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## Inferring ancestral range reconstruction based on trilobite records: a study-case on *Metacryphaeus* (Phacopida, Calmoniidae)

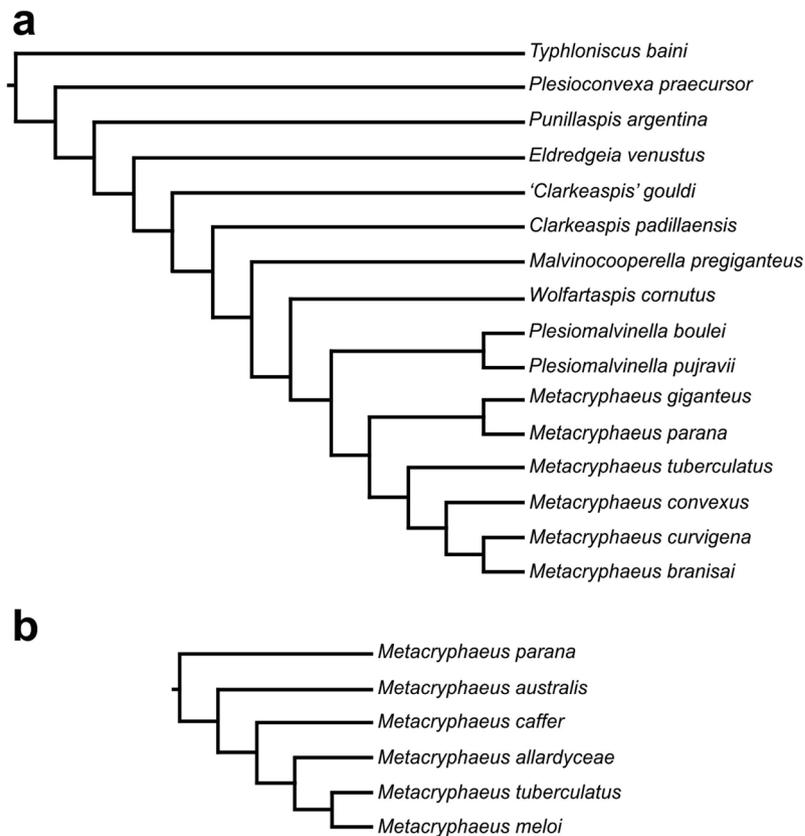
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*Metacryphaeus* is a calmoniid trilobite genus from the Devonian Malvinokaffric Realm, exclusive to the Gondwanan regions. It includes eleven species, which are for the first time included here in a single phylogenetic analysis. The resulting hypotheses establish relations among the *Metacryphaeus* species with few ambiguities, also suggesting the inclusion of both *Plesiomalvinella pujravii* and *P. boulei* within the genus, as originally considered. The results of palaeobiogeographic analyses employing the Dispersal-Extinction-Cladogenesis (DEC) model reinforce the hypothesis that Bolivia and Peru form the ancestral home of *Metacryphaeus*. The radiation of the genus to other Gondwanan areas took place during transgressive eustatic episodes during the Lochkovian–Pragian. The Lochkovian dispersal occurred from Bolivia and Peru to Brazil (Paraná and Parnaíba basins) and the Falklands, and Pragian dispersal occurred towards South Africa. Dispersal events from Bolivia and Peru to the Parnaíba Basin (Brazil) were identified during the Lochkovian–Pragian, suggesting the presence of marine connections between those areas earlier than previously thought.

The Malvinokaffric Realm includes a plethora of trilobites, including the Calmoniidae, which is composed of several genera (*e.g.*, *Calmonia* Clarke, 1913, *Typhloniscus* Salter, 1856, *Plesioconvexa* Lieberman, 1993, *Punillaspis* Baldis & Longobucco, 1977, *Eldredgeia* Lieberman, 1993, *Clarkeaspis* Lieberman, 1993, *Malvinocooperella* Lieberman, 1993, *Wolfartaspis* Cooper, 1982, *Metacryphaeus* Reed, 1907) reported from the Devonian rocks of Brazil, Argentina, Bolivia, Peru, Falkland Islands, and South Africa<sup>1–10</sup>. The present work focuses on the genus *Metacryphaeus*, which only includes Gondwanan species, namely: *M. tuberculatus* (Kozłowski, 1923), *M. kegeli* Carvalho *et al.*, 1997, *M. meloi* Carvalho *et al.*, 1997, *M. parana* (Kozłowski, 1923), *M. giganteus* (Ulrich, 1892), *M. convexus* (Ulrich, 1892), *M. curvigena* Lieberman, 1993, *M. branisai* Lieberman, 1993, *M. caffer* (Salter, 1856), *M. australis* (Clarke, 1913), and *M. allardyceae* (Clarke, 1913).

During the 1990s, Lieberman<sup>5</sup> presented the first phylogenetic analysis of the group including *Metacryphaeus*, represented by *M. parana*, *M. convexus*, *M. curvigena*, *M. branisai*, *M. giganteus*, and *M. tuberculatus*, among other calmoniids (Fig. 1a). Later, Carvalho *et al.*<sup>6</sup> (Fig. 1b) conducted a phylogenetic study of that genus, represented by *M. parana*, *M. australis*, *M. caffer*, *M. allardyceae*, *M. tuberculatus*, and *M. meloi*. More recently, Abe & Lieberman<sup>9</sup> presented a palaeobiogeographical area-taxon cladogram including all *Metacryphaeus* species, based on the tree provided by Lieberman<sup>5</sup>, with the manual insertion of additional species (*i.e.*, without carrying

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**Figure 1.** Previous phylogenetic models including *Metacryphaeus*: (a) Lieberman<sup>5</sup>; and (b) Carvalho *et al.*<sup>6</sup>.

out a new phylogenetic analysis). Those phylogenetic studies did not include all the species of *Metacryphaeus*. Accordingly, this study provides a new phylogenetic analysis including all species, in order to perform a new palaeobiogeographic analysis for the distribution of the genus.

The genus *Metacryphaeus* occurs in many Gondwanan geological units of Devonian age, including those in Brazil, Bolivia, Falkland Islands, Peru, and South Africa, spanning the Pragian to the Givetian–Frasnian<sup>3–6,11,12</sup> (Figs 2 and 3). It has been suggested that the genus originated and diversified in small basins of the Malvinokaffric Realm in Bolivia and Peru<sup>9</sup>. The records in this area are from the Pragian to the Givetian, including *M. giganteus*, *M. tuberculatus*, *M. parana*, *M. convexus*, *M. curvigena*, and *M. branisai*.

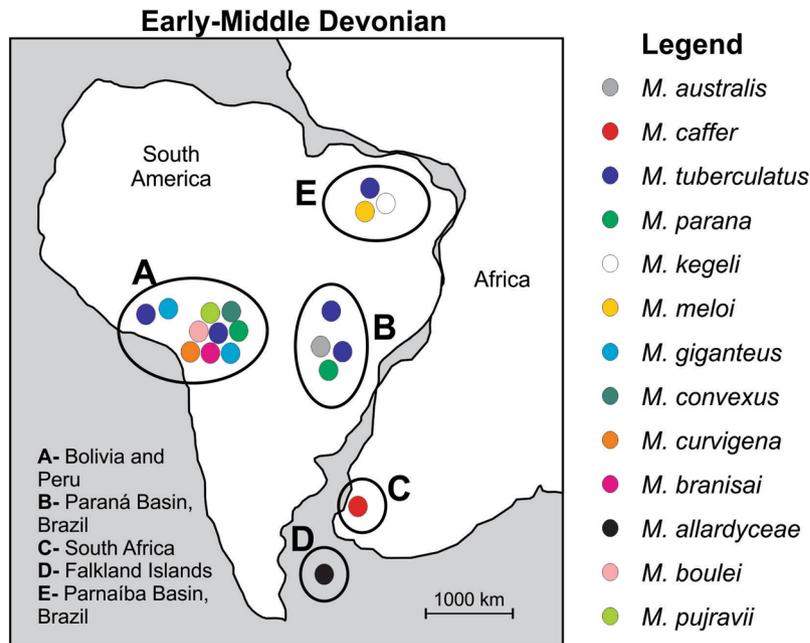
## Results and Discussion

**Phylogeny.** The parsimony analysis resulted in two MPTs of 132 steps (consistency index = 0.41 and retention index = 0.52; Fig. 4). The only topological difference between these two trees is the placement of *Metacryphaeus branisai*. The strict consensus is presented in Fig. 5, along with bootstrap probabilities and Bremer decay indices for each node.

*Plesiomalvinella boulei* and *P. pujravii* were found deeply nested within a clade of *Metacryphaeus* species. Accordingly, those two species are here referred to that genus, as previously proposed by Wolfart<sup>13</sup>. *Metacryphaeus* (including *M. boulei* and *M. pujravii*) is here supported by two synapomorphies: frontal lobe projecting beyond the cephalic anterior border in dorsal view (character 4) and uniformly divergent axial furrows from SO to the cephalic margin (character 19).

In contrast to Lieberman<sup>5</sup>, *Clarkeaspis gouldi* (Lieberman, 1993) and *C. padillaensis* (Lieberman, 1993) were grouped into a clade supported by four synapomorphies (Figs 4 and 5): cephalic anterior border (cranial) extended and pointed (characters 2 and 3); pentagonal glabella (character 6); 60 to 70% ratio between the basal glabellar width and the glabellar length (character 9). *Clarkeaspis* is here placed closer to *Metacryphaeus* (as its sister group) than in Lieberman<sup>5</sup>. The *Metacryphaeus* + *Clarkeaspis* clade is supported by a single synapomorphy (character 9, 0 → 1) and shows low bootstrap support (Fig. 5). The placement of *Malvinocooperella pregiganteus* (Lieberman, 1993) and *Wolfartaspis cornutus* (Wolfart 1968) as successive outgroups of the *Metacryphaeus* + *Clarkeaspis* (Figs 4 and 5), also differs from the arrangement seen in Lieberman<sup>5</sup>.

The present analysis recovered the clades formed by *Metacryphaeus giganteus* + *M. parana* (Figs 4 and 5) and *M. boulei* + *M. pujravii* (Figs 4 and 5), previously recognized by Lieberman<sup>5</sup>. Synapomorphies of the *M. giganteus* + *M. parana* clade are: 60 to 70% ratio between the basal glabellar width and the glabellar length (character 9), convergently acquired in *Clarkeaspis*; slender genal spine (character 36); dorsoventral height of the pygidium gradually decreasing posteriorly (character 39); 0.65 to 0.80 ratio between the maximum pygidial axial width and the maximum pygidial axial length (character 42). The *M. boulei* + *M. pujravii* clade is supported by six



**Figure 2.** Palaeobiogeographic distribution of the genus *Metacryphaeus* during the Early and Middle Devonian. Areas were divided into (A–E) for the palaeobiogeographic analysis. Note: *Plesiomalvinella boulei* and *P. pujravii* have been reassigned here to *Metacryphaeus*.

synapomorphies which are related to the presence of two symmetrical rows of sagittal spines on the posterior part of the glabella (character 15), the presence of one or two spines on L1 and L2 (characters 17 and 18), 0.15 and 0.25 ratio between the distance of posterior margin of the eyes to the axial furrow and the maximum glabellar width (character 25), the presence of four or five spines on the thoracic axial rings (character 37), and the prosopon covered by spines (character 48).

Our study also recovered new hypotheses for the relationships of *Metacryphaeus*, including a clade formed by *M. allardyceae*, *M. caffer*, *M. australis*, *M. meloi*, *M. kegei*, and *M. tuberculatus*. This is supported by four synapomorphies related to the shape and extension of the (cranial) cephalic anterior border (characters 2 and 3), the ratio between the sagittal length of L1 and the glabellar sagittal length (character 14), and the incision of the occipital furrow medially (character 29). The clade including *M. caffer*, *M. australis*, *M. meloi*, *M. kegei*, and *M. tuberculatus* is supported by four synapomorphies (Fig. 4a): glabella posteriorly elevated and declined anteriorly to S3 (character 8); 65 to 75°  $\alpha$  angle (character 22); rounded pygidial terminus (character 45); no spine on the pygidial terminus (character 46). Also, the clade formed by *M. tuberculatus*, *M. meloi*, and *M. kegei* is supported by four synapomorphies related to L2 and L3 that do not merge distally (character 13), 55 to 64°  $\beta$  angles (character 23), the connection of S2 and the axial furrow (character 24), and the lack of connection between the anterior margin of the eyes and the axial furrow (character 26) (Fig. 5). Two synapomorphies support the *M. caffer* plus *M. australis* clade: characters 9 (reverted to the plesiomorphic condition) and 41, which are respectively related to a ratio greater than 80% between the basal glabellar width and the glabellar length, and to 0.25 to 0.35 ratios between the maximum pygidial axial width and the maximum pygidial width.

The clade that includes all *Metacryphaeus* except for *M. convexus*, *M. curvigena*, and *M. branisai* (Fig. 4a) is supported by three synapomorphies related to a 0.15 to 0.25 ratio between the distance from the posterior margin of the eyes to the axial furrow and the maximum glabellar width (character 25), occipital furrow weakly incised medially (character 29), and 130 to 160°  $\gamma$  angle (character 34). Three synapomorphies support the group formed by *M. giganteus*, *M. parana*, *M. allardyceae*, *M. australis*, *M. caffer*, *M. meloi*, *M. kegei*, and *M. tuberculatus* (Fig. 4a): 0.25 to 0.34 ratio between sagittal length of L1 glabellar lobe and glabellar sagittal length (character 14), 0.3 to 0.4 ratio between the maximum exsagittal eyes length and the glabellar sagittal length (character 27), 0.60 to 0.80 ratio between maximal sagittal pygidial length and maximal transverse pygidial width (character 40). The position of *Metacryphaeus branisai* is variable in the two MPTs (Fig. 4), probably because its pygidium is unknown, implying the non-codification for characters 38 to 47.

In the phylogeny modelled by Lieberman<sup>5</sup>, *Metacryphaeus convexus* and *M. curvigena* are not considered sister taxa to all other *Metacryphaeus*. Instead, *M. curvigena* is considered the sister taxon to *M. branisai* and *M. convexus* the sister taxon to both (Fig. 1a). In our analysis, the clade formed by *M. convexus* and *M. curvigena* is supported by five synapomorphies: inclination of 10–20° of S3 in relation to SO (character 12); L2 and L3 not merged distally (character 13); cephalic axial furrows deep and broad (characters 20 and 21); evident connection between S2 and the axial furrow. Likewise, the affinities of *M. meloi* and *M. kegei* are supported by four synapomorphies. This is interesting because these species are endemic to the Parnaíba Basin (Brazil), as is their sister-taxon *M. tuberculatus*, the only other species of the genus known to that basin.

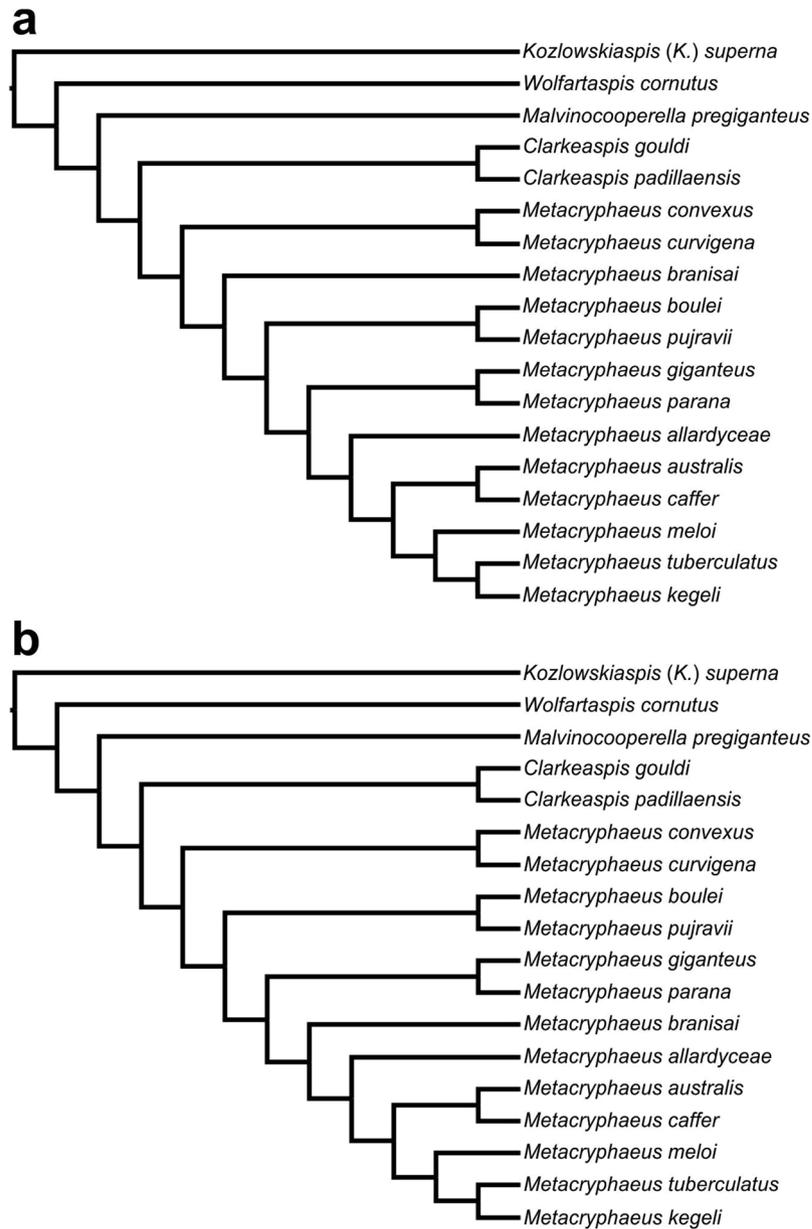
SPECIES	COUNTRY	GEOLOGIC UNIT	CHRONOSTRATIGRAPHIC DISTRIBUTION					
			Loch.	Prag.	Emsi.	Eife.	Give.	Fras.
<i>Metacryphaeus giganteus</i>	BOLIVIA	Icla Formation		—				
		Belén Formation			—			
	PERU	Cabanillas Formation			—			
<i>Metacryphaeus parana</i>	BOLIVIA	Icla Formation		—				
	BRAZIL	Ponta Grossa Formation		—				
<i>Metacryphaeus australis</i>	BRAZIL	Ponta Grossa Formation		—				
		São Domingos Formation			—			
		Chapada Group Unit 2 or 3			—			
<i>Metacryphaeus caffer</i>	SOUTH AFRICA	Voorstehoek Formation			—			
<i>Metacryphaeus tuberculatus</i>	BOLIVIA	Icla Formation		—				
		Limoncito Formation		—				
		Belén Formation			—			
		Sicasica Formation			—			
	PERU	Cabanillas Formation			—			
	BRAZIL	Ponta Grossa Formation		—				
		Chapada Group Unit 4				—		
Pimenteira Formation					—			
<i>Metacryphaeus meloi</i>	BRAZIL	Pimenteira Formation				—		
<i>Metacryphaeus kegeli</i>	BRAZIL	Pimenteira Formation				—		
<i>Metacryphaeus convexus</i>	BOLIVIA	Icla Formation		—				
<i>Metacryphaeus curvigena</i>	BOLIVIA	Icla Formation		—				
<i>Metacryphaeus branisai</i>	BOLIVIA	Icla Formation		—				
<i>Metacryphaeus allardyceae</i>	FALKLAND ISLANDS	Fox Bay Formation			—			
<i>Metacryphaeus boulei</i>	BOLIVIA	Icla Formation		—				
		Belén Formation			—			
<i>Metacryphaeus pujravii</i>	BOLIVIA	Icla Formation		—				
		Belén Formation			—			

**Figure 3.** Chronostratigraphic distribution of *Metacryphaeus*. Note: *Plesiomalvinella boulei* and *P. pujravii* have been reassigned here to *Metacryphaeus*. Abbreviations: Loch., Lochkovian; Prag., Pragian; Emsi., Emsian; Eife., Eifelian; Give., Givetian; Fras., Frasnian; Fame., Famennian.

**Palaeobiogeography.** Likelihood Ratio Test supports DEC M2 ( $w$  and  $j$  set as free parameters) as the best-fit model to our data (Table 1). The palaeobiogeographic reconstructions differ only slightly for the two MPTs, so we focus the discussion on the first MPT. The summary of biogeographic stochastic mapping (BSM) counts (Table 2) shows a predominance of dispersals among range change events (33.6% of total events) and, among those, founder events (19.6%) are slightly more frequent than anagenetic dispersals (14.1%). Vicariance was very uncommon according to our model, accounting only for 3.9% of the events (Table 2). Most dispersals occurred from Bolivia and Peru (A) to other areas, more frequently to the Paraná (B) and Parnaíba (E) basins (Table 3).

All three models estimate a 100% probability for Bolivia and Peru (A) as the ancestral area for the *Metacryphaeus* clade, as well as for most of its internal clades (Fig. 6; Supplementary Supple 3). The earliest *Metacryphaeus* records in this area are from the early Pragian<sup>4,5</sup>, but three range changes were estimated to have occurred earlier, during the late Lochkovian (Fig. 6): 1- the ancestor of *M. parana* and *M. giganteus* expanded its occurrence to encompass the Paraná Basin (B), with the former species maintaining this broader distribution and the latter restricted to B (subset sympatry) - in an alternative scenario, the ancestor of this clade is present only in Bolivia and Peru (A), with *M. parana* expanding its range to also the Paraná Basin (B); 2- *M. allardyceae* dispersed to the Falklands area (D); 3- the ancestor of *M. australis* and *M. caffer* dispersed to the Paraná Basin (B). During the early Pragian, *M. caffer* dispersed from the Paraná Basin to South Africa (C). It is interesting to note that those dispersal and expansion events likely occurred before the transgressive events on western Gondwana<sup>14–17</sup> dated between the late Pragian and the early Emsian (Fig. 6). Those areas (A, B, C, D) were eventually connected by transgressive-regressive cycles (Fig. 6), which promoted the faunal similarity observed among the Malvinokaffric fauna of the Early Devonian<sup>15,18</sup>.

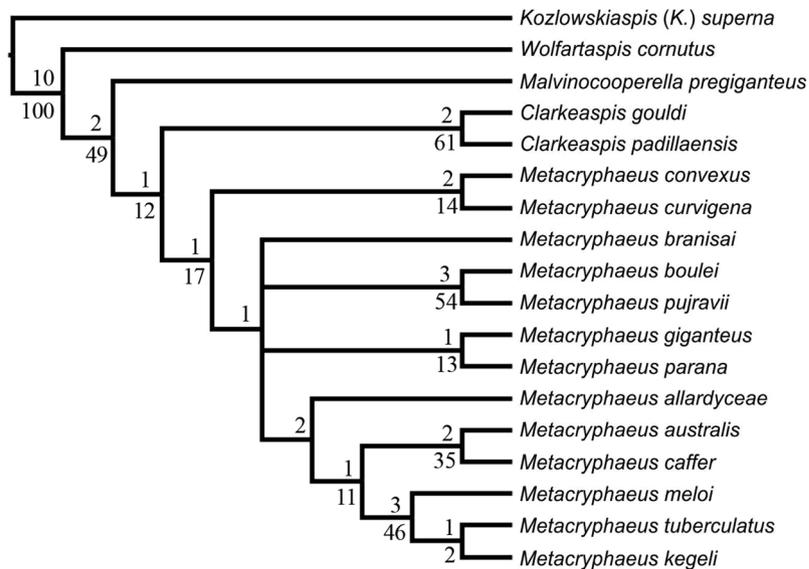
The last common ancestor of *Metacryphaeus meloi*, *M. kegeli*, and *M. tuberculatus*, and the node including only the latter two taxa were reconstructed with two almost equal probable ranges, either restricted to Bolivia and Peru (A) or a joint distribution (Fig. 6) also including the Parnaíba and Paraná basins (ABE). These different



**Figure 4.** (a,b) Two most parsimonious trees (132 long and consistency index of 0.41) calculated in the present phylogenetic analysis.

ancestral range reconstructions imply distinct processes of range changes, respectively: 1 - successive dispersals from Bolivia and Peru to the other areas (for an ancestral with distribution restricted to A), 2 - distribution expansions inferred as founder events (for an ancestral widely distributed in ABE). Nevertheless, in all cases *M. meloi* and *M. kegeli* became restricted to the Parnaíba Basin (E), whereas *M. tuberculatus* maintained (or reached) a widespread distribution (ABE), even though its earliest records, dated as late Eifelian and early Givetian, do not include the Parnaíba Basin<sup>4-6,11,12</sup>. Alternatively, but with lower statistical support, the ancestral range reconstruction hypothesized for the clades *M. meloi* + (*M. tuberculatus* + *M. kegeli*) and *M. tuberculatus* + *M. kegeli* could be AB, encompassing only their older records. This would imply expansion events towards the Parnaíba Basin (E) after the arrival of ancestors in the Paraná Basin (B).

The arrival of *Metacryphaeus* in the Parnaíba Basin may have occurred via two alternative routes (Fig. 6). A northern route (surrounding the northern margin of the South American continent) would impose no continental (landmass) barriers, but there would be climatic barriers related to the warmer waters the animals would need to overcome, as the Malvinokaffric Realm marks cooler areas. Also, faunas of this age on the northern margin of South-America belong to other realms, which lack *Metacryphaeus*. On the other hand, a route through the Amazon Basin (Fig. 6) would have presented no climatic or faunal barriers (cf.<sup>15,18,19</sup>). Even a continental barrier might not have been in place, as there were transgression events possibly connecting that basin to Bolivia and Peru. The lack of fossils of this age in the Amazon Basin, which could confirm such a dispersal route, is related



**Figure 5.** Strict consensus of the two MPTs with bootstrap values (using 1000 replicates; below) and Bremer support (above) indicated for each node.

Alternative Model	LnL	DF	Null Model	LnL	DF	Likelihood Ratio Test $p$
DEC + w	-32.41	3	DEC	-32.98	2	0.29
DEC + w + j	-29.87	4	DEC + w	-32.41	3	0.024

**Table 1.** Pairwise comparison of the results of the ancestral area reconstructions of nested DEC models on tree 1. Abbreviations: LnL, log-likelihood values; DF, degrees of freedom.

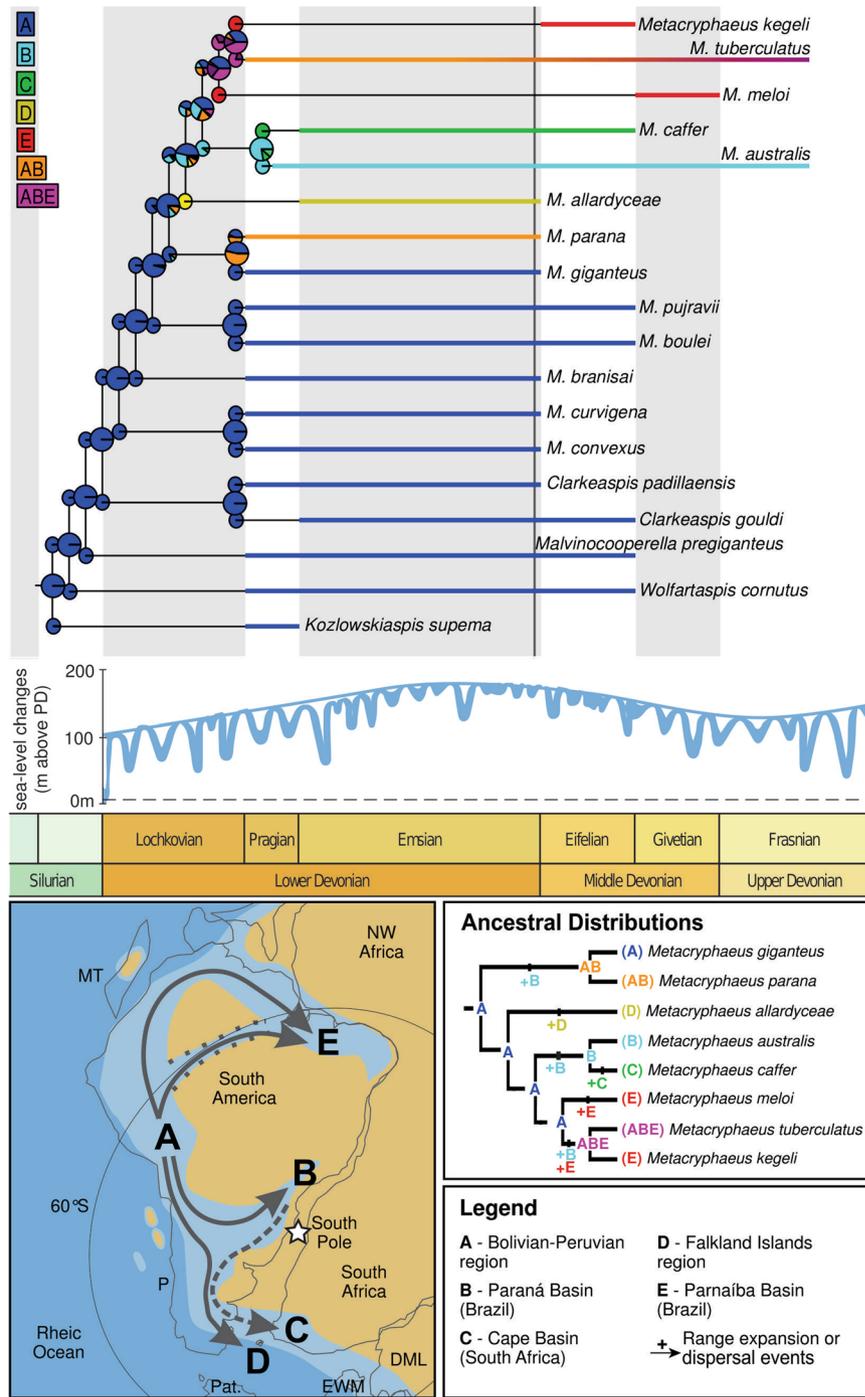
Type	Mean (SD)	%
range contractions (e)	0 (0)	0.0%
range expansion (d)	2.78 (0.60)	14.1%
founder events (j)	3.87 (1.33)	19.6%
all dispersals	6.65 (0.97)	33.6%
sympatry (y)	11.01 (0.81)	55.7%
subset speciation (s)	1.34 (0.93)	6.7%
vicariance (v)	0.78 (0.60)	3.9%

**Table 2.** Summary of BSM (Biogeographic Stochastic Mapping) counts based on DEC M2 model showing the mean, standard deviations (SD), and percentage of different types of biogeographic events.

	A	B	C	D	E
A	0 (0)	2.42 (0.64)	0.11 (0.31)	0.69 (0.46)	1.39 (0.55)
B	0.53 (0.69)	0 (0)	0.87 (0.34)	0.31 (0.46)	0.03 (0.17)
C	0.02 (0.14)	0.16 (0.37)	0 (0)	0 (0)	0 (0)
D	0 (0)	0.10 (0.30)	0.02 (0.14)	0 (0)	0 (0)
E	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)

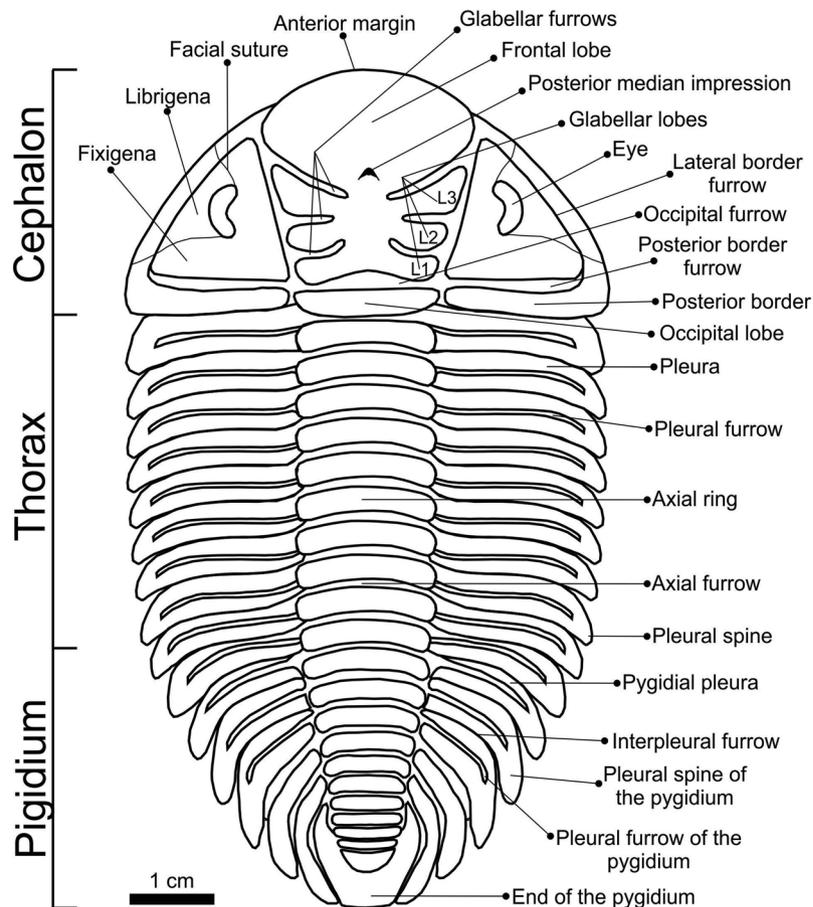
**Table 3.** Counts (and standard deviations in parentheses) of dispersal events averaged across 100 biogeographic stochastic mappings based on the biogeographic history of *Metacryphaeus* according to DEC M2 model. (A) Bolivia and Peru, (B) Paraná Basin, (C) South Africa, (D) Falkland Islands, and (E) Parnaíba Basin.

to the depositional gap present in the upper Lochkovian and lower Emsian of the basin (cf.<sup>20–25</sup>). This absence of Lochkovian–lower Emsian rocks is also observed in the Parnaíba Basin<sup>20,21,24</sup>, which hinders palaeobiogeographical inferences related to the presence/absence of *Metacryphaeus* in the Lower Devonian of this basin.



**Figure 6.** Ancestral area reconstructions based on DEC M2 model on the tree 1 (top), sea-level changes curves from Lochkovian to Frasnian (middle) based on Haq & Schutter<sup>55</sup>, and Lower Devonian palaeomap of Southern Gondwana (bottom) modified from Torsvik & Cocks<sup>56</sup>. Arrows on the palaeomap indicate inferred Lochkovian (full arrow) and Pragian (dashed arrow) dispersal routes for *Metacryphaeus* taxa. Additional abbreviations: DML, Dronning Maud Land, Antarctica; EWM, Ellsworth-Whitmore Mountains, Antarctica; MT, Mexican terranes; P, Precordillera Terrane, Argentina; Pat., Patagonia.

Other trilobite genera also have a broad Gondwanan distribution during the Devonian, e.g. the calmonioid *Eldredgeia*, with occurrences in the Bolivia, Brazil (Amazon and Parnaíba basins), and South Africa, and the homalonotid *Burmeisteria*, with records in the Brazil (Amazon, Parnaíba, and Paraná basins), Falkland Islands, South Africa, and Ghana<sup>1,15,19,26</sup>. Furthermore, the distribution of the brachiopods *Tropidoleptus carinatus* (Conrad, 1839) and *Australocoelia palmata* (Mooris & Sharpe, 1846), and the crinoids *Exaesiodiscus* Moore & Jeffords, 1968, *Laudonomphalus* Moore & Jeffords, 1968, *Monstrocrinus* Schmidt, 1941, and *Marettocrinus* Le Menn<sup>15,27-34</sup>, also reinforce that connections between the Bolivian-Peruvian region and the Amazon, Parnaíba,



**Figure 7.** Schematic drawing showing the major exoskeleton elements of the dorsal surface of *Metacryphaeus*.

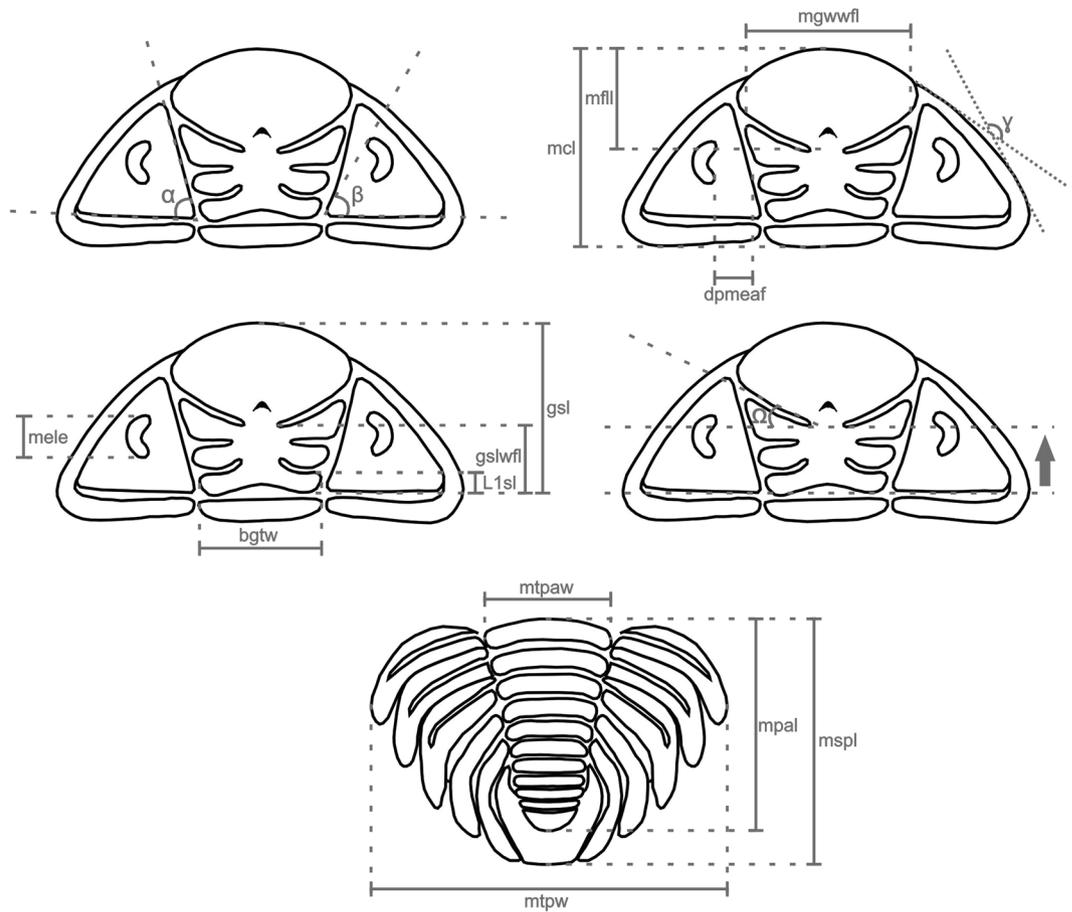
and Paraná basins were recurrent by the Middle Devonian (e.g.<sup>15,26</sup>). However, the dispersal and range expansion events highlighted in our biogeographic analyses (except that related to *M. caffer* dispersal from the Paraná Basin to South Africa) occurred during the late Lochkovian (Fig. 6). As such, our data suggest an earlier connection between all those Gondwanan regions, allowing *Metacryphaeus* trilobites to expand into the Paraná and Parnaíba basins via southeastern and northern/northeastern routes, respectively (Fig. 6). Another interesting fact is the diversification of *Metacryphaeus* in South America occurring earlier than its dispersal to South Africa (where it is represented by *M. caffer*). This was temporally the latest dispersal of the genus, taking place during the Pragian, and a separate event from the dispersal of *M. allardyceae* in the same direction (to the Falkland Islands), which occurred earlier.

## Methods

**Phylogenetic analysis.** The phylogenetic analysis conducted here was based on the phylogeny of Lieberman<sup>5</sup>, with extra characters and species added to the data matrix. The added species were *Metacryphaeus australis*, *M. caffer*, *M. kegei*, *M. meloi*, and *M. allardyceae*, as to encompass all valid species of the genus. Other ingroup taxa were defined according to the phylogenetic hypothesis of Lieberman<sup>5</sup> consisting of *Plesiomalvinella boulei*, *P. pujravii*, *Wolfartaspis cornutus*, *Malvinocooperella pregiganteus*, *Clarkeaspis gouldi*, and *C. padillaensis*. Also, according to Lieberman<sup>5</sup>, *Kozlowskiaspis (K.) superna* Braniša & Vaněk, 1973 was used to root of the phylogenetic trees.

Among the 48 characters employed here (see Appendix 1), 33 were taken or modified from Lieberman<sup>5</sup> and 15 are new (characters 7, 9, 12, 13, 14, 22, 23, 24, 25, 26, 27, 34, 40, 41, and 42), although based on characters used in phylogenetic analyses of other trilobite groups (e.g.<sup>35–42</sup>). The morphological elements of the exoskeleton are shown in Fig. 7 and all morphological relations/angles used in the 15 newly proposed characters were measured as indicated in Fig. 8.

Among the characters taken from Lieberman<sup>5</sup>, some scores were changed for some taxa based on our own interpretations. This is the case for characters 5 (changed from 0 to 1 in *Malvinocooperella pregiganteus*, *Metacryphaeus giganteus*, and *Me. branisai*), 18 (changed from 0 to 1 in *Me. branisai*), and 19 (changed from 0 to 1 in *Me. giganteus*). Other characters from Lieberman<sup>5</sup>, e.g. characters 9, 10, 12, 13, 19, 23, 24, and 34, were not used here because they either have too much variation between individuals of the same species or can be easily affected by taphonomic deformation. Some characters from Lieberman<sup>5</sup> were split into two or more characters, as in case of characters 2 and 3 (=character 1 of Lieberman<sup>5</sup>), 20 and 21 (=character 18 of Lieberman<sup>5</sup>), 30 and



**Figure 8.** Measurements used: mgwwfl = maximum glabellar width without consider the frontal lobe; mfl = maximum frontal lobe length; mcl = maximum cephalic length; dpmeaf = distance of posterior margin of the eyes to the axial furrow; mele = maximum exsagittal length of the eyes; bgtw = basal glabellar transverse width; gsl = glabellar sagittal length; gslwfl = glabellar sagittal length without consider the frontal lobe; L1sl = sagittal length of L1 glabellar lobe; mtpaw = maximum transverse pygidial axis width; mtpw = transverse maximum pygidial width; mspl = sagittal maximum pygidial length; mpal = maximum pygidial axis length;  $\alpha$  = angle between the axial furrow and the furrow of cephalic posterior border;  $\beta$  = angle between the cephalic posterior border furrow and a line traced from the posterior margin of the axial furrow to the anterior margin of the eyes;  $\gamma$  = angle between a straight line traced adjacent to the lateral genae (from the contact with the cephalic posterior furrow) and a line traced from the anterior part of the genae (from the contact of the axial furrow) in direction to the medial-posterior part of the genae;  $\Omega$  = S3 inclination in relation to SO.

31 (=character 25 of Lieberman<sup>5</sup>), 35 and 36 (=character 29 of Lieberman<sup>5</sup>), and 45, 46, and 47 (=character 36 of Lieberman<sup>5</sup>), following a contingential approach<sup>43</sup>.

Characters 1 to 36 are related to the cephalon, character 37 to the thorax, 38 to 47 to the pygidium, and 48 to the prosopon (Appendix 1 and 2). All characters are related to the dorsal surface of the exoskeleton and were treated as ordered. The data matrix was analyzed in search of the Most Parsimonious Trees (MPTs) using the software TNT version 1.1<sup>44</sup>. A heuristic search was conducted with 1,000 replicates, random addition of taxa (random seed 0), *Tree Bisection and Reconnection* (TBR) as branch swapping algorithm, and “hold” of 10 trees per replica. The recovered MPTs were summarized in a strict consensus tree. Bremer<sup>45</sup> decay indices and bootstrap proportions<sup>46</sup> were calculated using scripts incorporated in TNT. The data matrix was compiled in NEXUS format using the software Mesquite version 3.03 (702) and the tree images were generated with the software FigTree version 1.4.2.

**Palaeobiogeographical analysis.** We conducted palaeobiogeographic analyses to explore the distribution dynamic and biogeographical events that affected *Metacryphaeus* distribution through time in five areas pre-defined based on the known occurrences genus: Bolivia and Peru (A); Paraná Basin, Brazil (B); South Africa (C); Falkland Islands (D); and Parnaíba Basin, Brazil (E). Bolivia and Peru were treated as a single area due to their geographical proximity, strong palaeontological association, and co-occurrence of endemic species<sup>2,47</sup>. Only fossil taxa with accurate occurrence data and taxonomic identification were included. For this reason, taxa with doubtful assignation (*cf.*, *aff.*) were not considered in our analyses (*e.g.*<sup>48</sup>).

Ancestral area reconstructions were conducted using R (R Development Core Team 2013) package *BioGeoBEARS*<sup>49</sup>, which allows comparing the likelihood of our data given distinct models, choosing that with better fit<sup>50</sup>. We tested three nested models based on the LAGRANGE Dispersal-Extinction-Cladogenesis (DEC) model<sup>51,52</sup>: M0 contains the default parameters of the DEC models<sup>49</sup>; M1 has the addition of the free parameter  $w$ ; and M2 has the addition of the free parameters  $w$  and  $j$ . The free parameter  $w$  is a multiplier of the dispersal matrices and when set to 1 (e.g. in M0) the probabilities of dispersal events are based solely on the dispersal matrices and equal across all events<sup>53</sup>. The founder-event parameter  $j$  (included only in M2 and set to 0 in M0 and M1) allows range changes to areas distinct to that of the ancestor during a cladogenetic event<sup>49</sup>. We employed the Likelihood Ratio Test (LRT) to select the best model.

We used time-calibrated versions of the two MPTs, dividing them into two time slices, Silurian to Lower Devonian (430–395 Ma) and Middle to Upper Devonian (395–382 Ma). Based on that, we conducted a time-stratified analyses using time-specific dispersal multiplier and area matrices (see Supplementary suppl 2 and suppl 3). This allowed changing the distances and probabilities between the areas along these periods, simulating the continental transformations.

We also conducted a biogeographic stochastic mapping (BSM) on *BioGeoBEARS*<sup>54</sup> to estimate the number and type of biogeographical events. We conducted the BSM only for the first MPT, as the ancestral area reconstruction of both MPTs differ only slightly, and employed the parameters of the best-fit model of the ancestral area reconstruction<sup>53</sup>. The mean and standard deviation of event counts of 100 BSMs were used to estimate the frequencies of range change between the considered areas and of each kind of biogeographic event.

## Conclusions

This work provides new phylogenetic hypotheses for the relationships of all species within the genus *Metacryphaeus*, including the identification of the clades composed of (1) *M. caffer* and *M. australis*, (2) *M. tuberculatus*, *M. meloi*, and *M. kegei*, (3) *M. tuberculatus* and *M. kegei*, (4) *M. curvigena* and *M. convexus*, the latter two as sites clades. The position of *M. branisai* varied in the two recovered MPTs, probably due to the unknown pygidium for this specie. As *Plesiomalvinella pujravii* and *P. boulei* were positioned within the *Metacryphaeus* clade, these species were reinserted in that genus, as originally suggested by Wolfart<sup>13</sup>. Finally, the genus *Clarkeaspis* represents the immediate outgroup to *Metacryphaeus*.

The results of the palaeobiogeographic analyses with DEC models reinforce the interpretations of Lieberman<sup>5</sup> and Abe & Lieberman<sup>9</sup> that *Metacryphaeus* originated in the Lower Devonian of Bolivia and Peru, where they are represented by a higher taxonomic diversity. The radiation of *Metacryphaeus* to other Gondwanan regions probably occurred during the transgressive events in the Lochkovian–Pragian. In the Lochkovian, dispersals would have occurred to the Paraná Basin, in Brazil (*M. parana*, *M. australis*, *M. tuberculatus*), as well as to the Falklands area (*M. allardyceae*) and the Parnaíba Basin (*M. meloi*, *M. kegei*, *M. tuberculatus*). Pragian dispersal events were reconstructed only towards South Africa (*M. caffer*).

The ancestral area reconstructions for *Metacryphaeus* show dispersal events occurring earlier than expected, i.e. during the Early Devonian, even though the faunal similarities of Bolivia and Peru with the Parnaíba and Amazon basins are more prominent in the Middle Devonian, with the sharing of brachiopod (*Tropidoleptus* and *Australocoelia*), crinoid (*Exaesiodyscus*, *Laudonomphalus*, *Monstrocrinus*, and *Marettocrinus*), and other trilobite (*Eldredgeia* and *Burmeisteria*) taxa. The results presented here indicate that these areas were also somehow connected during the beginning of the Devonian, as to allow the dispersal of *Metacryphaeus*.

## Data Availability

The datasets analyzed during the current study are available in: <https://figshare.com/s/6b42cf2d4d0cadd7e11>.

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## Author Contributions

F.A.C. wrote the main manuscript text, prepared figures, conducted the phylogeny and paleobiogeography analyses. G.S.F. conducted the BioGeoBEARS analysis, wrote part of the Methods and Results (related to Palaeobiogeography), helped in the Figure 6 and in the palaeobiogeographical interpretation. S.S.N. helped in palaeobiogeography (methods and interpretation). M.C.L. and R.P.G. helped in taxonomy, phylogeny, and palaeobiogeography interpretations. All authors reviewed the manuscript.

## Additional Information

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