PHYLOGENETIC REVISION OF THE LATE ORDOVICIAN ORTHID BRACHIOPOD GENERA *PLAESIOMYS* AND *HEBERTELLA* FROM LAURENTIA

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ABSTRACT—The orthidine brachiopod genera *Plaesiomys* and *Hebertella* are significant constituents of Late Ordovician benthic marine communities throughout Laurentia. Species-level phylogenetic analyses were conducted on both genera to inform systematic revisions and document evolutionary relationships. Phylogenetic analyses combined discrete and continuous characters, from which character states were determined using a statistical approach, and utilized both cladistic and Bayesian methodologies. *Plaesiomys cutterensis*, *P. idahoensis*, and *P. occidentalis* are herein recognized as distinct species rather than subspecies of *P. subquadratus*. Similarly, *Hebertella montoyensis* and *H. prestonensis* are recognized as distinct species separate from *H. occidentalis,* and *H. richmondensis* is recognized as a distinct species rather than a geographical variant of *H. alveata. Hebertella subjugata* is removed from its tentative synonymy with *H. occidentalis* and revalidated.

The development of species-level evolutionary hypotheses for *Plaesiomys* and *Hebertella* provides a detailed framework for assessing evolutionary and paleobiogeographic patterns of Late Ordovician brachiopods from Laurentia. The geographic range of *Hebertella* expanded throughout Laurentia during the Richmondian into both intracratonic and marginal basins. *Plaesiomys subquadratus* participated in the Late Ordovician Richmondian Invasion. The recovered phylogenetic topology for *Plaesiomys* suggests that *P. subquadratus* may have migrated into the Cincinnati region from a basin situated to the paleo-northeast.

INTRODUCTION

ORTHID BRACHIOPODS were among the most common benthic organisms in Late Ordovician benthic marine communities. Despite their abundance, diversity, and excellent preservation, few species-level evolutionary hypotheses for orthid brachiopods have been constructed (e.g., Stigall Rode, 2005) and only one involves a Late Ordovician taxon (Wright and Stigall, in press). The purpose of this study is to develop phylogenetically informed taxonomic revisions for two significant genera representative of Late Ordovician orthid brachiopods: *Hebertella* and *Plaesiomys*. Phylogenetic hypotheses were developed by subjecting both discrete and statistically constrained continuous character data to parsimony and Bayesian analysis.

The phylogenetic revisions presented herein aim to revise the taxonomy and document evolutionary relationships among species in these genera from North America. In addition, the construction of evolutionary hypotheses for *Hebertella* and *Plaesiomys* may provide valuable data for constraining species-level analyses of paleobiogeographic patterns for Late Ordovician orthid brachiopods distributed throughout the Laurentian paleocontinent. For example, *Plaesiomys subquadratus* (Hall, 1847) participated in the Late Ordovician Richmondian Invasion, an event which introduced over 50 genera to the present-day Cincinnati region (Foerste, 1912; Meyer and Davis, 2009). The phylogenetic placement of *P. subquadratus* may be used to test competing paleobiogeographic hypotheses regarding the geographic source of the Richmondian invaders (see Stigall, 2010a).

TAXONOMIC BACKGROUND

Plaesiomys *systematics.*—The orthidine brachiopod genus *Plaesiomys* Hall and Clarke, 1892 ranges throughout the Late Ordovician (Katian to Hirnantian). *Plaesiomys* reached maximal diversity during the late Katian and is a significant constituent of benthic marine communities in Late Ordovician deposits of the Northern Hemisphere. Although several emended diagnoses have been published (e.g., Jin and Zhan, 2008; Macomber, 1970), previous taxonomic revisions of *Plaesiomys* focused on describing new species or shifting the status of *Plaesiomys* between a discrete genus or a subgenus within *Dinorthis* Hall and Clark, 1892. Although suggested by Macomber (1970), no prior study has utilized phylogenetic analysis to inform a comprehensive taxonomic revision or assess evolutionary relationships among species of *Plaesiomys* from North America.

Plaesiomys was erected by Hall and Clarke in 1892 to contain species with shells morphologically similar to *Orthis subquadrata* Hall, 1847. Hall and Clarke (1892) considered *Plaesiomys* to be closely allied with *Hebertella* Hall and Clarke, 1892, but *Plaesiomys* was synonymized with *Dinorthis* by Winchell and Schuchert (1893). There has been much controversy regarding the taxonomic relationship between *Plaesiomys* and *Dinorthis* (Jin and Zhan, 2001; Macomber, 1970; Schuchert, 1913; Schuchert and Cooper, 1932; Wang, 1949; Winchell and Schuchert, 1893). For example, Schuchert and Cooper (1932) considered *Plaesiomys* a subgenus of *Dinorthis*, whereas Williams and Wright (1965) reversed this treatment and considered *Dinorthis* a subgenus of *Plaesiomys*.

Although multiple criteria have been used to distinguish *Plaesiomys* and *Dinorthis*, generic differentiation hinges on whether the shell exterior is costate or multicostellate. Authors disagree about whether a continuum exists between the costate *Dinorthis* and the fully multicostellate *Plaesiomys* (Schuchert and Cooper, 1932; Winchell and Schuchert, 1893). Wang (1949) considered *Dinorthis* to encompass species exhibiting costae that

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TABLE *1*—Species included in phylogenetic analysis of *Plaesiomys*. Asterisk indicates outgroup.

Dinorthis meedsi arctica* Shuchert, 1900
Dinorthis sweeneyi* (Winchell, 1881)
Dinorthis venusta* Cooper, 1956
Plaesiomys anticostiensis (Shaler, 1865)
Plaesiomys belilamellosus Wang, 1949
Plaesiomys bellistriatus Wang, 1949
Plaesiomys carltona (Twenhofel, 1928)
Plaesiomys cutterensis Howe, 1966
Plaesiomys idahoensis Ross, 1949
Plaesiomys occidentalis Ladd, 1929
Plaesiomys proavitus (Winchell and Schuchert, 1892)
Plaesiomys subcircularis (Roy, 1941)
Plaesiomys subquadratus (Hall, 1847)

TABLE *2*—Species included in phylogenetic analysis of *Hebertella*. Asterisk indicates outgroup.

Doleroides tennesseensis* Cooper, 1956
Hebertella alveata Foerste, 1909a
Hebertella bursa Raymond, 1928
Hebertella frankfortensis Foerste, 1909b
Hebertella montoyensis Howe, 1966
Hebertella occidentalis (Hall, 1847)
Hebertella maria (Billings, 1862)
Hebertella parksensis Foerste, 1909b
Hebertella prestonensis Ladd, 1929
Hebertella richmondensis Foerste, 1909a
Hebertella subjugata (Hall, 1847)

do not branch or in which secondary costae are less coarse than primary costae, whereas he assigned all multicostellate species to *Plaesiomys*. Macomber's (1970) broader diagnosis of *Dinorthis* included multicostellate species in which the secondary costae occur only on the lateral margins of the shell. Williams and Harper (2000) reverted to Hall and Clarke's (1892) original designation and considered *Plaesiomys* and *Dinorthis* to be separate, distinct genera.

Jin and Zhan (2001) provided support for this distinction by noting that *Dinorthis* has coarse costae with rare evidence of bifurcation whereas *Plaesiomys* has fine costae and is always multicostellate. In addition, species of *Dinorthis* are typically rectimarginate whereas species of *Plaesiomys* are usually uniplicate (Jin and Zhan, 2001). In contrast to previous taxonomic treatments which considered the ventral muscle scars of *Plaesiomys* and *Dinorthis* indistinguishable (Schuchert, 1913; Schuchert and Cooper, 1932), Jin and Zhan (2001) noted two important differences: 1) the ventral muscle scars of *Dinorthis* are more strongly bilobed than those of *Plaesiomys* and exhibit a medial notch at the anterior margin of the muscle field, and 2) the anterior margin of the ventral adductor muscle scars extend to the medial notch in *Dinorthis* yet is enclosed within the diductor scars in *Plaesiomys*. The suite of characters identified by Jin and Zhan (2001) strongly supports the distinction of these two genera, and we accept their support of the monophyly of *Plaesiomys* as an underlying basis for this analysis.

The phylogenetic analysis of North American species of *Plaesiomys* presented herein provides a comprehensive taxonomic revision in which taxonomic designations are emended and evolutionary relationships are investigated among species distributed throughout the Laurentian paleocontinent.

Hebertella systematics.—The plectorthidine brachiopod genus *Hebertella* Hall and Clarke, 1892 occurs in Whiterockian (lower Sandbian) to Gamachian (Hirnantian) strata of Laurentia. Species of *Hebertella* reached maximal diversity and abundance throughout the Cincinnatian Series (upper Sandbian to Katian) and became significant constituents of the largely endemic Richmondian brachiopod fauna of Laurentia (Cocks and Torsvik, 2011; Schuchert and Cooper, 1932). Although several taxonomic revisions of *Hebertella* have been conducted (i.e., Schuchert and Cooper, 1932; Cooper, 1956; Walker, 1982), these have focused primarily on amending specific designations or diagnoses (Cooper, 1956; Walker, 1982). No prior study has utilized phylogenetic analysis to inform a comprehensive taxonomic revision or assess evolutionary relationships among species of *Hebertella*.

Hall and Clarke's (1892) original conception of *Hebertella* included a morphologically diverse set of species. Subsequently, many of these species were recognized as type species of distinct genera including *Glyptorthis* Foerste 1914a, *Eridorthis* Foerste, 1909a, *Austinella* Foerste, 1909a, and *Mimella* Cooper, 1930,

whereas other species were transferred to existing genera, such as *Plectorthis* Hall and Clarke, 1892. Schuchert and Cooper (1932) summarized these revisions and provided a less inclusive diagnosis in which they recognized species of *Hebertella* on the basis of a convexoconcave to unequally biconvex multicostellate exterior with an obcordate ventral muscle field surrounding a double-adductor scar ridge. Further, Cooper (1956) followed Schuchert and Cooper's (1932) revised diagnosis of *Hebertella* and transferred five species originally assigned to *Hebertella* into *Mimella*. Walker (1982) provided a partial taxonomic revision of *Hebertella* and synonymized the type species *H. sinuata* (Hall, 1847) with *H. occidentalis* (Hall, 1847). However, Walker's (1982) revision of *Hebertella* is incomplete because his investigation was geographically limited to Kentucky.

This analysis of *Hebertella* provides a comprehensive phylogenetically informed taxonomic revision by emending taxonomic designations and documenting evolutionary relationships among species distributed throughout the Laurentian paleocontinent.

TAXA ANALYZED

Plaesiomys analysis.—Specimens belonging to ten species of *Plaesiomys* occurring in Laurentia were examined for phylogenetic analysis (Table 1). All known Late Ordovician species available were examined for morphological character data except for *P. rockymontana* Wilson, 1926, a rare species only known from incomplete type specimens (Jin, personal commun., 2011). Species of *Plaesiomys* occurring outside of North America were excluded because this investigation is limited to assessing evolutionary patterns in Laurentian species. Because *Plaesiomys* and *Dinorthis* share many morphological features and have previously been considered sister taxa (Schuchert and Cooper, 1932), *Dinorthis* was chosen as the outgroup for character polarization. Three species of *Dinorthis* were included in the analysis: *D. meedsi arctica* Schuchert, 1900, *D. sweeneyi* (Winchell, 1881), and *D. venusta* Cooper, 1956. These species were chosen because the type specimens were well preserved and representative of *Dinorthis*. Unfortunately, the type species of *Dinorthis*, *Orthis pectinella* Emmons, 1942 is poorly preserved and consequently not sufficiently informative for character analysis (Jin et al., 2007).

Three subspecies of *Plaesiomys subquadratus* were included in phylogenetic analysis: *P. s. cutterensis* Howe, 1966, *P. s. idahoensis* Ross, 1959, and *P. s. occidentalis* Ladd, 1929. Each subspecies has well-preserved type material and was coded separately from Hall's (1847) types of *P. subquadratus* to test whether phylogenetic analysis upholds subspecific diagnoses.

Hebertella analysis.—Specimens assigned to ten Laurentian species of *Hebertella* were examined for phylogenetic analysis (Table 2). *Doleroides tennesseensis* Cooper, 1956 was selected as the outgroup for character polarization. This species were chosen because the type specimens were well preserved and representative of *Doleroides* Schuchert and Cooper, 1930, a plectorthidine

TABLE 3—Characters used in phylogenetic analysis of *Plaesiomys*.

General characters

1. Maximum width. The maximum shell width parallel to the hinge line. (0), narrow (≤ 21.452); (1), wide (≥ 25.049).
2. Relative inflation of the dorsal valve. Recorded as the ratio of the maximum dorsal height, measured perpendicular to the commissural plane, divided by the maximum width, measured parallel to the hinge line. (0), high (≥ 0.269); (1), low (≤ 0.239).
3. Relative inflation of the ventral valve. Recorded as the ratio of the maximum ventral valve height, measured perpendicular to the commissural plane, divided by the maximum width, measured parallel to the hinge line. (0), low (≤ 0.117); (1), high (≥ 0.120).
4. Shell thickness. Recorded as the total height of the individual divided by the maximum width, measured parallel to the hinge line. (0), low (≤ 0.329); (1), (≥ 0.364).
5. Comparative convexity of the valves. Recorded as the ratio of the ventral valve height, measured as the maximum vertical height of the ventral valve perpendicular to the commissural plane and the dorsal valve height, measured as the maximum vertical height of the ventral valve perpendicular to the commissural plane. (0), high (≥ 0.414); (1), low (≤ 0.413).
6. Depth of the shell. Ratio of the maximum shell length, measured perpendicular to the hinge line, divided by the maximum shell width, measured parallel to the hinge line. (0), low (≤ 0.781); (1), high (≥ 0.813).
7. Depth of the sulcus. Recorded as the ratio of the sulcus, measured as the vertical distance between the commissure at the center of the sulcus and the commissure at the break in the slope at the side of the sulcus, divided by shell thickness of the brachiopod. (0), high (≥ 2.743); (1), low (≤ 2.048).
8. Origin of the sulcus. Recorded as the ratio of the distance, measured perpendicular to the hinge line, from the ventral umbo to the beginning of a perceptible concave deflection in the ventral valve divided by the maximum length of the valve, measured perpendicular to the hinge line. (0), distal (≥ 0.531); (1), proximal (≤ 0.494).
9. Outline shape. (0), subelliptical; (1) subquadrate.
10. Costal density. Recorded as the number of costae per 5 mm at the anterior margin of the valves, divided by the maximum shell width measured parallel to the hinge line. (0) low (≤ 0.267); (1) high (≥ 0.359).
11. Presence of secondary costae. (0), absent to rare; (1) abundant.

Ventral valve characters

12. Length of the ventral muscle scars. Recorded as the ratio of the maximum length of the ventral muscle field, measured perpendicular to the hinge line, divided by the maximum shell length, measured perpendicular to the hinge line. (0), short (≤ 0.473); (1) long (≥ 0.499).
13. Height of the ventral cardinal area. Recorded as the ratio of the vertical distance from the hinge line to the top of the ventral interarea, measured perpendicular to the hinge line, divided by the ventral valve height, measured as the maximum vertical height of the ventral valve perpendicular to the commissural plane. (0), high (≥ 0.674); (1), low (≤ 0.662).
14. Angle of the ventral cardinal area. Recorded as the angle between the lateral boundaries of the ventral interarea. (0), high ($\geq 150°$); (1), low ($\leq 145°$).
15. Ventral umbonal angle. Recorded as the angle between the two limbs of the umbo when the dorsal valve is oriented parallel to the commissural plane. (0), high ($\geq 155°$); (1), low ($\leq 150°$).
16. Angle of the delthyrium. Recorded as the angle between the lateral edges of the delthyrial opening. (0), low ($\leq 50°$); (1) high ($\geq 60°$).
17. Posterior extension of the ventral umbo across the hinge line. Recorded as the ratio of the distance of extension of the ventral umbo, measured perpendicular to the hinge line, divided by the length of the hinge line. (0), high (≥ 0.063); (1), low (≤ 0.053).
18. Angle between the ventral interarea and the hinge line. Recorded as the angle at which the ventral interarea diverges from the commissural plane prior to incurving. (0), upright ($\geq 75°$); (1), inclined ($\leq 70°$).

Dorsal valve characters

19. Height of the dorsal cardinal area. Recorded as the ratio of the vertical distance from the hinge line to the top of the dorsal interarea, measured perpendicular to the hinge line, divided by the ventral valve height, measured as the maximum vertical height of the dorsal valve perpendicular to the commissural plane. (0), high (≥ 0.126); (1), low (≤ 0.049).
20. Dorsal umbonal angle. Recorded as the angle between the two limbs of the umbo when the dorsal valve is oriented parallel to the commissural plane. (0), high ($\geq 150°$); (1), low ($\leq 145°$).
21. Posterior extension of the dorsal umbo across the hinge line. Recorded as the ratio of the distance of extension of the dorsal umbo, measured perpendicular to the hinge line, divided by the length of the hinge line. (0), high (≥ 0.052); (1), low (≤ 0.049).

genus and potential sister taxon of *Hebertella* (Schuchert and Cooper, 1932; Williams and Wright, 1965).

Because Walker (1982) questioned whether *H. subjugata* (Hall, 1982) was a distinct species from *H. occidentalis*, data for *H. subjugata* was coded separately to test the taxonomic validity of *H. subjugata*. In addition, three taxa previously assigned subspecific ranks were included in phylogenetic analysis: *H. alveata richmondensis* Foerste, 1909a, *H. sinuata prestonensis* Ladd, 1929 and *H. occidentalis montoyensis* Howe, 1966. Each subspecies has well-preserved type material and was coded separately to test whether the phylogenetic analysis would uphold the subspecific diagnoses.

MATERIAL EXAMINED

Specimens from the type series of each species were examined for character analysis whenever possible. The type series for most species examined consisted of multiple specimens, thereby providing range of intraspecific morphological variation. Additional non-type and figured specimens from museum collections and the literature were analyzed when available to more accurately assess the total the range of morphological variability within each species. Specimens examined for each species are indicated in the Systematic Paleontology section.

Only data from specimens interpreted to be adult individuals were incorporated into the analysis. Ontogenetic stage was determined by surveying all specimens available for a given species as a group. Specimens were interpreted to be adults when the hinge line and commissure reached a morphology that was stable compared to other specimens of similar or larger sizes. For example, specimens that exhibited stable ventral and dorsal umbonal angles relative to other specimens of the same or larger sizes were classified as adults and included in our analyses. Furthermore, Schuchert and Cooper (1932) noted that small, articulated specimens of *Hebertella* are difficult to distinguish from *Plectorthis*. Small specimens interpreted as young individuals were, therefore, excluded to remove ontogenetic variation or incorrect generic diagnoses from impacting character state distributions.

Specimens were examined from the collections within the United States National Museum of Natural History (USNM); American Museum of Natural History (AMNH); University of Iowa Paleontology Repository (SUI), Academy of Natural Sciences of Philadelphia (ANSP), and the Yale Peabody Museum (YPM).

CHARACTERS AND CODING

A total of 21 characters comprising internal and external morphological traits were included within the *Plaesiomys* analysis (Table 3), and 18 characters were analyzed for the *Hebertella* analysis (Table 4). Both internal and external morphological characters were utilized because they have

TABLE 4—Characters utilized in phylogenetic analysis of *Hebertella*.

General characters

1. Maximum width. The maximum shell width parallel to the hinge line. (0), narrow ($\leq$24.618); (1), wide ($\geq$27.128).
2. Inflation of the dorsal valve. Recorded as the ratio of the maximum dorsal height, measured perpendicular to the commissural plane, divided by the maximum width, measured parallel to the hinge line. (0), low ($\leq$0.311); (1), high ($\geq$0.319).
3. Inflation of the ventral valve. Recorded as the ratio of the maximum ventral valve height, measured perpendicular to the commissural plane, divided by the maximum width, measured parallel to the hinge line. (0), low ($\leq$0.175); (1), high ($\geq$0.208).
4. Comparative convexity of the valves. Recorded as the ratio of the ventral valve height, measured as the maximum vertical height of the ventral valve perpendicular to the commissural plane and the dorsal valve height, measured as the maximum vertical height of the ventral valve perpendicular to the commissural plane. (0), high ($\geq$0.631); (1), low ($\leq$0.567).
5. Depth of the shell. Ratio of the maximum shell length, measured perpendicular to the hinge line, divided by the maximum shell width, measured parallel to the hinge line. (0), high ($\geq$0.770); low ($\leq$0.742).
6. Depth of the sulcus. Recorded as the ratio of the sulcus, measured as the vertical distance between the commissure at the center of the sulcus and the commissure at the break in the slope at the side of the sulcus, divided by shell thickness of the brachiopod. (0), shallow ($\leq$7.900); (1) deep ($\geq$10.490).
7. Width of the sulcus. Recorded as the ratio of the distance, measured parallel to the hinge line, between the inflection points on the sulcus, divided by the maximum width of the shell. (0), wide ($\geq$0.447); (1), narrow ($\leq$0.435).
8. Number of costae in the sulcus. Recorded as the total count of costae between the slope breaks at both sides of the sulcus measured parallel to the commissural plane. (0), many ($\geq$17); (1), few ($\leq$15).
9. Outline shape. (0), subelliptical; (1) subquadrate.
10. Termination of cardinal extremities. (0), rounded; (1) angular.

Ventral valve

11. Maximum width of the ventral muscle scars. Recorded as the ratio of the maximum width of the ventral muscle field, measured parallel to the hinge line, divided by the maximum valve width, measured parallel to the hinge line. (0), narrow ($\leq$0.251); (1), wide ($\geq$0.300).
12. Height of the ventral interarea. Recorded as the ratio of the vertical distance from the hinge line to the top of the ventral interarea, measured perpendicular to the hinge line, divided by the ventral valve height, measured as the maximum vertical height of the ventral valve perpendicular to the commissural plane. (0), high ($\geq$0.779); (1) low ($\leq$0.661).
13. Ventral umbonal angle. Recorded as the angle between the two limbs of the umbo when the dorsal valve is oriented parallel to the commissural plane. (0), low ($\leq$135°); (1), high ($\geq$140°).
14. Angle of the delthyrium. Recorded as the angle between the lateral edges of the delthyrial opening. (0), ($\leq$35°); (1), high ($\geq$40°).
15. Angle between the ventral interarea and the hinge line. Recorded as the angle at which the ventral interarea diverges from the commissural plane prior to incurving. (0), upright ($\geq$90°); (1), inclined ($\leq$85°).

Dorsal valve

16. Height of the dorsal cardinal area. Recorded as the ratio of the vertical distance from the hinge line to the top of the dorsal interarea, measured perpendicular to the hinge line, divided by the dorsal valve height, measured as the maximum vertical height of the ventral valve perpendicular to the commissural plane. (0), low ($\leq$0.104); (1), high ($\geq$0.129).
17. Dorsal umbonal angle. Recorded as the angle between the two limbs of the umbo when the dorsal valve is oriented parallel to the commissural plane. (0), low ($\leq$135°); (1), high ($\geq$140°).
18. Posterior extension of the dorsal umbo across the hinge line. Recorded as the ratio of the distance of extension of the dorsal umbo, measured perpendicular to the hinge line, divided by the length of the hinge line. (0), high ($\geq$0.052); (1), low ($\leq$0.049).

previously been demonstrated to be useful for constructing phylogenetic hypotheses of fossil brachiopods (Leighton and Maples, 2002; Stigall Rode, 2005; Wright and Stigall, in press) and form the basis of many specific diagnoses of the included taxa (Howe, 1966; Wang, 1949; Walker, 1982; Williams and Harper, 2002).

Although both internal and external characters were used, emphasis is placed upon external morphology in the analyses presented here because many potential internal morphological characters for species of *Plaesiomys* and *Hebertella* do not contain grouping information about species-level traits. Numerous internal characters were analyzed during the data collection stage of this analysis, but potential characters (such as adjustor scar width) that exhibited intraspecific variation greater than interspecific variation were excluded from the final analysis;

therefore, data on these traits are not presented here. For example, a character coding the shape of the ventral muscle scars for species of *Plaesiomys* does not contain useful information about grouping related species because morphological variation within populations of a single species, *Plaesiomys subquadratus*, in the collections of the NMNH is greater than the variation among the numerous *Plaesiomys* species also reposited in those collections. Although internal characters are useful for generic differentiation (e.g., Jin and Zhang, 2001), the intraspecific variation within these traits precludes their utility in a species-level phylogenetic analysis. In addition, although apomorphic characters are taxonomically important for specific diagnoses, all apomorphic internal and external species-level characters were excluded from parsimony analysis because they

TABLE 5—Data ranges for continuous characters of species analyzed in phylogenetic analysis of *Plaesiomys*.

	1	2	3	4	5	6	7
D. meedsi arctica	16.22–19.03	0.144–0.199	0.113–0.125	0.257–0.323	0.627–0.785	0.755–0.813	3.230
D. sweeneyi	22.17–22.48	0.120–0.161	0.137	0.298	0.856	0.744–0.790	2.550–7.838
D. venusta	20.97–24.36	0.332–0.333	0.085–0.118	0.319–0.350	0.366–0.510	0.781–0.797	2.571–2.919
P. anticostiensis	21.98–33.26	0.279–0.340	0.117–0.149	0.396–0.474	0.358–0.460	0.767–0.863	3.405–5.703
P. belilamellosus	22.49–25.20	0.389	0.129	0.518	0.331	0.832–0.858	0
P. bellistriatus	29.02–34.70	0.346	0.102	0.448	0.296	0.789–0.846	2.074
P. carltona	15.03–26.13	0.268	0.160	0.427	0.597	0.708–0.844	2.997
P. cutterensis	25.65–30.34	0.227	0.109–0.110	0.324	0.483	0.741–0.745	2.900
P. idahoensis	16.83–21.08	0.163–0.191	0.114–0.159	0.305–0.323	0.596–0.975	0.724–0.829	1.343–2.851
P. occidentalis	22.97–24.19	0.243–0.266	0.098–0.121	0.355–0.382	0.379–0.497	0.775–0.806	0–1.495
P. proavitus	18.69–22.24	0.190–0.285	0.047–0.214	0.190–0.332	0.165–0.373	0.697–0.842	0
P. subcircularis	20.76–21.49	0.151–0.294	0.146	0.298–0.440	0.497–0.968	0.803–0.851	0–1.915
P. subquadratus	27.72–37.48	0.214–0.304	0.064–0.142	0.142–0.413	0.298–0.443	0.762–0.901	0–3.853

contain no information about shared evolutionary history and are thus uninformative for phylogenetic analysis.

Both discrete and continuous characters were considered. Discrete characters are the most commonly used character type in phylogenetic analyses (Wiley and Lieberman, 2011). However, continuous characters have also been utilized previously to construct species-level phylogenetic hypotheses for clades of fossil invertebrates (Rode, 2004; Stigall Rode, 2005; Hopkins, 2011; Wright and Stigall, in press). When normalized to form a ratio, a continuous morphometric character forms a quasi-continuous distribution whereby the range of normalized variation may be differentiated into distinct classes and coded as discrete phylogenetic character states.

Continuous characters were coded based on the total range of morphometric values measured for each species presented in Tables 5 and 6. Measurements of continuous characters were separated into discrete states using a procedure similar to those suggested by Morton and Kincaid (1995) and Swiderski et al. (1998). Morphometric measurements were visually inspected by examining univariate frequency distributions and box plots. Cutoffs were determined by the presence of discontinuities, disjunct clusters, or changes in slope within the distribution (Hunt, 2007; Stigall Rode, 2005). Following visual separation of the data set into classes, potential character states were compared using analysis of variance (ANOVA). Due to potential heteroscedasticity between character states, the non-parametric Kruskal-Wallace test was also performed. In all cases, the Kruskal-Wallace test confirmed the results from ANOVA. Potential states for all characters were found to be highly distinct ($P<0.001$) with non-overlapping mean values within the 95% confidence interval. The expected range for each continuous character state was calculated as the mean ± 1 standard deviation (Tables 7, 8). If measurements for a species fell within a single expected range, only that state was coded; whereas if a species possessed measurements from multiple expected character states, it was coded as polymorphic. Character state distributions for species of *Plaesiomys* are presented in Table 9 and those of *Hebertella* species are presented in Table 10. All statistical procedures for separating continuous characters were performed using PAST (Hammer et al., 2001). Examples of morphometric-based characters are shown in Figure 1.

SEARCH METHOD

Tree topologies were estimated using both cladistic and Bayesian methodologies of inferring phylogenetic hypotheses. A cladistic approach uses maximum parsimony as the sole optimality criterion; whereas Bayesian estimation is model-based (Yang and Rannala, 2012). Although parsimony and model-based approaches may each represent a valid approach

for delimiting monophyletic groups sensu Hennig (1966), they differ on both philosophical and mathematical grounds (Felsen-stein, 2004; Wiley and Lieberman, 2011). Parsimony methods have enjoyed success as an approach amenable to both molecular and morphological data sets that requires few a priori assumptions of character evolution (Wiley and Lieber-man, 2011), yet parsimony techniques have been criticized for lacking explicit assumptions, tendency for long branch attrac-tion, and statistical inconsistency (Felsenstein, 2004; Sober, 2004; Yang and Rannala, 2012). Statistically powerful model-based techniques for inferring phylogenies have become increasingly popular among molecular biologists because they can account for observed changes within sequence data, yet they have been difficult to apply to morphological data and may need to be amended to accommodate realistic models of morpholog-ical character evolution (Spencer and Wilberg, 2013; Wagner, 2011). Because examining the efficacy of maximum parsimony versus model-based methods for estimating phylogenies with morphological characters is beyond the scope of this paper, we choose treat the issue empirically and present the results of both methods. Our results agree with Spencer and Wilberg's (2013) observation that tree topologies recovered using maximum parsimony and Bayesian methods are broadly similar, with the exception that our tree topologies are better resolved using maximum parsimony rather than Bayesian methods.

All parsimony analyses were conducted in PAUP* 4.0 (Swofford, 2002). A branch and bound search was used to determine the most parsimonious tree for the *Plaesiomys* character matrix whereas an exhaustive search was used to determine the most parsimonious tree for the *Hebertella* character matrix. All characters were treated as unweighted and unordered. Characters were optimized using accelerated transformation (ACCTRAN) and analyzed in MacClade 4.06 (Maddison and Maddison, 2003). For Bayesian phylogenetic inference, analyses of 20,000 generations each were performed in MrBayes 3.2 (Ronquist et al., 2011) using the Mk model of morphological evolution with a sampling frequency of 100 (Lewis, 2001).

Taxa exhibiting multiple character states were coded accordingly and treated as polymorphic. Parsimony and Bayesian methods differ in how they treat the evolution of polymorphisms. Parsimony algorithms treat each polymorphism as an independent acquisition whereas Bayesian methods treat polymorphic taxa as if it were a node with marginal likelihoods of $1/n$ for each observed state. Taxa examined in this study include a large number of polymorphic species; therefore, these data may be useful for future analyses using a mixture modeling approach to test different evolutionary scenarios for polymor-phic taxa (Pagel and Meade, 2004; Wagner, 2000). However, a test of these ideas is beyond the scope of this paper.

TABLE 5—Extended.

8	10	12	13	17	19	21
0.666	0.525–0.631	?	0.525–0.642	0.034–0.052	0.150–0.242	0.029–0.045
0.611	0.222–0.357	0.447	0.563	0.047–0.056	0.150	0.068
0.620–0.667	0.246–0.334	?	0.540–0.837	0.060–0.077	0.109–0.134	0.053–0.065
0.273–0.548	0.180–0.262	?	0.798–1.272	0.042–0.074	0.020–0.047	0.043–0.059
0.608	0.437–0.489	0.535	0.562	0.047	0.078	0.056
0.582	0.346	0.435–0.444	0.358	0.031	0.100	0.946
0	0.306–0.383	0.359	0.571	0.049	0.086	0.053
0.637	0.351–0.390	0.471–0.569	0.776	0.082	0.108	0.069
0.434–0.488	0.628–0.831	0.605	0.332–0.585	0.059–0.062	0.124–0.215	0.046–0.061
0.478–0.566	0.392–0.435	?	0.615–0.637	0.079–0.086	0.038–0.114	0.025–0.042
0.425–0.534	0.180–0.199	0.478–0.739	0.617–0.932	0.040–0.072	0.132–0.215	0.036–0.038
0.459–0.675	0.326–0.434	?	0.490–0.546	0.073–0.101	0.220–0.280	0.083–0.087
0–0.492	0.166–0.299	0.466–0.549	0.665–0.672	0.047–0.074	0.059–0.172	0.052–0.056

TABLE 6—Data ranges of morphometric characters for species included in phylogenetic analysis of *Hebertella*.

	1	2	3	4	5	6	7	11	12	16	18
D. tennesseensis	27.55–33.60	0.273–0.313	0.209–0.242	0.668–0.884	0.750–0.814	2.280–2.543	0.517–0.544	0.261–0.268	0.452–0.462	0.051–0.098	0.067–0.072
H. alveata	27.55–33.60	0.295–0.327	0.213–0.248	0.651–0.842	0.184–0.432	3.071–6.867	0.250–0.436	?	0.861–1.094	0.032–0.182	0.036
H. bursa	29.450	0.158	0.106	0.675	0.824	0.000	0.000	?	0.604	0.220	0.042
H. frankfortensis	18.14–26.66	0.323	0.132–0.187	0.579	0.664–0.890	4.822	0.475–0.492	0.209–0.324	0.458	0.117	0.066
H. occidentalis	20.30–47.95	0.274–0.464	0.114–0.289	0.593–0.860	0.666–0.843	1.799–15.644	0.291–0.618	0.254–0.732	0.451–1.688	0.025–0.167	0.031–0.072
H. maria	11.76–18.91	0.272–0.354	0.170–0.231	0.754–0.850	0.998–0.717	5.234–15.806	0.436–0.601	0.236	0.859–1.078	0.121–0.229	0.055–0.067
H. montoyensis	32.25–35.99	?	0.137–0.181	?	0.779–0.827	8.876–19.411	0.487–0.729	0.368–0.396	1.308–1.318	?	?
H. parksensis	24.48–26.88	0.281–0.374	0.131–0.245	0.460–0.871	0.739–0.780	9.369–10.633	0.431–0.490	0.232	0.442–0.691	0.042–0.064	0.019–0.036
H. prestonensis	44.19–46.80	0.345–0.454	0.145–0.204	0.421–0.450	0.780–0.868	12.436–15.879	0.336–0.381	0.293	1.378	0.097–0.113	0.048–0.082
H. richmondensis	31.330	0.334	0.289	0.867	0.781	7.098	0.588	?	0.777	0.135	0.048
H. subjugata	25.940	0.350	0.220	0.628	0.741	8.290	0.481	?	0.404	0.093	0.048

TABLE 7—Statistical separation of continuous characters in *Plaesiomys* analysis (SD=standard deviation).

Character	Range	Mean	SD
1. Maximum width			
(0) small	x≤21.425	18.662	2.790
(1) large	x≥25.045	29.104	4.055
2. Inflation of the dorsal valve			
(0) low	x≤0.239	0.206	0.033
(1) high	x≥0.269	0.307	0.038
3. Inflation of the ventral valve			
(1) low	x≤0.117	0.095	0.022
(0) high	x≥0.120	0.149	0.029
4. Shell thickness			
(1) low	x≤0.329	0.269	0.060
(0) high	x≥0.364	0.416	0.052
5. Comparative convexity of the valves			
(1) low	x≤0.413	0.337	0.076
(0) high	x≥0.414	0.611	0.197
6. Depth of the shell			
(1) low	x≤0.781	0.756	0.025
(0) high	x≥0.813	0.838	0.025
7. Depth of the sulcus			
(0) shallow	x≤2.048	1.001	1.047
(1) deep	x≥2.743	3.864	1.121
8. Origin of the sulcus			
(1) proximal	x≤0.494	0.420	0.074
(0) distal	x≥0.531	0.581	0.050
10. Costal density			
(1) low	x≤0.267	0.220	0.047
(0) high	x≥0.359	0.507	0.148
12. Length of the ventral muscle scars			
(1) short	x≤0.473	0.436	0.037
(0) long	x≥0.499	0.533	0.034
13. Height of the ventral cardinal area			
(1) low	x≤0.662	0.573	0.089
(0) high	x≥0.674	0.872	0.198
17. Posterior extension of the ventral umbo across the hinge line			
(1) low	x≤0.053	0.046	0.007
(0) high	x≥0.063	0.074	0.011
19. Height of the dorsal cardinal area			
(1) low	x≤0.094	0.064	0.030
(0) high	x≥0.126	0.183	0.057
21. Posterior extension of the dorsal umbo across the hinge line			
(1) low	x≤0.049	0.042	0.007
(0) high	x≥0.052	0.065	0.013

PLAESIOMYS PHYLOGENY

Results of phylogenetic analyses.—Parsimony analysis retrieved a single most parsimonious tree with a length of 92 steps (Figs. 2, 3). The consistency and retention indices are 0.696 and 0.576, respectively, which are significantly higher than those derived from similar sized matrices using randomly generated data at the α=0.05 level (Klassen et al., 1998). Bayesian analysis returned limited phylogenetic structure; however, the partitions recovered from Bayesian analysis were fully consistent with the topology recovered in parsimony analysis (Fig. 2). Confidence values for node support were recovered using 100 repetitions of a full-heuristic Jackknife analysis with 5% deletion (Freudenstein and Davis, 2002). Jackknife values for nodes compatible with the single most parsimonious tree are presented in Figure 2. Further support was assessed by calculating the g_1 statistic, a metric for assessing internal consistency and decisiveness within the dataset by examining the degree of skewness in the distribution of tree lengths (Huelsenbeck, 1991; Hillis, 1995). The g_1 statistic for 10,000 trees generated from the data matrix is −0.358, indicating strong phylogenetic signal within the data ($P<0.05$; Hillis and Huelsenbeck, 1992). In addition, markovian signal within the data set was assessed by a compatibility test (Alroy, 1994; Wilkinson, 1994). Results indicate higher compatibility of characters (74 or 210 possible character pairs) than expected by chance (Alroy, 1994; Wilkinson, 1994).

Recognition of clades.—Species of *Plaesiomys* form a monophyletic group supported by multiple synapomorphies and strong Jackknife support. Characters supporting the monophyly of

TABLE 8—Statistical separation of continuous characters in *Hebertella* analysis (SD=standard deviation).

Character	Range	Mean	SD
1. Maximum width			
(0) small	x≤24.618	21.220	3.413
(1) large	x≥27.128	33.413	6.285
2. Inflation of the dorsal valve			
(0) low	x≤0.311	0.294	0.017
(1) high	x≥0.319	0.356	0.037
3. Inflation of the ventral valve			
(1) low	x≤0.175	0.149	0.025
(0) high	x≥0.208	0.243	0.035
4. Comparative convexity of the valves			
(1) low	x≤0.567	0.473	0.094
(0) high	x≥0.631	0.740	0.109
5. Depth of the shell			
(1) low	x≤0.742	0.698	0.044
(0) high	x≥0.770	0.807	0.037
6. Depth of the sulcus			
(0) shallow	x≤7.900	5.630	2.060
(1) deep	x≥10.490	14.200	3.710
7. Width of the sulcus			
(1) narrow	x≤0.435	0.334	0.101
(0) wide	x≥0.447	0.527	0.080
11. Width of the ventral muscle scars			
(0) narrow	x≤0.251	0.236	0.015
(1) wide	x≥0.300	0.343	0.043
12. Height of the ventral cardinal area			
(1) low	x≤0.661	0.541	0.120
(0) high	x≥0.779	1.110	0.331
16. Height of the dorsal cardinal area			
(0) low	x≤0.104	0.070	0.034
(1) high	x≥0.129	0.169	0.040
18. Posterior extension of the dorsal umbo across the hinge line			
(1) low	x≤0.049	0.039	0.010
(0) high	x≥0.052	0.072	0.020

the genus include a subquadrate outline of the shell, a low angle of the ventral umbo, and the presence of secondary costae (characters 9, 11, and 16). Species of *Plaesiomys* are distributed among three clades (Fig. 2): a basal clade including *P. cutterensis* Howe, 1966, a clade including *P. carltona* (Twenhofel, 1928), and a clade including *P. bellistriatus* Wang, 1949.

The basal clade includes *Plaesiomys cutterensis* and *P. idahoensis* Ross, 1959, and their sister relationship is supported by low inflation of the dorsal valve, high costal density, and an inclined angle between the ventral interarea and hinge line (characters 2, 10, and 18). The sister relationship between the *P. carltona* and *P. bellistriatus* clades is supported by wide shell width, low inflation of the dorsal valve, high total shell height, and a ventral umbo located proximal to the hinge line (characters 1, 2, 4, and 17).

The monophyly of the clade comprising *P. carltona*, *P. subquadratus* (Hall, 1847), and *P. anticostiensis* (Shaler, 1865) is supported by a low height of the dorsal cardinal area and a proximal origination of the sulcus (characters 8 and 19). The

sister relationship between *P. anticostiensis* and *P. subquadratus* is supported by an elevated height of the ventral valve cardinal area (character 13). The monophyly of the *P. carltona* clade and the sister relationship between *P. subquadratus* and *P. anticostiensis* are both strongly supported by Jackknife values.

The pectinate clade comprising *P. bellistriatus*, *P. belilamellosus* Wang, 1949, *P. subcircularis* (Roy, 1941), *P. occidentalis* Howe, 1966, and *P. proavitus* (Winchell and Schuchert, 1892) is characterized by a high shell depth with relatively low convexity and a low depth of the sulcus (characters 5, 6, and 7) and is supported by Jackknife analysis. The clade comprising *P. belilamellosus* and species crownward is supported by extensive character evidence including highly inflated ventral valves, subelliptical outline, high costal density, long ventral valve muscle scars, low height of the ventral valve cardinal area, low dorsal umbonal angle, and a high angle between the ventral valve interarea and hinge line (characters 5, 9, 10, 12, 14, 18, and 20).

The monophyletic relationship among *P. subcircularis*, *P. occidentalis*, and *P. proavitus* is supported by relatively narrow shells width, low ventral umbonal angles, and a ventral umbo significantly extending over the hinge line (characters 1, 15, and 17). The sister relationship between *P. occidentalis* and *P. proavitus* is supported by a proximal dorsal umbo (character 21).

Discussion.—North American species of *Plaesiomys* originated in the Late Ordovician and underwent rapid diversification and subsequent dispersal throughout Laurentia during the mid-to late Katian (Fig. 4). Species of *Plaesiomys* most commonly occurred in intercratonic basins of the Laurentian mid-Continent, yet they also occurred in marginal and mixed platforms and formed a minor component of the Late Ordovician *Hiscobeccus* Fauna of Laurentia (Jin, 2001).

Species of *Plaesiomys* are hypothesized to have lived with their beaks down and their commissures oriented vertically (Richards, 1972; Alexander and Scharpf, 1990). Flume tank experiments by Alexander (1984) suggested the dorsibiconvex profile and relatively small interareas of typical *Plaesiomys subquadratus* would render the shell hydrodynamically unstable in that position if unattached. Species of *Plaesiomys* seem to have overcome this limitation by increasing their musculature and facilities for pedicle attachment. For example, species within both the *P. carltona* and *P. bellistriatus* subclades are characterized by large, thick shells with a ventral interarea located proximal to the hinge line.

A diagnostic feature of *Plaesiomys* relates to its multicostellate exterior which may be related to deterring epibionts (Richards, 1972). Alexander and Scharpf (1990) found that *P. subquadratus* shells had statistically lower inarticulate brachiopod epibionts than expected and also low rates of encrustation in general, which they attributed to the course costae of the species relative to other articulated brachiopods in the same deposit. Both the sister group

TABLE 9—Character state distribution for species included in phylogenetic analysis of *Plaesiomys* (X=0 and 1).

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
D. meedsi arctica	0	1	X	0	0	X	0	0	0	1	0	?	1	0	0	?	1	0	0	0	1
D. sweeneyi	0	1	1	0	0	0	0	0	X	0	0	0	1	1	1	0	1	0	0	0	0
D. venusta	0	0	0	0	X	0	0	0	0	0	0	?	0	0	0	0	0	X	0	0	0
P. anticostiensis	1	0	X	1	X	X	0	X	1	0	1	?	0	X	0	1	X	X	1	0	X
P. belilamellosus	1	0	1	1	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	0
P. bellistriatus	1	0	0	1	1	1	1	0	1	0	1	0	1	0	0	1	1	0	0	0	0
P. carltona	X	0	1	1	0	X	0	1	1	1	1	0	1	0	0	1	1	0	1	0	0
P. cutterensis	1	1	0	0	0	0	0	0	1	1	1	X	0	1	0	1	0	1	0	?	0
P. idahoensis	0	1	X	0	0	X	X	X	X	1	1	1	1	0	1	0	1	0	0	0	X
P. occidentalis	0	0	X	1	X	0	1	X	1	1	1	?	1	1	1	1	0	1	1	1	1
P. proavitus	0	X	X	0	1	X	1	X	0	0	1	1	X	1	1	1	X	1	0	1	1
P. subcircularis	0	X	1	X	0	1	1	X	0	1	1	?	1	1	1	1	0	1	0	1	0
P. subquadratus	1	X	X	X	X	X	X	1	1	0	1	X	0	0	1	1	X	0	X	1	0

TABLE 10—Character state distribution for species included in phylogenetic analysis of *Hebertella* (X=0 and 1).

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
D. tennesseensis	1	0	0	0	0	0	0	0	0	0	0	0	0	0	X	0	X	0
H. alveata	1	X	0	0	1	0	1	1	X	1	X	0	0	0	0	X	X	1
H. bursa	1	0	1	0	0	0	1	?	0	1	0	1	1	0	0	1	0	1
H. frankfortensis	0	1	1	1	X	0	X	1	0	0	0	1	0	1	0	0	0	0
H. maria	0	X	0	X	1	X	1	1	0	0	0	0	1	1	1	1	1	0
H. montoyensis	1	?	1	?	0	1	0	0	1	1	1	0	0	X	X	?	?	?
H. occidentalis	X	X	X	X	X	X	1	X	1	1	X	X	0	X	X	X	0	X
H. parksensis	0	X	X	X	X	1	1	0	0	0	0	1	0	0	1	0	1	1
H. prestonensis	1	1	1	1	0	1	0	0	1	1	1	0	1	0	1	0	0	X
H. richmondensis	1	1	0	0	0	0	0	0	0	X	1	1	1	0	1	1	0	1
H. subjugata	0	1	1	1	1	1	?	0	0	0	0	1	0	1	0	0	0	1

of *P. cutterensis* and *P. idahoensis* as well all species from *P. belilamelosus* crownward exhibit high costal density, which may indicate an increased resistance to specific epibionts (Richards, 1972). In addition, the epipunctae that characterize *Plaesiomys* may hinder epibionts (Jin et al., 2007) as they are functionally similar to punctae (Jin et al. 2007), which have been demonstrated to inhibit epibionts (e.g., Alexander and Scharpf, 1990).

Plaesiomys includes species that occupied a broad range of habitats and geographic areas. Species of *Plaesiomys* occur primarily in strata interpreted to have been deposited within normal to storm wave base (Holland and Patzkowsky, 1996), but they occur across multiple bathymetric gradients and tectonic settings (Patzkowsky and Holland, 2007). Several species, notably *P. bellistriatus*, *P. proavitus*, and *P. subquadratus*, attained large geographic ranges encompassing several tectonic basins (Table 11). For example, *P. bellistriatus* occurs in the Richmondian (upper Katian) age Maquoketa, Viola, and Aleman Formations across the mid-Continent region of Laurentia.

The combination of broad ecological tolerances and a high propensity for dispersal described and are both are characteristics of invasive species (Davis, 2009; Stigall, 2010b), and indeed *Plaesiomys* includes at least one species previously recognized as an invasive species: *Plaesiomys subquadratus* participated in the Late Ordovician Richmondian Invasion into the Cincinnati basin (Foerste, 1912; Stigall, 2010a). In the phylogenetic hypothesis presented in Figure 2, *P. subquadratus* is nested within a clade

FIGURE 1—Examples of morphometric-based measurements utilized in character analysis. *1, Plaesiomys bellistriatus* Wang, 1949, SUI 1820, holotype, ventral view ×1.2; *2*, lateral view, ×1.5; *3, P. subquadratus* (Hall, 1847), YPM S-728f, ventral interior, ×1.4; *4, P. subcircularis* (Roy, 1941), AMNH 4797, holotype, posterior view, ×2.2. Abbreviations: da=delthyrial angle (angle between the lateral boundaries of the ventral interarea); dvh=dorsal valve height; ia=interarea angle; msl=muscle scar length (maximum length of the ventral muscle field); w=maximum shell width.

consisting of two species, *P. anticostiensis* and *P. carltona*, from Anticosti Island (Table 11). The phylogenetic topology presented herein indicates that the common ancestor of *P. subquadratus, P. anticostiensis,* and *P. carltona* would likely have inhabited a geographic area in the portion of the Taconic foreland basin that extends toward the Anticosti Island region of Quebec (Wright and Stigall, 2012). No physical record of this ancestor is known, which may be due to limited outcrop availability of Late Ordovician deposits from that portion of the seaway. The implication of this ancestral reconstruction is that *P. subquadratus* may have invaded the Cincinnati region from the paleonortheast. This pattern conflicts with the hypothesized pathway of invasion for the orthid brachiopod *Glyptorthis insculpta* (Hall, 1847), which likely emigrated from the mid-Continent into the Cincinnati basin (Wright and Stigall, in press). The lack of a unidirectional source for the Richmondian Invasion suggests multiple pathways of invasion were utilized to facilitate the influx of invasive taxa into the Cincinnati basin. Further investigations are needed to assess whether or not invasion pathways for *P. subquadratus* or *G. insculpta* represent a general pattern for invader taxa.

HEBERTELLA PHYLOGENY

Results of phylogenetic analyses.—The exhaustive search retrieved a single most parsimonious tree of 67 steps (Figs. 3, 5). The consistency and retention indices are 0.731 and 0.591, respectively. These values are significantly higher than those derived from similar sized matrices using randomly generated data at the $\alpha=0.05$ level (Klassen et al., 1998). Bayesian analysis returned limited phylogenetic structure; however, the partitions recovered from Bayesian analysis were fully consistent with the topology recovered in parsimony analysis (Fig. 5).

Confidence values for node support were recovered using 100 repetitions of a full-heuristic Jackknife analysis with 5% deletion (Freudenstein and Davis, 2002). Jackknife values for nodes compatible with the single most parsimonious tree are presented in Figure 5. Further support was assessed by calculating the g_1 statistic, a metric for assessing internal consistency and decisiveness within the dataset by examining the degree of skewness in the distribution of tree lengths (Huelsenbeck, 1991; Hillis, 1995). The g_1 statistic is -0.603, which indicates strong phylogenetic signal within the data ($P<0.01$: Hillis and Huelsenbeck, 1992).

Recognition of clades.—The overall tree topology is balanced and is supported by multiple synapomorphies and very strong (>90%) Jackknife values (Fig. 5). Characters supporting the monophyly of *Hebertella* include a high inflation of the dorsal valve, a narrow sulcus width, and proximal dorsal umbo with respect to the hinge line (characters 2, 7, and 18).

The clade consisting of *H. alveata* Foerste, 1909a, *H. maria* (Billings, 1862), *H. richmondensis* Foerste, 1909a, and *H. bursa* Raymond, 1928 is characterized by having a relatively large
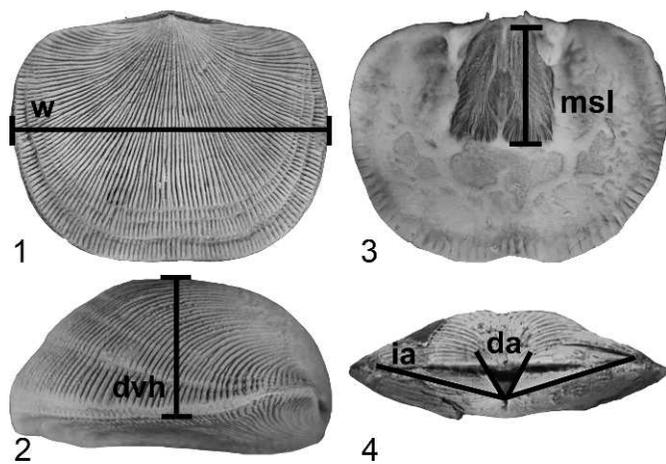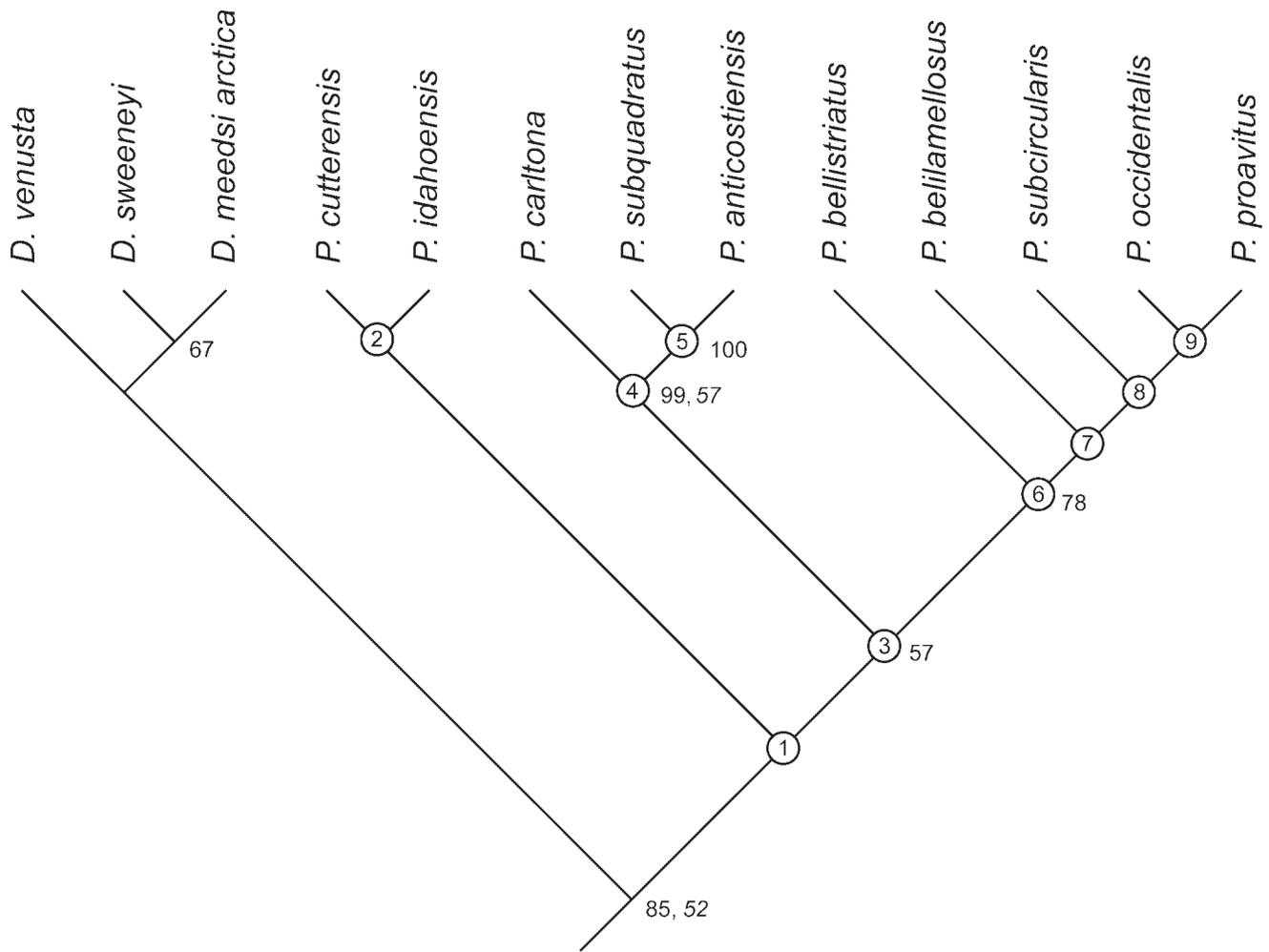
FIGURE 2—Single most parsimonious tree obtained from the character state distributions given in Table 9 as implemented in PAUP (Swofford, 2002). Nodes are numbered and circled. Values from Jackknife analysis are indicated next to supported nodes. Posterior probabilities from Bayesian analysis indicated in italics. Characters were optimized using ACCTRAN in MacClade (Maddison and Maddison, 2000). Unambiguous character changes listed below are denoted by parentheses: Node *1*, 9 (1), 11, (1), 16 (1); Node *2*, 2, (1), 10, (1), 18, (1); Node *3*, 1, (1), 2, (0), 4, (1), 17, (1); Node *4*, 8, (1), 19, (1); Node *5*, 13, (0); Node *6*, 5, (1), 6, (1), 7, (1); Node *7*, 3, (1), 9, (0), 10, (1), 12, (1), 14, (1), 18, (1), 20, (1); Node *8*, 1, (0), 15, (1), 17, (0); Node *9*, 21, (1).

dorsal cardinal area (character 16). The sister relationship between *H. alveata* and *H. maria* is supported by low shell depth, few ($\leq$15) costae in the sulcus, and a high ($>$140°) dorsal umbonal angle (characters 5, 8, and 17); whereas the sister relationship between *H. richmondensis* and *H. bursa* is supported by a low height of the ventral interarea and a high ($>$140°) umbonal angle (characters 12 and 13).

The clade comprising the remaining species is strongly supported by Jackknife values and is characterized by an inflated ventral valve, low comparative convexity between the valves, and a deep sulcus (characters 3, 4, and 6). This clade can be subdivided into two subclades of three species each. The first subclade includes *H. parksensis* Foerste, 1909b, *H. frankfortensis* Foerste, 1909a, and *H. subjugata* (Hall, 1847), whereas the second subclade consists of *H. occidentalis* (Hall, 1847), *H. montoyensis* Howe, 1966, and *H. prestonensis* Ladd, 1929.

Characters supporting the monophyly of the *H. parksensis* subclade include small (for the genus) maximum shell width and a low height of the ventral interarea (characters 1 and 12). *Hebertella frankfortensis* and *H. subjugata* form a sister group supported by a high ($>$40°) delthyrial angle relative to the commissural plane and an upright ($\geq$90°) angle between the ventral interarea and the hinge line (characters 14 and 15).

The monophyly of the *H. occidentalis* subclade is supported by 100% Jackknife support and based on the synapomorphies of a subquadrate shell outline and angular cardinal extremities (characters 9 and 10). The sister relationship between *H. montoyensis* and *H. prestonensis* is supported by a wide distance across the sulcus and wide ventral muscle scars (characters 7 and 11).

Discussion.—*Hebertella* originated in Laurentia during the Whiterockian (lower Sandbian) and persisted through the Gamachian (Hirnantian). Species of *Hebertella* reached maximal abundance during the Late Ordovician and rank among the most common and conspicuous fossils of shallow subtidal deposits in the type-Cincinnatian Series of eastern North America (Meyer and Davis, 2009; Stigall, 2010a). Although seven of the ten species included in this analysis occur within the Cincinnati Basin of Kentucky, Indiana, and Ohio, the geographic range of *Hebertella* extended beyond the confines of eastern North America into both marginal and interior cratonic basins (Billings, 1862; Howe, 1966; Ladd, 1929) (Table 12). Interbasinal range expansion in *Hebertella* occurred during the late Cincinnatian concomitant with a broader pattern of global brachiopod generic endemism whereby the Richmondian brachiopod fauna became
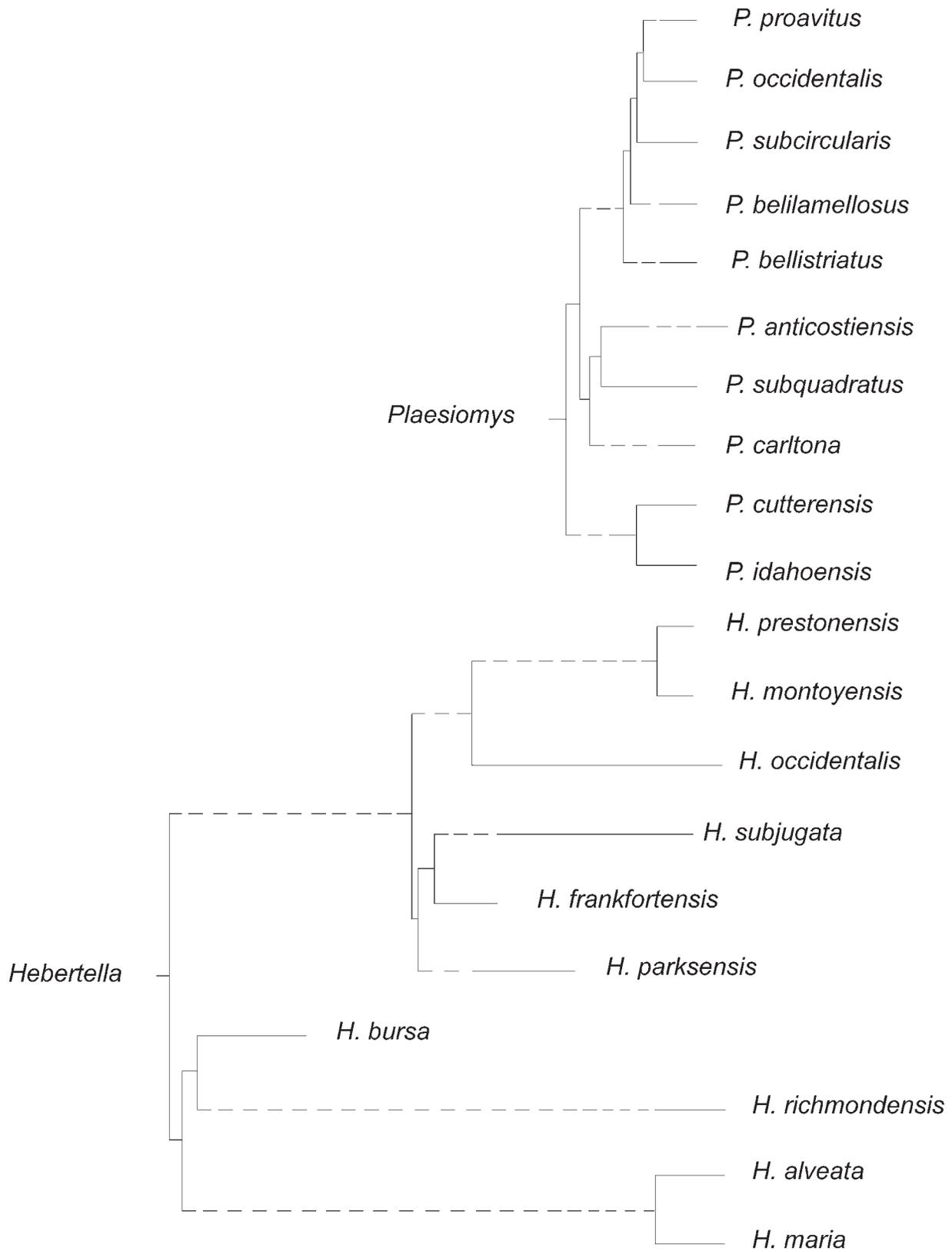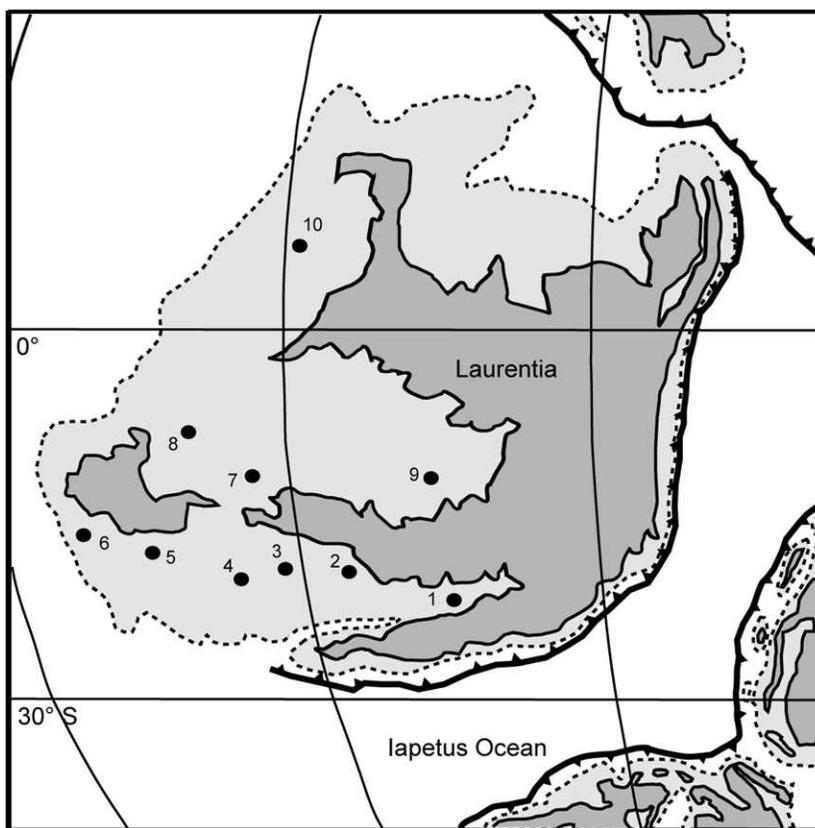
FIGURE 4—Late Ordovician paleogeography of Laurentia indicating basins where *Hebertella* and *Plaesiomys* species occurred. Dashed lines indicate shallow marine environments. *1*, Anticosti Island; *2*, Hudson Bay lowlands, Quebec; *3*, Ohio-Indiana-Kentucky region; *4*, Tennessee; *5*, Arbuckle Mountains, Oklahoma; *6*, Trans-Pecos, Texas; *7*, Iowa-Illinois-Minnesota region; *8*, Idaho; *9*, Baffin Island; *10*, Advance Mountains, British Columbia.

broadly yet uniquely established in Laurentia (Torsvik and Cocks, 2011).

Species of *Hebertella* occur primarily in rocks interpreted to have been deposited within normal to storm wave base (Holland and Patzkowsky, 1996). Paleoecological reconstructions of *H. occidentalis* suggest a lifestyle with the commissure oriented vertically and pedicle foramen flush to the substrate, which likely represented the general life habit for all species of *Hebertella* (Alexander, 1984; Richards, 1972). In addition, shells of *Hebertella* generally have large, cataeline to slightly apsacline ventral interareas which provide greater shell stability (Alexander, 1984). A wide sulcus is characteristic for the genus, which may have aided the feeding efficiency of the lophophore by enhancing the passive flow of nutrients (LaBarbera, 1981). *Hebertella alveata* and the species within the *H. occidentalis* subclade are characterized by having angular cardinal extremities; the increased length of the hinge provided a larger area of contact between the shell and the substrate and may represent an adaptation to high energy conditions (Richards, 1972). This feature is best developed in the highly alate shells of *H. alveata* from the Whitewater Formation in Indiana, a unit interpreted have been deposited in a nearshore environment with substantial interaction between waves and the seafloor (Meyer and Davis, 2009).

Species of *Hebertella* commonly occur in association with invasive taxa associated with the Richmondian Invasion, yet did not participate in the invasion process. Theoretical and empirical studies on invasive species indicate that invaders may exhibit ecological dominance over incumbents and may therefore threaten biodiversity (Davis; 2009; Rode and Lieberman, 2004; Stigall, 2010b). However, the influx of invaders did not drive species of *Hebertella* extinct nor facilitate local extirpation (Malizia and Stigall, 2011; Stigall, 2010a). Instead, incumbent Cincinnatian species persisted and *H. alveata* originated during the invasion interval. Paleobiogeographic analyses of faunal dynamics across the invasion interval suggest species of *Hebertella* were able to successful because they exhibited broad ecological tolerances facilitating large intrabasinal geographic ranges which may act as a buffer during biodiversity crises (Malizia and Stigall, 2011; Rode and Lieberman, 2004; Stigall, 2010a, 2012).

SYSTEMATIC PALEONTOLOGY

Specimens examined for species that require neither taxonomic revision nor lectotype designation are presented in Table 13. Each specimen listed belongs to a species of *Plaesiomys* or *Hebertella* that is considered valid herein. The original descriptions for these species are sufficient for diagnosis, and additional discussion is, therefore, not warranted here. The

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FIGURE 3—Phylogenetic relationships for species of *Plaesiomys* Hall and Clarke, 1892 and *Hebertella* Hall and Clarke, 1892 mapped onto geologic time. Time scale modified from Holland and Patzkowsky, 1996.

TABLE *11*—Stratigraphic and geographic distribution of *Plaesiomys*. Symbol † indicates Gamachian (Hirnantian), all other species are Richmondian (Katian).

Species	Stratigraphy	Geography	Source
P. anticostiensis	Ellis Bay Formation, Grindstone Member†	Anticosti Island	Jin and Zhan, 2008; Shaler, 1865
P. belilamellosus	Maquoketa Formation	Iowa	Wang, 1949
P. bellistriatus	Maquoketa Formation, Viola Formation, Aleman Limestone	Iowa, Illinois, Tennessee,Texas	Alberstabt, 1973; Howe, 1966; 1988; Wang, 1949
P. carltona	Vauréal Formation	Anticosti Island	Jin and Zhan, 2008; Twenhofel, 1928
P. cutterensis	Cutter Limestone	Texas	Howe, 1966
P. idahoensis	Saturday Mountain Formation	Idaho	Ross, 1959
P. occidentalis	Maquoketa Limestone	Iowa	Ladd, 1929; Wang, 1949
P. proavitus	Cape Limestone, Fernvale, Maquoketa, Viola Formations	Iowa, Illinois, Minnesota, Tennessee	Alberstabt, 1973; Howe, 1988; Winchell and Schuchert, 1892
P. subcircularis	Amadjuak Formation	Baffin Island	Roy, 1941
P. subquadratus	Liberty, Waynesville, Whitewater, Viola, Caution Creek Formations, and Avalanche Formations, Aleman Limestone	Indiana, Ohio, Oklahoma, Minnesota, Manitoba, British Columbia, west Texas	Alberstabt, 1973; Hall, 1847; Howe, 1966; Jin and Norford, 1996; Jin et al., 1997; Winchell and Schuchert, 1892

character state distribution data from the phylogenetic analysis presented in this paper (Tables 9, 10) may be combined with the original species descriptions to provide enhanced diagnoses.

Order ORTHIDA Schuchert and Cooper, 1932
Suborder ORTHIDINA Schuchert and Cooper, 1932
Superfamily ORTHOIDEA Woodward, 1852
Family PLAESIOMIDAE Schuchert, 1913

Subfamily PLAESIOMINAE Schuchert, 1913
Genus PLAESIOMYS Hall and Clarke, 1892

Type species.—Orthis subquadrata Hall, 1847.
Other species.—Austinella subcircularis Roy, 1941; *Dinorthis carltona* Twenhofel, 1928; *Dinorthis rockymontana* Wilson, 1926; *Orthis anticostiensis* Shaler, 1865; *O. proavitus* Winchell and Schuchert, 1892, *Plaesiomys belilamellosus* Wang, 1949; *P.*
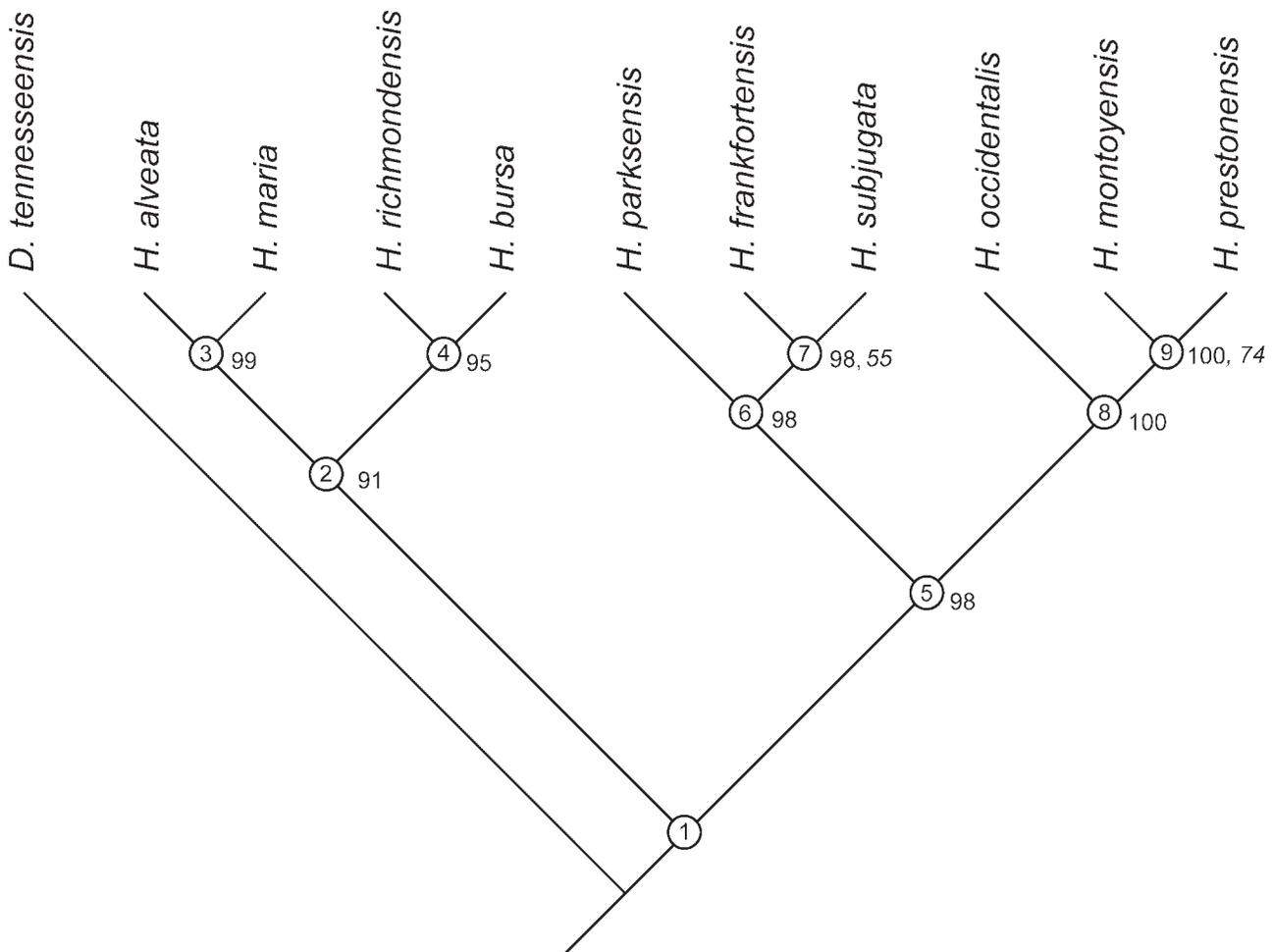

FIGURE 5—Single most parsimonious tree obtained from the character state distributions given in Table 10 as implemented in PAUP (Swofford, 2002). Nodes are numbered and circled. Values from Jackknife analysis are indicated next to supported nodes. Posterior probabilities from Bayesian analysis indicated in italics. Characters were optimized using ACCTRAN in MacClade (Maddison and Maddison, 2000). Unambiguous character changes listed below are denoted by parentheses: Node *1*, 2 (1), 7, (1), 18 (1); Node *2*, 16 (1); Node *3*, 5 (1), 8 (1), 17 (1); Node *4*, 12 (1), 13 (1); Node *5*, 3 (1), 4 (1), 6 (1); Node *6*, 1 (0), 12 (1); Node *7*, 14 (1), 15 (0); Node *8*, 9 (1), 10 (1); Node *9*, 7 (0), 11 (1).

TABLE 12—Stratigraphic and geographic distribution of *Hebertella*. Symbols: [x]=Whiterockian (lower Sandbian); *=Mohawkian (upper Sandbian to middle Katian); †=Cincinnatian (upper Katian to Hirnantian).

Species	Stratigraphy	Geography	Source
Hebertella alveata	Liberty and Whitewater formations†	Ohio and Indiana	Davis, 1985; Foerste, 1909a, 1910
Hebertella bursa	Athens Formation[x]	Tennessee	Raymond, 1928
Hebertella frankfortensis	Bigby-Cannon and Catheys formations*	Kentucky, Tennessee	Foerste, 1909b; Walker, 1982; Wilson, 1949
Hebertella montoyensis	Aleman and Cutter limestones†	Texas	Howe, 1966
Hebertella occidentalis	Arheim, Bellevue, Catheys, Leipers, Fernvale, Oregonia, Liberty, Whitewater, and Elkhorn formations*†	Indiana, Kentucky, Ohio, Tennessee	Hall, 1847; Howe, 1988; Wilson, 1949
Hebertella maria	Vauréal and Ellis Bay formations†	Anticosti Island	Billings, 1862; Jin and Zhan, 2008
Hebertella parksensis	Point Pleasant and Clays Ferry formations*†	Kentucky	Foerste, 1909b; Walker, 1982
Hebertella prestonensis	Maquoketa Formation†	Iowa	Ladd, 1929
Hebertella richmondensis	Whitewater Formation†	Indiana	Foerste, 1909a, 1910
Hebertella subjugata	Clays Ferry, Bellevue, and Waynesville formations†	Kentucky, Indiana, Ohio	Hall, 1847; Foerste, 1910; Walker, 1982

bellistriatus, Wang, 1949; *P. cutterensis* Howe, 1966; *P. idahoensis* Ross, 1959; and *P. occidentalis* Ladd, 1929. Species of *Plaesiomys* occurring outside of North America were excluded.

Diagnosis.—Genus of *Plaesiominae* with abundant bifurcating costellae and densely spaced epipunctae microstructure. Outline subquadrate to suboval, convexoconcave to dorsibiconvex; multicostellate, costae emplaced by bifurcation or intercalation, aditicules on costae and costellae, uniplicate to rectimarginate, epipunctae microstructure, densely spaced; ventral interarea short, apsacline, dorsal interarea orthocline to anacline; ventral muscle field subcordate, diductor scars large, adductor scars oval shaped, elongate, and enclosed within diductor muscle field, adjustor scars large with variable outline; posterior scars typically larger than anterior scars, divided longitudinally by a medial myophragm; myophore bilobate to trilobate, crenulated; brachiophores divergent. Emended from Williams and Harper (2000).

Occurrence.—Late Ordovician (late Sandbian to Hirnantian) of North America with possible occurrences in Kazakhstan, Estonia, Siberia, and the British Isles (see remarks below).

Remarks.—*Plaesiomys* has most frequently been compared with *Dinorthis* (e.g., Schuchert and Cooper, 1932; Howe, 1966). The external morphology of *Plaesiomys* differs primarily from *Dinorthis* in that *Plaesiomys* has well developed costellae, whereas costellae is absent or rare in *Dinorthis*. Additionally,

TABLE 13—Specimens examined for species that do not require taxonomic revision or lectotype designation. Asterisk indicates non-type specimens.

Species	Museum	Catalog number	Type
P. anticostiensis	MCZ	14679	Lectotype
	MCZ	147680	Paralectotype
	GSC	117925	*
	GSC	117926	*
	GSC	117929	*
P. belilamellosus	SUI	1804	Holotype
	SUI	1805	Paratype
	SUI	1806	Paratype
P. bellistriatus	SUI	1820	Holotype
	USNM	146550	*
	USNM	14655	*
P. carltona	GSC	2030k	Holotype
	YPM	10356	Paratype
	YPM	11129	Paratype
	GSC	uncataloged	*
P. subcircularis	AMNH	4797	Holotype
	AMNH	29423	Paratype
H. bursa	MCZ	110282	Holotype
H. maria	GSC	2271a	Lectotype
	GSC	2271b	Paralectotype
	GSC	2271c	Paralectotype
	YPM	157037	*
	YPM	161230	*
	YPM	516751	*

costae present in species of *Dinorthis* are typically much coarser than in *Plaesiomys*. Although setigerous shell perforations are present in both *Plaesiomys* and *Dinorthis*, they are more densely spaced in *Plaesiomys*. Internally, the ventral adductor muscle scars form an anterior notch in *Dinorthis* but are enclosed within the diductor scars in *Plaesiomys*. The multicostellate plaesiomids *Multicostellata* Schuchert and Cooper, 1931 and *Campylorthis* Ulrich and Cooper, 1942 also closely resemble *Plaesiomys*. *Plaesiomys* can be distinguished from *Multicostellata* by its convexoconcave profile and large adjustor muscles, whereas *Multicostellata* has subequally convex valves and small adjustor muscles. *Campylorthis* differs from *Plaesiomys* in possessing a perforated deltidium and a well-developed chilidium.

Species of *Plaesiomys* have been reported from outside of North America including the British Isles (Cocks, 2008; Hiller, 1980; Harper, 1984; Mitchell, 1977; Wright, 1964); Estonia (Oraspold, 1959), Kazakhstan (Popov et al., 2000), and Siberia (Kulkov and Severgina, 1989). However, the taxonomic validity of *Plaesiomys* occurring outside North America has been previously questioned based on shell microstructure (Jin and Zhan, 2008; Jin et al., 2007). Examining the original descriptions for these species supports Jin et al. (2007) and Jin and Zhan's (2008) assertions that some of these taxa are unlikely to belong within *Plaesiomys* sensu stricto, yet complete analyses of the extra-North American species is not within the scope of this analysis. Furthermore, many of these taxa were erected based on incomplete or poorly preserved material, which prohibits resolving an accurate placement for these taxa within a phylogenetic analysis.

PLAESIOMYS CUTTERENSIS Howe, 1966
Figure 6.9

1966 *Plaesiomys subquadratus cutterensis* HOWE, p. 249, pl. 29, figs. 7–12, 14.

Diagnosis.—Large species of *Plaesiomys* characterized by relatively few costae. Shell wider than long, hinge line narrow; outline subquadrate, total shell inflation low; costal density high, sulcus originating proximally; ventral interarea and delthryium oriented at a high angles to the hinge line; ventral muscle scars short to long; dorsal valve highly inflated. Emended from Howe (1966).

Types.—USNM 146558 (holotype); USNM 146559a, 1465591 (paratypes).

Occurrence.—Cutter Limestone, Montoya Group, Texas; Richmondian (upper Katian).

Remarks.—*Plaesiomys cutterensis* was originally described by Howe (1966) as a subspecies of *Plaesiomys subquadratus*. Howe (1966) differentiated specimens of *P. s. cutterensis* from *P.*

subquadratus by their considerably fewer costae. Although *P. cutterensis* typically has fewer costae, costal density (character 10) values between the specie are similar when normalized to maximum shell width because specimens of *P. cutterensis* are usually smaller than *P. subquadratus*. Character analysis reveals *P. cutterensis* is not a valid subspecies of *P. subquadratus* but rather a distinct species differentiated by a more distal origination of the sulcus, a more strongly inclined angle between the ventral interarea and hinge line, and a relatively lower angles of the ventral cardinal area and umbo. Therefore, *P. cutterensis* is herein elevated to specific status.

PLAESIOMYS IDAHOENSIS Ross, 1959
Figure 6.7, 6.8

1959   *Plaesiomys subquadratus idahoensis* Ross, p. 449, pl. 54, figs. 29, 30, 33, 34, 37, 38, 41, 42, pl. 55, figs. 22, 26, 27, 30, 31.

Diagnosis.—Small to moderate size *Plaesiomys* species with a wide hingeline and low ventral cardinal area. Shell outline subquadrate to subelliptical, highly convex valves of variable depth; costal density high relative to maximum width; ventral valve shallow to inflated, delthryium oriented at a high angle; ventral interior muscle field long; dorsal valve inflated with shallow to deep sulcus; dorsal interarea orthocline to apsacline; high dorsal umbonal angle. Emended from Ross (1959).

Types.—USNM 133239 (holotype); USNM 133240, 133241, 133242, and 133243 (paratypes).

Occurrence.—Saturday Mountain Formation, Idaho; Richmondian (upper Katian).

Remarks.—*Plaesiomys idahoensis* was considered a subspecies of *P. subquadratus* in the original description (Ross, 1959) on the basis that *P. idahoensis* is smaller with finer costae and a wider hinge than *P. subquadratus*. Phylogenetic analysis reveals *P. idahoensis* to be a distinct species more closely related to *P. cutterensis* than *P. subquadratus*, and it is correspondingly elevated to species status herein. As noted by Howe (1966), *P. idahoensis* can be distinguished from *P. cutterensis* by its smaller size, lower height of the ventral cardinal area, and a more obtuse interarea and umbonal angles on the ventral valve.

PLAESIOMYS OCCIDENTALIS Ladd, 1929

1929   *Dinorthis (Plaesiomys) subquadrata occidentalis* LADD, p. 402, pl. 5, figs. 7–9.
1949   *Plaesiomys subquadratus occidentalis* (Ladd); WANG, p. 5, pl. 2d, figs. 1–5.

Diagnosis.—Small *Plaesiomys* species with highly biconvex shell in which both dorsal and ventral umbos extending across the hinge line. Shell height large for genus; outline subquadrate, cardinal extremities rounded; costal density high; sulcus depth low, delthryium inclined; ventral interarea highly obtuse; ventral umbo extending significantly over the hinge line; dorsal umbo proximal, opening into a wide ($\geq 150°$) angle. Emended from Ladd (1929).

Types.—SUI 66504 (holotype); USNM 146553a–b, SUI 1807 (hypotypes).

Occurrence.—Maquoketa Shale, Iowa; Richmondian (upper Katian).

Remarks.—Ladd (1929) described *P. occidentalis* as a subspecies of *P. subquadratus* differing only with respect to the former having more rounded cardinal areas. Wang (1949) suggested that *P. occidentalis* more closely resembled *P. bellilamellosus*, and Howe (1966) considered the types of *P. occidentalis* and *P. bellilamellosus* to represent end members of a continuous spectrum between the two forms. Neither Wang (1949) nor Howe (1966), however; removed *P. subquadratus occidentalis* from its subspecific taxonomic rank. The topology

recovered from phylogenetic analysis indicates *P. occidentalis* is more closely related to *P. bellilamellosus* than *P. subquadratus*, yet *P. occidentalis* and *P. bellilamellosus* are not sister species and differ by six characters. *Plaesiomys occidentalis* is herein diagnosed as a distinct species. It differs from *P. bellilamellosus* by a smaller shell, low sulcus depth, subquadrate outline, low ventral umbonal angle, and having both the ventral and dorsal umbo extending significantly over the hinge line.

PLAESIOMYS PROAVITUS (Winchell and Schuchert, 1892)
Figure 6.5, 6.6

1892   *Orthis proavita* Winchell and Schuchert
1892   *Orthis petrae* (Winchell and Schuchert); SARDESON, pl. 5, figs. 18, 19.
1932   *Orthis (Dinorthis) proavita* (Winchell and Schuchert); BASSLER, pl. 25, figs. 16, 17.
1936   *Dinorthis proavitus* (Winchell and Schuchert); GREGOR AND BORN, pl. 1, figs. 4–6.
1949   *Plaesiomys proavita* (Winchell and Schuchert); WANG, p. 4, pl. 2, figs. e1–e6.
1949   *Plaesiomys planus* (Winchell and Schuchert); WANG, p. 6, pl. 3, figs. c1–c5.
1973 *Plaesiomys proavitus* (Winchell and Schuchert); ALBERSTADT, p. 24, pl. 2, figs. 1–5.

Diagnosis.—Small *Plaesiomys* species with low costal density and few secondary costae. Shell subelliptical; low total shell height valve convexity; costal density low, costae somewhat coarse; sulcus depth low; ventral interarea and umbonal angle acute for genus; high delthyrial angle; ventral muscle scars long. Emended from Winchell and Schuchert (1892).

Types.—Winchell and Schuchert (1892) did not designate a holotype. YPM S-703a is designated as the lectotype herein, and YPM S-703b (13 specimens) and YPM S-709a become paralectotypes.

Other material.—Following the synonymy listed in Wang (1949), the type material of *Hebertella clermontensis* Bradley, 1921 (MCZ 110301 [holotype]; MCZ 110549, 110550 [paratypes]) was examined and determined to belong to *P. proavitus*.

Occurrence.—Maquoketa Formation, Iowa, Illinois; Viola Formation, Oklahoma; Cape Limestone, Missouri, Fernvale Limestone, Tennessee; Richmondian (upper Katian).

Remarks.—This geographically widespread species is often confused in collections with *Dinorthis occidentalis* Okultich, 1943. The overall low costal density and fewer secondary costae of *P. proavitus* is unusual for a species of *Plaesiomys*, yet secondary costae are present and in greater abundance than typically seen in *Dinorthis* Furthermore, costae originate on each valve as in other species of *Plaesiomys*. Phylogenetic analysis confirms that the morphological resemblance to *Dinorthis occidentalis* is superficial because *P. proavitus* is placed well outside the *Dinorthis* clade at a derived position within *Plaesiomys*.

Although Winchell and Schuchert (1892) originally designated this species as *Orthis proavita*, the masculine suffix of *Plaesiomys proavitus* properly facilitates gender agreement (International Code of Zoological Nomenclature 34.2).

PLAESIOMYS SUBQUADRATUS (Hall, 1847)
Figure 6.1–6.4

1847   *Orthis subquadrata* HALL, p. 126, pl. 32a, fig. 1a–1o.
1873   *Orthis subquadrata* (Hall); MEEK, p. 94, pl. 9, fig. 2b–2g.
1892   *Plaesiomys subquadrata* (Hall); HALL AND CLARK, p. 196, pl. 5a, figs. 17–19.
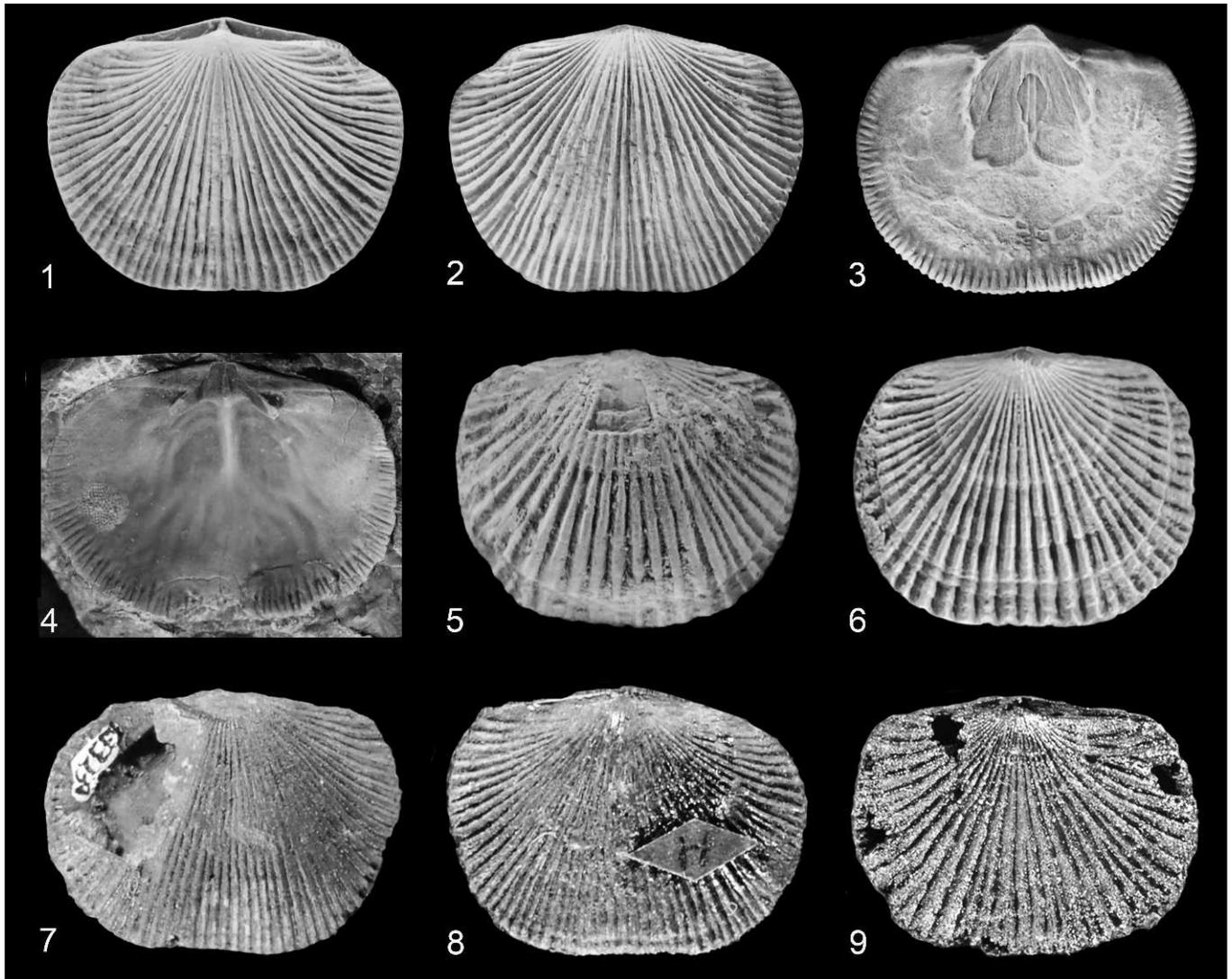1893   *Orthis (Dinorthis) subquadrata* (Hall); WINCHELL AND SCHUCHERT, p. 428, pl. 32, figs. 46–50.

FIGURE 6—*1*, *Plaesiomys subquadratus* (Hall, 1847), AMNH 30263, lectotype, ventral view, ×1.9; *2*, dorsal view, ×1.9; *3*, YPM S-728d, ventral interior, ×1.7; *4*, YPM S-238f, dorsal interior, ×1.7; *5*, *P. proavitus* (Winchell and Schuchert, 1892), YPM S-703a, lectotype, dorsal view, ×2.3; *6*, SUI 1808, ventral view, ×2.9; *7*, *P. idahoensis* Ross, 1949, USNM 133239, cast of holotype, dorsal view, ×2.6; *8*, ventral view, ×2.6; *9*, *P. cutterensis* Howe, 1966, USNM 268935, cast of holotype, ventral view, ×2.0.

1932 *Plaesiomys (Dinorthis) subquadrata* (Hall); SCHUCHERT AND COOPER, pl. 10, figs. 15, 17, 18, 24–26.

1959 *Plaesiomys subquadratus* (Hall); ROSS, p. 449, pl. 55, figs. 1, 6, 12, 14, 15, 18, 19, 23.

1965 *Plaesiomys (Plaesiomys) subquadrata* (Hall); WILLIAMS AND WRIGHT, p. H319, pl. 201, figs. 5a–3.

1966 *Plaesiomys* cf. *subquadratus* (Hall); HOWE, p. 247, pl. 29, figs. 1–6.

1973 *Plaesiomys subquadratus* (Hall); ALBERSTADT, p. 22, pl. 2, figs. 6–8.

1973 *Plaesiomys* cf. *subquadratus* (Hall); ALBERSTADT, p. 21, pl. 7, figs. 8a, 8b.

1985 *Plaesiomys subquadrata* (Hall); COOPER, p. 298, pl. 111, figs. 54–58.

1985 *Plaesiomys subquadrata* (Hall); DAVIS, pl. 8, figs. 5–7.

1996 *Plaesiomys subquadrata* (Hall); SCHWIMMER AND SANDY, pl. 16.2, figs. 11–13.

1996 *Plaesiomys* aff. *subquadratus* (Hall); JIN AND NORFORD, p. 25, pl. 2, figs. 1–7.

1997 *Plaesiomys subquadratus* (Hall); JIN, CALDWELL, AND NORFORD, pl. 1, figs. 1–4.

2000 *Plaesiomys subquadrata* (Hall); WILLIAMS AND HARPER, p. 747, pl. 540, figs. 1a–1d.

2008 *Plaesiomys subquadratus* (Hall); JIN AND ZHAN, pl. 4, figs. 14–20.

Diagnosis.—Large *Plaesiomys* species with wide, subquadrate shells characterized by high costal density. Valve convexity and inflation are variable, but valves are typically convexoconcave to dorsibiconvex; sulcus originates proximally; ventral muscle scars moderate to long, adjustor muscle scars variable; ventral and dorsal umbonal angles low. Emended from Hall (1847).

Types.—AMNH 20361–30267 are syntypes of Hall's (1847) original description; however, Hall (1847) did not designate a holotype. AMNH 30263 is therefore designated as a lectotype and the remaining specimens become paralectotypes.

Other material.—USNM 14655a–f, YPM S-697, S-728c-e.

Occurrence.—Waynesville, Liberty, and Whitewater Formations, Ohio and Indiana; Aleman Limestone, Texas; Viola Formation, Oklahoma; Avalanche Formation, British Columbia;
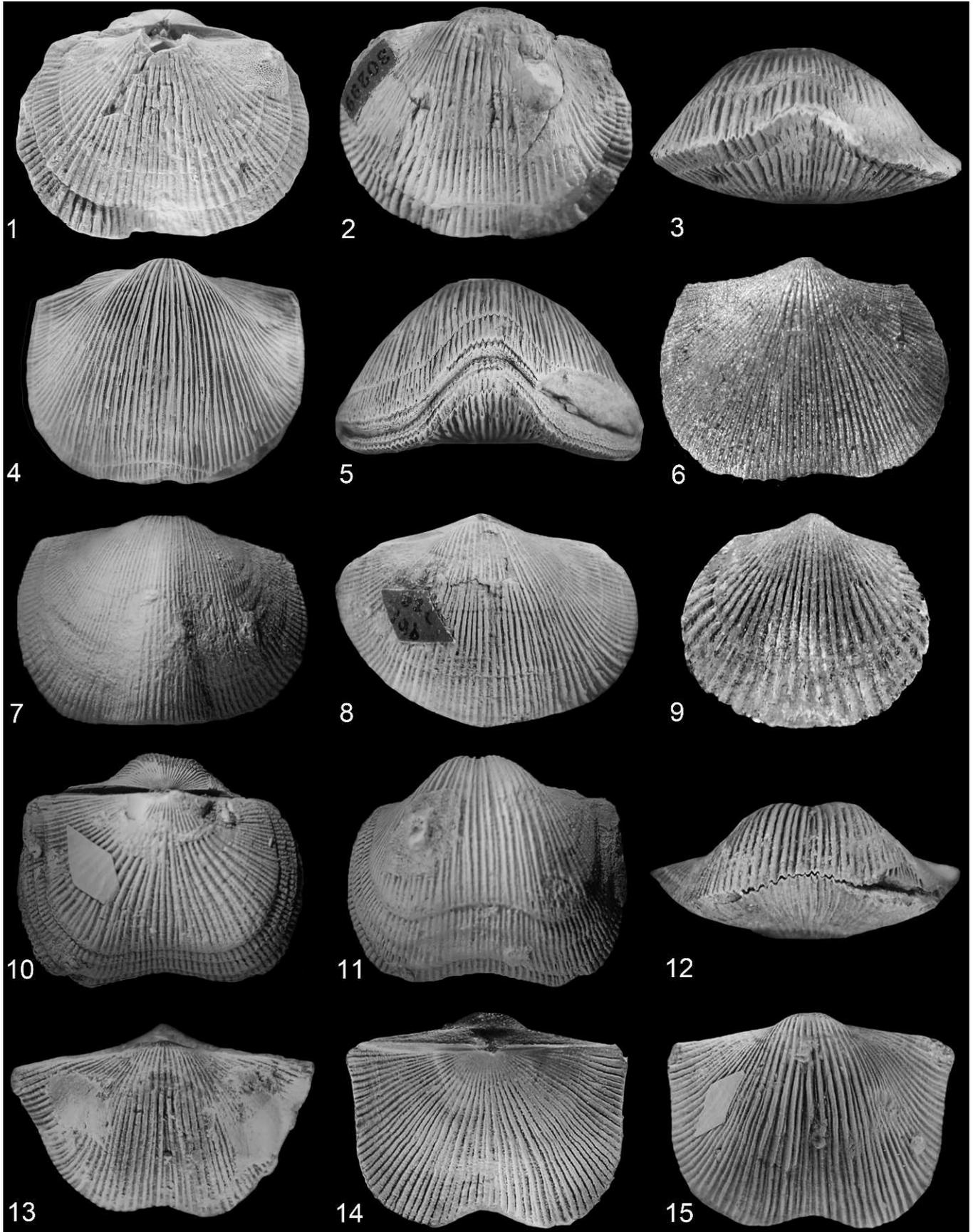
Caution Creek Formation, Manitoba; Richmondian (upper Katian).

Remarks.—Although several subspecies have been previously assigned to *P. subquadratus*, the phylogenetic analysis failed to uphold their subspecific status (see above). Consequently all former subspecies have been elevated herein to the rank of species. Character analysis reveals considerable morphological variation within *P. subquadratus* regarding relative valve inflations, convexity between the valves, total shell height, depth of the shell, depth of the sulcus, length of the ventral muscle scars, and the height of the dorsal cardinal area. Occurrences of *P. subquadratus* are geographically widespread throughout the Laurentian paleocontinent and range throughout the Richmondian (upper Katian). Given the widespread occurrences, substantial morphological variation may be attributed to differential population dynamics operating within a geographically widespread species.

Although Hall (1847) originally designated this species as *Orthis subquadrata*, Ross (1959) corrected the specific epithet to *Plaesiomys subquadratus* to facilitate gender agreement (ICZN 34.2).

Family PLECTORTHIDAE Schuchert and LeVene, 1929
Genus HEBERTELLA Hall and Clarke, 1892

Type species.—*Orthis occidentalis* Hall, 1847. Hall and Clarke (1892) originally designated *Orthis sinuata* Hall, 1847 as the type species of *Hebertella*. However, Walker (1982) synonymized *O. sinuata* with *O. occidentalis* Hall, 1847. *Orthis occidentalis* has page priority in Hall's (1847) original descriptions and is, therefore, the type species.

Other species.—*Hebertella alveata* Foerste, 1909a; *H. bursa* Raymond, 1928; *H. frankfortensis* Foerste, 1909b; *H. montoyensis* Howe, 1966; *H. parksensis* Foerste, 1909b; *H. prestonensis* Ladd, 1929; *H. richmondensis* Foerste, 1909a; *Orthis maria* Billings, 1862; *O. subjugata* Hall, 1847.

Diagnosis.—Genus of Plectorthidae with large, subquadrate shells characterized by obcordate ventral muscle scars with thickened margins and adductor scars tracks raised on a double median ridge. Pallial markings rare to absent. Valves are unequally biconvex to convexoconcave; multicostellate with aditicules; sulcus median, typically wide; cardinal extremities are rounded to alate; large ventral interarea, cataline to apsacline; dorsal cardinal area long, apsacline; brachiophore plates convergent; dorsal muscle scars quadripartite, weakly impressed, with posterior adductor scars larger than anterior. Juvenile or smaller shells may be semielliptical. Emended from Williams and Harper (2000).

Occurrence.—Whiterockian (lower Sandbian) to Richmondian (upper Katian) of North America and the Cautleyan (Katian) of Ireland.

Remarks.—*Hebertella* most closely resembles *Mimella* with respect to the exterior morphology of the shell, yet *Mimella* typically has a more convex ventral valve. Interiorly, species of *Hebertella* may be easily distinguished from *Mimella* based on ventral musculature. The ventral muscle scars in *Mimella* are characterized by deep diductor scars separated by an elongate and anteriorly expanded adductor scar trackway with well-developed pallial markings; conversely, in *Hebertella* the ventral adductor scars do not expand anteriorly and pallial markings are typically absent. Because small specimens of *Hebertella* may not be easily distinguished from *Plectorthis*, only large shells representing adult specimens should be considered useful for stratigraphic or paleobiologic inferences pending a taxonomic revision of *Plectorthis*.

Schuchert and Cooper (1932) noted that species of *Hebertella* are common in North America yet rare to unknown from Europe. Since their 1932 publication, possible species of *Hebertella* have been reported from outside North America including Kazakhstan (Popov et al., 2000), Tasmania (Laurie, 1991), and the British Isles (Reed, 1952; Wright, 1964). However, the generic affinity of the non-North American species has been disproven (Popov and Cocks, 2006; Jin and Zhan, 2008), except in the case of *Hebertella* sp. of Wright (1964). Unfortunately, the specimens described by Wright (1964) are incomplete or poorly preserved specimens; therefore, insufficient morphological data are available to include this taxon within a phylogenetic analysis.

HEBERTELLA ALVEATA Foerste, 1909a
Figure 7.12–7.15

1873 *Orthis occidentalis* (Foerste, 1909a); MEEK, p. 96, pl. 9, fig. 3.
1909a *Hebertella alveata* FOERSTE, p. 255, pl. 30, figs. 15–23.
1932 *Hebertella alveata* Foerste; SCHUCHERT AND COOPER, p. 60.
1982 *Hebertella alveata* Foerste; WALKER, p. M3.

Diagnosis.—Large *Hebertella* species with a wide hinge line containing angular to alate cardinal extremeties. Shell widest along the hinge line, outline semielliptical to subquadrate; sulcus narrow and shallow; dorsal valve variably inflated, with a broad medial depression extending from the beak to the commissure; dorsal umbo located proximal to the hinge line, not extending significantly beyond the hinge line. Emended from Foerste (1909a).

Types.—Foerste (1909a) described and figured two specimens yet did not designate a holotype. USNM 87146 (two articulated valves) is herein designated as the lectotype and USNM 78452 (two ventral valves) becomes a paralectotype.

Occurrence.—Liberty and Whitewater Formations, Ohio and Indiana; Richmondian (upper Katian).

Remarks.—*Hebertella alveata* occurs most commonly alongside *H. occidentalis* and *H. richmondensis* in the Liberty Formation, yet is easily distinguished by its biconvex profile, maximum shell width developed at the hinge line, pronounced angular to alate cardinal extremities, and a medial depression on the dorsal valve that extends to the commissure.

HEBERTELLA FRANKFORTENSIS Foerste, 1909b
Figure 7.9

1871 *Orthis frankfortensis* (Foerste, 1909b); JAMES, p. 10 [nomen nudum]
1909b *Hebertella frankfortensis* FOERSTE, p. 318–319, pl. 7, figs. 11a–b.
1932 *Hebertella frankfortensis* Foerste; SCHUCHERT AND COOPER, p. 60, pl. 11, fig. 21.
1982 *Hebertella frankfortensis* Foerste; WALKER, p. M3–M6, pl. 4, figs 18–40.

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FIGURE 7—*1, Hebertella occidentalis* (Hall, 1847), AMNH 30299, lectotype, ventral view, ×2.3; *2,* dorsal view, ×2.3; *3,* anterior view, ×2.4; *4, H. prestonensis* Ladd, 1929, SUI 66503, lectotype, dorsal view, ×1.3; *5,* anterior view, ×1.3; *6, H. montoyensis* Howe, 1966, USNM 268935, cast of holotype, ventral view, ×1.7; *7, H. parksensis* Foerste, 1909b, USNM 87054, lectotype, dorsal view, ×2.8; *8, H. subjugata* (Hall, 1847), AMNH 30290, holotype, dorsal view, ×2.1; *9, H. frankfortensis* Foerste, 1909b, USNM 258472, lectotype, ventral view, ×2.0; *10, H. richmondensis* Foerste, 1909a, USNM 87158, holotype, ventral view, ×1.7; *11,* dorsal view, ×1.7; *12, H. alveata* Foerste 1909a, USNM 87146a, lectotype, anterior view, ×2.2; *13,* ventral view, ×2.2; *14,* USNM 87146b, lectotype, ventral view, ×1.7; *15,* dorsal view, ×1.7.

Diagnosis.—Small, sparely costellate *Hebertella* species with a rounded outline and low sulcus. Shell outline semielliptical; costae coarse, bifurcation rare; cardinal extremities rounded; dorsal and ventral valves inflated, evenly biconvex; sulcus narrow to wide, shallow, with relatively few costae ($\leq$15) between inflection points; ventral interarea low, cataclie; delthyrium opening at a wide angle ($\geq$40°); dorsal interarea low, apsacline. Emended from Foerste (1909b).

Types.—Because Foerste (1909b) did not designate a holotype in his original description, USNM 258472 is herein designated the lectotype.

Other material.—USNM 258466, 258276, 258474, and 248477.

Occurrence.—Bigby-Cannon and Catheys Formations, Kentucky and Tennessee; Mohawkian (upper Sandbian to lower Katian).

Remarks.—*Hebertella frankfortensis* most closely resembles its sister species *H. subjugata*. Both are characterized by small size, a semielliptical outline, and rounded cardinal extremities, yet *H. frankfortensis* is readily distinguished from *H. subjugata* by its more rounded shell, shallower sulcus, and relatively coarse costae with rare bifurcations.

HEBERTELLA OCCIDENTALIS (Hall, 1847)
Figure 7.1–7.3

1847   *Orthis occidentalis* HALL, p. 127, pl. 32a, figs. 2a–2m, 14.
1847   *Orthis sinuata* (Hall); HALL, p. 128, pl. 32b, figs. 2a–2c.
1892   *Orthis sinuata* (Hall); HALL AND CLARKE, pl. 5a, figs. 1–8.
1910   *Hebertella occidentalis* (Hall); FOERSTE, pl. 2, figs. 1, 2.
1914b   *Hebertella latasulcata* (Hall); FOERSTE, p. 131, pl. 3, figs. 7a, 7b.
1932   *Hebertella occidentalis sinuata* (Hall); SCHUCHERT AND COOPER, pl. 11, figs. 14, 17, 19, 20, 22–26.
1961   *Hebertella occidentalis* (Hall); CASTER, DALVE, AND POPE, pl. 5, figs. 24, 25.
1961   *Hebertella sinuata* (Hall); CASTER ET AL., pl. 4, figs. 2–4.
1965   *Hebertella sinuata* (Hall); WILLIAMS AND WRIGHT, p. h325, pl. 205, figs. 5a–5e.
1982   *Hebertella occidentalis* (Hall); WALKER, p. m6, pl. 5, figs. 18–41.
1985   *Hebertella occidentalis* (Hall); DAVIS, p. 49, pl. 5, figs. 24, 25.
1988   *Hebertella occidentalis* (Hall); HOWE, p. 213, pl. 4, figs. 8–11.
1996   *Hebertella occidentalis* (Hall); SCHWIMMER AND SANDY, p. 224, pl. 16, figs. 24–26.
2000   *Hebertella sinuata* (Hall); WILLIAMS AND HARPER, p. 761, pl. 550, figs. 1a–1f.

Diagnosis.—Moderate to large *Hebertella* species with a subquadrate outline and a moderate to highly pronounced sulcus. Shell wider than long; shell depth variable, convexoconcave to unequally biconvex; cardinal extremities angular; sulcus wide with moderate to very high depth, typically well developed in larger specimens; ventral muscle scars of variable width; dorsal and ventral umbonal angles low (<135°). Emended from Hall (1847).

Types.—Hall (1847) did not specify a holotype in his original description, therefore AMNH 30298 is herein designated as the lectotype and AMNH 30299 becomes a paralectotype.

Other material.—AMNH 30406, USNM 258490, 258496, 258497, YPM S-388a, and ANSP 38106.

Occurrence.—Arnheim, Bellevue, Catheys, Leipers, Fernvale, Oregonia, Liberty, Whitewater, and Elkhorn Formations, Indiana, Kentucky, Ohio, and Tennessee; upper Mohawkian to Richmondian (lower to upper Katian).

Remarks.—This morphologically variable species was first described by Hall (1847) as separate from *H. sinuata* on the basis that the latter had a more highly developed fold and sulcus, more prominent costae, and a greater height of the dorsal valve. Meek (1873) and Cummings (1908) noted that intermediate forms exist between *H. occidentalis* and *H. sinuata*, and suggested that the two species represent morphological end members of a single species. Similarly, Schuchert and Cooper (1932) listed *H. sinuata* a subspecies of *H. occidentalis* and Howe (1966) found significant overlap between the two species using characters considered diagnostic by Hall (1847). Walker (1982) synonymized the two species (along with *H. subjugata*, see below) in his descriptions of *Hebertella* species from Kentucky, with the name *H. occidentalis* having page priority over *H. sinuata* in Hall's (1847) original descriptions. *Hebertella occidentalis* has a long stratigraphic range and is abundant in shallow subtidal facies throughout the Cincinnati Arch.

HEBERTELLA MONTOYENSIS Howe, 1966
Figure 7.6

1966   *Hebertella occidentalis montoyensis* HOWE, p. 255, pl. 30, figs. 15–23.

Diagnosis.—Large to very large species of *Hebertella* characterized by a highly developed sulcus and narrow ventral umbonal opening ($\leq$135°). Shell subquadrate; shell depth high; cardinal extremities angular; sulcus deep, narrow, with many ($\geq$17) costae; ventral valve inflated; ventral interarea large; ventral muscle scars wide. Emended from Howe (1966).

Types.—USNM 268935 (holotype), 146546.

Occurrence.—Aleman and Cutter Limestones, Texas; Richmondian (upper Katian).

Remarks.—*Hebertella montoyensis* was originally described by Howe (1966) as a subspecies of *H. occidentalis* from the Aleman and Cutter Limestones of the Hueco Mountains in Texas. Howe (1966) differentiated specimens of *H. montoyensis* from *H. occidentalis* because they had a much weaker sulcus. Character data supports Howe's (1966) distinction (character 7), yet *H. montoyensis* is herein recognized as a distinct species because phylogenetic analysis indicates *H. montoyensis* is more closely related to *H. prestonensis* than *H. occidentalis*.

HEBERTELLA PARKSENSIS Foerste, 1909b
Figure 7.7

1909b   *Hebertella maria-parksensis* FOERSTE, p. 319, pl. 7, figs. 6a, 6b.
1932   *Hebertella maria-parkensis* [sic] Foerste; SCHUCHERT AND COOPER, p. 60.
1982   *Hebertella parksensis* Foerste; WALKER, p. M8, pl. 5, figs. 1–12, 16, 17.

Diagnosis.—*Hebertella* species characterized by its small to moderate size, numerous bifurcations, and a ventral muscle field with an elevated marginal rim Shell outline semielliptical; highly multicostellate; cardinal extremities rounded; dorsal and ventral valves variably convex; sulcus narrow, deep, filled with numerous ($\geq$17) closely packed costae; ventral muscle field pronounced into a platform, with adductor scars elevated above diductor scars; ventral interarea low, orthocline; dorsal umbonal angle highly obtuse ($\geq$140°); dorsal interarea low, not extending significantly over the hinge line. Emended from Foerste (1909b).

Types.—Foerste (1909b) described two specimens in his

original description yet did not designate a holotype. USNM 87054 is herein designated a lectotype, and USNM 87055 becomes a paralectotype.

Other material.—USNM 258482.

Occurrence.—Point Pleasant and Clays Ferry Formations, Kentucky; Mohawkian (upper Sandbian to lower Katian).

Remarks.—Although Foerste (1909b) first described *H. parksensis* as *H. maria-parksensis*, Foerste (1909b) likely considered *H. parksensis* to be distinct from *H. maria* because later in the same publication he referred to the species as *H. parksensis*. Walker (1982) considered *H. parksensis* to be a valid species, and his taxonomic assessment is upheld by character analysis. Further, phylogenetic analysis indicates that *H. parksensis* is the sister taxon to the clade comprising *H. frankfortensis* and *H. subjugata* and is not closely related to *H. maria*.

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HEBERTELLA PRESTONENSIS Ladd, 1929
Figure 7.4, 7.5

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1929 *Hebertella sinuata prestonensis* LADD, p. 401, pl. 5, figs. 3–6.

Diagnosis.—Large to very large species of *Hebertella* characterized by a highly developed sulcus and obtuse ventral umbonal opening ($\leq$140°). Shell subquadrate; inflated dorsal and ventral valves, ventral valve with medial depression; sulcus very deep, narrow, many costae ($\geq$17) inserted between inflection points; ventral interarea strongly catacline; ventral muscle scars wide; dorsal umbo strongly apsacline. Emended from Ladd (1929).

Types.—Ladd (1929) described two specimens in his original description but did not designate a holotype. SUI 66503 is herein designated as the lectotype and USNM 71927 becomes a paralectotype.

Occurrence.—Maquoketa Formation, Iowa; Richmondian (upper Katian).

Remarks.—Ladd (1929) originally described *H. prestonensis* as a subspecies of *H. sinuata*, a junior synonym of *H. occidentalis*. However, Ladd (1929) must have considered *H. prestonensis* distinct because he listed more than six external morphological characters distinguishing the two species. Phylogenetic analysis supports removing *H. prestonensis* from subspecific taxonomic rank and it is elevated to specific status herein. The topology in Figure 5 indicates *H. prestonensis* is sister to *H. montoyensis* from the Montoya Group of Texas. The character state distribution in Table 10 reveals the two species only differ with respect the inclination of their ventral umbo (character 13). Because *H. montoyensis* is missing data for five characters, it is unclear whether further sampling would reveal *H. montoyensis* and *H. prestonensis* to be synonymous. Pending further sampling of non-type material, both species are herein considered valid, separate species.

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HEBERTELLA RICHMONDENSIS Foerste, 1909a
Figure 7.10, 7.11

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1909a *Hebertella alveata richmondensis* FOERSTE, p. 249, pl. 29, figs. 7–12, 14.
1910 *Hebertella alveata richmondensis*; FOERSTE, p. 55, pl. 5, fig. 10.
1932 *Hebertella alveata richmondensis*; SCHUCHERT AND COOPER, p. 60.

Diagnosis.—Large *Hebertella* species with a short hinge line and convexoconcave profile. Shell semielliptical; cardinal extremities variable; dorsal valve highly inflated; ventral muscle scars large; ventral interarea small, apsacline; ventral umbonal angle wide ($\geq$140°); dorsal valve with broad medial depression; dorsal cardinal area large; dorsal umbo wide, remaining proximal to the hinge line. Emended from Foerste (1909a).

Types.—USNM 87158 (holotype).

Occurrence.—Whitewater Formation, Indiana; Richmondian (upper Katian).

Remarks.—*Hebertella richmondensis* was originally described by Foerste (1909a) as a variant of *H. alveata* from the Whitewater Formation in Indiana. Foerste (1909a) described *H. richmondensis* as having a highly convex dorsal valve and much narrower hinge line, whereas *H. alveata* is generally biconvex and alate. However, phylogenetic analysis indicates that *H. richmondensis* is more closely related to *H. bursa* than *H. alveata*, differing from *H. alveata* by six characters related to shell depth, sulcus size and costae, and morphology of the ventral interarea (characters 5, 7, 8, 12, 13, 15). *Hebertella richmondensis* is, therefore, recognized as a distinct species herein. It is most readily differentiated by its convexoconcave profile, inflated dorsal valve with a broad medial depression extending anteriorly, and narrow hinge line.

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HEBERTELLA SUBJUGATA (Hall, 1847)
Figure 7.8

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1847 *Orthis subjugata* HALL, p. 249, pl. 29, figs. 7–12, 14.
1910 *Hebertella subjugata* (Hall); FOERSTE, p. 54, pl. 2, fig. 8.
1932 *Hebertella subjugata* (Hall); SCHUCHERT AND COOPER, p. 60.
1982 *Hebertella parksensis* (Hall); WALKER, pl. 5, figs. 13, 14.

Diagnosis.—Small to moderate size *Hebertella* species with a semielliptical outline and rounded cardinal extremities. Shell, much wider than long; ventral and dorsal valves inflated, unequally biconvex with steep dorsal valve lacking a medial depression; cardinal extremities rounded; sulcus deep, marked by many ($\geq$17) fine costae between inflection points; ventral interarea small, nearly catacline; delthyrial angle wide ($\geq$40°); dorsal and ventral umbos remaining proximal to the hinge line. Emended from Hall (1847).

Types.—AMNH 30290 (holotype).

Occurrence.—Clays Ferry, Bellevue, and Waynesville Formations in Kentucky, Indiana, and Ohio; Edenian to Richmondian (lower to upper Katian).

Remarks.—Hall (1847) differentiated specimens of *H. subjugata* from *H. occidentalis* on the basis of its smaller shell, semielliptical outline, finer costae, and a more prominent ventral umbo. Foerste (1910) furthered this distinction by noting that *H. subjugata* lacks a medial depression near the beak of the dorsal valve, whereas *H. occidentalis* has a medial depression terminating anteriorly. Walker (1982) questioned the taxonomic validity of *H. subjugata* in his discussion of *H. occidentalis* and *H. sinuata,* and he listed *H. subjugata* as a synonym of *H. occidentalis*. Although Walker's (1982) synonymy of *H. occidentalis* and *H. sinuata* has been supported by other authors (e.g., Cummings, 1908; Meek, 1873; Howe, 1966; Schuchert and Cooper, 1932), his synonymy of *H. subjugata* has not (Foerste, 1910; Schuchert and Cooper, 1932). Walker (1982) supported his synonymy of *H. subjugata* with *H. occidentalis* by citing Hall's (1847, p. 130) admission that they "are scarcely regarded as distinct, and are usually found mingled together in the collections". However, Hall's (1847) support is dubious because he included *Orthis subquadrata*, which is now recognized as the type species of *Plaesiomys*, in his admission. Moreover, the phylogenetic analysis presented here places *H. subjugata* outside the *H. occidentalis* subclade. Primary differences include its semielliptical profile and rounded cardinal extremities.

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CONCLUSIONS

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The orthid brachiopod genera *Plaesiomys* and *Hebertella* were both common and significant genera in Late Ordovician

benthic communities. Phylogenetic analysis has documented species-level evolutionary relationships and informed taxonomic revisions for both genera, thereby providing an evolutionary framework for future investigations examining potential drivers of paleobiogeographic differentiation among Late Ordovician brachiopod communities of the Laurentian paleocontinent. In addition, the data presented here may be combined with previous species-level phylogenetic hypotheses of invasive genera (e.g., Wright and Stigall, in press) to further constrain the biogeographic source of the Richmondian invaders.

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