

# CLADISTIC ANALYSIS OF EARLY–MIDDLE CAMBRIAN KOCHASPID TRILOBITES (PTYCHOPARIIDA)

FREDERICK A. SUNDBERG

Show Low High School, 500 W. Old Linden Road, Show Low, Arizona, <freds@show-low.k12.az.us>

**ABSTRACT**—Cambrian ptychopariids have defied most attempts at higher classification. Even at the generic level, there is no consensus as to what constitutes identification criteria in these morphologically conservative trilobites. The problem is more acute when there is a lack of knowledge about the different sclerites of species, the presence of species with morphologies intermediate between two genera, the naming of genera where incompletely known or poor quality specimens were used for type species, and the use of character checklists to generate diagnoses for higher taxa. This study on the kochaspid trilobites (Lower to Middle Cambrian) uses several available representatives of each genus to alleviate or assess some of these problems. Successive reweighting of characters is used for the assessment of 70 characters among 66 taxa as to their importance in forming clades. Results of this study include five important points about ptychopariid classification: 1) knowledge about noncranial sclerites is important for the proper placement of taxa that have generalized morphologies; 2) in contrast, taxa that have more derived cranial morphology can be accurately placed within a clade; 3) intermediate morphologies illustrate a close link between genera, but these forms can present nomenclatural problems in their placement; 4) although genera defined by type species based on incompletely described or poorly preserved specimens can create nomenclatural nightmares, other species assigned to these genera are not dependent on their previous taxonomic assignment for their placement in the cladogram; and 5) checklists of morphological characters cannot be used to recognize ptychopariid groups, since the level of homoplasy is too high and there are too many reversals of character states within a clade. Instead, a list of character states that *typify* a taxonomic group is more useful and will lead to a more stable classification.

This cladistic analysis of kochaspid trilobites indicates that 64 of the 70 characters were useful in the formation of clades. Fifty-six cranial, librigenal, thoracic, and pygidial characters were useful in typifying larger and smaller clades. The analysis also indicates that *Eokochaspis*, *Nyella*, and *Onchocephalus* are polyphyletic. Reassignments based on the cladistic analysis include *Schistometopus collaris* to *Caborcella*, and *Syspacephalus obscurus* to *Mexicella*.

## INTRODUCTION

A STABLE suprageneric classification of Cambrian ptychopariid trilobites has been elusive. An example of this instability is the classification for Upper Cambrian ptychopariids presented in Moore (1959), which was revised by Palmer (1965), Longacre (1970), and Stitt (1971); and subsequently revised by Ludvigsen and Westrop (1983), Westrop (1986), Ludvigsen et al. (1989), and Fortey and Chatterton (1988). The classification of Lower and Middle Cambrian ptychopariids is more tenuous, with some authors not using suprageneric classifications for at least some ptychopariids (e.g., Lochman, 1948; Rasetti 1951, 1955, 1963; Palmer and Halley, 1979; Robison, 1988; Babcock, 1994; Eddy and McCollum, 1998; Sundberg and McCollum, 2000, 2002, 2003a, 2003b).

This problem with ptychopariid trilobites has been long-standing. Ulrich (1929) referred to the assignment of genera to families and higher taxonomic units as “nothing better than a provisional arrangement” (p. 63). Resser (1935, 1938b, 1942) disliked assigning suprageneric classifications, citing that it would just add to the confusion that already existed. Whitehouse (1939) believed that it was not worth generating subfamilies until the morphology of ptychopariids was more completely known. Rasetti (1951) avoided suprageneric classification of the ptychopariids because intergrading forms made generic and familial subdivisions questionable. Palmer and Halley (1979) and Blaker and Peel (1997) disregarded the suprageneric taxa presented in the *Treatise of Invertebrate Paleontology* (Moore, 1959), citing that the generalized forms have no consistently recognized suprageneric taxa. Fortey (1990) suggested that one should be critical of almost all ptychopariid superfamilies. Other papers dissatisfied with the classifications of Cambrian ptychopariids include Palmer (1958, 1965), Ahlberg and Bergström (1978), Chang and Jell (1987), Pratt (1992), Melzak and Westrop (1994), Cotton (2001), and Fortey (2001).

## WHAT IS THE PROBLEM?

The problem with ptychopariid taxonomy has been blamed on their high degree of homoplasy (Rasetti, 1951; Fortey and Chatterton, 1988; Fortey, 1997), their generalized morphologies

(Lochman, 1947; Rasetti, 1951; Palmer, 1958; Schwimmer, 1975; Blaker and Peel, 1997; Fortey, 2001), the use of stratigraphy in constructing classifications (Fortey and Chatterton, 1988; Ludvigsen et al., 1989; Edgecombe, 1992; Westrop, 1995; Cotton, 2001; Fortey, 2001), and the failure to use stratigraphy or geography in constructing classifications (Rasetti, 1951, 1955; Palmer, 1965; Longacre, 1970; Stitt, 1983). All of these reasons add to the problem of ptychopariid classification, but they do not preclude a solution.

Four underlying problems presently hinder a solution to ptychopariid classification. First is the usual lack of articulated specimens or clearly associated sclerites that provide details of each part of the exoskeleton (see Sundberg and McCollum, 2002). Second is the incomplete description of many type species, some of which represent nominal genera for families (see Sundberg, 1999; Sundberg and McCollum, 2000). Third is the occurrence of intermediate forms between genera that make discrete breaks between taxa obscure (see Lochman, 1947; Rasetti, 1955; Palmer, 1965; Longacre, 1970; Westrop, 1992; Sundberg, 1994; Eddy and McCollum, 1998). And fourth is that different authors have different checklists of characteristics to define taxa (e.g., Lochman, 1947) and insist on using these lists.

## A POSSIBLE SOLUTION

Given the lack of success in establishing a stable classification of Cambrian ptychopariids by classical methods for the last 75 years, an approach that is untraditional in Cambrian trilobite taxonomy needs to be taken. This approach is cladistics. Cladistics provides a methodology that lays out its assumptions. Considerable controversy surrounds character selection, state weighting, state ordering, use of continuous characters, and integration of stratigraphy in cladistic analyses. However, in any cladistic analysis these assumptions are presented. If other scientists disagree with these assumptions, they have the data to reanalyze the results in their own fashion.

When trying to determine the relationship among genera, subfamilies, and families that contain high species diversity, ground

plan coding or exemplar taxa need to be used to reduce the high number of combinations that will be generated. Yeates (1995) discussed the pros and cons of using both methods and concluded that the use of exemplar taxa is the most repeatable method. Prendini (2001) discussed the process of selecting exemplar taxa. He emphasized that having hypotheses about relationships of species in a genus is preferred in selecting an exemplar taxon, suggesting that the exemplar taxon for that clade should be the basal member of the clade.

The cladistic studies of trilobites by Fortey and Chatterton (1988), Edgecombe (1992), and Babcock (1994) do not use exemplar taxa to represent their larger taxonomic groups. Lieberman (1998, 2001) has used exemplar taxa for genera in his analyses of the olenellids (either type specimens or representative species). In the latter studies, exemplar taxa were not selected due to their position in a clade. Not using exemplar taxa or not choosing them from the clade base is not a problem if the groups being studied are consistently divergent in character states (e.g., eodiscoids, agnostids, ptychopariids, and redlichids); however, a problem does exist where character states are variable within the terminal taxa (see Yeates, 1995; Prendini, 2001) or intermediate forms exist (e.g., within families of ptychopariids).

Reconstructing Cambrian trilobite phylogenies from the bottom up is suggested here. Cladistic analyses using several species are needed to determine the relationships among genera. This method allows for the use of intermediate forms that can provide valuable information linking two taxonomic groups and identifying larger clades. This type of analysis can then be used to identify the exemplar taxa to be used in larger scale cladistic studies. Presently, there are few papers that use several species to determine the phylogeny of Cambrian ptychopariids (e.g., Sundberg, 1999; Westrop and Ludvigsen, 2000; Cotton, 2001).

This paper will explore the phylogeny of the Middle Cambrian kochaspid trilobites using several species for the cladistic analysis. The kochaspids were recognized by Palmer (*in* Palmer and Halley, 1979) as an informal group characterized by their coarse granular ornamentation, prominently tapered glabella that tend to be slightly concave opposite the second pair of lateral glabellar furrows and with several pairs of moderately to strongly developed lateral glabellar furrows. Taxa presently included in this group by Palmer (*in* Palmer and Halley, 1979) and Sundberg and McCollum (2000, 2002, 2003a) are *Caborcella* Lochman, 1948; *Eokochaspis* Sundberg and McCollum, 2000; *Hadrocephalites* Sundberg and McCollum, 2002; *Kochaspis* Resser, 1935; *Kochiella* C. Poulsen, 1927; *Kochiellina* Palmer (*in* Palmer and Halley, 1979); *Kochina* Resser, 1935; and *Nyella* Palmer (*in* Palmer and Halley, 1979). These trilobites are common in strata ranging from the uppermost *Olenellus* to *Albertella* biozones of Laurentia (Walcott, 1886, 1917a, 1917b; C. Poulsen, 1927; Resser, 1939a; Lochman, 1948; Rasetti, 1951, 1957; Palmer *in* Merriam, 1964; V. Poulsen, 1964; Norford, 1968; Palmer and Halley, 1979; Sundberg and McCollum, 1997, 2000, 2002, 2003a, 2003b; Eddy and McCollum, 1998).

#### PHYLOGENETIC ANALYSIS

The cladistic analysis used 5 outgroups and 61 kochaspids and potentially related taxa. Authorship of species used is listed in Appendix 2. The outgroups were *Ptychoparella* sp. A, *Syspacephalus gregarius*, *Elrathina antiqua*, *Pachyaspis gallagari*, and *Pachyaspis deborra*. These outgroups were chosen based on their generalized morphology and their early age of origin (Early Cambrian or earliest Middle Cambrian). The ingroup was composed of taxa listed above that were previously assigned to the kochaspids by Palmer (*in* Palmer and Halley, 1979) and Sundberg and McCollum (2000, 2002, 2003b). *Amecephalites* Eddy and McCollum, 1998; *Amecephalus* Walcott, 1924; *Mexicella* Lochman,

1948; *Inglefieldia* C. Poulsen, 1927; *Onchocephalus* Resser, 1937; *Parapoulsenia* Rasetti, 1957; and *Tonopahella* Sundberg and McCollum, 2003b, were included in the study due to their age and similarity to some kochaspids.

Information about 70 presence/absence, multistate, and quantitative characters was compiled for the cladistic analyses (Appendix 1). A base weight of 1,000 steps was used unless otherwise noted (see below). Fifty characters were considered significant criteria for defining genera or higher taxa by Walcott (1886, 1916, 1917b), C. Poulsen (1927), Resser (1935, 1936, 1937, 1938a, 1939a, 1939b), Lochman (1948, 1952), Rasetti (1951, 1957), Moore (1959), V. Poulsen (1964), or Palmer (*in* Palmer and Halley, 1979) (Table 1). In addition to these characters, Sundberg (1999; Sundberg and McCollum, 2000, 2002, 2003a, 2003b) also considered an additional 15 characters significant for generic or higher classification. Two other characters were added (13—SO flexure and 37—offset of sutures) during the study because of their potential use in grouping taxa. Sundberg and McCollum (2000, 2002) used another three characters (26, 60, and 66) to differentiate species.

Many of the morphological features of Cambrian ptychopariids used by taxonomists are continuous characters. Of the 70 characters, 13 characters are quantitative. Other trilobite workers have used 12 of these quantitative characters to differentiate genera or higher taxonomic levels. Another character (palpebral lobe width) has been used by the author to differentiate genera. Although the use of quantitative characters is controversial, deletion of these characters eliminates valuable information for reconstructing the phylogeny (see Poe and Wiens, 2000). For example, a cladistic analysis of the kochaspid trilobites without the quantitative characters results in a highly unresolved strict consensus of 6,300 most parsimonious trees. To construct a resolved phylogeny, it is necessary to include these quantitative characters. The quantitative characters show continuous distributions and, thus, cannot be separated into states based on gap coding. The division of characters into individual states is based on a modified segment coding method similar to that used by Chappill (1989). Chappill used the *pool standard deviation* to determine ranges for each state (e.g., state 1 = 35–45 percent), and then assigned the mean of a species (e.g., 37 percent) to a state (=1) based on the mean's occurrence relative to the state's range. Due to the unequal sample size of species used here, the state ranges were based on the *standard deviation of the means* for all the species in the analysis. In addition, the mean  $\pm$  one standard deviation of a character for a species was used to determine the character state(s) for that species. In the example above, if the species had a range of 32–40 percent, then the species would be recorded as having character states 0 and 1. This approach gives variable species a range of states, which are recorded as a polymorphism. The quantitative characters had their weights adjusted such that a full range of character states (e.g., 0 to 4) would comprise 1,000 steps. Thus, each state change was a fraction of 1,000 (e.g., 250 steps). Only holaspides were measured for this analysis.

A potential problem with the use of quantitative characters is the correlation of those characters. An analysis of the 13 quantitative characters illustrates weak to moderate correlations ( $r = 0.006$  to  $0.669$ ), several which were significant ( $P < 0.05$ ). The angle of the posterior branch of the facial suture (character 38) was the most strongly correlated to the width and length of the posterior area of the fixigena (characters 33 and 34) and was used to represent both of the latter characters in the analysis.

Thirty-one other multistate characters document a range in character states; for example, furrows depth can range from absent to shallow to moderate depth to deep. The character state was determined by gap coding or comparison to specific taxa listed in

TABLE 1—Characters used by different authors (see text) to distinguish between trilobite taxa. The taxonomic level listed for each character indicates the highest level that an author used that character to distinguish taxa. S = species, G = genus, and F = family. Original weight refers to the weighting of the character states prior to reweighting based on RC; and percent of original is the percent of reweight of the original weight. \*Character not used in analysis.

Number	Character	Others	Sundberg	Original weight	Reweight	% of Original
1	Glabellar length	G	F	250	40	16
2	Glabellar tapering	F	G	200	9	5
3	Glabellar outline	F	F	500	39	8
4	Rounding of frontal lobe	G	G	500	39	8
5	Lateral furrow depth	F	F	500	65	13
6	Bifurcation of S1 and S2	G	F	1,000	0	0
7	Glabellar convexity	F	G	500	64	13
8	Location of deepest portion of axial furrow		G	1,000	63	6
9	Depth of axial furrow	G	F	500	67	13
10	Depth of SO	G	G	500	429	86
11	Occipital node	G	S	1,000	0	0
12	Occipital ring effacement	G	F	1,000	375	38
13	SO flexure			1,000	67	7
14	Occipital ring length	G	G	250	11	4
15	Preglabellar length	F	G	250	20	8
16	Border convexity	F	S	333	178	53
17	Anterior border tapering	G	F	500	41	8
18	Anterior border furrow curvature	G	F	333	15	5
19	Anterior border slope	G	G	500	37	7
20	Anterior border furrow depth	F	F	333	103	33
21	Anterior border furrow boss	G	G	500	8	2
22	Anterior border furrow secondary furrow		G	1,000	300	30
23	Median inbend	G	G	500	0	0
24	Broad inbend	G	S	1,000	333	33
25	Plectrum		F	1,000	1,000	100
26	Dorsal arching of anterior border		S	500	57	11
27	Fixigenal area elevated	F	G	333	52	16
28	Fixigenal width	G	F	250	5	2
29	Slope of anterior region of fixigena	G	F	500	77	15
30	Curvature of fixigena	G	G	1,000	25	3
31	Posterior border widens distally		G	1,000	22	2
32	Posterior border furrow extends to suture		G	1,000	111	11
33	Posterior area of fixigena length*	G	F	—	—	—
34	Posterior area width*	G	F	—	—	—
35	Anterior branch of facial suture direction	F	F	250	17	7
36	Anterior branch of facial suture bowing		G	500	37	7
37	Offset of sutures			1,000	156	16
38	Posterior branch of facial suture direction		G	333	25	8
39	Lateral extent of posterior branch nearly parallel		G	1,000	43	4
40	Palpebral lobe tilt	G	G	500	56	11
41	Palpebral lobe length	F	G	333	6	2
42	Palpebral lobe width		G	333	8	2
43	Palpebral lobe curvature	G	G	500	69	14
44	Direction of eye ridge	G	G	250	12	5
45	Eye ridge strength	F	S	500	46	9
46	Fine granules	G	G	1,000	34	4
47	Coarse granules	F	G	1,000	65	7
48	Librigenal spine length	G	G	333	265	80
49	Librigenal spine base width	G	G	500	630	126
50	Librigenal spine curvature		G	500	100	20
51	Border area cross section triangular	G	G	1,000	450	45
52	Librigenal field width	F	S	500	156	31
53	Pleural spine length	G		500	389	78
54	Pleural spine terminations	F	G	1,000	333	33
55	Fulcrum	G	G	1,000	429	43
56	Thoracic segment number	F	S	167	0	0
57	Pygidial outline	G	G	1,000	711	71
58	Rounding of anterolateral corners		G	1,000	22	2
59	Location of anterior corner	F	F	333	363	132
60	Vaulting of pygidium		S	1,000	1,000	100
61	Flat pleural fields	G	S	1,000	429	43
62	Pygidial spine/lobe length	F	S	333	1,000	300
63	Pygidial spines/lobes broad-based or narrow	F	G	1,000	1,000	100
64	Pygidial axis extends to near posterior margin	G	S	1,000	182	18
65	Axial ring number	G	G	333	40	21
66	Wrinkle marks on posterior portion		S	1,000	1,000	100
67	Pleural band development		F	500	61	12
68	Pleural furrows	G	G	1,000	103	10
69	Doubleure behind axis		G	1,000	1,000	100
70	Medial notch		G	500	127	30

Appendix 1. These multistate characters, because they are continuous, were weighted the same as the quantitative characters. Only three multistate characters were not weighted because they did not describe a range from one state to another. These are the location of the deepest portion of the axial furrows (8), pygidial outline (57), and spine/lobe base width (63).

Most multistate characters were treated as ordered based on changes from one state to another during ontogeny or if they represented gradational changes in slope, curvature, or length/width. The multistate characters that were considered unordered involved distinct morphological breaks of nongradational types (8, 57, 63) or involved characters where ontogeny did not support a gradation between states (3, 29, 45).

The characters used in this study are based on what trilobite workers considered important to delineate groups. However, homoplasy is believed to be a prominent feature of Cambrian ptychopariids. To determine which characters were useful in defining a species group and to de-emphasize those characters that display homoplasy, each character was reweighted using the option available through PAUP. Reweighting was done using the rescaled consistency index (RC) and was repeated three times until the cladogram and weights became consistent.

Cladograms were generated using PAUP's heuristic search with random addition of taxa (1,000 repetitions) and monophyletic in-group rooting (Swofford, 2003). ACCTRAN optimization was employed. Species with two or more states for a character had this character treated as polymorphisms instead of as an unknown state. Appendix 2 lists the character states for each species.

#### RESULTS

The analysis yielded a single most-parsimonious cladogram with a tree length of 64,524 steps, consistency index of 0.463, homoplasy index of 0.639, rescaled consistency index of 0.355, and retention index of 0.767 (Figs. 1, 2). The apomorphic changes at the nodes are listed in Appendix 3. In these results, the particular character numbers (Appendix 1) are listed in brackets with its state(s) in parentheses.

*Reweighting of characters.*—Through the iterative reweighting, four characters had their weights reduced to zero (Table 1) indicating that they were not useful in constructing clades. These characters were the bifurcation of S1 and S2 [6], occipital node [11], median inbend of anterior border furrow [23], and thoracic segment number [56]. An additional 51 characters had their weights reduced by 50 percent or more (Table 1), suggesting that these characters are of reduced importance in delineating clades in the kochaspids trilobites. Even though these characters had reduced weights, many of them still played an important role as apomorphic characters.

Eight characters maintained or exceeded 100 percent of their original weight. These characters include the presence of a plectrum [25], librigenal spine base width [49], location of the anterior corner of the pygidium [59], vaulting of the pygidium pleural fields [60], pygidial spine or lobe length [62] and basal width [63], wrinkle marks on posterior portion of pygidium [66], and the presence of the doublure behind axis [69]. Characters 25 and 66 are only found in two or three species of *Hadrocephalites*, which is why they maintained their original weight. In addition to these eight characters, another five characters had their weights adjusted to between 50 to 100 percent of their original weight (Table 1).

*Useful characters.*—Thirty-six cranidial, five librigenal, three thoracic, and 12 pygidial characters were used to characterize taxonomic groups. These character states did not necessarily define nodes in the cladogram, but represent common character states of the clade and thus can be used to characterize or typify a clade. Most of the apomorphic characters states are not used to

characterize the clades because they commonly display a considerable amount of changes and reversals (see below) within the clade they help define.

Thirty cranidial, librigenal, thoracic, and pygidial characters were useful in characterizing the larger clades in this analysis. Nineteen were cranidial features, including characters of the glabella (length [1], tapering [2], depth of the S1 and S2 [5], and axial furrow outline [3] and location of the deepest portion [8]), anterior border (tapering [17], furrow curvature [18], slope [19], interborder furrow [22]), fixigenae (ocular region slope [27], and anterior area slope [29]), posterior border (widening [31]), facial suture (direction of the anterior [35] and posterior branches [38]), bowing of anterior branch [36], and offset [37]), palpebral lobes (curvature [43]), and ocular ridges (direction [44]) and coarse granules [47]. Two important librigenal features were characters of the librigenal spines (base width [49]) and border (triangular cross section [51]). An important thoracic feature was the pleural rounding [54]. Pygidial features included the anterolateral corners (rounding [58] and position [59]), spine length [62], axis (length [64] and number of rings [65]), furrow development [68], double behind axis [69], and medial notch [70].

Twenty-six additional characters were also useful in characterizing genera and smaller clades. Seventeen were cranidial features, including characters of the glabella (convexity [7], rounding of the frontal lobe [4], flexure of the SO [13], depth of axial furrows [9] and SO [10], and occipital ring length [14]), preglabellar field (length [15]), anterior border (convexity [16], furrow depth [20], and dorsal arching [26]), fixigenae (width [28] and curvature [30]), palpebral lobe (tilting [40], length [41], and width [42]), ocular ridge (strength [45]), and granules (fine [46]). Three additional librigenal characters (librigenal area width [52] and spine length [48] and curvature [50]) were important for defining smaller clades. Two additional thoracic features included pleural terminations length [53] and the fulcrum development [55]. Four additional pygidial features of importance included vaulting of pygidium [60], pleural field convexity [61], spine base width [63], and pleural band development [67].

*Kochaspid clade.*—Palmer (*in* Palmer and Halley, 1979, p. 99) characterized the kochaspids by their coarse granular ornamentation [47(1)], prominently tapered glabellae [2(0,1)] that tend to be slightly concave opposite of the second pair (S2) of lateral glabellar furrows [3(1)], and with several pairs of moderately to strongly developed lateral glabellar furrows [5(1,2)]. The distribution of these characters in the cladogram (Fig. 1) illustrates a stepwise addition of these character states. Most of these states are present in *Caborcella*, *Hadrocephalites*, *Kochiella*, *Kochiellina*, *Nyella*, and *Tonopahella*, with one or two states found within some species of *Eokochaspis*, *Kochina*, and *Kochaspis*. Changes at node 118 included the presence of axial furrows being slightly concave in outline [3(1)]. Node 113 included the presence of moderately to strongly developed lateral glabellar furrows [5(1,2)]. The presence of coarse granules [47(1)] occurred at three nodes. The presence of strongly tapered glabella [2(0,1)] occurred in two groups in the clade.

Placing the morphological limits of the kochaspids based on the criteria prescribed by Palmer and the cladogram is difficult. Clearly those taxa above node 114 have most of the criteria. This would include *Amecephalus*, *Caborcella*, *Hadrocephalites*, *Kochaspis*, *Kochiella*, *Kochiellina*, *Kochina*, *Nyella*, *Tonopahella*, *Eokochaspis nodosa* (type species), *E. piochensis*, and *E. cabinnensis*. Other *Eokochaspis* species would not be included. However, the branch lengths between *E. longspina*, *E. delamarensis*, *E. metalaspis*, and *Amecephalites sundbergi* are relatively small (Fig. 2) and these taxa may just represent the more primitive forms of kochaspids and should also be included into the clade. The placement of taxa in the miscellaneous clade (Fig. 2) is more

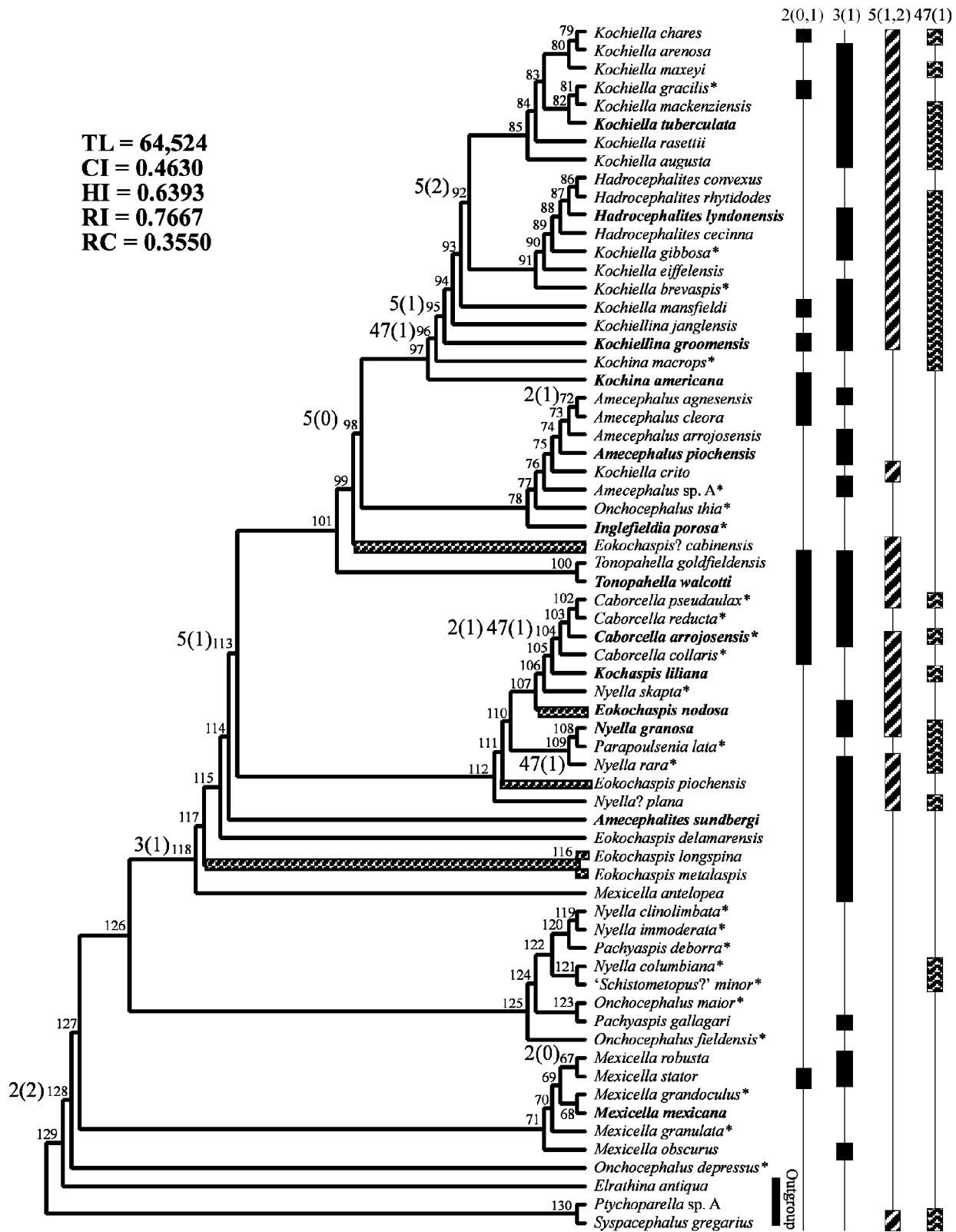


FIGURE 1.—The most parsimonious tree showing the distribution of character states considered by Palmer (in Palmer and Halley, 1979) as important in recognizing the kochaspid: 1) coarse granular ornamentation [47(1)], 2) prominently tapered glabella [2(0,1)], 3) axial furrows slightly concave opposite of the second pair (S2) of glabellar furrows [3(1)], and 4) moderately to strongly developed glabellar furrows [5(1,2)]. Stippled bars in the cladogram are representatives of *Eokochaspis* Sundberg and McCollum, 2000. Apomorphic character changes at nodes are listed in Appendix 3. An asterisk (\*) by a species' name indicates that it is only known from cranidia. Taxa listed in bold print are type species.

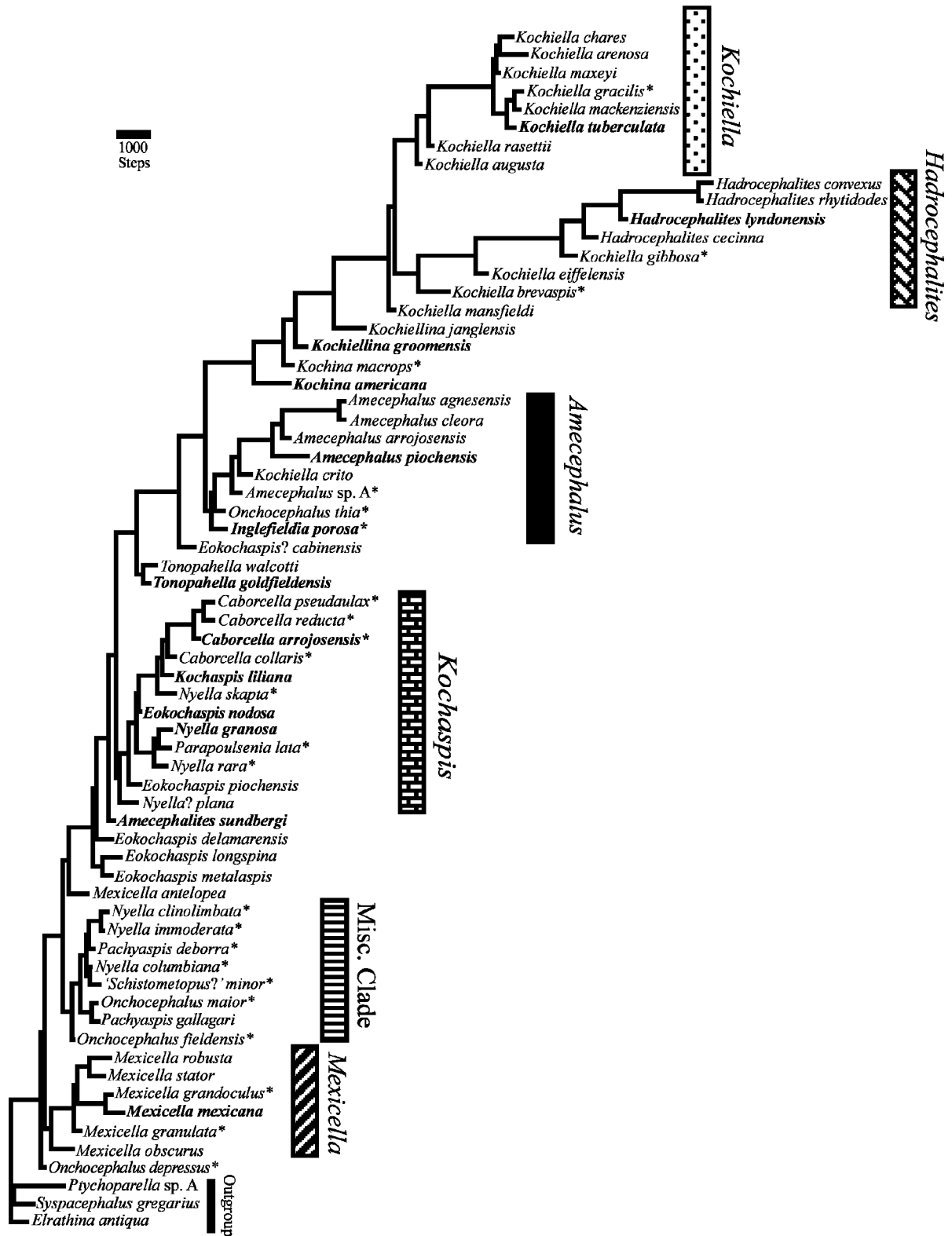


FIGURE 2—Phylogram showing the branch lengths between nodes and the major clades discussed in the text. An asterisk (\*) by a species' name indicates that it is only known from cranidia. Taxa listed in bold print are type species.

questionable, although the branch lengths leading to this clade are also relatively small.

*Other clades and subclades.*—A significant clade is the *Mexicella* clade, which is the sister group to the kochaspids. Within the kochaspid clade are the *Kochaspis*, *Hadrocephalites*, *Amecephalus*, and *Kochiella* subclades. Each clade is named for its prominent genus, with the exception of the *Kochaspis* clade. This clade is named for the type species *Kochaspis liliana*. These clades are discussed below as well as the nodes that link them together. Note that the apomorphic states that define the clades almost always vary within the clades. Thus, also presented below are the character states that typify most or all taxa in the clade.

The *Mexicella* + kochaspid clade (node 127) is defined by the apomorphic states: moderately short glabella [1(1)], moderate length occipital ring [14(2)], moderate curvature of the anterior border furrow [18(2)], posterior border widened distally [31(1)], direction of the anterior branch nearly parallel [35(2)], and a moderately posterolaterally direction of the ocular ridge [44(2)]. This clade can be characterized by the common occurrence of the short to moderately short glabella [1(0,1)], moderately tapered glabellar [2(1,2)], moderately strong curvature of the anterior border furrow [18(2)], nearly parallel direction of the anterior branch [35(2)], moderately to strongly posterolaterally directed ocular ridge [44(1,2)], pointed thoracic pleural terminations [54(1)], and anterolateral corners of the pygidium next to axial end or posterior [59(2,3)].

The *Mexicella* clade (node 71) is defined by the apomorphic states: shallow axial furrows [9(0)], strongly curved anterior border furrow [18(3)], downturned anterior border [19(2)], flat to nearly flat curvature of the fixigena [30(0)], short palpebral lobes [41(0)], and three pygidial rings [65(3)]. Character states that typify the clade are a moderately short length glabella [1(1)], moderately rounded frontal lobe [4(2)], low glabellar convexity [7(0)], shallow axial furrows [9(0)], shallow SO [10(0)], nontapering anterior border [17(0)], strongly curved anterior border furrow [18(3)], downturned anterior border [19(2)], very shallow anterior border furrow [20(0)], no dorsal arching of anterior border [26(0)], moderate downsloping of the anterior area of the fixigena [29(1)], flat to nearly flat curvature of the fixigena [30(0)], moderate to large angle of the posterior branch [38(2,3)], level palpebral lobes [40(0)], slight curvature of the palpebral lobe [43(0)], weak to absent ocular ridge [45(2)], no fine granules [46(0)], and absent or nearly absent librigenal spine [48(0)].

A clade of miscellaneous cranidia occurs as a sister group to the kochaspids. This clade consists of *Nyella clinolimbata*, *N. columbiana*, *N. immoderata*, *Onchocephalus fieldensis*, *O. maior*, *Pachyaspid deborra*, *P. gallagari*, and ‘*Schistometopus?*’ *minor*. Most of these taxa are only known from cranidia, and it is apparent from the discussions above that librigenal, thoracic, and pygidial characters are also needed to assess accurately the placement of these species. Without this morphological data, this clade may be an artificial grouping. Presently this clade (node 125) is defined by the apomorphic states: moderately tapered anterior border [17(2)], moderately deep anterior border furrow [20(2)], and strong pygidial median notch [70(2)]. This clade can be characterized by the straight axial furrow outline [3(0)], location of deepest portion of axial furrow next to L1 [8(0)], moderately tapered anterior border [17(2)], moderately deep anterior border furrow [20(2)], slight dorsal arching of anterior border [26(1)], downsloping of the fixigenal area [27(0)], moderate downsloping of the anterior area of fixigena [29(1)], and slight curvature of fixigena [30(1)].

*Eokochaspis* spp., *Mexicella antelopea*, and *Amecephalites sundbergi* form the basal members to the broader *Kochaspis* + *Amecephalus* + *Hadrocephalites* + *Kochiella* clade (node 118), which has the apomorphic states: slightly concave axial furrow

outline [3(1)], weak frontal area swelling [21(1)], strong downsloping of the anterior area of the fixigena [29(2)], large angle of the posterior branch of the facial suture [38(3)], and no fine granules [46(0)].

The *Kochaspis* + *Amecephalus* + *Hadrocephalites* + *Kochiella* clade (node 113) is defined by the apomorphic states: moderate depth of the S1 and S2 furrows [5(1)], no frontal swelling [21(0)], slight dorsal arching of the anterior border [26(1)], slight curvature of fixigena [30(1)], anterior branch slightly convergent [35(1)] and slightly bowed [36(1)], and moderately small angle of the posterior branch of the facial suture [38(1)]. This clade can be characterized by the slightly concave axial furrow outline [3(1)], deepest portion of the axial furrows adjacent to L2 and L3/L4 [8(1,2)], level or slightly upsloping ocular regions [27(1,2)], palpebral lobes with moderate to strong curvature [43(1,2)], and moderate to broad-based librigenal spines [49(1,2)].

The *Kochaspis* subclade (node 112) contains *Caborcella*, *Eokochaspis nodosa*, *E. piochensis*, *Kochaspis*, and *Nyella* and is defined by the apomorphic states: nontapering anterior border [17(0)] and strong dorsal arching of the anterior border [26(2)]. Character states that typify the clade are the moderately long [1(2)] and moderately convex glabella [7(1,2)], moderately long occipital ring [14(2)], slight to strong dorsal arching of the anterior border [26(1,2)], strong downslope of the anterior region of the fixigena [29(2)], moderately large angle of the posterior branch of the facial suture [38(2)], moderate wide [42(2)] and moderately curved palpebral lobes [43(1)], moderate width librigenal field [52(1)], short termination to the thoracic pleura [53(0)], rounded anterolateral corners of the pygidium [58(0)] located at axial midlength [59(1)], and moderate to strong pygidial medial notch [70(1,2)].

The *Amecephalus* + *Hadrocephalites* + *Kochiella* clade (node 101) is defined by the apomorphic states: triangular cross section of the librigenal border [51(1)] and wide and librigenal field [52(2)]. This clade can be characterized by the moderate depth to deep S1 and S2 [5(1,2)], nontapering anterior border [17(0)], slightly to moderately curved anterior border furrow [18(0,1)], anterior border secondary furrow [22(1)], slight to moderate downsloping of the anterior area of the fixigena [29(0,1)], uniform width posterior border [31(0)], low-angle direction of posterior branch [38(0,1)], broad-based librigenal spine [49(2)], triangular cross section of the librigenal border [51(1)], sharply rounded pygidial anterolateral corners [58(1)], and three to four pygidial axial rings [65(3,4)]. *Hadrocephalites* differs from the remaining clade in characters 22, 29, 38, 49, 51, and 58.

The *Amecephalus* subclade (node 78) has the apomorphic states: deepest portion of the axial furrows located next to L1 [8(0)], nontapering anterior border [17(0)] with no dorsal arching [26(0)], moderately wide fixigenae [28(2)], and moderately long [41(2)] and narrow [42(0)] palpebral lobes. Character states that typify the clade are the moderately tapered [2(1)] and low convexity glabella [7(0)]; shallow S1 and S2 [5(0)]; moderately long preglabellar area [15(2)]; concave [16(3)], nontapering [17(0)], and upturned anterior border [19(0)] with no dorsal arching [26(0)]; very shallow anterior border furrow [20(0)] with moderate curvature [18(1)]; slightly upsloping [27(1,2)] and flat fixigenal area [30(0)]; moderate downslope of the anterior region of the fixigena [29(1)]; sutures are not offset [37(0)]; moderately long to long [41(2, 3)] and narrow [42(0)] palpebral lobes; moderately posterolaterally directed ocular ridge [44(2)], fine granules [46(1)]; no coarse granulation [47(0)]; slightly curved librigenal spine [50(1)], triangular cross section of the librigenal border [51(1)]; fulcrum absent [55(1)]; three pygidial axial rings [65(3)]; and weak pygidial median notch [70(1)].

The *Hadrocephalites* + *Kochiella* clade with *Kochiellina* and

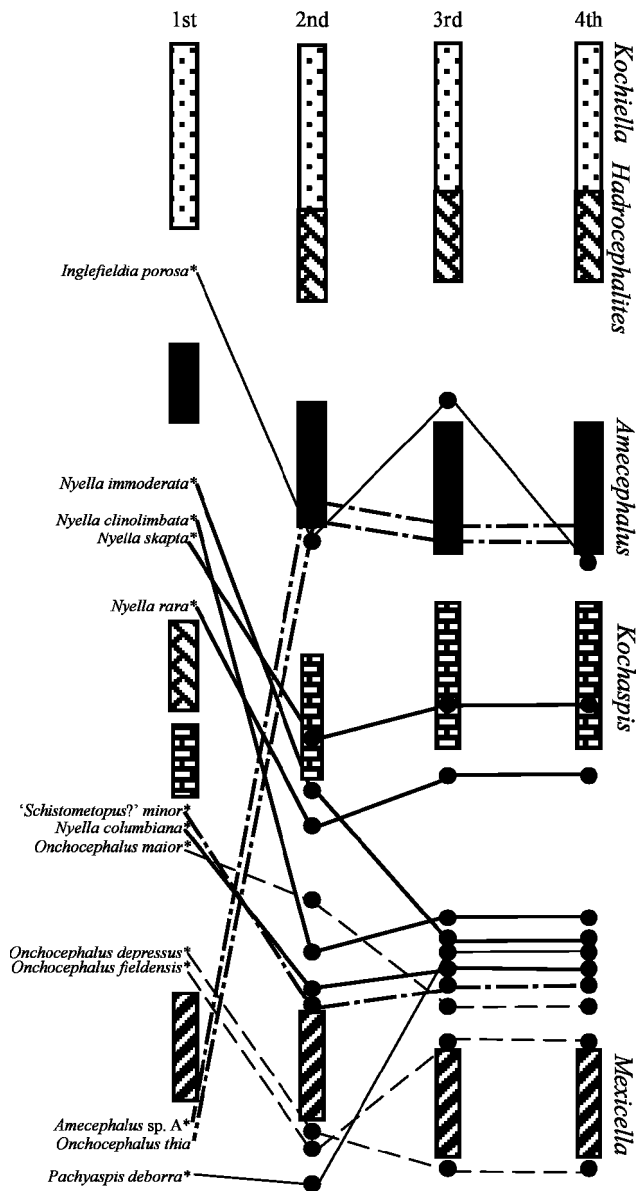


FIGURE 3—The change in distribution of the *Kochiella* C. Poulsen, 1927, *Amecephalus* Walcott, 1924, *Hadrocephalites* Sundberg and McCollum, 2002, *Kochaspis* Resser, 1935, and *Mexicella* clades in the four different iterations of the cladistic study. Also shown are several species known only from cranidia (\*) and how they shifted position during the different studies.

*Kochina* in the basal positions (node 97) is defined by the apomorphic states: slightly curved anterior border furrow [18(0)], slightly upsloping fixigenal area [27(2)], lateral extent to posterior branches not parallel [39(0)], wide palpebral lobes [42(2)], pygidial axis does not extend to near posterior margin [64(1)], doublure behind axis [69(0)], and no pygidial median notch [70(0)]. Character states that typify the clade are the level anterior border [19(1)], slightly upsloping fixigenal areas [27(2)], offset of the facial suture [37(1)], coarse granules [47(1)], pygidial axis that does not extend to posterior margin [64(1)], doublure behind axis [69(0)], and no pygidial median notch [70(0)].

The restricted *Hadrocephalites* + *Kochiella* subclade (node 92) is defined by the apomorphic states: moderately rounded frontal

lobe [4(1)], deep S1 and S2 [5(2)], posterior border widens distally [31(1)], slight bowing of the anterior branch of the facial suture [36(1)], and moderately long [41(2)] and moderately narrow [42(1)] palpebral lobes. Character states that typify the clade are deep S1 and S2 [5(2)], location of the deepest portion of axial furrow at L3/L4 [8(2)], slight bowing of the anterior branch of the facial suture [36(1)], strongly curved palpebral lobes [43(2)], pygidial anterolateral corners located posterior to axis [59(3)], pygidial spine or lobe present [62(1, 2, 3)], and strong to moderate development of the pleural furrows [68(0)].

The *Hadrocephalites* subclade (node 91) contains *Hadrocephalites* and some *Kochiella* species and is defined by the apomorphic states: moderately long glabella [1(2)], strong ocular ridge [45(0)], no triangular cross section of the librigenal border area [51(0)], and moderate width of librigenal field [52(1)]. Character states that typify the clade are moderately long to long glabella [1(2,3)], strong glabellar convexity [7(2)], deep axial furrows [9(2)], moderately deep anterior border furrow [20(2)], interborder furrow absent [22(0)], strong downslope of anterior region of fixigena [29(2)], posterior border widens distally [31(1)], strong bowing of anterior branches of facial suture [36(2)], moderate angle of the posterior branch of facial suture [38(1,2)], moderately narrow palpebral lobe [42(1)], strong ocular ridges [45(0)], moderate width of librigenal spine [49(1)], librigenal border not triangular in cross section [51(0)], moderate width of librigenal field [52(1)], subrectangular and transversely wide pygidium [57(1)], moderate to long pygidial spines [62(2,3)], narrow-based pygidial spines [63(1)], pygidial axis extends to near margin [64(0)], and strongly developed pleural bands [67(0)].

The *Kochiella* subclade (node 85) contains *Kochiella* and has the apomorphic states: moderately long preglabellar length [15(3)], concave anterior border [16(3)], low angle of the posterior branch of the facial suture [38(0)], lateral extent of posterior branches nearly parallel [39(1)], and long pleural spine length [53(2)]. Character states that typify the subclade are the relatively short glabella [1(0)], moderately rounded frontal lobe [4(1)], moderate depth axial furrows [9(1)], flexure of the occipital furrow [13(1)], short to moderately short occipital ring [14(0,1)], relatively long preglabellar area [15(3)], concave anterior border [16(3)] with no dorsal arching [26(0)], flat or nearly flat fixigena [30(0)], slight bowing of the anterior facial sutures [36(1)], slightly curved librigenal spine [50(1)], wide librigenal area [52(2)], poorly developed fulcrum [55(1)], vaulting of the pygidium [60(1)], flat pleural fields [61(1)], and moderately short [62(1)] and broad-based pygidial spines [63(0)].

*Taxonomic comments.*—The different cladistic analyses illustrate the labile arrangement of some taxa within the kochaspid (Fig. 3). This lability is the result of small differences between taxa and some taxa known only from cranidia (Fig. 2). Until more information has been collected and other taxa are added to the analysis, it is probably unwise to establish new taxonomic groups based on this cladistic analysis. However, through the many permutations of this analysis, there are several relevant comments about the taxonomic assignment of some species.

*Eokochaspis* is clearly polyphyletic. When named (Sundberg and McCollum, 2000, 2003a), this group of similar species was envisioned to be the “early kochaspid.” This analysis supports that idea, since the different species are located in the basal positions of four different clades.

*Nyella* is also polyphyletic. *Nyella granosa* (type species) and *N. rara* form sister taxa to *Kochaspis liliana* (type species) and *Caborcella*. *Nyella skapta* falls between *Eokochaspis nodosa* and *Kochaspis liliana*. *Nyella? plana* occurs at the base of the *Kochaspis* clade. *Nyella immoderata*, *N. columbiana*, and *N. clinolimbata* occur in the clade of miscellaneous cranidia. *Nyella columbiana*, *N. immoderata*, *N. clinolimbata*, *Nyella skapta*, and *N.*



*rara* are only known from cranidia and recovery of the other sclerites might change their position in the cladogram. These taxa had the tendency to shift in the cladogram during subsequent analyses (see Fig. 3).

*Onchocephalus* species illustrated by Rasetti (1951, 1957) occur in three different places in the cladogram. *O. depressus* occurs next to the outgroup at the base of the clade. *Onchocephalus maior* and *O. fieldensis* occur in the clade of miscellaneous cranidia adjacent to the *Mexicella* clade. *Onchocephalus thia* occurs near the base of the *Amecephalus* subclade. This again suggests a polyphyletic group, however, all of these species are known only from cranidia. Once again, they have a tendency to be relocated in the cladogram during different analyses (Fig. 3).

This analysis suggests that *Kochiella* is paraphyletic and in part leads to the development of *Hadrocephalites*. *Kochiella mansfieldi* occur at the base of the *Hadrocephalites* + *Kochiella* subclade and *Kochiella brevaspis*, *K. eiffelensis*, and *K. gibbosa* occur at the base of the *Hadrocephalites* subclade. However, the other sclerites of *K. brevaspis* and *K. gibbosa* are unknown. The pygidia of the *Hadrocephalites* and *Kochiella* are both spinose, but differ in appearance. It is possible that if the pygidia of *K. brevaspis* and *K. gibbosa* were known, they would move with *K. eiffelensis* and *K. mansfieldi* back into the *Kochiella* subclade.

*Pachyaspis gallegari* and *P. deborra* were originally used as part of the outgroup. Both taxa were removed from the outgroup to the ingroup by PAUP. They occur in the miscellaneous cranidia clade near the base of the cladogram.

Species that are reassigned to other genera, based on their occurrence in the cladogram are: *Schistometopus collaris* to *Caborcella* and *Syspacephalus obscurus* to *Mexicella*. The reassignment of other taxa is not recommended until more information about these taxa has been uncovered.

#### DISCUSSION

This study provides insight into the underlying problems of classifying the Cambrian ptychopariids. 1) The cladistic analysis shows taxa that are known only from cranidia can be reliably placed, if they contain enough derived characters. Those that cannot be reliably placed can have a significantly negative affect on tree stability and topology. 2) The presence of species assigned to genera based on poorly described type species or poorly preserved specimens usually do not negatively affect the topology. 3) Intermediate forms can show close ties between taxonomic groups, but dealing with the nomenclature of these forms can be problematic. 4) The use of checklists to delineate taxonomic groups is not practical in these Lower to Middle Cambrian trilobites. Each of these underlying problems is elaborated on below.

*Incomplete exoskeletons*.—Twenty-three species used in this analysis are only known from cranidia (those marked with an asterisk in Figs. 1–3). Placement of these taxa in the cladogram can be reliable if the cranidia have enough derived characters to show strong affiliation to a group. Examples of such taxa with significantly derived characters are *Mexicella granulata*, *M. grandoculus*, and *Kochiella gracilis*. *Caborcella* is also known only from cranidia and occurs consistently with *Kochaspis liliana*. The portions of the clade where these taxa occur are separated from the remaining portions by relatively long branches (Fig. 2).

In contrast, some taxa do not contain enough derived cranidial characters to show a strong affiliation to any group. Examples are *Onchocephalus* and *Nyella*. In the progressive reweighting, *Onchocephalus* spp., *Nyella skapta*, and *N. columbiana* had a tendency to shift positions in the cladogram (Fig. 3). In addition, *Inglefieldia porosa* (type species) also shifts within the *Amecephalus* + *Hadrocephalites* + *Kochiella* clade. (Note that *Inglefieldia affinis*, *I. inconspicua*, *I. groenlandia*, *I. discreta*, and *I. planilimbata* named by C. Poulsen [1927] have only minor differences to *I.*

*porosa* [based on the observations of plaster casts of type specimens] and are considered here as junior synonyms.) If the other sclerites of these species were better known, then their placement in the cladogram could significantly change. Given the short branch lengths linking the major clades within this cladogram (Fig. 2), this change in position could in turn change the position of the major clades as seen between the first and second iterations (Fig. 3).

*Type species*.—The effect of using poor quality specimens to define type species is illustrated by *Schistometopus* Resser, 1938a. The type species, *S. typicalis* Resser, 1938a, is based on a single internal mold of a partial cranidium that is crushed in shale. Due to the works of Rasetti (1951, 1957) and Palmer and Halley (1979), *Schistometopus* has become recognized as a common lower Middle Cambrian genus in western North America. However, because of the incomplete and poorly preserved type species and the lack of associated sclerites, Sundberg and McCollum (2002) considered *Schistometopus* as nomen dubium. Previous *Schistometopus* species now assigned to *Hadrocephalites* include *H. caria*, *H. cecinna*, and *H. convexus*. ‘*Schistometopus*’ *collaris* occurs in the *Caborcella* clade to which it is reassigned. ‘*Schistometopus*’ *minor* occurs in the basal miscellaneous cranidia clade with species of *Nyella*, *Pachyaspis*, and *Onchocephalus*. In contrast, using the different species of *Schistometopus* would have created problems in a noncladistic phylogenetic analysis or cladistic analyses using representative species or “generic” character states.

*Intermediate forms*.—The kochaspids contain many intermediate forms. *Eokochaspis* represents a very generalized genus that links other genera together, such as *Amecephalus*, *Kochaspis*, *Nyella*, and *Tonopahella*. In the *Amecephalus* + *Hadrocephalites* + *Kochiella* clade, *Kochina* and *Kochiellina* are also intermediate forms that bridge the gap between the subclades. The four species of these two genera form the basal branches of the *Hadrocephalites* + *Kochiella* clade.

Intermediate forms blur the lines between genera and make generic diagnosis difficult. What to do with these intermediate forms is a taxonomic problem. *Eokochaspis* is clearly a polyphyletic group. Do we broaden the definition of other groups to include these generalized forms? For example, should *E. nodosa* and *E. piochensis* be reassigned to *Kochaspis*? What about the three *Eokochaspis* species that form the base of the kochaspid clade or *E. cabinensis* that occurs at the base of the *Amecephalus* + *Hadrocephalites* + *Kochiella* clade? Do we assign them to their nearest neighbor *Amecephalites* or *Tonopahella*, respectively, and acknowledge these two genera as paraphyletic basal groups? Taxonomists will need to make these decisions, but there may be no satisfactory way to pigeon hole these intermediate taxa.

*Checklists*.—This cladogram has a homoplasy index of 0.639 (CI = 0.463), which is not unusually high (Sanderson and Donoghue, 1989), given the number of taxa and character states, plus the fact that this study was an ordered analysis. However, there are few character states that remain consistent in any clade, with most characters having many reversals and state changes. Thus, using a checklist of character states for a taxonomic diagnosis is not practical; there are too many exceptions to the rules. Instead, trilobite taxonomists will need to settle for a list of character states that are *typical* of the group and acknowledge that the absence of a characteristic morphology in a taxon does not preclude its inclusion into a higher taxonomic group.

#### CONCLUSIONS

The taxonomy of Lower and Middle Cambrian ptychopariids is messy. Given the level of homoplasy demonstrated in this analysis, using simple checklists of character states to identify taxonomic groups can only work if a considerable amount of latitude

is given when a species or genus does not completely fit the mold. An example is *Amecephalus*, which clearly falls within the more derived kochaspids, but was never included in Palmer's (*in* Palmer and Halley, 1979) original concept or by Sundberg and McCollum (2000, 2002, 2003a).

This study shows that 64 different characters are useful in delineating clades and subclades. However, very few apomorphic character states remained consistent in these clades. A more practical approach is listing character states that *typify* or are common within the clade. Fifty-six characters were useful in typifying clades, however these characters were not present in all members of the clade.

Whereas intermediate forms may provide links between taxa in a phylogenetic analysis, how to deal with their nomenclature is a taxonomic problem. These taxa do not fall clearly within a generic clade, but at the base of clades. Examples in this study include the basal groups *Amecephalites*, *Eokochaspis*, *Kochiellina*, *Kochina*, and *Tonopahella*. *Eokochaspis* is an excellent example, this polyphyletic taxon occurring at the base of the kochaspid, *Kochaspis*, and *Amecephalus* + *Hadrocephalites* + *Kochiella* clades.

Delineating suprageneric taxa from the cladogram generated here is inappropriate at this time. The kochaspids appear to be recognizable, but comparison to other groups like Alokistocaridae is needed before naming a new family. Determining the phylogenetic relationships among these ptychopariids is also hindered by the lack of information about the different sclerites for several taxa. Complete knowledge of the sclerites, especially from the less derived taxa (e.g., *Onchocephalus* and *Nyella*), could significantly alter the cladogram.

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## APPENDIX I: CHARACTERS

Linear measurements were made on actual specimens using an eyepiece scale with a binocular microscope (each scale division equal to 0.034 mm) or from photographs using calipers. Angles were measured using a protractor and degrees of arc were measured by overlying photographed specimens with a transparency marked with different degrees of arc. See Sundberg and McCollum (2000, 2002, 2003a) for measurements and abbreviations. For the standard deviation analysis, the number of measured holaspides for each taxon ranged from 1 to 13 (Appendix 2). \* = Characters not used in final cladistic analysis.

1. Glabellar length.—The length from posterior margin of occipital ring to anterior margin of frontal lobe (B<sub>1</sub>) as a percent of cranial length. States.—0 = 56 to 63, 1 = 64 to 71, 2 = 72 to 78, 3 = 79 to 86.
2. Glabellar tapering.—Based on the ratio of the basal glabellar width (K<sub>2</sub>) and the width at the ocular ridges (K<sub>0</sub>) as a percent of K<sub>0</sub> to K<sub>2</sub>. States.—0 = 56 to 62, 1 = 63 to 69, 2 = 70 to 76, 3 = 77 to 82, 4 = 83 to 89.
3. Axial furrow outline.—In plan view, the axial furrows can bow outward (convex), be straight, or bow inward (concave). States.—0 = straight, 1 = slightly concave, 2 = slightly convex.
4. Frontal lobe rounding.—The degree of roundness is based on comparisons made with *Caborcella arrojensis* (see Lochman, 1952, pl. 29, fig. 13; strongly rounded = 0) to *Mexicella robusta* (see Sundberg and McCollum, 2000, fig. 13.1; bluntly rounded = 2). States.—0 = very rounded, 1 = moderately rounded, 2 = bluntly rounded.
5. Depth of S1 and S2 lateral glabellar furrows.—This character is based on a comparison to the axial furrows of the same species or its absence. States.—0 = shallow (shallower than axial furrow, but easily visible), 1 = moderate (slightly shallower than axial furrows), 2 = deep (deep as axial furrows).
6. Bifurcation of the S1 lateral glabellar furrow. States.—0 = absent, 1 = present.
7. Glabellar convexity.—Based on the comparison of the glabellar profile as seen from the anterior margin to that of *Kochiella maxeyi* (see Rasetti, 1951, pl. 13, fig. 7; low = 0) to *Caborcella arrojensis* (see Lochman, 1952, pl. 29, figs. 11, 12; strongly rounded = 2). States.—0 = low, 1 = moderate, 2 = strong.
8. Location of deepest portion of axial furrows.—Determined relative to its adjacent glabellar lobe. States.—0 = L1, 1 = L2, 2 = L3/L4.
9. Depth of axial furrows.—Determined relative to end members: shallow = *Mexicella obscurus* (Palmer and Halley, 1979, pl. 7, figs. 6–12); and deep = *Hadrocephalites convexus* (Rasetti, 1951, pl. 13, figs. 17–22). States.—0 = shallow, 1 = moderate, 2 = deep.
10. Occipital furrow.—Occipital ring have a well-developed to faint occipital furrow (SO) transversely crossing the glabella. Shallow = *Amecephalus piochensis* (see Palmer, 1954, pl. 16, fig. 5), moderate = *Ptychoparella* sp. A (see Blaker and Peel, 1997, fig. 79), deep = *Caborcella arrojensis* (see Lochman, 1952, pl. 14, figs. 1–3). States.—0 = shallow, 1 = moderate, 2 = deep.
11. Occipital node or spine. States.—0 = present, 1 = absent.
12. Occipital ring distinct.—Distinct occipital rings have a well-developed occipital furrow (SO) transversely crossing the glabella. An indistinct ring has the medial portion of the occipital furrow directed posteriorly as in *Amecephalus piochensis* (see Palmer, 1954, pl. 16, fig. 5). States.—0 = nondistinct, 1 = distinct.
13. Occipital furrow flexure.—The medial portion of the occipital furrow (SO) is curved anteriorly. States.—0 = absent, 1 = present.
14. Occipital ring length.—The length from the occipital ring (E) as a percent of cranial length (A<sub>1</sub>). States.—0 = 14 to 17, 1 = 18 to 20, 2 = 21 to 24, 3 = 25 to 27, 4 = 28 to 31.
15. Preglabellar length.—Percentage of length (H) relative to the frontal area length (H + G<sub>1</sub>). States.—0 = 0 to 14, 1 = 15 to 30, 2 = 31 to 45, 3 = 46 to 61, 4 = 62 to 76.
16. Anterior border convexity viewed in sagittal cross section. States.—0 = strongly convex, 1 = convex, 2 = flat, 3 = concave.
17. Anterior border tapering.—This character is based on the comparison to other taxa that do not have tapering borders (0 = not tapering, *Kochiella maxeyi* Rasetti, 1951, pl. 13, figs. 5–8) to those moderately tapered (2 = moderately tapered, *Mexicella granulata* Eddy and McCollum, 1998, fig. 9.5–9.8). States.—0 = not tapering, 1 = slightly tapering, 2 = moderately tapering.
18. Anterior border furrow curvature.—Measured as degrees of arc. This is determined by 1) finding a circle that has the same curvature as the anterior border furrow and 2) determining the number of degrees of this circle defined by the two radii that terminate at the lateral extent of the furrow. The furrow was used instead of the anterior margin due to its greater width and more uniform curvature, thus providing a more accurate measure. States.—0 = 9 to 32, 1 = 33 to 55, 2 = 56 to 79, 3 = 80 to 103.
19. Anterior border slope.—Determined when the distal ends of the posterior area of the fixigenae and the anterolateral corners are oriented on the same horizontal plane. States.—0 = upturned, 1 = level, 2 = downturned.
20. Depth of anterior border furrow.—This is measured relative to comparison to different species and away from plectrums and medial swellings: poorly defined or shallow furrows = *Amecephalus piochensis* (see Palmer, 1954, pl. 16, fig. 5); moderately shallow furrows = *Nyella? plana* (see Sundberg and McCollum, 2003a, fig. 15.1); moderately deep furrows = *Eokochaspis piochensis* (see Sundberg and McCollum, 2000, fig. 12.1–12.3); and deep furrows = *Nyella rara* (see Rasetti, 1951, pl. 15, figs. 21–23). States.—0 = very shallow, 1 = moderately shallow, 2 = moderately deep, 3 = deep.
21. Frontal area swelling in anterior border furrow. States.—0 = absent, 1 = weak, 2 = strong.
22. Interborder furrow in either lateral border or genal spine. States.—0 = absent, 1 = present.
23. Median inbend of the anterior border towards frontal lobe.—This is typically a V-shaped inbend that either touches or approaches the frontal lobe of the glabella. States.—0 = absent, 1 = weak, 2 = strong.
24. Board inbend of the anterior border towards frontal lobe.—This is a broad U-shaped inbend that approaches the frontal lobe of the glabella. States.—0 = absent, 1 = present.
25. Plectrum. States.—0 = absent, 1 = present.
26. Dorsal (transverse) arching of anterior border.—Based on comparison to different species: flat, no arch = *Mexicella mexicana* (see Lochman, 1952, pl. 24, figs. 1–30); slight arch = *Kochina macrops* Rasetti (1951, pl. 19, fig. 19); strongly arched = *Nyella skapta* (see Rasetti, 1951, pl. 13, fig. 4). States.—0 = flat, 1 = slight, 2 = strong.
27. Fixigena area slope.—The slope of the ocular region of the fixigena, dorsally (up) or ventrally (down). States.—0 = downsloping, 1 = level, 2 = slightly upsloping, 3 = strongly upsloping.
28. Fixigenal width.—Measured (Fi) relative to basal glabellar width (K<sub>2</sub>). States.—0 = 41 to 51, 1 = 52 to 62, 2 = 63 to 73, 3 = 74 to 84, 4 = 85 to 96.
29. Downsloping of the anterior area of fixigena.—Determined when the distal ends of the posterior area of the fixigenae and the anterolateral corners are oriented on the same horizontal plane. States.—0 = slight, 1 = moderate, 2 = strong.
30. Curvature of fixigena.—Based on comparison to different species: flat or nearly flat = *Eokochaspis metalaspis* (see Palmer, 1958, pl. 25, fig. 8), slight = *Hadrocephalites convexus* (see Rasetti, 1951, pl. 13, fig. 22). States.—0 = flat/nearly flat, 1 = slight.
31. Posterior border widens distally.—This does not include the initial widening next to the occipital ring. States.—0 = no, 1 = yes.
32. Posterior border furrow extends to suture. States.—0 = yes, 1 = no.

- \*33. Posterior length of fixigena.—Measured ( $L_2$ ) relative to the basal glabellar width ( $K_2$ ).  
States.—0 = 19 to 26, 1 = 27 to 35, 2 = 36 to 43, 3 = 44 to 51.
- \*34. Width of posterior area of fixigena.—Measured ( $L$ ) relative to the basal glabellar width ( $K_2$ ).  
States.—0 = 52 to 68, 1 = 69 to 86, 2 = 87 to 103, 3 = 104 to 121, 4 = 122 to 138, 5 = 139 to 191.
35. Anterior branch of facial suture.—The number of degrees of the angle of suture from the anterior end of the palpebral lobe to the anterior border furrow measured from an exsagittal line from the junction of the suture and the palpebral lobe. Negative degrees indicate convergent sutures, positive degrees indicate divergent sutures.  
States.—0 = -30 to -18, 1 = -17 to -6, 2 = -5 to 7, 3 = 8 to 20, 4 = 21 to 33.
36. Anterior branch of facial suture bowing.—The lateral bowing of the anterior branch of the facial suture between the palpebral lobe and anterior border furrow.  
States.—0 = straight, 1 = slight, 2 = strong.
37. Offsetting of sutures.—Comparison of the points where the anterior branch and the posterior branch meets the palpebral lobe, whether they are in exsagittal alignment or near alignment or offset such as in *Kochiella maxeyi* (see Rasetti, 1951, pl. 13, fig. 5). This character is related to how parallel the palpebral lobes are to the sagittal axis of the cranidia. If parallel, then the sutures are not offset.  
States.—0 = not offset, 1 = offset.
38. Posterior branch of facial suture.—The number of degrees of the angle of suture from the lateral extent of the posterior border furrow to the posterior margin of the palpebral lobe measured from a transverse line from the posterior border furrow.  
States.—0 = 14 to 26, 1 = 27 to 40, 2 = 41 to 53, 3 = 54 to 67.
39. Lateral extent of posterior branches nearly parallel to each other.  
States.—0 = no, 1 = yes.
40. Palpebral lobe tilt.  
States.—0 = level, 1 = slightly tilted up, 2 = strongly tilted up.
41. Palpebral lobe length.—Measured ( $C$ ) relative to the glabellar length ( $B_1$ ).  
States.—0 = 21 to 29, 1 = 30 to 37, 2 = 38 to 46, 3 = 47 to 54.
42. Palpebral lobe width.—Measured ( $C_3$ ) relative to the palpebral length ( $C$ ).  
States.—0 = 20 to 27, 1 = 28 to 36, 2 = 37 to 45, 3 = 46 to 53.
43. Palpebral lobe curvature.—Based on comparison to different species: slight = *Eokochaspis metalaspis* (see Palmer, 1958, p. 25, fig. 11); moderate = *Hadrocephalites convexus* (see Rasetti, 1951, pl. 13, fig. 4); strong = *Kochiella augusta* (see Sundberg and McCollum, 2002, fig. 7.1–7.4).  
States.—0 = slight, 1 = moderate, 2 = strong.
44. Ocular ridge direction.—Measured ( $ER$ ) relative to the sagittal line.  
States.—0 = 58 to 64, 1 = 65 to 71, 2 = 72 to 78, 3 = 79 to 85, 4 = 86 to 92.
45. Ocular ridge strength.—Determined relative to species: strong = *Kochiella brevaspis* (see Sundberg and McCollum, 2002, fig. 8.1, 8.4–8.6) where the ocular ridges are easily visible; moderate = *Kochiella augusta* (Sundberg and McCollum, 2002, fig. 7.1–7.4) where the ocular ridges are slightly developed; and weak or absent = *Eokochaspis delamarensis* (Sundberg and McCollum, 2000, fig. 8.1–8.3, 8.6–8.9) where they are barely visible.  
States.—0 = strong, 1 = moderate, 2 = weak/absent.
46. Fine granules.  
States.—0 = absent, 1 = present.
47. Coarse granules. Some trilobites can contain both fine and coarse granules, or just fine or coarse granules.  
States.—0 = absent, 1 = present.
48. Length of librigenal spine. Determined relative to the librigenal length exclusive of the spine.  
States.—0 = absent/nub, 1 = short (less than 1/2), 2 = moderate (approx. 1/2), 3 = long (approximately the length of librigena).
49. Librigenal spine base width.—Determined relative to species: narrow based (trans.) = *Ptychoparella* sp. A (see Blaker and Peel, 1997, fig. 75); moderate = *Eokochaspis longspina* (Sundberg and McCollum, 2000, fig. 10.5); and wide = *Kochiella augusta* (Sundberg and McCollum, 2002, fig. 7.7).  
States.—0 = narrow, 1 = moderate, 2 = broad.
50. Librigenal spine curvature.—Determined relative to species: straight = *Tonopahella walcotti* (see Sundberg and McCollum, 2000, fig. 15.6); slight = *Eokochaspis longspina* (Sundberg and McCollum, 2000, fig. 10.5); and moderate = *Hadrocephalites rhytidodes* (Sundberg and McCollum, 2002, fig. 12.6).  
States.—0 = straight, 1 = slightly, 2 = moderately.
51. Librigenal border area cross section triangular.  
States.—0 = no, 1 = yes.
52. Librigenal field width.—Determined relative to species: narrow = *Eokochaspis longspina* (Sundberg and McCollum, 2000, fig. 10.5); moderate = *Ptychoparella* sp. A (Blaker and Peel, 1997, fig. 77.7); and wide = *Kochiellina groomensis* (Palmer and Halley, 1979, pl. 8, fig. 4).  
States.—0 = narrow, 1 = moderate, 2 = wide.
53. Thoracic pleural termination length.—The length of the thoracic spine or rounded end.  
States.—0 = short, one thoracic segment length; 1 = moderate, equal to one or two thoracic segment lengths; 2 = long, greater than two segment lengths.
54. Thoracic pleural termination.  
States.—0 = rounded, 1 = pointed.
55. Fulcrum.  
States.—0 = well developed; 1 = poorly developed, little difference in distal and proximal slope of thoracic segment.
56. Number of thoracic segments.  
States.—0 = 14, 1 = 15, 2 = 16, 3 = 17, 4 = 18, 5 = 19, 6 = 20.
57. Pygidial outline.  
States.—0 = suboval, 1 = subrectangular with transversely long axis, 2 = subsquare, 3 = subcircular, 4 = subrectangular with sagittally long axis.
58. Rounding of anterolateral corners.  
States.—0 = rounded, 1 = sharply rounded.
59. Position of pygidial anterolateral corners.—Measured relative to their position to the adjacent position to the axis.  
States.—0 = axial anterior margin, 1 = axial midlength, 2 = axial end, 3 = posterior of axis.
60. Vaulting of pygidium.—Pleural fields are either flat lying (or nearly so) or they are downsloping forming an inverted “V” shape in posterior view.  
States.—0 = absent, 1 = present.
61. Flat pleural fields.  
States.—0 = absent, 1 = present.
62. Pygidial spine/lobe length.—Measured relative to the pygidial length. States are based on gap coding.  
States.—0 = absent, 1 = approximately equal length, 2 = two to three times length, 3 = four or greater times length.
63. Pygidial spine/lobe base width.—States are based on gap coding.  
States.—0 = wide, 1 = narrow.
64. Pygidial axial length.—States are based on gap coding.  
States.—0 = extends to near posterior margin, 1 = does not extend to near posterior margin.
65. Number of pygidial axial rings.  
States.—1 to 5 = number of rings.
66. Wrinkle marks on posterior portion of pleural field.  
States.—0 = absent, 1 = present.
67. Development of pleural bands.—First anterior pleural band not used when determining character state.  
States.—0 = strong if they are wide and have high relief; 1 = moderate if they are easily seen and generally wide; 2 = weak/absent if they are narrow and have low relief.
68. Development of pleural furrows.  
States.—0 = strong/moderate, easily seen, 1 = weak/absent, if difficult to see.
69. Doublure behind axis.  
States.—0 = present, 1 = absent.
70. Median notch.—Determined relative to species: absent = *Hadrocephalites lyndonensis* (see Sundberg and McCollum, 2002, fig. 11.12); weak = *Eokochaspis delamarensis* (Sundberg and McCollum, 2000, fig. 8.13); and strong = *Eokochaspis longspina* (Sundberg and McCollum, 2000, fig. 10.10).  
States.—0 = absent, 1 = weak, 2 = strong.















## APPENDIX 3

Apomorphy list of the node changes in Figure 1. ACCTRAN optimization was used.

- 
- node 67 3(1), 14(1), 42(2), 52(2), 70(0)  
node 68 1(0), 8(2), 41(1), 59(2), 64(1), 65(2), 70(2)  
node 69 15(4), 17(0), 46(0)  
node 70 4(2), 10(0), 20(0), 29(0), 42(0), 58(0)  
node 71 9(0), 18(3), 19(2), 30(0), 41(0), 65(3)  
node 72 2(1), 8(2), 35(4), 53(2), 57(3), 59(0), 70(0)  
node 73 9(0), 40(0), 52(1)  
node 74 1(0), 4(2), 8(1), 10(0), 12(1), 36(1)  
node 75 20(0), 31(1), 35(3), 38(0), 39(0)  
node 76 3(1), 7(0), 14(1), 16(3), 19(0)  
node 77 30(0), 45(2), 46(0)  
node 78 8(0), 17(0), 26(0), 28(2), 41(2), 42(0)  
node 79 4(2), 29(0)  
node 80 5(2), 18(0), 28(3)  
node 81 8(0), 20(1), 27(3)  
node 82 15(1), 24(1), 38(1)  
node 83 13(1), 39(0), 41(1), 42(2), 56(2), 57(4), 60(1), 67(1)  
node 84 1(0), 5(1), 14(0), 20(0), 31(0), 68(0)  
node 85 15(3), 16(3), 38(0), 39(1), 53(2)  
node 86 25(1), 41(1), 44(0), 48(3), 62(3)  
node 87 4(0), 15(1), 28(0), 35(2), 66(1)  
node 88 1(3), 7(2), 9(2), 16(1), 18(0), 27(2), 28(1), 36(2), 39(1), 43(1)  
node 89 20(2), 29(2), 30(1), 35(1), 44(2), 62(2), 63(1), 64(0), 67(0)  
node 90 22(0), 27(1), 40(1), 49(1), 50(2), 58(1), 61(0), 68(0)  
node 91 1(2), 45(0), 51(0), 52(1)  
node 92 4(1), 5(2), 31(1), 36(1), 41(2), 42(1)  
node 93 8(2), 14(1), 21(0), 27(2), 28(2), 30(0), 43(2), 59(3), 62(1)  
node 94 26(0), 44(1), 57(1), 59(2)  
node 95 3(1), 4(2), 5(1), 7(0), 14(3), 17(0), 18(1), 21(1), 27(1)  
node 96 16(2), 37(1), 40(2), 47(1), 56(1), 61(1)  
node 97 18(0), 27(2), 39(0), 42(2), 64(1), 69(0), 70(0)  
node 98 5(0), 31(0), 49(2), 58(0), 65(3)  
node 99 3(0), 15(2), 22(1), 35(2), 36(0), 53(1), 55(1)  
node 100 2(1), 18(0), 39(0), 41(2), 42(0), 44(3), 50(0)  
node 101 51(1), 52(2), 56(2)  
node 102 4(2), 5(2), 27(2), 31(0), 41(1), 43(2)  
node 103 2(0), 3(1), 15(3), 16(3), 19(0), 20(0), 35(2), 36(0)  
node 104 4(0), 7(2), 8(2)  
node 105 2(1), 13(1), 23(0), 47(1)  
node 106 3(0), 10(2), 36(2), 45(1)  
node 107 9(2)  
node 108 8(0), 13(1)  
node 109 5(0), 16(0), 18(2), 28(0), 35(0), 44(1), 45(2), 47(1), 58(0), 65(3), 67(1)  
node 110 15(2), 17(1), 23(1), 38(2), 42(2), 70(2)  
node 111 1(2), 20(2), 29(2), 41(0), 45(0)  
node 112 17(0), 26(2)  
node 113 5(1), 21(0), 26(1), 30(1), 35(1), 36(1), 38(1)  
node 114 7(1), 8(1), 18(1), 27(1), 29(1), 45(1), 46(1)  
node 115 38(2), 43(1)  
node 116 18(3), 20(2), 52(0)  
node 117 30(0), 40(1), 49(1)  
node 118 3(1), 21(1), 29(2), 38(3), 46(0), 56(1)  
node 119 5(1), 9(2), 13(1), 38(1), 40(0), 41(2), 42(0), 43(1)  
node 120 39(0), 44(3)  
node 121 2(3), 14(1), 47(1)  
node 122 1(2), 18(1), 35(1), 36(1), 58(0), 67(1)  
node 123 3(1), 40(2), 42(2), 44(1), 64(1), 65(1)  
node 124 7(1), 15(2), 26(1), 40(1), 45(1)  
node 125 17(2), 20(2), 70(2)  
node 126 48(2)  
node 127 1(1), 14(2), 18(2), 31(1), 35(2), 44(2)  
node 128 2(2), 6(1), 7(0), 18(1), 35(1), 39(1), 41(1), 46(1), 54(1), 59(1)  
node 130 6(1), 26(1), 46(1)  
*Amecephalites sundbergi* 1(0), 21(2), 28(2), 40(2), 67(1)  
*Amecephalus agnesensis* 14(2), 15(3), 19(1), 28(4), 31(0), 36(2)  
*Amecephalus arrojensis* 1(1), 30(1), 35(2), 36(0), 38(1, 2), 39(1), 46(1)  
*Amecephalus cleora* 3(0), 28(1), 40(1), 45(1), 56(3)  
*Amecephalus piochensis* 15(3), 27(2), 31(0), 43(2), 45(1), 48(3), 50(2), 56(5), 58(1), 59(2), 67(1)  
*Amecephalus* sp. A 18(2, 3), 26(1), 30(1), 38(2), 40(0), 43(0)  
*Caborcella arrojensis* 17(0), 26(1), 42(1), 44(3), 46(0)  
*Caborcella collaris* 1(3), 13(0), 14(1), 18(0), 23(1), 27(0), 35(0)  
*Caborcella pseudaulax* 1(1), 9(1), 15(4), 18(2), 28(2), 30(0), 40(2), 45(0)  
*Caborcella reducta* 15(0), 19(1), 21(1), 32(1), 47(0)  
*Elrathina antiqua* 2(4), 7(2), 8(1), 17(2), 26(1), 31(1), 38(3), 42(3), 65(1), 70(2)  
*Eokochaspis delamarensis* 20(0), 48(1), 50(0)  
*Eokochaspis longspina* 21(2), 30(1), 45(1), 48(3), 58(0), 65(1), 70(2)  
*Eokochaspis metalaspis* 7(1), 8(1), 15(1), 17(2), 21(0), 23(2), 67(1)  
*Eokochaspis nodosa* 30(0), 38(3)
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## APPENDIX 3

Continued.

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- Eokochoaspis piochensis* 16(2), 18(0), 36(0), 50(0)  
*Eokochoaspis? cabinensis* 7(0), 8(2), 19(2), 21(1), 27(0), 41(0), 43(0), 44(0, 1), 52(1)  
*Hadrocephalites cecinna* 14(2), 16(0), 20(3), 45(1), 65(4)  
*Hadrocephalites convexus* 5(1), 15(0), 27(1), 37(0), 39(0), 65(2)  
*Hadrocephalites lyndonensis* 18(1), 19(2), 30(0), 42(2, 3), 43(2)  
*Hadrocephalites rhytidodes* 1(1, 2), 35(3), 38(0), 42(0)  
*Inglefieldia porosa* 13(1), 20(2), 36(1), 37(1), 43(2)  
*Kochaspis liliana* 1(1), 17(0), 26(1), 27(2), 30(0), 43(2)  
*Kochiella arenosa* 28(1), 44(0), 57(3), 65(2)  
*Kochiella augusta* 18(2), 27(1), 28(0, 1), 58(1)  
*Kochiella brevaspis* 7(1), 18(2), 27(3), 57(2), 65(2)  
*Kochiella chares* 2(1), 3(0), 8(0), 20(1), 27(1), 41(2, 3), 44(2, 3), 58(1), 65(4)  
*Kochiella crito* 3(2), 4(0), 5(1), 13(1), 29(0), 35(4), 46(1)  
*Kochiella eiffelensis* 3(0), 5(1), 8(0), 19(0), 31(0), 36(0), 47(0)  
*Kochiella gibbosa* 1(1), 4(2), 8(1), 17(1), 21(2), 26(2), 38(2), 40(2)  
*Kochiella gracilis* 2(1), 7(1), 15(2), 31(1), 38(0), 41(0), 44(0), 47(0)  
*Kochiella mackenziensis* 5(2), 9(0), 14(1), 41(2, 3), 44(2)  
*Kochiella mansfieldi* 1(0), 2(1), 14(0), 18(0), 29(0), 44(2)  
*Kochiella maxeyi* 36(2), 45(0)  
*Kochiella rasettii* 5(0), 36(2)  
*Kochiella tuberculata* 11(0), 16(2), 45(0)  
*Kochiellina groomensis* 2(1), 41(0), 48(1), 65(4)  
*Kochiellina janglensis* 7(1), 9(2), 21(2), 22(0), 29(2), 37(0), 40(0), 45(2), 67(1)  
*Kochina americana* 2(1), 9(2), 11(0), 14(1), 15(1), 19(2), 24(1), 38(0), 53(0), 56(3), 67(1), 68(0)  
*Kochina macrops* 4(0), 29(2), 30(0), 35(0), 36(2), 41(3)  
*Mexicella antelopea* 1(2), 14(1), 17(0), 19(2), 26(1), 36(1), 42(0), 52(2), 65(1), 70(0)  
*Mexicella grandocular* 14(3), 27(1), 28(2), 38(1), 41(2), 43(1)  
*Mexicella granulata* 8(1), 17(2), 18(1, 2), 27(1), 44(3)  
*Mexicella mexicana* 7(1), 9(1), 12(1), 44(3)  
*Mexicella obscurus* 3(1), 16(2), 26(2), 28(0), 38(3), 65(4), 67(0), 68(0)  
*Mexicella robusta* 15(2, 3), 29(1), 30(1), 36(1), 55(1), 58(1)  
*Mexicella stator* 2(0), 26(1), 31(0), 54(0), 56(6)  
*Nyella clinolimbata* 19(2), 26(2), 27(1), 28(2), 36(2)  
*Nyella columbiana* 18(2), 23(1), 41(0)  
*Nyella granosa* 4(2), 5(1), 14(1), 26(0), 30(0), 35(1), 38(0), 45(1)  
*Nyella immoderata* 23(2), 30(0), 36(0)  
*Nyella rara* 17(0), 18(3), 19(0), 20(3), 23(0), 27(0), 36(2), 40(2), 41(1, 2)  
*Nyella skapta* 5(2), 15(1), 16(0), 17(2), 20(3), 39(0), 43(0)  
*Nyella? plana* 21(1), 41(2), 47(1), 48(3), 67(1), 68(0)  
*Onchocephalus depressus* 15(2), 19(0), 28(0), 45(1)  
*Onchocephalus fieldensis* 19(0)  
*Onchocephalus maior* 9(2), 14(0, 1), 19(0), 23(1), 31(0), 41(0)  
*Onchocephalus thia* 2(3), 7(2), 17(2), 19(2), 27(0), 28(0)  
*Pachyaspis deborra* 8(1), 15(3), 18(0), 31(0), 38(3)  
*Pachyaspis gallagari* 4(2), 28(0), 38(1), 43(1), 45(0)  
*Parapoulsenia lata* 3(0), 7(2), 17(2), 18(1), 23(2), 36(0), 40(0), 43(0), 44(2, 3)  
*Prychoparella* sp. 20(2), 32(1), 52(2), 56(3), 65(3), 67(1), 68(0)  
*'Schistometopus?' minor* 1(3, 4), 7(2), 9(2), 11(0), 15(0), 17(0), 28(0)  
*Syspacephalus gregarius* 1(1), 4(2), 5(2), 6(0), 9(2), 10(2), 14(2, 3, 4), 19(2), 20(2), 21(2), 26(0), 27(1), 32(1), 40(1), 41(1), 44(4), 45(1), 46(0), 47(1), 56(0), 67(1), 68(0)  
*Tonopahella goldfieldensis* 13(1), 17(0), 20(0), 29(0), 46(0), 65(3)  
*Tonopahella walcotti* 4(2), 8(0), 30(0), 31(0), 58(0)
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