

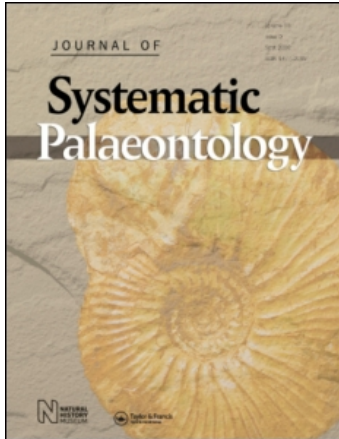
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Morphological diversity and biogeography of procolophonids (Amniota: Parareptilia)

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A recent phylogenetic analysis of procolophonid parareptiles is used as the basis for a study of morphological diversity (disparity) in these amniotes. Disparity values are compared in three groups of procolophonids (a paraphyletic series of basal taxa and two monophyletic sister groups: procolophonines and leptopleuronines), two ecophenotypic assemblages (one based upon inferred diet – non high-fibre versus high-fibre species; the other based upon cranial sculpture – non horned versus horned species), and two temporal assemblages (Lower Triassic versus Middle and Upper Triassic). The mean disparity values are comparable in the case of temporal and ecophenotypic assemblages. High-fibre species are marginally less disparate than non high-fibre species. The combined Middle and Upper Triassic species are slightly less disparate than Lower Triassic species. Finally, horned species are only slightly more disparate than non-horned species. The paraphyletic series of basal taxa and the leptopleuronines show similar disparity values, marginally higher than those for procolophonines. Phylogenetic analysis is also used to reconstruct the biogeographical history of procolophonids. Both ancestral area analysis and dispersal–vicariance analysis show that South Africa was the most likely ancestral area for procolophonids as a whole. North China – either as a single area or in combination with Russia or South Africa – was the most likely ancestral area for the leptopleuronine–procolophonine clade.

Keywords: Procolophonidae; morphospace; disparity; dispersal; ancestral area; phylogeny

Introduction

The clade Parareptilia (see Tsuji & Müller 2009 for a novel recent definition and a synoptic overview) consists of a diverse array of Permian and Triassic reptiles (*sensu* Modesto & Anderson 2004) of global distribution and great zoological significance, not least because several of them have been proposed, not without controversy, as the ancestors or near-ancestors of turtles (e.g. Reisz & Laurin 1991; Laurin & Reisz 1995; Lee 1995, 1997a; see also comments in Rieppel & Reisz 1999; Hill 2005; Rieppel 2001, 2007 and references therein). The group as a whole displays a wide variety of body shapes and sizes, exemplified by the gracile and fully aquatic mesosaurs (e.g. Oelofsen & Araújo 1983), the tiny bipedal bolosaurs (e.g. Berman *et al.* 2000) and the bulky, often heavily armoured pareiasaurs (e.g. Lee 1997b). In recent years taxonomic reviews and systematic efforts have improved our knowledge of these amniotes. As a result, detailed analyses of the intrinsic and external relationships of parareptiles as a whole, and of several constituent clades in this group, are now available (e.g. Rieppel & deBraga 1996; deBraga & Rieppel 1997; Modesto *et al.* 2003; Cisneros *et al.* 2004; Piñeiro *et al.*

2004; Jalil & Janvier 2005; Modesto 2006; Tsuji 2006; Modesto & Damiani 2007; Müller & Tsuji 2007; Reisz *et al.* 2007; Cisneros 2008a, b; Müller *et al.* 2008; Säilä 2008, 2009a; Sues & Reisz 2008; Tsuji & Müller 2008, 2009).

Procolophonoidea – one of the most species-rich clades of parareptiles – includes superficially lizard-like reptiles from the Permian and Triassic, diagnosed by (among other characters) the absence of a tabular, a contribution of the jugal to the ventral embayment of the posterior cheek, an emarginated ventral margin of the temporal region of the skull, and the absence of dentition on the transverse flange of the pterygoid (e.g. Modesto & Damiani 2007; Säilä 2008). Procolophonoids are the only parareptiles known to have survived the end-Permian mass extinction event, and have been widely discussed in the context of survivorship rate analyses across the Permian-Triassic boundary (examples of similar analyses applied to other tetrapod groups include: Modesto & Rychczynski 2000; Spencer & Benton 2000; Modesto *et al.* 2001, 2002, 2003; Benton *et al.* 2004; Cisneros *et al.* 2005; Ruta *et al.* 2007; Cisneros 2008a; Fröbisch 2008; Ruta & Benton 2008).

Procolophonoids are both morphologically and ecologically diverse (Cisneros 2006, 2008a). They have been

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recorded from all continents and encompass some forty species with a broad range of morphofunctional adaptations. For example, their dentition attests to a wide spectrum of feeding specializations in the herbivory guild (e.g. Gow 1977; Reisz & Sues 2000; Reisz 2006; Cisneros 2008a). Numerous taxa exhibit impressive cranial sculptures in the form of spikes and/or frills, the functional role of which may have been related to protection, display and/or recognition (e.g. Cisneros 2008c).

Procolophonoids provide an interesting case study for elucidating macroevolutionary trends, patterns of morphological transformation, and rates of character change in tetrapods in the aftermath of the end-Permian extinction (Benton *et al.* 2004). The group is amenable to these kinds of analyses because the study of its relationships is significantly advanced over those of other parareptiles, and thus permits the exploration of morphological variety using discrete character sets (e.g. Foote 1991, 1992; Wills *et al.* 1994; Roy & Foote 1997; Wills 1998; Brusatte *et al.* 2008; Ruta 2009; Young *et al.* 2010).

In recent years there has been a significant resurgence of interest in studies of biodiversity and ecological change through time, as well as in the impact of large-scale extinctions on diversification, especially in terrestrial environments. Several of these studies include analyses of morphological diversity (hereafter, disparity) which have found broad applications in both phylogenetic and macroecological frameworks (e.g. Wills *et al.* 1994; Wagner 1995, 1997; Foote 1997; Roy & Foote 1997; Wills 1998; Ciampaglio *et al.* 2001; Ciampaglio 2002; Villier & Korn 2004; Wesley-Hunt 2005; Stayton 2006; Botha & Angielczyk 2007; McGowan 2007; Brusatte *et al.* 2008; Sidlauskas 2008; Benton 2009; Ruta 2009; Young *et al.* 2010; for additional remarks, see also McGhee 1999; Eble 2000; Erwin 2007, 2008).

Here we use cladistic characters as a basis for disparity calculations and to construct a character-state 'morphospace'. We follow protocols outlined by Wills *et al.* (1994; see also Brusatte *et al.* 2008; Ruta 2009; Young *et al.* 2010). Generally, the approach we employ shows some similarities to protocols adopted in morphometric analyses (e.g. Zelditch *et al.* 2004; Stayton & Ruta 2006; Botha & Angielczyk 2007; Pierce *et al.* 2008; Young *et al.* 2010). However, the interpretation of a morphospace may be less straightforward in the case of cladistic data than in the case of landmarks and/or physical measurements (e.g. Wills *et al.* 1994; Villier & Korn 2004; McGowan 2007; Ruta 2009). The fundamental point is that both categories of data (physical measurements and/or landmarks on one hand, cladistic characters on the other) can be employed to describe shape and its variation. In the case of physical measurements and landmarks, shape is readily captured and visualized by geometric descriptors, whereas in the case of cladistic characters shape is quantified through different codings for alternative morphological conditions.

These two data categories should not be regarded as mutually exclusive or incompatible, as each is suited to specific targets and each presents advantages and limitations (see comments in Wills *et al.* 1994). Bearing this in mind, an empirical (*sensu* McGhee 1999) morphospace based upon cladistic data (i.e. a character-state multidimensional space), derived from a multivariate treatment of intertaxon distances, effectively depicts the morphological variety of taxa under study.

In the rest of this paper we use the largest clade within Procolophonoidea, the family Procolophonidae (see Cisneros 2008a, b; Tsuji & Müller 2009), as the basis for a disparity analysis (the first of its kind for parareptiles) using cladistic characters. We hope to pave the way for similar analyses in other parareptile groups, and to encourage exploration of other data sources (e.g. landmark-based geometric morphometrics).

Aims

In this paper we present a detailed analysis of morphological disparity in procolophonoids. Our investigation draws from a recently published phylogenetic analysis (Cisneros 2008a, b) of the group, and uses the cladistic data matrix of that study as the starting point for a quantitative treatment of the degree of morphological similarity among taxa and their distribution in morphospace (more accurately, a character-state space; e.g. Foote 1991, 1992; Wills *et al.* 1994; Roy & Foote 1997; McGhee 1999; McGowan 2007; Ruta 2009; Young *et al.* 2010).

Our goals are: (1) to explore patterns of morphospace occupation for procolophonoids as a whole and for constituent groups in this clade; (2) to quantify disparity for different sets of taxa grouped by stratigraphic age, ecological adaptations, phenotypical resemblance, and phylogenetic relatedness; and (3) to reconstruct a palaeobiogeographical scenario, including inferred modalities of dispersal and ancestral area distributions at different phylogenetic levels of procolophonid phylogeny.

Concerning ecological adaptations under point (2) above, we identify two broad 'categories' or 'assemblages' of procolophonoids based on their feeding specializations, identified a priori using tooth morphology. The first category consists of taxa adapted to feeding on high fibre vegetation, whilst the second category includes taxa that were adapted to feeding on softer plant material and/or insects (e.g. Colbert 1946; Gow 1977; Sues & Baird 1998; Cisneros 2006). Through this we seek to determine whether shifts in feeding adaptations were accompanied by changes in overall disparity. Concerning phenotypical resemblance under point (2), we establish a broad comparison between taxa that exhibit cranial armours and taxa that do not, the possession of cranial armour being taken as a proxy for overall similarity (though not necessarily for phylogenetic proximity). Through this we aim to test the hypothesis of an increased overall disparity among armoured taxa, most of which

are phylogenetically more derived than their armourless relatives.

Material and methods

Procolophonid diversity

An up-to-date list of known procolophonids (including as yet undescribed taxa) is shown in Part 1 of the Online Supplementary Material. Species are listed in stratigraphic order, but considerable uncertainty surrounds the age of numerous taxa, particularly in the Lower and Upper Triassic. Geographic provenance and stratigraphic occurrence are also reported.

Out of 43 recognized taxa, five appear to be dubious or extremely poorly known. Of the remaining 38 taxa, 22 have been considered in this study. The two species of *Phaantosaurus* and the four species of *Kapes* have been treated, in each case, as a single operational taxonomic unit. However, we have not tested the monophyletic status of each genus, which is part of an ongoing investigation. As a result 12 taxa in total have been left out. Several of these are still inadequately known, one (unnamed procolophonid from Australia) is currently under study, and another (*Anomoiodon*) has been considered in a recent cladistic analysis (Säilä 2008) published immediately after the analytical sections of this paper were completed. Finally, Schoch (in press) reported a procolophonid-like reptile from the German Middle Triassic. At least at genus level, however, the cladistic analysis that forms the basis for the present investigation (see Cisneros 2008a, b) provides adequate coverage of procolophonid diversity. It is the most comprehensive phylogenetic treatment of the group available to date, in terms of both number of taxa and characters (new cladistic analyses of procolophonids are currently being prepared by numerous authors; particularly important in this context is L. K. Säilä's revision of various Russian species; see also Säilä 2009a, b).

Phylogenetic analysis

The data matrix of Cisneros (2008b) was subjected to a maximum parsimony analysis with PAUP* 4.0b10 (Swofford 2002), after inclusion of *Pintosaurus magnidentis* (59 unordered and unweighted characters; two outgroup taxa; 22 ingroup taxa). The search settings were as follows: heuristic search with 5000 random stepwise addition replicates; tree bisection-reconnection branch-swapping algorithm (TBR), keeping one tree after completion of each replicate, and subsequently performing TBR on all trees in memory at the end of 5000 replicates with multiple tree saving option in effect. PAUP* retrieved 36 trees with length of 119 steps, global consistency index (CI) of 0.681 (excluding uninformative characters), global retention index (RI) of 0.8053, and global rescaled consistency

index (RC) of 0.5549. Most of the uncertainty revolves around the mutual relationships of the five basal taxa, *Coletta seca*, *Kitchingnathus untabeni*, *Phaantosaurus* spp., *Pintosaurus magnidentis* and *Sauropareion anoplus*. Furthermore, a trichotomy subtends *Procolophon trigoniceps*, *Teratophon spinigenis* and *Thelerpeton oppressus*. Reweighting characters based upon the maximum value (best fit) of their rescaled consistency indices yielded nine trees. The strict consensus shows a trichotomy subtending *Coletta*, *Pintosaurus* and *Sauropareion*, as well as a trichotomy (as in the unweighted analysis) subtending *Procolophon*, *Teratophon* and *Thelerpeton*. The (*Coletta*, *Pintosaurus*, *Sauropareion*) clade occupies a basal position in the weighted analysis, whilst *Phaantosaurus* spp. and *Kitchingnathus* emerge, in that order, as successively more closely related taxa to all remaining procolophonids. The trees from the weighted run are a subset of those from the unweighted run. No further reduction in the number of trees was obtained after additional rounds of weighting (five in total, after which no additional weighting was applied). With characters having equal weight and with the ordering scheme based upon Cisneros (2008b), PAUP* found 96 trees (length = 121 steps; CI = 0.6695, excluding uninformative characters; RI = 0.806; RC = 0.5462), the strict consensus of which is identical to that found with the unordered and unweighted characters. As this paper is not primarily concerned with a new phylogeny of procolophonids, we have not carried out additional analyses of the effect of taxon and/or character exclusion on the resolution of the consensus topology. Finally, concerning outgroup selection, the studies by Cisneros (2008a, b) used *Nyctiphruetus* and *Owenetta* spp. As for *Nyctiphruetus*, the senior author had a chance to observe a range of specimens that together provided a fairly complete picture of the anatomy of this parareptile. Therefore, this taxon was chosen as a suitable outgroup at the time of publication of the analyses that inform the present study. No detailed information on nyctoleterids was available at the time (see detailed references in Tsuji & Müller 2009). For the purposes of conducting disparity in procolophonids, the selection of outgroups did not pose problems, as the dataset seeks to capture traits relevant to the internal relationships of that clade. In addition, even the most basal parareptiles appear too derived to provide a suitable outgroup of procolophonids. In terms of biogeographic scenarios, we are currently exploring the influence of various outgroup selections on ancestral area reconstructions near the base of the major parareptile clades.

The choice of a tree does not affect disparity calculations, as these are based on the original data matrix. We selected one of the 36 equally parsimonious trees from the unweighted run (also corresponding to one of the trees from the weighted analysis) as the starting point for our discussion of dispersal routes (Fig. 1), but results (in terms of geographical area optimizations) based upon different

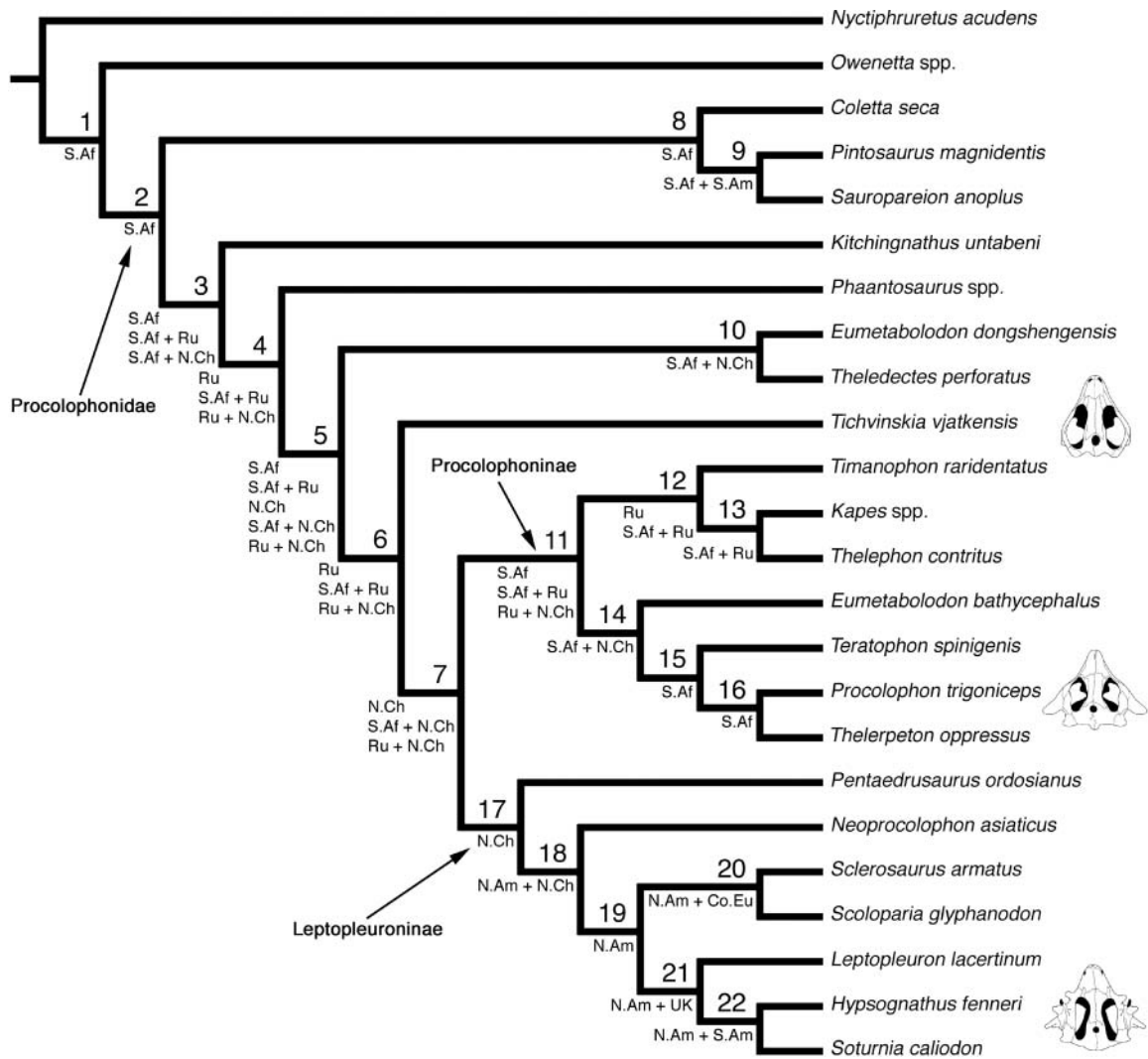


Figure 1. One of 36 equally parsimonious trees of procolophonids, derived from a maximum parsimony analysis in PAUP* of a data matrix consisting of 24 taxa and 59 unordered and unweighted characters (see text for details). Nodes discussed in the biogeography section of the text are numbered. Ancestral area reconstructions based on a DIVA analysis are plotted next to each node. At node 16, a possible dispersal to Antarctica (not shown) may have characterized the branch leading to *Procolophon*. Skull silhouettes (not to the same scale) are drawn next to the names of representative taxa. Area abbreviations: Co.Eu, Continental Europe; N.Am, North America; N.Ch, North China; Ru, Russia; S.Af, South Africa; S.Am, South America; Great Britain.

resolutions at the base of the strict consensus topology do not differ remarkably. The selected tree makes the best predictions in terms of patterns of skeletal change along the basal portion of procolophonid phylogeny (see also Cisneros 2008a, b; Säilä 2008, 2009a), and character-state changes near the root of this clade are currently being investigated. In the case of some biogeographical techniques (e.g. DIVA; see below), a fully resolved tree is needed. A more exhaustive treatment of the biogeographical history of procolophonids (and of other parareptiles), with a discussion of alternative branching patterns for various groups, will form the subject of a separate paper. For analyses of stratigraphical and phylogenetic concordance,

we performed calculations on all trees from the unweighted PAUP* analysis.

Stratigraphical data

Our main focus is not on the quality of the procolophonid record (for discussions see also Cisneros 2008a; Säilä 2009a, b), but on the general agreement between the branching order of taxa and their order of stratigraphical appearance. This is achieved through the use of various indices: Relative Completeness Index (RCI) (Benton 1994), Stratigraphic Consistency Index (SCI) (Huelsenbeck 1994), Gap Excess Ratio (GER) and modified Gap Excess Ratio (GER*). Note that RCI quantifies completeness of

the record rather than measures of fit (Wills *et al.* 2008). For a discussion of these indices, see Wills (1999, 2007), Finarelli & Clyde (2002), Hammer *et al.* (2001), Hammer & Harper (2006) and Wills *et al.* (2008). Calculations of most indexes are implemented in the software GHOSTS 2.3 (Wills 1999, 2007). Preliminary analyses of concordance between stratigraphy and phylogeny presented here will hopefully initiate detailed surveys of the procolophonid record and its quality, using both more comprehensive taxonomic sets and alternative tests (see methods in Angielczyk & Fox 2006; Marcot & Fox 2008; Wills *et al.* 2008).

Disparity analyses

Protocols for undertaking analyses of disparity are presented in numerous papers. Here we follow a set of techniques highlighted in a number of recent publications (see Brusatte *et al.* 2008; Ruta 2009). A more detailed explanation of these techniques can be found in Wills *et al.* (1994) and Wills (1998). For a general overview of disparity analyses, see Foote (1996, 1997), Wills (2001), Navarro (2003), Erwin (2007) and Foote & Miller (2007).

From data matrix to intertaxon distances. The data matrix assembled by Cisneros (2008a, b) was used to derive pairwise Euclidean distances among taxa. The latter were obtained with the software MATRIX 1.0 (Wills 1998). There are very few instances of uncertain character-state scores in the original dataset (about 0.02% of the total cell entries). There are several ways in which uncertain (as well as polymorphic) scores could be treated. One way is to replace them with question marks; another is to assign a known state to them. We opted for the introduction of a known state, while noting that the first option did not entail noticeable differences in either measures of mean disparity values or distribution of taxa in morphospace. All uncertainties were replaced consistently with the smallest of the states represented in the uncertainty coding (thus if a taxon was originally coded as 0/1, it received a score of 0; if it was coded as 1/2, it received a score of 1). No remarkable differences in the disparity calculations or morphospace plots were observed when alternative states were used (e.g. the highest state in the uncertainty coding). All question marks were replaced with 9, as per requirement of the MATRIX software to assign a number to unknown states that differs from all other states in the dataset. The character ordering and weighting schemes in Cisneros (2008a, b) were adopted in the input data file (Online Supplementary Material Part 2) exported to MATRIX 1.0. For a detailed account of MATRIX 1.0 options, see Wills (1998) and the manual annexed to the software (Brusatte *et al.* 2008; Ruta 2009). Tabulated Euclidean distances used in subsequent calculations are shown in Part 3 of the Online Supplementary Material. Below we elaborate briefly on the influence of autapomorphies on both disparity values and patterns of taxon distribution in morphospace.

From intertaxon distances to disparity indices.

Euclidean distances were subjected to a multivariate analysis (principal coordinates analysis; see also Wills *et al.* 1994; Wills 1998; Villier & Eble 2004), both to derive a set of scores for disparity calculations and to build a morphospace (more accurately, a character-state space) for procolophonids. Principal coordinates analysis (hereafter, PCoA) was carried out with the software GINKGO 1.5.5 (Cáceres *et al.* 2007), applying the Cailliez method of negative eigenvalue correction (Cailliez 1983; Legendre & Anderson 1998; Ruta 2009) and using the overall group centroid (point with coordinates averaged over the PCo coordinates of all taxa) as the origin of the coordinate axes in morphospace. The coordinates of each taxon on all PCo axes (PCo coordinates) were used to derive disparity indices. These coordinates are listed in Part 4 of the Online Supplementary Material.

For all disparity calculations we used the first 15 (out of 24) PCo axes, which explain at least 90% of the total variance. The software RARE 1.1 (Wills 1998) was used to output mean values of four disparity indices (sum and root-product of ranges, and sum and root-product of variances) and their associated 95% error bars (bootstrap resampling; 1000 replicates), as well as rarefaction profiles for each index. For explanations of commands in RARE 1.1, see Wills (1998) and the manual annexed to the software (Brusatte *et al.* 2008; Ruta 2009).

Apart from the two range-based and the two variance-based indices, other disparity metrics are available (Wills *et al.* 1994; Ciampaglio *et al.* 2001; Navarro 2003). However, range and variance metrics are extensively used and their significance is fairly intuitive. Range metrics measure the amount of morphospace occupied by taxa, whereas variance metrics measure the amount of taxon dispersal, i.e. the amount of dissimilarity among taxa (Wills *et al.* 1994; Ciampaglio *et al.* 2001; Villier & Korn 2004; Stayton & Ruta 2006).

From intertaxon distances to morphospace. Using the first three PCo axes (explaining cumulatively 45.73% of the total variance), we built a plot of both outgroup and ingroup taxa. The choice of the first three axes is only for the purpose of morphospace visualization. The morphospace summarizes information on a set of intertaxon distances derived from a cladistic matrix and is not akin to the concept of morphospace in geometric morphometrics. However, both types of morphospace depict aspects of shape change, as explained above. (e.g. Wills *et al.* 1994; Wills 1998, 2001; Zelditch *et al.* 2004; Foote & Miller 2007; Ruta 2009).

Palaeobiogeographical analyses

The reconstruction of the biogeographical histories of clades of Permian and Triassic amniotes is riddled with difficulties (e.g. Modesto 2000; Modesto & Rybczynski 2000; Cisneros *et al.* 2004; Reisz *et al.* 2007; Müller *et al.* 2008; Sues & Reisz 2008; Cisneros & Tsuji 2009), and

must await further discoveries and comprehensive phylogenetic reviews, especially following re-evaluation of numerous problematic taxa. A useful step towards a biogeographical treatment of parareptiles consists of producing more focused and targeted investigations, whereby estimates of the ancestral distribution of well-characterized clades are provided and subsequently tested in the light of broader taxonomic exemplars. Our discussion of procolophonid palaeobiogeography necessitates brief preliminary remarks on biogeographical analyses in general, and a clarification of what we seek to achieve through the reconstruction of ancestral geographic ranges.

Cladistic biogeography aims to understand relationships among geographic areas occupied by the terminal taxa in a phylogeny using information embodied in the geometry of the tree, i.e. the pattern of taxon relationships (e.g. Humphries & Parenti 1999; Ebach & Tangney 2006; Williams & Ebach 2007). Despite repeated claims that the study of historical biogeographical patterns of individual groups is not appropriate (Platnick & Nelson 1978), Engstoff (1993, p. 525) noted that "... taxon biogeography need not be abandoned: the diversity of distribution patterns requires not only a search for general patterns, but also inquiry into individual ones". The guiding principles underlying our approach to procolophonid biogeography are an attempt to merge the methodological and philosophical approaches of both traditional historical (narrative) and modern cladistic (analytical) biogeography. Thus, we are interested in searching for centres of origin (i.e. ancestral area ranges), area patterns, and reconstructing congruent area distributions and patterns of endemism, and analysing causal factors responsible for the observed range distributions (see Nelson & Platnick 1981; Patterson 1981; Rosen 1994; Smith 1994; Janvier 1996; Hunn & Upchurch 2001; Upchurch & Hunn 2002).

Two techniques of cladistic biogeography are applied here to procolophonids. Both rely upon tree topology and parsimony-based optimizations of ancestral areas. Whilst no method is perfect on its own, combined methods are likely to provide a more informed, albeit preliminary, framework for future, more refined analyses. Recent methods that use maximum-likelihood inferences of ancestral ranges and information on branch lengths (e.g. see Ree & Smith 2008) will be investigated in a separate publication.

Bremer's method. In his probabilistic approach to ancestral area reconstruction, Bremer (1992, 1995) devised a protocol for inferring which of the areas occupied by members of a widespread monophyletic group is most likely to belong to the original range of that group, i.e. the region where the group originated. In its original formulation, Bremer's method is applicable to extant clades with wide distributions (e.g. Engstoff 1995; Hausdorf 1995). However, Smith (1994) and Ruta (1998) extended its use to ancestral area reconstructions for entirely extinct monophyla.

The method assumes that the ancestor of a widely distributed, extant clade was probably limited rather than widespread if the individual taxa in that clade appear to be confined to restricted geographic regions. Furthermore, the method aims to formalize probabilistic arguments justifying the inclusion of a specific area in the ancestral range of a clade based upon the number of tree branches where the area in question occurs and the position of those branches relative to the tree root (see Engstoff 1993). The procedure for assessing the probability that the area (or areas) of occurrence of a terminal taxon is also part of the ancestral range for the entire clade to which that taxon belongs is summarized in two steps. Irreversible (i.e. Camin–Sokal) parsimony is employed in both steps to optimize the absence or presence of an area on the terminal branches.

Firstly, area absence is regarded as a derived condition, implying that the plesiomorphic distribution for the entire clade either includes or consists only of that area (all-loss/no-gain model). Secondly, area presence is regarded as a derived condition, so that the plesiomorphic distribution for the clade does not include the area of interest (all-gain/no-loss model). The tree in Fig. 1 was used for calculations. Next the total number of gains (G) and losses (L) was calculated for each area, and the G/L ratio was taken to represent the probability that an area belongs to the ancestral distribution of the entire clade. The ratios minimize the effect of equal probabilities of gains and losses implicit in the Bremer method. Finally, ratios were re-scaled to 1 by dividing them by the largest G/L to give ancestral area (AA) scores. The area(s) with the largest AA score is most likely to be part of the original clade's range (for a criticism of the Bremer method and its assumptions, see Ronquist 1994, 1995).

The probabilities of occurrence of the G/L ratios (or their AA transforms) are usually not determined in studies that apply the Bremer method. Here, we follow recommendations by Place & Abramson (2004), who proposed a simple technique to assess the significance of differences in the distribution of ratios. Firstly, we tested for the normal distribution of ratios. Secondly, we converted the ratios to Z-scores. Thirdly, we employed the Z-scores to assess the probabilities of the ratios. Thus "...[t]he right tail probability of the standard normal curve indicates the probability of occurrence of a ratio [by extension, an area] more extreme than the one tested" (Place & Abramson 2004, p. 153).

Ronquist's method. To obviate the limitations of irreversible parsimony optimizations of areas, an alternative method is explored. The method was devised by Ronquist (1996, 1997) and is known as dispersal–vicariance analysis, fully implemented in the software DIVA 1.1 (<http://www.ebc.uu.se/systzoo/research/diva/diva.html>). The method considers dispersal and extinction events, making no assumptions about limited or widespread ranges for ancestors. Also, it requires no information on nested patterns of area relationships.

A MacClade tree file was created using the topology in Fig. 1. Characters for all taxa were represented by areas. Each taxon was coded as either 0 or 1 for each area, signifying absence (non occurrence) or presence (occurrence), respectively. The optimal range distribution at each tree node may be represented either by a single area or by groups of areas. If several area optimizations appear to be equiprobable, these are plotted together at a node.

Area selection. The choice of geographical areas is based on distribution data in Part 1 of the Online Supplementary Material. Area optimization may be affected to a more or less significant degree by the merging or splitting of geographical regions. Visual inspection of palaeogeographical maps was used to identify suitable areas for biogeographical analyses. For example, if there are reasons to assume that different areas were always part of a single landmass (e.g. a terrane or a craton) during a time interval of interest, subdivision of this landmass into a number of distinct units may not be warranted. However, heterogeneity of a large region – e.g. in terms of physical, climatic and ecological factors – might make it desirable to consider distinct areas (e.g. at subcontinental level). Our selection of areas attempted to capture geographic spread whilst taking into account the distinctiveness of landmass domains. To reconstruct the palaeobiogeography of procolophonids, the following eight areas were chosen: South Africa, Russia, South America, North America, Great Britain, Europe (continental), North China and Antarctica. Excepting Great Britain, the areas are sufficiently large (continental or subcontinental scale) to enable us to infer plausible dispersal routes or local extinction events. Our conclusions do not differ if Great Britain and North America are merged into a single area (e.g. to reflect proximity of these regions in the Palaeozoic and early Mesozoic).

Results

Phylogeny and stratigraphy

A full list of values for the SCI, RCI, GER and GER* indices for all 36 trees is reported in a separate Excel file annexed to the Online Supplementary Material. SCI values range from 0.65 to 0.75. Thus, between 13 and 15 internal nodes (out of 20) in the fully resolved topologies are consistent, i.e. they have a sister taxon or sister group as old as, or older than them (Wills 1999). RCI values range from 42.105263 to 47.368421. GER values range from 0.556522 to 0.617391. The uncertainty (i.e. p value) that the observed GER and RCI metrics deviate from random varies between 0.04 and 0.12 (for 28 trees, $p < 0.05$). As GER is sensitive to tree shape, we also report values of GER*. These range from 0.999992 to 0.999998, indicating a strong correlation (significantly greater than a null distribution; see Wills *et al.* 2008) of each tree topology to stratigraphy.

Morphological diversity in procolophonids

Mean disparity values for various groups of species are plotted in Fig. 2. These groups are based upon phylogenetic proximity (Fig. 2A–D), stratigraphical age (Fig. 2E–H), pattern of dermal skull armour (Fig. 2I–L) and feeding adaptations (Fig. 2M–P). For each group we show mean values of the two range-based and two variance-based indices discussed above, with associated 95% confidence interval bars.

In quantifying disparity in relation to feeding specializations and the pattern of phenotypical resemblance associated with cranial sculptures, we have not introduced any additional measurements (e.g. meristic data related to dermal ornament or tooth crown morphology). This is because our primary focus is the construction of an empirical morphospace based upon a set of defined characters. However, we are currently exploring the impact of these additional data for future analyses that include a broader range of taxa and the use of multiple descriptors for disparity calculations (e.g. physical measurements, landmarks). It will be interesting to see how empirical morphospaces and relative disparity values are affected when combined discrete and continuous characters are used. In this respect our subdivisions of taxa into ecophenotypical groups precedes the actual analyses of disparity, in that such groups are predetermined based on overall resemblance and hypothesized dietary adaptations.

Mean disparity among groups. Visual inspection of the plots in Fig. 2A–D shows the same general pattern for the four indices. Mean disparity values for groups 1 (basal procolophonids) and 3 (leptopleuronines) are comparable, and only slightly larger than the mean value for group 2 (procolophonines). In all cases there is a considerable overlap among confidence interval bars. Thus, despite their broad spectrum of variation, especially evident in the array of cranial shapes and sculpture patterns, the three major procolophonid groups are almost equally diverse. The disparity indices exhibit different degrees of sensitivity to both sampling size and taxonomic practice (e.g. Wills *et al.* 1994; Foote 1997; Wills 1998; Ciampaglio *et al.* 2001; Villier & Eble 2004; Villier & Korn 2004). However, as the three groups considered here include approximately identical numbers of taxa (group 1: $n = 8$; group 2: $n = 7$; group 3: $n = 7$) and encompass a wide range of morphotypes (such as are represented by species exhibiting extreme cranial morphologies), we conclude that the observed disparity patterns reflect real biological signal.

To evaluate the impact of sampling intensity on disparity profiles among the three groups, we illustrate rarefaction profiles for each of the four indices (Fig. 3A–D). Almost invariably the mean disparity values for groups 1 and 3 are consistently larger than the mean value for group 2, even at very low sampling size. Furthermore, in the case of the two range-based indices (Fig. 3A, B) and the sum of variances

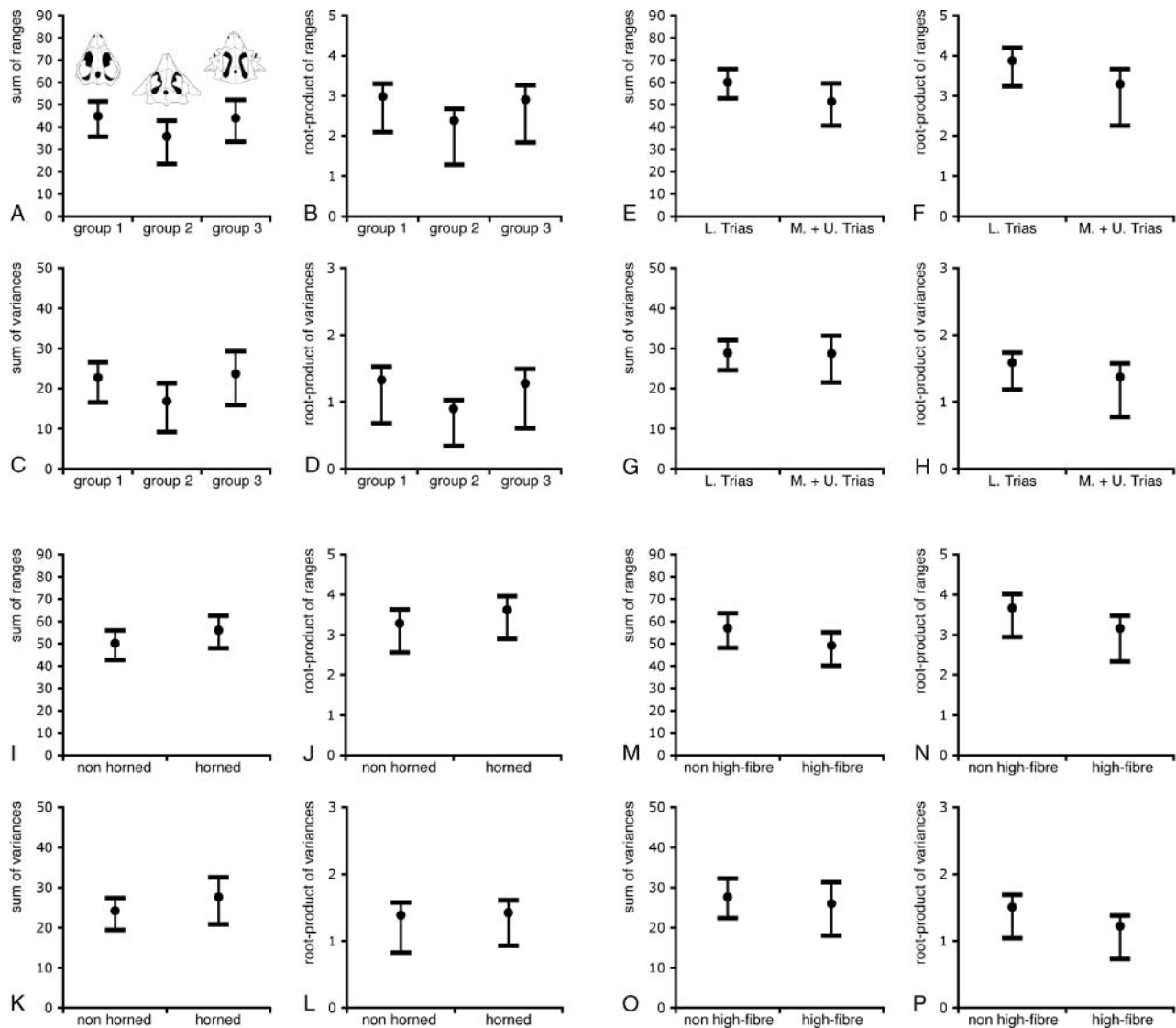


Figure 2. Mean values of four disparity indices and associated 95% confidence intervals for various clusters of taxa. Calculations are based upon a principal coordinates analysis of the intertaxon Euclidean distances derived from the cladistic data matrix, without inclusion of autapomorphies (see text for details). With reference to Fig. 1, the notations ‘group 1’, ‘group 2’ and ‘group 3’ refer, respectively, to the taxa comprised between, and including, *Coletta seca* and *Tichivinskia vjatkensis*, *Timanophon varidentatus* and *Thelerpeton oppressus*, and *Pentaedrusaurus ordosianus* and *Soturnia caliodon*. Species are grouped by A–D, phylogenetic proximity; E–H, stratigraphical age; I–L, pattern of dermal skull armour; and M–P, feeding adaptations. Skull silhouettes (not to the same scale) of representative taxa are shown (see also Fig. 1). Calculations exclude autapomorphies.

(Fig. 3C), the profiles of mean disparity values for groups 1 and 3 are closely appressed.

Taken together, these observations suggest that the evolution of procolophonids was characterized by a rather uniform spread of morphological variation both among the array of taxa preceding the procolophonine-leptopleuronine separation and within each of these two subfamilies. Procolophonines are invariably less morphologically diverse than leptopleuronines, particularly when variance-based indices are considered (Fig. 3C, D).

Assignments of taxa to each of the three main procolophonid groups, based on the topology shown in Fig. 1, are reported in Part 5 of the Online Supplementary Material.

Morphological diversity through time. The second set of disparity calculations refers to the grouping of species by age. The stratigraphical record of procolophonids continues to improve through a flurry of new discoveries; however, the overall distribution of species in time is still very patchy. This means that a detailed analysis of disparity changes cannot be satisfactorily undertaken using fine subdivisions

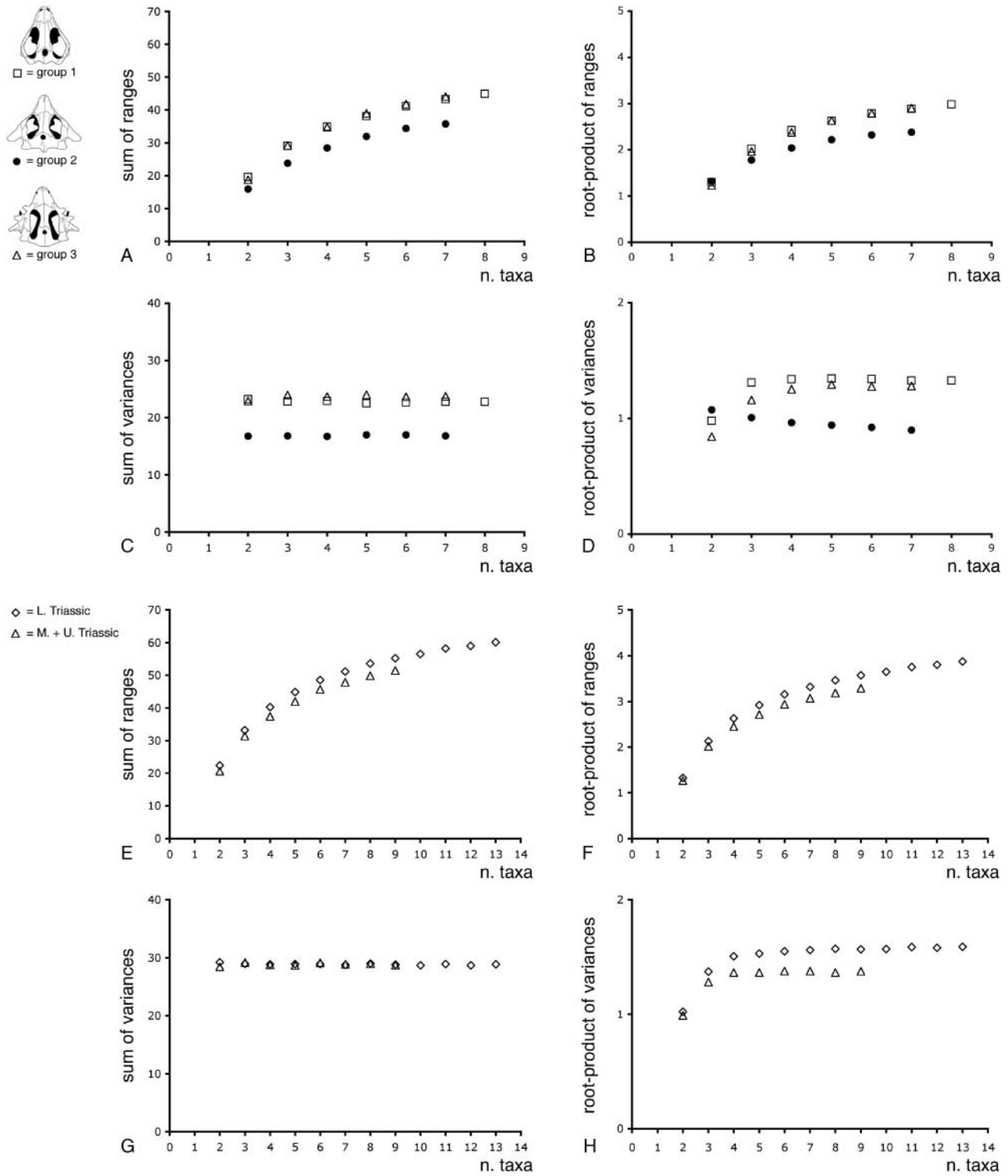


Figure 3. Rarefaction profiles of mean values of four disparity indices for different clusters of species grouped by A–D, phylogenetic proximity and E–H, stratigraphical age. Skull silhouettes (not to the same scale) of representative taxa are shown (see also Fig. 1). Calculations exclude autapomorphies.

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of the group's range (for examples of analyses of faunal turnover in speciose vertebrate groups, see Fröbisch 2008 and Ruta & Benton 2008). Therefore we provide only a crude estimate of disparity fluctuations during the Triassic. At the simplest level, taxa are assigned to two time bins, Lower Triassic ($n = 13$) and Middle + Upper Triassic ($n = 9$). The rationale for this is three-fold. Firstly, dubious, poorly known, fragmentary and/or undescribed taxa are not represented in the data matrix. Secondly, the age assignment for certain species is still unclear. Thirdly, the Middle and Upper Triassic record of procolophonids is rather sparse; for this reason a subdivision of species into separate Middle and Upper Triassic time bins does not appear to be feasible at present. Mean disparity values by age do not differ remarkably when the uncertain age of various taxa is taken into account and these taxa are transferred from one time bin to another.

As Fig. 2E–H shows, the mean disparity values of Lower Triassic procolophonids exceed slightly the mean value of Middle + Upper Triassic species for the two range-based indices and for the root product of variances. The mean values for the two age clusters are comparable for the sum of variances (Fig. 2G). Overall, differences in disparity are not remarkable, as illustrated by the large overlap between the confidence interval bars. At the broad temporal scale employed here, this finding implies that the group as a whole was characterized by a fairly constant level of morphological 'spread' during its evolutionary history. This conclusion is further strengthened by rarefied profiles of disparity (Fig. 3E–H) for the two time bins. The mean disparity values for the Lower Triassic are only marginally higher than those for the Middle + Upper Triassic. Overall, for each of the four disparity indices the two rarefied profiles follow each other's course very closely (but note a slight departure from this trend in the case of the root-product of variances; Fig. 3H).

Assignment of taxa to each of the two time bins is reported in Part 6 of the Online Supplementary Material.

Disparity and cranial armour. Numerous procolophonids carry peculiar dermal skull armours, mostly in the form of spines and spine-like projections. These vary in shape, size, position and number. *Neoprocolophon* exhibits a pair of short bulbous jugal spines (Young 1957); a pair of massive posterolateral quadratojugal spines account for more than 50% of cranial width in *Teratophon* (Gow 1977) and at least seven pairs of short slender spikes are visible along the jugal and the quadratojugal in adult specimens of *Scoloparia* (Sues & Baird 1998). In some cases the array of spines offers a remarkable example of convergence with extant North American horned lizards (Phrynosomatidae), as exemplified by the genus *Hypsognathus* (Sues *et al.* 2000). This astounding diversity of spine-bearing (horned) skulls contrasts with the relatively simple cranial morphology of other (non-horned) taxa. We are therefore interested

in contrasting overall disparity in taxa without ($n = 10$) and with cranial armour ($n = 12$). We note that horned taxa (leptopleuronines and most procolophonines) do not form a monophyletic group. Cranial armours are absent in the paraphyletic array of taxa preceding the evolutionary separation between procolophonines and leptopleuronines (e.g. Cisneros 2008b).

For all their diversity of cranial armours, horned procolophonids exhibit, on average, only slightly higher levels of disparity than their non-horned relatives. This is borne out by the plots in Fig. 2I–L. For brevity we have not reported rarefied disparity profiles, but their trend is similar to that found for age clusters (see above), i.e. the rarefied profiles are tightly appressed.

Assignment of taxa to each of the two main phenotypical assemblages is reported in Part 7 of the Online Supplementary Material.

Disparity and feeding strategies. A final set of disparity calculations relates to different food processing adaptations in procolophonids. Tooth morphology varies remarkably in this group, and this variation is probably associated with exploitation of different herbivorous niches. Examples of different dentition patterns include: slightly widened conical teeth (e.g. *Coletta*; Gow 2000); transversely expanded and mortar-like molariform teeth (e.g. *Hypsognathus*; Colbert 1946); transverse, multi-cusped and blade-like teeth (e.g. *Scoloparia*; Sues & Baird 1998); presence of a massive and dome-like posterior crushing tooth (e.g. *Haligonia* and *Thelephon*; Gow 1977; Sues & Baird 1998); and multiple rows of bulbous conical teeth bearing striking resemblance to those found in captorhinid reptiles (e.g. *Theledectes*; Gow 1977).

We return to a discussion of herbivorous adaptations in procolophonids below. Here we contrast disparity in two clusters of taxa, i.e. those that possess bicuspidate molariforms associated with mortar-like tooth surfaces ($n = 10$), and those that do not ($n = 12$). The latter assemblage also includes *Kitchingnathus* and *Scoloparia*, both of which exhibit bicuspidate teeth but no mortar-like surfaces. The former cluster includes taxa presumably adapted to feeding on high-fibre vegetation, a polyphyletic array including *Eumetabolodon bathycephalus*, *Procolophon*, *Thelerpeton*, *Teratophon*, *Pentaedrusaurus*, *Neoprocolophon*, *Sclerosaurus*, *Leptopleuron*, *Hypsognathus* and the tiny *Soturnia*. These high-fibre taxa are on average less morphologically diverse than their non-high fibre relatives, albeit only marginally so (Fig. 2M–P).

Assignment of taxa to the two main ecological groups is reported in Part 8 of the Online Supplementary Material.

Morphospace occupation. Figure 4 illustrates the pattern of morphospace occupation for all procolophonoid taxa included in the cladistic analysis. We present three 2D plots (Fig. 4A–C) and one 3D plot (Fig. 4D), all based on the first

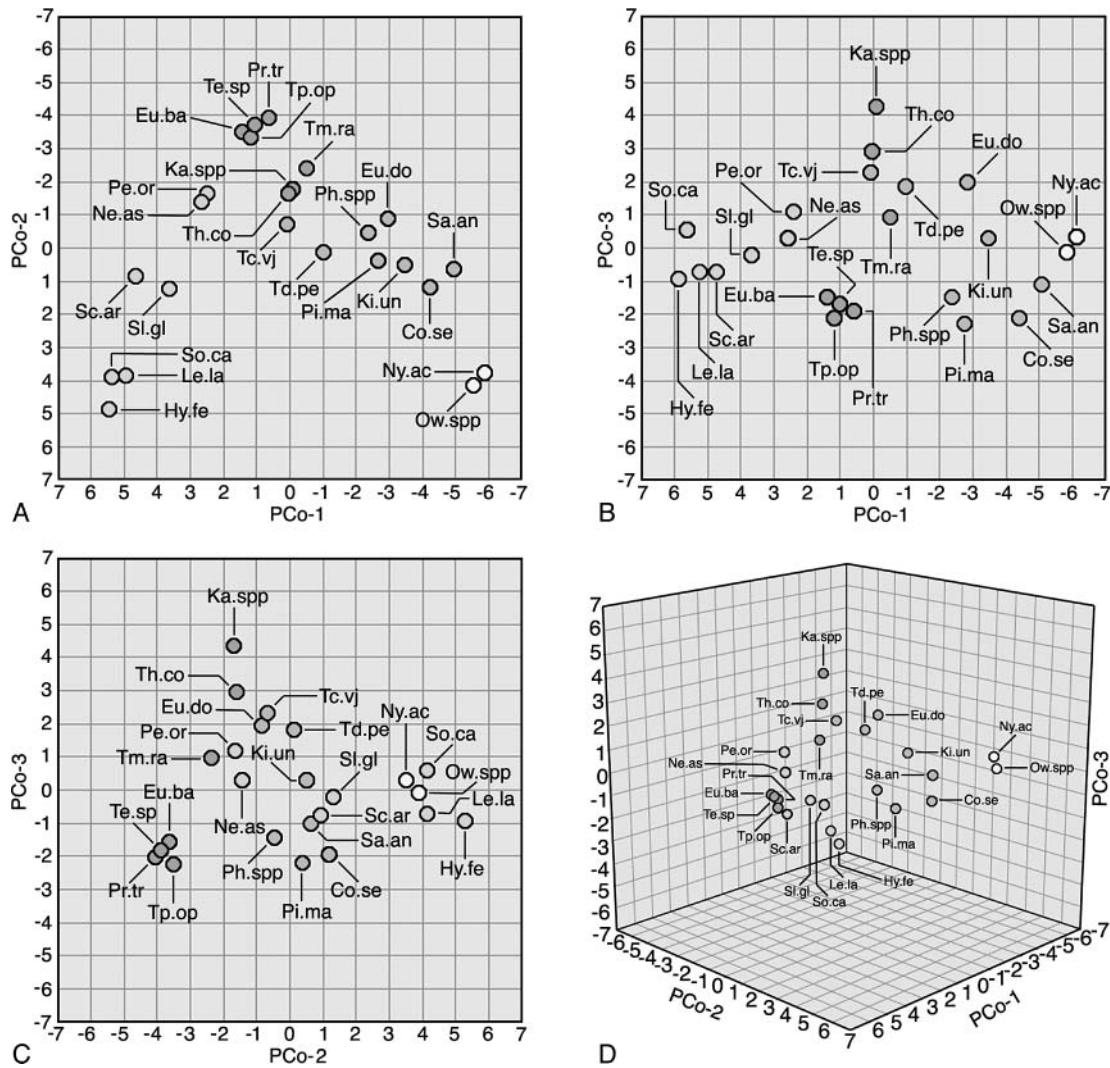


Figure 4. Representation of the three main groups of procolophonids in a character-state morphospace built from principal coordinate axes **A**, 1 and 2; **B**, 1 and 3; **C**, 2 and 3; and **D**, 1–3. Calculations exclude autapomorphies. Taxon abbreviations: Co.se, *Coletta seca*; Eu.ba, *Eumetabolodon bathycephalus*; Eu.do, *Eumetabolodon dongshengensis*; Hy.fe, *Hypsognathus fenneri*; Ka.spp, *Kapes* spp.; Ki.un, *Kitchingnathus untabeni*; Le.la, *Leptopleuron lacertinum*; Ne.as, *Neoprocolophon asiaticus*; Ny.ac, *Nyctiphruetus acudens*; Ow.spp, *Owenetta* spp.; Pe.or, *Pentaedrusaurus ordosianus*; Ph.spp, *Phaantosaurus* spp.; Pi.ma, *Pintosaurus magnidentis*; Pr.tr, *Procolophon trigoniceps*; Sa.an, *Sauropareion anoplus*; Sc.ar, *Scelosaurus armatus*; Sl.gl, *Scoloparia glyphanodon*; So.ca, *Soturnia caliodon*; Tc.vj, *Tichvinskia vjatkensis*; Td.pe, *Theledectes perforatus*; Te.sp, *Teratophon spinigenis*; Th.co, *Thelephon contritus*; Tm.ra, *Timanophon raridentatus*; Tp.op, *Thelepeton oppressus*.

three PCo axes. The percentages of the total variance associated with these axes are 24.92% (PCo-1), 14.39% (PCo-2) and 6.42% (PCo-3). Fig. 5 depicts four 2D plots based on the first two PCo axes illustrate hulls (convex polygons) delimiting clusters of taxa such as those described above: phylogenetic clusters (Fig. 5A); Lower Triassic versus Middle + Upper Triassic taxa (lower and upper hulls respectively; Fig. 5B); non-horned versus horned taxa (left and right hulls respectively; Fig. 5C); and non-high fibre versus high fibre taxa (left and right hulls respectively; Fig. 5D).

The different distributions of taxa in each of the clusters in Fig. 5 were subjected to a variety of tests to evaluate the

significance of the degree of separation between clusters. A detailed discussion of such tests can be found in Hammer & Harper (2006; see also Ruta 2009). All tests were carried out with the software PAST 1.79 (Hammer *et al.* 2001). They include: one-way nonparametric multivariate analysis of variance (npMANOVA), analysis of similarity (ANOSIM) and multivariate analysis of variance (MANOVA). The levels of significance for differences among clusters of taxa were assessed via 10,000 permutations of taxa for all analyses. Specifically, npMANOVA assesses similarities in distributions of variances in two or more groups through numerous permutations of the taxa in those groups

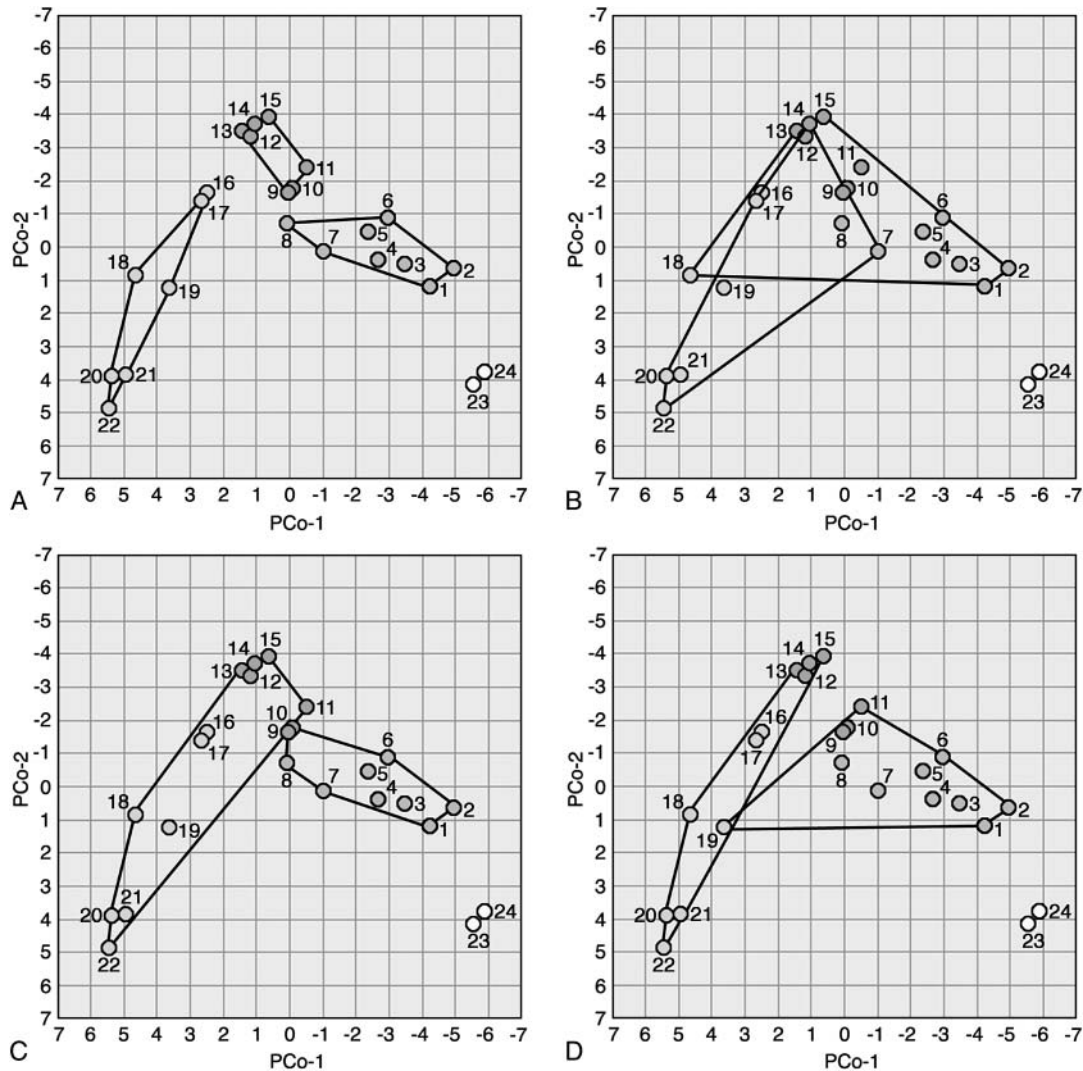


Figure 5. Representation of 2D plots based upon the first two PCo axes with hulls (convex polygons) delimiting clusters of taxa such as are described in the text, namely: **A**, phylogenetic groups; **B**, Lower Triassic versus Middle + Upper Triassic groups (lower and upper hulls, respectively); **C**, non-horned versus horned groups (left and right hulls, respectively); and **D**, non-high fibre versus high fibre groups (left and right hulls, respectively). Numbers appearing adjacent to the data points identify taxa, as follows: 1, *Coletta seca*; 2, *Sauropareion anoplus*; 3, *Kitchingnathus untabeni*; 4, *Pintosaurus magnidentis*; 5, *Phaantosaurus* spp.; 6, *Eumetabolodon dongshengensis*; 7, *Theledectes perforatus*; 8, *Tichvinskia vjatkensis*; 9, *Thelephon contritus*; 10, *Kapes* spp.; 11, *Timanophon raridentatus*; 12, *Thelepereton oppressus*; 13, *Eumetabolodon bathycephalus*; 14, *Teratophon spinigenis*; 15, *Procolophon trigoniceps*; 16, *Pentaedrusaurus ordosianus*; 17, *Neoprocolophon asiaticus*; 18, *Sclerosaurus armatus*; 19, *Scoloparia glyphanodon*; 20, *Soturnia caliodon*; 21, *Leptopleuron lacertinum*; 22, *Hypsognathus fenneri*; 23, *Owenetta* spp.; 24, *Nyctiphruretus acudens*.

(null hypothesis: groups have similar variances). ANOSIM compares the distances between groups with the distances within groups after distances are ranked (null hypothesis: ranked dissimilarities within groups have equal median and range). We also used the MANOVA/CVA function of PAST 1.79 to test for equality of means in different samples.

For each test we inputted the scores of all taxa on the first 15 PCo axes. Importantly, different inputs (e.g. PCo scores on the first three PCo axes) are likely to generate a different set of results (e.g. in terms of the significance of separation among clusters). As with disparity calculations, we chose

those axes that, together, explain at least 90% of the total variance. However, for ease of graphic representation, we show only the projections of taxa on the plane delimited by the first two PCo axes (Fig. 5). Results of all tests are shown in Part 9 of the Online Supplementary Material. Most tests returned significant results ($p < 0.05$), implying that selected groups of taxa (phylogenetic, phenotypical, and ecological, but not temporal) are significantly different.

Impact of autapomorphies. Calculations of disparity values and plots of species in a character-state morphospace

can be regarded as 'conservative', empirical (McGhee 1999) approaches to quantitative assessments of shape variation. In this context 'conservative' implies minimal assessments, such as those derived from the original character matrix. By their very nature character matrices tend to exclude autapomorphies as these have no impact on the reconstruction of trees. However, autapomorphies may alter disparity values and patterns of morphospace occupation to a more or less significant degree. A key point is to establish the extent to which relative disparity values (e.g. patterns of increasing or decreasing disparity among clades or stratigraphical groups) are affected by the inclusion of autapomorphies, as well as the extent to which the mutual positions of taxa in morphospace are altered. Changes in absolute values would not be critical if autapomorphy inclusion simply resulted in more or less isometric changes in morphospace occupation or did not alter the profiles of relative disparity (e.g. group 1 would always be consistently less disparate than group 2). Put simply, a uniform scatter of autapomorphies among the constituent taxa of a group would increase values proportionally, and the 'cloud' of taxa in morphospace would grow by maintaining similar proportions. The important issue is to establish whether significant changes in relative disparity values would be entailed by autapomorphy inclusion, which may be linked to remarkably heterogeneous distributions of unique traits in the taxa of interest.

A germane issue concerns autapomorphies identified as such a posteriori, i.e. character-state conditions that appear along distinct terminal branches (taxa that are not sister groups). These conditions are clearly distinct from unique features identified a priori. The latter are of immediate interest to us as they are not defined phylogenetically. They are also the most difficult to discern because there are different levels of organization at which an organism could be regarded as unique (e.g. genes; macroscopic anatomy). Also, incomplete preservation means that only some of the autapomorphies that are potentially discoverable can be coded for. Finally, further discoveries of new or better preserved taxa may imply a radical change in the status of a character (e.g. a trait formerly identified as being unique to a taxon may turn out to be shared by other taxa).

Acknowledging these problems, our list of unique features is necessarily limited, and likely to increase with future discoveries. However, this is not a limitation for our investigation. The empirical connotations of disparity and morphospace analyses imply that the results can only be usefully interpreted in the context of the selected data. It would therefore be interesting to see whether additional atomization of characters (such as may result from new procolophonid finds) will alter dramatically the relative positions of taxa in morphospace or the profiles of relative mean disparity among groups.

To evaluate the impact of autapomorphies on the groups of taxa discussed above, we added features deemed to be

unique (based on current knowledge of the group) to individual species. The augmented data matrix and derived Euclidean distances and PCo scores (Parts 10–12 of Online Supplementary Material) consist of an additional 27 characters (listed in Part 13 of Supplementary Online Material). Calculations of disparity were repeated for this new data matrix, and the results are reported in Fig. 6. Comparisons between Figs 2 and 6 shows that inclusion of autapomorphies affects very little the profiles of disparity for each of the species clusters discussed above. Whereas absolute disparity values for individual groups of taxa may change, relative values are almost unchanged, and even the amount of overlap between confidence intervals are very similar in the two sets of graphs. A more detailed investigation of the impact of autapomorphies on phylogeny-based analyses of disparity will be presented in a separate publication.

For brevity, we have not illustrated the pattern of species distribution in morphospace after the inclusion of autapomorphies. However, the pattern is very similar to that in Fig. 4. In order to assess the degree of congruence and similarity between autapomorphy-less and autapomorphy-based datasets, we performed two tests using the free software CADM (Legendre & Lapointe 2004; <http://www.bio.umontreal.ca/Casgrain/en/labo/index.html>). The input data consisted of two tabulations of intertaxon PCo distances (one for each dataset). Initially we carried out a global test to evaluate the null hypothesis of incongruence of the two PCo distances matrices, using Friedman's X^2 and Kendall's W statistics based on 999 permutations of matrix structure. The two matrices were given equal weights. Next we ran a Mantel test to evaluate the degree of resemblance among matrices and the associated permutational probabilities for the Mantel statistic (again using 999 replicates). A CADM global test (Friedman's $X^2 = 542.14001$; Kendall's $W = 0.98571$ using correction for tied ranks) returned a significant result ($p = 0.001$), implying that the two matrices of PCo distances are congruent (thus, autapomorphies do not influence overall matrix structure). Additionally, the degree of resemblance between the two matrices is high (Spearman correlation = 0.97142; $p = 0.001$).

Ancestral area reconstruction

Figure 1 shows the probable distribution of geographical areas for basal and internal nodes in one of the shortest trees from Cisneros (2008b) based on a dispersal–vicariance analysis. We discuss the results from this analysis first, before briefly addressing optimizations of areas using irreversible parsimony.

Dispersal–vicariance analysis. Reconstructed ancestral area distributions at different hierarchical levels of procolophonid phylogeny are shown in Fig. 1. If equally probable areas (or groups of areas) are likely to have been part of the ancestral range of a given node, they are listed on separate lines at the node in question. If a set of areas (as opposed

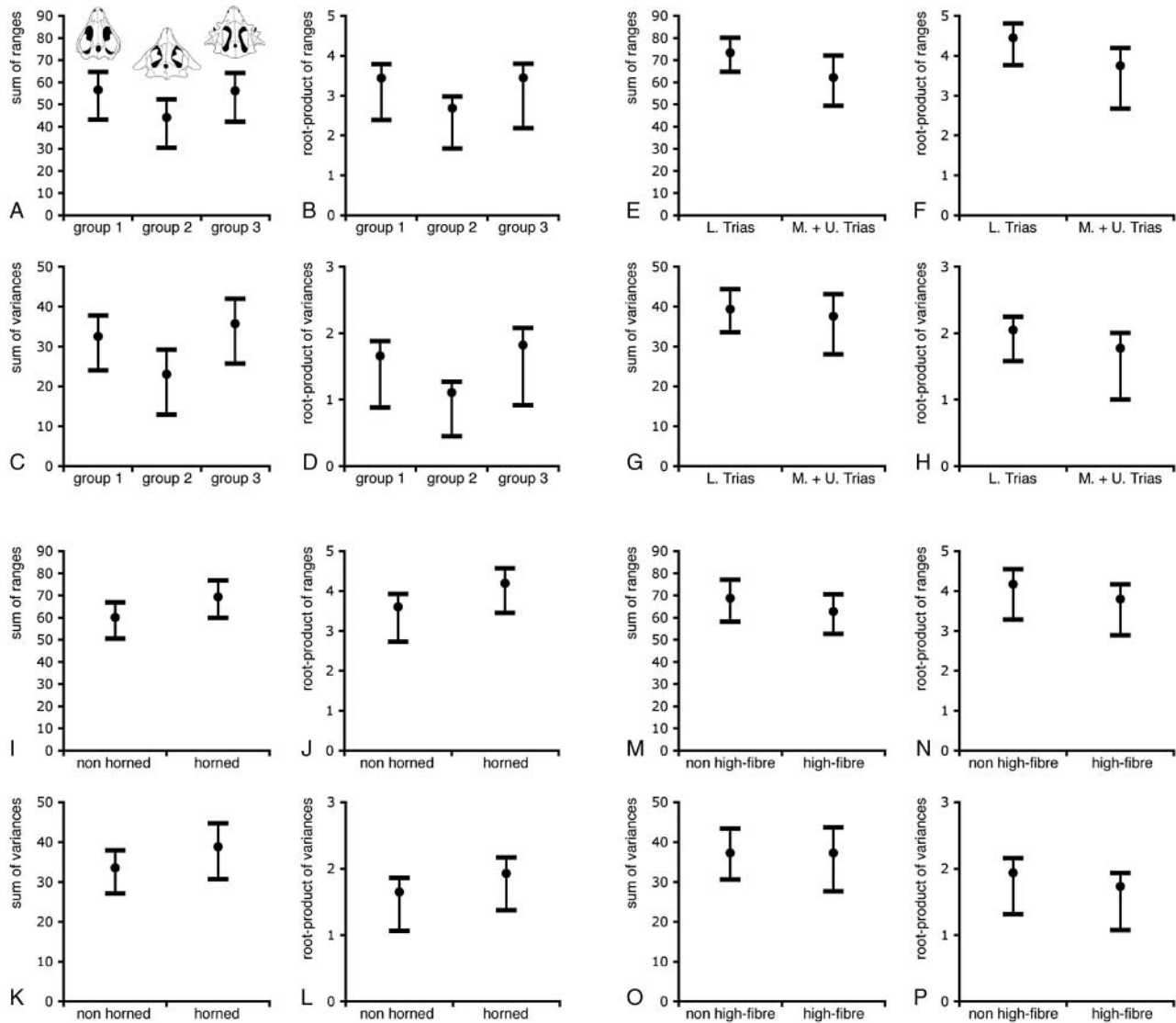


Figure 6. Mean values of four disparity indices and associated 95% confidence intervals for various clusters of taxa. Calculations are based upon a principal coordinates analysis of the intertaxon Euclidean distances derived from the cladistic data matrix, with inclusion of autapomorphies (see text for details and Fig. 2 for other notations).

to a single area) is likely to belong to the ancestral range of a node, a '+' sign separates all areas in that set.

Irreversible parsimony. Part 14 of the Online Supplementary Material reports the number of gains (G), losses (L) and G/L ratios for each of the terminal areas where taxa in Fig. 1 occurs. Inspection of the G/L ratios shows South Africa to be the most probable ancestral area for procolophonids, in agreement with the results of area optimizations from DIVA 1.1. Russia and North China successively form the second and third most likely ancestral area for the clade as a whole. All remaining areas show much lower probabilistic values. Given its assumptions (see above), the Bremer method is most effectively applied to the root of a tree (but see also Smith 1994; Ruta 1998). Therefore we do not list G/L scores for the less inclusive nodes in the phylogeny.

Probabilities of occurrence of G/L ratios are indicated by Z-scores and associated *p* values (Part 14 of Online Supplementary Material). The distribution of G/L ratios was tested for normality. However, given the relatively small number of observations ($n = 8$), commonly used normality tests, such as Kolmogorov–Smirnov (and most other available tests) may not be appropriate (e.g. Zar 1999; Sheskin 2007). Additionally, tests such as Shapiro–Wilk may provide spurious results if, as in the case of our tabulated G/L ratios, several values in the sample are identical. For these reasons we opted for a powerful alternative designed to function as an omnibus test, the D'Agostino–Pearson K^2 test (e.g. D'Agostino & Pearson 1973; D'Agostino & Stephens 1986). The test was carried out using the statistical program StatCat 3.6 (courtesy of Dr David J. Moriarty from California State Polytechnic University,

Pomona: <http://www.csupomona.edu/~djmoriarty/b211/index.html>)

We urge caution in interpretations of the results, as the sample size is smaller than the recommended minimum number of observations required for the test ($n = 20$). As a crude attempt at ensuring the optimal performance of the D'Agostino-Pearson K^2 statistic, we also \log_{10} -transformed the G/L values. However, several trial runs employing randomly generated sets of numbers (starting with $n = 8$, as per our sample) show that the test is able to detect non-normality where applicable (i.e. it rejects the null hypothesis of a Gaussian distribution).

When either the G/L ratios or their \log_{10} -transformed values were input, the test did not reject the null hypothesis of normality, i.e. the sample values conform to the Gaussian distribution (Part 14 of the Online Supplementary Material). We then used both the G/L ratios and their \log_{10} -transformed values to calculate Z-scores and corresponding p values, obtained with online calculators available at: <http://psych-www.colorado.edu/~mcclella/java/normal/normz.html>.

Part 14 of the Online Supplementary Material shows that the probability of South Africa belonging to the ancestral range of procolophonids is not significant at the $\alpha = 0.05$ level. However, as the level of non-significance is marginal, we conclude that a deviation from random of the probability of occurrence for this region is supported, albeit not strongly.

Discussion

Disparity

Despite their remarkable variety of morphofunctional specializations and their diverse array of skull shapes and/or proportions, procolophonids exhibit rather negligible differences in morphological diversity when taxa are grouped according to stratigraphical age, overall phenetic similarity (using cranial armour as a proxy), diet adaptations (such as those inferred from dentition patterns), or phylogenetic proximity. One possible biological explanation, at least for feeding strategies, is that procolophonids radiated rapidly into the herbivory guild ecospace (though some species may have fed on small invertebrates) and began to exploit a wide range of food sources thanks to their different dentition patterns. Significantly, profiles of relative disparity are not altered after inclusion of autapomorphic traits, many of which relate to tooth morphology (see Part 13 of Online Supplementary Material). The amount of morphological variety associated with feeding specializations thus appears to have been counterbalanced by character changes in other portions of the skeleton (e.g. conditions relating to remodelling of the cranial armour).

Disparity profiles through time (albeit at a rather crude level of temporal subdivision) and measures of dispar-

ity based upon tree shape together provide an interesting perspective on macroevolutionary changes among procolophonids. Disparity in the group appears to have stabilized around a 'threshold' value, with minimal fluctuations (e.g. slightly lower disparity in procolophonines relative to that in leptopleuronines, and in the basal grade group preceding the procolophonine-leptopleuronine separation). Pending further scrutiny and assembly of a more comprehensive data matrix, we suggest tentatively that observed patterns reflect the ability of individual procolophonid groups to exhaust character conditions (*sensu* Wagner 2000) equally rapidly. Alternatively, such groups may have been characterized by similar rates of character-state accumulation.

Biogeography

Reconstructed ancestral area distributions at the internal nodes of the procolophonoid tree (Fig. 1) support a simple scenario for the palaeobiogeographical history of this group, at least before the leptopleuronine-procolophonine separation.

At the node subtending the entire procolophonoid radiation, South Africa appears as the only possible ancestral range for the clade. This is plausible, as owenettids (e.g. Reisz & Laurin 1991; Reisz & Scott 2002; Modesto *et al.* 2003; Cisneros *et al.* 2004) have been thus far documented in Gondwana, namely South Africa and South America. From a theoretical standpoint, ancestral area reconstructions at the basal node of a phylogeny may be heavily influenced by outgroup selection and, more generally, by the topology of adjacent portions of the tree of life. A South African origin for procolophonoids certainly appears plausible under current palaeobiogeographical reconstructions, but it remains to be seen whether the ancestors of procolophonoids were present in South Africa only, whether they dispersed there from other areas, or whether they were present both in South Africa and in other areas.

Optimization of South Africa as a centre of origin for the clade is compatible with at least two scenarios. In the first, procolophonoid ancestors either migrated into South Africa or were already present in South Africa when the owenettid-procolophonid clade became separate from *Nyctiphruretus* and other parareptiles (e.g. Tsuji 2006; Reisz *et al.* 2007; Cisneros 2008b). In the second scenario, widespread procolophonoid ancestors present both in South Africa and in other areas went extinct in the latter but survived in the former.

Clearly, more stringent and decisive tests of the restricted versus widespread scenario for the ancestral distribution of procolophonoids must await both an exhaustive cladistic treatment of suitable outgroups and an encompassing palaeobiogeographical analysis of parareptiles as a whole.

The basal part of the procolophonid tree consists of a small clade (node 8) in which a dispersal event to South America occurs. This early South American dispersal is the

first of three recorded in the evolutionary history of the group (nodes 9, 16, 22).

At each of the nodes preceding the phylogenetic separation between leptopleuronines and procolophonines, South Africa forms either the sole ancestral region (nodes 1 and 2) or a component of some (but by no means all) equiprobable area clusters (in combination with either Russia or North China; nodes 3–7). Russia appears as the sole ancestral region in one of the equiprobable area optimizations at nodes 4 and 6, whilst North China forms the sole ancestral region in one of the equiprobable area optimizations at nodes 5 and 7.

Some of the reconstructed optimizations at nodes 3–7 may appear implausible as they consist of sets of widely separate areas (e.g. South Africa + North China, or South Africa + Russia). However, these are only estimates of geographical ranges of ancestors given the distributions of terminal taxa. Thus they need not reflect the actual extension of the area where ancestors were present. Inspection of nodes 3–7 suggests that during their initial diversification, procolophonids may have migrated along the arc-like set of terranes and continents (e.g. Australia, Cimmeria, Malaya and Chinese blocks) between mid southern Gondwana and Siberia. This northward dispersal may or may not have been accompanied by local extinctions. This scenario is corroborated, in part, by the presence of an as yet undescribed Induan basal taxon from the Arcadia Formation in eastern Australia (Bartholomai 1979; Cisneros 2006) which bridges the geographical gap between the records of procolophonoids in South Africa and North China during the Early Triassic.

Node 7 (leptopleuronine-procolophonine split) is characterized by three equiprobable area optimizations, all of which include North China (either as the sole ancestral region or in combination with South Africa or Russia). Biogeographical patterns exhibited by the two major procolophonid subfamilies differ remarkably. At the base of the leptopleuronine radiation (node 17) only North China forms part of the ancestral range. A subsequent dispersal is hypothesized to have occurred at node 18, leading to the colonization of Laurasia. The spread of taxa into Laurasia is indicated by node 19, coinciding with occurrences of leptopleuronines in North America, continental Europe and Great Britain (nodes 20 and 21). In the apical part of the leptopleuronine radiation, South America became occupied (node 22) again (cf. node 9 in the basal part of the tree).

As far as procolophonines are concerned, no simple and unequivocal dispersal pattern can be proposed, given the multiple equiprobable area optimizations at node 11: South Africa; South Africa + Russia; and Russia + North China. It is useful to contrast such optimizations with those at node 7 in order to make some sense of the subsequent scenarios of dispersal for this subfamily. A restricted distribution of the ancestors at nodes 7 and 11 – such as is implied by the occurrence of North China at node 7 and South Africa at node 11 – requires minimally one southward dispersal

into South Africa (node 11) followed by a further northward dispersal route to Russia in order to account for the distributions of taxa at nodes 12 and 13. Re-colonization of North China must have occurred between nodes 11 and 14 in order to explain the presence of a Chinese taxon subtended by node 14. A wider distribution of the ancestors at nodes 7 (e.g. South Africa + North China) and 11 (e.g. South Africa + Russia) implies a northward migration and colonization of Russia. In the simplest scenario, taxa dispersed from South Africa to Russia via North China and became extinct in the latter. Thus, the centre of subsequent dispersal routes (node 11) in fact consisted of two widely separated regions (South Africa and Russia), each housing a small and distinct procolophonine radiation (nodes 12 and 14). Once again, reappearance of a taxon in North China might be explained by a novel southward migration from Russia at node 14. Finally, we detail yet another dispersal scenario, this time hypothesizing that ancestors at nodes 7 and 11 were confined to Russia and North China. In this scenario, colonization of South Africa occurred independently in each of the two small clades subtended by node 11. This scenario partly explains the puzzling disjointed distributions of procolophonines in South Africa and Russia at node 12 by invoking an active role of North China in favouring northward and southward dispersal routes. A single southward dispersal event presumably occurred at node 14.

Note

Supplementary data can be viewed online.

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