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A taxonomic revision of the genus Procolophon and the phylogenetic relationships of Procolophonoid reptiles

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1 INTRODUCTION

1.1 Overview on procolophonids and related taxa

Procolophonids are small, lizard-like members of the Parareptilia, which appeared during the Late Permian and successfully radiated through Pangaea rapidly after the Permian-Triassic extinction event. Remains of this cosmopolitan clade have been found in several countries, on all continents. There are records in Antarctica, Australia, Brazil, Canada, China, Germany, Great Britain, Poland, Russia, South Africa, Switzerland and USA (von Huene, 1912; Colbert and Kitching, 1975; Bartholomai, 1979; Li, 1989; Ivakhnenko, 1983; Borsuk-Białynicka *et al*., 1999; Sues *et al*., 2000; Cisneros and Schultz, 2003). There are probable finds in Algeria and India (Lehman, 1981, Tripathi and Satsangi, 1963).

In a general way, they are distinctive from most parareptiles in possessing a short and wide body, relatively robust limbs, and one or more posterolateral processes in the cranium that give it a triangular outline. These characteristics represent a convergence with the much larger Permian pareiasaurids, from which procolophonids differ in a number of other features, such as enlarged orbits (orbitotemporal fenestrae) and labiolingually expanded teeth.

The fossil record of the Procolophonidae is best represented in the Lower Triassic of the Russian Cis-Uralia; in the Lower and Middle Triassic of the Karoo Supergroup of South Africa; and in the Upper Triassic of the Newark Supergroup in USA and Canada (Ivakhnenko *et al*. 1997, Sues and Bird 1998, Modesto and Damiani 2003). The majority of approximately 35 valid genera come from these basins. With the exception of a few Permian records based on fragmentary material, the Procolophonidae is a group mainly restricted to the Triassic.

The first procolophonid to be described was *Leptopleuron lacertinum* (Owen, 1851), based on a natural mould of an almost complete skeleton from the Lossiemouth beds (Upper Triassic) of Scotland. The same specimen was

redescribed by Mantell (1852) under the name *Telerpeton elginense*. Because Owen's description lacked illustrations and was published in a non-scientific journal, the name given by Mantell was preferred by many later researchers. Nevertheless, the rules of the International Code of Zoological Nomenclature give priority to Owen's name (Colbert, 1946). The phylogenetic position of *Leptopleuron lacertinum* remained obscure for decades, and different authors argued for its placement within the Lacertilia (e.g. Huxley, 1867) or the Rhynchocephalia (e.g. Broom, 1903) which included rhyncosaurs.

Another procolophonid, *Sclerosaurus armatus*, from the Upper Buntsandstein of Switzerland (Lower or Middle Triassic) was described by Meyer in 1857. The affinities of this taxon were not clear until the descriptions by von Huene (1912), based on more complete material, proposed relationships with *Procolophon* and *Leptopleuron* (this author had already suggested affinities within *Sclerosaurus* and *Procolophon* in 1902). This point of view was accepted by several authors (e.g. Nopcsa, 1923; Colbert, 1946; Kuhn, 1969) but also debated (Rieth, 1932; Ivakhnenko, 1979; Lee, 1995).

The genus *Procolophon* was described by Owen (1876) based on two crania, an adult and a juvenile, both collected at Donnybrook, Eastern Cape, in the South African Karoo. Based on these materials Owen proposed two species, *P. trigoniceps* and *P. minor*, and placed the new genus within his new family Mononaralia, in the order Theriodontia. According to this author, the characters that defined this family were an external nostril which is single or undivided, and the presence of more than three incisor teeth in the premaxillary bone. The first character has been shown to be an artefact of taphonomy or preparation in the holotypes.

In 1878, Seeley placed the genus *Procolophon* within the Rhynchocephalia. In 1888, however, he erected the suborder Procolophonia and placed it, together with the Pareiasauria (pareiasaurians were considered dinosaurs by Owen, 1876), within the Anomodontia. The order Anomodontia also included therapsids and

placodonts (Seeley, 1878). Later, Seeley (1892) included his Procolophonia within the Pareiasauria. Broom (1903) proposed that Procolophonia should be placed within the Rhynchocephalia, based on what he considered close affinities between *Procolophon* and *Palaeohatteria.* Later, Goodrich (1916) suggested that *Palaeohatteria* was not a rhynchocephalian, but had synapsid affinities.

Boulenger (1904) realized the affinities of the genus *Leptopleuron* lay with *Procolophon* (e.g. elongated orbits, transversely enlarged bicuspidated teeth, imperforate supratemporal roof), and included the former in the Procolophonia. He also placed this group within the assemblage of anapsid reptiles that Cope (1880) named the order Cotylosauria. Traditionally, this order has been considered to comprise three suborders: (1) Diadectomorpha, which included the families Diadectidae, Pareiasauridae and Procolophonidae (a family proposed by Lydekker, 1890); (2) Captorhinomorpha; and (3) Seymouriamorpha (Watson, 1917; Romer, 1933). The status of procolophonids within the Cotylosauria was supported by most authors (e.g. von Huene, 1912; Watson, 1914, 1917; Williston, 1925; Gilmore, 1928; Broom, 1936; Romer, 1933; von Huene, 1943; Colbert, 1946).

The monophyly of the group of anapsid reptiles named Cotylosauria was questioned by Olson (1947), who eliminated this group in his new classification of the Class Reptilia. In place of the Cotylosauria, this author proposed the subclass Parareptilia, which contained two orders: (1) Diadectia, including the suborders Seymouriamorpha, Diadectomorpha, Procolophonia and Pareiasauria; and (2) Chelonia. This group included only forms with a pronounced otic notch. In the same work, Olson placed the Infraclass Captorhina (Captorhinomorpha *sensu* Cope) in the new Subclass Eureptilia, which included also the infraclasses Synapsida, Parapsida, Euryapsida and Diapsida. The Eureptilia included only "typical reptiles characterized by lack of an otic notch or by a strong tendency towards its loss". The removal of Captorhina from Parareptilia (formerly Cotylosauria) was the major change in Olson's proposal. This classification was not widely accepted, and the Cotylosauria continued to be recognized by many

researchers (e.g. Ivakhnenko, 1973; Colbert and Kitching, 1975; Kemp, 1974; Gow, 1977a, 1977b).

The advent of cladistic methodology has brought to a general consensus of the placement of the Procolophonidae within the Parareptilia (Laurin and Reisz, 1995; Lee, 1997a; deBraga and Reisz, 1996; deBraga and Rieppel, 1997; Modesto, 1999; Sues *et al.*, 2000; deBraga, 2003; Modesto *et al*., 2001, 2002). Parareptilia is currently considered to be a more restricted group than originally proposed by Olson (1947) through the exclusion of the Diadectomorpha, Seymouriamorpha and Mesosauridae. In this sense Parareptilia includes the South African Millerettidae, the Laurasian Lanthanosuchoidea and the Bolosauridae, the Russian "nycteroleters", and the cosmopolitan Pareiasauria and Procolophonoidea (deBraga and Reisz, 1996; Modesto, 1999; Berman *et al.*, 2000; Reisz and Scott, 2002; deBraga, 2003).

Ivakhnenko (1979) proposed a subdivision of the Procolophonidae in three groups: Spondylolestinae, Procolophoninae and Leptopleuroninae. The Spondylolestinae was based in the poorly known genus *Spondylolestes* from South Africa and included procolophonids having less derived characters than the Procolophoninae. More recently the monophyly of this group has been questioned (Spencer and Benton, 2000). The Procolophoninae, based on *Procolophon*, included forms more derived than in the Spondylolestinae, but more primitive than in the Leptopleuroninae. Modesto *et al*. (2002) proposed a redefinition of the Procolophoninae and Leptopleuroninae groups in phylogenetic terms. In that work, the Procolophoninae is defined as the clade that includes all procolophonids that are more closely related to *Procolophon trigoniceps* than to *Leptopleuron lacertinum*. Therefore, the Leptopleuroninae is the clade that includes all procolophonids that are more closely related to *Leptopleuron lacertinum* than to *Procolophon trigoniceps*.

In 1939, Broom described *Owenetta rubidgei*, a small lizard-like reptile from the Upper Permian of South Africa. The author found several features in common

between the cranium of the new genus and that of the Triassic *Procolophon* (e.g. elongated orbits) suggestive of a close affinity. On the other hand, he considered that *Owenetta* was much more primitive than the latter (presumably based on the large number of simple conical teeth of *Owenetta*), and proposed the new family Owenettidae within the Procolophonia *sensu* Seeley (1888).

Owenettids have been recorded only in Gondwana, and the knowledge of this group has substantially increased in recent years. *Barasaurus besairei* is present both in the Upper Permian and the Lower Triassic of the Sakamena Formation, Madagascar (Piveteau, 1955; Smith, 2000; Ketchum and Barrett, 2004). This form is known from several good quality natural moulds, usually in an articulated state. A new *Owenetta* species, *O. kitchingorum*, was described for the *Lystrosaurus* Assemblage Zone (Early Triassic) of the South African Karoo by Reisz and Scott (2002). Modesto *et al*. (2003) described *Saurodectes rogersorum* also from this biozone. These authors questioned the monophyly of the two *Owenetta* species, based on the closer relationship of *O. kitchingorum* to *Saurodectes* than to *O. rubidgei*, as reflected in their phylogenetic analysis.

Recently, some procolophonoids that cannot be placed either in the Procolophonidae or in the Owenettidae have been recovered. These "stem-procolophonids" form a paraphyletic assemblage, exhibiting a combination of dental and other cranial characters from both the Procolophonidae and the Owenettidae. *Coletta seca* and *Sauropareion anoplus* were reported from the *Lystrosaurus* Assemblage Zone of South Africa (Gow, 2000; Modesto *et al.*, 2001, 2002). *Pintosaurus magnidentis* was collected in the Buena Vista Formation, Paraná Basin of Uruguay (Piñeiro *et al.*, 2004). This formation is usually correlated with the Lower Triassic Sanga do Cabral Formation of Brazil (Bossi and Navarro, 1991; Marsicano *et al.*, 2000; but see Piñeiro *et al.*, 2003 for a Permian correlation). These three genera are known only from holotypic cranial material, and the absence of collected postcrania precludes a better understanding of their relationships. The poorly known South African form *Spondylolestes rubidgei* (Broom, 1937), possessing wide but single-cusped marginal teeth, could

also be considered as a “stem-procolophonid”. The holotype and single specimen of *Spondylolestes* comes from Bethesda Road, Graaff-Reinet, Eastern Cape. Broom regarded this area to belong to the *Lystrosaurus* AZ, but the locality has been shown to belong to the *Dicynodon* AZ, of Late Permian age (Kitching, 1977).

1.2 Distribution of procolophonids in Pangea

Procolophonids have been found in several basins and formations around the world (Fig. 1). In Britain, *Kapes bentoni* is recorded from the Middle Triassic Otter Sandstone Formation (Spencer and Storrs, 2002) and *Leptopleuron lacertinum* in the Upper Triassic Lossiemouth Sandston Formation (Owen, 1851; Huxley, 1867; Boulenger, 1904; Spencer, 2000). Other procolophonids have been reported for the Upper Triassic fissure fillings in Britain, they include at least one undescribed taxon (Fraser, 1995; Spencer, 2000; Sues *et al.*, 2000) and the enigmatic *Tricuspisaurus thomasi* (Fraser, 1986) which could also be a trilophosaurid. The Lower-Middle Triassic Buntsandstein of Switzerland and Germany has yielded *Sclerosaurus armatus*, *Koiloskiosaurus coburgensis* and *Anomoiodon liliensterni* (von Huene, 1912; von Huene, 1939; Kuhn, 1969).

Three probable procolophonids are reported for the Permian of the Russian cis-Urals: *Microphon exiguus*, *Suchonosaurus minimus* and *Kinelia broomi* (Ivakhnenko, 1983; Bulanov, 2002). These taxa are only known from fragmentary, tooth bearing remains. Thirteen genera have been described from the Triassic of the Russian cis-Urals (Ivakhnenko, 1974, 1975, 1983; Novikov, 1991; Novikov and Orlov, 1992). A review of these taxa by Spencer and Benton (2000), suggested that several of the genera and species were founded on rather incomplete material and should not be considered valid. These authors recognized only five genera and thirteen species for the *gorizonts* of the cis-Uralia (listed stratigraphically); *Phaanthosaurus iguatjevi* and *P. simus*, Vokhmian Gorizont; ‘*Tichvinskia jugensis*’, Rybinskian Gorizont; *Orenburgia concinna*, Sludkian Gorizont; *O. bruma* and *Timanophon raridentatus*, Ustmylian Gorizont;

Tichvinskia vjatkensis, *Kapes amaenus*, *K. majmesculae*, *K. komiensis* and *O. enigmaticus*, Yarenskian Gorizont; and *K. majmesculae*, Donguz Gorizont.

In China, procolophonids have been recovered in the Ermaying Formation (Middle Triassic) and the Upper He Shang Gou Formation (Lower Triassic), both in north China. The former formation yielded *Neoprocolophon asiaticus* (Young, 1957) and the latter, *Pentaedrusaurus ordosianus* and *Eumetabolodon bathycephalus* (Li, 1983; Li, 1989). No precise stratigraphic information is available for a fourth procolophonid, *E. dongshengensis* (Li, 1989). Two additional procolophonids have also been described in China, *Santaisaurus yuani* and *Paoteodon huanghoensis* (Koh, 1940; Chow and Sun, 1960). Li (1989) considered the former to be an early lizard and the latter a *nomen dubium*.

The record of procolophonids in Australia comes from the Arcadia Formation, Lower Triassic, Queensland State (Bartholomai, 1979). Procolophonids are present in abundance in this formation and have not yet been described.

Colbert and Kitching (1975) described *Procolophon* remains recovered from the Fremouw Formation, in the Transantarctic Mountains, and assigned them to *Procolophon trigoniceps*. On the basis of the presence of *Lystrosaurus*, *Thrinaxodon* and *Procolophon*, the Fremouw fauna was correlated with the *Lystrosaurus* Assemblage Zone of South Africa and assigned an Early Triassic age.

Besides *Procolophon*, other procolophonids have been described from the South African Karoo. *Thelegnathus browni* was proposed by Broom (1905) based on an isolated maxilla from the *Cynognathus* Assemblage Zone (Early or Middle Triassic). Gow (1977a) proposed four new *Thelegnathus* species, based on a set of well preserved specimens recovered at the Subzone B (Hancox, 1988) of the *Cynognatus* Assemblage Zone (Anisian, Middle Triassic): *T. oppressus*, *T. perforatus*, *T. contritus* and *T. spinigenis*. Some of these species exhibit unique and bizarre adaptations for procolophonids, such as extremely elongated

quadratojugal processes in *T. spinigenis* and captorhinid-like multiple rows of marginal teeth in *T. perforatus*. A review of all *Thelegnathus* holotypes and referred material by Modesto and Damiani (2003) has shown that the holotype of the genus is non-diagnostic and *T. browni* is a *nomen dubium*. These authors also considered the remaining '*Thelegnathus'* species to be very distinctive from each other, and proposed new genera to accommodate them: *Thelerpeton oppressus*, *Theledectes perforatus*, *Thelephon contritus* and *Teratophon spinigenis*. Two other South African procolophonids, *Myocephalus crassidens* and *Microtheledon parvus* (Broom, 1905, 1936) were based on badly preserved, taphonomically altered material, and probably are *nomina dubia* (pers. obs.).

The records of procolophonids in South America come from the Paraná Basin. The genus *Procolophon* is present in the Sanga do Cabral Formation, in Rio Grande do Sul, Brazil, and has been used to correlate its associated fauna with the Early Triassic *Lystrosaurus* Assemblage Zone of South Africa (Lavina, 1983; Barberena *et al.*, 1985). *Procolophon* remains are abundant in the Sanga do Cabral Formation, though always present in disarticulated, reworked state. These have been referred to two different species *P. pricei* and *P. brasiliensis* (Lavina, 1983; Cisneros and Schultz, 2002). This species is also based mostly on palatal dentition characters. *Candelaria barbouri* was found in the Middle Triassic Santa Maria Formation (Price, 1947). This form lacks some distinctive characters of the Procolophonidae (e.g. labiolingually expanded teeth) and it is the subject of a reassessment in this thesis (see below). Another procolophonid, *Soturnia caliodon*, was also described in Rio Grande do Sul but in the Upper Triassic Caturrita Formation (Cisneros and Schultz, 2003). *Soturnia caliodon* is known from two specimens, a semi-articulated cranium and postcranium, and a partial cranium. This taxon represents the only known record of a leptopleuronine procolophonid in Gondwana.

In North America, procolophonids are known in the Dockum Group and the Chinle Formation of southwestern United States, and in the Newark Supergroup of eastern United States and Canada. In the Dockum Group *Libognathus sheddi* is

known from one left mandible, and it is considered a leptopleuronine procolophonid (Small, 1997; Spencer, 2000; Sues *et al*., 2000). At least two forms are known in the Upper Triassic Chinle Formation. *Colognathus obscurus* is only known from isolated marginal teeth (Murry, 1986; Heckert, 2004). These teeth are transversally expanded, bicuspid, similar to the upper teeth of the leptopleuronine procolophonids *Soturnia* and *Hypsognathus*. *Colognathus* tooth crowns are distinctive by the presence of vertical striations or fluting (Heckert, 2004). Another, unnamed procolophonid, is known from the Owl Rock Member of the Chinle Formation (Fraser *et al*., 2005). The genus *Chinleogomphius*, considered to be a procolophonid by Sues and Olsen (1993), was recently made a junior synonym of the archosauromorph *Trilophosaurus* (Heckert *et al*., 2006).

The first procolophonid to be described for the Newark Supergroup was *Hypsognathus fenneri* (Guilmore, 1928). This taxon is now relatively well known from several skeletons and natural moulds from the USA and Canada. The specimens come from the Newark, Hartford and Fundy basins, of Norian to Rhaetian age, Upper Triassic (Colbert, 1946; Baird, 1986; Sues *et al*., 2000). The Wolfville Formation of the Fundy Basin, in Nova Scotia, Canada, has yielded three more procolophonids: *Acadiella psalidodon*, *Haligonia bolodon*, *Scoloparia glyphanodon* (Sues and Baird, 1998). Another procolophonid, *Gomphiosauridion baileyae*, was described from the Upper Triassic Turkey Branch Formation in the Richmond Basin, Virginia, USA (Sues and Olson, 1993). This taxon was based on a fragment of a right maxilla with two teeth. The teeth of *Gomphiosauridion* are very similar to those of *Colognathus* due to the presence of vertical striations or fluting, and the former could be a junior synonym of the latter (Heckert, 2004).

1.3 Previous studies on *Procolophon*

The Early Triassic genus *Procolophon* is the most studied procolophonid and probably one of the best known Triassic reptiles. Natural casts, cranial and postcranial remains are locally abundant in the *Lystrosaurus* Assemblage Zone of the Beaufort Group in the Karoo (Groenewald and Kitching, 1995). Burrows

present in this assemblage zone have also been assigned to this genus (Groenewald, 1991). *Procolophon* is also known from the Fremouw Formation of the Transantartic Mountains (Colbert and Kitching, 1975), the Sanga do Cabral Formation of Southern Brazil (Lavina, 1983).

The genus *Procolophon* was described by Owen (1876), who proposed the species *P. trigoniceps* (type species, by page priority) and *P. minor*, the latter based on a small skull, of a juvenile individual (pers. obs.). Among the diagnostic characters of the new genus were the unusually large orbits, and the triangular shape of the skull from which the name *Procolophon* was derived (from the Greek words *pro*, "anterior" and *colophon*, "apex"). The locality provided by Owen was "Tafelberg, Cape of Good Hope", which has been shown to be incorrect by Watson (1914) and Broom (1936), who recognized the locality as Donnybrook, Queenstown District, Eastern Cape. Owen correctly assigned a Triassic age to the new materials.

Seeley (1878) erected the species *P. griersoni*, *P. cuneiceps* and *P. laticeps*, based on three new crania collected from the same region as that of the original material described by Owen. Seeley (1905) described two more *Procolophon* species, *P. platyrhinus* and *P. sphenorhinus*, based on materials which were also collected in the Donnybrook area. This proliferation of *Procolophon* species, described on the basis of characters presumably better explained by ontogenetic and taphonomic factors, and above all, based on specimens collected in the same area, lead Broom (1936) to synonymise *P. minor*, *P. griersoni*, *P. cuneiceps*, *P. laticeps*, *P. platyrhinus* and *P. spenorhinus* with the type species *P. trigoniceps*. In the same work, Broom created the new species *P. baini*, based on material from an unknown locality. This species was later synonymised with *P. trigoniceps* by Colbert and Kitching (1975). On the basis of several cranial features, including the presence of openings in the temporal region, Hamley and Thulborn (1993) re-erected the species *Procolophon laticeps* from the Lower Triassic of South Africa.

Neveling *et al*. (1999) reported a fossil fauna from the "impoverished zone" between the *Lystrosaurus* and the *Cynognathus* Assemblage Zones of South Africa. This fauna is characterized by the occurrence of some vertebrates characteristic of the above mentioned biozones and *Procolophon* in great numbers. The index tetrapods *Lystrosaurus* and *Cynognathus* have never been recorded from this level. The predominance of *Procolophon* in this assemblage, may suggest a correlation of these sediments with the Sanga do Cabral Formation of southern Brazil in which *Procolophon* is also common and *Lystrosaurus* is not recorded.

2 MATERIAL AND METHODS

2.1 Specimens

In addition to the literature, information for most procolophonoids was obtained from first hand examination of specimens in collections in different countries. The relevant specimens, including several holotypes, are listed in each chapter. Procolophonoids from the following institutions were studied (listed by country):

Australia. Queensland Museum, Brisbane (QMF): undescribed procolophonid, 6680, 6681, 6683, 6684, 6693, 6694, 6702, 6704, 6707, 6709, 9507, 18335, 49497, 49501, 49508, 49511, 49513, 49514, 49516, 49517, 49519.

Canada. Royal Ontario Museum (ROM): *Scoloparia glyphanodon*, 47487. Nova Scotia Museum (NSM): *Scoloparia glyphanodon*, 996GF82.1.

China. Institute of Vertebrate Palaeontology and Palaeoanthropology (IVPP): *Eumetabolodon bathycephalus*, V6064-70, V6166(1), V6166(2), V6167, V6168(1), V6168(2), V6169-75; *Eumetabolodon dongshengensis*, V6073; *Neoprocolophon asiaticus*, V866; *Pentaedrusaurus ordosianus,* V8735.

Brazil. Departamento Nacional de Produção Mineral, Rio de Janeiro, Brazil (DGM): *Candelaria barbouri*, 314R; Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre (MCN): *Procolophon pricei*, MCN PV1905; *Soturnia caliodon*, PV2738. Universidade Federal de Santa Maria, Santa Maria, Brazil (UFSM): *Candelaria barbouri*, 11076, 11131. Universidade Federal do Rio Grande do Sul, Porto Alegre (UFRGS): *Procolophon pricei*, PV231T; *Soturnia caliodon*, PV570T.

South Africa. Albany Museum, Grahamstown (AM): *Procolophon trigoniceps*, 358; *Sclerosaurus armatus* [plaster cast], 2480-2482. Bernard Price Institute for Palaeontological Research, Johannesburg (BP): *Owenetta rubidgei*, 1/1396;

Owenetta kitchingorum, 1/4195a, 1/4195b, 1/5398, 1/5882; *Nyctiphruretus acudens*, 1/5622; *Procolophon trigoniceps*, 1/966, 1/4014, 1/4248, 1/5927; *Teratophon spinigenis*, 1/4299; *Thelephon contritus*, 1/3512; *Thelerpeton oppressus*, 1/4538. *Theledectes perforatus*, 1/4585. Council for Geoscience, Pretoria (CGP): *Coletta seca*, GHG-228; *Procolophon trigoniceps*, 1-7, 1-9, 1-89, 1-108, 1-127, 1-256. Iziko South African Museum, Cape Town (SAM): *Barasaurus besairiei*, PK-K-8275, PK-K-8276, PK-K-8282; *Owenetta rubidgei*, PK-K-7582; indeterminate procolophonid, PK-7711. National Museum, Bloemfontein (NM): *Procolophon trigoniceps*, QR1447. Rubidge Collection, Graaff-Reinet, Eastern Cape (RC): *Owenetta rubidgei*, 50, 845.

United Kingdom. Natural History Museum, London (BMNH, specimens were loaned to BP): *Procolophon trigoniceps*, R1726, R4087; *Procolophon laticeps*, R3583, R1949.

United States of America. American Museum of Natural History, New York (AMNH): *Procolophon trigoniceps*, 5693, 9506; *Hypsognathus fenneri*, 1676-78. Peabody Museum of Natural History, New Heaven (YPM-PU): *Hypsognathus fenneri*, 55831; *Scoloparia glyphanodon*, 20588, 24504, 24506, 24501.

2.2 Preparation

Mechanical preparation using air-scribes and fine needles was carried out on several South African specimens. A very low concentrated solution of paraloid in acetone was employed as a fixative and to improve the visualization of sutures.

2.3 Illustration

Pencil illustrations of very small specimens were made on drawing paper with the aid of a *camera lucida*, larger specimens were illustrated using a “light table” to trace over photographs. Ink illustrations were made on tracing paper over

photographs. Ink and pencil drawings were corrected/improved using Paint and Photoshop 7.0 for Windows, respectively.

2.4 Phylogenetic analyses

Relationships among procolophonoids were evaluated using PAUP 3.1.1 (Swofford, 1993) in Chapter 3, and TNT (Tree Analysis Using New Technology) Version 1.0 for Windows (Goloboff *et al*., 2003, February 2006 update) in Chapter 5. In both cases, searches that provide exact solutions were employed, and polarization of the characters was done by using an outgroup.

3 PAPER: A PROCOLOPHONOID REPTILE WITH TEMPORAL FENESTRATION FROM THE MIDDLE TRIASSIC OF BRAZIL

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Abstract. The small tetrapod *Candelaria barbouri*, from the Middle Triassic of southern Brazil, is the first record of an owenettid procolophonoid outside of Africa and Madagascar. Originally described as a primitive procolophonid, a re-examination of the holotype as well as new material reveals that *C. barbouri* is in fact the youngest member of the Owenettidae, extending the chronological range of the group by more than ten million years. The recognition of *C. barbouri* as an owenettid points to a broader diversity and distribution for owenettids than hitherto thought. In addition, *C. barbouri* is the first member of the Owenettidae to exhibit temporal fenestrae, a discovery which draws attention to the significance of this feature in 'anapsid' reptiles.

Keywords. Owenettid, procolophonoid, anapsids, temporal fenestrae, Triassic

Cisneros, J.C., Damiani, R. Schultz, C., da Rosa, Á, Schwanke, C, Neto, L.W. and Aurélio, P.L.P. (2004) A procolophonoid reptile with temporal fenestration from the Middle Triassic of Brazil, *Proceedings of the Royal Society of London*, *Series B*, vol. 271, pp. 1541-1546.

3.1 Introduction

The proposed sister-group relationship between turtles and procolophonids (Reisz and Laurin, 1991) has attracted renewed interest in procolophonoid reptiles. Consequently, much new research has been published in recent years (see references in Modesto and Damiani, 2003), increasing substantially our knowledge of this group. The Procolophonoidea was proposed by Romer (1956) to unite the Procolophonidae and Owenettidae. The latter was erected by Broom (1939), who named *Owenetta rubidgei* from the Upper Permian of South Africa. Later, Piveteau (1955) described the owenettid *Barasaurus besairiei* from the Upper Permian Lower Sakamena Formation of Madagascar. No further owenettids were named until the descriptions of *Owenetta kitchingorum* (Reisz and Scott, 2002) and *Saurodectes rogersorum* (Modesto *et al.*, 2003), both from the Lower Triassic of South Africa.

Candelaria barbouri, from the Middle Triassic Santa Maria Formation of southern Brazil, was the first procolophonoid recorded in South America (Price, 1947). Price assigned the holotype to the Procolophonidae, although he recognized some primitive characters inconsistent with a Middle Triassic age. These included a large number of marginal teeth, orbitotemporal fenestrae that were not largely expanded, and the absence of quadratojugal 'horns'. Until now, the phylogenetic relationships of *Candelaria* have remained uncertain, mostly due to the poor preservation of the type specimen. Re-examination of the holotype, and the study of new material, leads us to reinterpret *Candelaria* as an owenettid rather than a procolophonid. As such, *Candelaria* represents not only the first record of the Owenettidae outside of Africa and Madagascar, but also the geologically youngest owenettid. In addition, the new specimens possess clearly visible temporal fenestrae, making *Candelaria* the first owenettid parareptile known to exhibit this historically important morphological feature. Together with the recurrent appearance of temporal fenestrae in parareptiles, this discovery casts further doubt on the significance of temporal fenestration for the classification of 'anapsid' reptiles.

3.2 Material and methods

In the holotype of *Candelaria* only the gross morphology is evident, because the skull roof and palate are damaged, and no sutures are visible. Consequently, most of the information we present here is taken from two newly recovered skulls. Like the holotype, these specimens exhibit the typical preservation of Santa Maria Formation fossils, in that re-crystallization of permineralized elements has resulted in some, relatively minor, osteological deformation (Holz and Souto-Ribeiro, 2000). Disarticulated postcranial remains were recovered in association with the new skulls, and may belong to the same taxon.

Procolophonoids studied for comparative purposes included the holotypes of *Owenetta kitchingorum* (BP/1/4195, Bernard Price Institute for Palaeontological Research, Johannesburg), *Owenetta rubidgei* (RC 50, Rubidge Collection, Graaff-Reinet), and *Coletta seca* (GHG 228, Council for Geoscience, Pretoria), and specimens of *Procolophon* (Bernard Price Institute for Palaeontological Research) and *Barasaurus besairiei* (South African Museum, Cape Town). Information on *Saurodectes rogersorum* and *Sauropareion anoplus* was taken from Modesto *et al.* (2001, 2003). Information on the Russian Permian 'nycteroleters' *Nyctiphruretus*, *Nycteroleter*, *Macroleter* and *Tokosaurus*, was taken from Tverdokhlebova and Ivakhnenko (1984) and Lee (1997).

3.3 Systematic palaeontology

Parareptilia Olson, 1947 (*sensu* deBraga and Reisz, 1996)
Procolophonoidea Romer, 1956 (*sensu* Lee, 1995)
Owenettidae Broom, 1939 (*sensu* Lee, 1995)
Candelaria barbouri Price, 1947

Revised diagnosis. Distinguished from all other owenettids by its relatively large size (at least 30% larger than all other known owenettid specimens) and by a suite of characters related to the presence of a temporal fenestra (figure 1): (1) Posterior process of the postorbital present, which extends well into the supratemporal; (2) lateral notch of supratemporal absent; (3) thin, concave temporal bar present posterior to the orbitotemporal fenestra; (4) supratemporal expanded ventrally; (5) squamosal dorsoventrally narrow, but anteroposteriorly elongate.

Holotype. DGM 314R, a poorly preserved skull and mandible in occlusion (Price, 1947), reposited in the Departamento Nacional de Produção Mineral, Rio de Janeiro, Brazil.

Locality and horizon. Collected in 1942 by an expedition of the Departamento Nacional de Produção Mineral at Sanga Pinheiros (S 29º46'19", W 52º44'54"), Candelaria County, Rio Grande do Sul State, Brazil. The sediments belong to the Dinodontosaurus Cenozone of the Santa Maria Formation (Paraná Basin), of Ladinian (late Middle Triassic) age (Abdala *et al*., 2001).

Referred material. UFSM 11076 and UFSM 11131, two complete skulls with mandibles in occlusion and associated postcrania, in the Universidade Federal de Santa Maria (UFSM), Rio Grande do Sul State, Brazil. These materials were collected by UFSM expeditions in 2000 and 2001 at a small outcrop (S 29°44'55", W 53°00'06") at 166,5 km along RST 287 Highway, Novo Cabrais County, Rio Grande do Sul State. These sediments pertain to the same horizon as the holotype.

3.4 Description

For the sake of brevity, only characters of phylogenetic relevance are reported here. A detailed description of the skulls and postcrania will be provided elsewhere. Here, we provide a reconstruction of the skull in dorsal and lateral views (Figure 1).

The known material of *Candelaria barbouri* indicates that it is a comparatively large owenettid species, the smallest skull (UFSM 11131) measuring 39 mm in length, and the largest (UFSM 11076) 49 mm. In contrast, the largest previously known owenettid skull, the type of *Owenetta rubidgei*, is 34 mm in length. In lateral view, the skull and mandible (in occlusion) of the holotype of *Candelaria* is 20 mm in height, which is at least twice the average height in other owenettids. As in all owenettids, the surface of the cranium lacks complex sculpturing, unlike the pitting characteristic of 'nycteroleters' and millerettids, or the bosses and/or projections characteristic of pareiasaurids and some procolophonids.

The premaxilla of *Candelaria* forms the anterior border of the external naris. As in other owenettids, it only contributes to the anterior portion of the ventral margin of the external naris. It bears five conical teeth that are longer than the anteriormost teeth in the maxilla.

The external naris of *Candelaria* is expanded posteriorly and accounts for half of the length of the snout. This is also the condition present in the owenettids *Barasaurus*, *O. rubidgei,* and *O. kitchingorum*, and in the 'nycteroleters' *Nyctiphruretus* and *Tokosaurus*. In procolophonids and most other parareptiles, however, the external naris comprises much less than half the length of the snout.

As in all parareptiles, the maxilla possesses an anterior dorsal expansion behind the external naris, and a large anterolateral foramen (Lee, 1995; Laurin and Reisz, 1995). A second, smaller foramen is adjacent to the anterolateral foramen, and a third below the margin of the orbitotemporal fenestra, as in all other owenettids in which the area is known, but not procolophonids. The maxilla bears between 21 and 23 teeth, which is close to the number present in *O. kitchingorum* (20 to 21 teeth), and, presumably, *Saurodectes*, judging from the size of the preserved maxillary teeth in the latter. The number of maxillary teeth present in Permian parareptiles (with the exception of pareiasaurids) is higher. For example, *O. rubidgei* bears approximately 30 maxillary teeth, a similar number to that in the

'nycteroleters' *Nyctiphruretus* and *Nycteroleter*. The reduction in dentition in Triassic owenettids is a direct result of the decrease in length of the maxilla, as first observed in *O. kitchingorum* (Reisz and Scott, 2002). This character could represent an apomorphy for these taxa. As in *O. kitchingorum*, the tooth directly below the anterolateral foramen is the largest in the maxilla. It has a wide base, is posteriorly recurved, and is followed by a series of progressively smaller, caniniform teeth. This caniniform region is absent in all other procolophonoids.

The nasal forms the dorsal margin of the external naris. Its contact with the prefrontal is not well preserved in any of the specimens. However, the anterior edge of the frontal terminates well behind the level of the anterior margin of the orbitotemporal fenestra, as in *O. kitchingorum*. This suggests that the prefrontals are sutured in the midline, separating the nasals from the frontals. In all other procolophonoids, the anterior edge of the frontal is positioned in front of the level of the orbitotemporal fenestra, contacting the nasal and precluding a midline contact between the prefrontals. The condition in *Saurodectes* is uncertain because of poor preservation. The nasals may also have contacted the frontals in *Candelaria*, but this would necessitate an unusual posterior expansion of the nasals.

A prominent crest, formed by the lateral margins of the prefrontal, frontal and postfrontal, borders the medial margin of each orbitotemporal fenestra. This structure, here termed the orbitotemporal crest, is present in all owenettids that we have observed, and in the 'nycteroleters' *Nyctiphruretus*, and, possibly, *Tokosaurus*. This character could be an apomorphy of owenettids that evolved independently in certain 'nycteroleters', or it represents an apomorphy of a more inclusive group comprising some 'nycteroleters' more closely related to owenettids than to other parareptiles.

The postfrontal contacts the supratemporal, precluding the parietal from contributing to the margin of the orbitotemporal fenestra. This is an owenettid autapomorphy (Reisz and Scott, 2002; Modesto *et al.* 2003).

The pineal foramen is located in a shallow fossa within the anterior portion of the parietals, and is positioned wholly posterior to the level of the orbitotemporal fenestra, as is characteristic of all other owenettids. Some unidentified elements at the back of the skull of UFSM 11076 could be interpreted as the remains of postparietals. However, the occipital area of the three known skulls is badly preserved and the presence of a postparietal cannot be assessed at present.
The most distinctive, and unexpected, feature of *Candelaria* is the presence of a temporal opening. Accordingly, the morphology of the bones of the cheek region of the skull has been considerably modified (figure 1). The fenestra is bordered by the postorbital anterodorsally, the supratemporal posterodorsally, and the squamosal ventrally, with a small contribution from the jugal anteroventrally. In dorsal view, a posterior process of the postorbital extends deep into the supratemporal. The latter is also characterised by being expanded ventrally, and in lacking the lateral notch characteristic of all other owenettids. The postorbital and the jugal form the narrow, anterior temporal bar. This bar is distinctly concave, so that the contact between these bones is not visible in dorsal view. The squamosal is dorsoventrally shallow, but more elongated than in other owenettids.

An acute temporal emargination between the jugal and the quadratojugal is present. This feature is characteristic of owenettids (Reisz and Scott, 2002), but occurs to a lesser degree in *Coletta* and *Sauropareion*.

As far as we can determine, the morphology of the palate of *Candelaria* is virtually indistinguishable from that of *O. kitchingorum*. In particular, the length of the palate in these taxa, as in all Triassic parareptiles, is much shorter than in their Permian relatives, judging from the relative distance between the tip of the transverse flange of the pterygoid and the posterior border of the basioccipital. As in all owenettids, *Candelaria* possesses a large number of palatal denticles arranged in long rows. This contrasts with the short rows of enlarged teeth characteristic of procolophonids.

The mandible of *Candelaria* cannot be fully described, because it remains firmly adducted to the skull in all specimens. However, its visible morphology is similar to that of other owenettids. Presumably, the number of dentary teeth is comparable to that of the upper marginal dentition, as also suggested by the position of the coronoid process. As in *O. kitchingorum*, the coronoid process is placed more anteriorly than in Permian owenettids. This feature may be related to the reduction in palatal length seen in the Triassic species, because the position of the coronoid process appears to be correlated with that of the transverse flange of the pterygoid.

3.5 Discussion

In order to determine the relationships of *Candelaria barbouri* among owenettids, we performed a phylogenetic analysis of all known owenettids and selected, well-known procolophonids. The results of this analysis (figure 2) indicate that *Candelaria* is the sister taxon of *O. kitchingorum* within a monophyletic Owenettidae. The Owenettidae can be diagnosed on the basis of four unequivocal synapomorphies (see Appendix A): the presence of a large postfrontal that contacts the supratemporal, the absence of an entepicondylar foramen, the presence of orbitotemporal crests, and the presence of broad, posteriorly expanded nostrils. Other characters typical of, though not exclusive to, owenettids are also present in *Candelaria*, and include the presence of an acute temporal emargination, a pair of anterolateral foramina on the maxilla, and a pineal foramen that is set within a shallow fossa.

The sister-group relationship between *Candelaria* and *O. kitchingorum* is supported by one unequivocal synapomorphy, the presence of posteriorly recurved maxillary teeth. Three further synapomorphies, the presence of a prominent anterior maxillary tooth, a short palate, and a midline contact between the prefrontals, also support this relationship but their distribution on the cladogram is equivocal. The long ghost lineage for *Candelaria* suggested by this relationship (figure 2) implies an unknown fossil record for owenettids spanning

most of the Early Triassic and the early part of the Middle Triassic. On a local scale, this may be partially explained by the sedimentary hiatus during that time period in southern Brazil. Our phylogenetic results also support those of Modesto *et al.* (2003) in that *O. kitchingorum* and *O. rubidgei* do not form a monophyletic group. Instead, the Triassic owenettids *Saurodectes*, *O. kitchingorum* and *Candelaria* form a natural group to the exclusion of the Permian owenettids. This tree topology necessitates a ghost lineage in the uppermost Permian for the Triassic owenettid clade (figure 2).

The presence or absence of temporal fenestrae has long played a major role in the classification of amniotes (e.g., Romer, 1956; Gauthier *et al*., 1989). Historically, four major types of temporal fenestration were recognized for systematic purposes, a synapsid, diapsid, euryapsid, and anapsid condition. The Parareptilia is generally recognized to be a group characterized, in part, by an anapsid temporal morphology. Indeed, the term Anapsida has been applied to the clade which includes parareptiles and mesosaurids (Modesto, 1999; Reisz and Scott, 2002). However, the significance of temporal fenestrae in anapsid phylogeny is questionable because of its repeated occurrence across several lineages (c.f., Hamley and Thulborn, 1993), as shown in figure 3. Temporal fenestration is absent in the most primitive anapsids, the Mesosauridae, but is present in all members of the Millerettidae (*Millerosaurus*, *Milleropsis* and young individuals of *Millereta;* Gow, 1972), all lanthanosuchoids (*Acleistorhinus*, *Lanthanosuchus*, *Lanthaniscus*; deBraga and Reisz, 1996), at least one 'nycteroleter' (*Tokosaurus*; Tverdokhlebova and Ivakhnenko, 1984), at least one procolophonid (*Procolophon laticeps*; Hamley and Thulborn, 1993), and at least one owenettid (*Candelaria*). In short, temporal fenestration is present in the most basal parareptiles, the millerettids, and in all other lineages except for pareiasaurids. This distribution implies that temporal fenestration has arisen independently in most parareptile lineages, but a more intriguing possibility is that it represents a synapomorphy of Parareptilia. The latter possibility will be explored in a forthcoming publication. For the moment, the recognition of temporal fenestrae in *Candelaria* may be viewed as further evidence for the independent development of temporal openings

in different parareptile lineages. We conclude that the absence of temporal fenestration may be of limited taxonomic significance for those amniotes traditionally perceived as ‘anapsids’.

The presence of temporal fenestrae in tetrapods has been explained as a means of reducing the weight of the skull in areas experiencing little or no stress, for expansion of the jaw adductor musculature, and/or for increasing the area for muscle attachment (Frazetta, 1968; Tarsitano *et al*., 2001). Interestingly, Colbert, (1946) suggested that the progressive enlargement of the orbitotemporal fenestrae within procolophonids, culminating in the leptopleuronines, may have been correlated with expansion of the adductor musculature. While there is no direct evidence for muscular expansion in derived leptopleuronines, we may speculate that the true temporal openings of *Candelaria* were functionally analogous to the enlarged orbitotemporal fenestrae in leptopleuronines.

Until now, owenettids were known only from the Upper Permian and lowermost Triassic of South Africa, and the Upper Permian of Madagascar. The recognition of *Candelaria* as an owenettid extends the known stratigraphic range of this group to Middle Triassic times, which significantly increases the entire chronological range of the Owenettidae. Biogeographically, it expands the known distribution of owenettids from what was then central Gondwana (South Africa and Madagascar) to western Gondwana (Brazil). Therefore, future discoveries of owenettids in Triassic sediments elsewhere in Gondwana could be expected.

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3.7 Appendix A: Phylogenetic characters

Characters 1-14 are taken from Modesto *et al*. (2003), with slight modifications to characters 1, 4, 8, and 13. Characters 15-21 are new characters. Additional information for *Sauropareion* taken from Damiani *et al*. (2004).

1. Premaxillary teeth number: five or more (0); fewer than five (1).
2. Maxillary fossa: absent (0); present (1).
3. Lacrimal: separated from ectopterygoid (0); contacts ectopterygoid (1).
4. Orbit posterior margin: anterior to or level with anterior margin of pineal foramen (0); posterior to it (1).
5. Pineal foramen: flush with skull roof (0); set within shallow fossa (1).
6. Postfrontal: large and contacts postorbital (0); large and contacts supratemporal (1); splint-like and separated from postorbital (2).
7. Squamosal ventral point: ends dorsal to ventral margin of quadratojugal (0); extends as far ventrally as quadratojugal (1).
8. Supratemporal: broader than long (0); approximately as broad as long (1); longer than broad (2).
9. Supratemporal lateral margin: straight (0); with lateral notch (1).
10. Postparietal: present (0); absent (1).
11. Vomerine dentition: present as small denticles (0); present as larger teeth (1).
12. Pterygo-palatine dentition: ‘continuous’ (0); stops in the middle of the palatine (1).
13. Temporal emargination: roughly straight (0); forms acute angle (1); broadly excavated (2).
14. Entepicondylar foramen: present (0); absent (1).
15. Prominent anterior maxillary tooth: absent (0); present (1).
16. Maxillary dentition formed by: straight conical teeth (0); posteriorly recurved teeth (1); conical and transversely widened teeth (2).
17. Orbitotemporal crests: absent (0); present (1).
18. Prefrontals: midline contact absent (0); midline contact present (1).

19. Nostril shape: subcircular, unexpanded posteriorly (0); broadly expanded posteriorly (1).
20. Maxillary tooth count: greater than 24 (0); fewer than 24 (1).
21. Palate length (i.e., distance between tip of transverse flange and basioccipital): long (0); short (1).

3.8 Appendix B: Data matrix

Character states for eight procolophonoid taxa and the outgroup taxon *Nycteroleter*. Character polarity denoted as follows: Primitive state=0; derived states=1 and 2; state unknown=?.

Nycteroleter	00?00	00000	00000	00000	0
O. rubidgei	00001	10111	001?0	01010	0
Barasaurus	00?01	10101	00110	01010	0
Saurodectes	??001	10111	??1??	01??1	?
O. kitchingorum	00001	10110	00111	11111	1
Candelaria	00?0?	1?1-?	001?1	11111	1
Coletta	11?01	00???	1?2?0	00001	1
Sauropareion	??111	21200	111?0	000?1	1
Procolophonidae	11110	21201	11200	20001	1

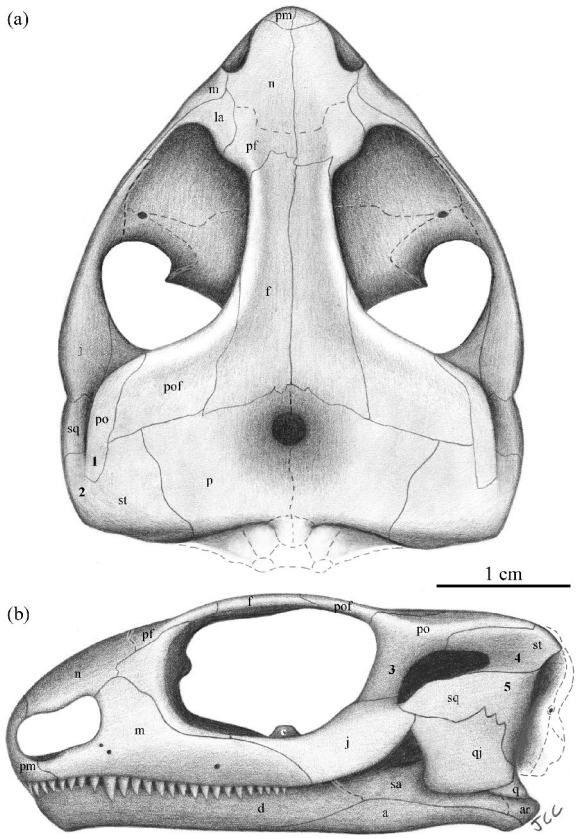


Figure 1. Reconstruction of the skull of the owenettid parareptile *Candelaria barbouri* (Price, 1947) from the Middle Triassic of Brazil, based on UFSM 11076, UFSM 11131 and DGM 314R. (*a*) Dorsal view; and (*b*) left lateral view. Characters 1-5 relate to the temporal fenestra and are listed in the diagnosis. Abbreviations: a, angular; ar, articular; c, coronoid process; d, dentary; f, frontal, j, jugal; la, lacrimal; m, maxilla; n, nasal; p, parietal; pf, prefrontal; pm, premaxilla; po, postorbital; pof, postfrontal; q, quadrate; qj, quadratojugal; sa, surangular; sq, squamosal; st, supratemporal.

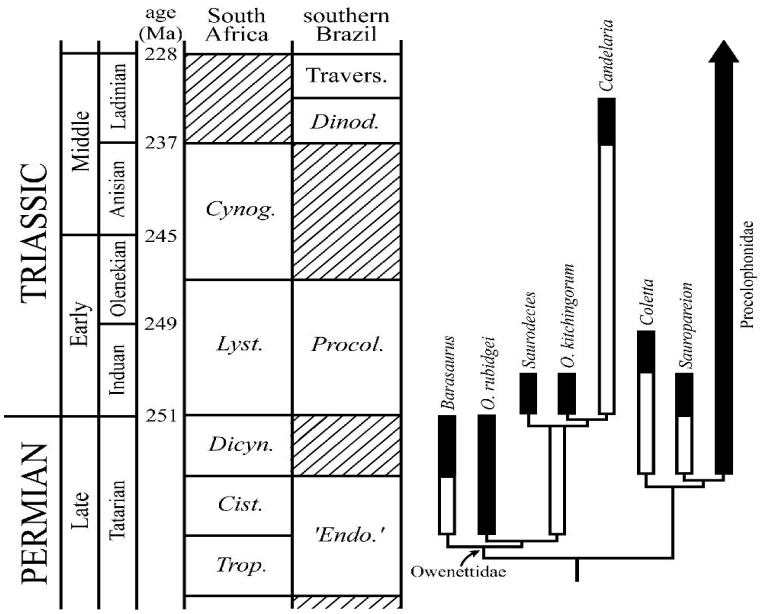


Figure 2. Stratocladogram of procolophonoid interrelationships, including ghost lineages (white extensions of black bars). The Owenettidae is a monophyletic taxon that includes *Candelaria*, while the Early Triassic taxa *Coletta* and *Sauropareion* are transitional forms between the Owenettidae and Procolophonidae. The phylogeny is based on a PAUP 3.1.1 (Swofford, 1993) analysis of the data matrix in Appendix 2, and represents one of two most parsimonious trees, chosen on the basis of greatest stratigraphic congruence, found using the branch-and-bound algorithm. Tree length=31 steps, consistency index=0.81, and rescaled consistency index=0.80. Biostratigraphy of South Africa from Rubidge (1995); southern Brazilian Triassic from Abdala *et al.* (2001); southern Brazilian Permian adapted from Langer (2000) and Malabarba *et al*. (2003). Hatchure indicates a sedimentary hiatus. Abbreviations: *Cist*., *Cistecephalus*; *Cynog*., *Cynognathus*; *Dicyn*., *Dicynodon*; *Dinod*., *Dinodontosaurus*; '*Endo*.', '*Endothiodon*'; *Lyst*., *Lystrosaurus*; *Procol*., *Procolophon*; Travers., Traversodontid; *Trop*., *Tropidostoma*.

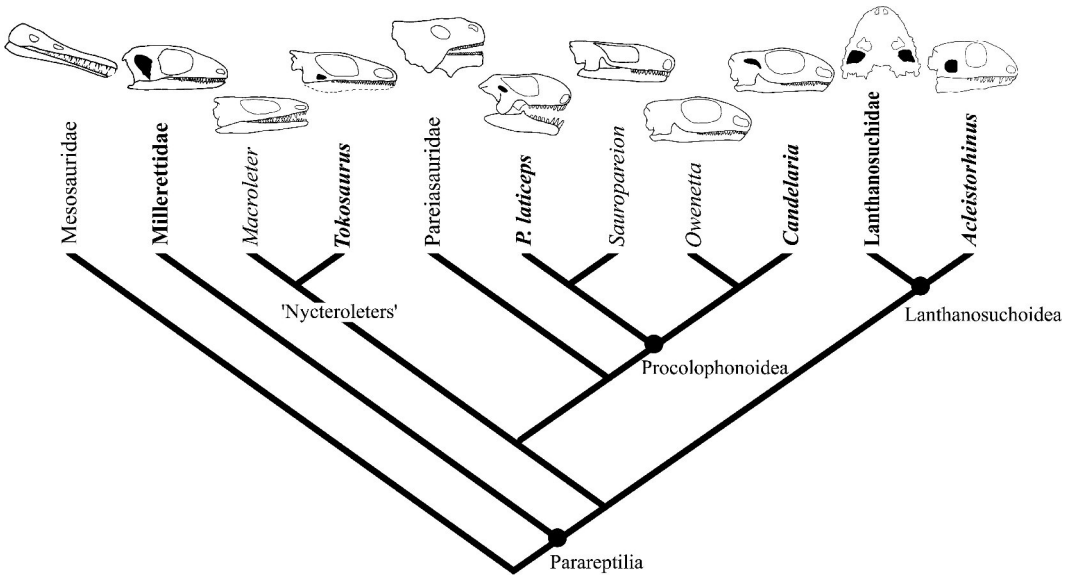


Figure 3. Simplified cladogram of 'anapsid' reptiles, showing distribution (in bold face) of all known taxa which possess temporal fenestrae (see discussion). Skull outlines, from left to right, are: *Stereosternum tumidum, Millerosaurus nuffieldi, Macroleter poezicus, Tokosaurus perforatus, Bradysaurus baini, Procolophon laticeps, Sauropareion anoplus, Owenetta kitchingorum, Candelaria barbouri, Lanthanosuchus watsoni* and *Acleistorhinus pteroticus*; temporal fenestrae are shaded in black. Phylogeny adapted from Reisz and Scott (2002). Drawings not to scale.

4 PAPER: TAXONOMIC STATUS OF THE TRIASSIC REPTILE *PROCOLOPHON* IN GONDWANA

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Abstract. The specific composition of the genus *Procolophon* in Brazil, South Africa and Antarctica is discussed in the light of new data. It is found that *P. pricei* and *P. brasiliensis*, two species proposed for Brazil, fit within the pattern of ontogenetic variation of the type species *P. trigoniceps*, and they are here considered junior synonyms. The South African species *P. laticeps*, characterized by the presence of a temporal fenestra, is no longer considered valid. The peculiar temporal openings of this species are here regarded as an anomalous condition without taxonomic significance. The only complete skull known from Antarctica shows a unique feature consisting of an elliptical depression in the palate. The interpretation of this structure is ambiguous as it may also be attributable to individual variation, and this specimen is provisionally kept within *P. trigoniceps*. Therefore, only the type species, *P. trigoniceps*, is recognized in Gondwana. This species occupies a wide geographic range, from the Paraná Basin to the Transantarctic Mountains.

Keywords. Procolophonidae, *Procolophon*, temporal fenestrae, Triassic, Gondwana.

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4.1 Introduction

Procolophon is a member of the Procolophonidae, a clade of small parareptiles that flourished across all Pangaea during the Triassic, becoming extinct during the time of the T/J boundary. *Procolophon* is known from hundreds of specimens, most of them found in the Lower Triassic of the South African Karoo, were it is outnumbered only by the ubiquitous dicynodont *Lystrosaurus* (Kitching 1977; Groenewald and Kitching 1995). The genus possesses a robust, wide torso and enlarged chisel-like teeth, both adaptations suggesting a high-fibre diet (Hotton *et al*. 1997); prominent quadratojugal processes confer a bizarre, triangular shape to the head (Fig. 1). Limb adaptations suggest that *Procolophon* was capable of burrowing (deBraga 2003) and burrow casts from the *Lystrosaurus* Assemblage Zone (AZ) of South Africa have been referred to this genus (Groenewald 1991). The genus is noteworthy because of the presence of some individuals with temporal openings, sometimes regarded as representing a different species (Hamley and Thulborn 1993). *Procolophon* has also been recovered from the Fremouw Formation of the Transantarctic Basin (Kitching *et al.* 1972; Colbert and Kitching 1975) and the Sanga do Cabral Formation of the Paraná Basin in Brazil (Barberena *et al*. 1981; Lavina 1983). In that country, two new *Procolophon* species were proposed (Lavina 1983; Cisneros and Schultz 2002). In the light of new data, this study reviews the taxonomic status of the Antarctic material, the Brazilian species and the specimens with temporal openings from South Africa.

Institutional abbreviations. AM, Albany Museum, Grahamstown, South Africa; AMNH, American Museum of Natural History, New York, USA; BMNH, Natural History Museum, London, United Kingdom; BP, Bernard Price Institute for Palaeontological Research, Johannesburg, South Africa; CGP, Council for Geosciences, Pretoria, South Africa; MCN, Museu de Ciências Naturáis, Porto Alegre, Brazil; NM, National Museum, Bloemfontein, South Africa; SAM, South African Museum, Cape Town, South Africa; RS, South African Museum (field

number), Cape Town, South Africa; UFRGS, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil.

Anatomical abbreviations. bo, basioccipital; ec, ectopterygoid; eo, exoccipital; f, vomerine "fang"; iv, interperygoid vacuity; j, jugal; m, maxilla; op, opisthotic; pl, palatine; pm, premaxilla; po, postorbital; pp, paroccipital process of the opisthotic, ps, parasphenoid; pt, pterygoid; q, quadrate; qj, quadratojugal; sf, suborbital foramen; so, supraoccipital; sq, squamosal; st, supratemporal; v, vomer.

4.2 Taxonomic history

Together with the description of the type species *Procolophon trigoniceps* (by page priority, Fig. 2), Owen (1876) proposed *P. minor* based on a juvenile skull. This was followed by five more species proposed by Seeley (1878, 1905): *P. griersoni*, *P. cuneiceps*, *P. laticeps*, *P. platyrhinus* and *P. sphenorhinus*. Some of the features used to distinguish these species are better explained by taphonomic, ontogenetic or individual variation. Besides, all seven of Owen's and Seeley's holotypes were collected by D. White from Donnybrook Farm, in the Eastern Cape Province of South Africa, leading Broom (1936) to recognize only the type species, *P. trigoniceps*. The non-validity of the additional species has been virtually unquestioned by later authors. Broom (1905) in turn, proposed another species, *P. baini*, based on a well preserved, almost complete skeleton collected by J.M. Bain or T. Bain at an unknown locality. This species was said to differ from *P. trigoniceps* mainly in the number of marginal teeth, but this character is known to be ontogenetically variable in the genus (Gow, 1977). *P. baini* was also sunk into junior synonymy with *P. trigoniceps* by Colbert and Kitching (1975).

The finding of a *Lystrosaurus* fauna in the Fremouw Formation of Antarctica yielded the first *Procolophon* remains from that continent (Kitching *et al.,* 1972). These remains were represented by one well preserved articulated skeleton plus a number of fragmentary specimens. Colbert and Kitching (1975) noted a number of peculiarities in the best Antarctic specimen, including very small quadratojugal

horns and relatively robust limbs, but decided that it fitted within the range of variation of the South African *P. trigoniceps* and referred all Antarctic material to this species. In Brazil, *Procolophon* was reported by Barberena *et al.* (1981) in the Sanga do Cabral Formation, in the state of Rio Grande do Sul, southern Brazil. This find consisted of one partial cranium and mandible, a second mandible and non-associated vertebral elements. These specimens were later described as a new species, *P. pricei* (Lavina, 1983). A later finding of a *Procolophon* cranium from a different locality to that of *P. pricei* was described as a new species, *P. brasiliensis* by Cisneros and Schultz (2002). Both Brazilian species were founded mainly on characters relating to the arrangement of the palatal dentition.

Hamley and Thulborn (1993) reviewed the status of the species *P. laticeps*. This species was said to differ from *P. trigoniceps* by the presence of a small temporal fenestra (Seeley, 1878, 1905). However, the authenticity of these small openings, which are present only in the holotype and a referred specimen of a genus that in South Africa is known from several specimens, was questioned almost from the beginning. They were regarded by some authors as an artefact of preparation or preservation (Broom, 1936; von Huene, 1912) and the species was neglected, a view endorsed by most later authors (e.g. Colbert, 1946; Kuhn, 1969; Colbert and Kitching, 1975; Carroll and Lindsay, 1985). Nevertheless, Hamley and Thulborn (1993) supported the view that the temporal openings were a natural feature in the hypodigm. The temporal fenestra was shown to be particularly well preserved in the holotype, and these authors re-erected the species *P. laticeps*. In addition, Hamley and Thulborn (1993) found four additional apomorphies to support the diagnosis of *P. laticeps*. Recent fieldwork in the *Lystrosaurus* AZ of South Africa has provided a new *Procolophon* specimen in which the presence of small temporal fenestrae is unequivocal; this specimen is discussed here.

Material and methods

Preparation by conventional methods (i.e. mechanical preparation using air-scribes and fine needles) was carried out on several specimens, including recently collected material and the holotypes of *P. trigoniceps*, *P. laticeps* and *P. pricei*. A

large number of *Procolophon* specimens were examined, most of them in South African collections, although only some are cited in the text. Specimens from other taxa studied for comparative purposes include the following: BP/1/4299, holotype of *Teratophon spinigenis*, BP/1/4587 syntype of *Teratophon spinigenis*, BP/1/4586 syntype of *Thelerpeton oppressus*, BP/1/4538 holotype of *Thelerpeton oppressus*, IVPP V6064 holotype of *Eumetabolodon bathycephalus*, IVPP V6175 *Eumetabolodon bathycephalus*.

4.3 Comparisons and discussion

4.3.1 The genus *Procolophon* in the Paraná Basin

The genus *Procolophon* is commonly found in the conglomeratic layers of the Sanga do Cabral Formation of Rio Grande do Sul State, southern Brazil (Langer and Lavina, 2000). However, these remains consist of disarticulated and reworked bones. The finding of two partial skulls from different localities, that differed from each other mainly in the arrangement of the palatal dentition, was the basis for the proposal of the new species *P. pricei* (Lavina, 1983) and *P. brasiliensis* (Cisneros and Schultz, 2002). These holotypes are discussed below.

Lavina (1983) distinguished *P. pricei* (Fig. 3B) from *P. trigoniceps* by the following characters: (i) snout shorter and more rounded; (ii) vomerine dentition arranged as an inverted “V”; (iii) posteromedial palatine tooth row not extending to the anterolateral region of the pterygoid; and (iv) interpterygoid vacuity distinctly larger.

The first character is an artefact of taphonomy, as the premaxillae of UFRGS PV0231T have been weathered, giving the snout a more rounded aspect. Character (ii) is consistent with the morphology of several *P. trigoniceps* specimens (Fig. 4), being distinctive only when compared with the stylised reconstruction of the palate of *P. trigoniceps* provided by Broili and Schröder (1936, fig. 6). Character (iii) is variable, and is found in juvenile *P. trigoniceps*

specimens (e.g. AMNH 5693, NM QR1447, Fig. 4D, E). An enlarged interpterygoid vacuity (character (iv)) is also seen in some *P. trigoniceps* specimens, especially in juveniles and subadults (e.g. specimen CGP 1-89, Fig. 4A). Thus, the supposedly diagnostic characters of *P. pricei* can be rejected as of a taphonomic nature, or due to individual variation or ontogeny.

Cisneros and Schultz (2002) proposed *P. brasiliensis* (Fig. 3A) based on the following characters: (i) vomer possessing a single tooth row extending over the entire bone, and reaching the pterygoid-vomer contact; (ii) a small diastema (or hiatus) in the posterior third of the row; and (iii) three vomerine fangs in the anterior part of the bone, arranged in a "V" shape, pointing forwards. Characters (i) and (ii) result from a misinterpretation of the position of the vomer-pterygoid contact in MCN PV1904. This suture was erroneously traced on what is in fact a transverse fracture of the anterior part of the pterygoid. The actual suture occurs anteriorly, in the place interpreted by these authors as a tooth hiatus of the vomerine row. Thus, the vomerine tooth row does not reach the vomer-pterygoid suture. Character (iii) is somewhat subjective. The three anterior vomerine teeth are large elements in the vomerine tooth row, but the anteriormost tooth is the largest element, its diameter at the base exceeding by *c.* 50% that of the two following enlarged teeth. The number of enlarged teeth in the vomer is actually variable in *P. trigoniceps*, and some old individuals have a number of them (e.g. BP/1/966, BP/1/4248, Fig. 4C, F). Thus, character (iii) is not a valid autapomorphy.

Re-examination of both diagnoses shows that there no current grounds to retain *P. pricei* or *P. brasiliensis* as valid species. Both Brazilian holotypes fit within the range of individual and ontogenetic variation of *P. trigoniceps*. The arrangement of the palatal dentition is particularly variable in *P. trigoniceps* and juveniles differ substantially from adults (pers. obs.). A comprehensive description of the pattern of tooth succession in the palate of *P. trigoniceps* is in preparation.

4.3.2 Specimens with temporal fenestrae from the Karoo Basin

The species *P. laticeps* was re-erected by Hamley and Thulborn (1993) on the basis that the temporal fenestrae noted in the two known specimens were real features. In addition, these authors pointed out four further autapomorphies for this taxon. The temporal region of these two individuals, and of a new specimen showing temporal fenestrae recently collected, all from South Africa, is discussed below.

BMNH R3583. The holotype of *P. laticeps* is a weathered but otherwise unaltered cranium and mandible (Fig. 5C). The temporal region is better preserved on the left side of the skull, where the fenestra can be seen. This region is not visible on the right side of the cranium, where it is covered with resin. The temporal fenestra (Fig. 6E, F) is subcircular, located between the postorbital, jugal, quadratojugal and squamosal bones. These bones contribute almost equally to the margins of the temporal opening. The postorbital bone forms the anterodorsal margin of the fenestra. Ventrally, this bone has a thin contact with the jugal, which forms the anteroventral edge of the opening. The quadratojugal forms the posteroventral border, and the squamosal the posterodorsal border. As noted by Hamley and Thulborn (1993), part of the dorsal rim of the opening, between the postorbital and squamosal bones, was slightly damaged in preparation. The rest of the structure is, however, well preserved.

BMNH R1949. This specimen was referred to *P. laticeps* by Seeley (1905) and Hamley and Thulborn (1993), and it has been repeatedly illustrated and discussed (see Seeley, 1889, 1905; von Huene, 1912; Carroll and Lindsay, 1985). The specimen consists of an articulated partial skeleton of a large-sized individual (Fig. 5B). The cranium lacks the tip of the snout and the left quadratojugal process, and some areas are weathered. The temporal fenestra (Fig. 6F-I) is preserved on both sides of the cranium. This structure is elliptical, and elongated in a posterodorsal to anteroventral direction. It is located between the postorbital, jugal and squamosal bones. The postorbital delimits the anterior and anterodorsal

borders of the fenestra. On both sides of the skull the margins of this bone have been slightly damaged by over-preparation. The openings should therefore be moderately more constricted than they appear now. Anteroventrally, the fenestra is bordered by a basin of the posterodorsal projection of the jugal. The jugal contribution to the margin of the fenestra is the shortest of the three bones that form this structure. The squamosal contribution is the longest, delimiting the posterodorsal to posteroventral margins. Posterodorsally, the squamosal contribution to the margin is concave, and ventrally it forms a straight, thin ventral projection that contacts the jugal. This bar excludes the quadratojugal from the margin of the opening.

CGP 1-127. A well-preserved medium-sized specimen (Fig. 5A), consisting of cranium and anterior part of postcranium, collected by Johann Neveling (for stratigraphic context, see Neveling, 2004). The temporal region is well preserved on both sides of the cranium. The opening (Fig. 6A-D) is subcircular and smaller than in other specimens, composed by the margins of the postorbital, jugal and squamosal bones. The postorbital forms the anterodorsal rim of the opening. Dorsally, this bone has a short contact with the squamosal that prevents the supratemporal from contributing to the dorsal margin of the fenestra. The squamosal forms the posterior border of the opening, and is less convex than the other two bones that form this structure. The squamosal sutures ventrally to the jugal, this short contact excluding the quadratojugal from the rim. The jugal forms the markedly convex ventral border of the orbit. In the right fenestra, this bone is positioned slightly more anteriorly than on the left side.

On the validity of *Procolophon laticeps*

The temporal fenestrae show clear discrepancies in the specimens discussed here. In the holotype, the temporal fenestra is considerably wide, being some 50 per cent larger than in CGP 1-127. This difference does not seem to be ontogenetic, because the skulls of both individuals are of comparable length (maximum cranial length: BMNH R3583 = 41.5 mm; CGP 1-127 = 42.4 mm), suggesting comparable ontogenetic stages. In the much larger cranium BMNH R1949, the

temporal openings are elongated, being longer dorsoventrally than in the holotype, but shorter anteroposteriorly. The quadratojugal contribution to the rim of the orbit is present only in the holotype. Furthermore, in this specimen the quadratojugal contributes to the rim to a larger extent than the jugal or the squamosal. In the remaining specimens, the temporal openings are formed exclusively by the jugal, squamosal and postorbital. It is difficult to infer an ontogenetic mechanism that can account for this variation in size, shape and composition of the temporal openings in all specimens, and it seems unlikely that they can be regarded as merely due to individual variation.

Besides the presence of temporal fenestrae, Hamley and Thulborn (1993) proposed four additional autapomorphies for *P. laticeps*. Because the bone surface of the skull of the holotype of *P. laticeps* is heavily weathered, these characters were mostly obtained from BMNH R1949, and presumably, by contrast with the holotype of *P. trigoniceps* and other specimens held at the Natural History Museum in London. Taking into account the new specimen with temporal openings, CGP 1-127, as well as a broader sample of *P. trigoniceps*, however, none of these characters seems diagnostic. These characters are: (i) contact between parietal and squamosal bones; (ii) ventrolateral extension of parietal on occipital surface; (iii) arched tip of paroccipital process; and (iv) contact between prefrontal and postfrontal. A contact between parietal and squamosal bones (character (i)) is not obvious in BMNH R1949. On both sides of this specimen, the anterodorsal margins of the squamosals are not well preserved, nor are the lateral margins of the parietals. No contact can be traced between these bones. The bone labelled as “parietal” in Hamley and Thulborn (1993, “pa” in fig. 3) is in fact the supratemporal. Character (ii), ventrolateral extension of parietal on occipital surface, is in fact present in BMNH R1949, but is also present in specimens with no temporal fenestrae, e.g. BMNH R4087 (see Carroll and Lindsay, 1985, fig. 5). The character is, therefore, not confined to specimens that bear temporal openings. With regard to character (iii), BMNH R1949 does posess an arched tip of the paroccipital process of the opisthotic (Fig. 7A), but this character is not present in the new specimen CGP 1-127 (Fig. 7B), where the

paroccipital process is well preserved and has been carefully prepared. Hence, this character cannot be considered diagnostic for *P. laticeps*. The peculiar morphology of the opisthotic in BMNH R1949 may be due to individual variation. In ventrolateral view, a very short contact is present between the tips of the prefrontal and postfrontal bones (Character (iv)) in BMNH R1949. This prefrontal-postfrontal contact is a highly variable character in *Procolophon*. It is not present in all specimens with temporal openings, and it is present in some specimens that do not possess temporal openings (e.g. CGP 1-108, pers. obs.).

Specimen CGP 1-127 was collected from the same locality and horizon as CGP 1-256 (Johann Neveling, pers. comm. 2005), the latter being a *Procolophon* specimen with no temporal fenestrae. Furthermore, the holotypes of both *P. trigoniceps* and *P. laticeps* were collected by D. White at Donnybrook Farm, Queenstown District, presumably from the same localized band of dark red mudstone, approximately one meter thick, within the Katberg Formation. This is the only stratum where *Procolophon* is known to occur at Donnybrook (Kitching, 1977). Unfortunately, no precise locality information is available for BMNH R1949. Thus, at least two of the three specimens referable to *P. laticeps* come from sites and horizons that have also produced *P. trigoniceps*. This implies sympatry for the two species, at least in two localities in the Eastern Cape Province of South Africa.

A number of factors, when combined, strongly suggest that *P. laticeps* is not a valid species: (1) the rarity of specimens with temporal openings, within a genus that is known from several well preserved crania; (2) the high variation in the morphology of the temporal openings among the specimens that have them; (3) the absence of additional autapomorphies for *P. laticeps*; and (4) the co-occurrence with *P. trigoniceps* of at least two of the three individuals known.

The phenomenon of sympatry is known to occur when there is a non-geographical mechanism of reproductive isolation among the species populations (Mayr, 1970; Dobzhansky, 1970). Sympatry, however, is an exceptional event in nature, and

intrageneric species are more likely to occupy different geographic areas (Mayr, 1970; Dobzhansky, 1970).

Thus, *P. laticeps* is here regarded as a junior synonym of *P. trigoniceps*. The temporal fenestration of *Procolophon* is considered to represent an anomalous or pathological feature of the three individuals in which it is known. When considering a large sample of individuals – as is the case in *Procolophon* (some hundred well preserved crania recovered at the Karoo Basin) – anomalous specimens should be expected. The temporal openings of *Procolophon* are smaller and much simpler than those of the procolophonoid *Candelaria barbouri* (see Cisneros *et al.,* 2004), and no more than a small genetic change would be necessary to activate the development of these openings in *Procolophon*. The mere embryological failure to close sutures of the relevant bones in the temporal region would result in this feature (Tarsitano *et al.*, 2001). This unusual condition was not necessarily disadvantageous, because judging by its size, BMNH R1949 represents an old individual.

4.3.3 The genus *Procolophon* in the Transantarctic Mountains

Among the *Procolophon* remains from the Transantarctic Mountains described by Colbert and Kitching (1975), one specimen is notable for its completeness and fine preservation, and offers the best comparisons with non-Antarctic *Procolophon* material. AMNH 9506 is a subadult individual, consisting of a cranium and articulated postcranium, including the 21st presacral vertebrae, ribs, pectoral girdle and forelimbs (Fig. 8A). Colbert and Kitching (1975) noted some peculiarities of AMNH 9506 when compared to known specimens of *P. trigoniceps*; including the fact that it has rather small quadratojugal processes and relatively robust forelimbs. They considered, however, that these traits fitted within the range of ontogenetic, individual or sexual variation of the type species, a view also endorsed here.

Recent preparation of the palate in AMNH 9506 has revealed an unusual feature of this Antarctic specimen, the only one in the collection of AMNH where the palate is preserved. It consists of a distinctive depression between the vomers (Fig. 8B). This structure is located in the posteromedial region of these bones, is elliptical and symmetrical, and the medial vomerine suture divides it through the midline. It is shallow (less than one millimetre in depth), but taking into account the postmortem dorsoventral compression of the cranium, the depression must have been deeper, although narrower, in life. The surface and margins of this inter-vomerine depression, except for small areas of subperiosteum damaged during preparation, are well preserved. It possesses regular borders and is roughly symmetrical, suggesting that it was a natural feature of the Antarctic procolophonid, not an artefact of taphonomy or preparation. No other *Procolophon* specimen from South Africa or southern Brazil shows this depression. AMNH 9506 is also peculiar because of the large number of foramina in the vomers. Although the number of these foramina is variable in *Procolophon*, no other specimen examined in this study possesses a number similar to AMNH 9506. It is possible, however, that the remarkable preservation of the palate in this specimen allows one to see more foramina than in other *Procolophon* specimens where this area has been prepared.

Although it is possible that this depression in the vomers may be of taxonomic significance, especially taking into account the provenance of AMNH 9506, far from both the Karoo and Paraná basins, it is considered unjustified to propose a new species based on this single small feature that could also be a result of mere individual variation. A similar depression was noted by Dias-da-Silva *et al*. (2006) in a large Brazilian specimen. As mentioned above, other particular features seen in this specimen are considered to fit within the known range of variation of *Procolophon trigoniceps* (Colbert and Kitching, 1975). If future work reveals that this feature is characteristic of *Procolophon* specimens from Antarctica, then it may be necessary to propose a new taxon to accommodate them.

4.4 Systematic palaeontology

Parareptilia Olson, 1947
Procolophonoidea Romer, 1956
Procolophonidae Lydekker, 1890
Procolophoninae Lydekker, 1890
Procolophon Owen, 1876

Type species. *Procolophon trigoniceps* Owen, 1876

Revised diagnosis. Robust procolophonid with adults possessing six to eight large bicuspid molariform teeth with mesiodistally-compressed, chisel-like crowns. In *Eumetabolodon* from China, and *Thelerpeton* and *Teratophon* from South Africa, adults may possess a similar number of molariform teeth, roughly comparable in morphology to those of *Procolophon*. In these taxa, however, molariform teeth are less compressed and more bulbous than in *Procolophon* (Fig. 9). In addition, the maxillary tooth row of *Procolophon* does not increase distally in labio-lingual length as in *Teratophon* and *Thelerpeton*. *Procolophon* can also be distinguished from all procolophonids except *Thelerpeton* by the presence of a single, prominent, posterolaterally directed quadratojugal spine, that does not exceed the orbitotemporal maximum width. Other procolophonids (e.g. *Eumetabolodon*, *Timanophon*) posses a single but much smaller, posterolaterally directed quadratojugal spine. Conversely, *Teratophon* possesses a single spine that greatly exceeds the maximum orbitotemporal width.

Comments. An additional putative diagnostic character for *Procolophon* is the loss of the fifth tarsal (Fig. 10), but the lack of postcranial information for most procolophonids precludes assessing whether this character represents a valid autapomorphy. DeBraga (2003) listed other distinctive, probably diagnostic features for the postcranium of *Procolophon.* Unfortunately this author based his

observations largely on SAM PK-7711, a specimen which is unlikely to belong to *Procolophon*. SAM PK-7711 is a huge postcranium collected on the farm Erf 1 Aliwal North, Free State Province, the type locality of the archosauromorph *Euparkeria.* These exposures belong to the Burgersdorp Formation, being referred to the middle part of the *Cynognathus* AZ (*Trirachodon* subzone, Hancox *et al*. in press). Hence, the age of the specimen is Middle Triassic, exceeding by a considerable margin the LAD of *Procolophon* based on diagnostic material (see below). Four procolophonids, formerly grouped within the genus "*Thelegnathus*", are known from this horizon, all established on cranial characters: *Thelephon contritus*, *Theledectes perforatus*, *Thelerpeton oppressus* and *Teratophon spinigenis* (Modesto and Damiani, 2003). The unusually large size of SAM PK-7711 suggests that is referable to *Teratophon spinigenis*, a robust procolophonid that commonly exceeds the size of other procolophonids known from South Africa.

Referred material. The *Procolophon* material comprises hundreds of specimens, being too numerous to be listed here. Major collections are held at the following South African institutions: AM, BPI, CGP, NM and SAM.

Localities. Sanga do Cabral Formation (Paraná Basin), Rio Grande do Sul State, Brazil; Katberg and lowermost Burgersdorp formations (Karoo Basin), Free Sate, Eastern Cape and KwaZulu Natal provinces, South Africa; and Lower Fremouw Formation (Transantarctic Basin), Shackleton Glacier, Transantarctic Mountains. (for a list of localities of specimens cited in the text, see Appendix).

Horizon. The temporal range of *Procolophon* is best documented for the Karoo Basin. The FAD of *Procolophon* is represented by a maxilla (RS 265) recorded at 116 m above the P/T boundary, in the Lower Katberg Formation (Botha and Smith, 2006), being located much higher than the FAD of the dicynodont *Lystrosaurus* (*c*. 41 m below the P/T boundary; Smith and Ward, 2001). The LAD of *Procolophon* is represented by a partial maxilla (CGP 1-9) and a partial left mandible (CGP 1-7) found in mudstones at the base of the Burgersdorp horizon 1,

a unit that represents the lower part of the Burgersdorp Formation in the proximal sector (Neveling, 2004). The genus surpasses the LAD of *Lystrosaurus* by a long way and co-existed at least briefly with the reptile *Palacrodon* and the amphibian *Trematosuchus* (Neveling, 1999, 2004; Damiani *et al.,* 2000), components of the *Cynognathus* Subzone A (Hancox *et al*. 1995). The temporal range of *Procolophon*, therefore, spans the upper part of the *Lystrosaurus* AZ (including the informal "*Procolophon* Abundance Zone" *sensu* Neveling, 2004) to the lowermost *Langbergia* Subzone (*c*. Late Induan-Olenekian, Early Triassic).

Procolophon trigoniceps Owen, 1876 (Figs. 2-8, 9C, 10)

v* 1876 *Procolophon trigoniceps* Owen p. 25, pl. 20, figs 4-7
1876 *Procolophon minor* Owen p. 26, pl. 20, figs 8-12
1878 *Procolophon griersoni* Seeley p. 797, pl. 22, figs 1-3
1878 *Procolophon cuneiceps* Seeley p. 799, pl. 22, figs 7, 8
v* 1878 *Procolophon laticeps* Seeley p. 801, pl 22, figs 4-6
v 1903 *Procolophon trigoniceps* Broom figs 4-6
1905 *Procolophon platyrhinus* Seeley p. 226, text-fig. 35
1905 *Procolophon sphenorhinus* Seeley p. 226, text-fig. 36
v* 1905 *Procolophon baini* Broom p. 332
1914 *Procolophon trigoniceps* Watson pls 1-3, text-figs 1-5
1936 *Procolophon trigoniceps* Broili and Schröeder figs 1-10, pls; pl. 3, figs 2-3; pl. 4-6
1974 *Procolophon trigoniceps* Kemp pl. 1, figs 1-4
1975 *Procolophon trigoniceps* Colbert and Kitching figs 1-24
vp 1977 *Procolophon trigoniceps* Gow text-figs 1-3, 5, 7 [*non* fig. 6 = new undescribed procolophonid]
p 1974 *Procolophon* van Heerden pls 1,2, 5-8, figs 1, 3-5 [*non* pls 3, 4, fig. 2 = temnospondyl]
v* 1979 *Procolophonoides baini* Ivakhnenko p. 13
v* 1983 *Procolophon pricei* Lavina p. 54, figs 1-9
1985 *Procolophon trigoniceps* Carroll and Lindsay figs 1, 3-14
v* 1987 *Procolophonoides baini* Ivakhnenko p. 52
v 1993 *Procolophon laticeps* Hamley and Thulborn figs 2-4
v* 2002 *Procolophon brasiliensis* Cisneros and Schultz figs 1, 2
vp 2003 *Procolophon trigoniceps* deBraga figs 1-3, 6-9, 18 [*non* figs 4, 5, 10-17 = cf. *Teratophon spinigenis*]

Holotype. BMNH R1726, a small-sized, almost complete cranium and mandible in occlusion. Collected by D. White at Donnybrook Farm, Eastern Cape Province, South Africa.

Diagnosis. See generic diagnosis above.

4.5 Biogeographical considerations

It is a valid question to ask whether a species of small terrestrial reptile could have such a wide geographic range in Gondwana, through the Paraná, Karoo and Transantarctic basins. Some modern lizards provide examples of wide distributions at species level for small reptiles that are comparable with, or even wider than, the geographic range that is proposed for *Procolophon trigoniceps* in this study. A number of Australian species, including the skinks *Tiliqua scincoides*, *T. rugosa*, *T. occipitalis*, *Menetia grey*, and the gecko *Heteronotia binoei*, have ranges that cover most of the continent, being excluded from the most arid regions of the Australian Desert (Cogger, 1979). The fact that these species are spread right across Australia suggests that they could have broader ranges if a larger area was available. An even larger distribution is shown by the agamid *Agama agama*; this species covers all Equatorial Africa (Enge *et al*., 2004). The lacertid *Zootoca vivipara* (formerly *Lacerta vivipara*) has probably the widest range of any modern lizard. It is found all across North Eurasia, from the British Isles east to the Japanese Archipelago (Surget-Groba *et al*., 2002). The range of this species, that is well known for having both viviparous and oviparous populations, includes high altitudes in the Alps, the Pyrénées and the Urals. The modern distribution of *Zootoca vivipara* is far wider than the distribution proposed for *Procolophon trigoniceps* in this study. It would not be unexpected though, that *Procolophon trigonicep*s may yet be found in a yet wider area than that currently known.

4.6 Conclusions

The holotypes of *P. pricei* and *P. brasiliensis* fit within the pattern of individual, and specially, ontogenetic variation of *P. trigoniceps*, and are here considered junior synonyms. The pattern of palatal dentition of *P. trigoniceps*, thus, is more complex than previously suspected, and juveniles may differ substantially from adults. The only complete Antarctic skull known differs from South African and

Brazilian specimens in having an elliptical depression in the vomers. The interpretation of this structure is ambiguous as it may also be regarded as due to individual variation, and this specimen is provisionally kept within *P. trigoniceps.* Further evidence from Antarctica would be necessary to confirm if this structure is present in other specimens, and if it should be regarded as taxonomically important.

The peculiar temporal openings of the South African species *P. laticeps* are here regarded as an authentic feature of these specimens, but their presence is interpreted as anomalous or pathological, and hence without taxonomic significance. The occurrence of temporal openings in *Procolophon* is intriguing, due to their presence in a number of other parareptile lineages (Cisneros *et al.*, 2004).

Only the type species *P. trigoniceps* is recognized in Gondwana, on the basis of available evidence. This species occupied a large geographical range, from the Paraná Basin to the Transantarctic Mountains.

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4.8 Appendix

Provenance of *Procolophon* specimens cited in the text

specimen	locality
AM 358	Fernrocks 192, Middelburg District, Eastern Cape Province, South Africa
AMNH 5693	Unknown locality, South Africa
AMNH 9506	Kitching Ridge, E of Shackleton Glacier, Transantarctic Mountains, 85°13'S/177°E
BMNH R1726	Donnybrook, Queenstown, Eastern Cape Province, South Africa
BMNH R3583	Donnybrook, Queenstown, Eastern Cape Province, South Africa
BMNH R1949	Unknown locality, Free State Province, South Africa
BMNH R4087	Haslope Hill, Tarkastad, Eastern Cape Province, South Africa
BP/1/966	Middelkraal, Tarkastad, Eastern Cape Province, South Africa
BP/1/4014	Hobbs Hill (Windvogelsberg), Cathcart, Eastern Cape Province, South Africa
BP/1/4248	Klipfontein 340 ("*Procolophon* Hill"), Bethulie, Free State Province, South Africa, 30º28'S/26º08'E
BP/1/5927b	Klipfontein 340 ("*Procolophon* Hill"), Bethulie, Free State Province, South Africa, 30º28'S/26º08'E
CGP 1-7	Odendaalstroom, Burgersdorp, Free State Province, South Africa
CGP 1-9	Odendaalstroom, Burgersdorp, Free State Province, South Africa
CGP 1-89	Elandskop 116, Tarkastad, Eastern Cape Province, South Africa
CGP 1-108	Palmietfontein 94, Tarkastad, Eastern Cape Province, South Africa
CGP 1-127	Hill and Dale 156, Tarkastad, Eastern Cape Province, South Africa
CGP 1-256	Hill and Dale 156, Tarkastad, Eastern Cape Province, South Africa
MCN PV1905	Rincão dos Weiss, Mata, Rio Grande do Sul State, Brazil, 29º33'27.35"S/53º26'56.43"W
NM QR1447	Klipfontein 340 ("*Procolophon* Hill"), Bethulie, Free State Province, South Africa, 30º28'S/26º08'E
RS 265	Farm Donald 207, Bethulie, Free State Province, South Africa, 30°24'52.3"S, 26°15'00.7"E
UFRGS PV231T	Dilermando de Aguiar, Santa Maria, Rio Grande do Sul State, Brazil, 29º49'37"S/54º13'55"W

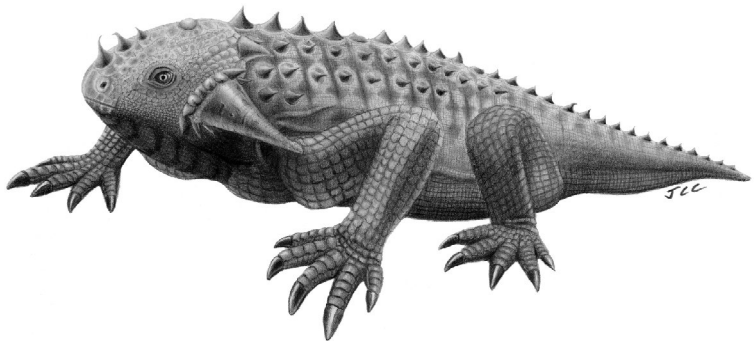


Figure 1. Life reconstruction of *Procolophon trigoniceps*. Note the presence of cheeks; quadratojugal processes covered by long keratinous spines; and large digging-claws. The skeleton of *Procolophon* entirely supports these features (Carroll and Lindsay, 1985; deBraga, 2003). Numerous minor keratinous spines are common over large or stocky-bodied modern lizards; these structures do not leave traces in the skeleton (e.g. *Iguana*, *Phrynosoma*, *Uromastix*; pers. obs.). The long quadratojugal and supratemporal spines of *Procolophon* may have acted as an anti-predatory mechanism, as in phrynosomatid lizards (Young *et al.*, 2004).

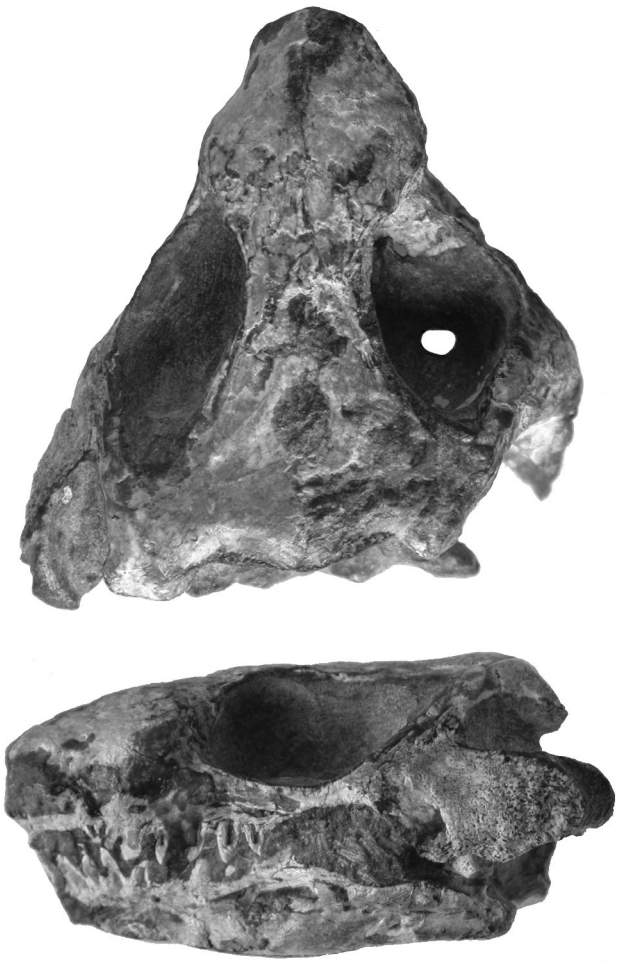


Figure 2. BMNH R1726 holotype of *Procolophon trigoniceps*, cranium in dorsal and left views.

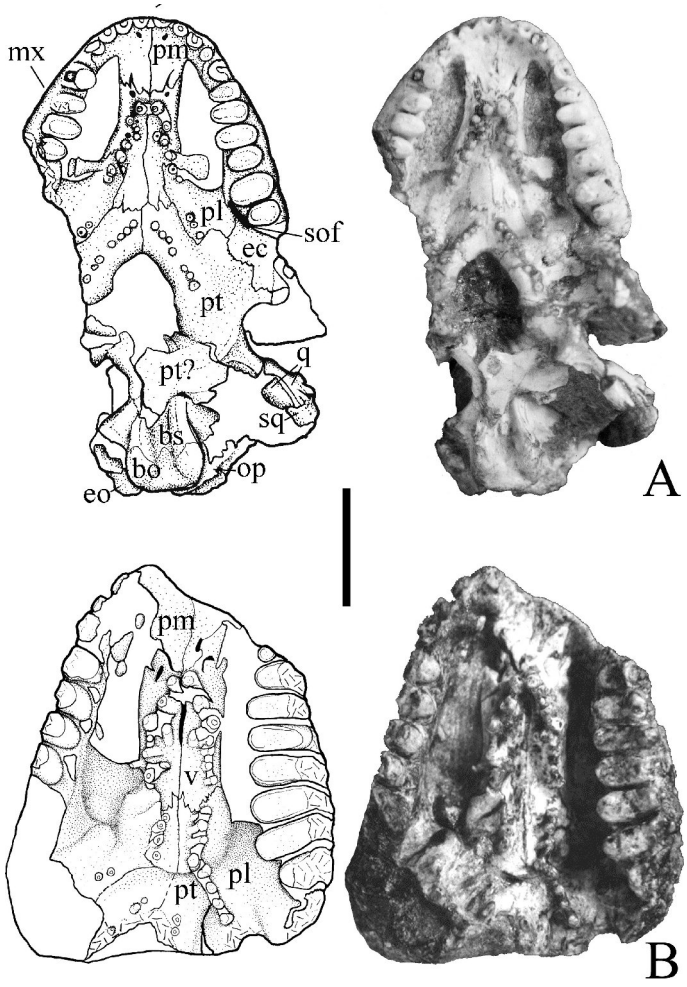


Figure 3. A, UFRGS PV231T holotype of *Procolophon pricei*, cranium in palatal view. B, MCN PV1904 holotype of *Procolophon brasiliensis*, cranium in palatal view. Scale bar represents 10 mm.

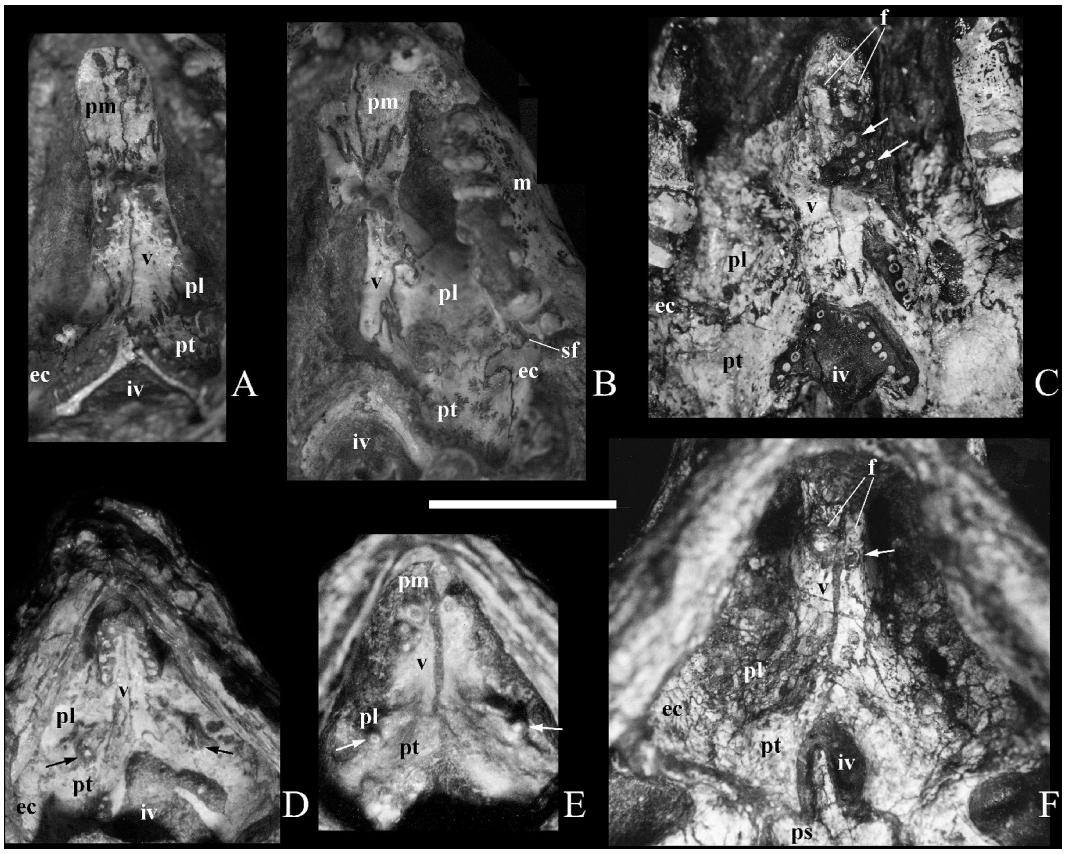


Figure 4. Palate of *Procolophon trigoniceps* specimens from the South African Karoo. A, CGP 1-89; B, BP/1/4014; C, BP/1/4248; D, NM QR1447; E, AMNH 5693; F, BP/1/966. Arrows in C and F indicate posterior enlarged vomerine teeth. Arrows in D and E indicate the last tooth in the pterygoid-palatine tooth row. The mandible is in occlusion in BP/1/4248, NM QR1447 and AMNH 5963. Scale bar is 10 mm for A-E and 17 mm for F.

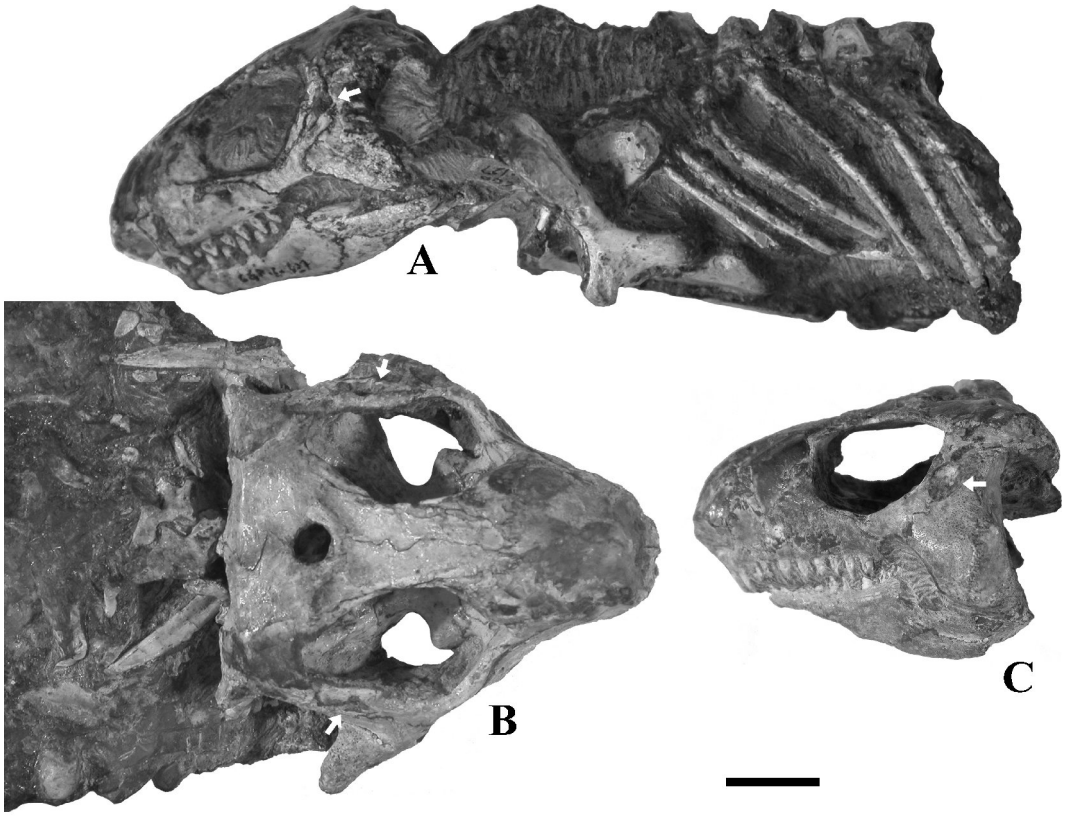


Figure 5. *Procolophon* specimens with temporal fenestrae. A, CGP 1-127; B, BMNH R1949; C, BMNH R 3583 holotype of *P. laticeps*. Scale bar represents 10 mm, arrows indicate temporal fenestrae.

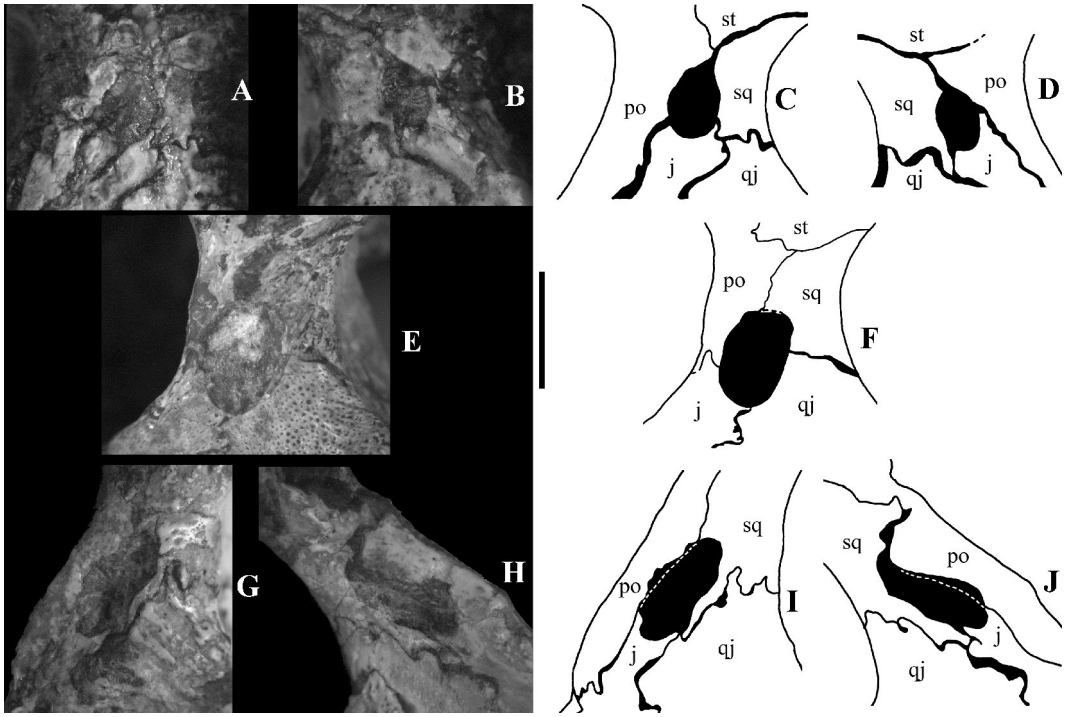


Figure 6. Temporal fenestrae in *Procolophon*. A, B, E, G, H, photographs; C, D, F, I, J, outline drawings. A-D, CGP 1-127. E, F, BMNH R3583 holotype of *P. laticeps*. G-J, BMNH R1949. A, C, E, F, G, I, left lateral views. B, D, H, J, right lateral views.

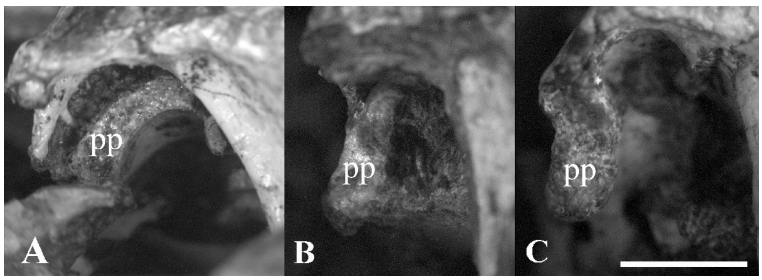


Figure 7. Paroccipital process of the right opisthotic in *Procolophon*, in lateral view. A. BMNH R1949. B, CGP 1-127. C, BMNH R4087. A and B are individuals with temporal openings. Scale bar represents 5 mm.

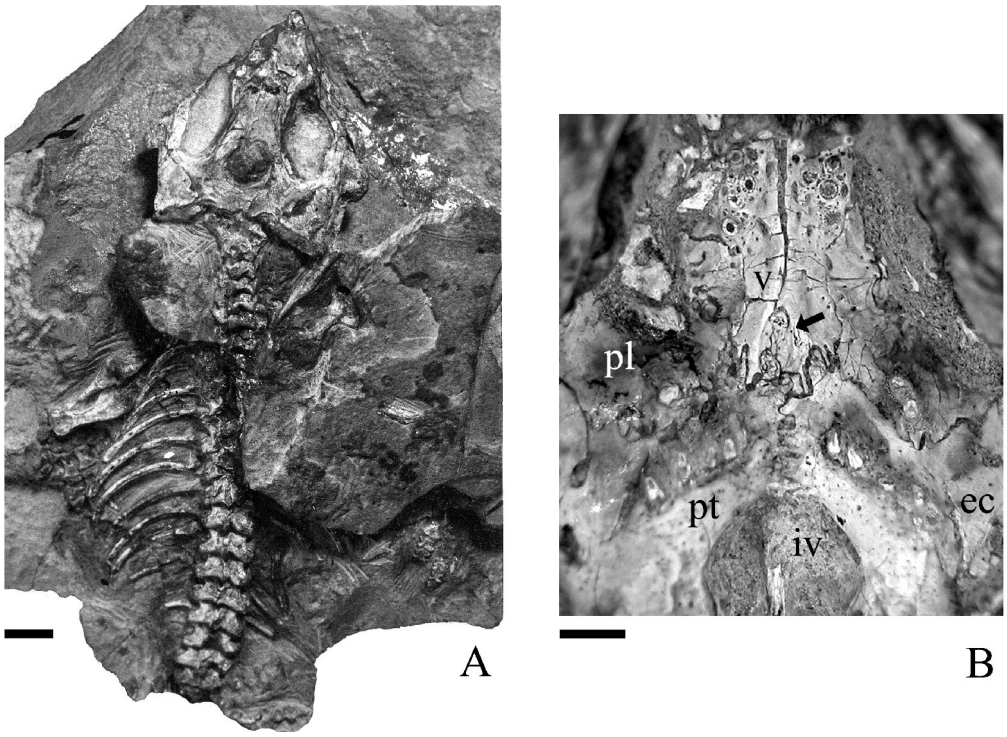


Figure 8. AMNH 9506, *Procolophon trigoniceps* from Shackleton Glacier, Transantarctic Mountains. A, skeleton in dorsal view. B, detail of palate in ventral view, arrow points to the depression between the vomers. Scale bars represent 5 mm (A) and 2 mm (B).

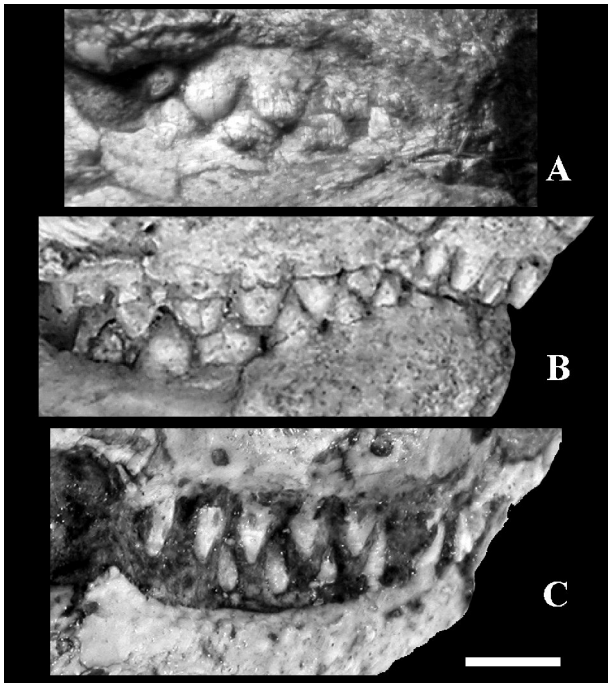


Figure 9. Comparison between A, *Teratophon spinigenis* (BP/1/4587), B, *Eumetabolodon bathycephalus* (IVPP V6064) and C, *Procolophon trigoniceps* (BP/1/5927b); showing differences in dentition. Scale bar represent 5 mm for A, B and 3.5 mm for C.



Figure 10. *Procolophon trigoniceps*, silicone impression of AM 358, a left hind limb in flexor aspect. The arrow in black shows the position where the fifth metatarsal should be located. The excellent preservation of this limb indicates that the absence of the fifth metatarsal in *Procolophon* is a natural feature rather than a post-mortem phenomenon as suggested by deBraga (2003). Although this specimen is smaller than other *Procolophon* individuals, all bones are well ossified. Scale bar is 5 mm.

5 PAPER : PHYLOGENETIC RELATIONSHIPS OF PROCOLOPHONID PARAREPTILES

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Abstract. The phylogenetic intrarelationships of procolophonid reptiles are determined via a comprehensive cladistic analysis using a data matrix of 22 taxa and 66 characters. Several taxa are included for the first time in a phylogenetic analysis and most of the characters are novel. The relationships within the group are more firmly resolved. Procolophoninae and Leptopleuroninae, two of the three traditional subdivisions of the Procolophonidae, are valid monophyletic groups, but Spondylolestinae is paraphyletic. A new group, Theledectinae, is erected. The latter clade consists of small procolophonids with a reduced marginal dentition and wide bulbous monocuspid teeth. A new basal genus from the Lower Triassic of South Africa is recognized, based on a specimen previously assigned to *Procolophon*. The Chinese genus *Eumetabolodon* and the former genus "*Thelegnathus*" from South Africa are shown to be paraphyletic. Bicuspid dentition, a distinctive character that is present in most procolophonids, evolved at least twice within the group. The successful radiation of the Procolophonidae during the Triassic is likely to be related to the development of feeding adaptations that allowed exploration of various ecological niches, particularly the exploitation of high-fiber herbivory. The scarcity of Permian records of procolophonids is examined, and the genus *Spondylolestes* from the Upper Permian of South Africa is considered a valid taxon with procolophonid affinities. Finally, a review of the procolophonid record from the Middle and Late Triassic reveals a global hiatus of procolophonids in Ladinian-Early Carnian rocks.

Key words. Parareptilia, Procolophonoidea, Procolophonidae, Triassic, phylogeny

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5.1 Introduction

The interrelationships of the Parareptilia have been the subject of deep scrutiny over the last two decades, producing a now accepted consensus of the monophyly of this group and an explicit phylogenetic definition (Gauthier *et al*., 1988; Laurin and Reisz, 1995; Lee, 1995; deBraga and Rieppel, 1997; Modesto, 2000; Berman *et al*., 2000). However, whereas the phylogeny of the Pareiasauridae, a major parareptile branch, acquired resolution through the work of Lee (1997a), the intrarelationships of the more diverse Procolophonidae remain poorly known.

Procolophonids represent the most successful radiation of the Parareptilia. Surviving the Mother of Mass Extinctions at the Permian-Triassic boundary, the group dispersed across Pangaea during the Early Triassic, and diversified until the Triassic-Jurassic boundary when it became extinct. More than 30 valid genera are known, from all continents. Most findings come from the South African Karoo, the Russian Cis-Urals, and the Newark Supergroup in Canada and USA. Typical procolophonid features include: small size (adults ranging from ~150-400 mm), extremely elongated orbits (orbitotemporal fenestrae), lateral cranial spikes, bulbous and/or bicuspid molariform teeth, short tale, and a wide, relatively robust body. Some of these features are present in other parareptiles, such as the bulbous teeth of the Bolosauridae, or the cranial spikes of the Pareiasauridae, but they were acquired independently by procolophonids.

A side effect of the proposed procolophonid affinity of turtles (Reisz and Laurin, 1991; Laurin and Reisz, 1995) has been a renewed interest in procolophonids and their close allies, the owenettids. In recent years, a number of papers describing new material and taxa have been published (Spencer, 2000; Spencer and Benton, 2000; Gow, 2000; Sues *et al*., 2000; Bulanov, 2002; Spencer and Storrs, 2002; Modesto *et al*., 2002; Cisneros and Schultz, 2003; Modesto and Damiani, 2003; Cisneros *et al*., 2004; Piñeiro *et al*., 2004; Fraser *et al*., 2004; Novikov and Sues, 2004). The first phylogenetic analyses of procolophonids were also published recently (Modesto *et al*., 2001, 2002; deBraga, 2003). These were preliminary

studies that included few, relatively well known taxa and small character state matrices. In this study, a larger analysis of procolophonid relationships is presented. Most of the characters employed here are new, and the majority of taxa considered in this study have not been included in previous phylogenetic analyses.

Institutional abbreviations

AM, Albany Museum, Gahamstown, South Africa; **BMNH**, Natural History Museum, London, UK; **BP**, Bernard Price Institute for Palaeontological Research, Johannesburg, South Africa; **CGP**, Council for Geoscience, Pretoria, South Africa; **IVPP**, Institute of Vertebrate Palaeontology and Palaeoanthropology, Beijing, China; **MCN**, Museu de Ciências Naturais, Porto Alegre, Brazil; **NM**, National Museum, Bloemfontein, South Africa; **PIN**, Palaeontological Institute, Moscow, Russia; **QMF**, Queensland Museum, Queensland, Australia; **RC**, Rubidge Collection, Graff-Reinet, Eastern Cape, South Africa; **SAM**, Izico: South African Museum, Cape Town, South Africa; **YPM**, Yale Peabody Museum, New Haven, USA.

5.2 Taxonomic background and previous analyses

Earlier classifications of procolophonid-like taxa usually distinguish between a group of mainly Triassic taxa, and one or more groups for the more primitive Permian taxa, whether including all groups as divisions of the family Procolophonidae (e.g. Colbert, 1946; Romer, 1956), or giving the Permian groups a family status (e.g. Kuhn, 1969). Ivakhnenko (1979) was the first author to recognize divisions within the Triassic procolophonids. This author subdivided the Procolophonidae into three subfamilies: Spondylolestinae, Procolophoninae and Leptopleuroninae. Within the Spondylolestinae, Ivakhnenko (1979) included the poorly known *Spondylolestes* plus a number of genera considered more primitive by him. Within the Procolophoninae, he included more typical procolophonids such as *Procolophon* and *Tichvinskia*. In the Leptopleuroninae, Ivakhnenko included the most derived taxa, such as *Leptopleuron* and *Hypsognathus*. Ivakhnenko (1979, 1987) did not consider the Permian forms

Owenetta, *Barasaurus* and *Nyctiphruretus* to be procolophonids, and placed them in the family Nyctiphruretidae. The Permian *Nycteroleter* and the problematic *Sclerosaurus* from the Buntsandstein were placed in their own families, Nycteroleteridae and Sclerosauridae, respectively.

Laurin and Reisz (1995), in their cladistic analysis of amniotes, did not include the genera *Owenetta*, *Barasaurus*, *Nyctiphruretus* or *Nycteroleter* in their definition of the Procolophonidae. The genus *Owenetta* was previously considered to be a procolophonid by these authors (Reisz and Laurin, 1991). Lee (1995, 1997a) included those four genera, and the Procolophonidae, as operational taxonomic units (OTUs) in his phylogenetic analyses. This author found an *Owenetta-Barasaurus* clade, and a *Nyctiphruretus-Nycteroleter* clade, the former being more closely related to the Procolophonidae than the latter. He applied the names Owenettidae to the *Owenetta-Barasaurus* node, Nyctiphruretidae to the *Nyctiphruretus-Nycteroleter* node, and Procolophonoidea for the Owenettidae-Procolophonidae dichotomy. The name Owenettidae had long been ignored by other authors since it was proposed by Broom (1939) for the genus *Owenetta*. In the reptile analysis by deBraga and Rieppel (1997), an Owenettidae-Procolophonidae clade was also found. These authors did not use owenettid genera as OTUs, nor did they consider *Nyctiphruretus* or *Nycteroleter*. Except for Reisz and Laurin (1991), who used information from *Owenetta* to code the Procolophonidae in their analysis, all other authors (Laurin and Reisz, 1995; Lee, 1995, 1997a; deBraga and Rieppel, 1997) coded the Procolophonidae mainly using information from the genus *Procolophon*, often considered to be a primitive member of the group.

The first phylogenetic analysis that included both owenettid and procolophonid genera as OTUs supported a monophyletic Owenettidae and Procolophonidae (Modesto *et al*., 2001). The analysis included four procolophonids, the recently described "stem-procolophonids" *Coletta* and *Sauropareion*, and the owenettids *Barasaurus*, *Owenetta rubidgei* and *Owenetta kitchingorum*, in a matrix of 25 characters. A second analysis by Modesto *et al*. (2002) focused on the

Procolophonidae, and included seven procolophonid genera and the "stem-procolophonid" *Coletta*. Their study confirmed two of the previous divisions proposed by Ivakhnenko (1979), namely the Procolophoninae and the Leptopleuroninae, but did not produce a clade that could be identified with the Spondylolestinae. A procolophonid phylogeny presented by deBraga (2003), employing some characters from Spencer (1994), included seven procolophonid genera, and seven outgroups (including *Barasaurus* and *Owenetta*). This analysis corroborated in most part the results from Modesto *et al*. (2001, 2002), producing a monophyletic Procolophonidae and Owenettidae, and a major dichotomy within Procolophonidae: Procolophoninae and Leptopleuroninae. However, the composition of Procolophoninae and Leptopleuroninae reported by deBraga (2003) differs notably from that of Modesto *et al*. (2002), partially explained due to the fact that these authors evaluated different genera. An interesting result of the analysis by deBraga (2003) was the placement of *Sclerosaurus* within the Procolophonidae. The status of this taxon as a procolophonid has been questioned by some authors (Rieth, 1932; Ivakhnenko, 1979, 1987; Lee, 1995, 1997a). A large number of the 60 characters used by deBraga (2003) were informative only of the relationships among the outgroups.

5.2.1 Nomenclatural remarks

The current definition of Procolophonidae is problematic. Laurin and Reisz (1995) defined Procolophonidae as "the last common ancestor of *Anomoiodon*, *Burtensia*, *Candelaria*, *Contritosaurus*, *Eumetabolodon*, *Hypsognathus*, *Kapes*, *Koiloskiosaurus*, *Leptopleuron*, *Macrophon*, *Microphon*, *Microtheledon*, *Myocephalus*, *Myognathus*, *Neoprocolophon*, *Orenburgia*, *Paoteodon*, *Procolophon* and *Thelegnathus*." This node-based definition is inapplicable because *Paoteodon* and *Thelegnathus* are *nomina dubia* (Li, 1989; Modesto and Damiani, 2003), whereas *Candelaria* and *Microphon* have been identified as, respectively, an owenettid and a seymouriamorph (Bulanov, 2002; Cisneros *et al*., 2004). Phylogenetic definitions that are less sensitive to changing tree topologies

are preferable, and stem-based definitions have been shown to be less vulnerable to floating taxa (see Modesto and Anderson, 2004).

Procolophonidae is here defined as all taxa more closely related to *Procolophon trigoniceps* Owen 1876 than to *Owenetta rubidgei* Broom 1939. Conversely, Owenettidae is defined as all taxa more closely related to *Owenetta rubidgei* Broom 1939 than to *Procolophon trigoniceps* Owen 1876. The more inclusive Procolophonoidea is defined as all taxa more closely related to *Procolophon trigoniceps* Owen 1876 than to *Pareiasaurus serridens* Owen 1876. These stem-based definitions have the additional benefit of avoiding the usage of unsuitable terms such as "stem-procolophonids" or "non-procolophonoid procolophonians" for taxa that fall outside the nodes employed in node-based definitions.

5.3 Analysis and methods

Relationships were evaluated using TNT (Tree Analysis Using New Technology) Version 1.0 for Windows (Goloboff *et al*., 2003a, February 2006 update). The search was performed using the Implicit Enumeration algorithm, which provides exact solutions (equivalent to the "branch-and-bound" option in other packages). Collapsing Rule 1 was employed during the search, which collapses branches if supported ambiguously, producing only conservative phylogenetic hypotheses with unequivocal support at all nodes (Coddington and Scharff, 1994). Collapsing ambiguously supported branches, together with the use of reductive coding (inapplicable characters: "?"), also diminish the problems arising from inapplicable character states (Strong and Lipscomb, 1999). Two measures of support were used to evaluate the tree: decay index (DI) and symmetric resampling (SR). DI ("Bremer support") reports absolute step differences between trees (Bremer, 1994). SR is not influenced by characters that are uninformative or irrelevant to the monophyly of a group, nor by additive characters. Such characters may affect bootstrapping or jackknifing analyses (Goloboff *et al*., 2003b).

5.3.1 Ingroup and outgroup

Twenty two procolophonids have been included in the ingroup. Many procolophonids are known from materials that are too incomplete, are not known from detailed descriptions and/or could not be examined first hand for this study, and could not be included in this analysis. The ingroup comprises well- or long-known taxa such as *Hypsognathus*, *Leptopleuron*, *Sclerosaurus*, *Neoprocolophon*, *Eumetabolodon*, *Pentaedrusaurus*, *Phaanthosaurus*, *Tichvinskia*, *Kapes* and *Procolophon*; and the more recently described *Scoloparia*, *Coletta*, *Sauropareion* and *Soturnia*. Priority has been given to anatomical information obtained by personal examination of specimens, including several holotypes (for sources of information and provenance of the taxa see Table 1).

The former genus "*Thelegnathus*" was present as a single OTU in the analyses by Modesto *et al*. (2002) and deBraga (2003). However, the type species "*Thelegnathus browni*" is a *nomen dubium*, and the remaining four species of the genus were assigned to new genera (Modesto and Damiani, 2003). These new genera, *Theledectes*, *Thelephon*, *Thelerpeton* and *Teratophon*, are included as OTUs in this analysis. The two species of the genus *Eumetabolodon*, *E. bathycephalus* and *E. dongshengensis*, have also been included separately herein, in order to test the monophyly of the genus. The possibility that *E. bathycephalus* and *E. dongshengensis* could represent different genera had already been expressed (Li, 1983). The genus *Kapes* has been coded largely based on the recent description by Novikov and Sues (2004) of a cranium referred to *K.* cf. *K. majmesculae*. The remaining species *K. amaenus*, *K. serotoninus* and *K. bentoni*, are based on specimens that are too incomplete to be included separately in the analysis. *Kapes* has been the subject of recent reviews which agree on the validity of these species (Spencer and Benton, 2000, Spencer and Storrs, 2002; Novikov and Sues, 2004). According to Novikov (1991), *Timanophon raridentatus* includes a cranium referred to *Burtensia burtensis* by Ivakhnenko (1979). Following Spencer and Benton (2000), only the species *Tichvinskia vjatkensis* is considered valid within the genus; and the genus name *Phaanthosaurus* is here

used instead of *Contritosaurus*, which is considered a junior synonym of the former by these authors. Only one species within the genus *Procolophon* has been considered in this study, following recent work (Cisneros *in press*) which recognizes only the species *P. trigoniceps*.

The analysis includes two unnamed procolophonids. Specimen BP/1/1187 was tentatively considered to be an unusual juvenile *Procolophon trigoniceps* by Gow (1977b: text-fig. 6). However, this author later expressed the view that BP/1/1187 could represent a new taxon (Gow, 2000). This conclusion is endorsed here following personal examination of the specimen, and BP/1/1187 is an OTU in this study. The procolophonid from the Lower Triassic Arcadia Formation of Australia (hereafter "Arcadia procolophonid") is also considered in this analysis. This taxon is represented by several well preserved specimens at the Queensland Museum, and is currently under study by R. Damiani and the author.

Owenettidae has been included in the analysis to test the monophyly of Procolophonidae. Although TNT does not allow assignment of more than one outgroup, Owenettidae is functionally a secondary outgroup. Characters for the Owenettidae have been coded based in major part from *Barasaurus besairiei* and *Owenetta rubidgei*, both of which occupy a basal position within the Owenettidae (Cisneros *et al*., 2004). It is worth mentioning that most previous analyses (Reisz and Laurin, 1991; Lee, 1995, 1997a; deBraga and Rieppel, 1997; deBraga, 2003) have coded *Owenetta* based on information from *Owenetta kitchingorum*. This species is more derived than the type species *O. rubidgei*, and the genus *Owenetta* is now considered to be paraphyletic (Modesto *et al*., 2003, Cisneros *et al*., 2004). The root of the tree is *Nyctiphruretus acudens*.

5.4 Character description

The majority of the 65 characters employed in this analysis are new. These include several dental and postcranial features. Characters taken or modified from other authors are indicated below. Some of these were recoded based on personal

observations or new information. Three postcranial characters in this study are at present uninformative because they could not be coded for several taxa currently known only from cranial remains. These characters have the potential of becoming informative in the future when they can be coded on the basis of more complete material and it is preferable that they remain available in the literature. In TNT character numeration begins with zero. Tooth nomenclature and orientation follows Smith and Dodson (2003).

5 Cranium surface (figure 1)

0. Premaxillary nasal process: 0, extends dorsally; 1, extends anterodorsally.
Primitively, the premaxillary nasal process is long in dorsal view; a derived state is recorded in some leptopleuronines in which this process is essentially restricted to the tip of the snout. From Modesto *et al.* (2001).

1. Maxilla premaxillary subnarial process: (0) present, (1) absent, (2) premaxilla posterodorsally expanded.
Primitively, the maxilla extends anteriorly below the margin of the external naris, in lateral view. This process is lost/not present in some procolophonids, where only the premaxilla forms the ventral margin of the external naris. A progression of this state is recorded in some procolophonids in which the premaxilla extends posterodorsally and contributes to the posterior border of the external naris. The character has been coded as ordered. The character is difficult to verify in *Hypsognathus* because the premaxilla and septomaxilla are apparently fused. Modified from Modesto *et al.* (2001).

2. Premaxillary ascending process: (0) dorsally projected, (1) anteriorly projected.
In *Nyctiphruretus* and owenettids, the ascending process of the premaxilla rises roughly vertically from the tooth margin, in lateral view, and the tip of the snout is adjacent to the level of the anteriormost premaxillary tooth. In the derived state, seen in most procolophonids, the ascending process of the premaxilla is projected

more anteriorly, and the tip of the snout considerably surpasses the level of the anteriormost premaxillary tooth. The derived condition also results in an external naris placed more anteriorly. *Tichvinskia* exhibits a somewhat intermediate condition and the character was coded as unknown for this taxon.

3. External naris: (0) anteroposteriorly elongated, (1) subcircular or dorsoventrally expanded.

The external naris of *Nyctiphruretus*, owenettids (*contra* Lee, 1995) and some procolophonids, is anteroposteriorly elongated. In the derived condition the external naris is smaller and more rounded, in some taxa being somewhat longer dorsoventrally (e.g. *Pentaedrusaurus*). Modified from Lee (1995).

4. Wide internarial bar: (0) absent, (1) present.

Primitively, the internarial bar of procolophonoids is thin and much of the external naris is visible in dorsal view. In the derived condition, seen in some procolophonids, the internarial bar is wider, so that the external naris is no longer exposed in dorsal view. This character is modified from Laurin and Reisz (1995). The authors incorrectly stated that the derived condition was a synapomorphy for Procolophonidae, because they based most observations for this clade on *Procolophon*.

5. Snout: (0) long and flat, (1) deep and short.

The anterior portion of the cranium is primitively long and flattened in lateral view. Derived forms usually exhibit a shorter and deeper snout, with a reversal to the long and flat condition in some leptopleuronines. See Figure 2 for an explanation of the criterion used to code this character.

6. Maxillary depression: (0) absent, (1) present.

The maxilla is flat in *Nyctiphruretus* and owenettids. A marked maxillary depression, posterior to the external naris, sometimes also comprising part of the nasal, is a derived condition in several procolophonids. A reversal occurs in some

leptopleuronines where this depression is weak or absent. From Modesto *et al*. (2001).

7. Prefrontal: (0) medial border straight, (1) medial border emarginated, (2) confined to the orbital rim.

Primitively the medial margin of the prefrontal is straight in dorsal view. Two derived conditions are recorded in procolophonids: (1) a medial expansion of this bone, but without contact between both prefrontals (a medial expansion with contact occurs in *Owenetta kitchingorum*); and (2) the complete reduction of its surface in dorsal view. Modified from Sues *et al.* (2000).

8. 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.

In *Nyctiphruretus*, owenettids, *Coletta* and *Phaanthosaurus*, the posterior rim of the orbitotemporal fenestrae does not reach the level of the pineal foramen. Progressive derived states (1, 2) of expansion of this structure are here coded based on the relation between the level of its posterior margin and the pineal foramen. State (3) is coded when the posterior border of the temporal fenestrae surpasses the posterior border of the pineal foramen in a distance equivalent to at least twice the length of the pineal foramen. The character is coded as ordered. The evolutionary significance of the posterior expansion of the orbitotemporal fenestrae was discussed by Colbert (1946: fig. 4) and Cisneros *et al*. (2004).

9. Posterior angle of opening of the orbitotemporal fenestra, in lateral view: (0) higher than 25°, (1) lower than 25°.

This character refers to the angle at the posterior intersection of lines that project from the ventral and dorsal margins of the orbitotemporal fenestra, measured in lateral view. In the primitive condition, the orbitotemporal fenestra is dorsoventrally high and this angle is wide. In the derived condition, present in

leptopleuronines, the orbitotemporal fenestra is dorsoventrally thinner and the angle of opening is less than 25° (see Fig 2).

10. Pineal foramen insertion: (0) in a shallow fossa, (1) flush with dorsal surface.

Primitively the pineal foramen is placed within a shallow fossa formed by the parietals. In the derived condition the parietals are flatter and the foramen is placed at the same level of the dorsal skull roof. From Modesto *et al*. (2002).

11. Contour of the pineal foramen: (0) rounded, (1) "teardrop shaped", (2) straight posterior border.

Primitively, the pineal opening is circular. Two derived states emerge in procolophonids: (1) an acute anterior margin which gives a "teardrop" shape to the opening is recorded in *Kapes* and *Thelephon*; and (2) a foramen with a straight posterior border in *Pentaedrusaurus*. In *Neoprocolophon* the pineal foramen appears to have a straight posterior border, but the margin is not well preserved and the character has been coded as an uncertainty among states zero and two.

12. Postfrontal: (0) contacts frontal, parietal and postorbital, (1) contacts frontal, parietal, postorbital and supratemporal, (2) contacts frontal and parietal only, (3) fused to parietal.

In *Nyctiphruretus* the postfrontal contacts the frontal, parietal and postorbital; in owenettids the postfrontal also contacts the supratemporal. The postfrontal becomes reduced in procolophonids: in some forms this bone only contacts the frontal and parietal (2); whereas it fuses to the parietal in a number of species (3). The condition in *Phaanthosaurus* is uncertain for states (1) and (2). Modified from Lee (1995) and Modesto *et al*. (2002).

13. Jugal lateral processes: (0) absent, (1) one, (2) two.

Primitively, the jugal of procolophonoids is a smooth bone that lacks spiny processes or bosses. A single, broad lateral projection in the jugal is a derived

feature of *Leptopleuron*; whereas *Sclerosaurus*, *Scoloparia* and *Hypsognathus* possess paired jugal spines.

14. Temporal ventral margin: (0) roughly straight, (1) acutely emarginated, (2) broadly excavated, (3) convex.

The ventral margin of *Nyctiphruretus* is smooth. An acute emargination between the jugal and quadratojugal is present in owenettids, *Coletta* and *Sauropareion*. This emargination becomes wider and more rounded in most procolophonids (e.g. *Procolophon*). The third derived state occurs in some leptopleuronines, in which a prominent anteroventral flange of the jugal constricts the ventral emargination, which becomes a small notch anteriorly located. Modified from Lee (1995) and Sues *et al*. (2000).

15. Quadratojugal lateral surface: (0) spineless, (1) one spine, (2) two or more spines.

Primitively the quadratojugal does not bear spines. A number of procolophonids present one quadratojugal spine, whereas some leptopleuronines possess two or more. The position and morphology of the spines in leptopleuronines are variable, and it is not clear if these spines are homologous to those present in other procolophonids. For this reason the character has not been coded as ordered. Modified from Modesto *et al*. (2002).

16. Squamosal ventral margin terminates: (0) at least as far ventrally as quadratojugal, (1) dorsal to quadratojugal.

The primitive condition of this character is present in *Nyctiphruretus* and most procolophonoids. The derived state in which the squamosal is shortened is recorded in owenettids and *Coletta*. From Modesto *et al*. (2001).

17. Posterior margin of the skull roof: (0) concave, (1) acute posterior process, (2) broad posterior emargination.

In the outgroup, the posterior edge of the skull roof is concave. In the Owenettidae and in *Sauropareion*, this border bears an acute projection formed by the

postparietals. In some procolophonids this acute projection is also present, but the postparietals are fused to the parietals (see character 19). Both conditions are here coded as state (1). In *Procolophon*, *Teratophon* and *Thelerpeton*, this projection is broader but its tip remains acute. State (2) is recorded in some leptopleuronines, in which the posterior border of the skull roof forms a broad, rounded emargination. This character is here seen as a progression from a concave posterior margin to a broad convex edge and it has been coded as ordered. A related character was proposed by Lee (1995).

18. Postparietal-parietal relation: (0) unfused, (1) fused.

Small postparietals are recorded in *Nyctiphruretus*, *Barasaurus* and *Sauropareion*. In *Nyctiphruretus* they are integrated into the posterior, concave margin of the skull roof, whereas in *Barasaurus* and *Sauropareion* they form a small median projection. The primitive condition for owenettids is uncertain, because postparietals are absent in *Owenetta rubidgei*. An acute median process at the posterior edge of the cranium is also present in a number of procolophonids, in the same place where the postparietals should be located, although no sutural contact is evident. This structure is presumably homologous to the projection formed by the postparietals in some owenettids and *Sauropareion*, indicating that the postparietals became fused to the parietals (see character 18).

19. Supratemporal posterolateral margin: (0) rounded, (1) acute, (2) prominent spine.

Primitively, the supratemporal has a broad, rounded posterolateral border. In the first derived state, this border is acute, but does not form a spine. In a number of procolophonids, a well developed ventrolateral spine is present. This character is coded as ordered.

5.4.2 Palate and braincase

20. Vomer width: (0) broader than choana, (1) roughly equal or narrower.

In *Nyctiphruretus*, owenettids, *Coletta* and *Sauropareion*, the vomer is a broad structure, being much wider than the internal naris. The vomers diminish in width in most procolophonids.

21. Epipterigoyd columella: (0) ends freely, (1) contact dorsally prootic and supraoccipital.

In *Tichvinskia*, *Procolophon* and the Arcadia procolophonid, the end of the epipterigoyd columella is not ossified and this bone does not contact the prootic and supraoccipital. This state is here tentatively considered as primitive, although the condition is not known in *Nyctiphruretus*. The derived condition is present in *Leptopleuron* and *Hypsognathus*. From Sues *et al.* (2000).

22. Quadrate: (0) roughly in line with the maxillary dentition, (1) well below the maxillary dentition.

Primitively the ventral surface of the quadrate is approximately in line with the alveolar level of the maxillary dentition. In leptopleuronines, the quadrate is notably positioned at a lower level.

23. Parasphenoid cultriform process: (0) directed anteriorly and tapers to sharp tip, (1) projects vertically as robust pillar.

In *Nyctiphruretus* and most procolophonoids the cultriform process of the parasphenoid is long, slender and horizontal. In the derived condition this process is robust and projected dorsally. From Sues *et al*. (2000).

24. Relation of basioccipital tuber and quadrate condyle: (0) approximately in line, (1) basioccipital projected far posteriorly.

In ventral view, the basioccipital tubera are placed close to or at the same level as the quadrate condyles in *Nyctiphruretus*, owenettids, *Tichvinskia* and the Arcadia procolophonid. In the derived state, recorded in several procolophonids, the basioccipital tubera are located far more posteriorly.

25. Occipital condyle: (0) uniform, (1) tripartite.

Primitively, the basioccipital is fused to the exoccipitals and the condyle appears unitary. In the derived condition, recorded in *Leptopleuron* and *Hypsognathus*, the sutures between these elements are present and the condyle becomes tripartite. From Sues *et al*. (2000).

5.4.3 Mandible (Figure 1)

26. Dentary ventral and dorsal surfaces: (0) nearly parallel, (1) oblique.
In most procolophonoids the ventral and dorsal surfaces of the mandible are approximately parallel. In leptopleuronines the dentary becomes notably deep posteriorly, and the angle of intersection of the lines projected from its ventral and alveolar levels is equal to or higher than 15 degrees.

27. Relation of articular bone to marginal dentary teeth: (0) roughly in line, (1) well below.
Primitively, the dorsal surface of the articular is approximately at the level of the alveolar margin of the dentary. In leptopleuronines, the articular is positioned well below this level. From Sues *et al*. (2000).

6.4.4 Dentition (Figure 2)

28. Premaxillary teeth number: (0) five or more, (1) four, (2) three, (3) two.
Nyctiphruretus and the owenettids possess five or more premaxillary teeth. The three derived states summarize the procolophonid trend to reduce the premaxillary dentition. This character has been coded as ordered. From Modesto *et al.* (2002).

29. Premaxillary teeth: (0) sub-equal in size, (1) enlarged mesialmost teeth.
In the primitive condition, all premaxillary teeth are conical or incisiform, and subequal in size. In the derived state, a large mesialmost incisor is present.

30. Maxillary anterior conical teeth: (0) present, (1) absent.

All maxillary teeth are conical in *Nyctiphruretus* and early procolophonoids. In some derived forms that develop expanded molariform teeth, one or more remnant conical teeth are still present in the anterior region of the maxilla. The derived state of this character is recorded in *Scoloparia* and *Leptopleuron*, where the anterior maxillary conical teeth are absent.

31. Maxillary teeth with labiolingually expanded bases: (0) absent, (1) present.

Primitively, the teeth have thin, rounded bases. In the derived condition the labiolingual length in basal cross section is longer than the mesodistal length. Modesto *et al*. (2003) coded the primitive state for *Coletta*, but the maxillary teeth in this form are labiolingually expanded (Fig. 2A). From Lee (1995).

32. Prominently bulbous teeth in the maxilla: (0) absent, (1) present.

In the primitive state all maxillary teeth are conical and long. Most procolophonids have teeth than can be described as bulbous. In some derived forms, however, the tooth are noticeably thicker and more bulbous than in more basal procolophonids. For the purpose of coding this character, a tooth is here considered "prominently bulbous" when its maximum mesodistal length, measured at the mid level of the basal-apical length, is equivalent or larger than 75% the basal-apical length. Accordingly, the chisel-like teeth of some forms such as *Procolophon* or *Scoloparia* are coded as (0).

33. Maxillary teeth cervices: (0) not constricted, (1) constricted.

The maxillary tooth cervix is relatively uniform in *Nyctiphruretus* and most procolophonoids. A constriction in the cervix of all maxillary teeth, visible in labial view, is present in some leptopleuronines.

34. Maxillary teeth cusps: (0) one, (1) two or more.

Primitively, the maxillary teeth are monocuspid. In the first derived state, recorded in most procolophonids, bicuspid molariform teeth are present. A variation of the derived state is represented by *Scoloparia*, which possesses

maxillary molariforms bearing two principal cusps, which are connected by a labiolingual ridge that bear a few cuspules.

35. Maxillary tooth number: (0) 40 or more, (1) 35 to 15, (2) 12 to ten, (3) eight to six, (4) five or less.

Earlier workers (e.g. Colbert, 1946) noticed a reduction in the number of marginal teeth during the evolution of procolophonoids. In *Theledectes perforatus*, a form with multiple rows of teeth both in the maxilla and dentary, it has been assumed that only the lateral-most tooth row is homologous to the marginal dentition of other procolophonids. Therefore, only this row has been used to count the maxillary tooth number. This character has been ordered.

36. Maxillary cheek teeth: (0) not inset, (1) inset.

Primitively, the external surface of the maxilla above the teeth is flat, and the lateral surfaces of the teeth are at the same level of the maxillary wall. In the derived condition, the area above the teeth is depressed and the teeth are inset from the maxillary surface. Modified from Modesto *et al*. (2001).

37. Deep occlusal depression in maxillary teeth: (0) absent, (1) present.

A marked depression between labial and lingual cusps in the maxillary crowns is a derived feature recorded in *Soturnia* and *Hypsognathus*.

38. Anterior vomerine dentition: (0) several denticles, (1) true teeth, (2) entirely absent.

In *Nyctiphruretus* and owenettids the anterior portion of the vomer is covered with several small denticles. True teeth, larger and bearing alveoli, although in smaller numbers, are present in most procolophonids. Teeth are absent on the anterior portion of the vomer of *Soturnia* and *Hypsognathus*. Modified from Lee (1995).

39. Vomerine denticles or teeth along posterior medial suture: (0) present, (1) absent.

Primitively, vomerine denticles or teeth are present on the posterior portion of the vomers, adjacent to the suture between them. The derived condition is recorded in *Coletta* and leptopleuronines. *Procolophon* is polymorphic for this character.

40. Palatine dentition: (0) denticles, (1) true teeth, (2) absent.

Palatine denticles are present in *Nyctiphruretus* and owenettids, whereas true teeth are present in most procolophonids. The palatine dentition is lost in *Leptopleuron* and *Hypsognathus*. Modified from Sues *et al*. (2000).

41. Pterygoid dentition: (0) present; (1) absent.

Primitively, pterygoid denticles or teeth are present. The derived condition is recorded in *Leptopleuron* and *Hypsognathus*. Modified from Sues *et al*. (2000).

42. Dentary tooth number: (0) 14 or more, (1) 12 to ten, (2) nine to eight, (3) seven to six, (4) five or less.

Primitively the dentary tooth number is high. There is a clear trend to decrease the number of dentary teeth in procolophonoids. The two known specimens of *Thelerpeton* are probably juveniles, and the character has been scored as uncertain between states (2) and (3). The criterion to code this character in *Theledectes perforatus* is the same as for character 35. The character has been coded as ordered.

43. Dentary incisors: (0) two or more, (1) one.

Primitively two or more dentary incisors are present. A single and prominent dentary incisor is recorded in some leptopleuronines.

44. Dentary labiolingually expanded teeth: (0) absent, (1) present.

See character 32.

45. Dentary prominently bulbous teeth: (0) absent, (1) present.

See character 33.

46. Dentary teeth cervices: (0) not constricted, (1) constricted.
See character 34.

47. Dentary molariform teeth cusps: (0) one, (1) two adjacent cusps, (2) two widely separated cusps.
Primitively, all dentary teeth are monocuspid. In the first derived state, seen in some procolophonids (e.g. *Kapes*, *Leptopleuron*), two small cusps, closely positioned, are present. The distance between labial and lingual cusps in these forms is equivalent to one cusp. The second derived condition is recorded in several procolophonids (e.g. *Tichvinskia*, *Procolophon*), where cusps are placed on the labial and lingual edges of a much expanded crown. *Scoloparia* has been scored as (2), although the dentary molariforms of this genus sometimes bear cuspules that connect the labial and lingual cusps. A reversal to the monocuspid condition occurs in *Soturnia*.

5.4.5 Axial skeleton

48. Posterior dorsal zygapophyses: (0) gracile, (1) robust.
In *Nyctiphruretus*, owenettids and some procolophonids, the zygapophyses on the posterior dorsal vertebrae are comparatively gracile. In the derived state, these zygapophyses become enlarged and "swollen".

49. Presacral pleurocentral ridge: (0) bearing a longitudinal sulcus, (1) longitudinal sulcus absent.
In *Nyctiphruretus*, the ventral ridge along the pleurocentrum of the presacral vertebrae bears a thin longitudinal sulcus. This sulcus is not recorded in owenettids and a number of procolophonids, but is present in *Procolophon* and probably represents a reversal. This character was described as a pleurocentral "double ridge" in Laurin and Reisz (1995).

50. Number of caudal vertebrae: (0) 20 or more, (1) 17 or less.

Primitively the number of caudal vertebrae is high. There is a significant reduction in the number of caudal vertebrae in *Procolophon* and *Sclerosaurus*.

51. Ossified presacral intercentra: (0) present, (1) absent.
Well developed intercentra are preserved in the presacral vertebrae of *Nyctiphruretus*, owenettids (although these are detached in some *Barasaurus* specimens) and a number of procolophonids. In *Sclerosaurus*, *Soturnia* and *Hypsognathus*, intercentra are not present, although there are spaces for them between each pleurocentra. These genera probably had cartilaginous intercentra.

52. Rib cage width: (0) short, (1) large.
Primitively the rib cage is relatively thin, and the thorax is more gracile. The derived state is recorded in some procolophonids, where the rib cage width is equal or greater than 70% of the glenoid-acetabular length.

5.4.6 Appendicular skeleton (Fig 3)

53. Posteromedial margin of lateral processes of the interclavicle: (0) concave, (1) straight.
In *Nyctiphruretus*, owenettids and some procolophonids, the posterior margins of the interclavicular lateral processes are smoothly concave. The derived condition is recorded in *Pentaedrusaurus* and *Sclerosaurus*, where the posterior margins of the bases of these processes are nearly perpendicular to the trunk of the interclavicle.

54. Interclavicle medial ridge: (0) smooth, (1) prominent.
Primitively, a wide but smooth ventral ridge is present in the trunk of the interclavicle, and is limited to the anterior portion of the interclavicle. In the derived state this ridge becomes narrow and more elevated, extending posteriorly. In some forms, the derived state may not be apparent, but the narrow ridge can be felt when touched.

55. Distal ends of interclavicular lateral processes: (0) straight, (1) posteriorly recurved.

In *Nyctiphruretus*, the interclavicular lateral processes are straight. In the derived condition, the tips are posteriorly recurved.

56. Ectepicondylar foramen on humerus: (0) present, (1) absent.

An ectepicondylar foramen is present in *Nyctiphruretus* and owenettids. This foramen is not recorded in any procolophonid. From Laurin and Reisz (1995).

57. Supinator process: (0) reduced, (1) prominent.

In the primitive state the entepicondyle is small and its external margin rises in a low angle from the humeral shaft. In the derived state, the supinator process is more prominent, emerging *c*. 90° from the shaft. Modified from Laurin and Reisz (1995).

58. Entepicondylar foramen on humerus: (0) present, (1) absent.

An ectepicondylar foramen is recorded in *Nyctiphruretus* and all procolophonids in which the humerus is known. Owenettids lack this feature. Laurin and Reisz (1995).

59. Non-terminal manual phalanges on digits ii, iii and iv: (0) long-slender, (1) short-robust.

In owenettids, the non-terminal manual phalanges on digits ii-iv are long, their length being more than 1.5 times their width. The condition is not known in *Nyctiphruretus*. In the procolophonids in which this character could be coded, these phalanges are notably short, with a length-width ratio of less than 1.5. Also in the derived condition, the epiphyses are usually bulbous, giving a robust appearance to the phalanges. The character is not measured on phalanges i and v because these tend to be more conservative. The condition is not known in *Nyctiphruretus*.

60. Length ratio of unguals/penultimate phalanges on manus: (0) unguals short, (1) unguals long.

In owenettids and most procolophonids, manual unguals are comparative in length to the penultimate phalanges, or moderately longer. This condition has been assumed to be primitive, although the character is not known in *Nyctiphruretus*. *Procolophon* and *Thelerpeton* possess manual unguals that are at least 50% longer than the penultimate phalanges.

61. Iliac anterior margin: (0) convex, (1) straight.

The anterior border of the ilium is convex in *Nyctiphruretus* and most procolophonids. A straight anterior margin is present in owenettids and *Sclerosaurus*.

62. Femur-humerus length ratio: (0) femur longer than humerus, (1) femur length equal to humerus.

In *Nyctiphruretus*, owenettids and *Tichvinskia*, the femur exceeds by up to 20% the length of the humerus. In the derived condition the femur and humerus are sub-equal in length.

63. Femur: (0) slender, (1) robust.

Primitively the femur is gracile. A femur is here considered "robust" when the ratio between the maximum length and the shortest width of the diaphysis, in lateral view, is less than nine. This is the condition present in procolophonids.

5.4.7 Dermal ossifications

64. Osteoderms: (0) absent, (1) present.

Primitively, osteoderms are absent. The derived state has only been found in *Sclerosaurus* and *Scoloparia*. However, these structures detach easily from the skeleton, and it is possible that they were present in other procolophonids. For this reason the character has been coded as missing data for most procolophonids, and only as primitive in taxa that are known from well preserved postcrania.

5.5 Results (Figs 4, 5)

The analysis produced a single most parsimonious tree with 134 steps. Clades here considered most relevant are discussed below. State transformations are indicated within brackets, and reversals are preceded by a minus sign.

5.5.1 Clade A: Procolophonidae Lydekker 1890

New definition. All taxa more closely related to *Procolophon trigoniceps* Owen 1876 than to *Owenetta rubidgei* Broom 1939.

Composition. *Coletta seca*, *Sauropareion anoplus*, BP/1/1187, *Phaanthosaurus* spp., *Tichvinskia vjatkensis*, Arcadia procolophonid, "*Eumetabolodon*" *dongshengensis*, *Theledectes perforatus*, *Timanophon raridentatus*, *Kapes* spp., *Thelephon contritus*, *Eumetabolodon bathycephalus*, *Procolophon trigoniceps*, *Thelerpeton oppressus*, *Teratophon spinigenis*, *Pentaedrusaurus ordosianus*, *Neoprocolophon asiaticus*, *Sclerosaurus armatus*, *Scoloparia glyphanodon*, *Leptopleuron lacertinum*, *Soturnia caliodon* and *Hypsognathus fenneri*.

Non-ambiguous synapomorphies

1(0→1):Maxilla premaxillary subnarial process absent.
3(0→1):External naris subcircular or dorsoventrally expanded.
6(0→1):Maxillary depression present.
28(0→1):Four premaxillary teeth.
31(0→1):Maxillary teeth with labiolingually expanded bases present.
35(1→2):Twelve to ten maxillary teeth.
38(0→1):Anterior vomerine dentition consisting of one to three rows of true teeth.
40(0→1):Palatine dentition formed by true teeth.

Comments. The Procolophonidae, as defined here, are a well defined group of parareptiles. The absence of postcranial information for the basalmost procolophonids *Coletta* and *Sauropareion* necessarily restricts the synapomorphies of the group to cranial, mainly dental characters.

5.5.2 Clade E

Composition. *Tichvinskia vjatkensis*, Arcadia procolophonid, "*Eumetabolodon*" *dongshengensis*, *Theledectes perforatus*, *Timanophon raridentatus*, *Kapes* spp., *Thelephon contritus*, *Eumetabolodon bathycephalus*, *Procolophon trigoniceps*, *Thelerpeton oppressus*, *Teratophon spinigenis*, *Pentaedrusaurus ordosianus*, *Neoprocolophon asiaticus*, *Sclerosaurus armatus*, *Scoloparia glyphanodon*, *Leptopleuron lacertinum*, *Soturnia caliodon* and *Hypsognathus fenneri*.

Non-ambiguous synapomorphies

8(1→2):Posterior margin of orbitotemporal fenestra beyond the posterior border of the pineal foramen.
12(2→3):Postfrontal fused to parietal.
29(0→1):Enlarged mesialmost premaxillary tooth.
35(2→3):Eight to six maxillary teeth.
42(1→2):Nine to eight dentary teeth.

Comments. Members of clade E display a notable reduction of both the maxillary and dentary dentition (characters 35 and 42). The condition where the posterior margin of the orbitotemporal fenestra surpasses the posterior border of the pineal foramen has been traditionally considered a very derived feature within the Procolophonidae (e.g. Colbert, 1946). The analysis indicates that this character state actually arose early in the evolution of procolophonids, and the condition in *Procolophon* and other procolophonines, where the orbitotemporal fenestra does not surpass the posterior border of the pineal foramen, constitutes a reversal (see below). The position of *Tichvinskia*, outside of the Procolophoninae clade, supports the results of Modesto *et al*. (2002), *contra* deBraga (2003).

5.5.3 Clade F: Theledectinae new taxon

Definition. All taxa more closely related to *Theledectes perforatus* (Gow, 1977a) than to *Procolophon trigoniceps* Owen 1876.
Composition. *Theledectes perforatus*, "*Eumetabolodon*" *dongshengensis* and the Arcadia procolophonid.

Non-ambiguous synapomorphies

7(0→1):Prefrontal medial border emarginated.
-31(1→0):Absence of maxillary teeth with labiolingually expanded bases.
42(2→3):Seven to six dentary teeth.
-44(1→0):Absence of dentary teeth with labiolingually expanded bases.

Comments. An interesting result of the analysis is this previously unrecognized clade, formed by procolophonids from south and east Pangaea. The most distinctive feature of the clade is the presence of enlarged, monocuspid marginal teeth with circular bases. These teeth are notably different from those of *Nyctiphruretus* or the owenettids, which also have circular bases but are much thinner and sharp.

The Chinese genus *Eumetabolodon* is paraphyletic. In the original description of this taxon, Li (1983: p. 572), regarding the differences between *E*. *bathycephalus* and "*E*". *dongshengensis*, stated that "the distinction might even be generic". In spite of the fragmentary nature of the holotype, it has been possible here to code "*E*". *dongshengensis* for some key characters, and the results confirm her initial suspicion that "*E*." *dongshengensis* represents a different genus. A re-description of this taxon is in progress, and a new genus name will be proposed in order to recognize only monophyletic genera. *Theledectes* (*Thelegnathus*) *perforatus*, the bizarre procolophonid with multiple rows of teeth from the *Cynognathus* AZ of South Africa, and the procolophonid from the Arcadia Formation, are also members of this clade. A review of the former, and a description of the latter, are in progress.

5.5.4 Clade H: "horned procolophonids"

Composition. *Timanophon raridentatus*, *Kapes* spp., *Thelephon contritus*, *Eumetabolodon bathycephalus*, *Procolophon trigoniceps*, *Thelerpeton oppressus*, *Teratophon spinigenis*, *Pentaedrusaurus ordosianus*, *Neoprocolophon asiaticus*, *Sclerosaurus armatus*, *Scoloparia glyphanodon*, *Leptopleuron lacertinum*, *Soturnia caliodon* and *Hypsognathus fenneri*.

Non-ambiguous synapomorphies

4(0→1):Wide internarial bar.
15(0→1):Presence of a quadratojugal spine.
19(0→1):Acute supratemporal posterolateral margin.
24(0→1):Basioccipital tuber projected far posteriorly than level of quadrate condyle.
52(0→1):Wide rib cage.
57(0→1):Prominent supinator process.

Comments. This clade is equivalent to procolophonines plus leptopleuronines, and its members can be readily identified by the presence of quadratojugal horns (this feature is lost in *Kapes* and *Thelephon*, see below) a feature that may have been acquired for defensive purposes (see Young *et al.*, 2004). These horned procolophonids are also characterized by a more robust postcranium, notably a wide rib cage, and a considerably larger size in comparison to earlier procolophonids and owenettids.

5.5.5 Clade I: Procolophoninae Lydekker 1890

Definition. All taxa more related to *Procolophon trigoniceps* Owen 1876 than to *Leptopleuron lacertinum* Owen 1851 (*sensu* Modesto *et al*., 2002).
Composition. *Timanophon raridentatus*, *Kapes* spp., *Thelephon contritus*, *Eumetabolodon bathycephalus*, *Procolophon trigoniceps*, *Thelerpeton oppressus* and *Teratophon spinigenis*.

Non-ambiguous synapomorphies

5(0→1):Snout deep-short
-12(3→2):Postfrontal contacts frontal and parietal only.

Comments. Procolophoninae, in this analysis, is a geographically diverse group formed by taxa from South Africa, Britain, Russia and China. This clade, however, is not well supported, requiring only one step to collapse. In a one-step suboptimal scenario, Procolophoninae is restricted to clade L, which is composed of the South African *Procolophon trigoniceps*, *Thelerpeton* (*Thelegnathus*)

oppressus and *Teratophon* (*Thelegnathus*) *spinigenis*, and the type species (by page priority) of the Chinese genus *Eumetabolodon*, *E. bathycephalus*. The analysis shows that only two species of the former genus *Thelegnathus* are closely related, namely *Thelerpeton oppressus* and *Teratophon spinigenis*. They form a trichotomy with the genus *Procolophon* (clade M), a more exclusive clade that is diagnosed by a reversal, the placement of the posterior margin of the orbitotemporal fenestra at the level of the posterior margin of the pineal foramen. A review of all species previously assigned to "*Thelegnathus*" is in progress by R. Damiani, S.P. Modesto and the author.

5.5.6 Clade K

Composition. *Kapes* spp. plus *Thelephon contritus.*

Non-ambiguous synapomorphies

7(0→1):Prefrontal medial border emarginated.
-10(1→0):Pineal foramen in a shallow fossa.
-15(1→0):Quadratojugal lateral surface spineless.

Comments. An unexpected result of the analysis is the close relationship between the South African *Thelephon* (*Thelegnathus*) *contritus* and the Laurasian genus *Kapes*. The latter was previously known only from tooth bearing fragments, and its addition to this analysis was only possible due to the recent description of a nearly complete cranium by Novikov and Sues (2004). Another possible synapomorphy of the *Kapes*-*Thelephon* clade is the presence of a prominent posterior tooth in the dentary. This is a variable feature within the genus *Kapes* which is clearly expressed in the species *K. amaenus* (Ivakhnenko, 1975: fig. 2), but it was not included in the analysis. On the other hand, *Thelephon* differs from *Kapes amaenus* in the presence of a prominent posterior tooth also in the maxilla (Modesto and Damiani, 2003: fig 4). Despite this difference, the crania of *Kapes* and *Thelephon* resemble each other closely. If *Thelephon* is not a valid taxon, as suggested by Modesto and Damiani (2003) who considered that the taxon lacks obvious cranial apomorphies, *Thelephon* may be regarded as a junior synonym of

Kapes. This assumption, however, would imply the existence of a trans-Pangaean genus. *Kapes* in turn, might be a junior synonym of the poorly known genus *Anomoiodon* from the Buntsandstein of Germany (Spencer and Storrs, 2002). Due to these nomenclatural problems, the clade has been left unnamed. A review of *Thelephon contritus*, based on a series of new specimens, is in progress by R. Damiani, S.P. Modesto, and the author.

5.5.7 Clade N: Leptopleuroninae Ivakhnenko 1979

Definition. All taxa more closely related to *Leptopleuron lacertinum* Owen 1851 than to *Procolophon trigoniceps* Owen 1876 (*sensu* Modesto *et al*., 2002).
Composition. *Pentaedrusaurus ordosianus*, *Neoprocolophon asiaticus*, *Sclerosaurus armatus*, *Scoloparia glyphanodon*, *Leptopleuron lacertinum*, *Soturnia caliodon* and *Hypsognathus fenneri*.

Non-ambiguous synapomorphies

9(0→1):Posterior angle of opening of the orbitotemporal fenestra, in lateral view, lower than 25°.
22(0→1):Ventral margin of quadrate below the level of the maxillary dentition.
26(0→1):Oblique dentary ventral and dorsal surfaces.
27(0→1):Articular well below the alveolar margin of dentary teeth.
39(0→1):Vomerine denticles or teeth along posterior medial suture absent.
42(2→3):Seven to six dentary teeth.
53(0→1):Straight posteromedial margin of lateral processes of the interclavicle.

Comments. This is a distinctive clade. The phylogenetic relationships of the Chinese procolophonids *Pentaedrusaurus ordosianus* and *Neoprocolophon asiaticus* are here resolved as the most primitive members of the Leptopleuroninae. Only one Gondwanan leptopleuronine is known, the recently described *Soturnia caliodon.* This may be due to preservational or collecting factors, because Upper Triassic rocks yielding small vertebrates are not common in Gondwana.

5.5.8 Clade P

Composition. *Leptopleuron lacertinum*, *Sclerosaurus armatus*, *Scoloparia glyphanodon*, *Soturnia caliodon* and *Hypsognathus fenneri*.

Non-ambiguous synapomorphies

-6(1→0):Maxillary depression absent.
13(0→2):Two jugal spines.
14(2→3):Temporal ventral margin convex.
15(1→2):Two or more quadratojugal spines.

Comments. This is the best supported clade within the Procolophonidae (DI=4, SR=97). It is composed of more derived leptopleuronines that exhibit very distinctive traits, such as the presence of multiple cranial spines. The problematic genus *Sclerosaurus* from the Buntsandstein is found in this clade. Leptopleuronine affinities for this genus were also reported by deBraga (2003). *Sclerosaurus* here constitutes the sister group of *Scoloparia* from Canada (clade O), a genus not considered in deBraga's (2003) analysis, both genera being the only procolophonids where the presence of osteoderms has been recorded. This character, however, could not be coded for a number of procolophonids because the postcranium is incomplete or not known at all. It should not be surprising that osteoderms are recorded in other forms when more or better specimens are found. Another possible member of clade P is the unnamed procolophonid from the Owl Rock Member of the Chinle Formation in USA (Fraser *et al*., 2004). Although poorly preserved, the specimen is clearly a leptopleuronine and shares some apomorphies known elsewhere only in *Leptopleuron*, *Soturnia* and *Hypsognathus*, such as the presence of a single dentary incisiform (Fraser *et al*., 2004).

5.5.9 General remarks

The analysis did not find a clade of basal procolophonids that could be identified as the Spondylolestinae. Ivakhnenko (1979) proposed this subfamily to include procolophonids considered primitive by him: *Spondylolestes*, *Phaanthosaurus*, *Contritosaurus*, *Candelaria*, *Procolophonoides* and *Neoprocolophon*. The genus

Procolophonoides was erected by Ivakhnenko (1979) for the species *Procolophon baini*, but this species is no longer recognized by most authors that have reviewed *Procolophon* due to the equivocal nature of the characters in which it was based, which can be explained through ontogeny (Colbert and Kitching, 1975; Gow, 1977b; Carroll and Lindsay, 1985; deBraga, 2003; Cisneros *in press*). In addition, *Candelaria* has recently been shown to be an owenettid (Cisneros *et al.,* 2004), and *Contritosaurus* can be considered a junior synonym of *Phaanthosaurus* (Spencer and Benton, 2000). Of the three remaining valid taxa, *Spondylolestes* was too incomplete to be included in this analysis, and only *Phaanthosaurus* and *Neoprocolophon* could be evaluated. The results show that *Phaanthosaurus* occupies a basal position and *Neoprocolophon* is a leptopleuronine.

The position of BP/1/1187 in the cladogram confirms Gow's (2000) suspicion that this specimen is not a juvenile *Procolophon trigoniceps*, but a representative of an undescribed taxon. The topology of the tree indicates that BP/1/1187 is the first procolophonid known to develop bicuspid molariforms. This early acquisition necessarily constitutes an independent phenomenon, because this specimen is the sister group of clade C, in which monocuspid marginal teeth are the primitive condition. This interesting new basal taxon will be the subject of a description to be published elsewhere.

The analysis supports the paraphyly of the former genus *Thelegnathus*, the four new genera proposed by Modesto and Damiani (2002) being here separated in three different clades: Theledectinae (clade E), clade J and clade L. Curiously, *Theledectes* (*Thelegnathus*) *perforatus* is here shown to be more closely related to an Australian and a Chinese procolophonid, than to any other South African form.

Previous workers on the phylogenetic relationships of parareptiles (Laurin and Reisz, 1995; Lee, 1995; deBraga and Rieppel, 1997) coded characters for the Procolophonidae mainly based on *Procolophon*, relying on the traditional assumption that this genus constitutes a primitive procolophonid. Despite its Early

Triassic age, the results indicate that the genus *Procolophon* actually represents a derived procolophonid.

The recognition in this analysis of the problematic taxon *Sclerosaurus armatus* as a member of the Procolophonidae, supports the results of deBraga (2003). Following Rieth's (1932) interpretation of *Sclerosaurus*, Lee (1995, 1997a) considered this taxon to be a "pareiasauroid", despite the fact that this genus exhibits a reduced marginal dentition with labiolingually expanded molariforms, both derived procolophonid traits that are not compatible with pareiasaurid affinities. In addition, *Sclerosaurus* possess orbits that are notably expanded (specimen AM 2482, *contra* Lee 1995, 1997a), a feature that further supports procolophonid relationships. The results of the present analysis are also consistent with the Early/Middle Triassic age of *Sclerosaurus*.

5.6 Evolutionary history and feeding ecology (Figures 6, 7)

One of the characters that diagnose Procolophonidae in this study is the appearance of teeth with labiolingually expanded bases, as seen in *Coletta* (Figs 2A, 6B). The presence of nearly isodont dentition, with ogival, unworn teeth, is suggestive of non-durophagous omnivory (Hotton *et al*., 1997). This pattern is followed by the acquisition of bulbous teeth (as defined in this study) by clade D (Figs 2B, 6C). The presence of blunted ogival teeth can be related to durophagous omnivory (Hotton *et al*., 1997). The dentitions of some of these procolophonids are comparable to those of modern durophagous lizards such as the varanid *Varanus niloticus* and the skink *Tiliqua scincoides*. However, there is a significant range of variation in the teeth of the Procolophonidae. *Theledectes* is notable for possessing multiple rows of bulbous teeth (Fig 6E) that resemble those of the Early Permian reptile *Captorhinus aguti*. *Kapes amaenus*, *Thelephon contritus* and *Haligonia bolodon* (the latter not included in this analysis; Carnian of eastern Canada, Sues and Bird, 1998) feature a prominent bulbous marginal tooth that may have worked as a nut cracker.

By developing adaptations for both durophagous and non-durophagous omnivory during the Early Triassic, procolophonids fulfilled an ecological niche that was left empty by captorhinids and bolosaurids, which did not survive the Permo-Triassic extinction. The absence of competitors probably was an important factor for the successful radiation of the Procolophonidae, which were present throughout Pangaea during the Early Triassic. Apart from procolophonids, small reptiles with adaptations for durophagous or non-durophagous omnivory are almost unknown in the Early Triassic.

The acquisition of labiolingually expanded crowns (Fig 6D) played a major role in procolophonids. This character has no reversals and it is noteworthy for appearing twice during the evolution of the group, independently acquired by BP/1/1187 and clade G. Whereas some forms that possess this character still may be considered durophagous omnivores (e.g. *Tichvinskia vjatkensis*), the labiolingually expanded crowns made possible the exploitation of a high-fiber herbivory niche by several members of this group. In most procolophonines and leptopleuronines, large occlusal areas of molariforms seem effective for processing tough, fibrous foods (Reisz and Sues, 2000, Figs 6G, L).

Procolophonids exhibit a progressive accumulation of cranial features concomitant with an enhanced mandibular action; some of these adaptations reached a peak in the leptopleuronines. These include: (a) the continuous expansion of the orbitotemporal fenestrae (see Colbert, 1946); (b) development of a high coronoid (this character was difficult to quantify and was not included in the analysis); (c) low articular (Fig 6H); (d) deep dentary (Fig 6I); and (e) the presence of marginal teeth inset from both the maxillary and dentary lateral surfaces (Fig 6F).

With the possible exception of the small *Soturnia caliodon*, the horned procolophonids (clade H) are significantly larger than owenettids and basal procolophonids, and the clade is diagnosed by an expanded rib cage. Both larger size and wide trunks represent adaptations in amniotes for a longer digestive

system and hosting endosymbiotic organisms that are necessary for the breakdown of cellulose (Sokol, 1967; Hotton *et al*., 1997; Cooper and Vitt, 2002). In modern herbivorous lizards there is a tendency towards a larger size compared to their omnivore and insectivore counterparts (Sokol, 1967; Cooper and Vitt, 2002). Only the horned procolophonids include presumably herbivorous forms, which suggests that this ecological niche only became possible for the Procolophonidae when a larger size and a wider trunk were acquired.

Two procolophonids with labiolingually expanded crowns seem to represent exceptions to herbivorous or durophagous diets. The marginal teeth of BP/1/1187 and the leptopleuronine *Scoloparia glyphanodon* differ notably from those of other procolophonids. Both forms possess mesodistally compressed molariforms with sharp labiolingual cutting edges. In these procolophonids, the cusps are thin and exhibit relatively less wear in comparison with *Procolophon* or other forms with labiolingually expanded crowns, which suggest that they were not employed in durophagy or in processing highly-fibrous plants. In *Scoloparia* additional cuspules connect the prominent labial and lingual cusps (Fig 6J), whereas in BP/1/1187 a number of sharp conical teeth are present anterior to the molariforms (Gow, 1977b, text-fig. 6). These dentitions would be very effective for the tearing and puncturing of arthropods and other small invertebrates. This mechanism of processing prey in the mouth hastens its digestion (Hildebrand, 1974) and predates modern gymnures and hedgehogs (Insectivora: Erinaceidae). Such dentition is indicative of similar ecological niches for *Scoloparia* and BP/1/1187.

As seen here, a plethora of adaptations for different feeding habits, ranging from insectivory to high-fiber herbivory, can be found in the *c*. 30 genera of known procolophonids. Whereas the development of different forms of omnivory and the absence of competitors allowed the colonization of Pangaea during the Early Triassic, the acquisition of specializations for high-fiber herbivory made possible further radiation and survival until Late Triassic times. The fossil record of *Procolophon* indicates that the presence of labiolingually expanded crowns in the group emerged as early as Late Induan (Fig. 7). This is somewhat earlier than the

first records of other Triassic tetrapods that also developed labiolingually expanded crowns: gomphodont cynodonts, bauriid therocephalians, and the enigmatic reptile *Palacrodon*; all from the Upper Olenekian of South Africa (*Cynognathus* subzone A; Neveling, 2004; Abdala *et al*., 2006). In summary, procolophonids fulfilled a variety of ecological niches during the Triassic, similar to those occupied today by some mammals such as rodents and insectivores, and durophagous lizards.

5.7 Biostratigraphic considerations (Figures 7, 8)

5.7.1 The Permian record of procolophonids

A Permian lineage for the Procolophonidae is implied by the minimum divergence time (Norell, 1992) of this group from the Owenettidae in the Late Wuchiapingian (Fig. 7). This long ghost record in part results from the assumption that the Owenettidae is a monophyletic group. Owenettids possess a good record before and after the P/T boundary. If some taxa currently included in the Owenettidae were discovered to be more closely related to procolophonids, the Permian ghost lineage of the Procolophonidae could be significantly or totally reduced. A review of the Owenettidae is beyond the scope of this study, and work in progress by S.P. Modesto may clarify this question. A few non-owenettid taxa with putative procolophonid affinities are present in the literature, and they may fill the Permian ghost lineage of the Procolophonidae. Unfortunately, these forms are known from very incomplete, fragmentary remains, and could not be included in this analysis, but they are discussed below.

***Spondylolestes rubidgei* Broom 1937**

The South African genus *Spondylolestes* has traditionally been considered to represent a primitive procolophonid (Colbert, 1946; Kuhn, 1969; Ivakhnenko, 1979, 1987). Broom (1937) tentatively assigned an Early Triassic age to *Spondylolestes*, based on the general appearance of the matrix around the fossil.

The holotype and only known specimen, however, was recovered in the Bethesda Road area, near Graaff-Reinet, Eastern Cape Province, a locality which yields Permian tetrapods including the index dicynodont *Dicynodon* (Kitching, 1977). Hence, the locality belongs to the *Dicynodon* Assemblage Zone, a horizon that is considered to be Changhsingian in age (Upper Tatarian; Kitching, 1995; Rubidge, 2005).

The holotype of *Spondylolestes* consists of a small, heavily weathered cranium and mandible in occlusion (Fig. 8). Although most sutures are not visible, the broad and triangular shape of the skull, enlarged orbits (orbitotemporal fenestrae) and the anteriorly directed ascendent process of the premaxilla (character 2, as shown by the internal mould of the premaxilla) indicate that *Spondylolestes* has procolophonid affinities. This is also supported by the low number of marginal teeth. Eight left maxillary teeth are preserved, and a total of ten maxillary teeth seems likely. A total of thirteen teeth were present in each dentary, including three missing teeth. *Spondylolestes* possesses considerably fewer marginal teeth than *Owenetta* and *Barasaurus* specimens of similar size, and in *Spondylolestes* these teeth are more robust, although not bulbous, suggesting that *Spondylolestes* is not an owenettid but a procolophonid. The total number of marginal teeth of *Spondylolestes* makes this genus comparable to *Coletta* and *Pintosaurus*. Contrary to *Coletta* and *Pintosaurus*, however, the teeth of *Spondylolestes* are not labiolingually expanded, but circular in basal cross section (Fig. 8E). The genus *Sauropareion* probably has a similar number of teeth as *Spondylolestes*. Although the holotype of *Sauropareion* is missing the snout, most of the maxilla is present, bearing at least eight teeth, which suggests a total of ten. It is not clear, however, if the marginal teeth of *Sauropareion* are strictly circular in basal cross section or slightly expanded labiolingually as in *Coletta* and *Pintosaurus*. The teeth of *Sauropareion* are not properly exposed to assess the contour of their bases, although Modesto *et al*. (2001) stated that the maxillary teeth seem "subcircular" and lacking the "transverse expansion", in comparison to more derived taxa such as *Phaanthosaurus* and *Procolophon* where this expansion is prominent.

The poor preservation of the holotype of *Spondylolestes* has led other authors to consider this taxon to be a *nomen dubium* (Spencer and Benton, 2000; Modesto *et al*., 2001). However, no owenettid or procolophonid is known to possess ten maxillary teeth, or 13 dentary teeth, with circular bases. If the marginal teeth of *Sauropareion* are shown to be strictly circular in basal cross-section and the total number comparable to *Spondylolestes*, the deeper skull of *Sauropareion* still allows the recognition of both taxa. In any case, *Spondylolestes* is easily distinguished from any Permian reptile and must be considered a valid taxon.

***Microphon exiguus* Ivakhnenko 1983**

The Russian genus *Microphon*, from the Orenburg Province in the Cis-Urals, has traditionally been considered a Late Tatarian representative of the Procolophonidae (Ivakhnenko, 1983; Modesto *et al*., 2001). The holotype and referred specimens, represented by isolated maxillae of very small size (as the name *Microphon* indicates), bear elongated teeth with longitudinally compressed crowns. Its identity as a procolophonid was questioned by Spencer and Benton (2000), due to the lack of unequivocal autapomorphies. The type series was recently re-studied and the individuals were re-identified as juvenile individuals of the seymouriamorph *Raphaniscus tverdochlebovae*, and *Microphon exiguus* is now considered its senior synonym by name priority (Bulanov, 2002).

***Suchonosaurus minimus* Tverdokhlebova and Ivakhnenko 1994**

Another Russian taxon that has been considered to represent a Permian procolophonid is *Suchonosaurus minimus*, from the Vologda region, Upper Tatarian of the Cis-Urals (Tverdokhlebova and Ivakhnenko, 1994). The holotype and only known specimen of *Suchonosaurus* consists of a very small maxilla bearing ten cylindrical teeth. Besides the statement that *Suchonosaurus* is similar to *Microphon*, the authors did not point out on which criteria they assigned this material to the Procolophonidae, and no obvious procolophonid apomorphies can be observed in the specimen as figured in Tverdokhlebova and Ivakhnenko

(1994). Furthermore, from the published illustrations it can be noticed that like *Microphon*, *Suchonosaurus* has a pleurodont dentition, a condition that has never been reported for a procolophonid or an owenettid. Both procolophonids and owenettids possess teeth well set in the bone, whether these are within distinct sockets or not (Gow, 1977b; Sues and Olsen, 1993; Small, 1997; pers. obs. in *Owenetta rubidgei* BP/1/1396), a condition that is usually termed "prototheco dont". Considering the absence of procolophonid autapormophies, and the presence of pleurodont dentition, it is unlikely that *Suchonosaurus* represents a valid procolophonid.

***Kinelia broomi* Bulanov 2002**

Bulanov (2002) described a new procolophonid, *Kinelia broomi*, from Vozdvizhenka, in the Orenburg region (Vyatkian Gorizont, Upper Tatarian of the Cis-Urals, Tverdokhlebov *et al*., 2005). The taxon, based on a partial right mandible, shows non-acrodont conical teeth, with labiolingually expanded bases, similar to those present in *Coletta seca* (Fig. 2A). Because the presence of transversally expanded tooth bases is an autapomorphy of the Procolophonidae, as shown in this study, *Kinelia* can be considered an early member of this group, probably related to *Coletta seca*.

***Pintosaurus magnidentis* Piñeiro *et al*. 2004**

Another possible Permian procolophonid was recently described. *Pintosaurus magnidentis*, from the Buena Vista Formation of Uruguay, is in many features similar to *Coletta seca* (Piñeiro *et al*., 2004). Like *Coletta*, *Pintosaurus* possesses single cusped, conical maxillary teeth with labiolingually expanded bases (pers. obs.). The dentary teeth also exhibit this pattern (pers. obs.), a feature that *Pintosaurus* shares with *Coletta* and *Kinelia*. *Pintosaurus* and *Coletta* also share the absence of posterior vomerine teeth along the medial suture, and the same number of maxillary teeth (twelve). *Pintosaurus* and *Coletta* are in fact so similar that they could be considered congeneric. The age of the Buena Vista Formation,

however, is not well established. While Piñeiro *et al*. (2003) considered it to be Late Permian, based on the presence of presumed varanopid remains, other authors consider it to be a lateral equivalent of the Sanga do Cabral Formation from southern Brazil (e.g. Bossi and Navarro, 1991), which has yielded the index taxon *Procolophon* and, therefore, should be Late Induan or Olenekian. Whereas the status of *Pintosaurus* as a procolophonoid related to *Coletta* is well established, the age of this intriguing taxon remains uncertain.

Based on the evidence discussed above, only *Kinelia broomi* from Russia and *Spondylolestes rubidgei* from South Africa can safely be considered taxa with procolophonid affinities, of Permian age, likely to fill the ghost lineage of this group in the Late Permian.

5.7.2 The Ladinian-Early Carnian record of procolophonids

Leptopleuroninae (clade N) is the only clade that has members that reached Late Triassic times. The stratigraphic range of this group spans at least from the Early Anisian to the Late Rhaetian. However, no record of leptopleuronines, or other procolophonids, are known in the Ladinian, and only one fragmentary record is known in the Early Carnian (see below). This results in a global procolophonid hiatus of more than 15 Ma and some Lazarus taxa (Fig. 7).

The Middle Triassic Santa Maria Formation of southern Brazil produces the procolophonoid *Candelaria barbouri*. *Candelaria* is found in the *Dinodontosaurus* AZ of this formation, a horizon which is considered to be Lower Ladinian (Abdala *et al*., 2001). However, *Candelaria barbouri* is now considered to be the sister group of *Owenetta kitchingorum* (Cisneros *et al.,* 2004), and this taxon does not fill the global procolophonid hiatus in the Ladinian. Being by far the most recent of the owenettids, *Candelaria* could be considered a living relict at the time the Santa Maria sediments accumulated. No other procolophonoid is known in the Ladinian.

Two fragmentary records of possible procolophonids are reported for the Lower/Middle Carnian of North America. These are *Gomphiosauridion baileyae* and *Xenodiphyodon petraios*, both from the Turkey Branch Formation of Canada (Sues and Olsen, 1993). *Gomphiosauridion* is based on a maxillary fragment with two molariforms; these teeth are labiolingually expanded, with a labial and a lingual cusp separated by a transverse ridge. This material seems referable to a procolophonid, but the fragmentary nature of the specimen precludes assessment of its affinities within the group. *Xenodiphyodon* is known from a partial dentary bearing nine teeth. The taxon is remarkable for having six anterior teeth that are mesodistally elongated, and three labiolingually expanded posterior molariforms. The posterior molariforms bear three cusps. If *Xenodiphyodon* is not a trilophosaurid, it may represent a leptopleuronine procolophonid. The three posteriormost teeth of *Xenodiphyodon* are comparable to those present in the leptopleuronine *Scoloparia*, and the very deep dentary of *Xenodiphyodon* supports leptopleuronine affinities. The absence/scarcity of Ladinian and Lower Carnian global records of procolophonids may be due to a preservational or collecting artifact. Ladinian rocks that produce microvertebrate faunas are scarce.

5.8 Conclusions

Procolophonidae is a monophyletic group, and its relationships are now more firmly resolved. Two of the three traditional divisions of the Procolophonidae, Procolophoninae and Leptopleuroninae, are valid monophyletic groups. Spondylolestinae, however, is paraphyletic. A new group, Theledectinae, is here erected, a clade which includes the procolophonid from the Arcadia Formation of Australia. The genus *Eumetabolodon* is paraphyletic. *Eumetabolodon bathycephalus* is a procolophonine whereas "*E.*" *dongshengensis* is a theledectine and must be placed in a new genus. This study confirms that the former genus *Thelegnathus* is also paraphyletic. A new procolophonid is here recognized based on BP/1/1187, a specimen previously assigned to the genus *Procolophon*. The Chinese genera *Pentaedrusaurus* and *Neoprocolophon* are the basalmost members of the Leptopleuroninae, and the problematic genus *Sclerosaurus* from

Switzerland is also a leptopleuronine. The genus *Spondylolestes* from South Africa is considered a valid taxon but its phylogenetic relationships remain tentative. Both *Spondylolestes* and the Russian *Kinelia* are likely to fill the ghost lineage of the Procolophonidae in the Permian. There is a global hiatus of procolophonid records in the Ladinian and Lower Carnian. Bicuspid dentition, a very distinctive trait of the group, evolved at least twice in procolophonids. The successful radiation of the Procolophonidae during the Triassic might be related to the variability of the dentition of procolophonids. This allowed exploration of various ecological niches, particularly the exploitation of high-fiber herbivory by several members of the group.

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5.10 APPENDIX: DATA MATRIX

Ordered characters are indicated by a plus sign. Question marks represent inapplicable characters or missing information. A=0,1; B=1,2; C=2,3; D=3,4; E=0,2.

			+	+	+	+	+	+	
	+	1111111111	2222222222	3333333333	4444444444	5555555555	6666666		
Taxon	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	012345		
Nyctiphruretus	0000000000	0000000000	0?00000000	0000000000	0000000000	000000000?	?0000		
Owenettidae	0000000000	00101011A0	0?00000000	0000010000	0000000001	000001001	001000		
Coletta	0101001000	0020101???	0?0???0010	0100020011	?000?000??	??0????????	?????		
Sauropareion	???????010	0020100100	0?0???00??	??000C001?	10???0????	??0????00?	?????		
BP/1/1187	??11?01???	?0?020?1?0	??0???0?B0	0100120???	??001002??	??????????	?????		
Phaanthosaurus spp.	0111011000	??B0??????	1??????020	0110020010	1?10110???	??????????	?????		
E. dongshengensis	??????11??	???0??????	1?????????	000003001?	1?C?0000??	??????????	?????		
Arcadia proc.	0110001120	1030200110	10000000B1	001003001?	1030010001	?000111?01	00110		
Theledectes	???????12?	103020?11?	??????0?21	00100300??	?030010???	???????00?	?????		
Tichvinskia	01?1001020	1030200110	1000000021	0110131010	1?2011020?	0?0???100?	?0010		
Timanophon	??????1020	1120210010	1?0010?02?	011013?010	1020110???	??????????	?????		
Kapes	0111111120	0130200111	1?0???0021	0110131010	1030A101??	??????????	?????		
Thelephon	???????120	012020?111	??????0???	?1101D101?	10???1????	??????????	?????		
E. bathycephalus	?211111020	1020210??2	1?0?100021	0110131010	1020110?1?	??????????	?????		
Procolophon	0211111A10	1020210112	1000100021	A10013101A	1020100210	1010111101	10110		
Thelerpeton	?2?111?010	1020210112	1?0?1?0021	01101D1010	10C0110???	???011???1	1????		
Teratophon	?211111A10	10C0210112	1?00100021	0110131010	10C0?10?1?	??1011110?	????0		
Pentaedrusaurus	0B11101021	1230210111	1?1???1121	0110131?11	1030110B11	?0?1111101	0?110		
Neoprocolophon	???1111?11	1E?021?21B	1?1???????	?1??1D1?11	?0????????	??????????	?????		
Sclerosaurus	????????3?	10?232?2??	??????????	?11?141???	???2??????1	1111??11?1	01111		
Scoloparia	1????00031	1?3232?2?1	??????1?31	11001D10??	??301002??	??????????	????1		
Leptopleuron	1?11??0221	102132?211	1111?1113?	1111141?11	2131???1??	0?1???????	????0		
Soturnia	?1????0???	??????????	1?1???1131	0111141127	??41011001	?1?????00?	?????		
Hypsognathus	A?11A00231	1032321B12	1111111131	0111141121	2141?111?1	?11?????0?	????0		

Table 1. Taxa, literature consulted for anatomical information, and provenance of materials used in this analysis. Names in bold indicate first hand study of non-type material, asterisks indicate that the holotype was examined. *Sclerosaurus* was studied through plaster casts (AM 2480-2482) of the holotype. Specimen BP/1/1187 has not yet been designated as a holotype, likewise, the Arcadia procolophonid lacks a holotype. Additional information for some taxa was obtained through photographs.

Nyctiphruretus acudens	Efremov 1940, Ivachnenko 1979, Efremov1987, Lee 1995, 1997b	Mezen Fauna, Cis-Urals, Russia
Barasaurus besairiei	Meckert 1995	Sakamena F., Madagascar
Owenetta rubidgei*	Reisz and Scott 2002	Balfour F., South Africa
*Coletta seca**	Modesto *et al*. 2002	Katberg F., South Africa
Sauropareion anoplus	Modesto *et al*. 2001, Damiani *et al*. 2003	Balfour F., South Africa
BP/1/1187	Gow 1977b	Katberg F., South Africa
Phaanthosaurus spp.	Ivachnenko 1974, Spencer and Benton 2000	Vokhmian Gorizont, Cis-Urals, Russia
*Eumetabolodon dongshengensis**	Li 1983	?Shiquianfeng Group, northern China
Arcadia procolophonid		Arcadia F., eastern Australia
*Theledectes perforatus**	Modesto and Damiani 2003	Burgersdorp F., South Africa
Tichvinskia vjatkensis	Ivachnenko 1973, 1979, Spencer and Benton 2000	Yarenskian Gorizont, Cis-Urals, Russia
Timanophon raridentatus	Ivachnenko 1979, Novikov 1991, Spencer and Benton 2000	Ustmylian Gorizont, Cis-Urals, Russia
Kapes spp.	Ivachnenko 1975, Novikov 1991, Novikov and Sues 2005, Spencer and Benton 2000, Spencer and Storrs 2002	Otter Sandstone F., UK; Yarenskian and Donguz gorizonts, Cis-Urals, Russia
*Thelephon contritus**	Modesto and Damiani 2003	Burgersdorp F., South Africa
Eumetabolodon bathycephalus*	Li 1983	Upper Heshanggou F., north China
Procolophon trigoniceps*	Gow 1977b, Carroll and Lindsay 1985, deBraga 2003	Sanga do Cabral F., Brazil; Katberg F., S. Africa; and Fremouw F., Antarctica
Thelerpeton oppressus*	Modesto and Damiani 2003	Burgersdorp F., South Africa
Teratophon spinigenis*	Modesto and Damiani 2003	Burgersdorp F., South Africa
*Pentaedrusaurus ordosianus**	Li 1989	Upper Heshanggou F., northern China
*Neoprocolophon asiaticus**	Young 1957	Middle or Upper Ermaying F., northern China
Sclerosaurus armatus	Von Huene 1912, Colbert 1946	Upper Buntsandstein, Switzerland
Scoloparia glyphanodon	Sues and Bird 1998	Wolfville F., eastern Canada
Leptopleuron lacertinum	Boulenger 1904, von Huene 1912, Spencer 2000	Lossiemouth Sandstone F., Britain
Soturnia caliodon*	Cisneros and Schultz 2003	Caturrita F., southern Brazil
Hypsognathus fenneri	Colbert 1946, Sues *et al*. 2000	Blomidon F., New Heaven F. and Passaic F., eastern Canada and USA

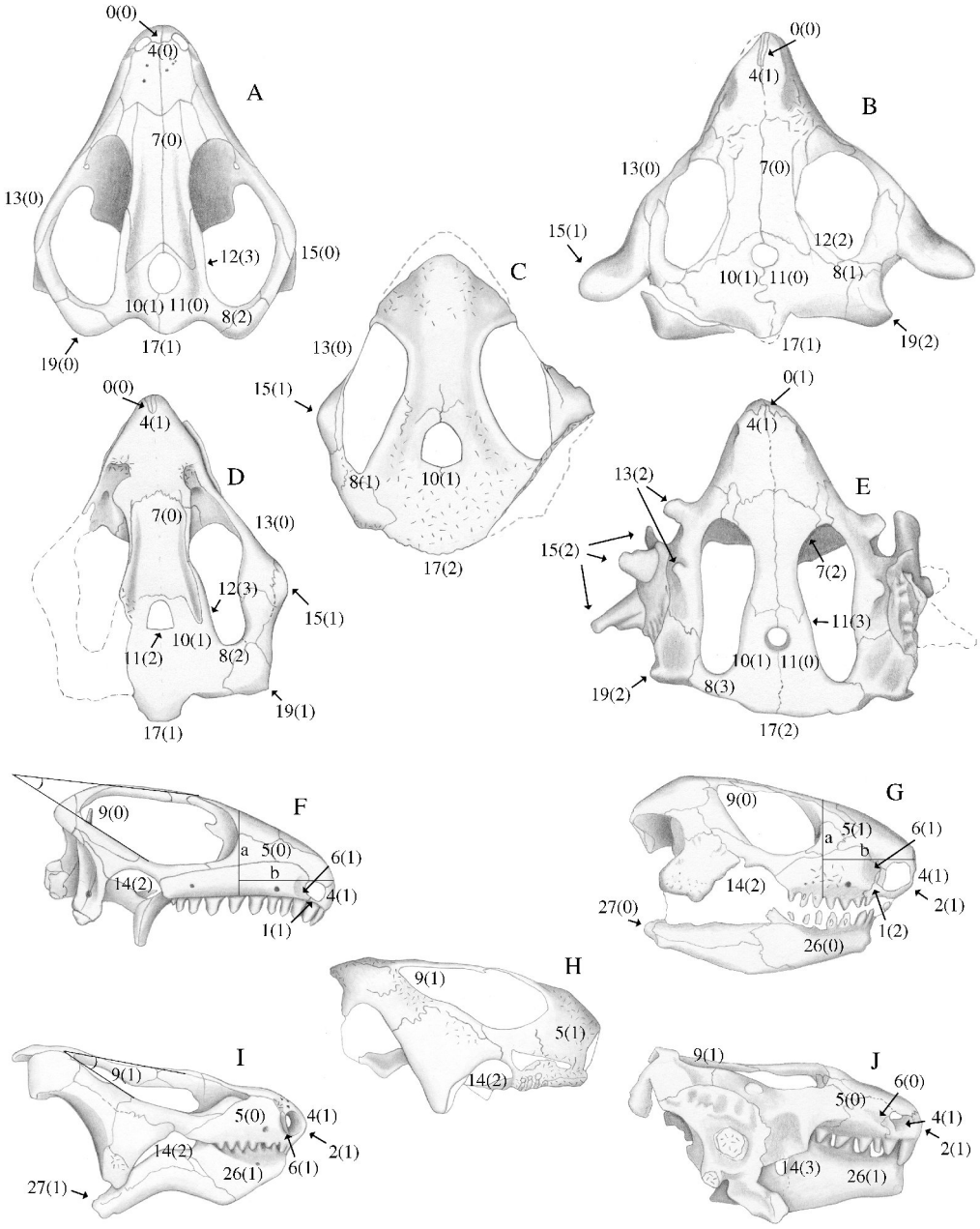


Figure 1. Skulls of procolophonids in dorsal (A-E) and right lateral (F-J) view, showing some characters used in this study (states indicated in brackets). A, *Tichvinskia vjatkensis* (PIN 954/1); B, *Procolophon trigoniceps* (NM QR3201); C, *Neoprocolophon asiaticus* (IVPP V866); D, *Pentaedrusaurus ordosianus* (IVPP V8735); E, *Hypsognathus fenneri* (YPM 55831); F, *Tichvinskia vjatkensis* (PIN 954/1); G, *Procolophon trigoniceps* (BMNH R4087); H, *Neoprocolophon asiaticus* (IVPP V866); I, *Pentaedrusaurus ordosianus* (IVPP V8735); J,

Hypsognathus fenneri (YPM 55831). All drawn from originals except *Tichvinskia*, redrawn from Ivakhnenko (1979), presumably reconstructed. Note that the sutures in *Neoprocolophon* differ from Young (1957). Coding of character 5: A vertical line (a) is traced from the cranial roof to the alveolar margin, tangencial to the anterior border of the orbitotemporal fenestra, and a line (b) is traced from (a) to the tip of the snout, perpendicular to (a). The snout is considered "long and flat" if (a) is shorter than (b); and "deep and short" if (a) is equal or longer than (b). Because the tip of the snout is not fully preserved in *Neoprocolophon*, coding of this character was based on a conservative estimation of the total length of the snout. Drawings not to scale.

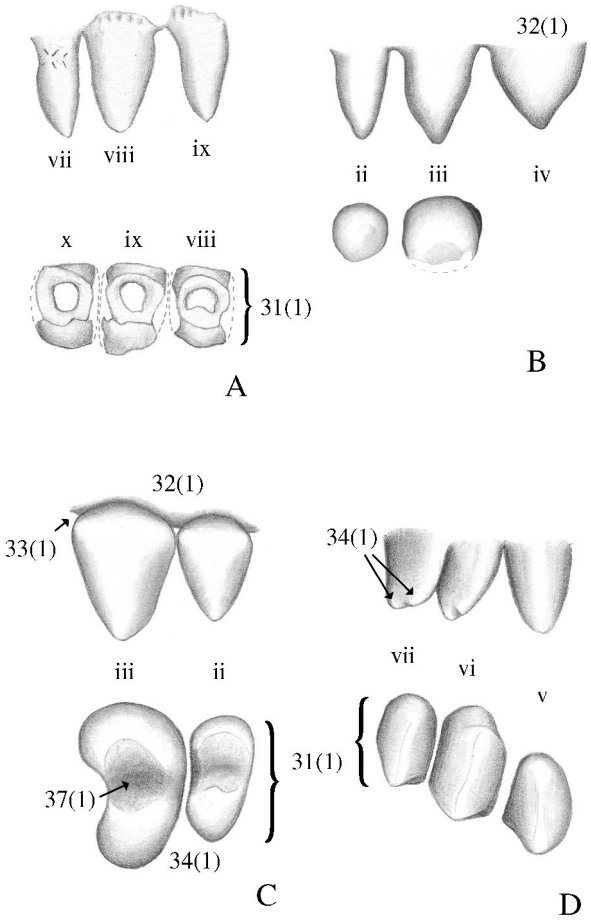


Figure 2. Maxillary teeth of procolophonids showing some characters from this study. A, *Coletta seca* (CGP/1/1003), left vii-ix in labial view, and right vii-ix in occlusal view (note that cusps are missing); B, Arcadia procolophonid (QMF 49510), left ii-iv in labial view, and left ii-iii in occlusal view; C, *Soturnia caliodon* (MCN PV2738) right ii-iii molariforms in lingual and occlusal views; D, *Procolophon trigoniceps* (SAM PK-K9998), right v-vii in labial (slightly posterior) and occlusal views. Drawings not to scale.

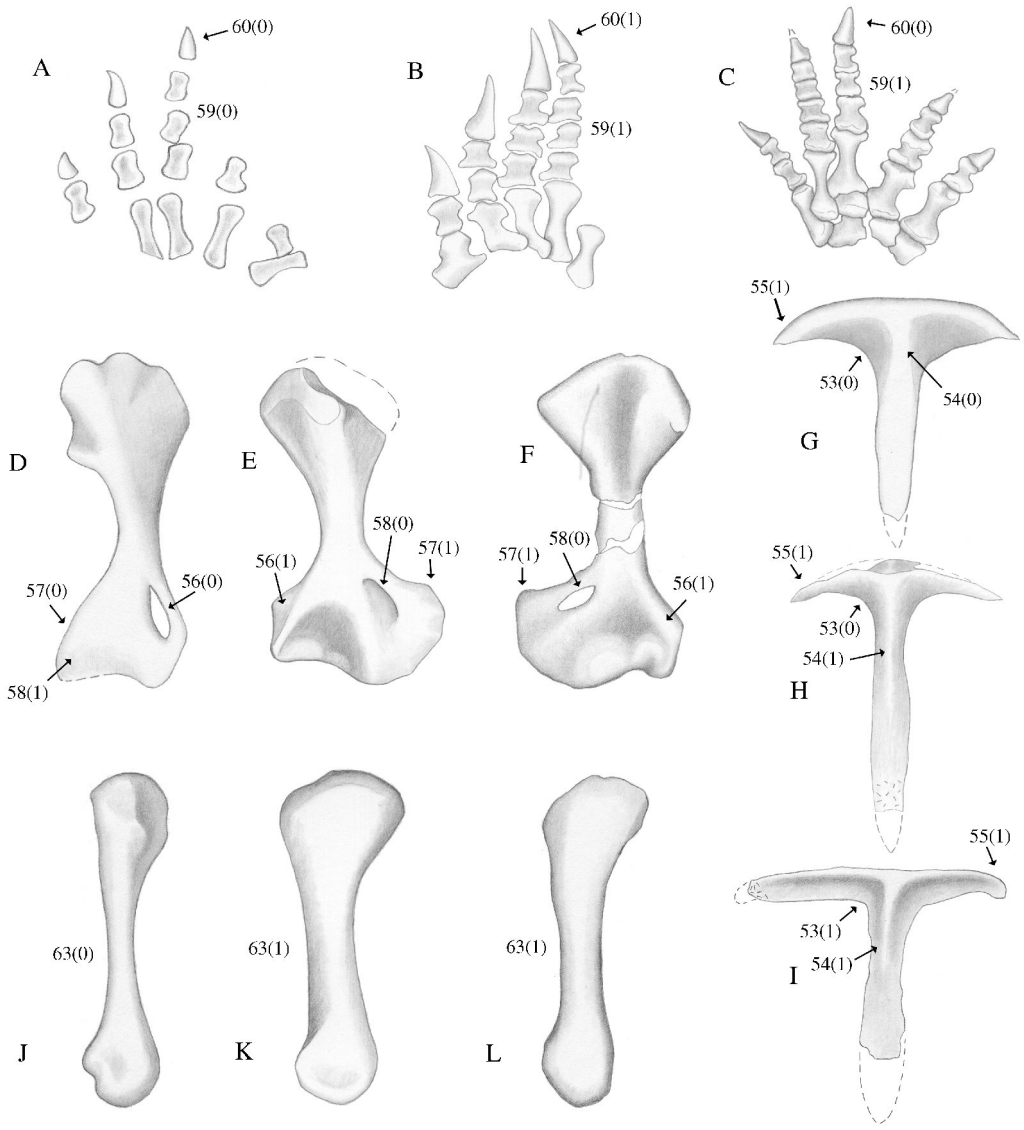


Figure 3. Postcranial elements of procolophonoids, showing some characters from this study. A-C, manus; D-F, humerus, G-I, interclavicle, J-L, femur. *Barasaurus besairiei*: A, manus (SAM PK-K8275); D, right humerus, dorsal view (SAM PK-K-8282); G, interclavicle, ventral view (SAM PK-K8276); J, right femur, anterior view (SAM PK-K-8282). *Procolophon trigoniceps* (BP/1/962): B, right manus, dorsal view; E, right humerus, ventral view; H, interclavicle, ventral view; K, right femur, anterior view. *Pentaedrusaurus ordosianus* (IVPP V8735): C, left manus, dorsal view; F, left humerus, ventral view (note that it differs from Li, 1989); I, interclavicle, ventral view; L, right femur, anterior view. Drawings not to scale.

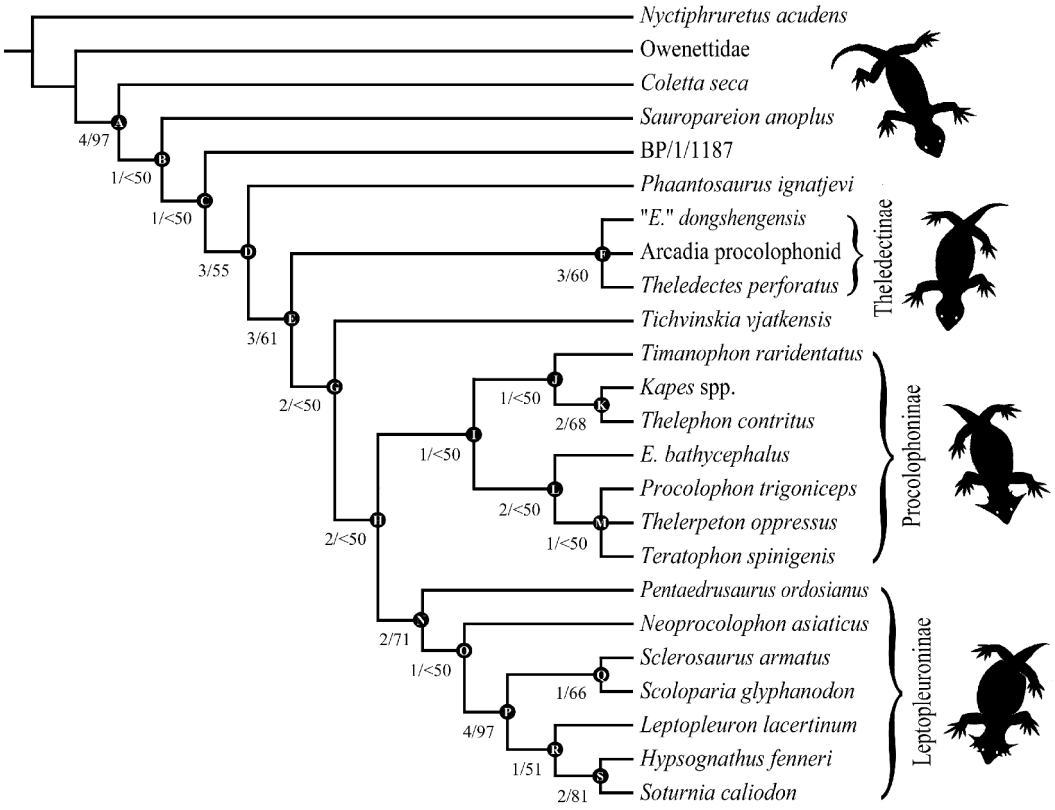


Figure 4. Single most parsimonious tree. Tree length=134 steps, consistency index (excluding uninformative characters) = 0.642, retention index = 0.796. DI and SR values are given next to each node (DI/SR, respectively). DI values were calculated from 6967 trees. SR was performed with 5000 replicates and 10 repetitions (p=0.33) under Traditional Search option (random addition sequences plus tree bisection-reconnection).

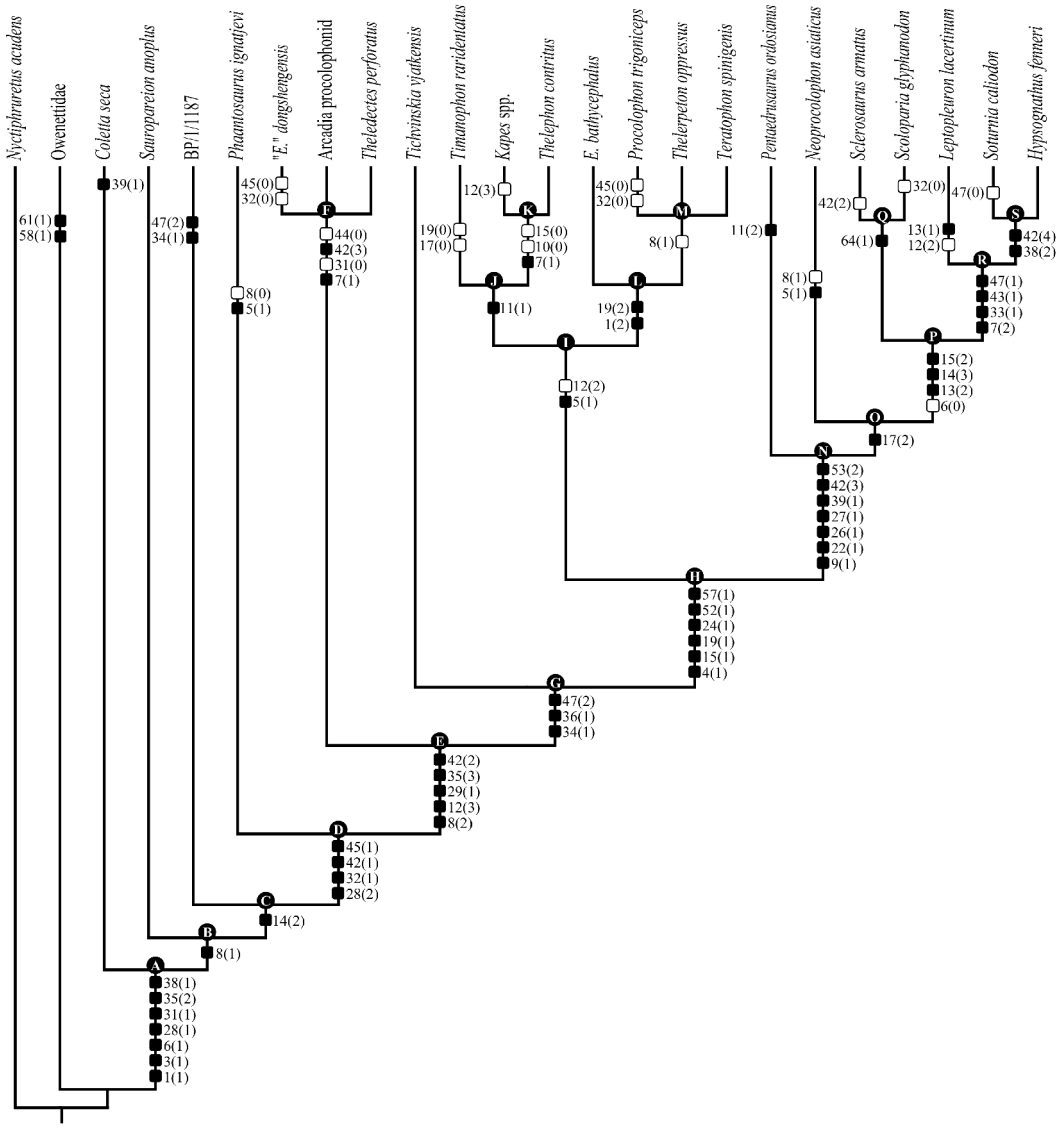


Figure 5. Single most parsimonious tree showing non-ambiguous synapomorphies for clades, and autapomorphies for terminal taxa. Reversals are indicated by white boxes.

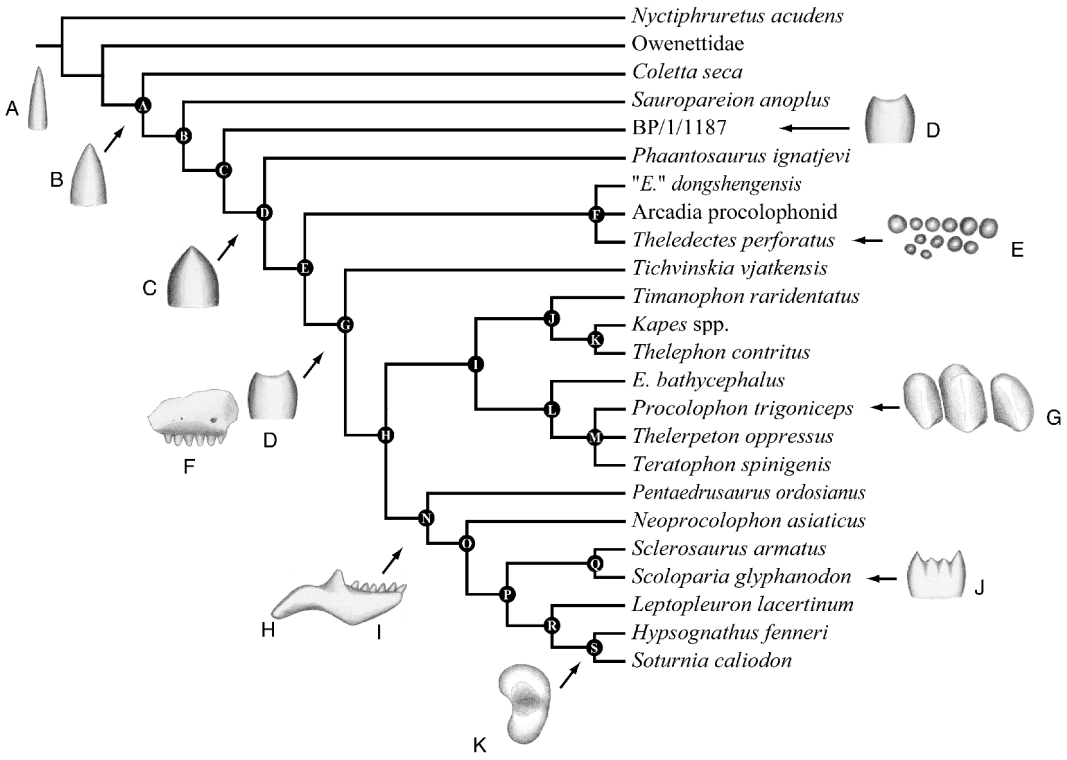


Figure 6. Single most parsimonious tree showing important feeding-related acquisitions in Procolophonids. A, thin conical tooth with circular base, medial (plesiomorphic state); B, tooth with labiolingually expanded base, mesial view; C, bulbous tooth, mesial view; D, bicuspid tooth, mesial view; E, multiple tooth rows; F, teeth inset from the lateral maxillary surface; G, molariforms with large occlusal areas; H, low articular; I, deep dentary; J, sharp, multiple cusped molariform; K, molariform with large occlusal area and a deep occlusal depression.

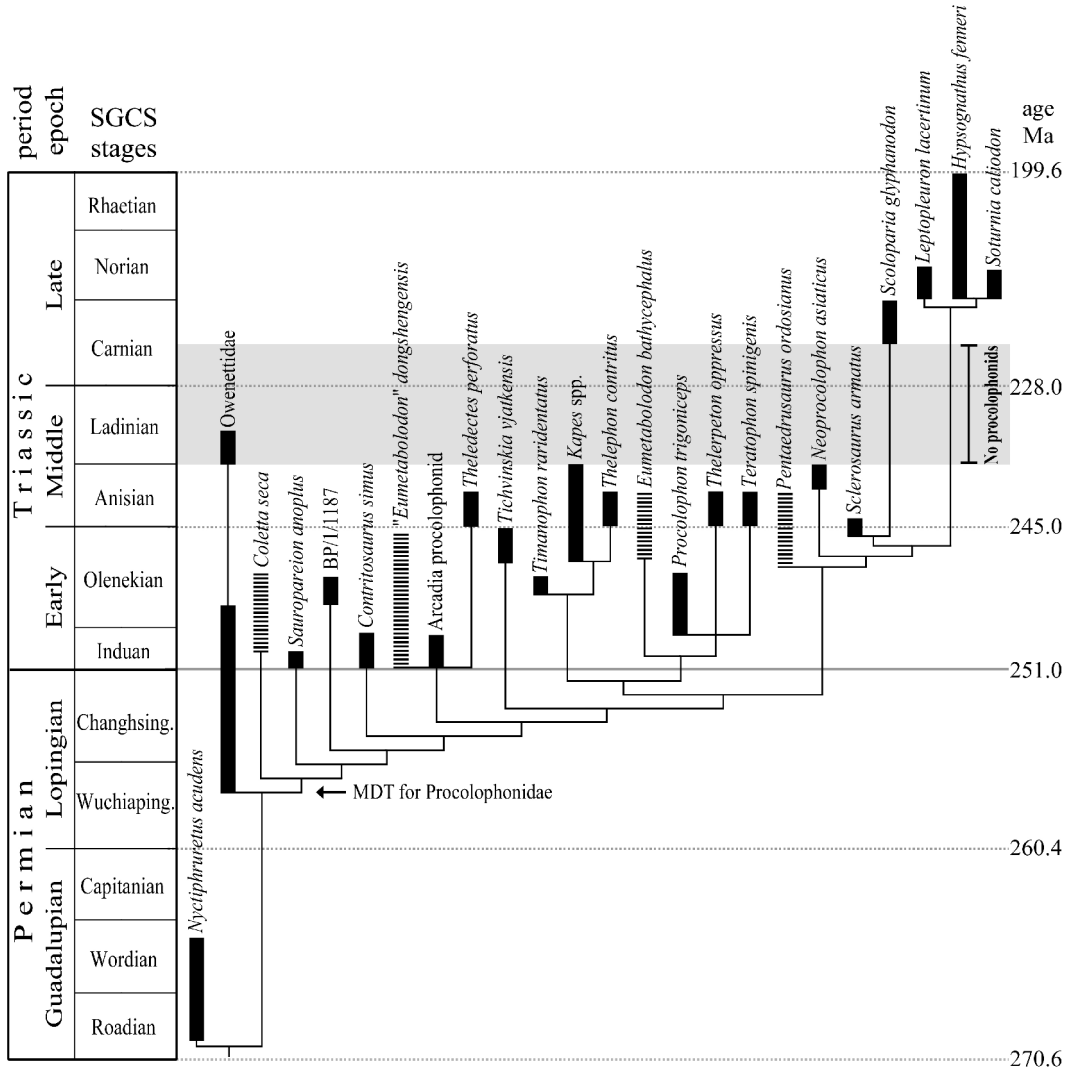


Figure 7. Single most parsimonious tree and the geological record of procolophonoids. Black bars represent the stratigraphic ranges, dashed bars represent uncertain stratigraphic ranges. The global hiatus of procolophonid records in Ladinian-Lower Carnian rocks is represented in gray. The minimum divergence time (MDT) of the Procolophonidae from the Owenettidae predicts the existence of a procolophonid as early as the Late Wuchiapingian. Stratigraphic ranges of taxa and geological dates based on: Li (1989), Lucas (1999), Smith (2000), Spencer and Benton (2000), Sues *et al*. (2000), Modesto *et al.* (2002), Cisneros *et al.* (2004), Rubert and Schultz (2004), Golubev (2005), Sennikov and Golubev (2005) and Hancox *et al.* (in press). SGCS (Standard Global Chronostratigraphic Scale) stages after Gradstein and Ogg (2004).

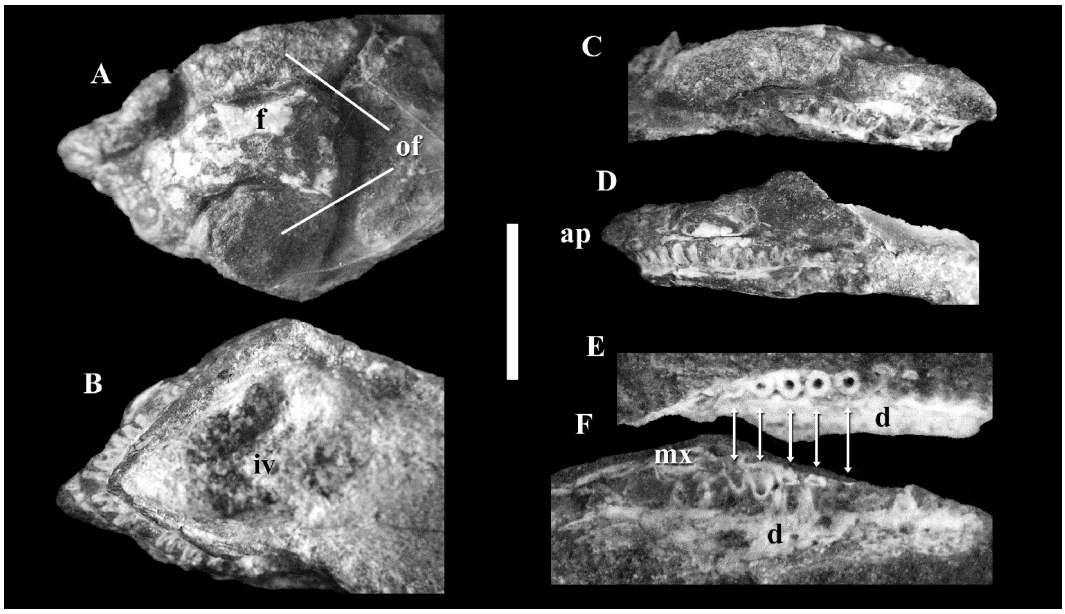


Figure 8. Cranium of *Spondylolestes rubidgei*, RC 3, holotype. **A**, dorsal; **B**, ventral; **C**, right lateral; and **D**, left lateral views of the skull. **E** and **F**, fragments of left maxilla and dentary in occlusion; **E**, dorsal view, showing maxillary dentition in basal cross-section; and **F**, lingual view showing both dentitions. Abbreviations: **ap**, ascendent process of the premaxilla; **d**, dentary; **f**, frontal; **iv**, interpterigoyd vacuity; **mx**, maxilla. Arrows indicate correspondence among maxillary teeth. Scale bar represents 5 mm for **A**-**D**, and 10 mm for **E** and **F**.

6 PAPER: A BASAL PROCOLOPHONID REPTILE FROM THE EARLY TRIASSIC OF SOUTH AFRICA

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Abstract. A new procolophonid reptile, *Kitchingnathus untabeni* gen. et sp. nov., is described from the uppermost strata of the *Lystrosaurus* Assemblage Zone of the Karoo Basin, South Africa. The new taxon co-occurs with the well known and more derived form *Procolophon trigoniceps*. *Kitchingnathus untabeni* is the basal member of a procolophonid clade that excludes *Coletta seca* and *Sauropareion anoplus* from South Africa. However, the new taxon exhibits some derived features such as the presence of transversally elongated, bicuspid teeth. Character optimisation indicates that bicuspid teeth were acquired independently by the new taxon, and originated twice in procolophonid evolution.

Key words. Parareptiles, procolophonids, *Lystrosaurus* Assemblage Zone, Triassic, South Africa.

Cisneros, J.C. A basal procolophonid reptile from the Early Triassic of South Africa. *Palaeontology* (submitted)

6.1 Introduction

The Early Triassic *Lystrosaurus* Assemblage Zone (AZ) of the Karoo Basin is characterised by relatively low tetrapod diversity and the dominant presence of the dicynodont *Lystrosaurus* (Kitching, 1977). Collecting in the *Lystrosaurus* AZ has traditionally been neglected due to the monotony of *Lystrosaurus* findings (Kitching, 1977), a genus that comprises up to 95% of the vertebrates in this horizon (Groenewald and Kitching, 1995). The procolophonoid *Procolophon* is also found in this biozone, occurring in isolated but usually large concentrations (Groenewald and Kitching, 1995). Procolophonoids are the only clade of parareptiles that survived the Permo-Triassic extinction event and constitute part of the Early Triassic recovery fauna of the Karoo Basin (Modesto *et al*., 2001; Smith and Botha, 2005). The group radiated throughout Pangaea, and its last members are known from Upper Triassic rocks in Brazil, Britain, Canada and USA (Sues *et al*., 2000; Cisneros and Schultz, 2003; Fraser *et al*., 2005).

In recent years renewed attention has been given to the tetrapods of the *Lystrosaurus* AZ, resulting in the description of the new procolophonoids *Owenetta kitchingorum* (Reisz and Scott, 2002), *Saurodektes rogersorum* (Modesto *et al*., 2003), *Coletta seca* (Gow, 2000) and *Sauropareion anoplus* (Modesto *et al*., 2001), and new temnospondyl amphibians (Damiani *et al*., 2000; Damiani and Welman, 2001). In 1977 Gow mentioned a procolophonid specimen from the *Lystrosaurus* AZ that differed from the genus *Procolophon* in the dentition. However, Gow (1977) concluded that this specimen was a juvenile *Procolophon* and the apparent differences were due to ontogeny. Later, Gow (2000) changed his view and stated the possibility that the fossil could represent a new taxon. Based on this specimen, a new genus of basal procolophonid is described herein.

Institutional abbreviations. BP, Bernard Price Institute for Palaeontological Research, Johannesburg; SAM, Iziko: South African Museum, Cape Town.

6.2 Systematic palaeontology

PARAREPTILIA Olson, 1947
PROCOLOPHONOIDEA Romer, 1956
PROCOLOPHONIDAE Lydekker, 1890

***Kitchingnathus* gen. nov.**

Etymology. In honour of the late James W. Kitching, a prominent South African palaeontologist and collector of the specimen; and from the greek *gnathus*, mandible.

Type species. *Kitchingnathus untabeni* sp. nov.

Diagnosis. Autapomorphies of the new taxon include: Six to seven conical teeth and nine to ten chisel-like bicuspid molariforms. Bicuspid molariforms smaller and thinner than in other procolophonids, with labial cusps taller than lingual cusps. A long posterior process of the maxilla that extends along the rim of the subtemporal emargination as much as the quadratojugal.

In addition, the new taxon differs from the similar form *Sauropareion anoplus* by having a broader subtemporal emargination and a posterior median parietal projection, and from *Coletta seca* by possessing a deeper cranium and bicuspid teeth. It is further distinguished from the co-occurring *Procolophon trigoniceps* by a number of characters (see below), including a longer snout and the absence of quadratojugal horns.

***Kitchingnathus untabeni* sp. nov.**
Figs 1-4
1977 *Procolophon trigoniceps* Gow text-fig. 6

Etimology. An isiZulu term meaning “from the mountain”, a reference to the locality where the fossil was collected.

Holotype. BP/1/1187, skull and partial postcranium (Text-fig. 1), in the collection of Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg. Collected by James W. Kitching in October of 1952.

Locality and horizon. Hobbs Hill (Windvogelsberg), west of Cathcart, Eastern Cape Province, South Africa; middle-upper Katberg Formation, Beaufort Group, Karoo Supergroup, uppermost *Lystrosaurus* AZ, late Early Triassic.

Remarks. Besides the holotype of *Kitchingnathus untabeni*, the locality Hobbs Hill has yielded several *Procolophon trigoniceps* specimens collected during field trips led by James W. Kitching in 1952 and 1966. Kitching (1977) assigned the fossiliferous horizons of this locality to the uppermost *Lystrosaurus* AZ. The matrix surrounding BP/1/1187 is a bright red sandstone, characteristic of the middle-upper Katberg Formation and lowermost Burgersdorp Formation (Johann Neveling pers. comm. 2006). In the Cathcart area only rocks of the Katberg Formation and Jurassic dolerites are exposed (Geological Survey of South Africa, 1976). Therefore, *Kitchingnathus untabeni* was most likely collected in the middle or upper horizons of the Katberg Formation. This stratigraphic assessment is consistent with the presence of the index genus *Procolophon* at the locality. The occurrence of *Procolophon* in South Africa is restricted to between the middle part of the Katberg Formation and the lowermost Burgersdorp Formation (Neveling, 2004; Smith and Botha, 2005).

6.3 Description

Cranium

The cranium of BP/1/1187 (Figs 1, 2) is compressed laterally and fractured loosely along the midline, resulting in the separation of right and left sides before burial of the specimen. Most of the left side of the cranium is missing or buried within the matrix, and some unidentified flat bones that lay below the posterior

margin of the right side of the cranium presumably belong to the left side. A tooth bearing fragment may represent a portion of the left maxilla exposed in medial view (Fig 1, ?lmx). The right side of the cranium has been carefully prepared (Fig. 2A) and provides most of the information for the new taxon.

Kitchingnathus possesses a gracile skull. The snout is elongated, and slightly deeper than in *Coletta seca*, being comparable to that of *Tichvinskia vjatkensis* from Russia (see Ivakhnenko, 1973). The external surface of the snout is not well preserved, and it is not possible to trace the sutures of the premaxilla, nasal, maxilla and frontal in this area. The external naris is subcircular. Although damaged, a depression is present on the anterior portion of the maxilla and probably part of the nasal, adjacent to the posterior margin of the external naris. No septomaxilla is preserved.

Sixteen upper right marginal teeth are present, being a relatively large marginal tooth count for a procolophonid. Only *Coletta seca* from South Africa is known to have a comparable upper tooth count, 15 and 16, on the left and right side respectively (Modesto *et al*., 2002). Owenettids, however, have considerably higher upper tooth counts (e.g. more than 30 in *Owenetta rubidgei*, Reisz and Scott, 2002). The premaxilla-maxilla suture is not preserved, but a maximum of four premaxillary teeth is likely. All premaxillary teeth and the first few maxillary teeth are conical. The conical tooth region comprises seven teeth, and extends to the level of the anterior maxillary foramen. Their apices are slightly recurved. These teeth are thicker than the conical teeth present in owenettids, but less bulbous than the conical teeth of *Procolophon*. The crown of the seventh tooth is preserved partially as a natural mould. There is a diastema between the seventh tooth and the eighth tooth. Although this space is large enough to hold another tooth, no socket or pulp is present. If the diastema is not the result of tooth replacement it may constitute an additional autapomorphy for *Kitchingnathus*. The molariform region comprises nine teeth. The crowns of the eighth and the sixteenth teeth, the latter being the last maxillary tooth, are fully exposed. These teeth are molariform, with labiolingually expanded bases the maximum width of

which occurs at the base. The crowns are bicuspid. The labial cusp is higher than the lingual cusp, and the cusps are connected by a labiolingual ridge.

The rim of the orbitotemporal fenestrae is formed by the lacrimal, prefrontal, parietal, postfrontal, jugal, and presumably the postorbital. Only portions of the lacrimal and prefrontal can be traced. As in other procolophonids, a small lateral extension of the frontal reaches the orbitotemporal fenestra, precluding the prefrontal and postfrontal from contact in dorsal view. The postfrontal is not fused to the parietal as in *Tichvinskia* (Ivakhnenko, 1973), *Kapes* (Novikov and Sues, 2004), *Hypsognathus* (Sues *et al*., 2000) and other genera. The postfrontal is long and narrow, decreasing in width towards its anterior edge.

The subtemporal emargination is broad, in contrast with the genus *Sauropareion*, in which the emargination is acute and narrow as in owenettids (Modesto *et al*., 2001). The subtemporal emargination is formed by the maxilla, jugal and quadratojugal. The posterior process of the maxilla is unusually long and thin, and contributes as much as the jugal to the border of the subtemporal emargination. In other procolophonids, the posterior process of the maxilla is shorter and contributes less than the quadratojugal, or is completely excluded from the rim of the subtemporal emargination. A portion of the transverse flange of the pterygoid or ectopterygoid can be seen through the subtemporal emargination, but it is not possible to identify the suture between these elements. The quadratojugal appears to be higher than wide, although its complete width cannot be assessed because the otic notch lays covered with matrix. The quadratojugal lacks the lateral spine characteristic of other procolophonids. Part of the quadrate is visible below the quadratojugal. The squamosal and postorbital are covered by the dislocated supratemporal.

The right half of the pineal foramen is present. It is essentially circular as in most procolophonids. The parietal is broad and has a long contact with the supratemporal. The fronto-parietal suture is not preserved. A smooth process extends from the posterior margin of the parietal which forms half of the median parietal projection present in many procolophonids. The large supratemporal

resembles very closely that of *Sauropareion*. It is essentially rectangular, its anteroposterior length being larger than its mesolateral length. The supratemporal possesses a flat occipital surface that is equivalent to approximately half of the dorsal surface. There is no evidence for postparietals.

Mandible

The right mandibular ramus (Figs 2B, 3A) is exposed in lateral view. The anterior and posterior portions of this ramus are missing, and its ventral surface is damaged. Posteriorly, a long element that lays partially below this ramus likely represents the dislocated quadrate process of the right pterygoid. Most of the dentary is present but its sutures with other elements in the mandible are poorly preserved. Parts of the splenial are visible through the damaged ventral portion of the mandible. Most of this bone was presumably covered in life by the dentary in lateral view. Thirteen teeth are preserved in the right dentary; the anteriormost teeth are missing. The first preserved tooth in the dentary is well exposed. It is monocuspid and conical, subcircular in basal cross-section, and its maximum diameter width occurs at the base. The two following teeth are partially covered by matrix, and they are likely conical in shape. Only one cusp is visible on each of them, positioned roughly at the centre of the crown. The fourth tooth preserved is molariform. It is labiolingually expanded and the only cusp preserved is positioned labially. The two following teeth are smaller in height and are probably replacement teeth. Their crowns, and those of the following teeth, were prepared. These are molariform, and, like in the upper teeth, the labial cusps are higher than the lingual cups and are connected by a labiolingual ridge.

The left ramus (Figs 2A, 3B-C) is exposed in medial view. It is heavily weathered and only part of the dentary is present. The teeth are fractured at the base and their pulp cavities are exposed. Their roots are shallow and firmly ankylosed to sockets, without space for periodontal ligament, a mode of implantation usually termed protothecodont (Small, 1997). Most crowns are well preserved. The dentition of this ramus is probably complete and it comprises 15 teeth. The three mesialmost

teeth are preserved mainly as natural moulds and are conical, presumably monocuspid. These are followed by four more conical, monocuspid teeth. Eight bicuspid molariforms are present. The last molariform is preserved as a mould.

Postcranium

The partial postcranium (Fig. 1) is exposed in dorsal view. Due to its poor preservation only preliminary observations can be made. The vertebral column was not preserved except for the sacrals, adjacent vertebrae, and a few isolated vertebrae. Some thoracic and sacral ribs are present, as well as gastralia. None of the thoracic ribs are preserved for their full length, so it is not possible to see if the thoracic rib cage is expanded as in derived procolophonids. Part of the pectoral girdle is present mainly as a mould. This includes the interclavicle, a portion of the left clavicle, and paired coracoids. The right coracoids are better preserved than the left ones. Both anterior and posterior coracoids are essentially rounded. Coracoids are not known in most procolophonids, but in *Procolophon* (BP/1/962) and in a specimen probably referable to *Teratophon spinigenis* (SAM-PK-K7711, pers. obs.), the posterior coracoid is anteroposteriorly elongated (deBraga, 2003, figs. 3, 5; note that this author assigns SAM-PK-K7711 to *Procolophon*).

The only visible portion of the pelvic girdle lies adjacent to the pectoral girdle. This may be the result of the specimen being in a curled-up position before dying and/or postmortem disarticulation. At least two sacral vertebrae can be distinguished based on the presence of sacral ribs. Both ribs are preserved on the first sacral vertebrae and a right rib lays on the second sacral vertebrae. The distal portions of these ribs are expanded and overlapping. A count of three sacral vertebrae, however, is likely. Three sacrals are normal for procolophonids and owenettids (see Ivakhnenko, 1979; Reisz and Scott, 2002; deBraga, 2003). Sacral ribs may have become detached from the third sacral vertebra. The right ilium is partially preserved. It is articulated to two sacral ribs and extends posteriorly parallel to the third putative sacral vertebra. The right femur is preserved in articulation with the ilium. A metapodial is preserved between the right femur and

the cranium, but it is not possible to confirm if it belongs to the forelimb or the hindlimb. Four digits have been tentatively identified in this metapodial.

6.4 Discussion

A cladistic analysis indicates that *Kitchingnathus untabeni* is a basal member of the Procolophonidae (Fig. 5, for details see Chapter 5). *Kitchingnathus* is the sister group of all procolophonids excluding *Coletta seca* and *Sauropareion anoplus*. Character optimisation suggests that the bicuspid marginal dentition present in *Kitchingnathus* arose independently. Bicuspid teeth are absent in all parareptile lineages except for the Procolophonidae and the Bolosauridae. In both groups, bicuspid teeth constitute a major acquisition that allowed the exploitation of durophagous and/or high-fibre herbivorous niches (Colbert, 1946; Gow, 1977b, Hotton, 1997).

Monocuspid teeth are the primitive condition in the sister group of *Kitchingnathus* (Fig. 5), a clade that has a decay index of three and is diagnosed by four non-ambiguous synapomorphies: (1) presence of three premaxillary teeth; (2) ten to 12 dentary teeth; (3) “prominently bulbous” teeth in the maxilla; and (4) “prominently bulbous” teeth in the dentary (a tooth is considered prominently bulbous when its maximum mesodistal length, measured at the mid level of the basal-apical length, is equivalent or superior to 75% the basal-apical length [see Chapter 5]). The analysis indicates that the bicuspid tooth condition arose again later in a clade that comprises the genus *Tichvinskia* together with the subdivisions Procolophoninae and Leptopleuroninae. Most procolophonids are included in this clade.

The feeding habits of *Kitchingnathus* were probably different from those of derived procolophonids, such as *Procolophon* or *Hypsognathus*, which are traditionally considered to be durophagous/herbivorous (Colbert, 1946; Gow, 1977). Unlike *Procolophon*, the cusps in the molariforms of the new taxon are sharp and the crowns are not notably worn, a condition that is not compatible with the practice of durophagy or high-fibre herbivory (Hotton, 1997). The presence of

numerous conical teeth and small molariforms with sharp cusps instead suggests an insectivorous niche. The dentition of *Kitchingnathus* indeed resembles that of modern hedgehogs, which use their teeth to tear and puncture a variety of invertebrates.

With the discovery of *Kitchingnathus untabeni*, there are now five procolophonoids known for the Katberg Formation of the Beaufort Group. The new taxon co-occurs with the well known and abundant form *Procolophon trigoniceps* at the type locality for *Kitchingnathus*, Hobbs Hill. Two other procolophonoids reported in this formation may overlap the stratigraphic range of the new genus. These are the recently described *Coletta seca* (Gow, 2000) and *Owenetta kitchingorum* (Reisz and Laurin, 2002). The precise stratigraphic position of *Coletta* within the Katberg Formation is uncertain (Modesto *et al*., 2002). *Owenetta kitchingorum* was first reported for the underlying Palingkloof Member of the Balfour Formation (Damiani *et al*., 2003) but there is a record probably in the lower or middle part of the Katberg Formation (Abdala *et al*., 2006). The procolophonid *Sauropareion anoplus*, also known from the Palingkloof Member, has been recently reported for the Lower Katberg Formation, below the First Appearance Datum of *Procolophon trigoniceps* (Modesto *et al*., 2006).

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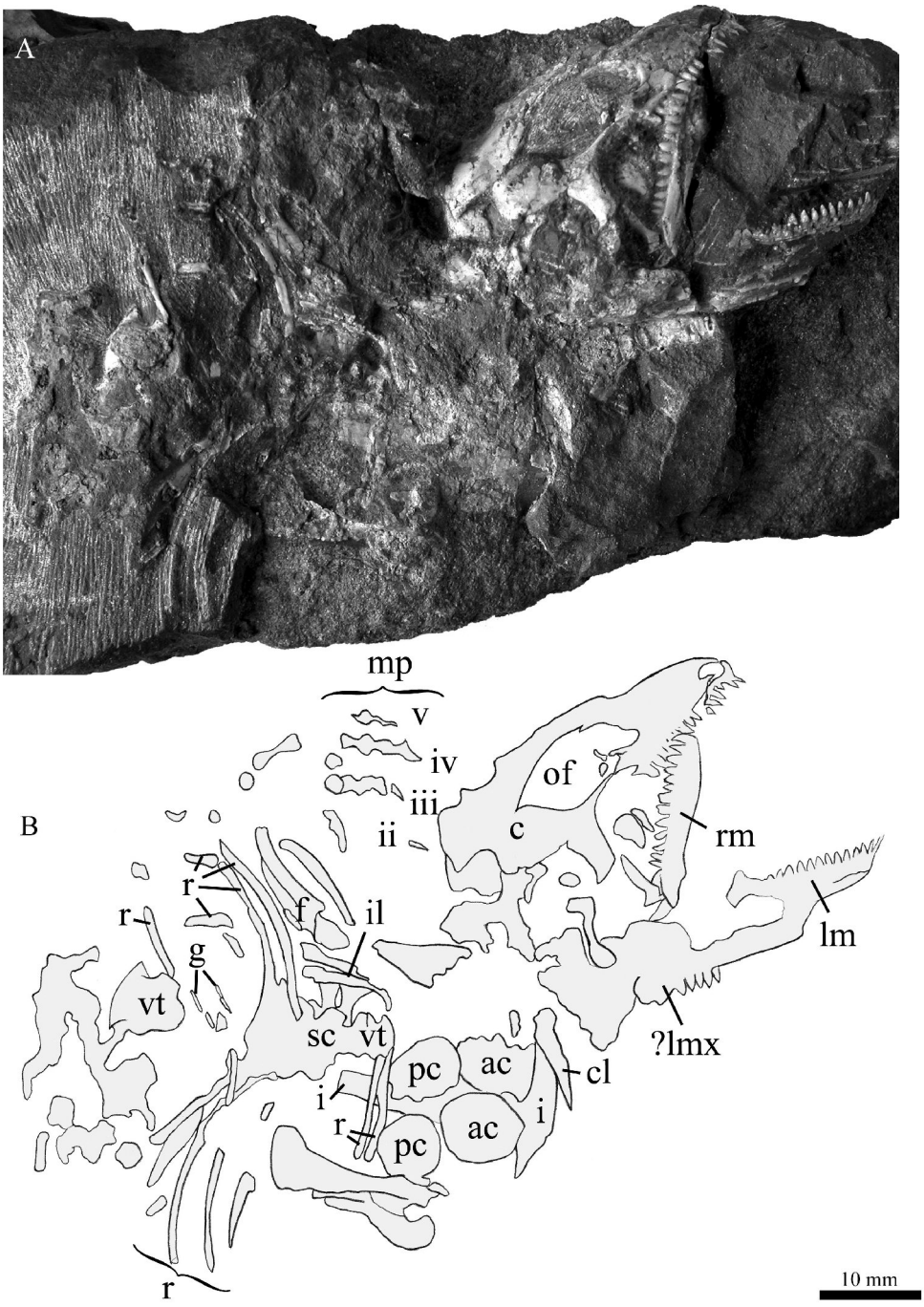


Figure 1. A, *Kitchingnathus untabeni* n. g. n. sp., Lower Triassic, South Africa, BP/1/1187, holotype, photograph of the skeleton; B, outline of the skeleton. Abbreviations: ac, anterior coracoid; c, clavicle; cr, cranium; g, gastralia; i, interclavicle; il, ilium; f, femur; lm, left mandibular ramus; lmx, left maxilla; mp, metapodial; of, orbitotemporal fenestra; r, rib; rm, right mandibular ramus; sc, sacrum; vt, vertebra. Digits are identified with Roman numerals ii-v. Postcranial bones that could not be identified are not labelled.

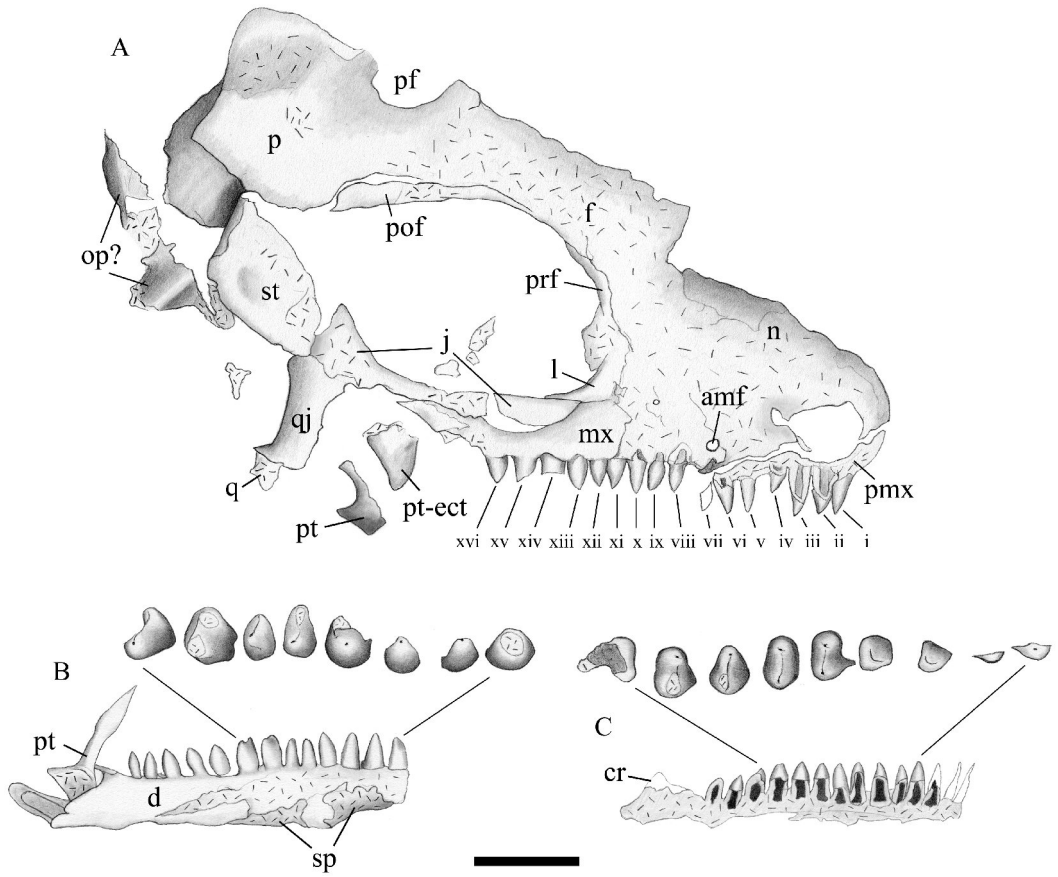


Figure 2. *Kitchingnathus untabeni* n. g. n. sp., Lower Triassic, South Africa, BP/1/1187, holotype. A, cranium, right view. B, right mandible in lateral view and selected teeth in occlusal view. C, left mandible in medial view and selected teeth in occlusal view. Abbreviations: amf, anterior maxillary foramen; d, dentary; cr, coronoid; f, frontal; j, jugal; l, lacrimal; mx, maxilla; n, nasal; op, opisthotic; p, parietal; pf, pineal foramen; pmx, premaxilla; pof, postfrontal; prf, prefrontal; pt, pterygoid; q, quadrate; qj, quadratojugal; sp, splenial; st, supratemporal; ect, ectopterygoid. Unshaded surfaces represent features preserved as natural casts. Roman numerals indicate tooth positions. Scale bar represents 5 mm, except for dentitions in occlusal view where it represents 2 mm.

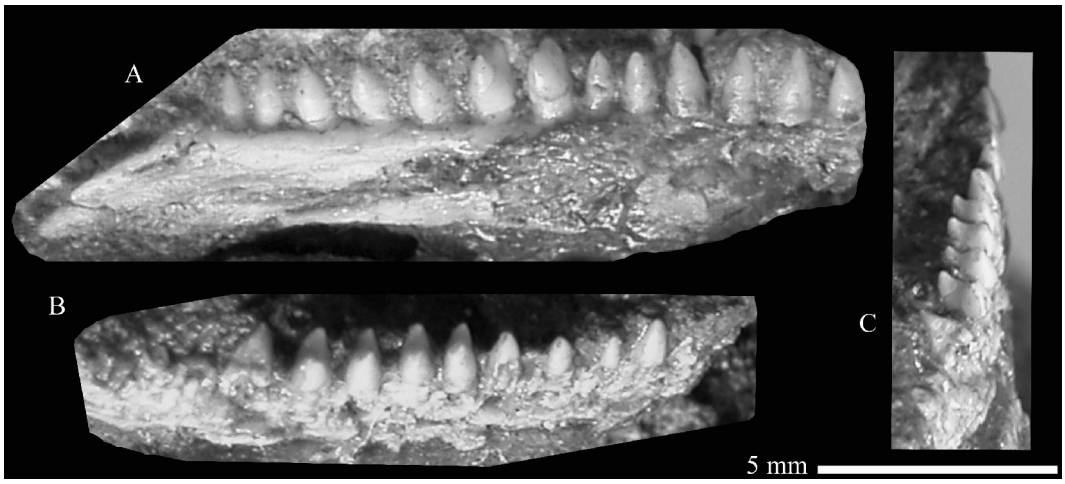


Figure 3. *Kitchingnathus untabeni* n. g. n. sp., BP/1/1187. Photographs of lower dentition. A, right mandible, lateral view. B, left mandible, dorsolateral view. C, left mandible, posterodorsal view.

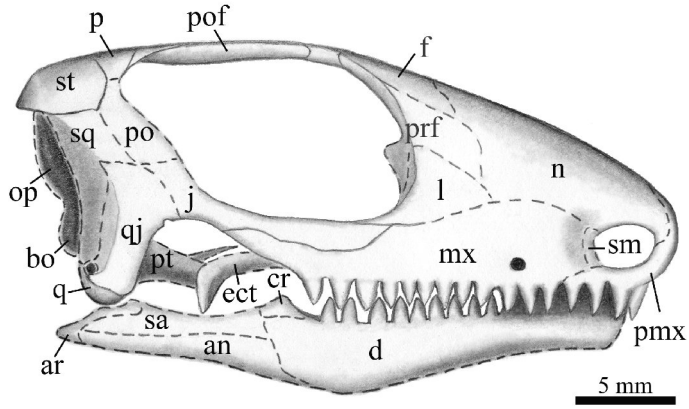


Figure 4. *Kitchingnathus untabeni* n. g. n. sp., BP/1/1187. Reconstruction of the skull in lateral view. Abbreviations: an, angular; ar, articular; bo, basioccipital; d, dentary; cr, coronoid; ect, ectopterygoid; f, frontal; j, jugal; l, lacrimal; mx, maxilla; n, nasal; op, opisthotic; p, parietal; pf, pineal foramen; pmx, premaxilla; po, postorbital; pof, postfrontal; prf, prefrontal; pt, pterygoid; q, quadrate; qj, quadratojugal; sa, surangular; sq, squamosal; st, supratemporal; ect, ectopterygoid.

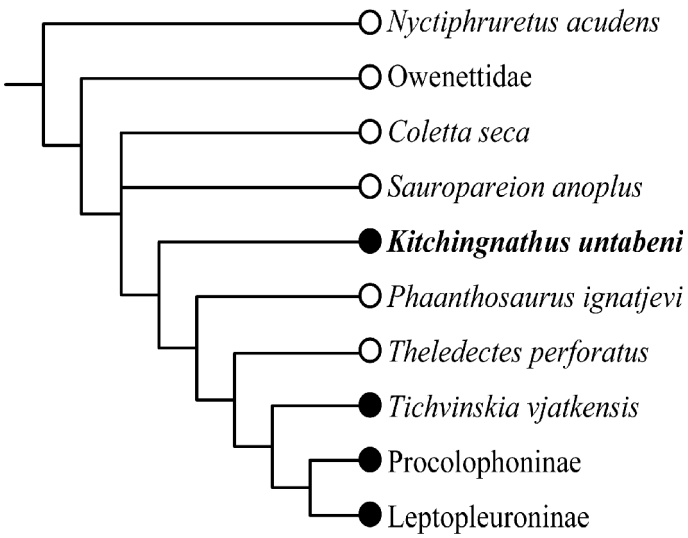


Figure 5. Simplified cladogram of procolophonid relationships. The presence of bicuspid marginal teeth is indicated by closed circles. For details see Chapter 5.

7. DISCUSSION

This research on procolophonoid parareptiles has highlighted and clarified aspects relating to their morphology, which in turn have provided a framework for performing more comprehensive phylogenetic analyses. Biogeographic and biostratigraphic implications of this study are summarized below.

7.1 Considerations on morphology and evolution

The presence of temporal fenestration in the owenettid *Candelaria barbouri* and in some specimens of the genus *Procolophon* is a remarkable characteristic, and draws attention to the presence of this character in other parareptilian clades. Temporal fenestrae are also known to be present in bolosaurids, a clade now identified as a member of the Parareptilia (Berman *et al*., 2000). This group was not considered in the paper presented in Chapter 3. In addition, the presence of a temporal fenestra was also recently documented for the "nycteroleter" *Macroleter poezicus* from the Middle Permian of Russia (Tsuji, 2005). The increasing number of reports of a temporal opening in parareptilian lineages adds weight to the hypothesis proposed in Chapter 3 that this structure may in fact be a primitive feature for most parareptiles.

The presence of a temporal fenestra in *Candelaria* and *Procolophon* is an independent acquisition as these genera constitute derived taxa within Owenettidae and Procolophonidae respectively. Furthermore, the most primitive members of these clades do not possess temporal openings. Despite the presence of a temporal fenestra in *Procolophon laticeps*, this species has been synonymized with the type species *P. trigoniceps*, and is therefore no longer considered valid (see Chapter 4). Nevertheless, this synonymy does not invalidate the discussion presented in Chapter 3, namely that the occurrence of temporal openings is a frequent phenomenon among "anapsids". Hence, the presence of a temporal fenestra is a valid, polymorphic character in *P. trigoniceps*.

Another character that has important implications is the appearance of bicuspid marginal dentition in procolophonids. Following to the phylogenetic relationships presented in Chapter 6, the bicuspid dentition of the new genus *Kitchingnathus* (BP/1/1187) was acquired independently from all other procolophonids. This does not represent the first instance of parallel acquisition of this kind of dentition among parareptiles because bolosaurids also developed independently expanded bicuspid teeth, similar to those of the procolophonids.

The acquisition of transversally expanded bicuspid teeth played a major role in procolophonid evolution, pre-adapting the group for processing high-fibre items. Procolophonids are notoriously the first Triassic tetrapod group to explore this ecological niche. The appearance of transversally expanded molariforms in procolophonids is followed by a number of adaptations to improve jaw mechanics (see Chapter 5) and the expansion of the thoracic cage. This last character suggests the presence of endosymbiotic organisms (Hotton *et al*., 1997). These adaptations proved to be important for the group as they are present in most members including the highly successful *Procolophon trigoniceps*.

7.2 Biostratigraphic remarks

7.2.1 The appearance of bicuspid dentition

The presence of bicuspid dentition in procolophonids has been considered relevant for biostratigraphic subdivision of the East European Platform (e.g. Shishkin *et al*., 2000). These authors note that the occurrence of *Phaanthosaurus* and *Contritosaurus* (the latter is considered a junior synonym of the former [Spencer and Benton, 2000]), is restricted to the Induan. These are the only Triassic procolophonids with monocuspid marginal teeth in the East European Platform. The appearance of the first procolophonid with bicuspid teeth, "*Tichvinskia*" *jugensis* (the genus is considered paraphyletic by Spencer and Benton, 2000), occurs in the Rybinskian Gorizont, a biostratigraphic unit that is equivalent to the earliest Olenekian. This taxon is succeeded stratigraphically by

Orenburgia concinna, *O. bruma*, *Timanophon raridentatus*, *Tichvinskia vjatkensis*, *Kapes amaenus*, *K. majmesculae* and *K. komiensis.* All these genera have bicuspid teeth and occur in Olenekian gorizonts, with *Kapes majmesculae* occurring also in the Anisian Donguz Gorizont. The presence of isodont and heterodont procolophonids has been used to distinguish between Induan and Olenekian strata in the East European Platform by Borsuk-Białynicka *et al*. (1999, 2003). Those authors proposed an Olenekian age for a microvertebrate assemblage in Poland, mainly based on procolophonid tooth-bearing fragments not identifiable at the generic level.

This biostratigraphic pattern seems valid in Gondwana as well, even when taking into consideration the independent acquisition of bicuspid teeth by the new taxon *Kitchingnathus untabeni*. The South African genera *Kitchingnathus* and *Procolophon* (the latter known also from Brazil and Antarctica) represent the earliest known heterodont procolophonids in Gondwana, and because of their occurrence in upper Katberg Formation strata, they are likely to extend into the Olenekian. The underlying Palingkloof Member of lowermost Triassic age yields owenettids and the procolophonid *Sauropareion*, all with monocuspid dentitions. Earliest Triassic rocks in Australia yield an undescribed procolophonid which also has monocuspid teeth. It seems that, on a global scale, bicuspid dentition emerges after the Induan in at least two different procolophonid lineages.

Biostratigraphic application of the two evolutionary stages in procolophonoid dentition should be done with caution, because some lineages with monocuspid teeth survived beyond the Induan. These include *Theledectes peforatus*, the procolophonid with multiple rows of teeth from the *Cynognathus* Assemblage Zone (Anisian) of South Africa and the owenettid *Candelaria barbouri* from the Ladinian of southern Brazil. Thus, whereas the occurrence of procolophonids with bicuspid dentition may be a reliable indicator of post-Induan rocks, procolophonoid monocuspid teeth do not necessarily indicate pre-Olenekian rocks.

7.2.1 The age of the Sanga do Cabral Formation

The absence of the dicynodont *Lystrosaurus* from the Sanga do Cabral Formation of the Paraná Basin of Brazil is noteworthy considering that *Procolophon* remains are common in this unit. *Lystrosaurus* represents by far the most abundant component of the *Lystrosaurus* AZ in the Karoo Basin (Groenewald and Kitching, 1995) where *Procolophon* occurs. Recent work in Karoo strata has shown that *Lystrosaurus* reaches its peak of abundance in the lower part of the Katberg Formation whereas *Procolophon trigoniceps* is absent in the Palingkloof Member of the Balfour Formation and the lowermost Katberg Formation (Botha and Smith, 2006; see Chapter 4). *Procolophon* reaches its peak of abundance in the upper part of this formation, a horizon in which *Lystrosaurus* is rare or absent, this horizon has been informally termed "*Procolophon* abundance zone" (Neveling, 2004). The common occurrence of *Procolophon* in the Sanga do Cabral Formation and the current absence of confirmed *Lystrosaurus* records in this unit suggests that its fauna can be correlated with the "*Procolophon* abundance zone" of Neveling (2004) that is present in the upper part of the Katberg Formation.

7.2.2 The Ladinian-Carnian hiatus of procolophonids

Procolophonids had a global distribution during the Triassic. In this context, the absence of procolophonid records in Ladinian and Lower Carnian rocks is notable. This long procolophonid hiatus reflects at least in part the scarcity of tetrapod records in rocks of this age in South Africa and Russia, the two countries that produce most procolophonid finds. Rocks of this age are represented in Russia by the Bukobay Gorizont (Shishkin *et al*., 2000). In this unit tetrapods occur in disarticulated, fragmentary state, and the reptiles found have been poorly studied (Shishkin *et al*., 2000). In South Africa this horizon is represented by the Molteno Formation but the tetrapod record of this unit constitutes only of dinosaur footprints (Raath *et al*., 1990). However, It is not possible to explain the absence of procolophonids in other regions where Ladinian rocks have produced tetrapods in abundance, such as South and North America. A taphonomic and/or collecting

artefact may be related to the current absence of procolophonids in these continents.

7.3 Biogeography

The results of this study suggest that the Procolophonidae, as defined herein, originated and underwent early diversification in Gondwana. The sister group of the Procolophonidae, the Owenettidae, has only Gondwanan members (Figure 1). These are found in Brazil, South Africa and Madagascar, and include two Permian forms, the South African *Owenetta rubidgei* and the Malagasy *Barasaurus besairiei*. The first appearance datum of *Owenetta rubidgei* is in the Upper Permian *Cistecephalus* Assemblage Zone (Kitching, 1977) and this taxon constitutes the oldest safely identified procolophonoid.

The three most basal procolophonids included in the phylogenetic analysis in Chapter 6 are also Gondwanan, namely *Coletta seca*, *Sauropareion anoplus* and the new taxon *Kitchingnathus untabeni*, all from South Africa. None of these genera are from the Permian. The only Permian procolophonids recognized in this work are the South African *Spondylolestes rubidgei* and the Russian *Kinelia broomi*. The presence of a Late Permian Russian procolophonid complicates the hypothesis of a Gondwanan origin for the group, specially because of the uncertain phylogenetic position of this taxon. However, it seems unlikely that the Procolophonidae originated in Laurasia since there are no records of Laurasian owenettids. Based on the available data, it seems that owenettids and procolophonids split during the Late Permian in Gondwana, with a subsequent migration of the latter clade colonized Laurasia soon thereafter. *Kinelia broomi* is likely a more derived taxon than *Spondylolestes rubidgei*, as suggested by the presence of teeth with labiolingually expanded bases, in contrast with the teeth with circular bases in the South African species.

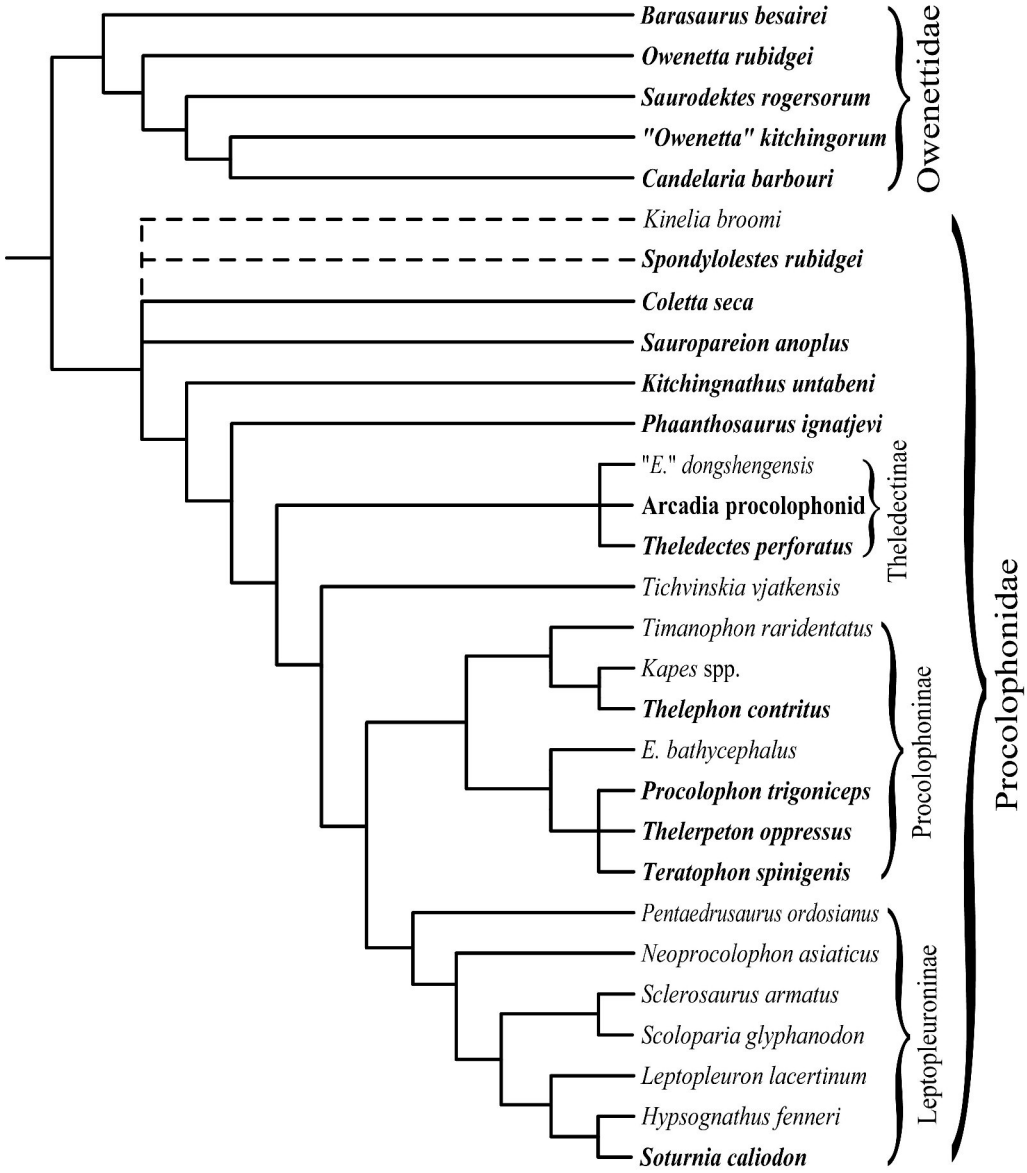


Figure 1. Composite cladogram of the Procolophonoidea, adapted from the phylogenetic analyses performed in chapters 3 and 6. *Spondylolestes rubidgei* and *Kinelia broomi* were not included in the cladistic analyses and their phylogenetic positions are tentative.

8. CONCLUSIONS

The presence or absence of a temporal fenestrae can no longer be used as a major criterion for classification of reptiles. The increasing reports of "anapsid" reptiles with temporal fenestration makes it desirable to abandon the use of the term "anapsid" with taxonomic connotations. A single species of the genus *Procolophon* is recognized across Gondwana. The relationships of the Procolophonidae are more firmly resolved. A phylogenetic analysis reveals that Procolophoninae and Leptopleuroninae are valid monophyletic groups but Spondylolestinae is paraphyletic. The appearance of bicuspid dentition in procolophonoids during the Olenekian plus the broad geographical distribution of some taxa such as *Procolophon*, *Kapes* and *Hypsognathus* make the group relevant in continental biostratigraphy. A review of procolophonid findings worldwide reveals a hiatus of records in the Ladininan and part of the Carnian. The genus *Spondylolestes* is considered a valid taxon and it represents the only known Permian procolophonid in Gondwana. The new taxon *Kitchingnathus untabeni*, in addition to other recent discoveries in the *Lystrosaurus* Assemblage Zone, highlights the potential of this biozone traditionally considered to have a low tetrapod diversity. Procolophonoids were the most diverse and successful clade of the Parareptilia. A plethora of feeding related adaptations combined with a small size seem to be the most important factors for the survival of this group from Late Permian to Late Triassic times.

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APPENDIX: PUBLISHED PAPERS AND PARALLEL PRODUCTION

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