (17 Feb. 2017)

Women in Science Panel, Panel Member, Sam Houston State University Department of Biological Sciences, Huntsville, TX. (2 December 2016)

Sam Houston State University 2016 Undergraduate Research Symposium, Moderator, Huntsville, TX. (23 April 2016)

First grade class dinosaur presentation, Huntsville Elementary School, Huntsville, TX. (2 March 2016)

## REVIEWER

Journal of Herpetology

## PEER REVIEWED PUBLICATIONS

**K. M. Jenkins**, E. Stelling, J. D. Daza. (*prep*). The appendicular skeleton of a Mid-Cretaceous lizard (Squamata: Scincoidea) preserved in burmite.

**K. M. Jenkins**, P. J. Hancox, P. J. Lewis. (*accepted*). The first record of *Diplichnites* in the Triassic of the Karoo Basin. *Palaeontologia Electronica*.

**K.M. Jenkins**, M.E.H. Jones, T. Zikmund, A. Boyde, J.D. Daza. 2017. A review of tooth implantation among rhynchocephalians (Lepidosauria). *Journal of Herpetology* 51:300-306. <https://doi.org/10.1670/16-146>

## OTHER PUBLICATIONS

**K.M. Jenkins**, E. Stelling, and J. D. Daza. 2017. The appendicular skeleton of a mid-Cretaceous lizard (Squamata: Scincoidea?) [abstract]. In: Society of Vertebrate Paleontology 77<sup>th</sup> Annual Meeting Program and Abstracts.

**K.M. Jenkins** and P.J. Lewis. 2016. Phylogenetic Position of *Palacrodon*: an enigmatic early Triassic diapsid from Southern Gondwana [abstract]. In: Society of Vertebrate Paleontology 76<sup>th</sup> Annual Meeting Program and Abstracts.

K. Bergstrom, **K.M. Jenkins**, J. Levy, R.J. Velasquez, P.J. Lewis, and T. Campbell. 2016. Computed tomography survey of supernumerary molars in extant orangutans with implications for studies of the primate fossil record [abstract]. In: Paleoanthropological Society 2016 Annual Meeting.

## PRESENTATIONS

**K.M. Jenkins**, E. Stelling, and J. D. Daza. 2017. The appendicular skeleton of a mid-Cretaceous lizard (Squamata: Scincoidea?). Society of Vertebrate Paleontology 77<sup>th</sup> Annual Meeting, Calgary, Canada 23-26 August 2017.

**K.M. Jenkins**. 2017. My friend, *Palacrodon*. Three Minute Thesis Semi-finals, Sam Houston State University, Huntsville, Texas 8 March 2017.

-Three Minute Thesis Finals, Sam Houston State University, Huntsville, Texas, 4 April 2017.

- K.M. Jenkins.** 2016. How well does dentition inform a tree? SHSU Systematics Symposium, Sam Houston State University, Huntsville, Texas 8 December 2016.
- K.M. Jenkins** and P.J. Lewis. 2016. Phylogenetic Position of *Palacrodon*: An Enigmatic Early Triassic Diapsid from Southern Gondwana. Society of Vertebrate Paleontology 76<sup>th</sup> Annual Meeting, Salt Lake City, Utah 26-29 October 2016.
- K.M. Jenkins.** 2016. Diversity in tooth morphology in extinct rhynchocephalians. Sam Houston State University Herpetology Symposium, Sam Houston State University, Huntsville, Texas 29 April 2016.
- K. Bergstrom, **K.M. Jenkins**, J. Levy, R.J. Velasquez, P.J. Lewis, and T. Campbell. 2016. Computed Tomography Survey of Supernumerary Molars in Extant Orangutans with Implications for Studies of the Primate Fossil Record. Paleoanthropological Society 2016 Annual Meeting, Atlanta, Georgia 12-13 April 2016.
- K.M. Jenkins**, J. Levy, K. Bergstrom, R.J. Velasquez, P.J. Lewis, and Timothy Campbell. Use of Computed Tomography Survey to Reveal Hidden Structures and a Survey of Supernumerary Molars within *Pongo pygmaeus*. Texas Academy of Science Annual Meeting, Texas Tech University Llano River Field Station, Junction, Texas, 3-4 March 2016.