

# PHYLOGENETIC RELATIONSHIPS OF PROCOLOPHONID PARAREPTILES WITH REMARKS ON THEIR GEOLOGICAL RECORD

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**SYNOPSIS** The phylogenetic intrarelations of procolophonid parareptiles are determined via a comprehensive cladistic analysis using a data matrix of 21 taxa and 58 characters. Most taxa are included for the first time in a phylogenetic analysis and 27 characters are novel. The relationships within the group are more firmly resolved than in previous analyses. Procolophoninae and Leptopleuroninae, two of the three traditional subdivisions of the Procolophonidae, are valid monophyletic groups, but Spondylolestinae is polyphyletic. The Chinese genera *Pentaedrusaurus* and *Neoprocolophon* are the most primitive members of the Leptopleuroninae. A new group, Theledectinae, is erected. The latter clade consists of small procolophonids with a reduced marginal dentition and wide bulbous monocuspid teeth. *Eumetabolodon* from China and the former genus '*Thelegnathus*' from South Africa are shown to be polyphyletic. 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-fibre herbivory. The scarcity of Permian records of procolophonids is examined and the genus *Spondylolestes* from the Upper Permian of South Africa is considered to be a valid taxon with procolophonid affinities. Finally, a review of the records from the Middle and Upper Triassic reveals a procolophonid global hiatus of more than 15 Ma in Ladinian–Lower Carnian rocks.

**KEY WORDS** Parareptilia, Procolophonidae, Triassic, phylogeny

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## INTRODUCTION

The interrelationships of the Parareptilia have been a subject of 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 & Reisz 1995; Lee 1995; deBraga & Rieppel 1997; Berman *et al.* 2000; Modesto 2000). However, whereas the phylogeny of the Pareiasauridae, a major parareptile branch, acquired resolution through the work of Lee (1997a), no comprehensive cladistic analyses of the Procolophonidae have been published.

Procolophonids represent the most successful radiation of Parareptilia. Extending beyond the Mother of Mass Extinctions (Erwin 1993) 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 finds come from the South African Karoo, the Russian Cis-Urals and the Newark Supergroup in Canada and the USA. Typical procolophonid features include: small size (adults ranging from ~150–400 mm), elongated orbits (orbitotemporal fenestrae), bulbous and/or bicuspid molariform teeth and a short tail; some forms possess lateral cranial spikes 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 & Laurin 1991; Laurin & 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 (Gow 2000; Spencer 2000; Spencer & Benton 2000; Sues *et al.* 2000; Bulanov 2002; Modesto *et al.* 2002; Spencer & Storrs 2002; Cisneros & Schultz 2003; Modesto & Damiani 2003; Cisneros *et al.* 2004; Piñeiro *et al.* 2004; Fraser *et al.* 2004;

Novikov & Sues 2005). 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 data matrices. In this study, a larger analysis of procolophonid relationships is presented. Many 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, Grahamstown, South Africa.  
**BMNH** = Natural History Museum, London, UK.  
**BP** = Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, 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.  
**RC** = Rubidge Collection, Camdeboo Municipality, Eastern Cape, South Africa.  
**SAM** = South African Museum, Cape Town, South Africa.  
**YPM** = Yale Peabody Museum, New Haven, USA.

## TAXONOMIC BACKGROUND AND PREVIOUS ANALYSES

Earlier classifications of procolophonid-like taxa usually distinguished between a group of mainly Triassic taxa and one or more groups of 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 recognise divisions within the Triassic procolophonids. He 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) did not consider the Permian forms *Owenetta*, *Barasaurus* and *Nyctiphruetus* to be procolophonids and he placed them in the family Nyctiphruetidae. The Permian *Nycteroleter* and the problematic *Sclerosaurus* from the Buntsandstein were placed in their own families, Nycteroleteridae and Sclerosauridae, respectively. This classification was retained by Ivakhnenko (1987) with minor changes.

Laurin & Reisz (1995), in their cladistic analysis of amniotes, did not include the genera *Owenetta*, *Barasaurus*, *Nyctiphruetus* or *Nycteroleter* in their definition of the Procolophonidae. The genus *Owenetta* had previously been considered to be a procolophonid by these authors (Reisz & Laurin 1991). Lee (1995, 1997a) included those four genera, as well as the Procolophonidae, as operational taxonomic units (OTUs) in his phylogenetic analyses. That author found an *Owenetta*–*Barasaurus* clade and a *Nyctiphruetus*–*Nycteroleter* clade, the former being more closely related to the Procolophonidae than the latter. He applied the names Owenettidae to the *Owenetta*–*Barasaurus* node, Nyctiphruetidae to the *Nyctiphruetus*–*Nycteroleter* node and Procolophonoidea to 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 & Rieppel (1997), an Owenettidae–Procolophonidae clade was also found. Those authors did not use owenettid genera as OTUs, nor did they consider *Nyctiphruetus* or *Nycteroleter*. Except for Reisz & Laurin (1991), who used information from *Owenetta* to code the Procolophonidae in their analysis, all other authors (Laurin & Reisz 1995; Lee 1995, 1997a; deBraga & 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 procolophonoids *Coletta* and *Saur-opareion*, as well as 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 *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*). That analysis corrob-

orated, for the most part, the results from Modesto *et al.* (2001, 2002), producing a monophyletic Procolophonidae and Owenettidae, with 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 by 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 for the relationships among the outgroups.

### Nomenclatural remarks

The current definition of Procolophonidae is problematic. Laurin & Reisz (1995) defined Procolophonidae as ‘the last common ancestor of *Anomoiodon*, *Burtensia*, *Candelaria*, *Conritosaurus*, *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 & Damiani 2003), whereas *Candelaria* and *Microphon* have been identified as, respectively, an owenettid and a seymouriamorph (Bulanov 2002; Cisneros *et al.* 2004). Procolophonidae is here defined as all taxa more closely related to *Procolophon trigoniceps* Owen, 1876 than to *Owenetta rubidgei* Broom, 1939.

## ANALYSIS AND METHODS

Relationships were evaluated using Tree Analysis Using New Technology (TNT) Version 1.1 for Windows (Goloboff *et al.* 2003a). The search was performed with all characters having equal weights, using Implicit Enumeration (Hendy & Penny 1982), a branch-and-bound algorithm which provides exact solutions. 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 & Scharff 1994). Two measures of support were used to evaluate the tree: decay index (DI: Bremer 1994) and symmetric resampling (SR). SR is not influenced by characters that are uninformative or irrelevant to the monophyly of a group, or by ‘ordered’ characters. Such characters may affect bootstrapping or jackknifing analyses (Goloboff *et al.* 2003b).

### Ingroup and outgroup

Twenty one procolophonids have been included in the ingroup. Many procolophonids are known from material that is too incomplete, does not possess a detailed description and/or could not be examined first hand for this study, and hence they could not be included in this analysis. The ingroup comprises well- or long-known taxa such as *Hypsognathus*, *Scoloparia*, *Leptopleuron*, *Sclerosaurus*, *Neoprocolophon*, *Eumetabolodon*, *Pentaedrusaurus*, *Phaanthosaurus*,

**Table 1** Taxa, literature consulted for anatomical information and provenance of materials used in this analysis.

Taxa studied	References	Provenance
<b><i>Nyctiphoretus acudens</i></b>	Efremov 1940; Ivakhnenko 1979, 1987; Lee 1995, 1997b	Mezen Fauna, Cis-Urals, Russia
<b><i>Barasaurus besairiei</i></b>	Meckert 1995	Sakamena F., Madagascar
<b><i>Owenetta rubidgei</i>*</b>	Reisz & Scott 2002	Balfour F., South Africa
<i>Coletta seca</i> *	Modesto <i>et al.</i> 2002	Katberg F., South Africa
<i>Pintosaurus magnidentis</i> *	Piñeiro <i>et al.</i> 2004	Buena Vista F., Uruguay
<i>Sauropareion anoplus</i>	Modesto <i>et al.</i> 2001; Damiani <i>et al.</i> 2003	Balfour F., Katberg F., South Africa
<i>Phaanthosaurus</i> spp.	Ivakhnenko 1974; Spencer & Benton 2000	Vokhmian Gorizont, Cis-Urals, Russia
<i>Eumetabolodon dongshengensis</i> *	Li 1983	?Shiqianfeng Group, northern China
<i>Theledectes perforatus</i> *	Modesto & Damiani 2003	Burgersdorp F., South Africa
<i>Tichvinskia vjatkensis</i>	Ivakhnenko 1973, 1979; Spencer & Benton 2000	Yarenskian Gorizont, Cis-Urals, Russia
<i>Timanophon raridentatus</i>	Ivakhnenko 1979; Novikov 1991; Spencer & Benton 2000	Ustmylian Gorizont, Cis-Urals, Russia
<i>Kapes</i> spp.	Ivakhnenko 1975; Novikov 1991, Novikov & Sues 2005; Spencer & Benton 2000; Spencer & Storrs 2002	Otter Sandstone F., UK; Yarenskian and Donguz gorizonts, Cis-Urals, Russia
<i>Thelephon contritus</i> *	Modesto & Damiani 2003	Burgersdorp F., South Africa
<b><i>Eumetabolodon bathycephalus</i>*</b>	Li 1983	Upper Heshanggou F., north China
<b><i>Procolophon trigoniceps</i>*</b>	Gow 1977b; Carroll & Lindsay 1985; deBraga 2003	Sanga do Cabral F., Brazil; Katberg F., Burgersdorp F., S. Africa; and Fremouw F., Antarctica
<b><i>Thelerpeton oppressus</i>*</b>	Modesto & Damiani 2003	Burgersdorp F., South Africa
<b><i>Teratophon spinigenis</i>*</b>	Modesto & Damiani 2003	Burgersdorp F., South Africa
<i>Pentaedrusaurus ordosianus</i> *	Li 1989	Upper Heshanggou F., northern China
<i>Neoprocolophon asiaticus</i> *	Young 1957	Middle or Upper Ermaying F., northern China
<i>Sclerosaurus armatus</i>	Huene 1912; Colbert 1946	Upper Buntsandstein, Switzerland
<b><i>Scoloparia glyphanodon</i></b>	Sues & Baird 1998	Wolfville F., eastern Canada
<i>Leptopleuron lacertinum</i>	Boulenger 1904; Huene 1912; Spencer 2000	Lossiemouth Sandstone F., Britain
<b><i>Soturnia caliodon</i>*</b>	Cisneros & Schultz 2003	Caturrita F., southern Brazil
<b><i>Hypsognathus fenneri</i></b>	Colbert 1946; Sues <i>et al.</i> 2000	Blomidon F., New Heaven F. and Passaic F., eastern Canada and the USA

Names in bold indicate first hand study of non-type material; asterisks indicate that the holotype was examined. *Sclerosaurus* was studied through casts (AM 2480–2482) of the holotype. Additional information for some taxa was obtained through photographs. F. = Formation.

*Tichvinskia*, *Kapes* and *Procolophon*; and the more recently described *Coletta*, *Sauropareion*, *Soturnia* and *Pintosaurus*. Priority has been given to anatomical information obtained by personal examination of specimens and casts, 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 now considered to be a *nomen dubium* and the remaining four species of the genus were assigned to new genera (Modesto & 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 has already been expressed (Li 1983). The genus *Kapes* has been coded largely on the basis of the recent description by Novikov & Sues (2005) 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 this analysis. *Kapes* has been the subject of recent reviews that agree on the validity of these species

(Spencer & Benton 2000; Spencer & Storrs 2002; Novikov & Sues 2005). According to Novikov (1991), *Timanophon raridentatus* includes a cranium referred to *Burtensia burtensis* by Ivakhnenko (1979). Following Spencer & 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 those authors. The remains of the type species of *Phaanthosaurus*, *P. ignatjevi*, are too incomplete to be included as a single OTU, and the information for this study has been taken mainly from *P. simus*. Only one species within the genus *Procolophon* has been considered in this study, following recent work (Cisneros *in press*) which recognises only the species *P. trigoniceps*.

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 on the basis of, in the main, *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 & Laurin 1991; Lee 1995, 1997a; deBraga & Rieppel 1997; deBraga 2003) have coded *Owenetta* on the basis of 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*.

## CHARACTER DESCRIPTION

A large number of the 58 characters employed in this analysis are new (see Appendix A: Data matrix). They include several dental and postcranial features. Characters taken or modified from other authors are indicated below. Some of these were recoded on the basis of personal observations or new information. Four 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 & Dodson (2003).

### Cranium surface (Fig. 1)

0. *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 ordered. The character is difficult to verify in *Hypsognathus* because the premaxilla and septomaxilla are apparently fused. Modified from Modesto *et al.* (2001).

1. *External naris: (0) posterior or at level of first premaxillary tooth, (1) anterior to first premaxillary tooth.*

In *Nyctiphruretus* and owenettids, the anterior border of the external naris, in lateral view, is located posterior or roughly at the level of the anterior border of the first premaxillary tooth. In the derived state, seen in most procolophonids, the snout is located much more anteriorly and surpasses considerably the anterior border of the first premaxillary tooth. A reversal is recorded in *Hypsognathus* and *Soturnia*.

2. *External naris: (0) anteroposteriorly elongated, (1) sub-circular 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).

3. *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 & Reisz (1995). Those authors incorrectly

stated that the derived condition was a synapomorphy for Procolophonidae because they based most observations for this clade on *Procolophon*.

4. *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 Fig. 1 for an explanation of the criteria used to code this character and Appendix B for ratios of snout height/length in procolophonids. The only known complete skull of *Kapes* (PIN 4365/40) is probably a juvenile and, considering that the proportions of the snout may be considerably influenced by ontogeny, this character has not been coded for this genus.

5. *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).

6. *Prefrontal: (0) medial border straight, (1) medial border with a medial process, (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 process that extends toward the midline, but without contact between prefrontals (a medial contact between prefrontals anterior to frontals occurs in *Owenetta kitchingorum*); and (2) the complete reduction of its surface in dorsal view. Modified from Sues *et al.* (2000).

7. *Posterior margin of orbitotemporal fenestra: (0) anterior to posterior margin of pineal foramen, (1) at level of posterior-most point of the pineal foramen, (2) beyond the posterior border of the pineal foramen, (3) considerably beyond the posterior border of the pineal foramen.*

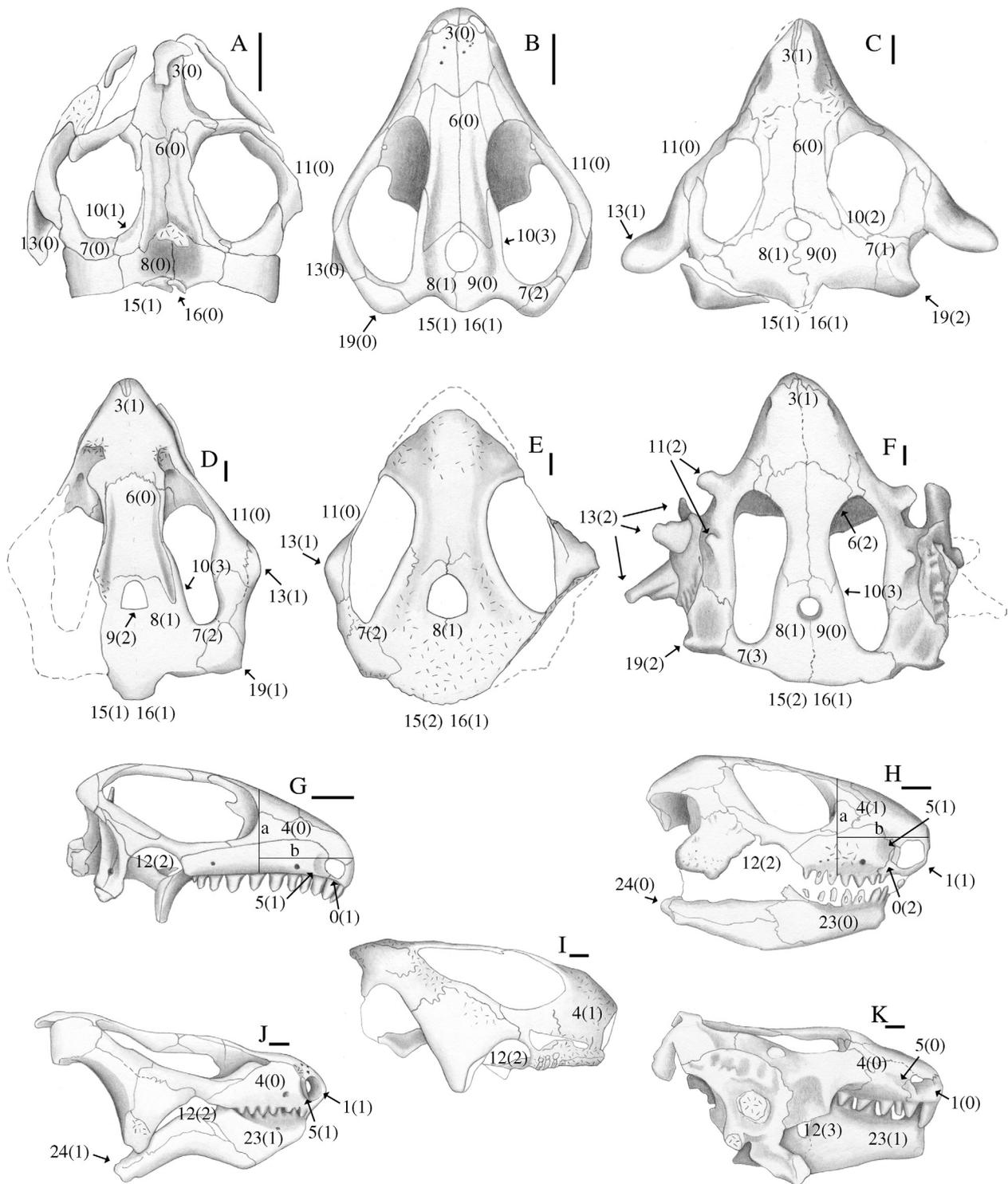
In *Nyctiphruretus*, owenettids, *Coletta* and *Phaanthosaurus*, the posterior rim of the orbitotemporal fenestra does not reach the level of the pineal foramen. Progressively derived states (1, 2) of expansion of this structure are here coded on the basis of the relationship between the level of its posterior margin and the pineal foramen. State 3 is coded when the posterior border of the temporal fenestra 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 fenestra was discussed by Colbert (1946: fig. 4) and Cisneros *et al.* (2004).

8. *Pineal opening 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 as the dorsal skull roof. From Modesto *et al.* (2002).

9. *Contour of the pineal opening: (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 that gives a 'teardrop' shape to the opening is recorded in *Kapes* and *Thelephon*; and (2) a foramen



**Figure 1** Crania of procolophonoids in dorsal (A–F) and right lateral (G–K) views, showing some characters used in this study (states indicated in brackets). **A**, *Barasaurus besairiei* (SAM PK-K8275); **B**, *Tichvinskia vjatzensis* (PIN 954/1); **C**, *Procolophon trigoniceps* (NM QR3201); **D**, *Pentaedrusaurus ordosianus* (IVPP V8735); **E**, *Neoprocolophon asiaticus* (IVPP V866); **F**, *Hypsognathus fenneri* (YPM 55831); **G**, *Tichvinskia vjatzensis* (PIN 954/1); **H**, *Procolophon trigoniceps* (BMNH R4087); **I**, *Neoprocolophon asiaticus* (IVPP V866); **J**, *Pentaedrusaurus ordosianus* (IVPP V8735); **K**, *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 4 (G–H): a vertical line (a) is traced from the cranial roof to the alveolar margin, tangential to the anterior border of the orbitotemporal fenestra, and a second line (b) is traced from (a) to the tip of the snout, perpendicular to (a). The snout is considered ‘long and flat’ if  $a/b < 0.8$ , and ‘deep and short’ if  $a/b \geq 0.8$  (see Appendix B for ratios). 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. Scale bar = 5 mm.

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 between states 0 and 2.

10. *Postfrontal*: (0) contacts frontal, parietal and postorbital, (1) contacts frontal, parietal, postorbital and supratemporal, (2) contacts frontal and parietal only, (3) absent and area occupied by parietal or fused to parietal.

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 is absent 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).

11. *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.
12. *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).
13. *Quadratojugal lateral surface*: (0) spineless, (1) one spine, (2) two or more spines.  
Primitively the quadratojugal does not bear spines. A number of procolophonids possess 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 this character has not been coded as ordered. Modified from Modesto *et al.* (2002).
14. *Squamosal ventral margin terminates*: (0) at least as far ventrally as quadratojugal, (1) dorsal to quadratojugal in the tympanic notch.  
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, *Coletta* and *Hypsognathus*. From Modesto *et al.* (2001).
15. *Posterior margin of the skull roof*: (0) concave, (1) acute posterior process, (2) broad posterior emargination.

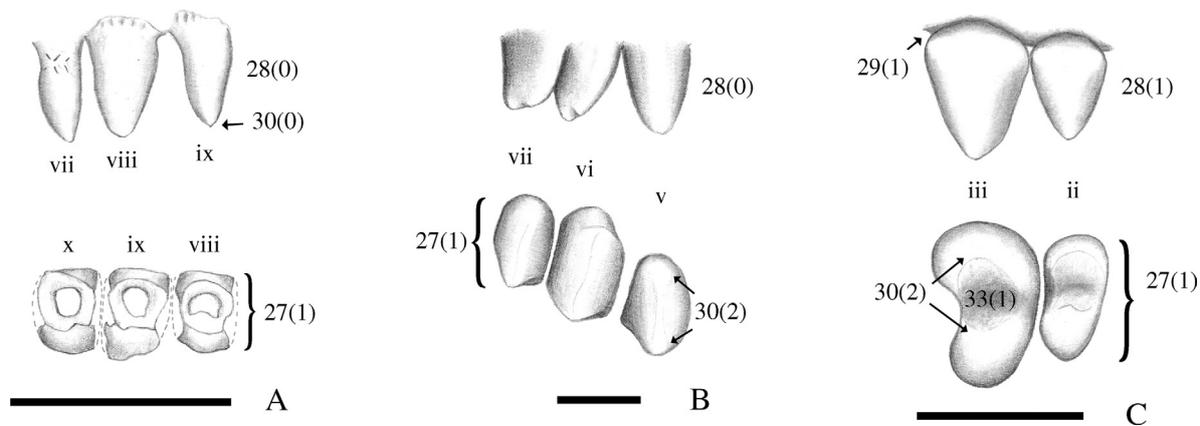
In the outgroup, the posterior edge of the skull roof is concave (0). In some owenettids and *Sauropareion*, this border bears an acute projection (1) formed by the postparietals. In some procolophonids this acute projection is also present, but the postparietals are absent or fused to the parietals (see character 16). 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. A related character was proposed by Lee (1995). The character is polymorphic (1, 2) in *Hypsognathus*.

16. *Postparietals*: (0) present, (1) absent/fused.  
Small postparietals are recorded in *Nyctiphruretus*, *Owenetta kitchingorum*, some *Barasaurus* specimens (pers. obs. on SAM PK-K8275) and *Sauropareion* (0). The primitive condition for owenettids is uncertain, because postparietals are not recorded in *Owenetta rubidgei*. In *Nyctiphruretus* they are integrated into the posterior, concave margin of the skull roof, whereas in *Barasaurus*, *Owenetta kitchingorum* and *Sauropareion* they form a small median projection (see character 15). Postparietals are absent or fused to parietals in most procolophonids (1). Modified from Modesto *et al.* (2002).
17. *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.

## Palate and braincase

18. *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.
19. *Epipterygoid columella*: (0) ends freely, (1) contacts dorsally prootic and supraoccipital.  
In *Tichvinskia* and *Procolophon*, the end of the epipterygoid 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).
20. *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).
21. *Relation of basioccipital tuber and quadrate condyle*: (0) approximately at the level, (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 and *Tichvinskia*. In the derived state, recorded in several procolophonids, the basioccipital tubera are located far more posteriorly.
22. *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 is tripartite. From Sues *et al.* (2000).



**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**, *Procolophon trigoniceps* (SAM PK-K7890), right v–vii in labial (slightly posterior) and occlusal views; **C**, *Soturnia caliodon* (MCN PV2738) right ii–iii molariforms in lingual and occlusal views. Scale bar = 2.5 mm.

### Mandible (Fig. 1)

23. *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°.

24. *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).

### Dentition (Fig. 2)

25. *Premaxillary teeth number: (0) five or more, (1) four, (2) three, (3) two.*

*Nyctiphruetus* and the owenettids possess five or more premaxillary teeth. The three derived states summarise the procolophonid trend to reduce the premaxillary dentition. This character has been coded as ordered. From Modesto *et al.* (2002).

26. *Premaxillary teeth: (0) sub-equal in size, (1) enlarged mesial-most teeth.*

In the primitive condition, all premaxillary teeth are conical or incisiform and sub-equal in size. In the derived state, a large mesial-most incisor is present. A similar character was proposed by Piñeiro *et al.* (2004).

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

Primitively, the maxillary teeth have rounded bases. In the derived condition, seen in most procolophonids, 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). A reversal to rounded bases is recorded in *Theledectes* and *E. dongshengensis*. From Lee (1995).

28. *Presence of prominently bulbous teeth in the maxilla: (0) absent, (1) present.*

Most procolophonids have teeth that can be described as bulbous. In some procolophonids, however, one or more maxillary teeth can be considerably wider in labial view. For the purpose of coding this character, a tooth is here considered ‘prominently bulbous’ when its mesodistal length, measured at the mid level of the basal–apical length, is equivalent or superior to 60% the basal–apical length (see Fig. 2).

29. *Maxillary teeth cervixes: (0) not constricted, (1) constricted.*

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

30. *Maxillary teeth cusps: (0) one, (1) two, (2) two and anterior monocuspid teeth absent.*

Primitively, the maxillary teeth are monocuspid. In most procolophonids, bicuspid molariform teeth are recorded (1), but one or more remnant monocuspid teeth are still present in the anterior region of the maxilla. All monocuspid maxillary teeth are absent (2) in *Leptopleuron*, *Scoloparia* and *Soturnia*. The character is polymorphic (1, 2) in the genus *Procolophon*, where some specimens lack anterior monocuspid maxillary teeth. This character has been ordered.

31. *Maxillary tooth number: (0) 40 or more, (1) 35 to 15, (2) 12 to 10, (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 in both 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.

32. *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 as 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).

33. *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*.
34. *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).
35. *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 some basal procolophonids and leptopleuronines. *Procolophon* is polymorphic for this character.
36. *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).
37. *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).
38. *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.
39. *Dentary teeth in basal cross-section: (0) circular, (1) labiolingually expanded, (2) mesodistally elongated.*  
The dentary teeth of *Nyctiphruretus* and owenettids are circular in basal cross-section (0). Most procolophonids have labiolingually expanded dentary teeth (1) that match with the maxillary molariforms. In some species within the genus *Kapes* and in *Soturnia*, however, the dentary teeth that occlude with the upper molariforms are much narrower than their upper counterparts, being mesodistally elongated (2). State 2 may be present in other leptopleuronines such as *Hypsognathus* and *Leptopleuron* but their dentary teeth are not well known.
40. *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 state 2, although the dentary molariforms of this genus sometimes bear

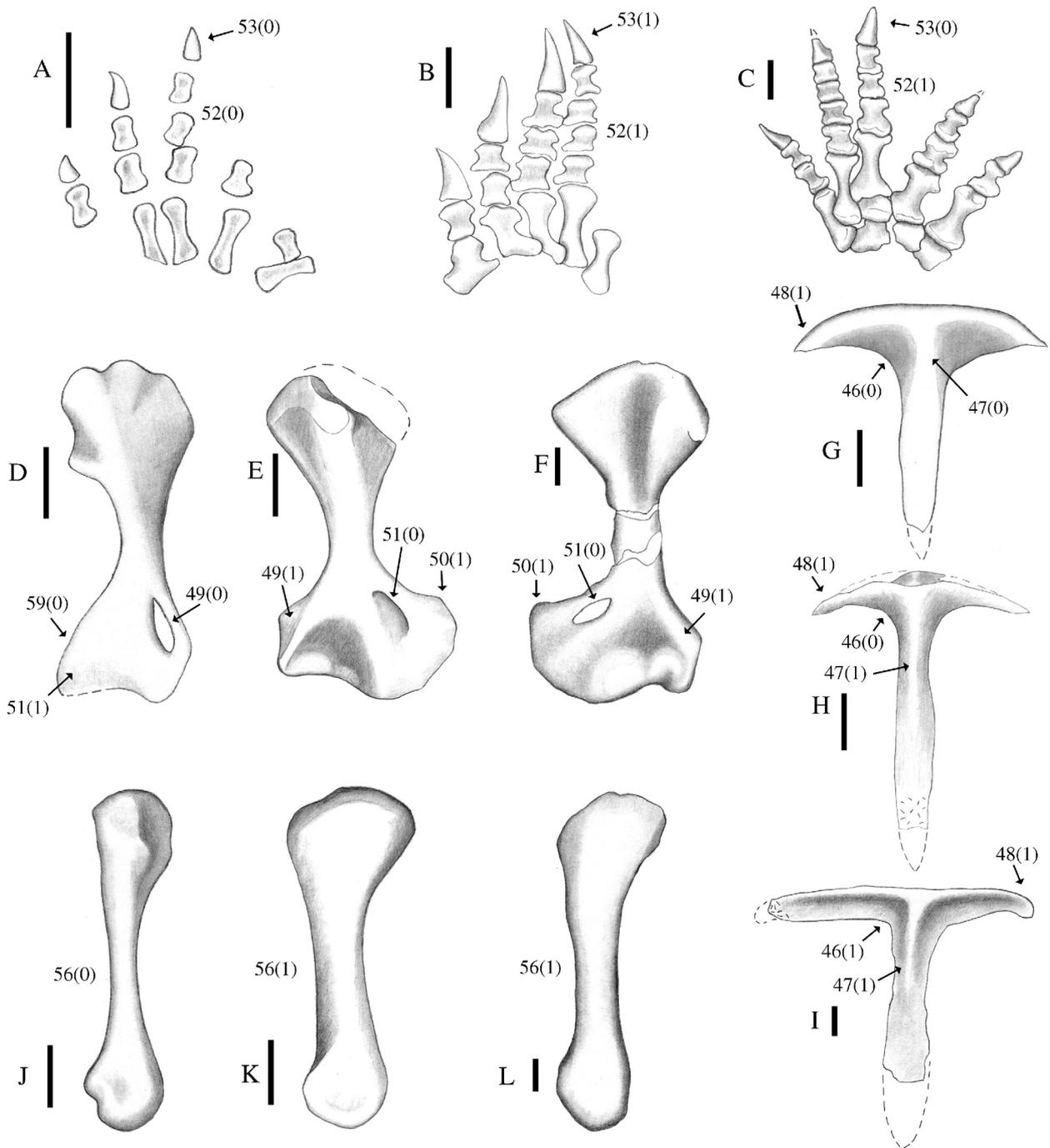
cusps that connect the labial and lingual cusps. A reversal to the monocuspid condition occurs in *Soturnia*. This character has been ordered.

### Axial skeleton

41. *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'.
42. *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 & Reisz (1995).
43. *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*.
44. *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 *Soturnia* and *Hypsognathus* intercentra are not recorded, although there are spaces for them between each pleurocentra. These genera probably had cartilaginous intercentra.
45. *Rib cage: (0) narrow, (1) broad.*  
Primitively the rib cage is relatively narrow and the thorax is more gracile. The derived state is recorded in some procolophonids, where the rib cage width is equal to or greater than 70% of the glenoid–acetabular length.

### Appendicular skeleton (Fig. 3)

46. *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*, where the posterior margins of the bases of these processes are nearly perpendicular to the trunk of the interclavicle.
47. *Interclavicle medial ridge: (0) smooth, (1) prominent.*  
Primitively, a wide but smooth ventral ridge is present in the trunk of the interclavicle and it is limited to the anterior portion of the interclavicle. In the derived state this ridge becomes narrow and more elevated, extending posteriorly.
48. *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.
49. *Ectepicondylar foramen or groove on humerus: (0) present, (1) absent.*



**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. Scale bar = 5 mm.

An ectepicondylar foramen or groove is present in *Nyctiphruetus* and owenettids. No foramen or groove is known in the ectepicondyle of procolophonoids. Modified from Laurin & Reisz (1995).

50. *Entepicondylar process*: (0) reduced, (1) prominent. In the primitive state the entepicondyle is small and its external margin rises in a low angle from the hu-

meral shaft. In the derived state, the entepicondylar process is more prominent, emerging *ca.* 90° from the shaft.

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

An entepicondylar foramen is recorded in *Nyctiphruetus* and all procolophonids in which the humerus is

known. Owenettids lack this feature. From Laurin & Reisz (1995).

52. *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 *Nyctiphruetus*. 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 proximal and distal ends 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.

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

In owenettids and most procolophonids, manual unguals are comparable in length to the penultimate phalanges, or moderately longer. This condition has been assumed to be primitive, although the character is not known in *Nyctiphruetus*. *Procolophon* and *Thelerpeton* possess manual unguals that are at least 50% longer than the penultimate phalanges. A similar character was proposed by deBraga (2003).

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

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

55. *Femur–humerus length ratio: (0) femur longer than humerus, (1) femur length equal to humerus.*

In *Nyctiphruetus*, 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 (see Appendix B for ratios of femur/humerus length).

56. *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 9. This is the condition present in procolophonids.

## Dermal ossifications

57. *Osteoderms: (0) absent, (1) present.*

Primitively, osteoderms are absent. The derived state has been found only 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. From Laurin & Reisz (1995) and Lee (1995).

## RESULTS

The analysis produced four most parsimonious trees (MPTs) with 116 steps. Clades from the strict consensus tree (Fig. 4) that are here considered most relevant are discussed below. Non-ambiguous synapomorphies present in all trees are listed. State transformations are indicated within brackets and reversals are preceded by a minus sign (Fig. 5).

## 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*, *Pintosaurus magnidentis*, *Sauropareion anoplus*, *Phaanthosaurus* spp., ‘*Eumetabolodon*’ *dongshengensis*, *Theledectes perforatus*, *Tichvinskia vjatkensis*, *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.

- 0(0 → 1): Maxilla premaxillary subnarial process absent.
- 2(0 → 1): External naris subcircular or dorsoventrally expanded.
- 5(0 → 1): Maxillary depression present.
- 25(0 → 1,2): Three to four premaxillary teeth.
- 27(0 → 1): Maxillary teeth with labiolingually expanded bases present.
- 31(1 → 2): Ten to 12 maxillary teeth.
- 34(0 → 1): Anterior vomerine dentition consisting of true teeth.

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

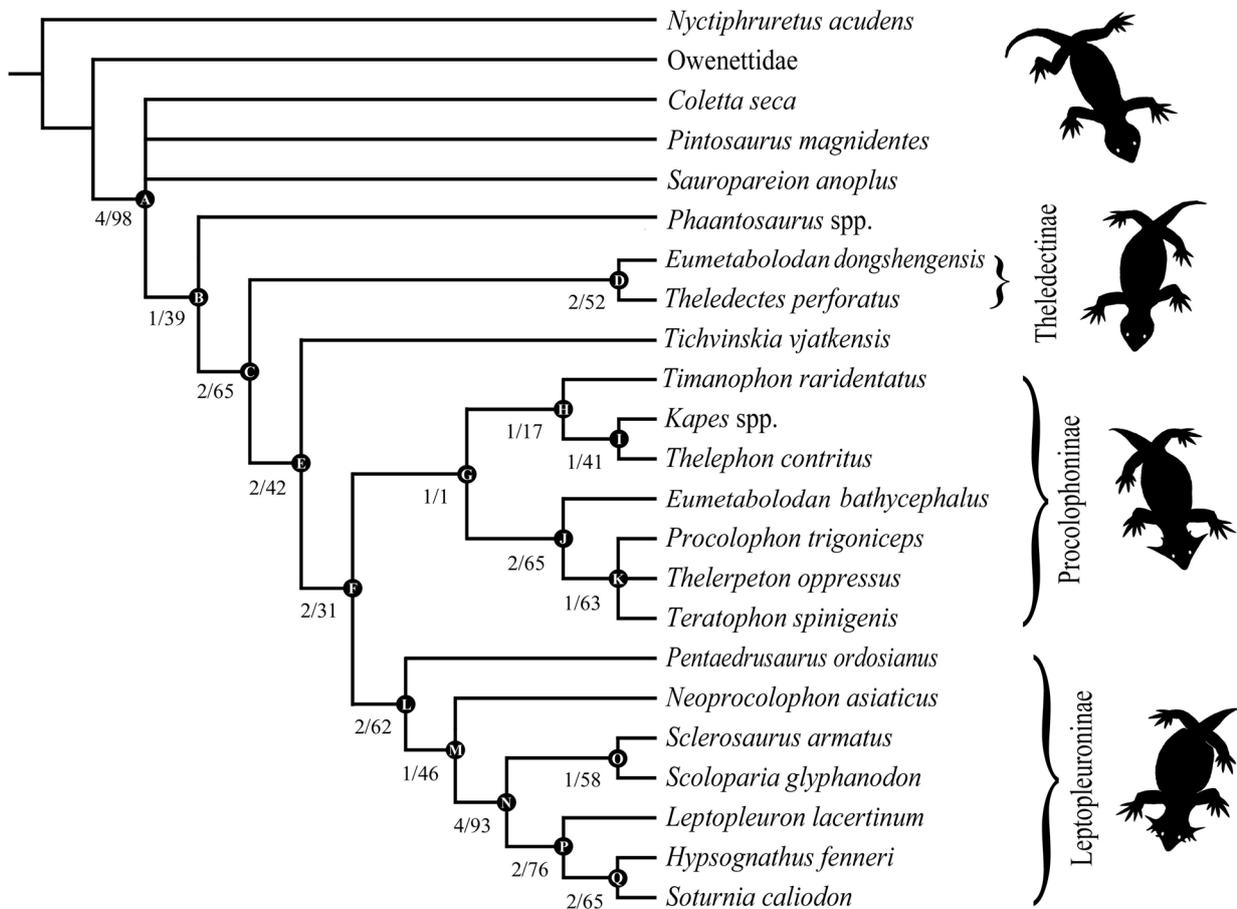
## Clade C

COMPOSITION. ‘*Eumetabolodon*’ *dongshengensis*, *Tichvinskia vjatkensis*, *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.

- 7(0,1 → 2): Posterior margin of orbitotemporal fenestra beyond the posterior border of the pineal foramen.
- 10(1,2 → 3): Postfrontal fused to parietal.
- 26(0 → 1): Enlarged mesial-most premaxillary tooth.
- 31(2 → 3): Six to eight maxillary teeth.

COMMENTS. Members of clade C display a notable reduction of both the maxillary and dentary dentition. 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



**Figure 4** Strict consensus tree from four most parsimonious trees. Statistics for each most parsimonious tree: tree length = 116 steps, consistency index (excluding uninformative characters) = 0.69, retention index = 0.82. Decay index (DI) and symmetric resampling (SR) values are given next to each node (DI/SR, respectively). DI values were calculated from 17,019 trees. SR was performed with 10,000 replicates and 10 repetitions ( $P = 0.33$ ) using the Traditional Search option (random addition sequences plus tree bisection-reconnection).

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).

#### Clade D: Theledectinae new taxon

**DEFINITION.** All taxa more closely related to *Theledectes perforatus* (Gow, 1977a) than to *Procolophon trigoniceps* Owen, 1876.

**COMPOSITION.** *Theledectes perforatus* and ‘*Eumetabolodon*’ *dongshengensis*.

**NON-AMBIGUOUS SYNAPOMORPHIES.**

- 6(0 → 1): Prefrontal medial border with a medial process.
- 27(1 → 0): Absence of maxillary teeth with labiolingually expanded bases.
- 39(1 → 0): Dentary teeth with circular bases.

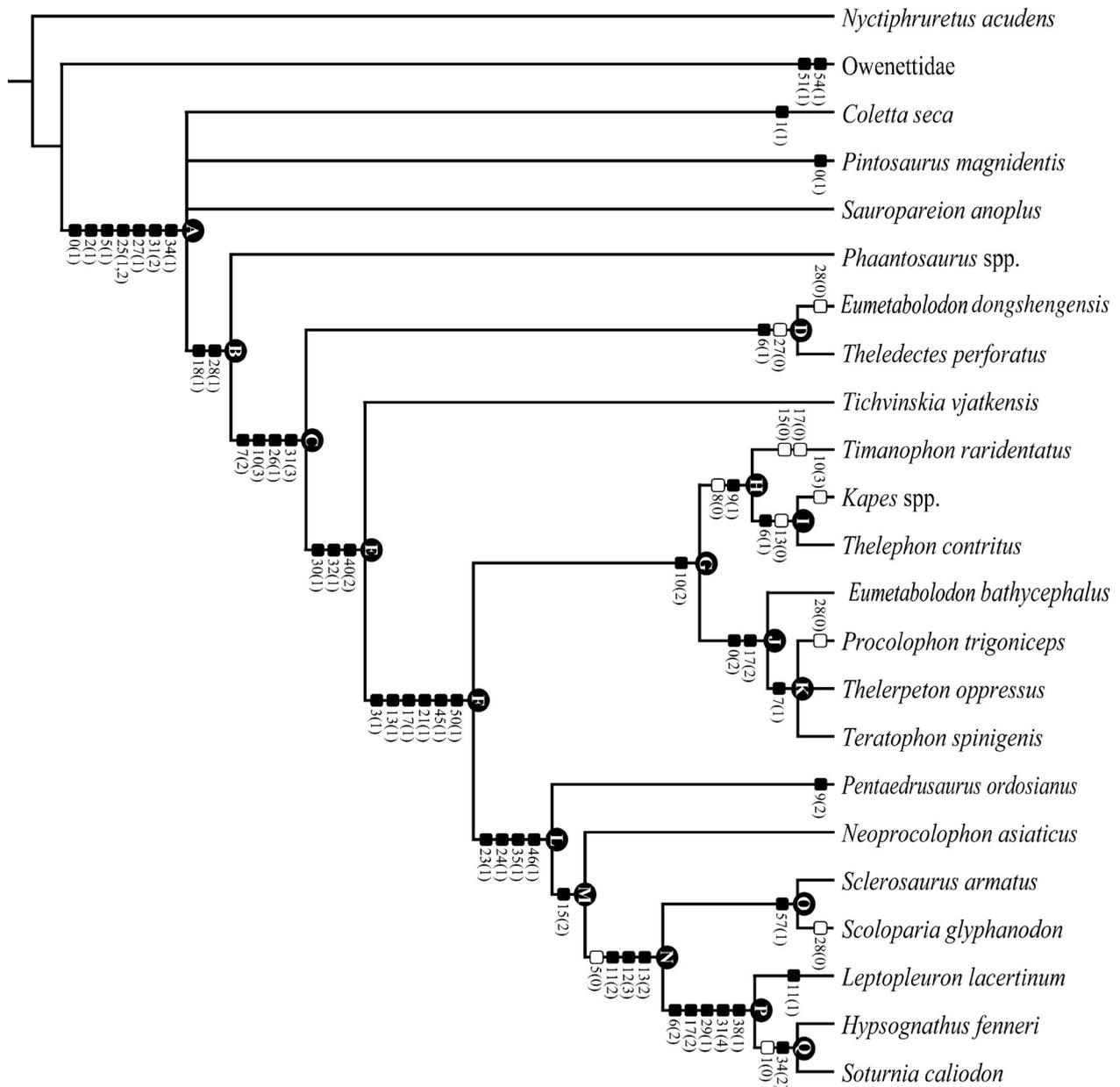
**COMMENTS.** An interesting result of the analysis is this previously unrecognised clade, formed by two small procolophonids from South Africa and China. The most distinctive feature of the clade is the presence of enlarged, monocuspid marginal teeth with circular bases. These teeth are notably

different from those of the owenettids, which also have circular bases but are much thinner and sharp.

The Chinese genus *Eumetabolodon* is polyphyletic. In the original description of this taxon, Li (1983: 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 Li’s 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 recognise only monophyletic genera. The other member of this clade is *Theledectes* (*Thelegnathus*) *perforatus*, the bizarre procolophonid with multiple rows of teeth from the *Cynognathus* Assemblage Zone of South Africa.

#### Clade F: ‘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*.



**Figure 5** Non-ambiguous synapomorphies and autapomorphies in the strict consensus tree. Reversals are indicated by white boxes.

#### NON-AMBIGUOUS SYNAPOMORPHIES.

- 3(0 → 1): Wide internarial bar.
- 13(0 → 1): Presence of one quadratojugal spine.
- 17(0 → 1): Acute supratemporal posterolateral margin.
- 21(0 → 1): Basioccipital tuber projected far more posteriorly than the level of the quadrate condyle.
- 45(0 → 1): Wide rib cage.
- 50(0 → 1): Prominent entepicondylar 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 characterised by a more robust postcranium, a wide rib cage and a considerably larger size in comparison to earlier procolophonids and owenettids.

#### Clade G: 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.

- 10(3 → 2): Postfrontal contacts frontal and parietal.

**COMMENTS.** Procolophoninae, in this analysis, is a geographically diverse group formed by taxa from South Africa, Britain, Russia and China. This clade, however, is very poorly supported. In a one-step suboptimal scenario, Procolophoninae is restricted to clade J, which is composed

of the South African *Procolophon trigoniceps*, *Thelepeton* (*Thelegnathus*) *oppressus* and *Teratophon* (*Thelegnathus*) *spinigenis*, as well as the type species (by page priority) of the Chinese genus *Eumetabolodon*, *E. bathycephalus*. This group is characterised by a maxilla with a premaxillary subnarial process that is posterodorsally expanded (character 0) and a supratemporal with a prominent posterolateral spine (character 17). The analysis shows that only two species of the former genus *Thelegnathus* are closely related, namely *Thelepeton oppressus* and *Teratophon spinigenis*. They form a trichotomy with the genus *Procolophon* (clade K), a more exclusive clade that is diagnosed by the placement of the posterior margin of the orbitotemporal fenestra at the level of the posterior margin of the pineal foramen, a convergence with *Sauropareion anoplus*. A review of all species previously assigned to ‘*Thelegnathus*’ is in progress.

### Clade I

COMPOSITION. *Kapes* spp. plus *Thelephon contritus*.

NON-AMBIGUOUS SYNAPOMORPHIES.

- 6(0 → 1): Prefrontal medial border with a medial process.
- 13(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 & Sues (2005). 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 this analysis. However, *Thelephon* differs from *Kapes amaenus* in the presence of a prominent posterior tooth, also in the maxilla (Modesto & 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 & 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 *Anomiodon* from the Buntsandstein of Germany (Spencer & 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.

### Clade L: 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.

- 23(0 → 1): Oblique dentary ventral and dorsal surfaces.
- 24(0 → 1): Articular well below the alveolar margin of dentary teeth.
- 35(0 → 1): Vomerine denticles or teeth along posterior medial suture absent.
- 46(0 → 1): Straight posteromedial margin of lateral processes of the interclavicle.

COMMENTS. The phylogenetic relationships of the Chinese procolophonids *Pentaedrusaurus ordosianus* and *Neoprocolophon asiaticus* are here resolved as the most primitive members of the Leptopleuroninae. The problematic genus *Sclerosaurus* from the Buntsandstein is a member of this clade. Leptopleuronine affinities for this genus were also reported by deBraga (2003). 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.

### Clade N

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

NON-AMBIGUOUS SYNAPOMORPHIES.

- 5(1 → 0): Maxillary depression absent.
- 11(0 → 2): Two jugal spines.
- 12(2 → 3): Temporal ventral margin convex.
- 13(1 → 2): Two or more quadratojugal spines.

COMMENTS. This is the best supported clade within the Procolophonidae (DI = 4, SR = 91). It is composed of more derived leptopleuronines that exhibit very distinctive traits, such as the presence of multiple cranial spines. *Scoloparia* from Canada here constitutes the sister group of *Sclerosaurus* (clade O), 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 if osteoderms are recorded in other forms when more or better specimens are found. Another possible member of clade N is the unnamed procolophonid from the Owl Rock Member of the Chinle Formation in the 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).

### 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*, *Contritrosaurus*, *Candelaria*, *Procolophonoides* and *Neoprocolophon*. The genus *Procolophonoides* was erected by Ivakhnenko (1979) for the species *Procolophon baini*, but this species is no longer recognised by most authors that have reviewed *Procolophon* due to the equivocal nature of the characters on which it was based, which can be explained

through ontogeny (Colbert & Kitching 1975; Gow 1977b; Carroll & Lindsay 1985; deBraga 2003; Cisneros *in press*). In addition, *Candelaria* has recently been shown to be an owenettid (Cisneros *et al.* 2004) and *Contritrosaurus* can be considered a junior synonym of *Phaanthosaurus* (Spencer & 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 analysis supports the polyphyly of the former genus *Thelegnathus*, the four new genera proposed by Modesto & Damiani (2002) being here separated in three different clades: Theledectinae (clade D), clade I and clade K. Curiously, *Theledectes* (*Thelegnathus*) *perforatus* is here shown to be more closely related to a Chinese procolophonid than to any other South African form.

Previous workers on the phylogenetic relationships of parareptiles (Laurin & Reisz 1995; Lee 1995; deBraga & 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, closely related to Middle Triassic forms.

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* possesses 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 more consistent with the Early/Middle Triassic age of *Sclerosaurus*.

### Evolutionary history and feeding ecology

One of the characters that diagnose Procolophonidae in this study is the appearance of teeth with labiolingually expanded bases, as seen in *Coletta* (Fig. 2A). 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 B. 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 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 & Baird 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 was probably 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 played a major role in procolophonid evolution. This character has no reversals. Whereas some forms that possess this character may still be considered durophagous omnivores (e.g. *Tichvinskia vjatkensis*), the labiolingually expanded crowns made possible the exploitation of a high-fibre herbivory niche by several members of this group (the term 'herbivory' is here used for an animal that is expected to feed nearly exclusively on plant material). In most procolophonines and leptopleuronines, large occlusal areas of molariforms seem effective for processing tough, fibrous foods (Reisz & Sues 2000).

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; (d) deep dentary; and (e) the presence of marginal teeth inset from both the maxillary and dentary lateral surfaces.

With the possible exception of the small *Soturnia caliodon*, the horned procolophonids (clade F) 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 for hosting the endosymbiotic organisms that are necessary for the breakdown of cellulose (Sokol 1967; Hotton *et al.* 1997; Cooper & Vitt 2002). In modern herbivorous lizards there is a tendency towards a larger size compared to their omnivore and insectivore counterparts (Sokol 1967; Cooper & 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.

One procolophonid with labiolingually expanded crowns seems to represent an exception to herbivorous or durophagous diets. The marginal teeth of the leptopleuronine *Scoloparia glyphanodon* differ notably from those of other procolophonids. This form possesses mesodistally compressed molariforms with sharp labiolingual cutting edges. In this procolophonid, the cusps are thin and exhibit relatively less wear in comparison with *Procolophon* or other forms with labiolingually expanded crowns, which suggests that they were not employed in durophagy or in processing highly-fibrous plants. In *Scoloparia* additional cuspules connect the prominent labial and lingual cusps of maxillary teeth. This dentition 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 a similar ecological niche for *Scoloparia*.

As seen here, a plethora of adaptations for different feeding habits, ranging from insectivory to high-fibre

herbivory, can be found in the approximately 30 genera of known procolophonids. Whereas the development of different forms of omnivory and the absence of competitors allowed the colonisation of Pangaea during the Early Triassic, the acquisition of specialisations for high-fibre herbivory made possible further radiation and survival until Late Triassic times.

The first appearance datum of *Procolophon*, in the *Lystrosaurus* Assemblage Zone of South Africa (Fig. 6; Botha & Smith 2006), indicates that the presence of teeth with labiolingually expanded crowns in the Procolophonidae emerged earlier than in other Triassic tetrapods that also developed labiolingually expanded crowns: gomphodont cynodonts, bauriid thercephalians and the enigmatic reptile *Palacrodon*; all from the overlying *Cynognathus* subzone A of South Africa (Neveling 2004; Abdala *et al.* 2006b). 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.

## BIOSTRATIGRAPHICAL CONSIDERATIONS

### 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. 6). This long ghost lineage results in part 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, but 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, except for *Pintosaurus*, 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 in the Camdeboo Municipality (formerly 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. 7). Although most sutures are not visible, the broad and triangular shape of the skull, enlarged orbits (orbito-

temporal fenestrae) and the anteriorly directed external naris (character 1) 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 10 maxillary teeth seems likely. A total of 13 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. 7E). 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 10. 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.

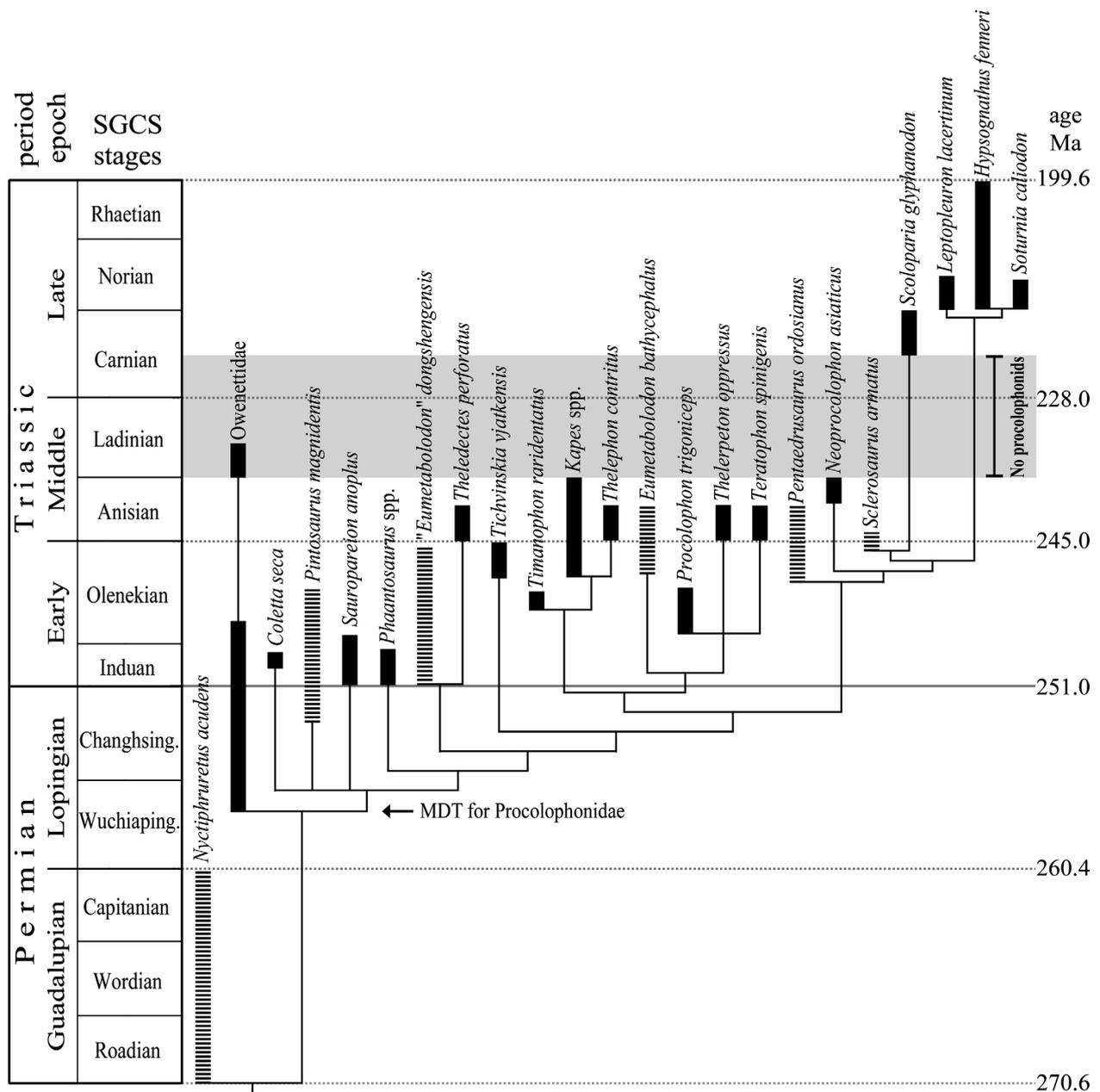
The poor preservation of the holotype of *Spondylolestes* has led other authors to consider this taxon to be a *nomen dubium* (Spencer & Benton 2000; Modesto *et al.* 2001). However, no owenettid or procolophonid is known to possess 10 maxillary teeth, or 13 dentary teeth, with circular bases. If the marginal teeth of *Sauropareion* are shown to be strictly circular in basal cross-section and if the total number is 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 & 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 *Raphanicus tverdochlebovae*, hence *Microphon exiguus* is now considered its senior synonym by name priority (Bulanov 2002).

#### *Suchonosaurus minimus* Tverdokhlebova & 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 & Ivakhnenko 1994). The holotype and only known specimen of *Suchonosaurus* consist of a very small maxilla bearing 10 cylindrical teeth. Besides the statement that *Suchonosaurus* is similar to *Microphon*, the authors did not point out on which criteria they assigned this material



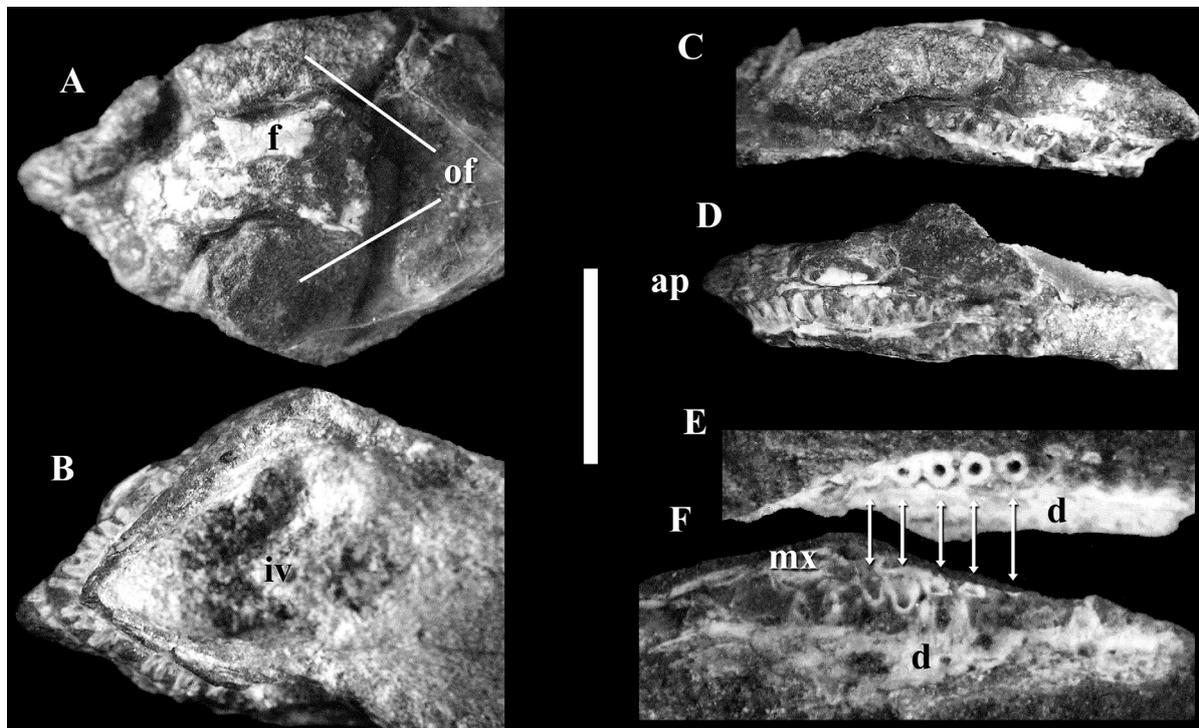
**Figure 6** Strict consensus tree and the geological record of procolophonoids. Black bars represent the stratigraphical ranges, dashed bars represent uncertain stratigraphical ranges. The global hiatus of procolophonid records in Ladinian–Lower Carnian rocks is represented in grey. The minimum divergence time (MDT) of the Procolophonidae from the Owenettidae predicts the existence of a procolophonid as early as the Late Wuchiapingian. Stratigraphical ranges of taxa and geological dates have been adapted from: Li (1989); Lucas (1999); Smith (2000); Spencer & Benton (2000); Sues *et al.* (2000); Modesto *et al.* (2002, 2006); Cisneros *et al.* (2004); Rubert & Schultz (2004); Golubev (2005); Sennikov & Golubev (2005); Abdala *et al.* (2006a). SGCS (Standard Global Chronostratigraphic Scale) stages after Gradstein & Ogg (2004).

to the Procolophonidae and no obvious procolophonid apomorphies can be observed in the specimen as figured in Tverdokhlebova & Ivakhnenko (1994). Furthermore, from the published illustrations it can be seen 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 & Olsen 1993; Small 1997; pers. obs. in *Owenetta rubidgei* BP/1/1396), a condition that is usually termed ‘protothecodont’. Considering the absence of procolophonid autapomorphies 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; Tverdokhlebova *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



**Figure 7** 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**, interpterigoid vacuity; **mx**, maxilla; **of**, orbitotemporal fenestrae. Arrows indicate correspondence among maxillary teeth. Scale bar = 5 mm for **A–D**, and 10 mm for **E** and **F**.

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 procolophonid of possible Permian age was recently described. *Pintosaurus magnidentis*, from the Buena Vista Formation of Uruguay is, in this analysis, nested in a polytomy with *Coletta seca*, *Sauropareion anoplus* and a clade that includes all other procolophonids (Fig. 4; see results above). 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* from Russia. *Pintosaurus* and *Coletta* also share the absence of posterior vomerine teeth along the medial suture and the same number of maxillary teeth (12). The age of the Buena Vista Formation, however, is not well established. This formation is usually considered to be a lateral equivalent of the Sanga do Cabral Formation from Rio Grande do Sul, Brazil (Bossi & Navarro 1991), which has yielded the index taxon *Procolophon* and, therefore, could be Lower Triassic. Recently, however, Piñeiro *et al.* (2003) considered it to be Upper Permian, mainly on the basis of the presence of varanopid vertebrae. Dias-da-Silva *et al.* (2006) have pointed out that the varanopid vertebrae reported for the Buena Vista Formation have diapsid features, which make their identification as varanopid questionable. Whereas the status of *Pintosaurus* as a procolophonid is well established in this analysis, problems with the correlation of the Buena Vista Formation preclude the confident assignment of a Permian age to this taxon.

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.

#### The Ladinian–Early Carnian record of procolophonids

Leptopleuroninae (clade L) is the only clade that reached Late Triassic times. The stratigraphical range of this group extends at least from the Early Anisian to the Late Rhaetian. However, no record of leptopleuronines, or other procolophonids, is known from the Ladinian and only one fragmentary record is known from the Early Carnian (see below). This results in a global procolophonid hiatus of more than 15 Ma and some Lazarus taxa (Fig. 6).

The Middle Triassic Santa Maria Formation of southern Brazil produces the procolophonoid *Candelaria barbouri*. *Candelaria* is found in the *Dinodontosaurus* Assemblage Zone of this formation, a horizon which is considered to be Ladinian (Cisneros *et al.* 2004). 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 taxonomic relict at the time the Santa Maria sediments accumulated. No other procolophonid 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 & 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 posterior-most 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 artefact. Ladinian rocks that have produced microvertebrate faunas are scarce.

## CONCLUSIONS

Procolophonidae is a monophyletic group and its relationships are now more firmly resolved than in previous works. Two of the three traditional divisions of the Procolophonidae, Procolophoninae and Leptopleuroninae, are valid monophyletic groups. Spondylolestinae, however, is polyphyletic. A new group, Theledectinae, is here erected. The genus *Eumetabolodon* is polyphyletic. *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 polyphyletic. The genus *Spondylolestes* from South Africa is considered a valid taxon but its phylogenetic relationships remain tentative. Both *Spondylolestes* and the Russian *Kinellia* are likely to fill the ghost lineage of the Procolophonidae in the Permian. The Chinese genera *Pentaedrusaurus* and *Neoprocolophon* are the basal-most members of the Leptopleuroninae and the problematic genus *Sclerosaurus* from Switzerland is also a leptopleuronine. The recognition of these taxa as leptopleuronines considerably extends the range of this clade, traditionally regarded to be Late Triassic, to at least the Early Anisian. The earliest leptopleuronines are separated from the latest members of this clade by a global hiatus of at least 15 Ma in the Ladinian and Lower Carnian, where no procolophonids are known. 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-fibre herbivory by several members of the group.

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## APPENDIX B: MEASUREMENT RATIOS

### Ratios of snout height/length (character 4)

Primitive state: *Nyctiphruetus acudens*: 0.57; *Coletta seca*: 0.59; *Leptopleuron lacertinum*: 0.6; Owenettidae: 0.67; *Tichvinskia vjatkensis*: 0.7; *Hypsognathus fenneri*: 0.74.

Derived state: *Teratophon spinigenis*: 0.87; *Pentaedrusaurus ordocianus*: 0.89; *Procolophon trigoniceps*: 0.89; *Phaantosaurus simus*: 0.9; *Thelerpeton oppressus*: 0.99;

*Neoprocolophon asiaticus*: ~1; *Eumetabolodon bathycephalus*: 1.33.

### Ratios of femur/humerus length (character 55)

Primitive state: *Nyctiphruetus acudens*: 1.21; Owenettidae (*Barasaurus*): 1.14.

Derived state: *Pentaedrusaurus ordocianus*: 1.1; *Tichvinskia vjatkensis*: 1.06; *Sclerosaurus armatus*: 1.06; *Procolophon trigoniceps*: 1.02.