PHYLOGENETIC ANALYSIS OF SOME BASAL EARLY CAMBRIAN TRILOBITES, THE BIOGEOGRAPHIC ORIGINS OF THE EUTRILOBITA, AND THE TIMING OF THE CAMBRIAN RADIATION

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ABSTRACT—This paper presents a phylogenetic analysis of the ''Fallotaspidoidea,'' a determination of the biogeographic origins of the eutrilobites, and an evaluation of the timing of the Cambrian radiation based on biogeographic evidence. Phylogenetic analysis incorporated 29 exoskeletal characters and 16 ingroup taxa. In the single most parsimonious tree the genus *Fallotaspidella* Repina, 1961, is the sister taxon of the sutured members of the Redlichiina Richter, 1932. Phylogenetic analysis is also used to determine the evolutionary relationships of two new species of ''fallotaspidoids'' distributed in the White-Inyo Range of California that have been previously illustrated but not described. These species had been referred to *Fallotaspis* Hupé, 1953, and used to define the occurrence of the eponymous *Fallotaspis* Zone in southwestern Laurentia. However, these two new species need to be reassigned to *Archaeaspis* Repina *in* Khomentovskii and Repina, 1965. They are described as *Archaeaspis nelsoni* and *A. macropleuron*. Their phylogenetic status suggests that the *Fallotaspis* Zone in southwestern Laurentia is not exactly analogous to the *Fallotaspis* Zone in Morocco, where that division was originally defined. Thus, changes to the biostratigraphy of the Early Cambrian of southwestern Laurentia may be in order. Furthermore, specimens of a new species referable to *Nevadia* Walcott, 1910, are recognized in strata traditionally treated as within the *Fallotaspis* Zone, which is held to underlie the *Nevadella* Zone, suggesting further biostratigraphic complexity within the basal Lower Cambrian of southwestern Laurentia.

Phylogenetic analyses of the Olenellina and Olenelloidea, along with the phylogenetic analysis presented here, are used to consider the biogeographic origins of the eutrilobites. The group appears to have originated in Siberia. Biogeographic patterns in trilobites, especially those relating to the split between the Olenellid and Redlichiid faunal provinces are important for determining the timing of the Cambrian radiation. Some authors have argued that there was a hidden radiation that significantly predated the Cambrian, whereas others have suggested that the radiation occurred right at the start of the Cambrian. The results from trilobite biogeography presented here support an early radiation. They are most compatible with the notion that there was a vicariance event relating to the origin of the redlichiinid trilobites, and thus the eponymous Redlichiid faunal province, from the ''fallotaspidoids,'' whose representatives were part of the Olenellid faunal province. This vicariance event, based on biogeographic patterns, is likely related to the breakup of Pannotia which occurred sometime between 600–550 Ma, suggesting that the initial episodes of trilobite cladogenesis occurred within that interval. As trilobites are relatively derived arthropods, this suggests that numerous important episodes of metazoan cladogenesis precede both the earliest trilobitic part of the Early Cambrian, and indeed, even the Early Cambrian.

INTRODUCTION

IN THIS study, phylogenetic patterns are evaluated among the basal group of trilobites within the Redlichiina Richter, 1932, the paraphyletic ''Fallotaspidoidea'' [paraphyly designated using quotation marks following the convention of Wiley (1979)]. They share primitive characters, such as the absence of facial sutures, with representatives of the Olenellina Walcott, 1890, yet they also possess derived characters that indicate they are more closely related to the Redlichiina. Thus, the ''Fallotaspidoidea'' are a grade group within and transitional to the rest (sutured members) of the Redlichiina, and they include taxa that share a close common ancestry with the Olenellina, the basal eutrilobite clade (Lieberman, 1998, 2001). The ''fallotaspidoids'' and basal representatives of the Redlichiina are characterized by several features discussed by Lieberman (1998, 2001) which allow them to be consistently distinguished from the Olenellina. These features include: the width (tr.) of the glabella diminishes anteriorly; the frontal lobe is relatively short (sag.), with a length roughly equal to the length of L0; the ocular lobes contact the entire lateral margin of the frontal lobe; and the ocular lobes gradually decrease in height between the midpoint of the ocular lobes and the axial furrows. The phylogenetic position of the ''fallotaspidoids'' suggests that they are broadly transitional to all or almost all other trilobites (exclusive of the Olenellina) according to phylogenies of the Trilobita presented by Fortey and Whittington (1989), Fortey (1990), Ramsköld and Edgecombe (1991) and Fortey and Owens (1997). [The precise position of the Agnostida within or outside of this clade of trilobites is still the subject of debate (e.g., Fortey and Whittington, 1989; Fortey, 1990; Ramsköld and Edgecombe, 1991; Shergold, 1991; Bergström, 1992; Babcock, 1994;

Fortey and Theron, 1994; Fortey and Owens, 1997; and Edgecombe and Ramsköld, 1999).] The ''fallotaspidoids'' thus have a pivotal position in the evolutionary history of the trilobites. Furthermore, their stratigraphic position within the Early Cambrian signifies that they are important exemplars of the Cambrian radiation.

Phylogenetic analysis is used to determine the taxon within the ''Fallotaspidoidea'' that shares the most recent common ancestry with the Olenellina and also the taxon within the ''Fallotaspidoidea'' that is the sister group of the rest of the Redlichiina. [Genera such as *Bigotina* Cobbold, 1935 and *Lemdadella* Sdzuy, 1978 were used as exemplars for the Redlichiina following the conclusions of Palmer and Repina (1993) and Palmer and Rowell (1995) that these are basal sutured redlichiines.] Phylogenetic analysis also is used to determine the phylogenetic position of taxa figured by Nelson (1976), but not described, which were provisionally referred to *Fallotaspis* Hupé, 1953. These taxa are biostratigraphically and biogeographically significant and are discussed more fully below. Morphological terminology follows that of Palmer and Repina (1993), Geyer (1996), Whittington et al. (1997), and Lieberman (1998, 1999a). One new term is introduced, midinterocular ridge, which refers to the extension of the intergenal ridge [of Palmer and Repina (1993) and Geyer (1996)] onto the interocular area.

PHYLOGENETIC ANALYSIS

Taxa analyzed.—A total of 16 taxa within the ''Fallotaspidoidea'' and the Redlichiina were subjected to phylogenetic analysis. All adequately preserved species within the ''Fallotaspidoidea'' were analyzed. The outgroup taxon chosen was a consensus node,

which represented the character codings for the hypothetical ancestor of all the Olenellina, using the characters considered in this analysis. Explanation of how the character states of this node were determined is provided below.

A few taxa, because of doubtful taxonomic affinities, a very poor state of preservation, or the unavailability of very limited material were not considered in the phylogenetic analysis conducted herein but do merit discussion. For example, as mentioned by Lieberman (2001), one taxon, which had formerly been assigned to the "fallotaspidoids," *Bradyfallotaspis fusa* Fritz, 1972, by Fritz (1972), Palmer and Repina (1993, 1997), and Lieberman (1998) needs to be reassigned to the Olenellina because it bears the hallmark traits of that suborder. In particular, it has a relatively long (sag.) frontal lobe, and the ocular lobe contacts only the posterior part of the lateral margin of the frontal lobe. Therefore, it was not included in the phylogenetic analysis conducted herein. Similarly, Lieberman (1998, 2001) discussed *Geraldinella corneiliana* Fritz, 1995. This species had been assigned to the "Fallotaspidoidea" by Fritz (1995) and by Palmer and Repina (1993, 1997) [in Palmer and Repina (1993) it was referred to as GENUS A Fritz, 1993], but it needs to be reassigned to the Olenellina because again it bears the hallmark traits of that suborder enumerated above for *Bradyfallotaspis fusa*. Palmer and Repina (1993, 1997) assigned *Selindella gigantea* Repina, 1979 to the "Fallotaspidoidea." This taxon is very poorly preserved, but it does appear to have a relatively long (sag.) frontal lobe, and the ocular lobe may contact only the posterior part of the lateral margin of the frontal lobe. Therefore, this species is likely referable to the Olenellina. Because of this and its poor state of preservation, which hinders determination of its precise taxonomic affinities, it was excluded from phylogenetic analysis. *Wolynaspis unica* Chernysheva *in* Kir'ianov and Chernysheva, 1967 appears to be closely related to such "fallotaspidoids" as *Daguinaspis* Hupé and Abadie, 1950, and *Choubertella* Hupé, 1952, as Palmer and Repina (1993, 1997) suggested; however, it is extremely poorly preserved and known from very limited material. Therefore, again it was excluded from phylogenetic analysis.

Characters and character states.—Phylogenetic patterns were determined by parsimony analysis of the following 29 holaspid exoskeletal characters. Characters are roughly arranged in manner they appear, from anterior to posteriormost point, on exoskeleton. No autapomorphies are included in the character list. (0) represents the primitive state for the "Fallotaspidoidea."

1) Anterior border near but not directly anterior of frontal lobe—(0) very short, length (exsag.) less than or equal to one-half length (sag.) of L0, (1) moderately long, length (exsag.) equal to 0.85 to 1.1 times length (sag.) of L0, (2) very long, length (exsag.) equal to approximately 1.5 times length (sag.) of L0.

2) Anterior cephalic border developed as—(0) flattened ledge, (1) rounded ridge.

3) Anterior border—0) prominently separated from extraocular area by furrow, (1) not prominently separated from extraocular area by furrow.

4) Plectrum—(0) absent or not prominently developed, (1) present.

This character was coded as state 0 for *Choubertella* and *Daguinaspis* based on the work of Geyer (1996).

5) Frontal lobe of glabella—(0) contacts anterior border furrow, (1) does not contact anterior border furrow.

6) Length (sag.) of preglabellar field—(0) preglabellar field absent, (1) equal to 0.25 to 0.7 times length (sag.) of L0, (2) equal to 1.5 to 2.0 times length (sag.) of L0, (3) 0.9 to 1.2 times length (sag.) of L0.

7) Prominent parafrontal band anterior of LA—(0) not visible in dorsal view, (1) visible in dorsal view.

8) Anterior margins of frontal lobe at each side of midline deflected posteriorly at—(0) roughly 40 degree angle relative to transverse line, (1) roughly 10 to 20 degree angle relative to transverse line.

9) Outer band of ocular lobe near lateral margin of L4—(0) does not expand prominently exsagittally adaxial of glabella, (1) expands prominently exsagittally adaxial of glabella.

10) Anterior part of ocular lobe—(0) does not deflect strongly anteriorly near L3, (1) deflects strongly anteriorly near L3.

11) Anterior tip of visual surfaces opposite—(0) adaxial part of S3, (1) point between adaxial part of S2 and S3, (2) anterior of adaxial tip of S3.

In some specimens of *Fallotaspis bondoni* (Neltner and Poctey, 1949) the anterior tips of the visual surfaces may be opposite S2.

12) Line from posterior tip of ocular lobe to junction of posterior margin of lobe with glabella—(0) forms 0 to 20 degree angle with sagittal line, (1) forms 35 to 45 degree angle with sagittal line.

13) Posterior tips of ocular lobes developed opposite—(0) medial part of distal margin of L0, (1) S0, (2) opposite or anterior of medial part of distal margin of L1.

14) Width (tr.) of interocular area—(0) approximately equal to 1 to 1.5 times width of ocular lobe at its midlength, (1) about half to two-thirds width (tr.) of ocular lobe at its midlength, (2) equal to two to three times width (tr.) of ocular lobe at its midlength.

15) Orientation of S3—(0) convex, (1) slightly inclined abaxially at −10 to 10 degree angle relative to transverse line, (2) straight, inclined posteriorly abaxially at roughly 30 to 45 degree angle relative to transverse line.

16) Orientation of S2—(0) straight, abaxially directed inward and posteriorly at roughly 35 to 45 degree angle relative to transverse line, (1) straight, abaxially directed forward at roughly 10 degrees relative to transverse line, (2) convex, abaxially directed inward and posteriorly at roughly 10 degree angle relative to transverse line.

17) Shape of S1—(0) transverse or faintly convex anteriorly, (1) sinuous.

18) Anterolateral lobes on L0 and L1—(0) absent, (1) present.

Anterolateral lobes are absent from all specimens of *Choubertella spinosa* Hupé, 1953, except in one deformed internal mold. They were therefore coded as absent for this taxon.

19) Axial part of L0—(0) smooth or with faint node present, (1) with spine present.

20) Midinterocular ridge—(0) not visible, (1) prominently developed.

21) Orientation of midinterocular ridge—(0) midinterocular ridge absent, (1) inclined at roughly 10 degree angle relative to sagittal line, (2) diagonal, inclined at roughly 45 degree angle relative to sagittal line.

22) Extraocular region opposite L1—(0) broad, width (tr.) greater than or equal to 65 to 75 percent of the width of the glabella at L1, (1) narrow, width (tr.) 35 to 50 percent of the width of the glabella at L1, (2) very narrow, essentially absent.

Lemdadella antarcticae Palmer *in* Palmer and Rowell, 1995 was coded as having states 1 and 2 for this character. In this case, the polymorphic coding signified that state 0 clearly was not present; it did not signify that both states 1 and 2 were actually present.

23) Genal spine—(0) present, (1) not well developed or absent.

24) Functional facial sutures—(0) absent, (1) present.

25) Length (exsag.) of pleural spine on T3—(0) comparable in length (exsag.) to length of spines on T2, T4–T6, (1) very long (exsag.), extending back the length (sag.) of the entire thorax (this character state is equivalent to the spine of T4 being greatly reduced), (2) moderately long (exsag.), extending back three to eight segments.

Fallotaspis typica Hupé, 1953, was coded as having states 1 and 2 for this character. In this case, the polymorphic coding

TABLE *1*—Character state distributions for taxa used in phylogenetic analysis. Characters and character states are as listed in text. Missing data are indicated by "?". Character numbers are listed at top of table. Character states listed as "V", "W", "X", "Y", and "Z" are polymorphic, where "X" = (0&1), "Y" = (1&2), "Z" = (0&2), "W" = (0&1&2), and "V" = (1&3).

	0000000001 1234567890	1111111112 1234567890	222222222 123456789
Olenellina Node	0000000000	00W00Z0000	0000Z0000
Repinella sibirica	00001V0100	?001?110?0	010001???
Profallotaspis jakutensis	0000131100	1110111011	2200?????
Pelmanaspis jurii	0000131100	1110111011	2100?????
Eofallotaspis tioutensis	0010131100	1102?01101	1100?????
Daguinaspis ambroggii	0010131110	01X2200001	221000000
Choubertella spinosa	0110121110	1102200011	221001011
Fallotaspis typica	2100001100	0110201111	1000Y1???
F. bondoni	1100XX1101	10001Z1111	100021000
Parafallotaspis grata	1001121100	2102021101	1000??001
Archaeaspis hupei	2001111010	0100100111	1100?????
A. nelsoni	1101131000	100020??11	100001???
A. macropleuron	1101111001	000020??01	100010???
Fallotaspidella musatovi	1001111110	0110110100	0000?????
Bigotina bivallata	11011V1X10	11Y2021000	0101??111
Lemdadella antarcticae	1001111X00	1120100000	0X01??111
L. linaresiae	1101111100	X112120000	010101111

signified that state 0 clearly was not present; it did not signify that both states 1 and 2 were actually present.

26) Anterolateral nodes on thoracic axis—(0) faint to absent, (1) prominent.

27) Pygidium—(0) with axis indistinctly separated from pleural field, (1) with axis distinctly separated from pleural field.

28) Number of pygidial axial rings in addition to terminal segment—(0) one, (1) four to five.

29) Pygidial axial rings—(0) poorly divided, (1) well divided.

The codings for the taxa analyzed are given in Table 1. The Olenellina, as mentioned above, was treated as a single consensus node, representing the hypothesized ancestral morphology of that suborder. To code this node, taxa considered by Lieberman (1998), Lieberman (2001) and where applicable by Lieberman (1999a) were coded for all of the characters used in the phylogenetic analysis presented above. Those characters that vary within the Olenellina but which are absent or do not vary within the "Fallotaspidoidea" were not considered. Using the cladogram for the Olenellina from Lieberman (2001), character codings were assigned to the terminal taxa and parsimoniously optimized to the various nodes of the tree: specifically, the basal node of the Olenellina, using the trace changes option of MacClade v. 3.04 (Maddison and Maddison, 1992). The character states representing the codings of the ancestral node were entered into the data matrix in Table 1. Such an approach to coding the outgroup was utilized for several reasons. First, including all of the species considered in Lieberman (1998, 1999a, 2001) in this analysis would have greatly magnified the number of taxa considered, creating a potentially intractable phylogenetic problem. By contrast, using just a few of these species as the outgroup would not necessarily have captured the ancestral state of the Olenellina at its point of divergence from the taxa analyzed herein, and thus would have been inaccurate. Therefore, some alternate method of coding an outgroup was necessary. Various authors have debated the relative merits of using individual species versus supraspecific taxa to code outgroups (or terminal taxa). For example, Rice et al. (1997) endorsed the use of supraspecific taxa in phylogenetic analysis and thus would have approved of the method used herein. By contrast, Wiens (1998) and Prendini (2001) argued that supraspecific taxa should generally be avoided and individual species should be used. However, even Wiens (1998) and Prendini (2001), who typically favored the use of individual species in phylogenetic analysis did argue that supraspecific can be legitimately used

in phylogenetic analysis in the case when "the supraspecific taxon is coded with plesiomorphic states determined in previous lower-level analyses of internal relationships within the supraspecific taxon" (Prendini, 2001, p. 291). This case is the one encountered herein, and therefore the method used to code the outgroup stands on solid theoretical grounds.

Parsimony analysis.—These data were subjected to a heuristic search using PAUP 4.0 beta version 2a (Swofford, 1998) with a stepwise addition sequence with 100 random replications and the TBR option. All multistate characters were treated as unordered (nonadditive) in the absence of clear criteria for ordering them. One most parsimonious tree was recovered of length 106 steps (Fig. 1). The retention index of this tree is 0.58, and the consistency index excluding uninformative characters is 0.53. The value of the consistency index is near the mean value of data sets of this size based on Archie (1989) and Sanderson and Donoghue (1989) and is also within the range of consistency indices for phylogenies of this size (in terms of numbers of taxa) generated using molecular sequence data (Klassen et al., 1991). The value of the consistency index significantly exceeds values derived from similarly sized data matrices constructed from random data (consistency index of 0.21) at the 0.05 level of significance, based on Klassen et al. (1991). This suggests that there is reasonable phylogenetic signal in these character data and also supports the contention of Lieberman (1998, 2001) that morphological variation in trilobites, if evident as homoplasy, was not unduly extreme in the Early Cambrian [see discussion in McNamara (1986), Hughes (1991), and Lieberman (1998)].

To assess overall phylogenetic signal within the database, 1,000 random trees were generated from the character data in Table 1 ten separate times using PAUP 4.0. For each iteration, the distribution of these tree lengths was evaluated and the g_1 statistic, a measure of tree-length skewness, was obtained. The mean value from these 10 iterations was -0.47 which differs at the 0.01 level of significance from g_1 values obtained from cladograms generated using random character data. This implies strong phylogenetic signal in the character data (Hillis, 1991).

PTP tests (Faith, 1991; Faith and Trueman, 1996) were performed using PAUP to assess the phylogenetic signal in the character data of Table 1. This method was described in detail by Faith (1991), Swofford et al. (1996), and Faith and Trueman (1996). Two separate PTP tests were implemented. In the first, the character data for all taxa were randomized 1,000 times, and in each of these replications a heuristic stepwise search with a random addition sequence and five replications was used to find the most parsimonious cladogram based on the random data. The PTP value was <0.001, a highly significant value, implying good cladistic structure and phylogenetic signal in the database. A similar protocol was followed in a PTP test that only randomized the ingroup taxa. Again, the PTP was <0.001, implying good phylogenetic signal.

A bootstrap analysis also was done using PAUP 4.0 (Swofford, 1998) to determine the support for each of the nodes that appear in the most parsimonious cladogram. One hundred bootstrap replications were employed in a stepwise search that used five random replications per bootstrap replication, and groups were retained that were compatible with the 50 percent majority rule consensus tree. The confidence values for the nodes of the tree duplicated in the bootstrap analysis are given in the caption for Figure 1. Many but not all of the nodes appear in both the bootstrap consensus tree and the most parsimonious tree. In a similar test of cladogram support and phylogenetic structure the jackknife analysis of PAUP 4.0 (Swofford, 1998) was implemented; the jackknife percentage value chosen was ten percent, equivalent to three characters in this database. As with the bootstrap analysis, groups were retained that were compatible with the 50 percent
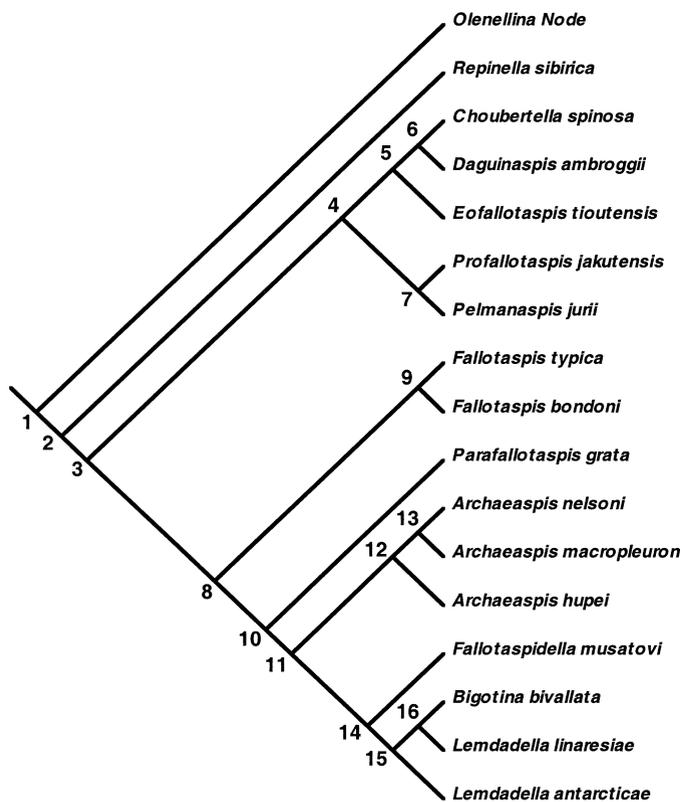
FIGURE *1*—The most parsimonious tree of length 106 steps produced from analysis of character data in Table 1 with PAUP 4.0 (Swofford, 1998). Cladogram constructed using a heuristic search with a stepwise addition sequence and 100 random replications. All characters were treated as unordered. The retention index is 0.58 and the consistency index excluding uninformative characters is 0.53. The following nodes of the tree were supported by the following jackknife confidence values (see text for jackknife procedure used): Node *3* = 0.73; Node *4* = 0.53; Node *5* = 0.67; Node *6* = 1.00; Node *7* = 0.96; Node *8* = 0.52; Node *9* = 0.80; Node *10* = 0.34; Node *11* = 0.30; Node *12* = 0.36; Node *13* = 0.52; Node *14* = 0.68; Node *15* = 0.98; Node *16* = 0.98. The following nodes of the tree were supported by the following bootstrap confidence values (see text for bootstrapping procedure utilized): Node *3* = 0.45; Node *4* = 0.17; Node *5* = 0.37; Node *6* = 0.77; Node *7* = 0.74; Node *8* = 0.16; Node *9* = 0.35; Node *13* = 0.24; Node *14* = 0.39; Node *15* = 0.74; Node *16* = 0.76. The following branch support values (Bremer, 1994) were recovered for the following nodes: Node *6* = 2; Node *7* = 1; Node *15* = 1; Node *16* = 1. Total tree support (Bremer, 1994) is 0.05. Character states are placed at nodes [using MacClade v. 3.0.4 (Maddison and Maddison, 1992)], with the characters given in the text. The apomorphic state is given in parentheses. Brackets indicate equivocal character states which are ambiguous because of missing data, polymorphisms, or multiple equally parsimonious resolutions. Equivocal characters are placed only at their basal phylogenetic position, and only unambiguous reversals are shown, except for multistate characters. Node *1,* 5[0, 1], 6[0, 1, 3], 8[0, 1], 15[0, 1], 17[0, 1], 22[0, 1], 26[0, 1]; Node *2,* 5(1), 8(1), 17(1), 26(1); Node *3,* 7(1), 12(1), 15(1), 20(1), 21[0, 1, 2]; Node *4,* 6(3), 11(1), 21[1, 2], 22[1, 2]; Node *5,* 3(1), 14(2), 15[1, 2]; Node *6,* 9(1), 15(2), 17(0), 21(2), 22(2), 23(1); Node *7,* 13(1), 16(1), 19(1), 21(2); Node *8,* 1(1), 6[0, 1, 2, 3], 18(1), 21(1), 22(0); Node *9,* 2(1), 5[0, 1], 6[0, 1], 19(1), 25(2); Node *10,* 4(1), 29(1); Node *11,* 6(1), 17(0); Node *12,* 8(0), 19[0, 1]; Node *13,* 2(1), 12(0), 15(2); Node *14,* 13(1), 20(0), 21(0); Node *15,* 11(1), 18(0), 22[0, 1], 24(1), 27(1), 28(1); Node *16,* 2(1), 14(2), 16(2), 22(1).

majority rule consensus tree. The confidence values for the nodes of the tree duplicated in the jackknife analysis are also given in the caption for Figure 1. Again, many but not all of the nodes appear in both the jackknife consensus tree and the most parsimonious tree.

A Bremer branch support analysis (Bremer, 1994) also was conducted to examine the support of the different individual nodes of the cladogram. Seventy-eight (78) trees of length less than or equal to 107 steps, 1,019 trees of length less than or equal to 108 steps, and 8,534 tees of length less than or equal to 109 steps were found before the analysis was terminated when a completely polytomous ingroup was recovered. Individual branch support values are given in the caption of Figure 1. The total support index (Bremer, 1994) for the tree is 0.05.

SUPRAFAMILIAL CLASSIFICATION WITHIN THE "FALLOTASPIDOIDEA"

The phylogenetic analysis conducted herein and the study of Lieberman (1998) suggested that the "Fallotaspidoidea" are paraphyletic. At this time, it is recommended that the paraphyletic group name be restricted to the grade in Figure 1 down the tree relative to *Bigotina* and *Lemdadella*. Within this paraphyletic superfamily, however, some monophyletic clades can be identified. One group includes *Choubertella*, *Daguinaspis*, *Eofallotaspis* Sdzuy, 1978, *Profallotaspis* Repina *in* Khomentovskii and Repina, 1965, and *Pelmanaspis* Repina, 1990. This clade is referred to as the family Daguinaspididae Hupé, 1953, and within it is the synonymous subfamily Daguinaspidinae. *Fallotaspis*, which contains several species, two of which were considered in the phylogenetic analysis conducted herein, is assigned to the now monogeneric Fallotaspididae Hupé, 1953. Finally, *Archaeaspis* is assigned to the Archaeaspididae Repina, 1979, which is now also monogeneric. Palmer and Repina (1993, 1997) had included *Fallotaspidella* Repina, 1961, within the Archaeaspididae. If this taxonomic assignment were to be continued, that family would be paraphyletic because they are not sister taxa. However, the phylogeny in Figure 1 suggests that Palmer and Repina (1993, 1997) were correct in asserting a close relationship between *Archaeaspis* and *Fallotaspidella*. Repina (1979), Ahlberg et al. (1986), and Palmer and Repina (1993, 1997) suggested a close relationship between *Fallotaspis* and *Parafallotaspis* Fritz, 1972, and though they do not appear to be sister taxa, their conclusions are broadly supported by the analysis conducted herein.

Parafallotaspis, *Repinella* Geyer, 1996, and *Fallotaspidella* could be assigned to new, monotypic families based on phylogenetic topology and rules of classification, but this taxonomic strategy was not followed here in order to avoid establishing new, monospecific families. Based on phylogenetic topology, *Repinella* is the basal representative of the "Fallotaspidoidea." Among the "fallotaspidoids," *Fallotaspidella* shares the most recent common history with such sutured representatives of the Redlichiina as *Bigotina* and *Lemdadella*.

The degree of confidence we can have in the hypothesis that the Laurentian taxa informally referred to the genus *Fallotaspis* actually belong to *Archaeaspis* can be quantified using the topology-dependent permutation test (T-PTP test) of Faith (1991), available in PAUP 4.0 Swofford (1998). This test was conducted using a search that randomized ingroup taxa only and employed a stepwise, random addition sequence with five random iterations per replication with a total of 1,000 replications. Two constraint trees were used. In the first, *Fallotaspis*, *Archaeaspis*, and the sutured Redlichiina each were constrained to be monophyletic (on the presumption that these relationships were confidently known). In the second, only *Archaeaspis* was constrained to be monophyletic. If it is assumed in the case of either constraint tree that *a*

priori these taxa are closely related then the p-value for the T-PTP test is 0.001, a highly significant value. This implies that there is strong support for a close relationship between the two new Laurentian species of *Archaeaspis* and *A. hupei* Repina *in* Khomentovskii and Repina, 1965, to the exclusion of species of *Fallotaspis* or indeed, any other representative of the "Fallotaspidoidea" or the basal Redlichiina. Recently, however, Harshman (2001) has challenged aspects of the T-PTP test, suggesting that it may not be a valid test of an *a priori* hypothesis of monophyly. Thus, the results presented here for the T-PTP test may need qualification.

If either of the relationships used in the constraint tree is postulated *a posteriori* a Bonferroni (or some other) correction is necessary in order to avoid Type I error. This can be applied simply and conservatively using a model of probabilistic grouping. In the case of the constraint tree that assumed just *Archaeaspis* was monophyletic, there are 16 ingroup taxa and the possible number of ways of recognizing groups of three species within a larger group of 16 species is 16!/13!*3! = 560. With 560 possible combinations, for an observation to be globally statistically significant at the 0.05, it must actually be significant at a value equal to 1 minus the 560th root of 0.95. This equals 9.16×10^{-5} which is smaller than 0.001. Thus, if applied *a posteriori,* the T-PTP test is no longer significant. In the constraint tree that assumed *Archaeaspis*, *Fallotaspis*, and the Redlichiina were monophyletic there are 16 ingroup taxa and four groups, two with three members, one with two members, and one with eight members. The possible number of ways of assigning these groups is 16!/(3!*3!*2!*8!) = 7,207,200. Thus again, if applied *a posteriori,* the T-PTP test is no longer significant.

BIOGEOGRAPHIC ORIGINS OF THE EUTRILOBITES AND THE TIMING OF THE CAMBRIAN RADIATION

Introduction.—The timing of the Cambrian radiation is a topic that has been extensively debated (see Gould, 1989; Signor and Lipps, 1992; Fortey et al., 1996; Knoll, 1996; Raff, 1996; and Lieberman, 1999b). Some have argued that the Cambrian radiation significantly predates the Neoproterozoic-Cambrian boundary (e.g., Darwin, 1859; Davidson et al., 1995; Fortey et al., 1996; Fortey and Owens, 1997; Wray et al., 1996; Ayala et al., 1998; Xiao et al., 1998; Fortey, 2001) whereas others have suggested that the radiation occurred just before the start of the Cambrian (McNamara, 1986; Gould, 1989; Hughes, 1991; Valentine et al., 1994). The former view implies a long, cryptic history of metazoan diversification; the latter implies a more literal reading of the fossil record. Either view has significant, yet divergent, implications for our understanding of the tempo and mode of evolution during this critical episode in the history of life.

The biogeographic origin of the eutrilobites is potentially informative for determining the timing of the Cambrian radiation because trilobites are among the first undoubted metazoans to appear in the fossil record. Furthermore, trilobite faunas in the Early Cambrian were already differentiated biogeographically. Fortey et al. (1996) and Fortey and Owens (1997) have argued that this fact provides evidence that trilobites, and thus, by phylogenetic association, other crown-group metazoan taxa must have been diversifying for a significant period of time before they first appeared in the fossil record. Their arguments are compelling and warrant further attention (Lieberman, 1999b).

The biogeographic patterns Fortey et al. (1996) and Fortey and Owens (1997) discussed involve the split between the Olenellid and Redlichiid faunal provinces. The Olenellid province comprises Laurentia, Siberia, and Baltica. The Redlichiid province comprises Australia, Antarctica, and China. Areas of overlap between these two provinces occur in northern Africa and southern Europe. These two faunal provinces are defined on the basis of their eponymous trilobite taxa: for example, the Olenellina but also, critically, the "Fallotaspidoidea" in the case of the Olenellid faunal province, and the Redlichiina, exclusive of the "Fallotaspidoidea," in the case of the Redlichiid faunal province. It is now clear though that the "Fallotaspidoidea" are linked phylogenetically to the Redlichiina (Lieberman, 1998, 1999b). Thus, the evolutionary disjunction between the Olenellina on the one hand and the "Fallotaspidoidea" plus Redlichiina on the other, should tell us something about the biogeographic relationship between the Olenellid and Redlichiid faunal province. Specifically, the traditional Olenellid faunal province must be in some sense paraphyletic.

As discussed by Lieberman (1999b), Fortey et al. (1996) and Fortey and Owens (1997) predicted that the early biogeographic distribution of the eutrilobites should have included Laurentia, Siberia, and much of Gondwana, particularly China, Antarctica, and Australia. They further predicted that subsequent biogeographic patterns within the eutrilobites should have followed a pattern of vicariant differentiation with ever decreasing geographic ranges, along the line of the biogeographic division of the earth into two faunal provinces. Fortey et al. (1996) and Fortey and Owens (1997) related the biogeographic disjunction between the Olenellid and Redlichiid faunal provinces to an early vicariance event dating to the separation between western Laurentia and part of what later became Gondwana during the breakup of Rodinia.

To understand the nature and timing of such potential vicariance events it is helpful to consider some of the tectonic changes occurring in this region. There has been an extensive amount of tectonic research aimed at identifying cratons that were situated on the western margin of Laurentia during the Neoproterozoic. Evidence suggests these may have included Australia, parts of eastern Antarctica, and the North and South China blocks (Dalziel, 1991, 1992, 1997; Hoffman, 1991; Moores, 1991; Stump, 1992; Young, 1992; Moyes et al., 1993; Powell et al., 1993; Li et al., 1995, 1996; Torsvik et al., 1995, 1996; Unrug, 1996, 1997; Scotese, 1997; Wingate et al., 1998; Karlstrom et al., 1999; Prave, 1999; Waggoner, 1999). Most authors suggest this breakup occurred between 700 Ma and 800 Ma (e.g., Moyes et al., 1993; Powell et al., 1993; Li et al., 1995, 1996; Torsvik et al., 1995, 1996; Unrug, 1996, 1997; Dalziel, 1997; Scotese, 1997; Karlstrom et al., 1999; Waggoner, 1999). Some have suggested though that breakup occurred around 550 Ma (e.g., Bond et al., 1984; Veevers et al., 1997), whereas Dalziel (1991, 1992) put the breakup anytime between 550 Ma and 750 Ma. Finally, Prave (1999) identified two phases of rifting along the western margin of Laurentia, one at 700 Ma and one at 600 Ma. Thus, the most corroborated geological hypothesis suggests that separation between the western margin of Laurentia and parts of China, Antarctica, and Australia occurred around 700 Ma, with the important caveat that the hypothesis that final separation of these plates occurred 100–150 Ma later has been somewhat corroborated and has not been definitively refuted. Thus, the vicariance event Fortey et al. (1996) and Fortey and Owens (1997) associate with initial divergence events, the breakup of Rodinia, implied that early trilobite lineages had originated before 700 Ma.

There are also important tectonic events that occur after the breakup of Rodinia but before the start of the Cambrian. Among the most important of these is the assembly of another supercontinent, Pannotia, which formed around 600 Ma (Dalziel, 1992, 1997; Scotese, 1997). The precise geometry of this supercontinent is debated, but it appears that Amazonia and parts of present day South America (especially Amazonia) were in contact with the eastern margin of Laurentia. Baltica (Scandinavia and the eastern European platform) was also in contact with the northern margin of Amazonia and the north-eastern margin of Laurentia, while Siberia was in contact with the northern margin of Laurentia.

Finally, East Antarctica, India, South and North China, Australia, and other smaller terranes were in contact with the eastern margin of Amazonia and modern day western Africa. Pannotia began to break apart over the interval 600–550 Ma (Dalziel, 1997; Faill, 1997; Scotese, 1997; Unrug, 1997; Scotese et al., 1999).

The phylogenetic analysis presented herein, as well as those of Lieberman (1998, 1999a, 2001), are used to evaluate the biogeographic origin of the eutrilobites and test the biogeographic predictions of Fortey et al. (1996) and Fortey and Owens (1997). These are related, but distinct propositions. The former involves determining the biogeographic state of the root node of the eutrilobites, while the latter involves determining the biogeographic state of the node at the split between the representatives of the Olenellid and Redlichiid faunal provinces, which, as described above, involves the branching point between the "Fallotaspidoidea" and the basal representatives of the Redlichiina. As described above, Fortey et al. (1996) and Fortey and Owens (1997) linked early events in trilobite evolution to episodes of vicariance. If such events had occurred, they would have involved first a widespread ancestral distribution at what should properly be viewed as the node separating the "fallotaspidoids" from the basal redlichiinids, with subsequent divergence events associated with contracting range. Conceivably, a widespread distribution further down the trilobite tree, at the base of the eutrilobites, might also still be compatible with an early vicariance event. A vicariance event of this type might correspond to the approximately 700–800 Ma breakup of Rodinia or potentially even to the 600–550 Ma breakup of Pannotia, depending on the biogeographic states on the tree. Either date implies that the true radiation of the Metazoa significantly predated the Cambrian radiation, with the biogeographic event corresponding to the Rodinia breakup necessitating the longer cryptic Cambrian radiation.

It is also conceivable that the ancestral eutrilobite or the ancestor at the branching point between the "Fallotaspidoidea" and the basal redlichiinids did not have a widespread ancestral biogeographic distribution. This alternative biogeographic pattern would involve an ancestral species with a narrow geographic distribution that subsequently underwent range expansion such that eventually the range of the trilobites came to comprise essentially all of the core elements of Rodinia (or Pannotia) including Laurentia, Baltica, Siberia, Australia, Africa, and China. This biogeographic pattern could be more compatible with a metazoan radiation right around the Early Cambrian.

Methods.—To pursue this analysis, the phylogeny generated from cladistic analysis shown in Figure 1 was combined with the phylogeny of the Olenelloidea by Lieberman (1999a, fig. 23), and the phylogenies of Lieberman (1998, figs. 1 and 2; 2001, fig. 1) to create a supertree of the type described by Sanderson et al. (1998) and Ree and Donoghue (1999) (Fig. 2). This phylogeny was also converted to an area cladogram (Fig. 2) by substituting the species names for the geographic distribution of the taxa (see Brooks and McLennan, 1991; Wiley et al., 1991; Lieberman and Eldredge, 1996). The biogeographic regions considered were: Siberia; southern Europe-northern Africa (comprising France, Sardinia, Spain, and Morocco); Avalonia (comprising parts of present day eastern Massachusetts, eastern Newfoundland, England, and Wales); southwestern Laurentia (comprising parts of present day southern California, Nevada, and the Caborca region of Mexico); northwestern Laurentia (comprising western Canada); eastern Laurentia [comprising the sedimentary deposits extending through Alabama, Virginia, Pennsylvania, New York, Vermont, Quebec, and western Newfoundland (see Barnaby and Read, 1990), eastern Ellesmere Island, Greenland, Svalbard, and northwestern Scotland]; Baltica; East Antarctica; and Australia-south China. These are all distinct geological regions characterized by large

numbers of endemic species. The Early Cambrian faunas of Australia and south China were treated as one biogeographic region because they were represented in this analysis by a single exemplar that occurred in both regions (the Redlichiina exclusive of the "Fallotaspidoidea"). Certainly there is a biogeographic distinction between Australia and south China, but this analysis could not discern biogeographic relationships among these two regions. Southern Europe and northern Africa were also distinct biogeographic regions during the Neoproterozoic and Cambrian. They too were treated as a single biogeographic region in this analysis because they were closely related biogeographically in the Early Cambrian (Fortey and Cocks, 1992) and also because few taxa from southern Europe could be considered in this study, and species poor regions can artifactually map as biogeographically basal (Fortey and Cocks, 1992; Lieberman, 1997). After substituting species' biogeographic states for their taxonomic names at the terminals of the tree, the ancestral biogeographic state of the eutrilobites and also the ancestral biogeographic state at the divergence between the "fallotaspidoids" and the redlichiinids was determined.

Biogeographic areas were treated as a multistate character [described by Lieberman (2000)] and these were optimized to nodes, including the ancestral node of the tree, using the modified version of the Fitch (1971) parsimony algorithm described by Lieberman (2000). The Fitch algorithm allows for unordered transformations between multistate characters. This method was used, rather than Bremer's (1992) ancestral area analysis, which may be problematic because it treats each biogeographic region as an irreversible character that is mapped to a tree using Camin-Sokal parsimony. Ronquist (1994, 1995) questioned whether areas should be treated as irreversible characters because this assumption is valid only if dispersal is irreversible and a region cannot be subsequently reinvaded and numerous biogeographic studies (see for example Lieberman, 2000) have in fact demonstrated that the converse is true. Furthermore, Ronquist (1994, 1995) suggested that there is no reason why we should assume that an area can be invaded only a single time and there are no biogeographic processes that would always produce such a result. Thus, he concluded that using Camin-Sokal parsimony to optimize individual areas to a cladogram one at a time is flawed. Instead, Ronquist (1994, 1995) argued that allowing dispersals to occur as unordered, reversible events was probably more realistic; therefore, he concluded that Fitch parsimony (the optimization procedure used above) should be used to optimize characters (areas) to trees.

Results.—The results are shown in Figure 2, though only the biogeographic states of the nodes crucial to this analysis are given for the purposes of brevity and clarity. Range expansions are represented by a change or increase in the overall number of biogeographic regions occupied between adjacent nodes and adjacent nodes and terminal taxa. Vicariance is represented by a contraction in the overall number of biogeographic regions occupied between adjacent nodes and adjacent nodes and terminal taxa. The biogeographic state of the root node is Siberia (labeled "A" in Fig. 2), suggesting that the eutrilobites originated in that region and moved outward. The limited distribution of this root node suggests that the biogeographic origins of the eutrilobites and there subsequent divergence were not compatible with strict vicariance. However, the critical biogeographic patterns, at least in relation to the timing of the Cambrian radiation, involve the branching point between the "fallotaspidoids" and the redlichiinids (the node labeled "B" in Fig. 2). This ancestral biogeographic distribution encompassed a much broader range, comprising Siberia and southern Europe-northern Africa. Close to this branch point (at the node labeled "C" in Fig. 2) the distribution is even larger, comprising Siberia, southern Europe-northern Africa, and also northwestern Laurentia. Furthermore, one of the divergence
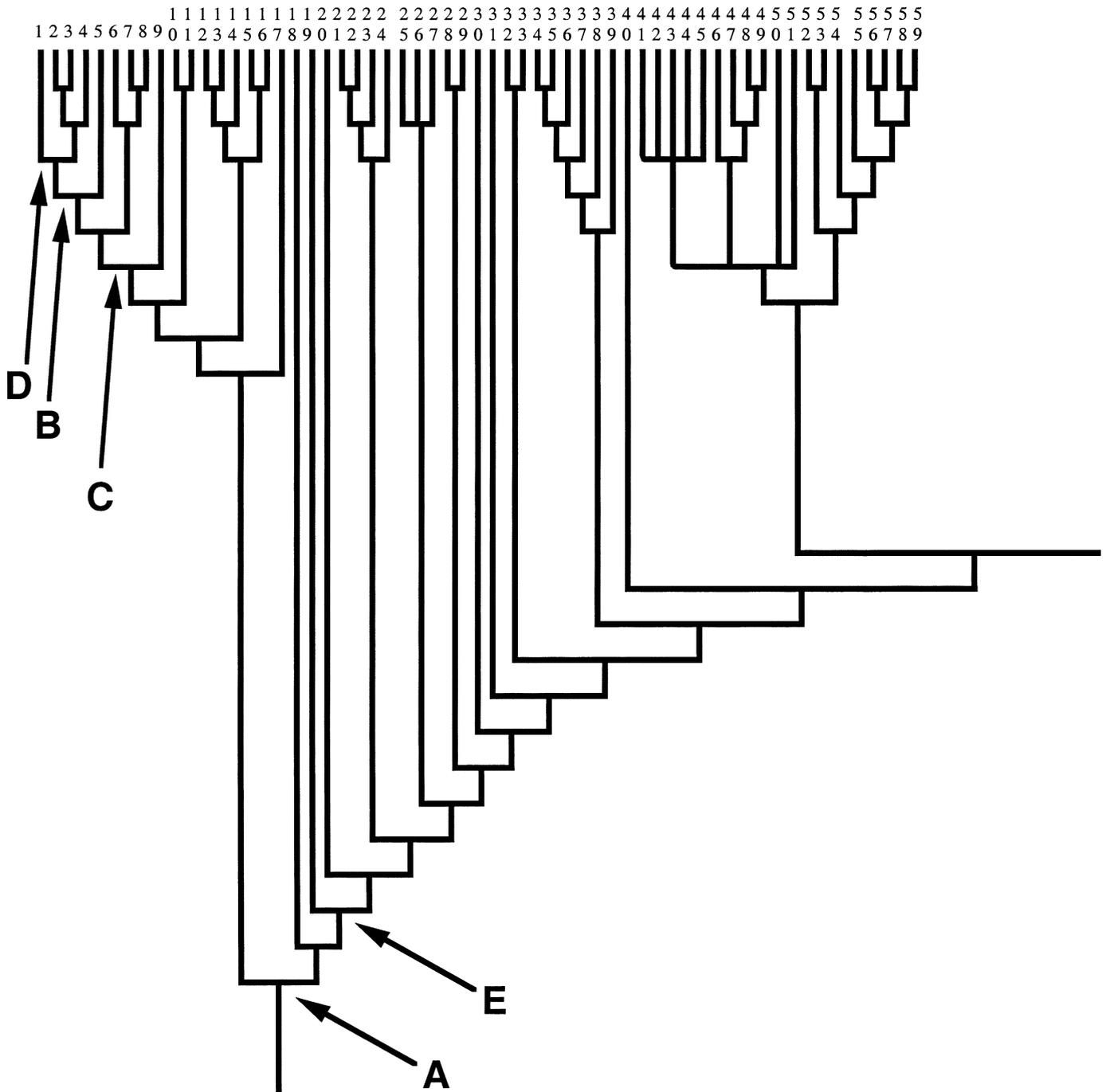
FIGURE 2—Phylogenetic supertree for basal eutrilobite taxa produced by combining the cladogram in Figure 1 with those in Lieberman (1998, figs. 1 and 2, 1999a, fig. 23, and 2001, fig. 1) where taxa labeled 1–4 belong to the Redlichiina, taxa labeled 5–17 belong to the ''Fallotaspidoidea,'' and taxa labeled 18–119 belong to the Olenellina. The numbers at the terminal nodes refer to species names and an area cladogram can be produced by substituting the geographic distribution of the taxon for the species name, where *0* = Siberia; *1* = southern Europe-northern Africa; *2* = Avalonia; *3* = southwestern Laurentia; *4* = northwestern Laurentia; *5* = eastern Laurentia; *6* = Baltica; *7* = Antarctica; and *8* = Australia-south China. Biogeographic regions are discussed in greater detail in the text. Species names and biogeographic states are: **1.** Other Redlichiina—*1, 7, 8*; **2.** *Lemdadella linaresiae* Liñán and Sdzuy—*1*; **3.** *Bigotina bivallata* Cobbold—*1*; **4.** *L. antarcticae* Palmer *in* Palmer and Rowell—*7*; **5.** *Fallotaspidella musatovi* Repina, 1961—*0*; **6.** *Archaeaspis hupei* Repina *in* Khomentovskii and Repina—*0*; **7.** *A. macropleuron* new species—*3*; **8.** *A. nelsoni* new species—*3*; **9.** *Parafallotaspis grata* Fritz—*4*; **10.** *Fallotaspis bondoni* (Neltner and Poctey)—*1*; **11.** *F. typica* Hupé—*1*; **12.** *Choubertella spinosa* Hupé—*1*; **13.** *Daguinaspis ambroggii* Hupé and Abadie—*1*; **14.** *Eofallotaspis tioutensis* Sdzuy—*1*; **15.** *Pelmanaspis jurii* Repina—*0*; **16.** *Profallotaspis jakutensis* Repina *in* Khomentovskii and Repina—*0*; **17.** *Repinella sibirica* (Repina *in* Khomentovskii and Repina)—*0*; **18.** *Pseudojudomia egregia* Egorova *in* Goryanskii and Egorova—*0*; **19.** *Plesionevadia burri* (Walcott)—*2*; **20.** *Nevadia weeksi* Walcott—*3*; **21.** *Nevadella cartlandi* (Raw *in* Walcott)—*2*; **22.** *N. eucharis* (Walcott)—*4*; **23.** *N. mountjoyi* Fritz—*4*; **24.** *N. perfecta* (Walcott)—*4*; **25.** *Cirquella nummularia* Fritz—*4*; **26.** *C. espinata* Fritz—*4*; **27.** *C. nelsoni* Lieberman—*3*; **28.** *Bradyfallotaspis fusa* Fritz—*4*; **29.** *Paranevadella* subgroenlandicus Repina *in* Khomentovskii and Repina—*0*; **30.** *Cambroinyoella wallacei* Lieberman—*3*; **31.** *Geraldinella corneiliana* Fritz—*4*; **32.** *Cambro-*

pallas telesto Geyer—*1*; **33.** *Andalusiana cornuta* Sdzuy—*1*; **34.** *Neltneria jacqueti* (Neltner and Poctey)—*1*; **35.** *Bondonella typica* Hupé—*1*; **36.** *Judomia tera* Lazarenko—*0*; **37.** *Sdzuyomia lotzei* (Richter and Richter)—*1*; **38.** *Callavalonia callavei* (Lapworth)—*2*; **39.** *Callavia broeggeri* (Walcott)—*2*; **40.** *Gabriellus* sp.—*4*; **41.** *Olenellus parvofrontatus* Fritz—*4*; **42.** *O. transitans* (Walcott)—*5*; **43.** *O. nevadensis* (Walcott)—*3*; **44.** *O. roddyi* Resser and Howell—*5*; **45.** *O. clarki* (Resser)—*3*; **46.** *O. thompsoni* (Hall)—*5*; **47.** *O. robsonensis* (Burling)—*4*; **48.** *O. crassimarginatus* Walcott—*5*; **49.** *O. getzi* Dunbar—*5*; **50.** *O. agellus* Resser and Howell—*5*; **51.** *O. romensis* Resser and Howell—*5*; **52.** *Mesolenellus svalbardensis* (Kielan)—*5*; **53.** *M. hyperborea* (Poulsen)—*5*; **54.** *Mesonacis fremonti* (Walcott)—*3*; **55.** *M. bonnensis* (Resser and Howell)—*5*; **56.** *M. vermontanus* (Hall)—*5*; **57.** *M. eagerensis* (Best)—*4*; **58.** M. hamoculus (Cowie and McNamara)—*5*; **59.** M. cylindricus (Palmer *in* Palmer and Halley)—*3*; **60.** *Elliptocephala lundgreni* (Moberg)—*6*; **61.** *E. mirabilis* (Poulsen)—*5*; **62.** *E. logani* (Walcott)—*4, 5*; **63.** *E. parvifrons* (Fritz)—*4*; **64.** *E. paraoculus* (Fritz)—*4*; **65.** *E. laxocules* (Fritz)—*4*; **66.** *E. mediocris* (Poulsen)—*5*; **67.** *E. walcotti* Lieberman—*4*; **68.** *E. praenuntius* (Cowie)—*5*; **69.** *E. bicensis* (Walcott)—*5*; **70.** *E. asaphoides* Emmons—*5*; **71.** *E. sequomalus* (Fritz)—*4*; **72.** *Wanneria walcottana* (Wanner)—*5*; **73.** *Holmiella falcuta* Fritz—*4*; **74.** *H. preancora* Fritz—*4*; **75.** *Esmeraldina rowei* (Walcott)—*3*; **76.** *Palmettaspis parallela* Fritz—*3*; **77.** *P. consorta* Fritz—*3*; **78.** *P. lidensis* (Fritz)—*3*; **79.** "*P.*" *cometes* (Fritz)—*3*; **80.** *Schmidtiellus mickwitzi torelli* (Moberg)—*6*; **81.** *S.* sp.—*6*; **82.** *S. reetae* Bergström—*6*; **83.** *Kjerulfia lata* Kiaer—*6*; **84.** *Baltobergstroemia mobergi* (Bergström)—*6*; **85.** "*B.*" *sulcata* (Bergström)—*6*; **86.** "*B.*" sp.—*1*; **87.** *Holmia kjerulfi* (Linnarsson)—*6*; **88.** "*H.*" *laponica* Ahlberg and Bergström—*6*; **89.** "*H.*" *palpebra* (Ahlberg)—*6*; **90.** *Fritzolenellus reticulatus* (Peach)—*5*; **91.** *F. lapworthi* (Peach)—*5*; **92.** *F. truemani* (Walcott)—*4*; **93.** *Mummaspis occidens* (Walcott)—*4*; **94.** *M. macer* (Walcott)—*5*; **95.** *M. muralensis* (Fritz)—*4*; **96.** *M. oblisooculatus* Fritz—*4*; **97.** *M. truncatooculatus* (Fritz)—*4*; **98.** *Laudonia bispinata* Harrington—*4*; **99.** *L. amputata* Fritz—*4*; **100.** *Bristolia bristolensis* (Resser)—*3*; **101.** *B. fragilis* Palmer *in* Palmer and Halley—*3*; **102.** *B. harringtoni* Lieberman—*3*; **103.** *B. mohavensis* (Hazzard and Crickmay)—*3*; **104.** *B. insolens* (Resser)—*3*; **105.** *B.* sp.—*4*; **106.** *B. anteros* Palmer *in* Palmer and Halley—*3*; **107.** *Fremontella halli* (Walcott)—*5*; **108.** *Lochmanolenellus mexicana* (Lochman *in* Cooper et al.)—*3*; **109.** *Nephrolenellus multinodus* (Palmer *in* Palmer and Halley)—*3*; **110.** *N. jasperensis* Lieberman—*4*; **111.** *Bolbolenellus euryparia* (Palmer *in* Palmer and Halley)—*3*; **112.** *B. altifrontatus* (Fritz)—*4*; **113.** *B. sphaerulosus* (Fritz)—*4*; **114.** *B. hermani* (Kindle and Tasch)—*5*; **115.** *B. groenlandicus* (Poulsen)—*5*; **116.** *Olenelloides armatus* Peach—*5*; **117.** *Biceratops nevadensis* Pack and Gayle—*3*; **118.** *Peachella brevispina* Palmer *in* Palmer and Halley—*3*; **119.** *P. iddingsi* (Walcott)—*3*. Synonymies for all these taxa are given in Lieberman (1998, 1999a, 2001, and herein). Areas were optimized to ancestral nodes using the modified version of Fitch (1971) parsimony described by Lieberman (2000). Only some nodal states are shown for the purposes of brevity and clarity, where: "*A,*" the ancestral biogeographic state of the eutrilobites, is Siberia; "*B,*" the ancestral biogeographic state at the divergence of the "fallotaspidoids" and the redlichiinids, is Siberia and southern Europe-northern Africa; "*C,*" the ancestral biogeographic state shortly before the divergence between the "fallotaspidoids" and the redlichiinids, is Siberia, southern Europe-northern Africa, and northwestern Laurentia; "*D,*" the ancestral biogeographic state of the redlichiinids, is southern Europe-northern Africa and Antarctica; and "*E,*" the ancestral biogeographic state of all of the Olenellina exclusive of *Pseudojudomia egregia*, is Siberia, Avalonia, and southwestern Laurentia.

events between nodes "C" and "B" on Figure 2 appears to involve vicariance, as there is a contraction in range associated with one of the cladogenetic events. After the divergence between the "fallotaspidoids" and the redlichiinids there is evidence for both vicariance and range expansion within the redlichiinids, as the node labeled "D" in Figure 2 no longer occurs in Siberia, but also includes a new area.

Discussion.—The initial distribution of the trilobites was relatively narrow, as they were confined to Siberia. Subsequently, the group expanded its range to encompass all of the Earth's major cratonic blocks. Range expansions or shifts in these early trilobites could have involved either episodes of traditional dispersal (sensu Humphries et al., 1988), dispersion (see Lieberman, 2000), or geo-dispersal (sensu Lieberman and Eldredge, 1996; Lieberman, 1997). The patterns of subsequent range expansion and vicariance in Early Cambrian trilobites can be discerned by tracing the patterns of character change along the nodes of the tree, and between the nodes and terminals of the tree shown in Figure 2.

In the case of the "fallotaspidoids," the range expansions first involved movement into northern Africa followed by movement

into western Laurentia. There were subsequent range expansions by the Redlichiina into Antarctica, Australia, and China. In the case of the Olenellina, the range expansions first involved movement into western Laurentia and Avalonia, the node labeled "E" in Figure 2, with other regions like Baltica and eastern Laurentia invaded subsequently.

There are also several key vicariance events relating to the origin of the redlichiinids from the "fallotaspidoids." These specifically involve the nodes labeled "D," "C," and "B" in Figure 2. The biogeographic state for the last common ancestor of the "fallotaspidoids" and the redlichiinids is Siberia and northern Africa-southern Europe (node "B" in Fig. 2). The ancestral biogeographic state of the Redlichiina plus the derived "fallotaspidoids" *Parafallotaspis*, *Archaeaspis*, and *Fallotaspidella* was even broader, and also encompassed western Laurentia. Thus, immediately prior to the divergence between the "fallotaspidoids" and the Redlichiina, there was a broadly distributed biogeographic fauna, which subsequently became broken up by vicariance. In a fundamental sense, this involved the split between the Olenellid and Redlichiid faunal provinces. As Lieberman (1999b) argued, the eponymous Redlichiid faunal province is derived from the eponymous (and paraphyletic) Olenellid faunal province. The split between these faunal provinces can be broken down into several steps. The first involved vicariance events separating Siberia and northern Africa-southern Europe from an area that included these regions and also western Laurentia (nodes "C" and "B" in Fig. 2). Then, the final event associated with the origin of the Redlichiid faunal province (and the origin of the Redlichiina), labeled node "E" in Figure 2, involved both vicariance and range expansion. Based on cladogram topology it appears that at least initially the Redlichiina were excluded from Siberia, and occurred in southern Europe-northern Africa and Antarctica. Australia and China (and eventually Siberia) were occupied shortly thereafter.

On the whole, the biogeographic patterns recovered here are broadly confluent with the predictions of Fortey et al. (1996) and Fortey and Owens (1997), and suggest that the trilobites have a cryptic history that extends back into the Neoproterozoic, and thus prior to the Cambrian radiation. However, the patterns of vicariance do not correspond exactly to those predicted by Fortey et al. (1996) and Fortey and Owens (1997). Specifically, they argued that the biogeographic patterns should involve vicariant events between taxa ancestrally distributed across western Laurentia, China, Australia, and Antarctica which subsequently became differentiated during the breakup of Rodinia. The biogeographic patterns retrieved here and shown in Figure 2 do not show evidence for vicariance involving these regions, and instead indicate vicariance involved western Laurentia, Siberia, and southern Europe-northern Africa. This vicariant pattern suggests a uniform trilobite fauna was once distributed across south-western Laurentia, the margins of Gondwana, and Siberia. These regions were in contact until the breakup of Pannotia, which various tectonic studies place as occurring between 600–550 Ma. Thus, based on the phylogenetic and biogeographic evidence, trilobites were likely in place across these regions before 550 Ma and perhaps as far back as 600 Ma. Either of these dates is well before the first appearance of trilobites in the fossil record. As trilobites are highly derived metazoans, biogeographic patterns do indeed support a cryptic Cambrian radiation of the Metazoa, though the period of cryptic divergence, at least based on patterns from trilobite biogeography, may not have been as long as that Fortey et al. (1996) and Fortey and Owens (1997) argued for.

IMPLICATIONS OF PHYLOGENETIC ANALYSIS FOR EARLY CAMBRIAN BIOSTRATIGRAPHY

The ranges of trilobite taxa are among the fundamental data used to biostratigraphically subdivide the Lower Cambrian because of their great abundance and diversity in this interval (e.g.,

Walcott, 1910; Resser and Howell, 1938; Fritz, 1972, 1992; Palmer and Halley, 1979; Palmer and Repina, 1993; Geyer, 1996; Landing et al., 1998). Although the development of a workable global stratigraphy of the Early Cambrian has been complicated due to problems correlating between highly endemic faunas (Landing, 1992), significant progress has been made (e.g., Ahlberg, 1991; Fritz, 1992; Palmer and Repina, 1993; Geyer and Landing, 1995; Geyer and Palmer, 1995; Knoll, 1996; Landing et al., 1998; Hollingsworth, 1999a, 1999b; McCollum and Sundberg, 1999). The fundamental biostratigraphic units recognized in the Early Cambrian of Laurentia are, in ascending order, the *Fallotaspis* Zone, the *Nevadella* Zone, and the *Bonnia-Olenellus* Zone (sometimes referred to simply as the *Olenellus* Zone). Although this biostratigraphy represents a highly advanced state of knowledge and is unlikely to change significantly in the future, subtle modification may be necessary and is underway (e.g., Hollingsworth, 1999a, 1999b, 1999c). For instance, Lieberman (1999a) argued that what has traditionally been referred to as the genus *Olenellus* Hall, 1862 is actually a polyphyletic assemblage of taxa. This signifies that there may be some problems with the definition of the eponymous *Olenellus* Zone. Therefore, there may be some potential problems correlating this zone.

In detailed studies of the Early Cambrian biostratigraphy of Morocco, Geyer and Landing (1995) and Geyer (1996) discussed the difficulty of using olenelloid and redlichioid trilobites for global correlations. Geyer (1996) particularly emphasized the problems inherent with the informally defined *Fallotaspis* Zone in Laurentia. The presence of this zone in Laurentia has been discussed in several studies including those of Fritz (1972, 1992), Nelson (1976, 1978), and Palmer and Repina (1993). The stratigraphic refinements of these authors are detailed and represent significant advances over earlier studies. However, because of the difficulties of correlation discussed by Landing (1992), subtle refinements may be in order. One potential area that may need modification involves the boundaries of the *Fallotaspis* Zone in Laurentia. Potential changes to the definition of this zone are in progress and were described by Hollingsworth (1999a, 1999b, 1999c). This topic merits some attention, however, based on the results of phylogenetic analysis presented herein. The stratigraphic distribution of the *Fallotaspis* Zone in Laurentia is constrained by the presence of several taxa including the trilobite genus *Parafallotaspis* Fritz, 1972, known from northwestern Laurentia (Fritz, 1972, 1992) and also some trilobites from southwestern Laurentia figured and discussed by Nelson (1976) and discussed by Nelson (1978), and informally referred to *Fallotaspis*. *Fallotaspis* also occurs in Morocco (Hupé, 1953; Palmer and Repina, 1993; Geyer, 1996), suggesting a potential for biostratigraphic correlation between the Laurentian sections and the marginal Gondwanan sections of Morocco [similarly, Palmer and Repina (1993) referred to a *Fallotaspis* Zone in Siberia, and also suggested that *Fallotaspis* occurs in Avalonia, again indicating the potential for large scale Early Cambrian biostratigraphic correlations, although no species of that genus are known to occur either in Siberia or Avalonia]. However, Geyer (1996) discussed how *Fallotaspis* has a long stratigraphic range in Morocco and may not be a particularly useful biostratigraphic marker. Further complicating matters are some modifications that need to be made to the provisional generic assignments of Nelson (1976, 1978) for some of the trilobites he collected from the White-Inyo mountains of California. Although he originally suggested that these belonged to the genus *Fallotaspis*, these actually belong to *Archaeaspis* based on the phylogenetic analysis conducted herein. The type species of this genus is *Archaeaspis hupei* Repina *in* Khomentovskii and Repina, 1965, which according to Palmer and Repina (1993) occurs in the *Pagetiellus anabarus* Zone in Siberia. Thus, in addition to the convincing arguments in Geyer (1996)

and Hollingsworth (1999a, 1999b, 1999c), simply on phylogenetic grounds the species from southwestern Laurentia should not be used to correlate between Laurentia and Morocco. *Archaeaspis* may, though, allow for potential correlations between Laurentia and Siberia.

Additional insights to Early Cambrian stratigraphy are indicated by material discovered from the White-Inyo Mountains of California. Specimens discussed and illustrated below are known from that part of the Campito Formation traditionally assigned to the *Fallotaspis* Zone. Although these taxa are not described because of the limited material available, they are clearly referable to *Nevadia* based on characters described below. Specimens with similar taxonomic affinities and in a similar biostratigraphic position were discussed by Hollingsworth (1999a, 1999b, 1999c). Traditionally, the *Nevadella* Zone is held to everywhere post date the *Fallotaspis* Zone, yet one taxon used to define the *Nevadella* Zone, the genus *Nevadia*, actually first appears in the *Fallotaspis* Zone, indicating further refinements to the regional Early Cambrian biostratigraphy of western Laurentia may be in order. In light of Geyer's (1996) detailed analysis of the *Fallotaspis* Zone in Morocco, and Hollingsworth's (1999a, 1999b, 1999c) detailed analyses of possibly correlative units in Laurentia, both discussed already, this implies that aspects of the earliest trilobitic biostratigraphic divisions in the Early Cambrian may be those that change the most in the future.

TAXA ANALYZED AND SYSTEMATIC PALEONTOLOGY

Most of the taxa treated in phylogenetic analysis do not need a detailed synonymy list or discussion, and these are simply listed. The other taxa are treated in a systematic paleontology section, where detailed diagnoses and descriptions are provided for two new species. For other taxa, previous diagnoses are sufficient, and these can be augmented using the characters and character codings in Table 1.

Collections from the following institutions were examined in the course of coding various specimens for phylogenetic and biogeographic analysis: University of Kansas Natural History Museum (Division of Invertebrate Paleontology) (KUMIP); Los Angeles County Museum of Natural History (LACMIP).

Abbreviated list of taxa analyzed, significant material examined, and where applicable recent publication with synonymy list or general discussion.—*Repinella sibirica* (Repina *in* Khomentovskii and Repina, 1965) see Geyer (1996); *Daguinaspis ambroggii* Hupé and Abadie, 1950, see Geyer (1996); *Choubertella spinosa* Hupé, 1953, see Geyer (1996); *Eofallotaspis tioutensis* Sdzuy, 1978, see Geyer (1996); *Profallotaspis jakutensis* Repina *in* Khomentovskii and Repina, 1965; *Pelmanaspis jurii* Repina, 1990; *Fallotaspis typica* Hupé, 1953, see Geyer (1996); *Fallotaspis bondoni* (Neltner and Poctey, 1949), see Geyer (1996); *Parafallotaspis grata* Fritz, 1972; *Archaeaspis hupei* Repina *in* Khomentovskii and Repina, 1965; *Fallotaspidella musatovi* Repina, 1961; *Bigotina bivallata* Cobbold, 1935, see Pillola (1993); *Lemdadella linaresiae* Liñán and Sdzuy, 1978; *Lemdadella antarcticae* Palmer *in* Palmer and Rowell, 1995- KUMIP 218060, 218074–218079, 218118, 218120, 218121, 218141, 218143, 218147–218150, 218177.

Order REDLICHIIDA Richter, 1932
Suborder REDLICHIINA Richter, 1932
Superfamily "FALLOTASPIDOIDEA" Hupé, 1953
Family FALLOTASPIDIDAE Hupé, 1953
Genus FALLOTASPIS Hupé, 1953

Discussion.—Several taxa discussed in Geyer (1996) have been referred to *Fallotaspis*. Of these, two exemplars were subjected to phylogenetic analysis because of their excellent state of preservation and completeness: *F. typica* and *F. bondoni*. One other taxon which was not subjected to phylogenetic analysis but deserves mention here is "*Fallotaspis*" *ljungeri* (Kautsky). It was discussed and figured by Bergström (1973), and is based on very poorly preserved material that was not available for study. It may or may not be referable to the "Fallotaspidoidea."

Family ARCHAEASPIDIDAE Repina, 1979
Genus ARCHAEASPIS Repina *in* Khomentovskii and Repina, 1965

Type species.—*Archaeaspis hupei* Repina *in* Khomentovskii and Repina, 1965.
Other species.—*A. nelsoni* n. sp., *A. macropleuron* n. sp.
Diagnosis.—Frontal lobe of glabella does not contact anterior border furrow; plectrum present; anterior margins of frontal lobe at each side of midline deflected posteriorly at roughly 40 degree angle relative to transverse line; length (sag.) of preglabellar field equal to 0.25–0.7 times length (sag.) of L0; posterior tips of ocular lobes developed opposite medial part of distal margin of L0; orientation of S2 straight, abaxially directed inward and posteriorly at roughly 35–45 degree angle to transverse line; midinterocular ridge prominently developed, inclined at roughly 10 degree angle relative to sagittal line.

Discussion.—A diagnosis of this genus has recently been presented by Palmer and Repina (1993, 1997) but a few new characters that have emerged from the cladistic analysis conducted herein are also given above. These can augment the original morphological characterization of the genus as well as what was presented in Palmer and Repina (1993, 1997). Originally *Archaeaspis* was thought to be confined to the Siberian platform (e.g., Palmer and Repina, 1993, 1997), but new species described below from the White-Inyo Mountains of California suggest that this genus has a broader distribution spanning both Laurentia and Siberia. These new species are represented by specimens that were informally referred to both *Fallotaspis* and *Judomia* by Nelson (1976). The assignment of this material to *Judomia* can no longer be advocated because these specimens lack the defining characters of the Olenellina discussed above and in Lieberman (1998, 2001). Although similar in many respects to *Fallotaspis*, these taxa do differ in a few key features, suggesting they are more closely related to *Archaeaspis*. In particular: they have a plectrum; the frontal lobe does not contact the anterior border furrow (this character state is present in some specimens of *F. bondoni*); the anterior margins of the frontal lobe at each side of the midline are deflected posteriorly at a roughly 40 degree angle relative to a transverse line whereas in *Fallotaspis* they are deflected posteriorly at a roughly 10–20 degree angle relative to a transverse line; and finally, the new species of *Archaeaspis* either have spines on T3 that are very short (exsag.), with a length roughly equal to the length (exsag.) of the spines on T2 or T4–T6, or they have a T3 with length (exsag.) greater than the length (sag.) of the entire thorax; by contrast, in *Fallotaspis* T3 is typically moderately long, extending back three to eight segments, except in some specimens of *F. typica* where it may be longer (exsag.) than the length (sag.) of the entire thorax.

Hughes and and Jell (1992) and Rushton and Hughes (1996) have described how tectonic deformation of specimens can produce interesting alterations in trilobite morphology that may lead conspecific taxa to masquerade as evolutionarily divergent forms. Although some of the morphological characters differences described above that distinguish the Laurentian species identified as *Archaeaspis* from typical species of *Fallotaspis* could conceivably be produced by artifacts of tectonic deformation, the characters involving the condition of the plectrum, the preglabellar field, and the thoracic spines cannot be. Furthermore, it is inconceivable that a realistic model of tectonic deformation could consistently and

always in the same manner produce the same morphology in numerous specimens of species of *Archaeaspis* from several distinct localities separated by many miles, and in some cases significant thicknesses of strata. Finally, the species of *Archaeaspis* from Laurentia described here are the only two described representatives of the "Fallotaspidoidea" in Laurentia to date, again indicating that tectonic deformation has not produced chronic specimen mis-identification in this case.

Based on the phylogeny in Figure 1, a putative convergent similarity the Laurentian species of *Archaeaspis* share with *Fallotaspis* is the condition of the anterior cephalic border, which is developed as a rounded ridge in these taxa.

Reassigning the Californian specimens to *Archaeaspis* has biostratigraphic and biogeographic implications. Originally, the presumed presence of *Fallotaspis* in the Lower Cambrian beds of Laurentia was used for biostratigraphic correlation with Moroccan sections. This was challenged by Geyer (1996), based on the pattern of distribution of taxa in Morocco. The revised taxonomy of these species further questions these correlations. Instead, prospects for correlation may emerge with the Siberian sections: *Archaeaspis hupei*, which is closely related to *A. nelsoni* and *A. macropleuron*, is known from the lower *Pagetiellus anabarus* Zone (Palmer and Repina, 1993). Based on correlations given by Palmer and Repina (1993), the inferred relative ages of the southwestern Laurentian sections may need to be adjusted upwards. The changing taxonomic assignment also implies the potential for a biogeographic link between Laurentia and Siberia as opposed to between Laurentia and Morocco. This makes more sense on tectonic grounds as Laurentia and Siberia were presumed to be in contact perhaps into the Early Cambrian (Pelechaty, 1996; Lieberman, 1997), whereas an Early Cambrian tectonic link between Laurentia and Morocco appears more tenuous.

<div align="center">

ARCHAEASPIS NELSONI new species
Figure 3.1, 3.3, 3.5–3.7, 3.9

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Fallotaspis sp. NELSON, 1976, p. 31, pl. 1, top row, second from right; 1978, p. 121.
Judomia sp. NELSON, 1976, p. 31, pl. 2, top row, second from right, pl. 2, bottom right, pl. 2, second row, second from left; 1978, p. 121.
?*Judomia* sp. NELSON, 1976, p. 31, pl. 2, bottom row, second from right.

Diagnosis.—Length (sag.) of preglabellar field roughly 0.9–1.2 times length (sag.) of L0; anterior tip of visual surfaces between S2 and S3; axial part of L0 with spine; length (exsag.) of pleural spine on T3 roughly equal to length (exsag.) of pleural spines on T2, T4–T6; prominent anterolateral nodes on thoracic axis.

Description.—Cephalic length (sag.) 70–80 percent of width (tr.). Anterior cephalic border rounded ridge, length (exsag.) between lateral margins of LA (L4) and genal spine angle roughly equal to length (sag.) of L0. Frontal lobe about 20–25 percent length (sag.) of glabella; frontal lobe does not contact anterior border furrow; plectrum visible; anterior margin of frontal lobe at each side of midline deflected posteriorly at roughly 40 degree angle relative to a transverse line; lateral margins of LA proximal to lateral margins of L0; lateral margins of LA convergent anteriorly; L2 and L3 do not merge distally; line from anterior to posterior edge of ocular lobe forms roughly 10–20 degree angle relative to sagittal line; S0–S3 straight, with medial edge declined posteriorly; width (tr.) of glabella opposite margins of L1 constricted relative to width at lateral margins of L0; posterior edge of ocular lobe opposite medial margin of L0; ocular lobes weakly elevated from extraocular area; posterior margin of L0 with axial spine medially; genal spine prominently developed; genal spine angle opposite distal margin of L0; midinterocular ridge prominently developed, inclined at roughly ten degree angle relative to

sagittal line; width (tr.) extraocular area opposite L1 approximately 70 percent width of glabella at L1.

Indeterminate number (>6) of thoracic segments. Anterior margin of T1 strongly telescoped by posterior margin of cephalon. Anteromedian margin of third thoracic pleural segment transverse; third thoracic segment only slightly macropleural, pleural spine on T3 roughly equivalent in length (exsag.) to length of pleural spine on T2, T4–T6; anterior margin of thoracic pleural furrow on third segment directed weakly posteriorly. Thoracic pleural spines on segments two to five developed as short projections extending approximately two thoracic segments back; thoracic pleural furrows extend roughly entire width of inner pleural region. Anterolateral nodes on thoracic axis prominent.

Type.—Holotype LACMIP 7371 (Fig. 3.1), partial cephalon and thorax from LACMIP locality 6748, Early Cambrian, *Fallotaspis* Zone, Montenegro Mbr., Campito Fm., Inyo Co., CA, Blanco Mtn. USGS quad., SE¼, NE¼, NE¼, sec. 32, T7S, R35E, in small gully just east of north end of Cedar Flat, White-Inyo Mountains.

Etymology.—Named for Clem Nelson, emeritus professor, University of California at Los Angeles, and White Mountain Research Station, who collected the material this species is based on and kindly allowed me to study it.

Other material examined.—LACMIP 7361, 7367, 7371, 7375, 7989, 7991, 26824 (nine unnumbered cephala).

Occurrence.—In addition to LACMIP locality 6748, Early Cambrian, *Fallotaspis* Zone, Inyo Co., CA, White-Inyo Mtns.: LACMIP locality 6749, Montenegro Mbr., Campito Fm., Blanco Mtn. USGS quad., SE¼, NE¼, SE¼, sec. 13, T6S, R35E, on small hill just south of east-west road leading to Silver Canyon; and LACMIP locality 6824, Campito Fm., Bishop USGS quad, NW¼, SE¼, sec. 24, T5S, R33E, on south facing dip slope on north side of small east-west canyon on east side of road.

Discussion.—Some of the specimens that Nelson (1976, pl. 2) figured and referred to the genus *Judomia* Lermontova, 1951 do appear to have been referable to that genus. In particular, those specimens that are figured on the top row, far right, the middle row, far left, and the bottom row, far left are likely specimens of *Judomia*. They have typical characters of the Olenellina and Judomioidea, such as the relatively long (sag.) frontal lobe, and the ocular lobes merging with the entire lateral margins of the frontal lobe, and are discussed more thoroughly in Lieberman (2001). However, other specimens that Nelson (1976) referred to *Judomia* actually are "fallotaspidoids" and represent specimens of *Archaeaspis nelsoni*. These specimens lack the characters of the Olenellina [which are given in Lieberman (1998) and Lieberman (2001)]. A few of the specimens on Nelson's (1976) pl. 2 are too poorly preserved to determine their precise taxonomic affinities and they may or may not be "fallotaspidoids."

The morphology of *A. nelsoni* is similar to that of *A. macropleuron* and they map as sister species on the phylogeny in Figure 1. They differ principally in the condition of the following morphological features: T3 has relatively longer (exsag.) pleural spines in *A. macropleuron* than in *A. nelsoni*; in the condition of the glabella, which is relatively longer (sag.) and closer to the anterior border furrow in *A. macropleuron* than in *A. nelsoni*; in the condition of the anterior part of the ocular lobe which deflects strongly anteriorly near L3 in *A. macropleuron* but not in *A. nelsoni*; and in the condition of the anterior margin of the visual surfaces which are relatively farther forward in *A. macropleuron* than in *A. nelsoni*. They also occur in a very similar set of localities. It is conceivable that these relatively minor differences actually represent sexual dimorphs of a single species rather than two distinct species. However, at this time two distinct species were described since no other cases of such pronounced sexual
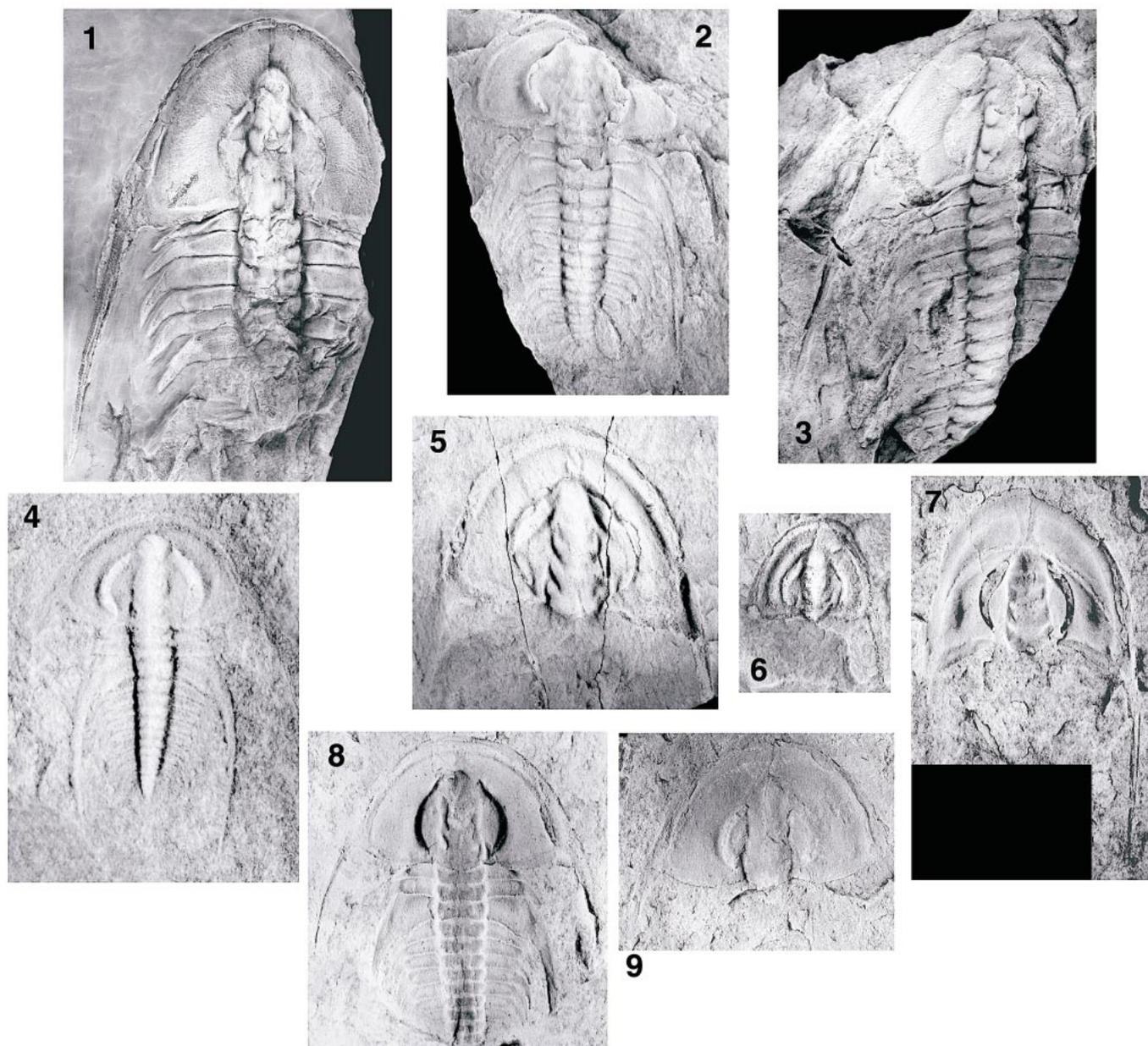
FIGURE 3—*Archaeaspis* spp. Repina *in* Khomentovskii and Repina, 1965, Early Cambrian, *Fallotaspis* Zone, Inyo Co., CA, White-Inyo Mtns., Montenegro Mbr., Campito Fm. *1, 3, 5–7, 9, A. nelsoni* n. sp. *1,* Dorsal view of holotype cephalon and partial thorax, LACMIP 7371, ×2, LACMIP locality 6748; *3,* dorsal view of partial cephalon and thorax, LACMIP 7991, ×1, LACMIP locality 6748; *5,* dorsal view of cephalon, LACMIP 7361, ×2, LACMIP locality 6824; *6,* dorsal view of cephalon, LACMIP 7375, ×2, LACMIP locality 6824; *7,* dorsal view of cephalon, LACMIP 7367, ×2, LACMIP locality 6749, showing crescentic ridge roughly paralleling anterior cephalic margin, probably indicative that this specimen is a molt and the ridge is an impression of the rostral plate that slid backwards during molting (R. A. Robison, pers. comm.); *9,* dorsal view of cephalon, LACMIP 7989, ×2, LACMIP locality 6748; *2, 4, 8, Archaeaspis macropleuron* n. sp., LACMIP locality 6748, *2,* dorsal view of partial cephalon and thorax, LACMIP 7993, ×2; *4,* dorsal view of nearly complete holotype, LACMIP 7362, ×5; *8,* dorsal view of nearly complete external mold, LACMIP 7363, ×2.

dimorphism are known among the ''fallotaspidoids'' or the Ole-nellina.

ARCHAEASPIS MACROPLEURON new species
Figures 3.2, 3.4, 3.8, 4.1, 4.2

Fallotaspis sp. NELSON, 1976, p. 31, pl. 1, top row, far left and second from left, middle row all but far right, bottom row second from left and far right; 1978, p. 121.

Diagnosis.—Preglabellar field short (sag.); anterior part of oc-ular lobe deflects strongly anteriorly near L3; anterior tips of vi-sual surfaces developed opposite adaxial part of S3; axial part of L0 with faint node; length (exsag.) of pleural spine on T3 roughly equal to length (sag.) of entire thorax; prominent anterolateral nodes on thoracic axis absent.

Description.—Same as for *A. nelsoni* except: Cephalic length (sag.) 60–70 percent of width (tr.). Width (tr.) extraocular area
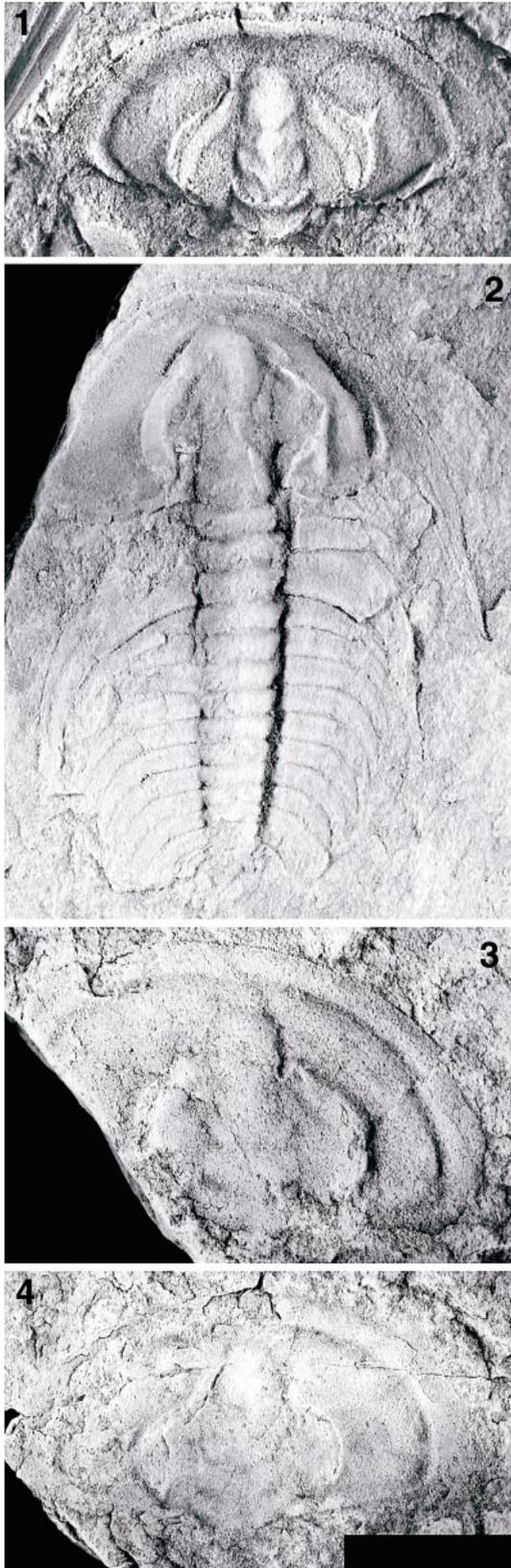
opposite L1 approximately 70–80 percent width of glabella at L1.

Approximately 16–17 thoracic segments; length (exsag.) of pleural spine on T3 greater than length (sag.) of entire thorax; thoracic pleural spines on segments five to eight developed as short projections extending approximately two to three thoracic segments back; thoracic pleural furrows extend roughly entire width of inner pleural region. Anterolateral nodes on thoracic axis not prominent.

Type.—Holotype LACMIP 7363 (Fig. 3.4), cephalon and partial thorax from LACMIP locality 6748, Early Cambrian, *Fallotaspis* Zone, Montenegro Mbr., Campito Fm., Inyo Co., CA, Blanco Mtn. USGS quad., SE¼, NE¼, NE¼, sec. 32, T7S, R35E, in small gully just east of north end of Cedar Flat, White-Inyo Mountains.

Etymology.—Named for the large pleural spine on T3.

Other material examined.—LACMIP 7362, 7363, 7366, 7990, 7992–7996, 26748 (three unnumbered cephala and two unnumbered complete specimens), 26749 (five unnumbered cephala and one unnumbered complete specimen), 26789 (one unnumbered cephalon), 26823 (two unnumbered cephala).

Occurrence.—In addition to LACMIP locality 6748, Early Cambrian, *Fallotaspis* Zone, Inyo Co., CA, White-Inyo Mtns.: LACMIP locality 6749, Montenegro Mbr., Campito Fm., Blanco Mtn. USGS quad., SE¼, NE¼, SE¼, sec. 13, T6S, R35E, on small hill just south of east-west road leading to Silver Canyon; LACMIP locality 6789, Campito Fm., Waucoba Mtn. USGS quad., SW¼, SE¼, sec. 20, T8S, R35E, just northwest of small hill (8,080 ft) on 8,000 ft contour, approximately 1,900 ft southeast of VABM 8250; and LACMIP locality 6823, Campito Fm., Waucoba Springs USGS quad., SE¼, SE¼, sec. 4, T11S, R37E, in small gully just southeast of 6,640 ft closed contour at 6,560 ft.

Discussion.—Most of the specimens Nelson (1976) figured and referred to as *Fallotaspis* on his plate one belong to *A. macropleuron*. However, one of these specimens figured on the top row, second from the right appears to represent a specimen of *A. nelsoni* on the basis of its relatively long (sag.) preglabellar area. The specimens on the top row at the far right and on the bottom row two from the right are referable to *Cambroinyoella wallacei* Lieberman, 2001. This taxon is discussed extensively in Lieberman (2001). The two specimens on Nelson's (1976, pl. 1), bottom row, far left, and the middle row, far right, are too poorly preserved to determine their taxonomic affinities.

Suborder OLENELLINA Walcott, 1890
Superfamily ''NEVADIOIDEA'' Hupé, 1953
Genus NEVADIA Walcott, 1910
NEVADIA sp.
Figure 4.3, 4.4

Material examined.—LACMIP 7997, 7998.

Occurrence.—Early Cambrian, *Fallotaspis* Zone, Inyo Co., CA, White-Inyo Mtns.: LACMIP locality 6748, Early Cambrian, Montenegro Mbr., Campito Fm., Inyo Co., CA, Blanco Mtn. USGS quad., SE¼, NE¼, NE¼, sec. 32, T7S, R35E, in small gully just east of north end of Cedar Flat; and LACMIP 6789, Campito Fm., Waucoba Mtn. USGS quad., SW¼, SE¼, sec. 20, T8S, R35E, just northwest of small hill (8,080 ft) on 8,000 ft contour, approximately 1,900 ft southeast of VABM 8250.

Discussion.—Two poorly preserved partial cephala from the

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FIGURE 4—Early Cambrian, *Fallotaspis* Zone, Inyo Co., CA, White-Inyo Mtns., Montenegro Mbr., Campito Fm. *1, 2, Archaeaspis macropleuron* n. sp. *1,* dorsal view of cephalon, LACMIP 7366, ×6, LACMIP locality 6749; *2,* dorsal view of partial cephalon and thorax, LACMIP 7996, ×2.4, LACMIP locality 6748. *3, 4, Nevadia* sp., LACMIP locality 6748. *3,* dorsal view of partial cephalon, LACMIP 7997, ×2.2; *4,* dorsal view of partial cephalon, LACMIP 7998, ×3.

Fallotaspis Zone represent specimens referable to the ''Nevadioidea.'' [The ''Nevadioidea'' are discussed more fully in Lieberman (2001)]. Specifically, these two specimens have the ocular lobes contacting the posterior margins of the frontal lobe, the ocular lobes gradually decrease in dorso-ventral elevation between the mid-point of the ocular lobes and the axial furrows, and the frontal lobe is relatively long (sag.), roughly equal to the length (sag.) of L0 and L1. Within the ''Nevadioidea'' they are not likely to be closely related to *Plesionevadia* Lieberman, 2001 because they have a prominent anterior cephalic border furrow, they do not have a very long (exsag.) parafrontal band, the posterior tips of the ocular lobes are not opposite S0, they lack a raised swelling in the interocular area, and the interocular area is relatively narrow. They differ from *Cirquella* Fritz, 1993, because they have relatively broad (tr.) extraocular areas and the ocular lobes do not contact the entire lateral margin of the frontal lobe. These specimens may be similar to or conspecific with the specimens referred to by Hollingsworth (1999c) informally as *Paranevadella* Palmer and Repina, 1993. However, if so, that generic assignment is not correct because *Paranevadella* is characterized by having the ocular lobes contacting the entire lateral margin of the frontal lobe, and by having the posterior border of the cephalon deflected much further posteriorly near the genal spine than near L0. The genera the two partial cephala from the *Fallotaspis* Zone share the most features with are *Nevadia* or *Nevadella* Raw, 1936. The one character that suggests these specimens have a closer relationship with *Nevadia* is the condition of S0, which is straight in the two specimens and in *Nevadia* whereas S0 is typically convex in *Nevadella*. However, because of the poor state of preservation, several character state distributions for these specimens cannot be determined in detail and therefore they could be conceivably referred to *Nevadella* instead so the assignment to *Nevadia* should be treated as tentative. Other characters visible in the specimens include the condition of: the anterior cephalic border, which has a length (exsag.) roughly equal to the length (sag.) of L0; the anterior margins of the frontal lobe, which at each side of the midline are deflected posteriorly at a roughly 40 degree angle relative to a transverse line; the width (tr.) of the glabella, which uniformly constricts from its posterior to anteriormost point; the posterior tips of the ocular lobes are opposite the medial part of the distal margins of L0; the cephalic posterior border, which is roughly transverse; the width (tr.) of the extraocular region, which is about 70 percent of the width of the glabella at L1; and the genal spine angle, which is developed opposite the medial part of the distal margin of L0. At this time these specimens are not described as new species because the material available is relatively poor, and Hollingsworth's (1999c) work in progress suggests that describing this material at this time may not be prudent as new, potentially closely related or conspecific material may come to light shortly. Among species of *Nevadia*, this new material from the White-Inyo Mountains differs from *N. bacculenta* (Fritz, 1972) because its cephalic posterior border is transverse instead of being deflected posteriorly near its lateral margins, and because the interocular area is relatively broad (tr.); it differs from *N. fritzi* Lieberman, 2001 because its cephalic posterior border is transverse instead of being deflected posteriorly near its lateral margins, and because the ocular lobes are relatively longer (exsag.). The material from the White-Inyos most closely resembles *N. faceta* (Fritz, 1972), *N. weeksi* Walcott, 1910, and *N. gracile* (Walcott, 1910).

LEMDADELLA Sdzuy, 1978

Discussion.—In the phylogeny in Figure 1 the two species of *Lemdadella* do not map as sister taxa, suggesting that this genus may be paraphyletic. However, a more formal designation of the paraphyly of the genus *Lemdadella* is not pursued at this time

because of the relatively limited coverage that basal, sutured species belonging to the Redlichiina had in this phylogenetic analysis. The genera *Bigotina* and *Lemdadella* were chosen as limited exemplars to assess relative phylogenetic patterns within the ''Fallotaspidoidea.'' It is likely that the addition of more taxa within the Redlichiina but outside of the ''Fallotaspidoidea'' is needed to obtain a complete picture of the evolutionary relationships of *Lemdadella* and *Bigotina* to one another, and of course to other suture bearing redlichiine taxa.

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