

# EVOLUTIONARY AND BIOGEOGRAPHICAL IMPLICATIONS OF PHYLOGENETIC ANALYSIS OF THE LATE PALAEOZOIC TRILOBITE *PALADIN*

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**ABSTRACT.** Phylogenetic analysis of 19 species assigned to the Carboniferous and Permian trilobite genus *Paladin* produced a single most parsimonious tree with four distinct branches termed Clades A to D. Clade A is made up of six species that are geographically restricted to the interior shelf regions of the United States and are assigned to *Kaskia*. Clade B of five species, which includes *Paladin morrowensis* (Mather), is known from the southern and western United States; these five species conform morphologically to the original diagnosis of *Paladin*. Clade C consists of five Viséan to Namurian species from western and eastern Europe and at least three of the species should be assigned to *Weberides*. Clade D consists of two late Carboniferous and one early Permian species from the Ukraine, western Russia, and Spitsbergen. This clade is distinct from all the others analysed and probably represents a yet unnamed genus.

**KEY WORDS:** Trilobita, Carboniferous, evolution, phylogenetics, palaeobiogeography.

*PALADIN* is one of the most widespread and long-lived late Palaeozoic trilobite genera. It ranges from the early Carboniferous (early Viséan) to Late Permian (Guadalupian), a duration of nearly 100 million years. Examination of systematic literature indicates that approximately 50 species are assigned to this genus worldwide (Hahn and Hahn 1970; Osmólska 1970; Kobayashi and Hamada 1980). A number of these species from the late Carboniferous and Permian can be reassigned *a priori* to other genera. Some clear examples of this are *P. gruenewaldi* (Möller, 1867), *P. roemeri* (Möller, 1867), and *P. pyriformis* Chamberlain, 1969. The first two species, by lacking an anterior border, are more appropriately assigned to *Tripoetus* Kobayashi and Hamada, 1979; the last, which displays a medial preoccipital lobe, should be assigned to *Pseudophillipsia* (*Carniphillipsia*) Hahn and Brauckmann, 1975. It is not clear from the current analysis whether the Permian species previously assigned to *Paladin* and herein assigned to *Neokaskia* and *Tripoetus* are derived from the early Carboniferous *Paladin* stock. This unresolved question may warrant future study. Even with the reassignments considered above, there are still approximately 40 species that can be attributed to *Paladin*, all of which are from the Carboniferous.

Although the revised stratigraphical range of *Paladin* spans most of the Carboniferous, North American representatives are restricted to the Viséan and Namurian (Osagean–Morrowan) as outlined as ‘Stage 2’ of Brezinski (1999). The relatively complete marine record for the Carboniferous and Permian of North America notwithstanding, it is puzzling why this long-ranging and cosmopolitan genus has never been recognized outside the Stage 2 limits documented by Brezinski (1999). This perplexing stratigraphical and geographical restriction spurred the current study. Because this genus is such an important component of the Carboniferous trilobite faunas of the United States, a taxonomic re-evaluation was undertaken in an attempt to understand better the phylogeny and systematic relationships of *Paladin*.

## *Taxonomic confusion*

Weller (1936) erected *Paladin* on a Namurian species from the southern United States, *Griffithides morrowensis* Mather, 1915. Characterised by a forwardly expanding glabella, large posteriorly located palpebral lobes, anterior border, and bordered pygidium, according to Weller, *Paladin* was similar to

*Kaskia*, which he erected in the same publication. He noted that *Kaskia* differed from *Paladin* by lacking the distinct anterior border, and had more forwardly located palpebral lobes, but that there were several species which exhibited morphologies intermediate between the two type species. This gradation in morphology has through time posed a considerable amount of confusion when subsequent species were assigned to either genus. Whittington (1954) recognized this gradation in morphology between the two and chose to consider *Kaskia* a subgenus of *Paladin*. Whittington (1954, p. 5) also noted that some of the European species assigned to *Weberides* by Reed (1942) might also be assignable to *Paladin*. Cisne (1967) also noted the difficulty in separating *Kaskia* from *Paladin* and considered the two to be congeneric. The lumping of *Kaskia* and *Weberides* under *Paladin* was accepted by Hahn and Hahn (1970), Osmólska (1970), and most subsequent workers, with the exception of Kobayashi and Hamada (1980) who continued to separate *Weberides* as a distinct genus.

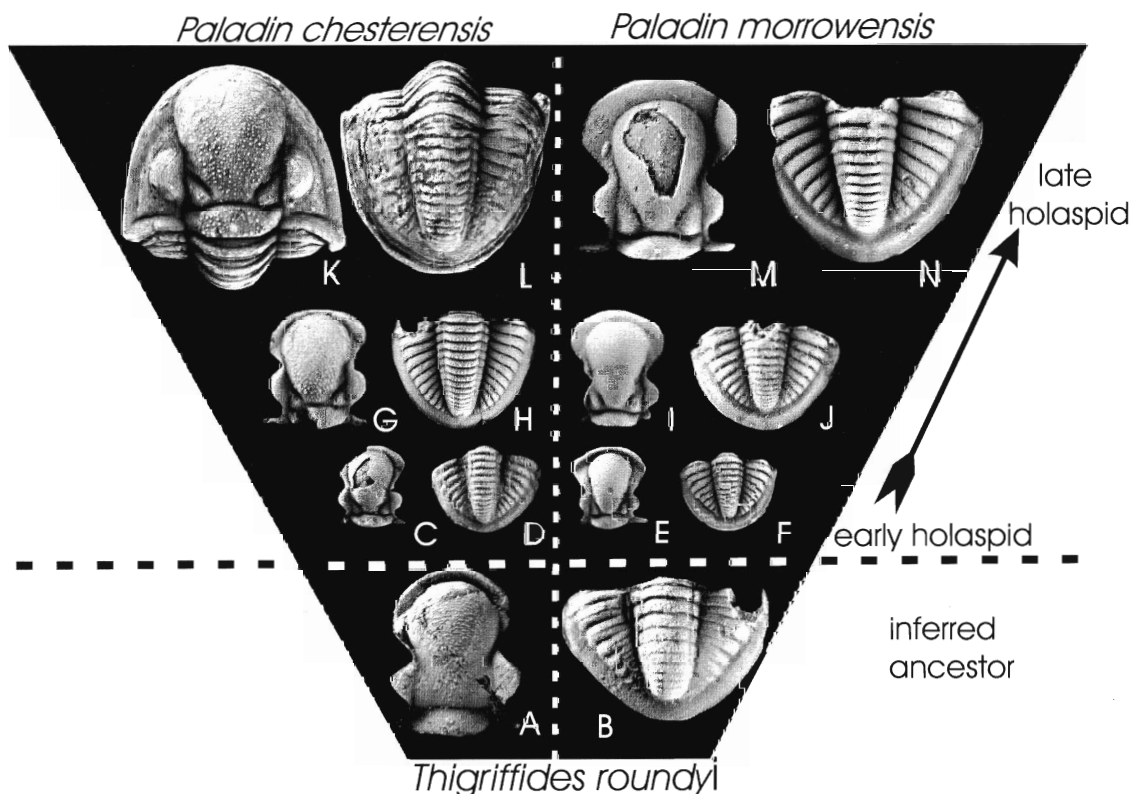
#### PUTATIVE ANCESTRAL MORPHOLOGY

Throughout the earliest Carboniferous (Tournaisian) the characteristic phillipsiid morphology consisted of a forwardly tapering to parallel-sided glabella, narrow, forward-located, palpebral lobes, and borderless pygidium. The few exceptions include *Griffithides*, *Bollandia*, *Griffithidella*, and *Thigriffides*. It can be surmised that the widespread Viséan and Namurian *Paladin* probably originated from one of these possible ancestors. Although Weller (1936), in his original remarks on the genus, proposed that *Paladin* was derived from *Griffithides*, this is not a likely ancestral candidate since it is characterized by narrow palpebral lobes located forward on a cranidium that lacks an anterior border, and has a long pygidium that is weakly bordered. Furthermore, it is unlikely that *Griffithides* served as a precursor to *Paladin* since both genera have the same stratigraphical ranges. *Bollandia* also is characterized by small, forward-located palpebral lobes, and lacks an anterior cranial border, consequently, as with *Griffithides*, it is not a likely ancestor to *Paladin*. The large, posteriorly located palpebral lobes, forwardly expanding glabella, anterior cranial border, and distinctly bordered pygidium are pleisiomorphic characters that point to only two other potential ancestral genera, *Griffithidella* and *Thigriffides*. The former has ten thoracic segments, a very short pygidium, and a narrow glabella that, in some species, is forwardly converging or medially constricted. These characters tend to suggest that *Griffithidella* is also an improbable ancestor to *Paladin*.

Hahn and Hahn (1967, fig. 5) suggested that *Paladin* was derived from the early Carboniferous *Thigriffides*. This was agreed by Owens (*in* Owens and Hahn 1993), but alternatively, Owens and Hahn (1993) suggested that *Rhenogriffides* Hahn *et al.*, 1987 may have supplied the ancestral stock for *Paladin*. Although *Rhenogriffides* shares a superficial resemblance to *Paladin*, it is characterized by transversely narrow palpebral lobes, a poorly defined anterior border, and glabella with parallel to slightly forward-tapering sides. Clearly, *Thigriffides*, with its large posteriorly located palpebral lobes, forwardly expanding glabella, and anterior border, has a closer resemblance to *Paladin*, and is more tenable as the ancestor. These presumed pleisiomorphic characters, although widespread in the middle to late Carboniferous, are unusual in the Tournaisian.

The dearth of ontogenetic studies for late Palaeozoic trilobites hinders phylogenetic reconstruction based on ontogenies. However, comparison of variation through the holaspid stage of several species aids reconstruction of ancestral morphologies. Text-figure 1 illustrates such holaspid variation of *P. morrowensis* (Mather, 1915) and *P. chesterensis* (Weller, 1936). Notwithstanding the marked morphological divergence exhibited by larger holaspid specimens, smaller, and presumably younger, individuals show a marked interspecific morphological convergence. This is interpreted to suggest that these species share a common ancestral history. The putative ancestor which will be used in subsequent analysis is *Thigriffides roundyi* (Girty, 1926) (Text-fig. 1).

While there have been no detailed ontogenetic studies of North American species of *Paladin*, Clarkson and Zhang (1991) provided detailed documentation of morphological changes shown by *P. eichwaldi shunnerensis* (King, 1914) from Great Britain. The marked similarity between the early holaspid individuals of *P. chesterensis* (Weller, 1936), *P. eichwaldi* (Fischer v. Waldheim, 1825), and *P. morrowensis* (Mather, 1915) allows a reasonable interpretation that the European taxa assigned to



TEXT-FIG. 1. A–B, morphology in inferred ancestor *Thigriffides roundyi* (CFM 51952, US National Museum 3523, respectively). C–N, morphological variation of cranidia and pygidia observed in individuals of increasing size through the holaspid stage of *Paladin chesterensis* (Weller, 1936) and *P. morrowensis* (Mather, 1915). C–D, small holaspid individuals of *P. chesterensis* (Carnegie Museum of Natural History (CM) 41720–41721). E–F, small holaspid individuals of *P. morrowensis* (CM 41724–41725). G–H, middle holaspid individuals of *P. chesterensis* (CM 41722–41723). I–J, middle holaspid individuals of *P. morrowensis* (CM 41726–41727). K–L, larger holaspid individuals of *P. chesterensis* (Chicago Field Museum (CFM) 34437). M–N, larger holaspid individuals of *P. morrowensis* (CM 41728–41729). All photographs  $\times 2.0$ .

*Paladin* and the North American representatives share a close common ancestry (see Clarkson and Zhang, 1991, figs 12–13; text-fig. 3).

#### PHYLOGENETIC ANALYSIS

The plethora of apparently gradational morphologies displayed by species assigned to *Paladin*, and exemplified by the *Paladin-Kaskia* conundrum, is confusing both to traditional taxonomy and phylogeny reconstruction. Because of this, modern phylogenetic procedures were chosen to analyse a number of species assigned to *Paladin*. The initial phylogenetic study, which concentrated on 11 North American species, produced a single tree with a distinct two-branch topology which reflects a dichotomy of taxa into two separate clades. Because these results are mirrored in later analyses they will not be discussed here. The topology produced in this early analysis raised a question regarding the relationship between these North American clades and the European representatives of the genus. This question led to the inclusion in the analysis of an additional eight species known from Europe, five from the Viséan and Namurian and three from Westphalian to Stephanian. The Viséan–Namurian species are: *P. cuspidatus* (Reed, 1943),

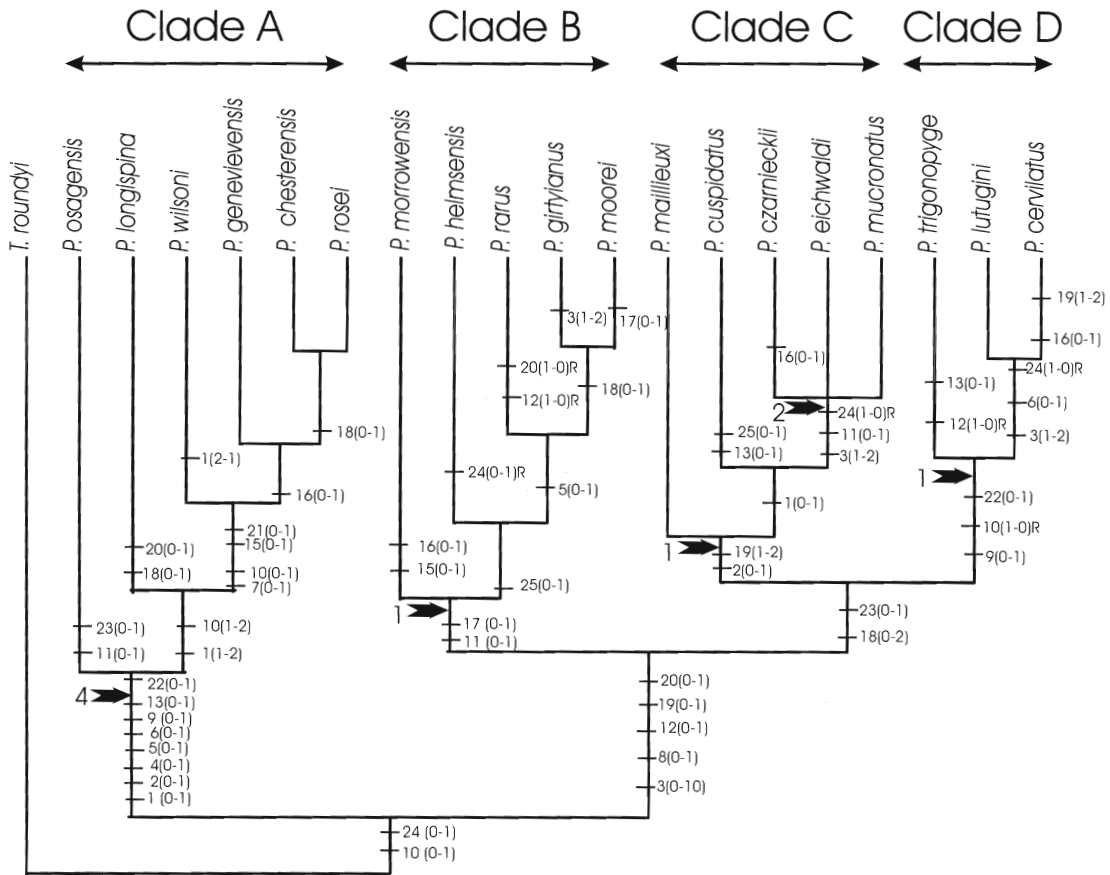
TABLE 1. List of characters and character-states used in phylogenetic analysis of *Paladin* ingroup using *Thigriffides roundyi* as an outgroup.

1. Anterior border. Distinct and wide (0). Narrow (1). Indistinct to obsolete (2).
2. Anterior border furrow. Shallow (0). Absent (1).
3. Shape of the base of glabella. Quadrate (0). Subrounded (1). Acutely rounded (2).
4. Palpebral midline position. Less than or equal to 0.35 cranial length (0). Greater than 0.35 cranial length (1).
5. Palpebral outline. Nearly semicircular (0). Crescentic (1). Narrow (2).
6. Character of S1. Shallow (0). Narrow, deeply incised (1).
7. Lateral border. Sharply furrowed (0). Indistinct furrow rounded at margin (1).
8. Occipital furrow longitudinal profile. Narrowly incised (0). V-shaped profile (1).
9. L2–3 present. No (0). Yes (1).
10. Posterior facial sutures. Short curved (0). With a short straight section (1). With a long straight section (2).
11. L1 outline. Suboval (0). Subtriangular (1).
12. L1 position with respect to glabella base. Sub-even (0). Behind glabella base (1).
13. S1 trace. Straight (0). Recurved posteriorly (1).
14. Pygidial/Axial width ratio. Less than or equal to 0.33 (0). Greater than 0.33 (1).
15. Pleural furrow. Well incised (0). Shallow-narrow (1).
16. Interpleural furrows. Distinct, except on most posterior ribs (0). Distinct on only anteriormost ribs (1).
17. Axial terminus outline. Broadly rounded (0). Sharply rounded with tapered extension (1).
18. Pygidial outline. Parabolic (0). Semi-elliptical (1). Lanceolate (2).
19. Pygidial border. Evenly wide (0). Slightly wider posterior (1). Posteriorly extended (2).
20. Pleural field convexity (transverse). Arched (strongly convex) (0). Flattened exsagittal (low convexity) (1).
21. Pygidial border slope. Less than lateral part of pleural field slope (0). Equal to pleural fields (1). Flanged (2).
22. L1 depressed in height relative to posterior of glabella. Yes (0). No (1).
23. Pygidium axial transverse profile. Rounded (0). Subtrapezoidal (1).
24. Cranial width at  $\Delta$  relative to  $\beta$ .  $\Delta$  greater than  $\beta$  (0).  $\Delta$  equal to or less than  $\beta$  (1).
25. Shape of sutures at  $\beta$ . Broadly rounded (0). Acutely rounded (1).

*P. czarnieckii* Osmólska, 1970, *P. eichwaldi* (Fischer v. Waldheim, 1825), *P. maillieuxi* (Demanet, 1938), and *P. mucronatus* (M<sup>c</sup>Coy, 1844). The three late Carboniferous species are: *P. cervilatus* (Weber, 1933), *P. lutugini* (Weber, 1933), and *P. trigonopyge* Osmólska, 1968.

The 19 *Paladin* species comprising the ingroup were compared using 25 morphological characters. These taxa were examined using PAUP 4.0 in beta version employing a heuristic search command with simple addition. All characters were unordered and of equal weight, and are summarised in Table 1. The list of character states for each ingroup species is given in the Appendix. A single most parsimonious tree was retained by the analysis (Text-fig. 2). This most parsimonious tree, of length 62 steps, produced a consistency index of 0.48 and a retention index (RI) of 0.80. The topology of the single most parsimonious tree displayed four separate branches, labelled Clades A to D. The sister clades, Clades A and B, were produced by the initial analysis of North American species; these two groups maintained their integrity during the more comprehensive analysis. Bremer indices, an indication of branch stability, were calculated for this topology and are plotted on their respective branches on Text-figure 2. The total support index (ti) of 0.15 was calculated from the branch supports, and suggests a fairly stable topology. Fifty per cent consensus trees also were produced by bootstrap and jack-knife analyses to test the stability of the four-branch topology. Although the four-branch topology was retained in the bootstrap analysis, Clade B was lost during jack-knife analysis. However, during both analyses several of the taxa were removed from Clades C and D. The possible significance of these omissions is discussed below.

Clade A consists of six species: *P. osagensis* Cisne, 1967, the oldest representative of the genus; *P. chesterensis* (Weller, 1936); *P. genevievensis* (Walter, 1924); *P. longispina* (Strong, 1872); *P. rosei* Cisne, 1967; and *P. wilsoni* (Walter, 1924). This clade ranges from early to late Viséan (late Osagean–middle Chesterian). The large number of characters that define this group (see Text-fig. 2) directly reflects that it was the ingroup defined in the earlier analysis. The result of the large number of synapomorphies is a



TEXT-FIG. 2. Single most parsimonious cladogram of 19 ingroup taxa assigned to *Paladin*. Characters 1–25 given in Table 1; assigned character states given in Appendix. Distribution of characters given on branches; R denotes a reversal to an ancestral state. Bremer branch support index number given in dark numbers to left of arrows at branch locations. Cladogram generated by Treeview (Page 1996).

relatively high Bremer branch index of 4. This branch is also retained on the consensus trees produced by bootstrap and jack-knife analyses.

Clade B is made up of the remaining five North American species: *P. girtyianus* Hahn and Hahn, 1970; *P. helmsensis* Whittington, 1954; *P. moorei* (Branson, 1937); *P. morrowensis* (Mather, 1915); and *P. rarus* Whittington, 1954. Species of this clade range in age from the late Viséan to late Namurian (middle Chesterian–middle Morrowan). Although this branch is defined by a low Bremer branch index of 1, both sister clades A and C have much higher indices, which serve to isolate the low stability branch between them. Although this branch is retained on the consensus tree from the bootstrap analysis, it is lost during the jack-knife analysis.

The branch defining Clade C is created by the five Viséan–Namurian species from Europe. This group contains *P. cuspidatus* (Reed, 1943), *P. czarnieckii* Osmólska, 1970, *P. eichwaldi* (Fischer v. Waldheim, 1825), *P. maillieuxi* (Demanet, 1938), and *P. mucronatus* (M<sup>c</sup>Coy, 1844). *Paladin czarnieckii* Osmólska, 1970, *P. eichwaldi* (Fischer v. Waldheim, 1825), and *P. mucronatus* (M<sup>c</sup>Coy, 1844) produce an unresolved polytomy. Bremer indices on this branch occur at the node at the base of the branch and between the three polytomous species and their sister species. This later index may suggest that the three unresolved species represent a separate clade from the two non-polytomous species. This is further suggested by the bootstrap

and jack-knife consensus trees, which each maintain the three polytomous European species as a separate branch. This polytomy suggests that the characters used in the analysis of North American species is not sufficiently discriminating for all European species. Clearly, further analysis of this clade is warranted to evaluate whether the three unresolved species indeed represent a separate group that is not differentiable by the current characters utilized. The three unresolved species are characterized by the shape of the glabellar base, a narrow anterior cranial border, broadly rounded anterior facial suture, and posterior elongation of the pygidial border.

The fourth clade, termed here Clade D, is made up of the three species from upper Carboniferous–lower Permian strata. Both *P. cervilatus* (Weber, 1933) and *P. lutugini* (Weber, 1933) are known from the Westphalian of the Donets Basin of Ukraine, whereas *P. trigonopyge* (Osmólska, 1968) is known from lower Permian (Asselian) strata of Spitsbergen. Although this branch has a Bremer index of only 1, it is maintained on the consensus trees for both the bootstrap and jack-knife analyses, albeit without *P. trigonopyge* (Osmólska, 1968). The removal of *P. trigonopyge* (Osmólska, 1968) from this branch during both of the variance analyses raises questions about its relationship to this clade as well as other *Paladin* clades.

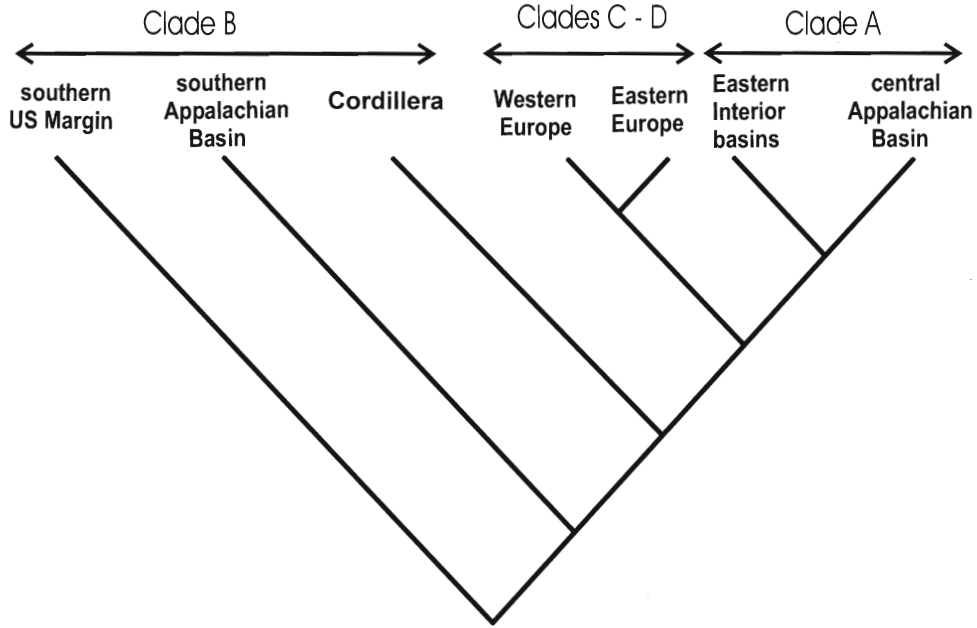
#### PALAEOGEOGRAPHICAL IMPLICATIONS

The four clades delineated by phylogenetic analysis of 19 ingroup species assigned to *Paladin* reflect subgroups that are not only differentiable on a phylogenetic basis but also on palaeogeographical grounds. In an effort to evaluate possible vicariance patterns within the ingroup species, Brookes Parsimony Analysis (BPA) was conducted (Text-fig. 3).

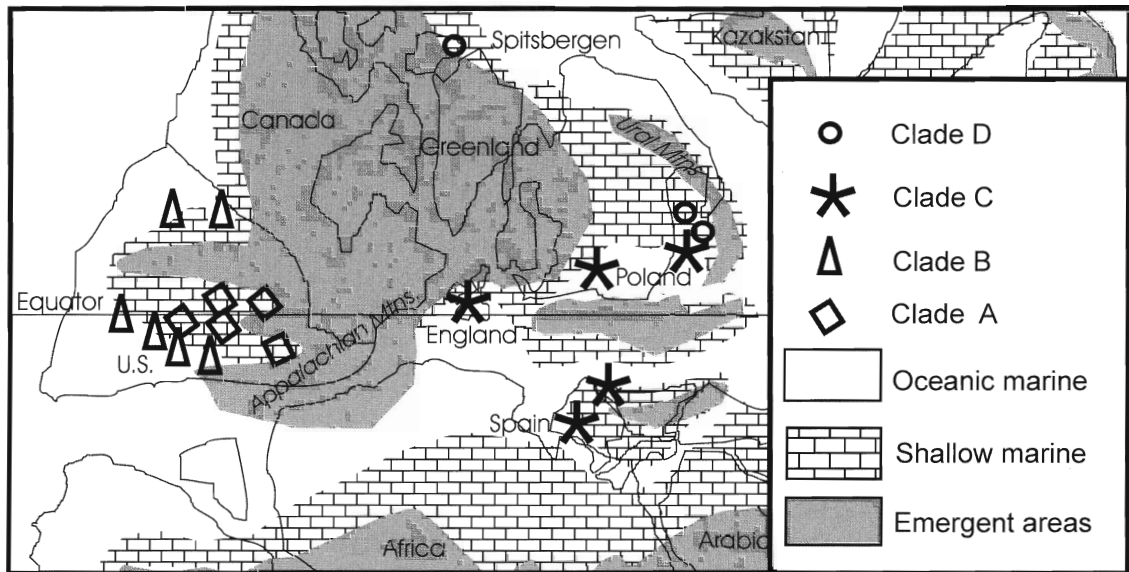
The ingroup species are present in seven separate geographical areas (Text fig. 4). Clade A is present in the central Appalachian Basin (Area 1), the Illinois and Michigan basins, and upper Mississippi Valley area (Area 2). Clade B is present in the southern Appalachian Basin (Area 3), Cordilleran region (Area 4), and the southern United States (Arkansas, Oklahoma, and Texas) (Area 5). Clade C is present in western Europe, including the United Kingdom, Belgium, Spain, and France (Area 6), as well as eastern Europe (Germany, Poland, Czech Republic, Ukraine, and Spitsbergen) (Area 7). Clade D is known only from the Ukraine and Spitsbergen.

Utilizing BPA with the above-defined areas, a single area cladogram was derived (Text-fig. 3), with a consistency index of 0.92 and 38 steps long. This single area cladogram reveals an interesting vicariance pattern, but one that might be intuitively expected. On the retained tree, Area 5, the southern margin of the United States, represents the ancestral area. Sister areas to this ancestral area are both the southern Appalachian Basin and the Cordillera. These three areas are the known sites where species of Clade B occur. Western Europe and eastern Europe are sister areas to one another, as they form a branch which is a sister area to both the Cordillera and eastern Interior areas of the United States. The European branch contains species of Clades C and D. Perhaps the most derived areas are 1 and 2 which contain species of Clade A.

Because the area cladogram produces relationships that are consistent with the cladogram in Text-figure 2, a number of palaeogeographical inferences may be proposed (Text-fig. 4). The restriction of Clade B to Areas 3, 4, and 5 is consistent with both phylogenetic and environmental occurrences. Area 5, the area where the type species of *Paladin* is known, juxtaposes the known area of occurrence of *Thigriffides roundyi* (Girty, 1926), the interpreted ancestor of *Paladin*. Brezinski (1998) found that this ancestral species inhabited presumed deep water, starved basin deposits off the southern margin of the United States during the Tournaisian. *Paladin*, the interpreted descendant of *Thigriffides*, is known from shelf edge and deeper off-shelf deposits of Arkansas and Oklahoma (Sutherland and Manger 1979). The environments that produced these deposits represent a variety of water depths from shallow, shelf edge, sand shoals, to relatively deeper, off-shelf shales. Although these rocks were deposited in a range of water depths the environments that produced them appear to be relatively long-lived and stable through time. This is indicated by the lack of interbedded lithologies and facies shifts (Sutherland and Manger 1979). The other areas where Clade B is known can also be attributed to similar environmental settings.



TEXT-FIG. 3. Area cladogram derived from phylogenetic cladogram illustrated in Text-figure 2 using Brookes Parsimony Analysis (BPA) (see Wiley 1988). Geographical areas are described in text. Cladogram generated by Treeview (Page 1996).



TEXT-FIG. 4. Palaeogeographical reconstruction of the pan-equatorial region during the Viséan. Continental and shelf area reconstructions from Scotese and McKerrow (1990). Symbols represent approximate locations where species of *Paladin* are known and clade in which they are assigned.

Another inference suggested from Text-figures 2 and 3 is that western Europe served as an ancestral area for eastern Europe. Although this inference is based on the area cladogram, it may be premature to make such an interpretation based on the limited number of species used in the current analysis.

Lastly, the most derived areas, the Eastern Interior areas of the United States and the central Appalachian Basin, were the sites where Clade A is present. Clade A occurrences are within deposits of interbedded marine and non-marine strata; the former were deposited in relatively shallow marine environments during cyclothemic iterations of sea level (Swann 1964; Brezinski 1983, 1989). It is suggested here that these interior basins allowed for the allopatric isolation of these taxa, permitting this lineage to evolve with little exchange with the ancestral southern areas.

#### TAXONOMIC SIGNIFICANCE

While there is a dearth of information about the ontogenetic development of species of *Paladin*, morphological similarities within the early holaspid stage of a number of the species of *Paladin* argue for a shared ancestry (Text-fig. 5). The divergence of the 19 ingroup species into four, phylogenetically, palaeogeographically, and in some cases palaeoecologically, distinct groups suggests that a taxonomic separation may be warranted and that the current procedure of lumping the taxa together is inadvisable.

The branch stability of Clade A along with its palaeogeographical segregation in the central Appalachian, Illinois, and Michigan basins argues that this clade has significant divergence from its proposed ancestor. Interestingly, the position of these species on this branch of the cladogram is congruent with the stratigraphical occurrence of these species. *Paladin osagensis* Cisne, 1967, the earliest representative known (early Viséan), is succeeded, stratigraphically, by *P. longispina* (Strong, 1872) (middle Viséan strata), *P. wilsoni* (Walter, 1924) and *P. genevievensis* (Walter, 1924) (late middle Viséan), and finally by *P. rosei* Cisne, 1967, and *P. chesterensis* (Weller, 1936) (late Viséan). All of these factors point strongly towards Clade A being a distinct monophyletic group. One of the most derived species on this branch, *P. chesterensis* (Weller, 1936), was originally designated the type species of the genus *Kaskia* by Weller (1936). Considering the factors discussed above, it is herein recommended that the genus *Kaskia* be re-erected and that the species discussed herein as Clade A be assigned to it.

Some morphological attributes that should be used to characterise large holaspid individuals of *Kaskia* include a narrow, indistinct, anterior border, a subquadrate base of the glabella, long straight section of the posterior branch of the facial sutures, narrow, crescentic palpebral lobes, a broad, indistinct, trough-like, lateral border furrow, and a semielliptical pygidium, with shallow pleural furrows.

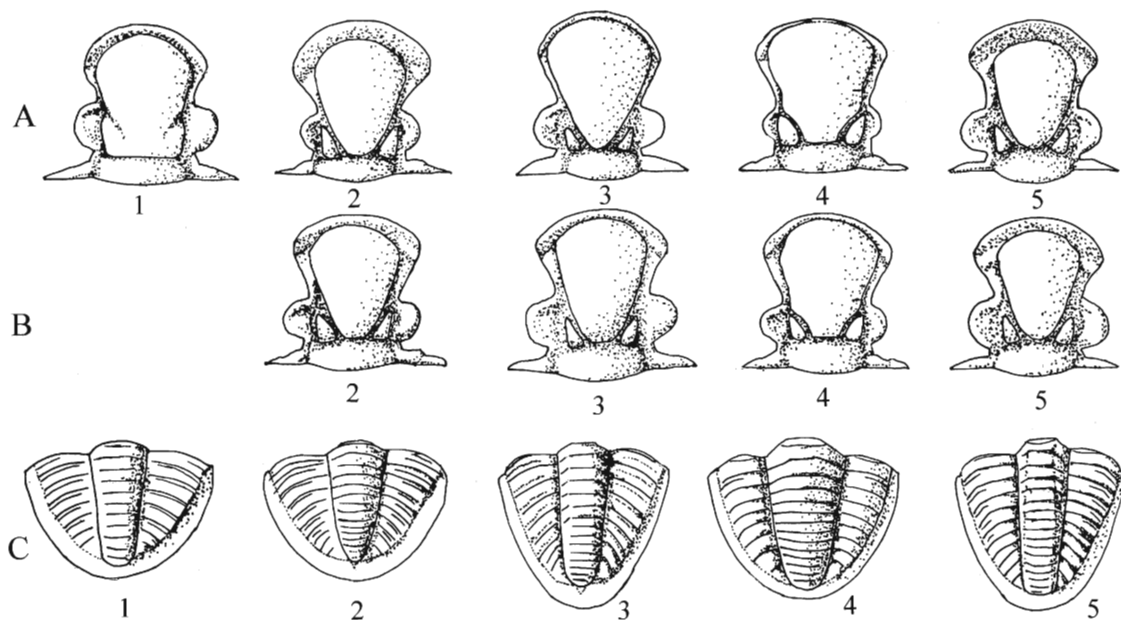
The branch stability of Clade C is manifested with two separate support values. Although the entire branch has a Bremer branch support number of 3, the unresolved polytomy of *P. czarnieckii* Osmólska, 1970, *P. eichwaldi* (Fischer v. Waldheim, 1825), and *P. mucronatus* (M<sup>c</sup>Coy, 1844) has an additional support value of 2 and is retained in both the bootstrap and jack-knife analyses. This trichotomy points to the possibility that Clade C, when examined more thoroughly, might provide a separation of the western European species into two separate and recognizable groups. Clade C is present in Europe and there is currently no known overlap of geographical distribution with it and members of clades A or B.

An important taxon within Clade C is *Paladin mucronatus* (M<sup>c</sup>Coy, 1844). Reed (1942) erected *Weberides* based on this taxon, and although other species within this clade do not show the terminal mucro on the pygidium, they do exhibit a broadening of the posterior pygidial border. Furthermore, the triangular outline to the pygidium is not seen in either Clades A or B. It is herein recommended that the unresolved species of Clade C be returned to the resurrected *Weberides*. Further analysis is needed to determine if *P. cuspidatus* (Reed, 1943) and *P. maillieuxi* (Demagnet, 1938) should be assigned to *Weberides* or to a separate genus.

Characters which redefine this genus include the pygidial character mentioned above, in addition to the acutely rounded posterior base of the glabella, large palpebral lobes that are commonly broader than the cranial width at  $\beta$ , and narrow anterior border that lacks a border furrow. While the current analysis suggests that perhaps more than one clade is represented by these species, sufficient information is currently not available to delineate such a separation.

While Clade B has a relatively low Bremer index, it is retained by bootstrap analysis, but lost during





TEXT-FIG. 5. Sketches of general cranidial morphologies shown by holaspid individuals of the various *Paladin* clades as well as that of the presumed ancestral morphology of *Thigriffides roundyi* (Girty, 1926) cranidium (A1) and pygidium (C1). Smaller holaspid cranidial morphologies (row B), larger holaspid cranidial morphologies (row A), and holaspid pygidial morphologies (row C). Column 2, *Paladin morrowensis* (Mather, 1915); column 3, *P. chesterensis* (Weller, 1936); column 4, *P. eichwaldi* (Fischer v. Wildhelm, 1825); and column 5, *P. lutugini* (Weber, 1933).

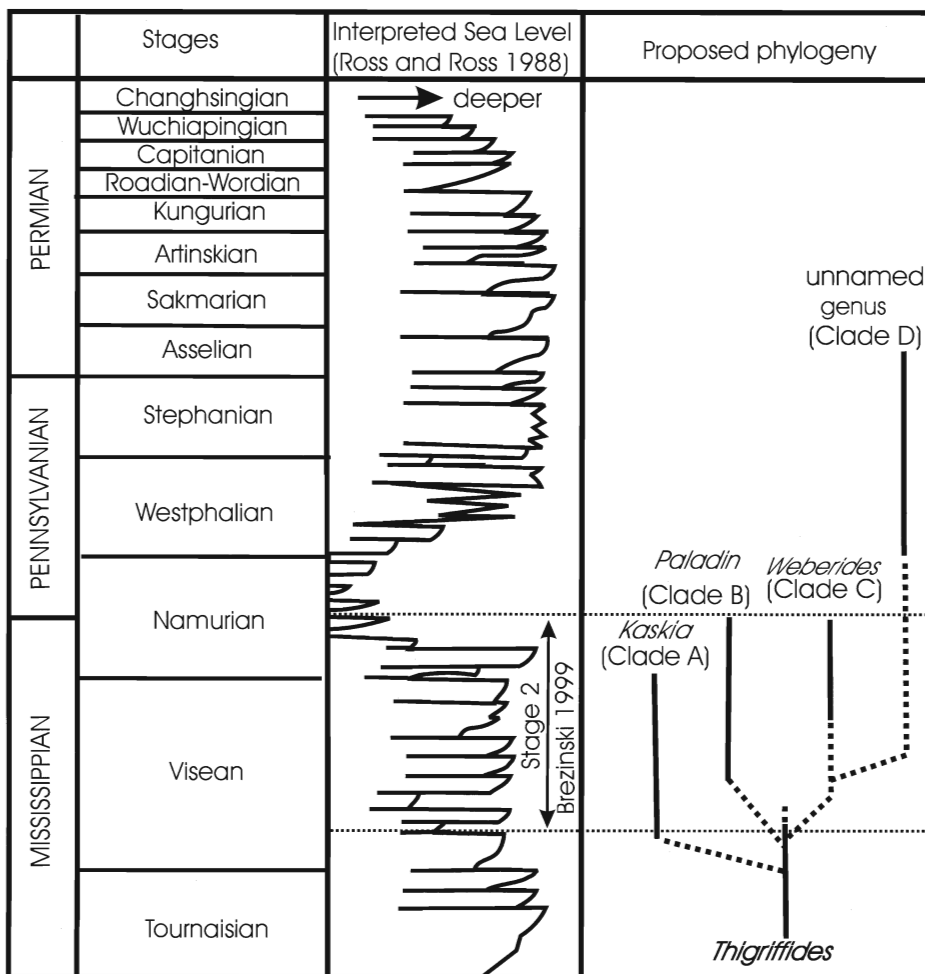
jack-knife analysis. This clade contains the type species of *Paladin*, *P. morrowensis* (Mather, 1915), as well as some of the more definitively assigned *Paladin* species (e.g. *P. helmsensis* Whittington, 1954, *P. girtyianus* Hahn and Hahn, 1970). Because the species of this clade exhibit a morphological separation from the other species examined, it should be considered a separate genus from either of its sister clades. Therefore, the characteristics of Clade B should be considered as those that typify the true *Paladin* morphology.

Refined morphological characteristics that typify *Paladin* are the subrounded base to the glabella, parabolic outline to the pygidium, sharply tapered terminus to the pygidial axis, and distinct anterior border, commonly separated from the front of the glabella by a shallow, narrow border furrow.

Clade D, like Clade B, has a relatively low Bremer support index of 1. However, a branch formed by two of the taxa, *P. cervilatus* (Weber, 1933) and *P. lutugini* (Weber, 1933), is retained on both the bootstrap and jack-knife consensus trees. Notwithstanding that this clade (or at least part of it) forms a derived branch separate from the other clades, the current analysis, based only on photographs of the type material, is insufficient to be certain that these species are truly a separate and distinct group. Therefore, it would be imprudent with the current information to erect a separate genus to include these species. Further analysis of these species as well as other late Carboniferous species such as *P. subbakewellensis* Osmólska, 1970 is needed.

#### EVOLUTIONARY INTERPRETATIONS

The phylogenetic analysis presented here suggests that many of the taxa currently assigned to *Paladin* can be referred to a number of other genera. Similarity of morphology within the early holaspid stages, especially among the mid-Carboniferous genera, indicates their shared ancestry. A proposed phylogeny, consistent with the cladogram illustrated in Text-figure 2, is presented in Text-figure 6. The interpreted



TEXT-FIG. 6. Hypothesis of phylogeny based on phylogenetic and palaeogeographical reconstructions presented in Text-figures 2–4. Sea level curve from Ross and Ross (1988), and dashed lines delineate Stage 2 of North American trilobite evolution as outlined in Brezinski (1999).

ancestor, *Thigriffides*, ranged through most of the Tournaisian, and inhabited deeper water, basal deposits. During the early Viséan, the early representatives of the *Kaskia* lineage appeared and migrated into the depositional basins of the shallow shelf interior of the central and eastern United States. In these quasi-isolated locations, this lineage evolved into the derived morphology seen in *Kaskia chesterensis* Weller, 1936. During the middle Viséan, a second lineage with morphologies consistent with true *Paladin* individuals was derived from the putative ancestral *Thigriffides* stock. The *Paladin* lineage inhabited areas along the margin of the late Mississippian and earliest Pennsylvanian shelves of the southern and western United States. Coincident with this lineage was the derivation of another lineage (or group of lineages) that inhabited the periphery of the Rheic seaway of Europe and western Russia and Ukraine and are manifested in the genus *Weberides*. This lineage, or group of lineages, arose in the middle to late Viséan and survived into the early Namurian.

The termination of the *Kaskia*, *Paladin*, and *Weberides* lineages by the middle Namurian indicates an extinction episode that spanned a considerable geographical area. This is consistent with the

interpretations of Brezinski (1999) that the Stage 2 of North American trilobite evolution was terminated during the mid-Carboniferous eustatic fall in sea level (Saunders and Ramsbottom 1986). The appearance of a *Paladin*-like morphology appears after this extinction may be the result of the Donets Basin of eastern Ukraine serving as a refuge during the mid-Carboniferous regression. Thus, the Westphalian and Stephanian taxa currently assigned to *Paladin* may represent Lazarus taxa (Jablonski 1986) that appeared during late Carboniferous submergence. Alternatively, these species may represent a convergent, late Carboniferous morphology.

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#### REFERENCES

- BRANSON, C. C. 1937. Stratigraphy and fauna of the Sacajawea formation, Mississippian, of Wyoming. *Journal of Paleontology*, **11**, 650–660.
- BREZINSKI, D. K. 1983. Paleocology of the Upper Mississippian trilobite *Paladin chesterensis* in southwestern Pennsylvania. *The Compass of Sigma Gamma Epsilon*, **61**, 2–7.
- 1989. Late Mississippian depositional patterns in the north-central Appalachian Basin, and their implications to Chesterian hierarchical stratigraphy. *Southeastern Geology*, **30**, 1–23.
- 1998. Lower Mississippian trilobites from starved basin deposits of the south-central United States. *Journal of Paleontology*, **72**, 718–725.
- 1999. The rise and fall of late Paleozoic trilobites in the United States. *Journal of Paleontology*, **73**, 164–175.
- CHAMBERLAIN, C. K. 1969. Carboniferous trilobites: Utah species and evolution in North America. *Journal of Paleontology*, **43**, 41–68.
- CISNE, J. L. 1967. Two new trilobites of the genus *Paladin*. *Journal of Paleontology*, **41**, 1267–1273.
- CLARKSON, E. N. K. and ZHANG, X.-G. 1991. Ontogeny of the Carboniferous trilobite *Paladin eichwaldi shunnerensis* (King 1914). *Transactions of the Royal Society of Edinburgh: Earth Sciences*, **82**, 277–295.
- DEMANET, F. 1938. La faune des Couches de passage du Dinantien, au Namurien dans le synclinorium de Dinant. *Mémoires du Musée Royal d'Histoire Naturelle Belgique, Series 1*, **84**, 201 pp.
- FISCHER VON WALDHEIM, G. 1825. Trilobiten. 54. In EICHWALD, E. *Geognostico-zoologicae per ingriam marisque Baltici provincias nec non de trilobitis observationes*, Kasan, 58 pp.
- GIRTY, G. H. 1926. The macrofauna of the limestone of Boone age. 24–43. In ROUNDY, P. V., GIRTY, G. H. and GOLDMAN, M. I. (eds). *Mississippian formations of San Saba County, Texas*. US Geological Survey, Professional Paper, **146**, 63 pp.
- HAHN, G. and BRAUCKMANN, C. 1975. Revision zweier Trilobiten-Arten aus dem Perm Asiens. *Geologica et Palaeontologica*, **9**, 117–124.
- and HAHN, R. 1967. Zur Phylogenie der Proetidae (Trilobita) des Karbons und Perms. *Zoologische Beiträge*, **13**, 303–349.
- — 1970. Trilobitae carbonici et permici II. 161–335. In WESTPHAL, F. (ed.). *Fossilium Catalogus I. Animalia*. 's Gravenhage, 531 pp.
- — and BRAUCKMANN, C. 1987. Die trilobiten des belgischen Kohlenkalkes (Unter-Karbon) 9. *Piltonia* und Nachtrage. *Geologica et Palaeontologica*, **21**, 137–167.
- JABLONSKI, D. 1986. Causes and consequences of mass extinctions: a comparative approach. 183–229. In ELLIOT, D. K. (ed.). *Dynamics of extinctions*. John Wiley and Sons, New York, 294 pp.
- KING, W. B. R. 1914. New trilobites from the Millstone Grit of North Yorkshire. *Geological Magazine, Series 6*, **1**, 390–394.
- KOBAYASHI, T. and HAMADA, T. 1979. Permo-Carboniferous trilobites from Thailand and Malaysia. *Contributions to the Geology and Palaeontology of Southeast Asia, CCI*, **20**, 1–21.
- — 1980. Carboniferous trilobites of Japan in comparison with Asian, Pacific, and other faunas. *Palaeontological Society of Japan, Special Paper* **23**, 132 pp.
- MATHER, K. F. 1915. The fauna of the Morrow Group of Arkansas and Oklahoma. *Bulletin of Science Laboratories of Denison University*, **18**, 59–284.
- McCoy, F. 1844. *A synopsis of the character of Carboniferous limestone fossils of Ireland*. McGlassen and Gill, Dublin, 274 pp.

- MÖLLER, V. 1867. Über die trilobiten der Steinkohlenformation des Ural, nebst einer Übersicht und einigen Ergänzungender bisherigen Beobachtungen über Kohlen-Trilobiten im Aligemeinen. *Bulletin of the Imperial Society of Moscow*, **40**, 120–200.
- OSMÓLSKA, H. 1968. Two new trilobites from the Treskelodden beds of Hornsund (Vestspitsbergen). *Acta Palaeontologica Polonica*, **13**, 605–617.
- 1970. Revision of non-cyrtosymbolinid trilobites from the Tournaisian–Namurian of Eurasia. *Palaeontologica Polonica*, **23**, 165 pp.
- OWENS, R. M. and HAHN, G. 1993. Biogeography of Carboniferous and Permian trilobites. *Geologica and Palaeontologica*, **27**, 165–180.
- PAGE, R. D. M. 1996. Treeview: an application to display phylogenetic trees on personal computers. *Computer Applications in Biosciences*, **12**, 357–358.
- REED, F. R. C. 1942. Some new Carboniferous trilobites. *Annals and Magazine of Natural History, Series 11*, **9**, 649–672.
- 1943. The genera of British Carboniferous trilobites. *Annals and Magazine of Natural History, Series 11*, **10**, 54–65.
- ROSS, C. A. and ROSS, J. P. 1988. Late Paleozoic transgressive-regressive deposition. 227–247. In WINGUS, C. K., POSAMENTIER, H., ROSS, C. A. and KENDALL, C. G. ST. C. (eds). *Sea level changes: an integrated approach*. Society of Economic Paleontologists and Mineralogists, Special Publication, **42**, 407 pp.
- SAUNDERS, W. B. and RAMSBOTTOM, W. H. C. 1986. The mid-Carboniferous eustatic event. *Geology*, **14**, 208–212.
- SCOTSE, C. and MCKERROW, W. S. 1990. Revised world maps and introduction. In MCKERROW, W. S. and SCOTSE, C. R. (eds). *Palaeozoic palaeogeography and biogeography*. Geological Society of London, Memoir, **12**, 210 pp.
- STRONG, E. A. 1872. Notes upon the fossil remains of the Lower Carboniferous limestone exposed at Grand Rapids, Michigan. *Kent Science Institute, Miscellaneous Papers*, **3**, 6 pp.
- SUTHERLAND, P. K. and MANGER, W. L. 1979. Ozark and Ouachita shelf-to-basin transition Oklahoma-Arkansas. *Ninth International Congress of Carboniferous Stratigraphy and Geology, Guidebook*, **19**, 81 pp.
- SWANN, D. H. 1964. Late Mississippian rhythmic sediments of the Mississippi Valley. *Bulletin of the American Association of Petroleum Geologists*, **48**, 637–658.
- WALTER, O. T. 1924. Trilobites of Iowa and some related Paleozoic forms. *Iowa Geological Survey, Annual Report*, **31**, 169–400.
- WEBER, V. N. 1933. Trilobites of the Donetz Basin. *Transmissions of the United Geological and Prospecting Service of the U.S.S.R.*, Facsimile, **225**, 1–69 [In Russian], 69–89 [In English].
- WELLER, J. M. 1936. Carboniferous trilobite genera. *Journal of Paleontology*, **10**, 704–714.
- WHITTINGTON, H. B. 1954. Two silicified Carboniferous trilobites from West Texas. *Smithsonian Miscellaneous Collections*, **122**, 1–16.
- WILEY, E. O. 1988. Parsimony analysis and vicariance biogeography. *Systematic Zoology*, **37**, 271–290.

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## APPENDIX

*Character states for ingroup relative to outgroup species*

			11111	11112	22222
	12344	67890	12345	67890	12345
<i>Thigriffides roundyi</i>	00000	00000	00000	00000	00000
<i>Paladin chesterensis</i>	21011	11012	00111	10100	11011
<i>Paladin wilsoni</i>	21011	11012	00111	00000	11011
<i>Paladin genevievensis</i>	11011	11012	00111	10000	11011
<i>Paladin rosei</i>	21011	11012	00111	10100	11011
<i>Paladin longispina</i>	21011	10012	00100	001?1	01?11
<i>Paladin osagensis</i>	11011	10011	10100	0???0	01110
<i>Paladin morrowensis</i>	00100	00101	11001	11011	01010
<i>Paladin girtyianus</i>	00201	00101	11000	01111	00011
<i>Paladin helmsensis</i>	00101	00101	11000	01011	00000
<i>Paladin rarus</i>	01101	00101	10000	01010	00011
<i>Paladin moorei</i>	00101	00101	11000	00111	00011
<i>Paladin czarnieckii</i>	11200	00101	11000	10221	00100
<i>Paladin eichwaldi</i>	11200	00101	11000	00221	00100
<i>Paladin mucronatus</i>	11200	00101	11000	00221	00100
<i>Paladin cuspidatus</i>	11100	00101	01100	00221	00111
<i>Paladin maillieuxi</i>	01100	00101	01000	00221	00110
<i>Paladin lutugini</i>	00200	1?110	01000	00211	01100
<i>Paladin cervilatus</i>	00200	1?11?	01000	10221	011?0
<i>Paladin trigonopyge</i>	00100	0?110	00100	00211	01110