



## A combined morphometric and phylogenetic revision of the Late Ordovician brachiopod genera *Eochonetes* and *Thaerodonta*

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**Abstract.**—Systematic revision of the Late Ordovician brachiopod genera *Eochonetes* Reed, 1917 and *Thaerodonta* Wang, 1949 was conducted utilizing specimen-based morphometric and species-level phylogenetic analyses. Previous studies had recognized *Thaerodonta* and *Eochonetes* as either distinct taxonomic entities or synonyms. New multivariate and phylogenetic analyses confirm the synonymy of *Thaerodonta* with *Eochonetes* and provide a framework to assess evolutionary and ecological patterns within the clade. Multivariate analyses were employed to delineate species in morphospace and provided information on potential species relationships. Phylogenetic analysis was used to produce an evolutionary framework for taxonomic revision and identify character evolution within the clade. Most species previously assigned to *Thaerodonta* are transferred to *Eochonetes*, and three others are excluded from *Eochonetes* and provisionally referred to other sowerbyellid genera. Three new species (*Eochonetes maearum* new species, *E. voldemortus* new species, *E. minerva* new species) are described, one species (*Leptaena saxea* Sardeson, 1892) is synonymized with *E. recedens* Sardeson, 1892, and one subspecies (*Thaerodonta mucronata scabra* Howe, 1965) is rejected. This study demonstrates that a combination of complementary approaches and data types has the potential to advance interpretations beyond analyses confined to single analytical tools. Specifically, multivariate analyses provide constraints on species boundaries, whereas species-level phylogenetic analyses provide frameworks to examine morphological, ecological, and biogeographic evolution within a clade.

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### Introduction

Studies of fossil morphology and systematics provide key data for most areas of paleontological investigation. Descriptions of new taxa and systematic revisions provide the framework on which additional analyses of evolution, biogeography, and diversity can be developed (e.g., Lieberman, 2000; Cracraft, 2001; Friis et al., 2010; Bauer and Stigall, 2014). During the past 25 years, new tools, e.g., phylogenetic methods and advanced computational programs (e.g., Huelsenbeck and Ronquist, 2001; Swofford, 2002; Maddison and Maddison, 2003), have emerged to provide expanded opportunities for systematic analyses and create potential for ever more detailed understanding of the history of life. The adoption of these tools has varied substantially among specialists of various clades; detailed phylogenetic and multivariate analyses are common in vertebrate paleontology, but comparatively less common within invertebrate systematics. Specifically, most systematic revisions of brachiopod genera have been conducted based on detailed qualitative or quantitative analyses of overall morphology (e.g., Popov et al., 2002; Cocks, 2005; Thomsen et al., 2006), but have lacked explicit phylogenetic frameworks to examine the evolutionary history of a clade. In this study, we examine

whether a combination of phylogenetic and morphometric techniques can improve on prior inferences of evolutionary history among a set of species previously assigned to the Late Ordovician strophomenid genera *Eochonetes* Reed, 1917 and *Thaerodonta* Wang, 1949. We examine and contrast potential inferences derived from specimen-based morphometric analyses, taxon-based phylogenetic analyses, and the possible extension of these results for addressing evolutionary, biogeographic, and ecological patterns within these species.

Species assigned to *Thaerodonta* were distributed across the palaeocontinent of Laurentia during the Late Ordovician, whereas species assigned to *Eochonetes* were concentrated within the peri-Laurentian terrains of Scoto-Appalachia and Anticosti Island. The taxonomic history of these genera is complex, reflecting conflicting opinions about whether or not the included species comprise a single lineage or multiple distinct lineages. *Eochonetes* was originally considered closely related to *Chonetes* Fischer de Waldheim, 1830 and *Sowerbyella* Jones, 1928, but has generally been accepted as a distinct genus since 1965. Following its initial description, the genus *Thaerodonta* has been synonymized with three different genera, most notably with *Eochonetes* (Cocks and Rong, 1989, 2000; Cocks, 2005, 2013), and rerecognized as a valid taxon on eight

**Table 1.** Taxonomic status changes of the genera *Eochonetes* and *Thaerodonta* over the past century.

Year	Taxonomic Status	Author
1917	<i>Eochonetes</i> erected as a subgenus of <i>Chonetes</i>	Reed
1928	<i>Eochonetes</i> recognized as a subgenus within <i>Sowerbyella</i>	Jones
1949	<i>Thaerodonta</i> erected as distinct genus	Wang
1965	<i>Thaerodonta</i> recognized as distinct genus	Howe
1965	<i>Thaerodonta</i> synonymized with <i>Eoplectodonta</i>	Muir-Wood & Williams
1965	<i>Eochonetes</i> recognized as a distinct genus	Muir-Wood & Williams
1967	<i>Thaerodonta</i> recognized as distinct genus	Havliček
1972	<i>Thaerodonta</i> recognized as distinct genus	Howe
1974	<i>Thaerodonta</i> recognized as distinct genus	Amsden
1977	<i>Thaerodonta</i> synonymized with <i>Eoplectodonta</i>	Mitchell
1981	<i>Thaerodonta</i> recognized as distinct genus	Rõõmusoks
1989	<i>Thaerodonta</i> synonymized with <i>Sowerbyella</i> ( <i>Eochonetes</i> )	Cocks & Rong
1997	<i>Thaerodonta</i> recognized as distinct genus	Jin et al.
2000	<i>Thaerodonta</i> synonymized with <i>Eochonetes</i>	Cocks & Rong
2001	<i>Thaerodonta</i> recognized as distinct genus	Jin & Zhan
2003	<i>Thaerodonta</i> recognized as distinct genus	Candela
2005	<i>Thaerodonta</i> synonymized with <i>Eochonetes</i>	Cocks
2013	<i>Thaerodonta</i> synonymized with <i>Eochonetes</i>	Cocks

separate occasions over the last century (Table 1; Howe, 1965; Havliček, 1967; Howe, 1972; Amsden, 1974; Rõõmusoks, 1981; Jin et al., 1997; Jin and Zhan, 2001; Candela, 2003).

The primary difference between *Eochonetes* and *Thaerodonta* is the presence of ventral hinge-line canals visible on internal molds of *Eochonetes* but not on any individuals recognized as *Thaerodonta* (Cocks and Rong, 1989). The ventral tubules, or canals, of *Eochonetes* do not penetrate the exterior of the shell, and therefore, do not appear to extend into external spines as in true chonetids (Reed, 1917; Jones, 1928). In the majority of *Eochonetes* specimens, the canals are not preserved (Cocks and Rong, 1989). However, few *Thaerodonta* specimens are preserved as molds, and thus taphonomic biases likely indicate that the lack of recognition of this character among *Thaerodonta* species is not particularly meaningful. All other morphological characters of *Eochonetes* closely resemble *Thaerodonta*, including the hinge-line denticulation of dorsal denticles and ventral fossettes (Cocks and Rong, 1989).

Although the relationship between *Thaerodonta* and *Eochonetes* has previously been assessed based on character data, these comparisons have lacked an explicit phylogenetic framework that could help clarify the evolutionary positions of species assigned to these genera. In this study, we examine whether *Thaerodonta* and *Eochonetes* are distinct evolutionary lineages first by assessing species validity through multivariate morphometric analysis and then by generating a species-level phylogenetic hypothesis through parsimony analysis. Results of these two morphological analyses are then used to provide the basis for a comprehensive, phylogenetically informed taxonomic revision of species previously assigned to *Eochonetes* and *Thaerodonta*.

## Materials and methods

Interspecific and intraspecific variation is widespread within species of *Thaerodonta* and *Eochonetes* (Howe, 1972; Jin and Zhan, 2001). Therefore, character-based morphometric analysis

was employed to establish species boundaries and validate specific assignments. The multivariate analyses provide a basis to interpret generic and species relationships in the context of morphological space, but only incorporate a subset of all potentially informative characters. Subsequent species-level phylogenetic analysis employed morphometrically constrained species as the focal taxa and incorporated additional character data to reconstruct evolutionary relationships. The combined results of the two analyses provide the basis for the systematic revision.

**Taxa analyzed.**—Twenty-seven operational taxonomic units (OTUs) were analyzed from museum collections, including 20 validly described species and seven OTUs in open nomenclature (Table 2). Morphological data were collected for 397 specimens including all available type and numerous nontype specimens (Supplemental Data 1, 2). Nontype specimens were included to better characterize the degree of intraspecific variation and because type specimens were not always available or able to provide sufficient character data for analysis. Nontype specimens that were chosen for measurement were based on: prior specific assignment, presence of dorsal denticles, and geographic occurrence in North America, the British Isles, or Estonia (Fig. 1; Table 3). Only specimens interpreted as adults were included within the study. Maturity was determined based on the presence of a well-developed bema and muscle scars. When identified, juvenile specimens typically exhibited the same outline shape as the adults but were of smaller size with less-pronounced internal features. Individuals of notably small size for the species or that lacked well-developed internal features were excluded from analysis.

Species listed in Table 7 are considered to be valid taxa. The original descriptions for most of these species are sufficient for diagnoses and further discussion is not necessary. Character state distribution data in Table 6 and Supplemental Data 4 and 5 can be combined with previously published descriptions to provide enhanced diagnoses. For a complete list of specimens examined, see Supplemental Data 1.

**Repositories and institutional abbreviations.**—Repositories of specimens are indicated by the following abbreviations: AMNH, American Museum of Natural History; BGS, British Geological Survey; FMNH, Field Museum of Natural History; GLAHM, Hunterian Museum, Glasgow, Scotland; GSC, Geological Survey of Canada; NHM, Natural History Museum, London; OUIP, Ohio University Invertebrate Paleontology Collections; SNMOH, Sam Noble Museum of Oklahoma History; SUI, University of Iowa Paleontological Repository; TUG, University of Tartu, Museum of Geology; USNM, United States National Museum of Natural History; YPM, Yale Peabody Museum.

**Characters analyzed.**—Measurements were collected for a series of length, width, angles, and amounts or counts of specific features on the interior and exterior surfaces of specimen valves. These included both qualitative and quantitative characters reflecting external and internal attributes of both valves (Fig. 2). Characters were organized in groups pertaining to external and internal features of ventral or dorsal valves. Similar characters have been used in previous morphometric analyses of Ordovician brachiopods (e.g., Sohrabi and Jin, 2013; Sproat and Jin, 2013) and to generate

**Table 2.** Distribution of OTUs among analyses within the study. \* = outgroup.

Species Examined (OTU)	Morphometric Analysis			Phylogeny	Excluded
	Dorsal	Ventral			
<i>Sowerbyella rugosa</i> * Meek, 1873	–	–	x	–	
<i>Sowerbyella socialis</i> * Cooper, 1956	–	–	x	–	
<i>Eochonetes advena</i> Reed, 1917	x	x	x	–	
<i>Thaerodonta</i> aff. <i>T. clarksvillensis</i> ; Macomber, 1970	x	–	x	–	
<i>Thaerodonta aspera</i> Wang, 1949	x	x	x	–	
<i>Eochonetes celticus</i> Mitchell, 1977	–	x	x	–	
<i>Thaerodonta clarksvillensis</i> Foerste, 1912	x	x	x	–	
<i>Thaerodonta</i> cf. <i>T. recedens</i> ; Howe, 1965	x	x	x	–	
<i>Thaerodonta</i> cf. <i>T. recedens</i> ; Ross, 1957	–	–	–	x	
<i>Thaerodonta</i> cf. <i>T. recedens</i> ; Alberstadt, OU coll.	–	–	–	x	
<i>Thaerodonta convexa</i> Rõõmusoks, 1981	–	–	–	x	
<i>Thaerodonta dignata</i> Wang, 1949	x	x	x	–	
<i>Eochonetes glabra</i> Dewing, 1999	x	x	x	–	
<i>Thaerodonta johnsonella</i> Amsden, 1974	x	x	x	–	
<i>Thaerodonta magna</i> Howe, 1965	x	x	x	–	
<i>Thaerodonta minnesotensis</i> Sardeson, 1892	–	–	x	–	
<i>Thaerodonta moelsi</i> Rõõmusoks, 1981	–	–	–	x	
<i>Thaerodonta mucronata</i> Howe, 1965	x	x	x	–	
<i>Thaerodonta mucronata scabra</i> Howe, 1965	–	–	–	x	
<i>Thaerodonta nubila</i> Rõõmusoks, 1981	–	–	–	x	
<i>Thaerodonta recedens</i> Sardeson, 1892	x	x	x	–	
<i>Thaerodonta saunjaensis</i> Rõõmusoks, 1981	–	–	x	–	
<i>Thaerodonta saxeae</i> Sardeson, 1892	x	x	x	–	
<i>Thaerodonta</i> sp.; Ross, 1959	x	–	x	–	
<i>Thaerodonta</i> sp.; Ross, USNM coll.	–	–	x	–	
<i>Eochonetes vaurealensis</i> Dewing, 1999	x	x	x	–	

phylogenetic hypotheses in other groups of articulated brachiopods (e.g., Leighton and Maples, 2002; Stigall Rode, 2005; Wright and Stigall, 2013, 2014). They also form the basis for many specific diagnoses within the focal genera (e.g., Wang, 1949; Howe, 1965; Macomber, 1970; Amsden, 1974).

Both qualitative characters (based on character states interpreted as homologous) and quantitative characters (based on measurements of specific organisms; Wiley and Lieberman, 2011) were included in this analysis. Both character types have been successfully utilized in previous morphometric and phylogenetic analyses of brachiopods and other clades (e.g., Stigall Rode, 2005; Hunt, 2007; Hopkins, 2011; Sohrabi and Jin, 2013; Sproat and Jin, 2013; Wright and Stigall, 2013, 2014). Recent analyses by Hopkins (2011) demonstrated that inclusion of continuous characters within phylogenetic analyses significantly increases phylogenetic resolution.

Continuous values were used directly for morphometric analysis. For phylogenetic analysis, continuous characters were standardized by dividing the measurement by the maximum width of the valve (typically the hinge line) of the specimen. For complete valves, denticles were counted for each cardinal extremity and averaged for the individual. In specimens in which only part of the hinge line was preserved, denticles were counted on one cardinal extremity for each individual. The angle between the cardinal extremity and the hinge line were treated similarly.

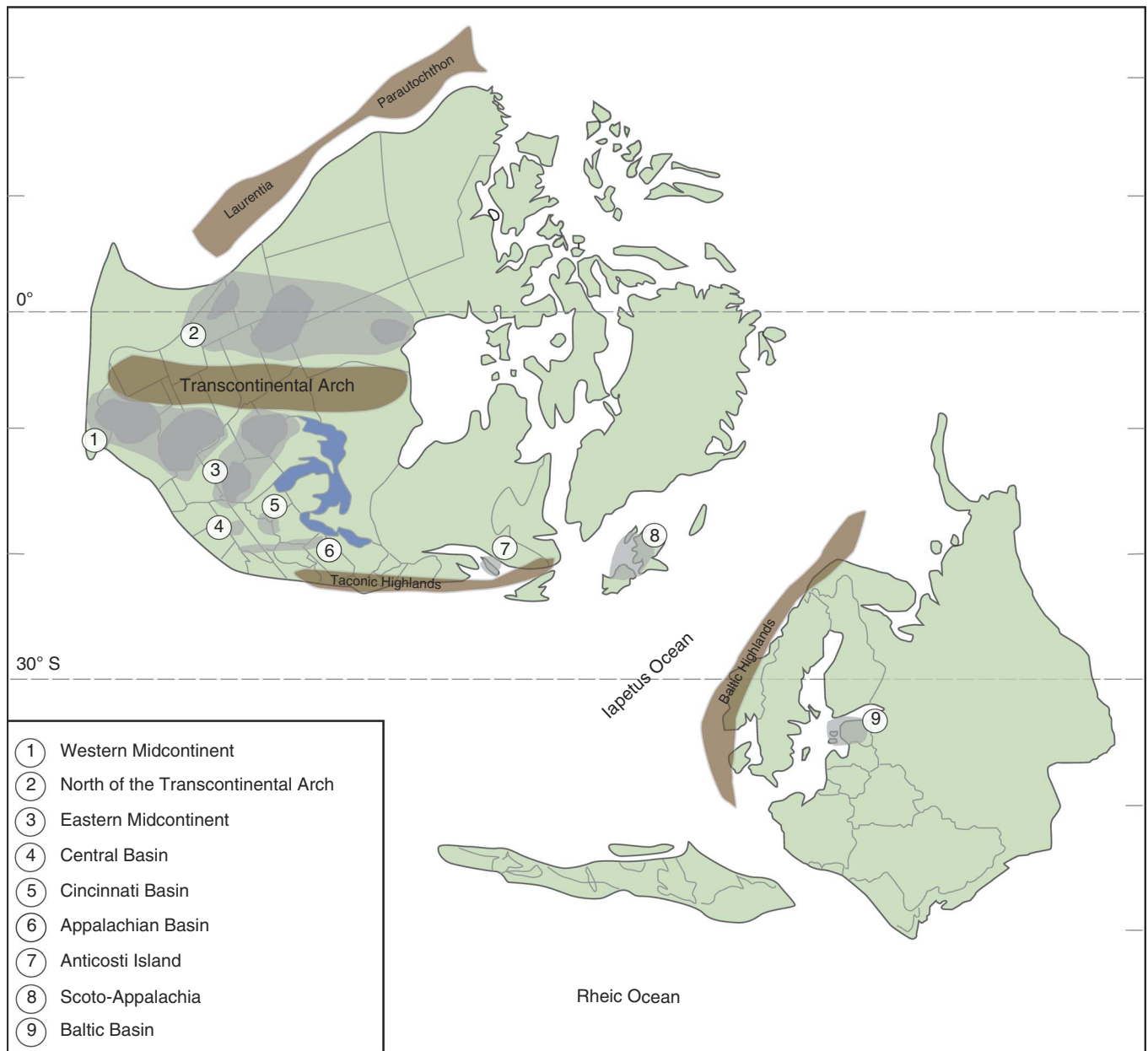
**Morphometric analysis.**—Each specimen for which all characters described could be measured was included in the morphometric analysis. This constrained the data set to 56 specimens within 14 OTUs for dorsal valve analysis and 41 specimens within 13 OTUs for ventral valve analysis (Table 2; Supplemental Data 3, 4). The suite of characters captures overall morphology within the genera and provides a robust framework for multivariate analysis. Similar characters

have been used to distinguish *Thaerodonta* and related genera as well as to delineate species within *Eochonetes* and *Thaerodonta* (e.g., Wang, 1949; Macomber, 1970; Cocks, 2013).

Principal components analysis (PCA) was used to: (1) examine the separation of the genera *Thaerodonta* and *Eochonetes* based on the species previously assigned to each genus; and (2) test individual species boundaries prior to phylogenetic analysis. PCA applies a linear transformation to the original data set to produce an uncorrelated set of variables while minimizing residual variance (Dunteman, 1989). The correlation algorithm normalizes the characters in order to create even weighting for variables measured in different units (Hammer et al., 2001; Sohrabi and Jin, 2013). This technique is intended for use with continuous character data (James and McCulloch, 1990; Etter, 1999), and it is commonly used in analyses of morphometric character data, i.e., analysis of fossil brachiopods (e.g., Sohrabi and Jin, 2013) or fossil or modern humans (White et al., 2003). Analyses were conducted using JMP Pro 11 (SAS Institute Inc., 2009).

To visualize how each type of character influenced the output, two variations of morphometric analyses were conducted: (1) the data set was analyzed in full as described above; and (2) analyses were repeated with characters considered to have potential to skew the results (i.e., length and width) removed. Minor differences occurred among these treatments, as noted below, but the primary results of (1) were repeated in the alternate treatment. Thus, discussion below will focus on analysis (1) unless otherwise indicated.

**Phylogenetic analysis.**—Eighteen OTUs were included in the phylogenetic analysis, including 16 ingroup and 2 outgroup taxa. Two species of *Sowerbyella*, *S. rugosa* Meek, 1873 and *S. socialis* Cooper, 1956 were coded for outgroup comparison because *Sowerbyella* has been considered to be the sister group or ancestral clade from which *Eochonetes* and *Thaerodonta*



**Figure 1.** Palaeogeographic reconstruction of Laurentia and Peri-Iapetan terranes during the Late Ordovician. Structural elements of exposed land, e.g., the Transcontinental Arch, Taconic Highlands, Laurentia Parautochthon, and Baltic Highlands, are outlined, shaded in brown, and labeled. Geographic areas discussed herein are in shaded numbered polygons; these include: (1) Western Midcontinent (Texas and Oklahoma basins); (2) North of the Transcontinental Arch (Bighorn, Williston, and Hudson Bay basins); (3) Eastern Midcontinent (Iowa and Illinois basins); (4) Central Basin (Nashville Dome); (5) Cincinnati Basin; (6) Appalachian Basin; (7) Anticosti Island; (8) Scoto-Appalachia (Scotland and Ireland); and (9) Baltic Basin. Modified from Cocks and Torsvik (2011) and Torsvik and Cocks (2013).

evolved (Howe, 1972; Cocks and Rong, 1989; Sloan, 2005). Based on results of the morphometric analysis and preliminary phylogenetic reconstructions, *T. saxea* Sardeson, 1892 and *T. recedens* Sardeson, 1892 were combined as a single OTU for phylogenetic analysis. All other OTUs listed in Table 1 were coded for potential inclusion within the phylogenetic analysis. However, only those listed in Table 2 were found to convey phylogenetic signal, as described below.

Inclusion of numerous taxa with very sparse character data can cause topological instability or incorrect placement of taxa within the output cladograms (e.g., Gauthier, 1986; Novacek,

1992; Wilkinson and Benton, 1995; Gao and Norell, 1998; Wiens, 2003; Wiley and Lieberman, 2011). However, certain taxa with a substantial number of missing characters can still influence tree topology in positive ways (Wiens, 1998, 2003, 2006), thus the inclusion of some taxa with missing character data is preferable to excluding all species with incomplete character sets out of hand because that approach can result in inadequate data about the evolution of the clade (= missing taxa). Following Wiens (2006), taxa with missing character data were retained in this analysis if they provided phylogenetic structure.

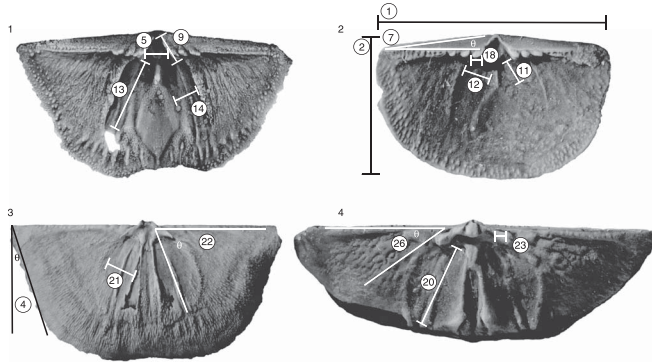
**Table 3.** Geographic, stratigraphic, and temporal distribution for species examined.

Species	Age	Stratigraphy	Geography	Reference
<i>Eochonetes advena</i>	Late Katian	Lower Quarrel Hill Fm. Lady Burn Starfish Beds	Ayrshire, Scotland	Reed, 1917
<i>Thaerodonta</i> aff. <i>T. clarksvillensis</i>	Late Katian	Bighorn Fm., Rock Creek Beds	Johnson Co., Wyoming	Macomber, 1970
<i>Thaerodonta aspera</i>	Middle Katian	Maquoketa Fm. Maquoketa Fm., Elgin Mbr.	Winneshiek Co., Iowa Cape Girardeau Co., Missouri	Wang, 1949
<i>Eochonetes celticus</i>	Early–Late Katian	Member III of the Bardahessiagh Fm., Killey Bridge Fm.	Pomeroy, Ireland	Candela, 2002
<i>Thaerodonta clarksvillensis</i>	Late Katian	Liberty Fm. Waynesville Fm. Penitentiary Mbr. Selkirk Mbr. Cat Head Mbr. Dog Head Mbr. Portage Chute Fm. Surprise Creek Fm. Caution Creek Fm. Chasam Creek Fm. Churchill River Grp. Red River Fm. Aleman Fm.	Concord, Kentucky Southwest Ohio and Southeast Indiana Southern Manitoba	Foerste, 1912; Howe, 1988 Foerste, 1912; Howe, 1979, 1988 Jin & Zhan, 2001
<i>Thaerodonta</i> cf. <i>T. recedens</i>	Late Katian Late Katian	Cutter Fm. Viola Grp., Welling Fm.	Hudson Bay	Jin et al., 1997
<i>Thaerodonta convexa</i>	Middle–Late Katian	Kõrgessaare Fm.	Montana Hudspath Co., Texas Culberson Co., Texas El Paso Co., Texas Carter Co., Oklahoma Pontotoc Co., Oklahoma	Ross, 1957 Howe, 1965 Alberstadt, OU coll.
<i>Thaerodonta dignata</i>	Middle Katian	Lower Maquoketa Fm. Maquoketa Fm., Clermont Mbr.	Paope, Estonia Hiiu Co., Estonia Saxby, Estonia Winneshiek Co., Iowa	Rõõmusoks, 1981 Wang, 1949
<i>Eochonetes glabra</i>	Late Katian–Hirnantian	Ellis Bay Fm.	Anticosti Island, Quebec	Dewing, 1999
<i>Thaerodonta johnsonella</i>	Hirnantian	Edgewood Grp., Leemon Fm.	Cape Girardeau Co., Missouri	Amsden, 1974
<i>Thaerodonta magna</i>	Middle–Late Katian	Aleman Fm.	Hudspath Co., Texas	Howe, 1965
<i>Thaerodonta minnesotensis</i>	Early–Middle Katian	Galena Group, <i>Orthisina</i> Bed no. 6	Kenyon, Minnesota Berne, Minnesota	Sardeson, 1892
<i>Thaerodonta moelsi</i>	Middle–Late Katian	Kõrgessaare Fm.	Hiiu Co., Estonia Lääne Co., Estonia	Rõõmusoks, 1981
<i>Thaerodonta mucronata</i>	Middle–Late Katian	Aleman Fm.	Hudspath Co., Texas	Howe, 1965
<i>Thaerodonta mucronata scabra</i>	Late Katian	Cutter Fm.	El Paso Co., Texas	Howe, 1965
<i>Thaerodonta nubila</i>	Late Katian–Hirnantian	Adila Fm.	Lääne Co., Estonia Haapsalu, Estonia	Rõõmusoks, 1981
<i>Thaerodonta recedens</i>	Late Katian	Maquoketa Fm., <i>Leptaena</i> Bed no. 13	Spring Valley, Minnesota	Sardeson, 1892
<i>Thaerodonta saunjaensis</i>	Middle Katian	Saunja Fm.	Harju Co., Estonia Tõrma quarry, Estonia Mäemetsa, Estonia	Rõõmusoks, 1981
<i>Thaerodonta saxea</i>	Middle–Late Katian	Fernvale Fm.	Cape Girardeau Co., Missouri Valmeyer, Illinois Pulaski, Tennessee	Sardeson, 1892 Bassler, 1932
<i>Thaerodonta</i> sp.	Late Katian	Maquoketa Fm., Wykoff Mbr. Maquoketa Fm., Elgin Mbr. Saturday Mountain Fm.	Bristol Twp., Minnesota Winneshiek Co., Iowa Lemhi Range, Idaho	Sardeson, 1892 Wang, 1949; Howe, 1965 Ross, 1959
<i>Thaerodonta vaurealensis</i>	Middle–Late Katian	Bighorn Dolomite Vaureal Fm.	Johnson Co., Wyoming Anticosti Island, Quebec	Ross, 1957 Dewing, 1999

To determine whether taxa provided phylogenetic signal, multiple analyses were conducted that alternately inserted and removed OTUs with missing data during repeated analyses to examine changes in tree topology to test the hypothesis that these species retained potential to drive tree topology.

The minimum number of characters required to positively impact tree topology in this dataset was ~10 characters (one-third of the full suite). The taxa excluded from the final phylogenetic analyses (Table 2) did not further resolve the tree but rather caused tree topology to collapse. Morphological data for excluded OTUs were typically severely limited due to lack of preserved valve interiors.

Thirty morphological characters were utilized in the phylogenetic analysis (Table 4). Continuous characters were normalized and converted into discrete data for phylogenetic analysis following the protocol of Wright and Stigall (2013). Continuous measurements were unordered and plotted to determine natural breaks (e.g., change in slope or discontinuities) of variation. The natural breaks in the data were utilized to create bins of discrete states via gap coding (see Mickevich and Johnson, 1976; Archie, 1985; Thiele, 1993; Swiderski et al., 1998). The mean and standard deviation values were calculated for each bin and used to define character state ranges following Morton and Kincaid (1995) and Wright and Stigall (2013, 2014). After separation of character states, the statistical significance of the prospective character ranges was assessed using one-way analysis of variance (ANOVA). Classes of morphological characters were found to be highly unequivocal ( $P < 0.001$ ) with nonoverlapping mean values at the 95% confidence interval. The character state range was calculated as the mean of each state  $\pm 1$  standard deviation (Table 5). OTUs were coded as exhibiting a single character state if all measurements for specimens of that OTU fell



**Figure 2.** Examples of locations of linear and angular measurements used in the analyses on representative specimens. (1) Ventral interior of *Thaeorodonta magna*, USNM 145048. (2) Ventral interior of *Eochoonetes glabra*, GSC 113889. (3) Dorsal interior of *Thaeorodonta aspera*, SUI 1886. (4) Dorsal interior of *Thaeorodonta clarksvillensis*, USNM 88274. 1 = maximum width; 2 = shell length; 4 = angle between hinge and cardinal extremity; 5 = delthyrium size; 7 = ventral interarea angle; 9 = dental plate length; 11 = adductor scar length; 12 = adductor scar width; 13 = diductor scar length; 14 = diductor scar width; 18 = primary teeth size; 20 = adductor scar length; 21 = adductor scar width; 22 = angle between muscle scar and hinge; 23 = socket width; 26 = angle between brachial process and hinge.

**Table 4.** Characters utilized for phylogenetic analysis. Other than for character 1, measurements (in mm) were standardized by maximum width of the specimen. See Table 6 for statistical separation of continuous characters.

#### External Characters

1. Maximum width. Widest region of the valve, measured parallel to the hinge line: (0) small ( $\leq 12.64$ ); (1) medium ( $14.75 \leq x \leq 18.57$ ); (2) large ( $\geq 20.33$ ).
2. Shell length. Greatest shell length, measured perpendicular to the hinge line: (0) small ( $\leq 0.56$ ); (1) medium ( $0.60 \leq x \leq 0.64$ ); (2) large ( $\geq 0.69$ ).
3. Shell height. Measure of the convexity of the ventral valve: (0) low ( $\leq 0.16$ ); (1) medium ( $0.19 \leq x \leq 0.22$ ); (2) high ( $\geq 0.26$ ).
4. Angle between hinge and cardinal extremity. Angle between the hinge line and curvature of the cardinal extremity: (0) narrow ( $\leq 29^\circ$ ); (1) moderate ( $30^\circ \leq x \leq 36^\circ$ ); (2) wide ( $\geq 38^\circ$ ).
5. Delthyrium size. Width of the median aperture, typically covered by pseudodeltidium: (0) small ( $\leq 0.07$ ); (1) medium ( $0.08 \leq x \leq 0.10$ ); (2) large ( $\geq 0.11$ ).
6. Costal density. Number of costae per 5 mm, taken in the center of the valve: (0) few ( $\leq 27$ ); (1) many ( $\geq 29$ ).
7. Angle of ventral interarea. Angle between the ventral interarea and the cardinal extremity: (0) small ( $\leq 10^\circ$ ); (1) medium ( $11^\circ \leq x \leq 13^\circ$ ); (2) large ( $\geq 14^\circ$ ).
8. Hinge line equivalent to maximum width: (0) no; (1) yes.

#### Ventral Valve Internal Characters

9. Dental plate length. Length from the hinge line to the farthest extent of the dental plate: (0) short ( $\leq 0.09$ ); (1) long ( $\geq 0.10$ ).
10. Muscle scar angle. Angle between the center of the muscle scar to the hinge line: (0) narrow ( $\leq 62^\circ$ ); (1) wide ( $\geq 64^\circ$ ).
11. Ventral adductor scar length. Adductor muscle scar length, typically as long as the extent of the median septum prior to bifurcation: (0) short ( $\leq 0.12$ ); (1) long ( $\geq 0.14$ ).
12. Ventral adductor scar width. Adductor muscle scar width, typically from median septum to lateral ridge that extends from the dental plate: (0) narrow ( $\leq 0.11$ ); (1) narrow ( $\geq 0.12$ ). {both "narrow"?
13. Ventral diductor scar length. Diductor muscle scar length, including the adductor muscle field: (0) short ( $\leq 0.25$ ); (1) long ( $\geq 0.27$ ).
14. Ventral diductor scar width. Diductor muscle scar width, taken outside of the adductor muscle field: (0) narrow ( $\leq 0.12$ ); (1) wide ( $\geq 0.13$ ).
15. Primary teeth size (width): (0) small ( $\leq 0.05$ ); (1) large ( $\geq 0.05$ ).
16. Accessory teeth (number): (0) zero; (1) one; (2) two.
17. Fossettes (number): (0) absent; (1) few ( $\leq 7$ ); (2) many ( $\geq 8$ ).
18. Lateral ridge strength. Development of lateral ridge in comparison to the median septum (the most dominant feature of the internal structures): (0) weak; (1) strong.
19. Tubules. Hinge line canals, forming at oblique angles to the hinge line: (0) absent; (1) present.

#### Dorsal Valve Internal Characters

20. Dorsal adductor scar length: (0) short ( $\leq 0.24$ ); (1) moderate ( $0.30 \leq x \leq 0.34$ ); (2) long ( $\geq 0.35$ ).
21. Dorsal adductor scar width: (0) narrow ( $\leq 0.16$ ); (1) moderate ( $0.17 \leq x \leq 0.19$ ); (2) wide ( $\geq 0.19$ ).
22. Muscle scar angle. Angle between the center of the muscle scar (typically aligning with the lateral ridge) to the hinge line: (0) narrow ( $\leq 61^\circ$ ); (1) moderate ( $63^\circ \leq x \leq 67^\circ$ ); (2) wide ( $\geq 70^\circ$ ).
23. Socket size. Width of the primary socket: (0) small ( $\leq 0.06$ ); (1) large ( $\geq 0.06$ ).
24. Accessory sockets (number): (0) zero; (1) one; (2) two.
25. Denticles (number): (0) absent; (1) few ( $\leq 7$ ); (2) many ( $\geq 8$ ).
26. Brachial process angle. Angle between the hinge and the cardinal process: (0) narrow ( $\leq 28^\circ$ ); (1) moderate ( $29^\circ \leq x \leq 31^\circ$ ); (2) wide ( $\geq 33^\circ$ ).
27. Lateral ridge strength. Development of the lateral ridge compared to the median ridges (the most dominant feature of the internal structures): (0) weak; (1) strong.
28. Bema. Raised ridges (which provide support for the lophophore) surrounding muscle scar field within the dorsal valve: (0) absent; (1) present.
29. Bema strength. Development of the bema compared to the median septum: (0) weak; (1) strong.
30. Raised muscle scars. Dorsal muscle scars raised on a calcified layer: (0) absent; (1) present.

**Table 5.** Statistical separation of quantitative morphological characters. All characters measured in millimeters. Continuous characters other than character 1 were standardized by the maximum width of the specimen. SD = standard deviation.

Character	N	Mean	SD	Range (mean $\pm$ SD)	ANOVA
<b>1. Maximum Width</b>					
(0) small	20	11.34	1.292	$x \leq 12.636$	$p < 0.001$
(1) medium	38	16.66	1.914	$14.746 \leq x \leq 18.574$	
(2) large	20	22.06	1.727	$x \geq 20.331$	
<b>2. Shell Length</b>					
(0) small	35	0.526	0.038	$x \leq 0.564$	$p < 0.001$
(1) medium	34	0.621	0.02	$0.601 \leq x \leq 0.641$	
(2) large	8	0.747	0.06	$x \geq 0.687$	
<b>3. Total Height</b>					
(0) small	22	0.141	0.018	$x \leq 0.159$	$p < 0.001$
(1) medium	25	0.207	0.016	$0.191 \leq x \leq 0.223$	
(2) large	10	0.319	0.055	$x \geq 0.264$	
<b>5. Delthyrium Size</b>					
(0) small	9	0.062	0.007	$x \leq 0.068$	$p < 0.001$
(1) medium	29	0.091	0.01	$0.081 \leq x \leq 0.102$	
(2) large	8	0.123	0.013	$x \geq 0.110$	
<b>9. Dental Plate Length</b>					
(0) small	11	0.079	0.009	$x \leq 0.088$	$p < 0.001$
(1) large	10	0.105	0.006	$x \geq 0.099$	
<b>11. Ventral Adductor Scar Length</b>					
(0) small	11	0.109	0.014	$x \leq 0.123$	$p < 0.001$
(1) large	11	0.152	0.015	$x \geq 0.137$	
<b>12. Ventral Adductor Scar Width</b>					
(0) small	11	0.097	0.011	$x \leq 0.109$	$p < 0.001$
(1) large	11	0.139	0.017	$x \geq 0.122$	
<b>13. Ventral Diductor Scar Length</b>					
(0) small	9	0.22	0.03	$x \leq 0.250$	$p < 0.001$
(1) large	13	0.298	0.027	$x \geq 0.271$	
<b>14. Ventral Diductor Scar Width</b>					
(0) small	13	0.098	0.019	$x \leq 0.116$	$p < 0.001$
(1) large	9	0.163	0.033	$x \geq 0.130$	
<b>15. Primary Teeth Size</b>					
(0) small	11	0.035	0.013	$x \leq 0.047$	$p = 0.001$
(1) large	7	0.054	0.005	$x \geq 0.054$	
<b>20. Dorsal Adductor Scar Length</b>					
(0) small	3	0.231	0.006	$x \leq 0.237$	$p < 0.001$
(1) medium	16	0.321	0.02	$0.301 \leq x \leq 0.341$	
(2) large	3	0.42	0.069	$x \geq 0.351$	
<b>21. Dorsal Adductor Scar Width</b>					
(0) small	7	0.13	0.03	$x \leq 0.159$	$p < 0.001$
(1) medium	11	0.178	0.008	$0.170 \leq x \leq 0.185$	
(2) large	4	0.22	0.026	$x \geq 0.194$	
<b>23. Socket Size</b>					
(0) small	12	0.05	0.006	$x \leq 0.056$	$p < 0.001$
(1) large	8	0.07	0.007	$x \geq 0.063$	

within the range for that character state. Alternately, the taxon was coded as polymorphic for the character if the specimen data were distributed within two or more of the defined character states (Table 6; Supplemental Data 5).

A cladistic approach using maximum parsimony was employed to reconstruct phylogenetic relationships. Studies comparing the model-based approaches with parsimony have reported conflicting results regarding which methodology is more successful (Pol and Siddall, 2001; Kolaczkowski and Thornton, 2004; Wright and Hillis, 2014; Xu and Pol, 2014). Many of these studies utilized large datasets with a vast amount of character data (e.g., Wright and Hillis, 2014; Xu and Pol, 2014). Studies that have explicitly addressed the efficacy of parsimony versus model-based approaches have established that maximum parsimony is equally successful in general (Rindal and Brower, 2011) and could be more powerful in particular for analyses of fossil taxa (Spencer and Wilberg, 2013). Our study has a much smaller data set, and there is little information, at present, for small data sets on model-based approaches versus parsimony. Parsimony-uninformative characters, including autapomorphies, were removed from the analysis but would be beneficial in a Bayesian approach. Analyses were conducted in

PAUP\*4.0b10 (Swofford, 2002) using the branch and bound search method. All characters were equally weighted and unordered. Taxa exhibiting multiple character states were treated as polymorphic. Accelerated transformation (ACCTRAN) was utilized to optimize and analyze characters in MacClade 4.06 (Maddison and Maddison, 2003).

### Morphometric analysis

*Generic discrimination.*—When analyzed as a group, specimens previously attributed to *Thaerodonta* constitute a large region of morphospace in the PCA plot. Specimens attributed to *Eochonetes* occupy a comparatively smaller region of morphospace (Fig. 3). These two populations overlap substantially in multivariate space.

*Species discrimination.*—Multivariate analyses of individual OTUs demonstrate considerable overlap among taxa in morphospace (Fig. 3). In most cases, OTUs representing taxa in open nomenclature plot separately from the formal species with which they had been previously aligned. The restriction of some OTUs to single data points within only the ventral or dorsal

**Table 6.** Character state distribution for OTUs included in the phylogenetic analysis of *Thaerodonta* and *Eochonetes*. Character states indicated as W = (0 and 1 and 2); X = (0 and 1); Y = (1 and 2); Z = (0 and 2). Acronyms indicating location of species in open nomenclature: TX = Texas; ID = Idaho; WY = Wyoming. ? = missing data; \* = outgroup (*Sowerbyella*).

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30		
<i>E.advena</i>	X	W	?	X	?	?	?	X	X	0	X	X	X	X	1	X	0	X	1	1	1	0	X	?	0	0	0	0	?	0		
<i>T. aspera</i>	2	0	0	0	0	X	0	1	0	1	1	1	0	0	0	2	1	1	?	X	0	2	X	2	1	0	1	1	0	0		
<i>T. aff. T. clarksvillensis</i>	X	Y	X	X	0	1	Z	1	?	?	?	?	?	?	?	?	?	?	?	1	X	1	X	0	0	0	0	1	0	0		
<i>E. celticus</i>	1	X	?	1	?	?	?	0	1	0	1	1	0	0	?	?	?	?	0	1	?	?	?	?	?	?	?	?	?	?		
<i>T. clarksvillensis</i>	Y	X	W	X	X	X	X	1	0	0	1	1	1	1	0	1	0	1	0	X	1	X	X	?	0	X	0	1	1	0		
<i>T. cf. T. recedens (TX)</i>	Y	X	W	0	X	?	X	1	1	X	1	1	1	1	X	2	0	1	?	1	1	1	X	?	1	1	1	1	0	0		
<i>T. dignata</i>	0	0	X	X	1	1	1	1	1	0	0	0	0	X	0	2	1	0	?	?	?	?	?	?	?	1	1	1	0	?	0	
<i>T. johnsonella</i>	X	X	0	0	0	1	?	1	0	X	0	0	0	0	1	X	X	0	?	1	1	1	1	1	1	1	0	1	1	1	0	
<i>T. magna</i>	2	W	Y	X	X	?	Y	1	0	X	X	X	X	X	W	X	X	X	?	1	1	1	X	1	1	X	1	1	1	X	0	
<i>T. mucronata</i>	2	0	W	1	1	?	1	1	0	1	0	1	X	1	1	2	1	0	?	X	0	1	0	?	1	0	1	1	0	0	0	
<i>T. recedens</i>	Y	W	W	X	Y	1	X	X	1	X	1	1	1	0	0	Z	1	X	0	Y	W	Y	X	Y	Y	Z	1	1	0	0	0	
<i>T. sp. (ID)</i>	0	0	0	1	0	?	0	1	?	?	?	?	?	?	?	?	?	?	?	0	0	1	0	?	1	1	?	0	?	0	0	
<i>T. sp. (WY)</i>	X	1	0	1	X	?	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0
<i>E. vaurelensis</i>	X	X	X	0	X	?	1	1	1	1	1	1	1	1	X	2	0	1	0	1	1	1	0	1	?	1	1	1	1	1	0	0
<i>E. glabra</i>	W	X	2	0	X	1	1	1	1	0	0	0	0	0	0	2	0	?	0	1	1	1	1	0	1	0	1	1	1	0	1	1
<i>T. saunjaensis</i>	X	Y	Y	0	Y	?	1	0	?	?	?	?	?	?	?	?	?	?	?	?	1	X	1	1	0	0	0	0	1	0	0	0
<i>T. minnesotensis</i>	X	Y	Y	?	?	0	?	1	?	?	?	?	?	?	?	?	?	?	?	1	1	X	1	?	0	0	?	1	1	0	0	
* <i>S. socialis</i>	X	1	X	0	X	0	2	1	X	0	1	0	X	X	1	0	0	0	?	1	0	0	1	?	?	0	0	0	1	1	1	1
* <i>S. rugosa</i>	1	0	X	0	0	0	X	1	?	?	?	?	?	?	?	?	?	?	?	X	X	0	X	0	0	0	0	0	1	1	1	1

analyses limits the extent of potential interpretation for some OTUs. Nevertheless, several clear patterns emerge from the PCA plots.

Ventral valve analysis shows many of the North American species clustering near each other on the right side of the plot, whereas the two *Eochonetes* species from Scoto-Appalachia (i.e., *E. advena* Reed, 1917 and *E. celticus* Mitchell, 1977) overlap on the left side of the plot. When length and width are removed from the set of included characters, the occupied species area in morphospace shifts only slightly. There is less separation among North American *Thaerodonta* species, other than *T. johnsonella* Amsden, 1974, which remains entirely isolated on the far left. *Thaerodonta saxea* is the only species occupying a morphospace field entirely overlapping that of other species; this could indicate a lack of differing morphological features distinguishing *T. saxea* from other taxa, notably *T. recedens*.

Dorsal valve analysis results in a similar grouping of North American species on the right side of the x-axis, but with greater overall separation than the ventral valve analysis. Removing length and width from the characters changed the orientation of *Thaerodonta magna* Howe, 1965, *T. mucronata* Howe, 1965, and *T. aspera* Wang, 1949. These three species shifted from their original location to the far right, closer to the large grouping. The other species remained in their original locations. Again, the morphospace of *T. saxea* completely overlaps that of other North American species. *Thaerodonta mucronata* also displays a high degree of overlap with the other North American species.

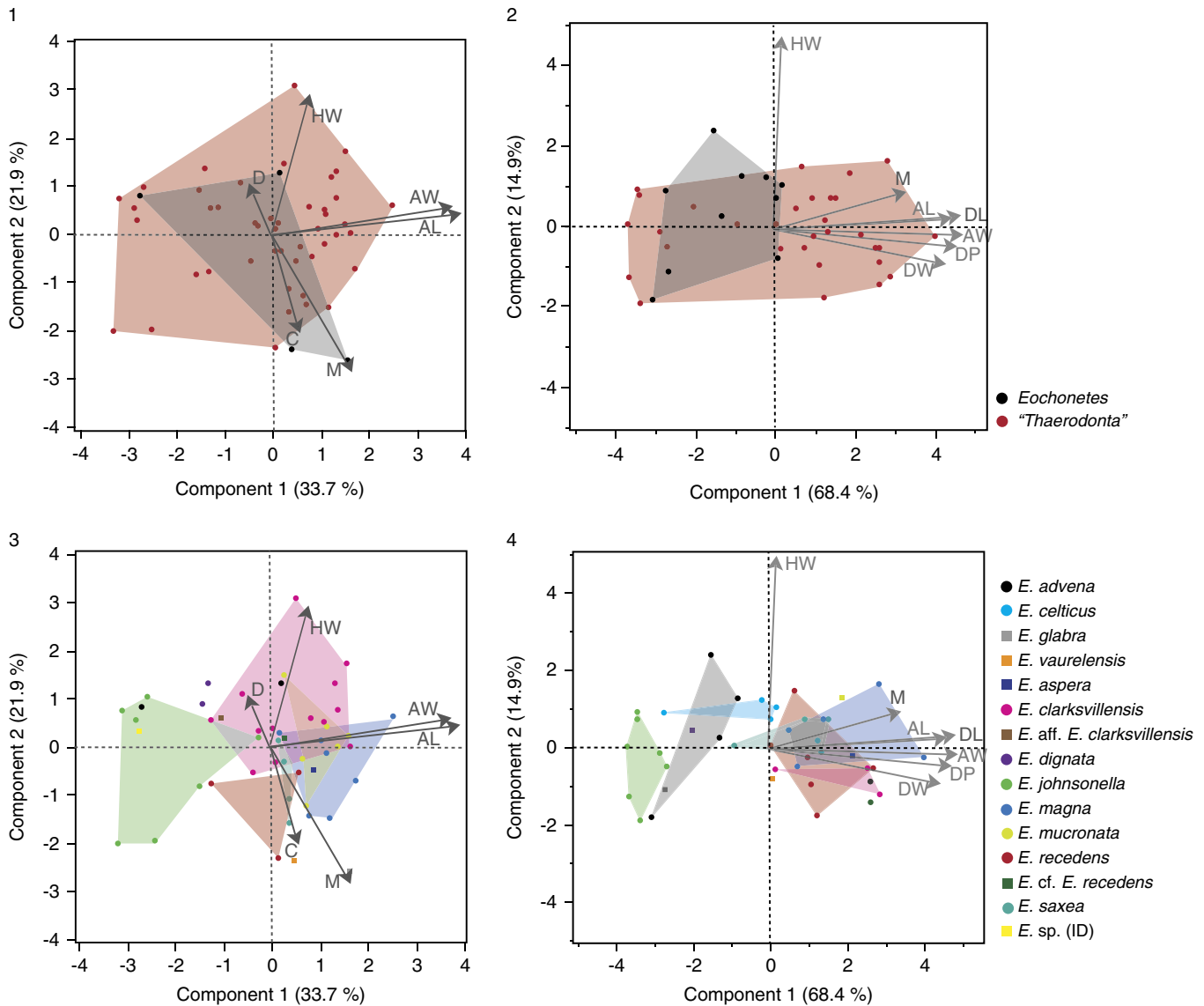
**Morphometric discussion.**—*Eochonetes* does not significantly differ from *Thaerodonta* in morphospace based on the character data utilized. Thus, the two genera are interpreted as lacking significant differences among the general morphological attributes analyzed in the multivariate analyses. This lack of distinction supports the previously hypothesized (e.g., Cocks and Rong, 1989) synonymy of these two genera, which will be explored more fully below in discussion of the phylogenetic analysis.

Most of the OTUs analyzed exhibited differentiation in morphospace. Taking into account the plots of both valves, species that exhibited a moderate to high degree of separation within morphospace are interpreted as valid, discrete taxa. The high degree of overlap exhibited between or among certain species indicates that a close examination of their validity should be tested in a phylogenetic framework. For example, the consistent overlapping occupation of morphospace between *T. saxea* and *T. recedens* indicates high morphological similarity and suggests that additional scrutiny of the distinction of these species using more character data is warranted. Howe (1972) also noted that it is difficult to confidently separate members of these two species when examining large populations.

**Implications.**—Reconstructing species boundaries of extinct organisms is challenging (see discussion by Allmon and Yacobucci, in press). Both ecophenotypic and taphonomic biases can impact species recognition in the focal clade. These challenges can be exacerbated in taxa, e.g., brachiopods, that exhibit differential growth based on environmental conditions (Rudwick, 1970) or in instances where preservation of key diagnostic characters is strongly controlled by taphonomy (e.g., many Cambrian arthropods). Within *Eochonetes*, the recognition of hinge-line tubules is highly influenced by preservation style, and variations in valve morphology have been previously attributed to environmental influences (e.g., Howe, 1965).

The results of the morphometric analyses presented here suggest caution in over interpreting results based on single characters. Indeed, our analyses demonstrate that different subsets of the morphological data analyzed provide distinct and complementary information about species identity. In this dataset, species that occupied overlapping morphospace of one valve often exhibited differentiation in the other, e.g., compare the positions of *Thaerodonta clarksvillensis* (Foerste, 1912) and *T. recedens*, or the directional vectors in Figure 3.1 and 3.2. Furthermore, the multivariate analyses were repeated with overall length and width included, overall length and width excluded, and with the addition of discrete data (e.g., counts) to determine how the resulting plot was affected. Removing





**Figure 3.** Results of generic (1–2) and species (3–4) separation in morphospace for dorsal (left column) and ventral (right column) valves. AL = adductor length; AW = adductor width; C = cardinal process angle (dorsal valve); D = denticle count (dorsal valve); DL = diductor length (ventral valve); DP = dental plate length (ventral valve); DW = diductor width (ventral valve); HW = angle between hinge line and cardinal extremity (dorsal valve); M = muscle scar angle to hinge line; square = single occurrence of a species on the plot; circle = multiple data points.

overall size reduced the loading for PC1, but had limited influence on the position of data in morphospace. Moreover, experimentation with including or excluding different types of data (i.e., measurements, angles, or counts) showed that the nonmeasurement data has a greater effect on the resulting plot. Thus, incorporating data from both valves and also exploring the impact of various data partitions was critical to understanding the morphospace occupation of the species.

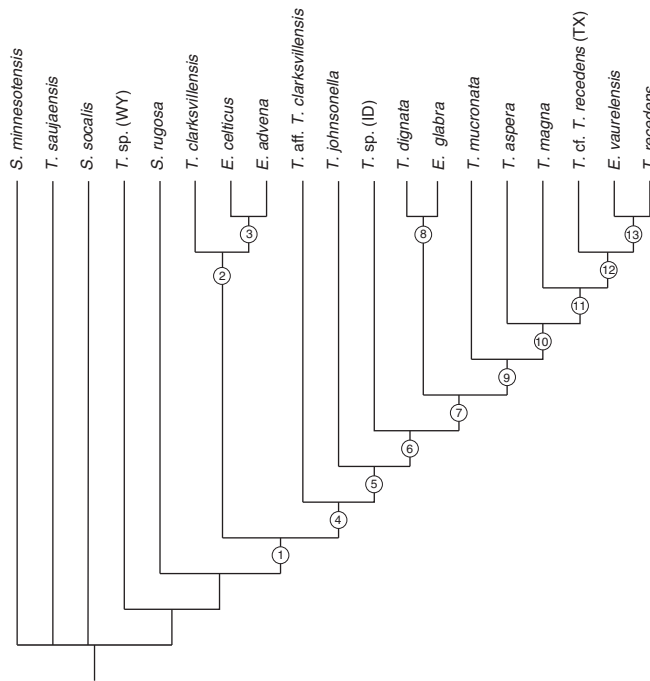
The morphological analysis was a valuable precursor to the subsequent phylogenetic analysis because it provided a framework to experiment with various character types and test species boundaries in morphospace. Because morphometric analysis examines overall similarity within a subset of all possible character data, multivariate techniques do not provide a direct hypothesis of evolutionary relationships the way that synapomorphy-based phylogenetic analysis does. However,

these methods provide an outstanding platform on which to test hypotheses of morphological or ecological discrimination of species, which can resolve certain sets of research questions and is a necessary foundation for phylogenetic analysis.

### Phylogenetic analysis

**Results.**—Parsimony analysis yielded three most parsimonious trees with lengths of 217 steps (Fig. 4). The consistency and retention indices are 0.866 and 0.642, respectively, for these trees, which exceed the values derived from equivalently sized randomized data sets at the  $\alpha = 0.05$  level (Klassen et al., 1991). Support was further 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 (Hillis and Huelsenbeck, 1992).

The  $g_1$  statistic for 10,000 random trees generated via heuristic search from the data matrix is -0.442. This is significantly higher than within a random data set and significant at the  $\alpha = 0.01$  level (Hillis and Huelsenbeck, 1992), which signifies substantial phylogenetic structure within the data.



**Figure 4.** Strict consensus tree generated via the branch and bound method utilizing data from Table 6 in PAUP\*4.0b10 (Swofford, 2002). Tree length is 217 steps. The retention index is 0.642, and the consistency index is 0.866. Character states for nodes were optimized using MacClade 3.04 (Maddison and Maddison, 2003) utilizing ACCTRAN optimization. Node numbers are circled on the cladogram; character and character state follows node number in the following description. Character states that change unambiguously at each node: Node 1, 11(0), 25(1), 30(0); Node 2, 12(1); Node 3, 19(1); Node 4, 6(1), 22(1); Node 5, 17(2), 25(2), 27(1); Node 6, 23(0), 29(0), Node 7, 7(1), 16(2); Node 8, 9(1); Node 9, 10(1), 12(1); Node 10, 4(0), 11(1), 18(1); Node 11, 13(1), 21(1), 26(2); Node 12, 9(1); Node 13, 17(1).

**Recognition of clades.**—Recovered tree topology (Fig. 4) indicates that species previously assigned to *Eochonetes* and *Thaerodonta* do not form distinct evolutionary lineages. Specifically, species referred to as *Eochonetes* appear at three isolated positions within a larger clade dominated by *Thaerodonta* species. Thus, neither *Eochonetes* nor *Thaerodonta* as previously defined is monophyletic. However, species previously referred to the two genera do form a clade when combined together, thus *Eochonetes* and *Thaerodonta* together form a single monophyletic genus. The name *Eochonetes* has priority and therefore is the correct taxonomic unit for this genus. We therefore support transferring all OTUs above node 1 in Figure 4 to *Eochonetes* and designating *Thaerodonta* as a junior subjective synonym of *Eochonetes* as indicated in Figure 5. Two species formerly assigned to *Thaerodonta*, *T. saunjaensis* Rõõmusoks, 1981 from Estonia and *Thaerodonta* sp. from Wyoming optimize within the outgroup species and are excluded from the revised *Eochonetes* clade. A complete list of species previously assigned and the taxonomic status recognized herein is presented in Table 7.

Monophyly of the ingroup (the revised *Eochonetes* clade) is supported by the presence of accessory teeth, the presence of denticles on the dorsal valve (Fig. 6.1), and the lack of raised muscle scars. Maximum shell width, length, and height are variable throughout the ingroup and many species exhibit polymorphic characters. The maximum width typically occurs at the hinge line; although one or more individuals of a few species (i.e., *E. celticus*, *E. advena*, *E. dignata* Wang, 1949, and *E. saxea*) exhibit hinge lengths less than the maximum width. In some individuals, the commissure is slightly raised in the center rather than lying flat, but well-developed fold and sulcus structures are absent at the species level. Delthyrial width varies among species, but a pseudodeltidial covering is consistently present. The bema is always present among ingroup species, although the height of the bema, compared to the median ridges, is variable between and within species. Primary teeth are consistently present, but size (Fig. 6.2) varies among species.

**Table 7.** Original taxonomic assignments of operational taxonomic units and the revised interpretations herein. Species now excluded from *Eochonetes* are listed at the bottom of the table. Asterisks denote taxa requiring systematic revision.

Previous Interpretation	Revised Interpretation	Figure
<i>Chonetes (Eochonetes) advena</i> Reed, 1917	<i>Eochonetes advena</i>	7.5–7.8
<i>Thaerodonta</i> aff. <i>T. clarksvillensis</i> Macomber, 1970	<i>Eochonetes maeorum</i> n. sp.	7.12–7.15
<i>Thaerodonta aspera</i> Wang, 1949	<i>Eochonetes aspera</i>	8.15–8.18
<i>Eochonetes celticus</i> Mitchell, 1977	<i>Eochonetes celticus</i>	7.9–7.11
<i>Thaerodonta clarksvillensis</i> Foerste, 1912	<i>Eochonetes clarksvillensis</i>	7.1–7.4
<i>Thaerodonta</i> cf. <i>T. recedens</i> ; Howe, 1965	<i>Eochonetes minerva</i> n. sp.	9.1, 9.4
<i>Thaerodonta</i> cf. <i>T. recedens</i> ; Ross, 1957	<i>Eochonetes</i> cf. <i>E. recedens</i>	not figured
<i>Thaerodonta</i> cf. <i>T. recedens</i> ; Alberstadt, SNOMNH	<i>Eochonetes</i> cf. <i>E. recedens</i>	not figured
<i>Thaerodonta dignata</i> Wang, 1949	<i>Eochonetes dignata</i>	8.1–8.4
<i>Sowerbyella (Eochonetes) glabra</i> Dewing, 1999	<i>Eochonetes glabra</i>	8.5–8.11
<i>Thaerodonta johnsonella</i> Amsden, 1974	<i>Eochonetes johnsonella</i>	7.16–7.19
<i>Thaerodonta magna</i> Howe, 1965	<i>Eochonetes magna</i>	8.19–8.21
<i>Thaerodonta mucronata</i> Howe, 1965	<i>Eochonetes mucronata</i> *	8.12–8.14
<i>Thaerodonta mucronata scabra</i> Howe, 1965	<i>Eochonetes mucronata</i> *	8.12–8.14
<i>Thaerodonta recedens</i> Sardeson, 1892	<i>Eochonetes recedens</i> *	9.7–9.13
<i>Thaerodonta saxea</i> Sardeson, 1892	<i>Eochonetes recedens</i> *	9.7–9.13
<i>Thaerodonta</i> sp.; Ross, 1959	<i>Eochonetes voldemortus</i> n. sp.	7.21–7.23
<i>Thaerodonta</i> sp.; Ross, 1957	<i>Eochonetes maeorum</i> n. sp.	7.12–7.15
<i>Sowerbyella (Eochonetes) vaurealensis</i> Dewing, 1999	<i>Eochonetes vaurealensis</i>	9.2–9.3, 9.5–9.6
<i>Thaerodonta minnesotensis</i> Sardeson, 1892	<i>Sowerbyella minnesotensis</i>	not figured
<i>Thaerodonta saunjaensis</i> Rõõmusoks, 1981	<i>Sowerbyella saunjaensis</i>	10.14–10.16
<i>Thaerodonta moelsi</i> Rõõmusoks, 1981	<i>Eoplectodonta moelsi</i>	10.9–10.10
<i>Thaerodonta convexa</i> Rõõmusoks, 1981	<i>Plectodonta convexa</i>	10.11–10.12
<i>Thaerodonta nubila</i> Rõõmusoks, 1981	<i>Plectodonta nubila</i>	10.13



**Figure 5.** Cladogram from Figure 4 relabeled with revised taxonomic names and scaled against the Late Ordovician timescale. Observed ranges indicated by solid lines; ghost lineages indicated by dashed lines. Time scale modified from Cohen et al. (2014). Stratigraphy correlated from sources listed in Supplemental Data 6.

The basal *Eochonetes* clade is composed of *E. clarksvillensis*, *E. celticus*, and *E. advena* (Figs. 5, 7). Monophyly of this clade is supported by wide ventral adductor scars and the appearance of hinge-line denticles (Fig. 6.1). The sister relationship of *E. celticus* and *E. advena* is supported by the presence of ventral tubules along the hinge line.

Monophyly of the remaining *Eochonetes* species is supported by an increased dorsal muscle scar angle as well as high costal density. Each node of this pectinate portion of the tree is supported by 100% agreement in the strict consensus tree and is supported by character evidence. Monophyly of *E. johnsonella* (Fig. 8) plus crownward species is supported by the synapomorphies of increased fossette/denticle count and better-developed lateral ridges in the dorsal muscle scar field (Fig. 6.3). Monophyly of species including *E. voldemortus* n. sp. (Fig. 7) crownward is supported by a well-developed bema and decreased socket size.

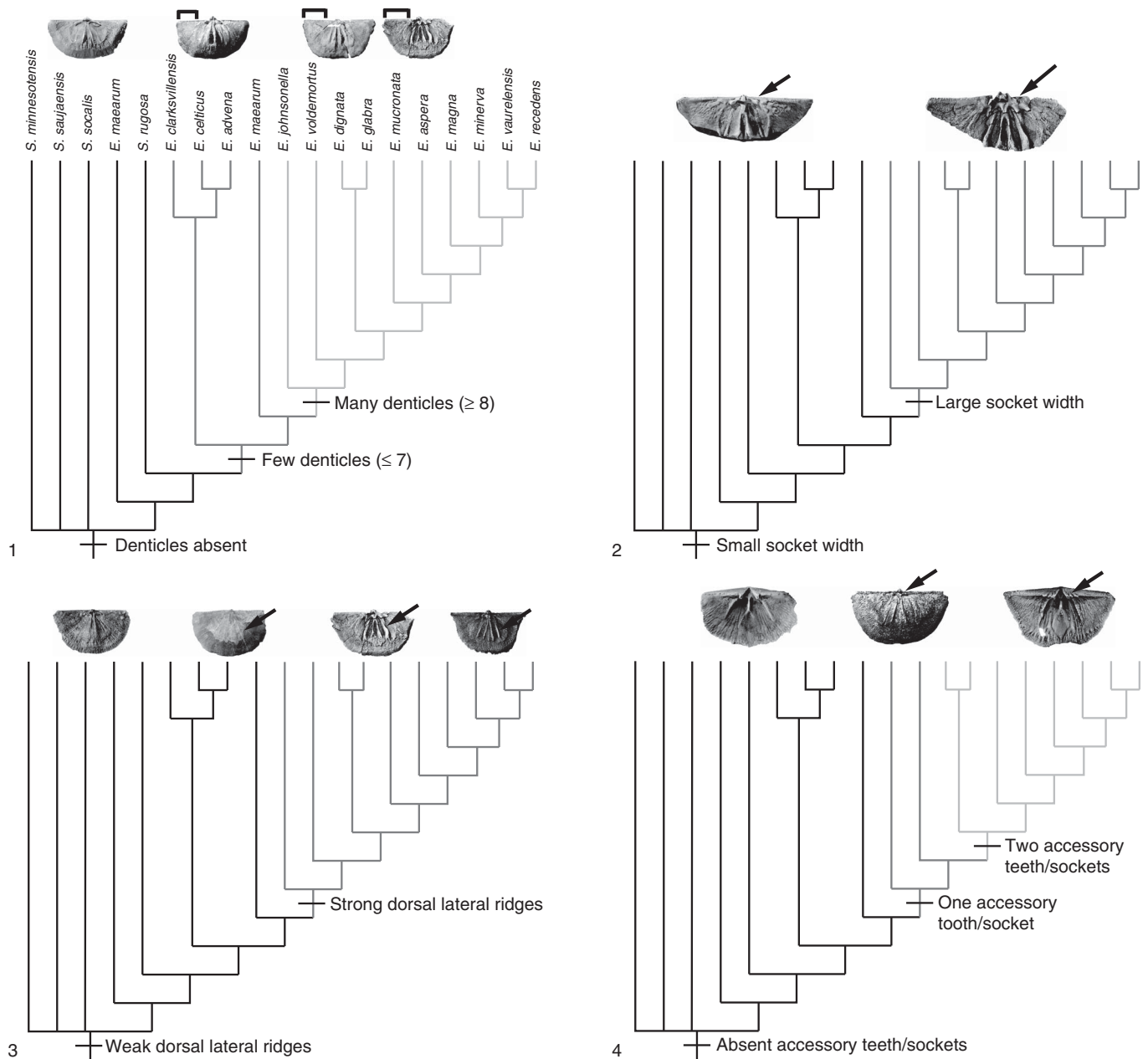
Monophyly of the species from *Eochonetes dignata* (Fig. 8) crownward is supported by the synapomorphies of an increased number of accessory teeth (Fig. 6.4) and a wide ventral interarea angle. The sister relationship of *E. dignata* and *E. glabra* Dewing, 1999 (Fig. 8) is supported by long dental plates. Monophyly of *E. mucronata* (Fig. 8) through *E. recedens* (Fig. 9) is supported by character evidence including wide ventral adductor muscle scars and a wide angle between the ventral muscle scars and the hinge line. Monophyly of *E. aspera*

(Fig. 8) and more derived species is supported by increased strength of the ventral lateral ridges, increased ventral adductor scar length, and a narrower angle between the cardinal extremity and the hinge line.

Monophyly of the species *Eochonetes magna* (Fig. 8) plus crownward species is supported by increased dorsal adductor scar width, increased ventral diductor scar length, and a large cardinal process angle. Increased dental plate length is the synapomorphy supporting the monophyly of *E. minerva* n. sp., *E. recedens*, and *E. vaurealensis* Dewing, 1999 (Fig. 9). The sister group relationship of *E. recedens* and *E. vaurealensis* is supported by decreased fossette numbers.

*Evolutionary and ecological implications.*—The most notable character suites within a phylogenetic context include the development of hinge-line dentition and musculature within the clade (Fig. 7). Notably, both musculature and dentition become more robustly developed during the evolution of the clade. Increased robustness in these features has often been considered to be indicative of adaptation to higher energy depositional environments in other brachiopod taxa (Cocks, 1970; Hurst, 1975), and *Eochonetes* species appear reflective of that overall trend.

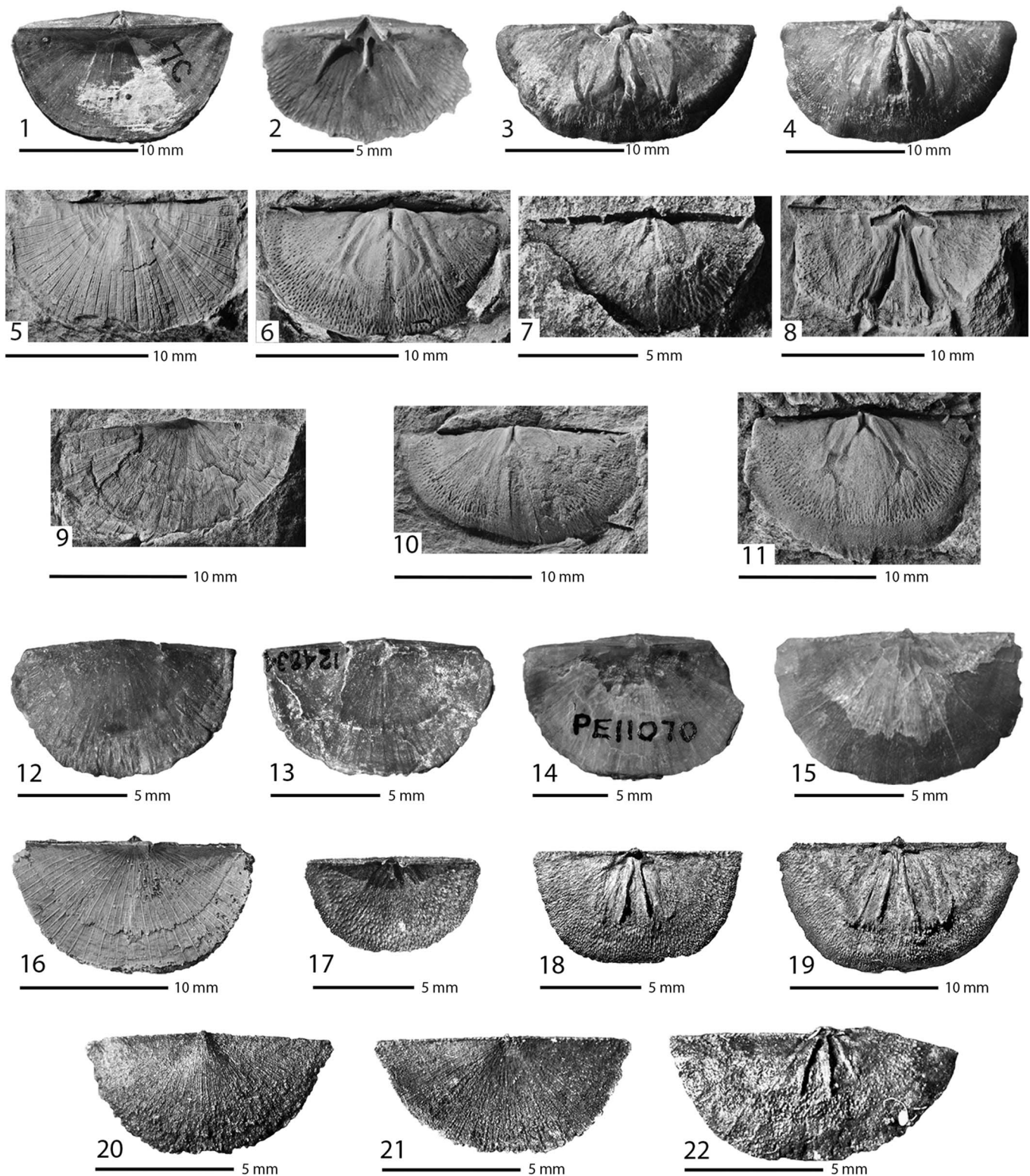
Species of closely related genera, e.g., *Sowerbyella* and *Eoplectodonta*, lack developed hinge-line denticulation; the development of denticles and accessory teeth begins with the



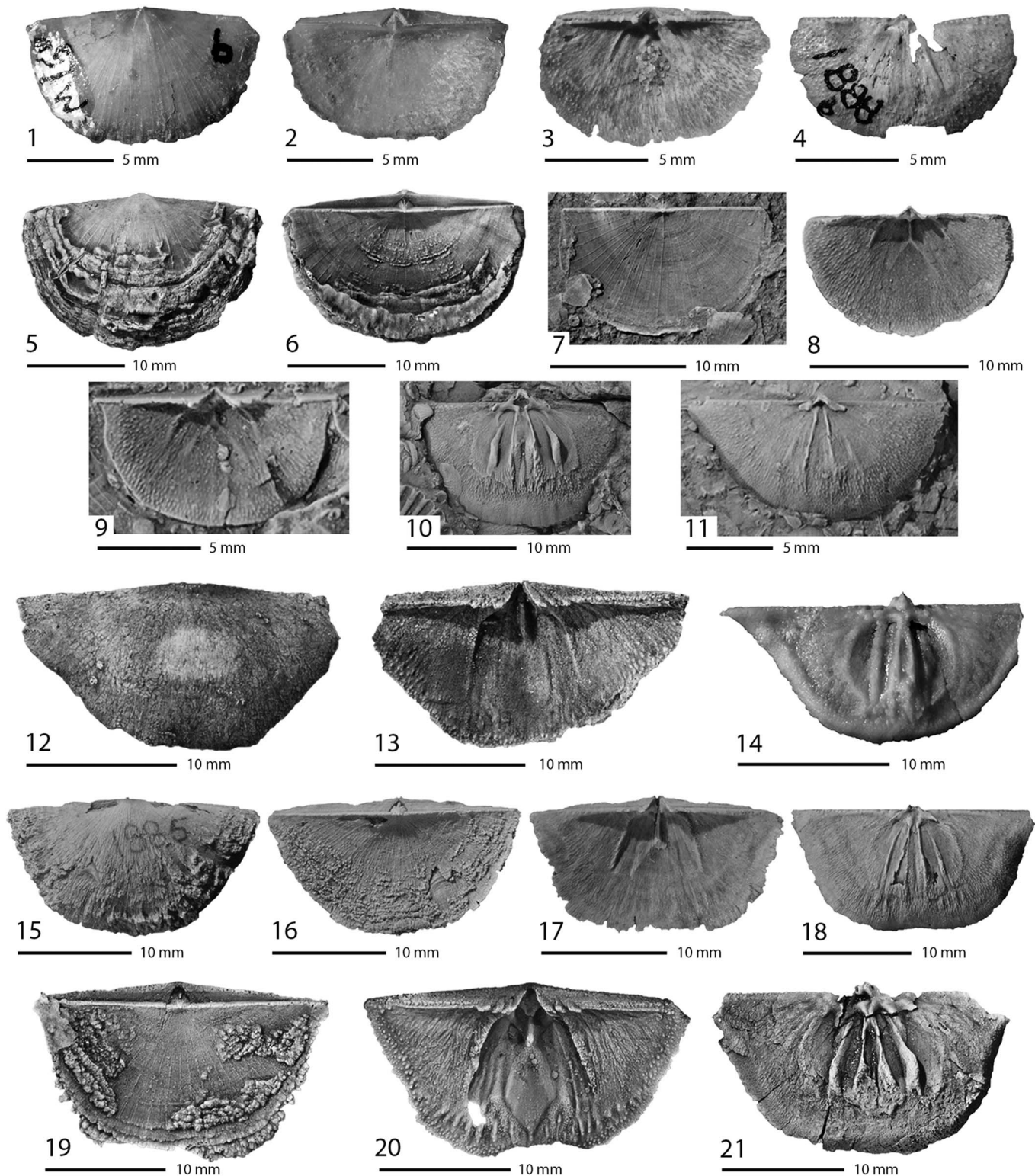
**Figure 6.** Cladograms depicting character evolution shown through change in color of the branches as well as character shifts at ancestral nodes. (1) Denticles. (2) Socket size. (3) Dorsal lateral septa. (4) Accessory sockets/teeth.

evolution of the *Eochoonetes* clade. *Eochoonetes* primarily radiated into shallower water environments than those occupied by *Sowerbyella* species, e.g., *S. sericea* (Sowerby, 1839) (early Katian) occurred in high abundance in the shallow-shelf benthic assemblages (Cocks, 2013). Notably, the contemporaneous *E. advena*, which is part of the basalmost *Eochoonetes* clade, occupied a similar deepwater environment that was dominated by siltstone and mudstone deposition (Donovan et al., 2002). *Eochoonetes advena* exhibits the synapomorphic fossettes, but limited additional hinge line development. Conversely, *E. recedens*, which occurs abundantly in the storm-influenced shelf environment of the Maquoketa Formation, Elgin Member (Sloan, 2005), exhibits well-developed hinge-line denticulation including one or two accessory teeth and numerous denticles

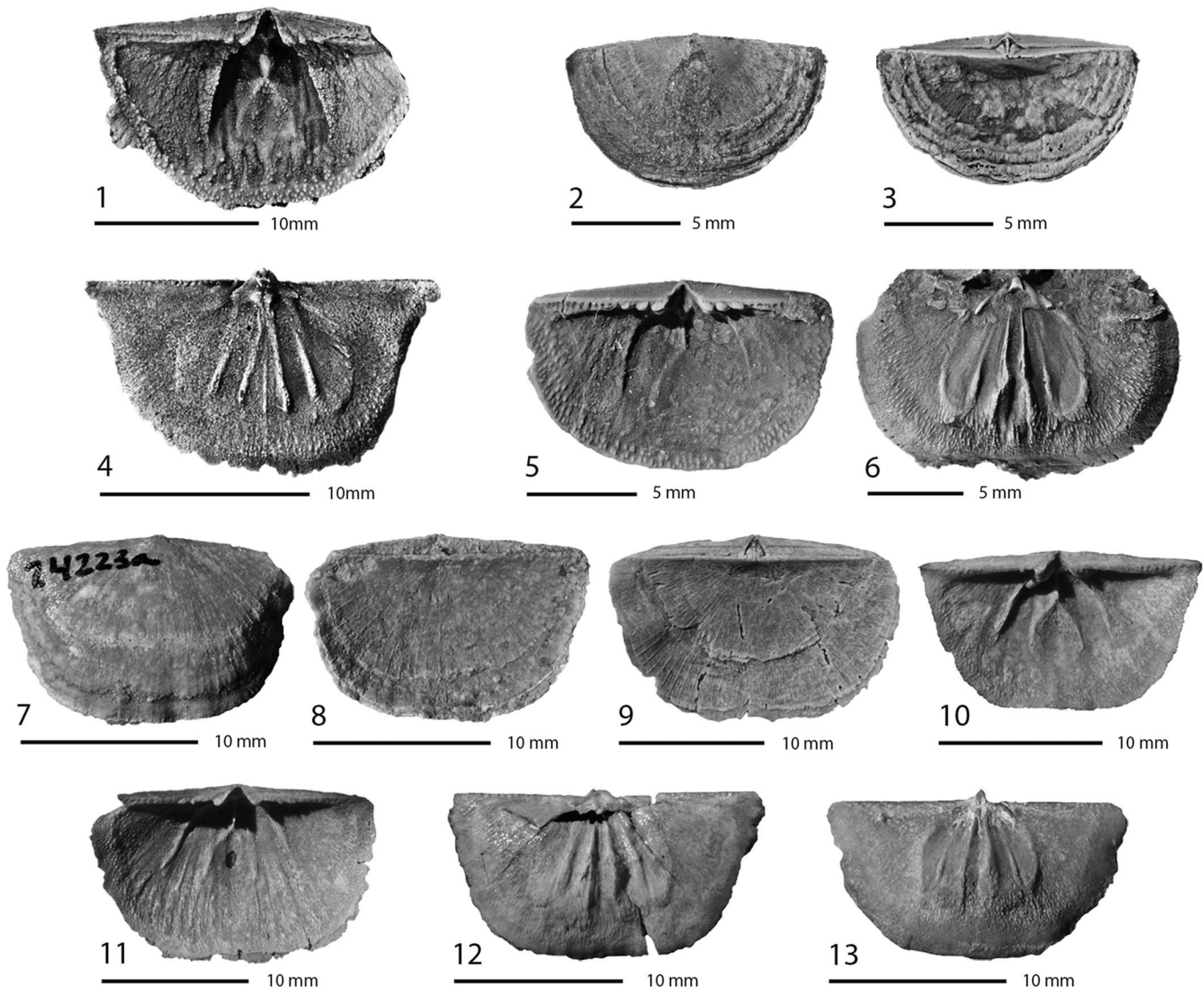
concentrated in the center of the hinge line. Other species with well-developed denticulation include *E. magna* (Fig. 8.19–8.21) and *E. mucronata* (Fig. 8.12–8.14) from the Aleman Formation of Texas, which is composed of intercalated, thin-bedded carbonate and cherty dolostone deposited in a midramp location (Howe, 1959; Pope, 2004). Both species have accessory teeth, numerous (10–20) denticles along their hinge line, deeply incised muscle scars with prominent ridges, and attain the maximum size of any *Eochoonetes* species. Overall, the distribution of morphological features among taxa results in a clade-wide pattern in which species present in higher energy environments exhibit enhanced hinge-line denticulation as well as more deeply incised muscle scars than their counterparts found in lower energy environments.



**Figure 7.** (1–4) *Eochoonetes clarksvillensis* (Foerste, 1912); (1) dorsal exterior (USNM 87151 7C); (2) ventral interior (OUIP 1547); (3) dorsal interior (USNM 88274); (4) dorsal interior (USNM 87151 7B). (5–8) *Eochoonetes advena* Reed, 1917; (5) dorsal exterior (GLAHM L-3190); (6) ventral interior (GLAHM L-2719 [6]); (7) ventral interior (GLAHM L-1806[20]); (8) dorsal interior (GLAHM L-2884[4]). (9–11) *Eochoonetes celticus* Mitchell, 1977; (9) ventral exterior (BGS NIL 5312); (10) ventral interior (BGS NIL 9114); (11) ventral interior (BGS GU 983). (12–15) *Eochoonetes maeorum* n. sp.; (12) ventral exterior (USNM 124834); (13) dorsal exterior (USNM 124838); (14) dorsal exterior (FMNH PE 11070); (15) dorsal interior (FMNH PE 11072). (16–19) *Eochoonetes johnsonella* (Amsden, 1974); (16) dorsal exterior (SNMOH 6679); (17) ventral interior (SNMOH 6680); (18) dorsal interior (SNMOH 6678); (19) dorsal interior (SNMOH 6679). (20–22) *Eochoonetes voldemortus* n. sp.; (20) ventral exterior (USNM 133257); (21) dorsal exterior (USNM 133257); (22) dorsal interior (USNM 133258).



**Figure 8.** (1–4) *Eochonetes dignata* (Wang, 1949); (1) ventral exterior (USNM 560301); (2) dorsal exterior (USNM 560301); (3) ventral interior (SUI 1888a); (4) dorsal interior (SUI 1888b). (5–11) *Eochonetes glabra* (Dewing, 1999); (5) ventral exterior (GSC 113897); (6) dorsal exterior (GSC 113900); (7) dorsal exterior (GSC 113900b); (8) ventral interior (GSC 113900a); (9) ventral interior (GSC 113910); (10) dorsal interior (GSC 113908a); (11) dorsal interior (GSC 113908b). (12–14) *Eochonetes mucronata* (Howe, 1965); (12) ventral exterior (USNM 145038); (13) ventral interior (USNM 145038); (14) dorsal interior (USNM 145039k). (15–18) *Eochonetes aspera* (Wang, 1949); (15) ventral exterior (SUI 1885); (16) dorsal exterior (SUI 1885); (17) ventral interior (SUI 1886a); (18) dorsal interior (SUI 1886b). (19–21) *Eochonetes magna* (Howe, 1965); (19) dorsal exterior (USNM 145047); (20) ventral interior (USNM 145048); (21) dorsal interior (USNM 145049).



**Figure 9.** (1, 4) *Eochonetes minerva* n. sp.: (1) ventral interior (USNM 145043); (4) dorsal interior (USNM 145045). (2–3, 5–6) *Eochonetes vaurealensis* (Dewing, 1999): (2) ventral exterior (GSC 113879); (3) dorsal exterior (GSC 11379); (5) ventral interior (GSC 113889); (6) dorsal interior (GSC 11893). (7–13) *Eochonetes recedens* (Sardeson, 1892): (7) ventral exterior (USNM 24223a); (8) dorsal exterior (USNM 24223a); (9) dorsal exterior (SUI 1883, previously *Thaerodonta saxea*); (10) ventral interior (SUI 1881); (11) ventral interior (SUI 1884, previously *T. saxea*); (12) dorsal interior (SUI 1882); (13) dorsal interior (USNM 24691k).

In addition to informing evolutionary and ecological analyses, phylogenetic hypotheses can also provide a framework for biogeographic analysis. A recent phylogenetic biogeographic study by Bauer and Stigall (2014), utilized the topology presented herein to investigate biogeographic evolution with the *Eochonetes* clade. Their results indicated that *Eochonetes* likely originated in basins north of the Transcontinental Arch (Fig. 1), exhibited early dispersal into the northern midcontinental region, and later evolved predominately by vicariant speciation (Bauer and Stigall, 2014).

## Discussion

All analyses within this study support the synonymy of *Thaerodonta* with *Eochonetes*. In addition, three new species have been identified and five species previously assigned to *Thaerodonta* or *Eochonetes* have been reassigned to other genera. Morphometric analyses aided in morphological delineation of the species and

genera, and phylogenetic analyses provided additional insight into evolutionary patterns within the clade. The combination of these methods provided a framework for comparing data types (e.g., discrete versus quantitative characters) and produced a level of insight greater than could be attained by either alone. For taxa classified primarily by discrete characters, single approach analyses might be sufficient. However, combination approaches, such as the one employed herein, have the potential to provide greater analytical power, particularly when working with variable taxa characterized primarily by quantitative features.

## Systematic paleontology

Superfamily Plectambonitoidea Jones, 1928  
 Family Sowerbyellidae Öpik, 1930  
 Subfamily Sowerbyellinae Öpik, 1930  
 Genus *Eochonetes* Reed, 1917

*Type species.*—*Eochonetes advena* Reed, 1917 from the upper Katian Lady Burn Starfish Beds, Farden Member, South Thraeve Formation, Girvan, Scotland.

*Diagnosis.*—Cardinal extremities acute to alate, exterior unequally costellate with multiple costae between two stronger costae. Profile concavoconvex. Ventral valve with posterior conical cavities, delthyrial thickening, and hinge-line fossettes. Dorsal valve with hinge-line denticles, thickened notothyrium, median ridge short then bifurcating, and consistently present but variably developed bema.

*Occurrence.*—Katian to Hirnantian age strata of the United States, Canada, Scotland, and Ireland.

*Description.*—Ventral valve moderately convex; interarea long, orthocline to apsacline; fossettes developed along all or part of hinge length. Pseudodeltidium small, convex, apical, often rounded. Teeth usually small; crural fossettes deep; dental plates thick, extending anteriorly into lateral ridges of muscle scar field; accessory teeth well developed. Oblique infilled canals rarely present along hinge line of moldic specimens, not extending exteriorly. Delthyrial cavity divided by strong horizontal thickening between base of dental plates and median septum. Muscle-scar field bilobed anteriorly; median septum sharp, bifurcating anteriorly; adductor scars small, oval to subtriangular, posteriorly located; diductor scars longer, straight, stretching anteriorly.

Dorsal valve gently concave, with short hypercline interarea; denticles prominent, developed along part or all of hinge length, often irregularly spaced; sockets and accessory sockets on either side of cardinal process. Cardinal process short, elevated; chilidial plates strong, attached to brachial process, separated from cardinal process by deep grooves; floor of notothyrium thickened. Muscle scar field separated medially by two high ridges; adductor scars elongate; adductor scars elongate, straight, each separated centrally by lateral ridge of variable height. Bema present, variably developed, encompassing muscle scar field. Emended from Wang (1949).

*Other species.*—*Chonetes (Eochonetes) advena* Reed, 1917 from the Lower Quarrel Hill Formation and Lady Burn Formation of the Drummuck Subgroup (upper Katian), Girvan, Scotland; *Thaerodonta aspera* Wang, 1949 from the Elgin Member of Maquoketa Formation (upper Katian), Winneshiek County, Iowa; *Eochonetes celticus* Mitchell, 1977 from the Member III of the Bardahessiagh Formation (lower Katian) and Killey Bridge Formation (upper Katian), Pomeroy, County, Tyrone, Northern Ireland; *Thaerodonta dignata* Wang, 1949 from the lower Maquoketa Formation (upper Katian), Clermont County, Iowa; *Plectambonites glabra* Shaler, 1865 from the Ellis Bay Formation (Hirnantian), Anticosti Island, Québec, Canada; *Thaerodonta johnsonella* Amsden, 1974 from the Leemon Formation (Hirnantian), Cape Girardeau County, Missouri; *Thaerodonta magna* Howe, 1965 from the Aleman Formation (middle Katian), Hueco Mountains, Hudspeth County, Texas; *Eochonetes maeorum* n. sp. from the Bighorn Formation, Rock Creek Beds (upper Katian), Johnson County, Wyoming; *Eochonetes minerva* n. sp. from the Cutter

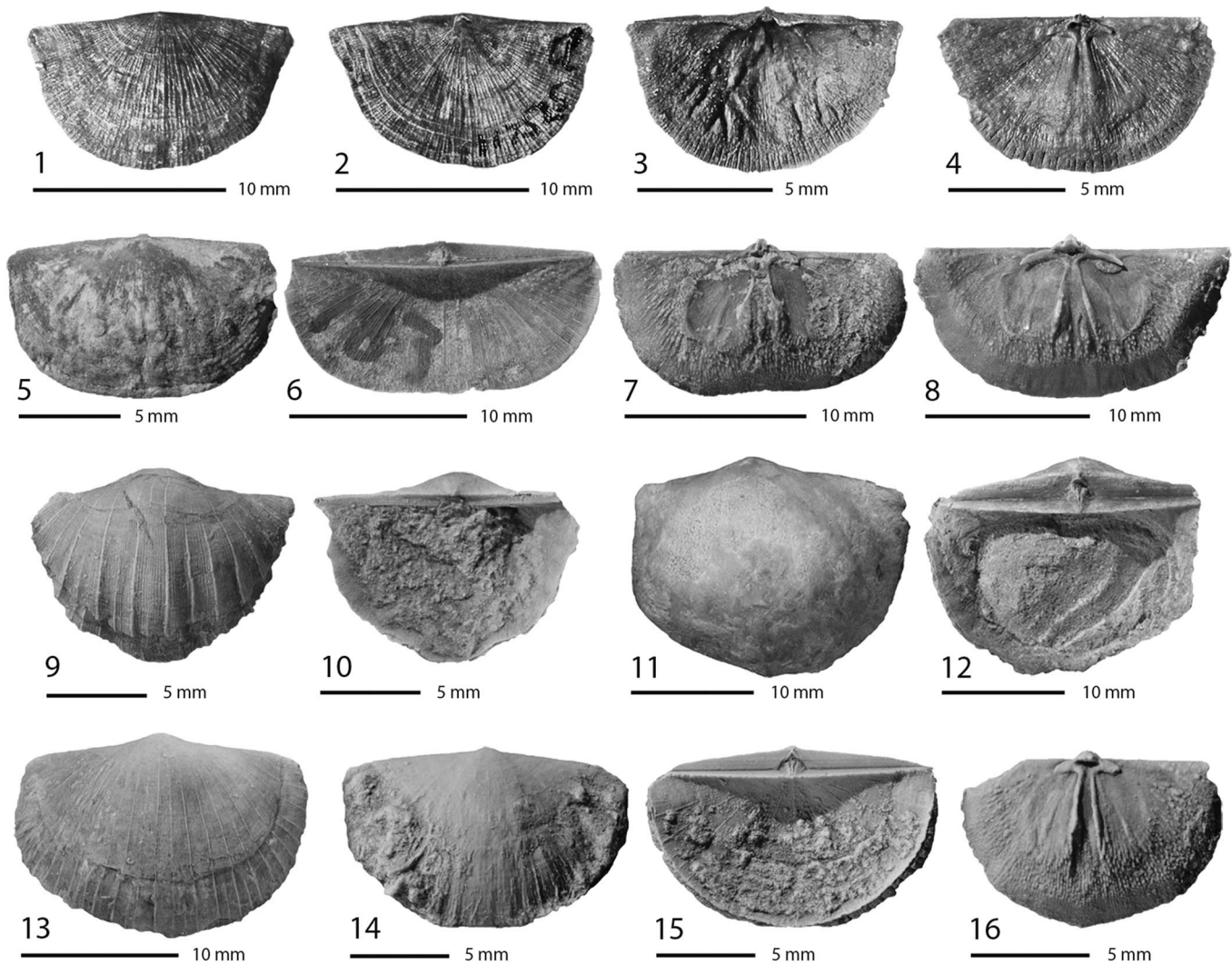
Formation, El Paso County, and Aleman Formation (middle–upper Katian), Culberson County, Texas; *Thaerodonta mucronata* Howe, 1965 from the Aleman Formation (middle Katian), Hudspeth and El Paso Counties, Texas; *Leptaena recedens* Sardeson, 1892 from the Maquoketa Formation (middle Katian), Spring Valley, Fillmore County, Minnesota, and Arnheim Formation (upper Katian), Tennessee; *Plectambonites rugosaclarksvillensis* Foerste, 1912 from the Waynesville and Liberty formations (upper Katian), Butler, Warren, and Clarksville counties, Ohio, and Lewis County, Kentucky; *Sowerbyella (Eochonetes) vaurealensis* from the Lavache through Homard members of the Vaureal Formation (upper Katian), Anticosti Island, Québec, Canada; *Eochonetes voldemortus* n. sp. from the Saturday Mountain Formation (upper Katian), South Lemhi Range, Idaho.

*Remarks.*—The previous separation of *Thaerodonta* and *Eochonetes* was based primarily on the presence of ventral hinge-line canals in species attributed to *Eochonetes* but absent in species of *Thaerodonta*. The differentiation of these genera based on a single character prone to preservation bias is not supported by this analysis. Morphospace analyses detailed above demonstrate that *Eochonetes* and *Thaerodonta* are not distinguishable in general shell features (Fig. 3). The phylogenetic hypothesis generated indicates *Eochonetes* and *Thaerodonta* are not discrete evolutionary lineages. Species previously referred to *Eochonetes* share closer relationships to species previously referred to as *Thaerodonta* than to each other. This indicates that neither of the previous concepts of *Eochonetes* and *Thaerodonta* is monophyletic, however, the combined set of species does form a monophyletic lineage with respect to the outgroup taxa. Therefore, these species are transferred into a single monophyletic genus herein. Because the name *Eochonetes* Reed, 1917 was described earlier, it has priority over *Thaerodonta* Wang, 1949 and is the correct generic name for this clade.

*Eochonetes* was originally erected based on the specimens discovered in the Starfish Beds (upper Katian) of the Drummuck Subgroup in Thraeve Glen, Scotland. Reed (1917) described the ventral hinge-line canals as being characteristic of the superfamily Chonetoidea. The canals were preserved as small rods along the hinge of moldic specimens, but they do not correspond with external spines and are therefore not homologous with the spines of true chonetids (e.g., Racheboeuf, 2000). All other characteristics, internal and external, of *Eochonetes* align more appropriately with the family Sowerbyellidae (Jones, 1928; Cocks and Rong, 2000; Cocks, 2013). Results of this investigation support the assignment of *Eochonetes* to Sowerbyellidae.

Species of *Eochonetes* are abundant in Katian strata of North America and some have been assigned to *Sowerbyella* (Fig. 10.1–10.8), which is characterized by similar external and internal structures. Specifically, the semicircular outline, variably costellate exterior surface ornamentation, and the bifurcated median septum in the ventral valve of *Eochonetes* resemble those of *Sowerbyella* (Wang, 1949). Both *Sowerbyella* and *Eochonetes* possess similar ventral and dorsal muscle scar fields and have similar cardinalia (Howe, 1972). *Eochonetes* is distinguished from *Sowerbyella* on the basis of





**Figure 10.** (1–4) *Sowerbyella socialis* Cooper, 1956; (1) ventral exterior (USNM 117525a); (2) dorsal exterior (USNM 117525a); (3) ventral interior (USNM 117527a); (4) dorsal interior (USNM 117527b). (5–8) *Sowerbyella rugosa* Meek, 1873; (5) ventral exterior (OUIP 183a); (6) dorsal exterior (OUIP 183b); (7) dorsal interior (OUIP 183e); (8) dorsal interior (OUIP 183f). (9–10) *Eopectodonta moelsi* (Rõõmusoks, 1981); (9) ventral exterior (TUG 1371-8); (10) dorsal exterior (TUG 1371-8). (11–12) *Plectodonta convexa* (Rõõmusoks, 1981); (11) ventral exterior (TUG 1971-12); (12) dorsal exterior (TUG 1971-12). (13) *Plectodonta nubila* (Rõõmusoks, 1981); ventral exterior (TUG 1371-15). (14–16) *Sowerbyella saunjaensis* (Rõõmusoks, 1981); (14) ventral exterior (TUG 1371-11); (15) dorsal exterior (TUG 1371-11); (16) dorsal interior (TUG 1371-19).

well-developed hinge-line denticulation (accessory teeth and denticles), a less divergent brachial process, a narrower muscle field, and an increased delthyrial thickening that produces two small conical cavities in the posterior region of the ventral valve.

*‘Thaerodonta’* was previously synonymized with *Eopectodonta* Kozłowski, 1929 on the basis of similar characters, i.e., hinge-line denticulation and the presence of divergent dorsal lateral ridges (Muir-Wood and Williams, 1965; Mitchell, 1977). Howe (1972) questioned this synonymy, because *Eochonetes* lacks the well-developed medium septum and external oblique rugae, which are considered generic traits of *Eopectodonta*. Fundamentally, the problem with the *‘Thaerodonta’-Eopectodonta* synonymy is that the hinge-line denticulation in the two genera is opposite in nature; *Eochonetes* has dorsal denticles with corresponding ventral fossettes, whereas *Eopectodonta* has ventral denticles with corresponding dorsal fossettes (Howe, 1972). The primary difference

supports independent, rather than homologous, acquisition of hinge-line denticulation in these two lineages.

*Rejection of previously assigned species.*—Five species previously assigned to the *Eochonetes* clade are herein transferred to other genera (Table 7). *Leptaena minnesotensis* Sardeson, 1892 from the *Orthosina* Bed, Kenyon, and Galena Series Bed, (lower Katian) Berne, Minnesota is transferred to *Sowerbyella*. This species lacks dorsal denticles and clusters with *Sowerbyella* in the phylogenetic analysis (Fig. 4) based on features of raised muscle scars and a high angle between the brachial process and hinge line. *Thaerodonta saunjaensis* Rõõmusoks, 1981 (Fig. 10.14–10.16) from the Saunja Formation, (middle Katian), Miaremtsa, Estonia is likely assignable to *Sowerbyella*. The dorsal valve appears to lack denticles, and this taxon grouped within the *Sowerbyella* out-group in the phylogenetic analyses (Fig. 4). The lack of denticles suggests that *T. saunjaensis* could belong to *Sowerbyella*

rather than *Eochonetes*. However, the scarcity of specimens with preserved interiors renders this assignment tentative. *Thaerodonta moelsi* Rõõmusoks, 1981 (Fig. 10.9, 10.10) from the Kõrgessaare Formation, (middle Katian), Kõrgessaare, Estonia is transferred to *Eoplectodonta*. This species possesses a length to width ratio ( $=0.71$ ) that falls within the *Eochonetes* spectrum ( $=0.39\text{--}0.77$ ) but at the high end and well above the mean ( $0.57$ ,  $N = 333$ ). This species exhibits an anacline ventral interarea and the dorsal interarea has an increased inclination relative to the cardinal area instead of the orthocline to apsacline ventral interarea that characterizes *Eochonetes*. In addition, the ventral valve lacks the characteristic delthyrial thickening and posterior conical cavities of *Eochonetes*. Finally, *T. moelsi* possesses a true median septum within the dorsal valve and has dorsal fossettes with corresponding ventral denticles, which are diagnostic of *Eoplectodonta*. *Thaerodonta convexa* Rõõmusoks, 1981 (Fig. 10.11, 10.12) from the Kõrgessaare Formation, (middle Katian), Paopa, Estonia is transferred to *Plectodonta*. This species exhibits extreme convexity, attaining approximately double the ventral valve height of the average *Eochonetes* specimen, and a significantly greater length to width ratio than exhibited by *Eochonetes* species. The interarea of *T. convexa* is anacline and the dorsal interarea differs from the orthocline to apsacline ventral interarea of *Eochonetes*. In addition, *T. convexa* exhibits increased inclination of the ventral interarea toward the cardinal area. The lack of a true median septum supports the assignment of this species to *Plectodonta* instead of *Eoplectodonta*. *Thaerodonta nubila* Rõõmusoks, 1981 (Fig. 10.13) from Adila Formation, (Hirnantian), Kaapsalyski Cliff, Estonia is transferred to *Plectodonta*. This species is more quadrate and has a less-curved beak than either *T. convexa* and *T. moelsi*. Compared to *Eochonetes*, this species has a greater shell height ( $=6.06$  mm), which coincides with the end of the *Eochonetes* continuum ( $=0.45\text{--}8$  mm), but the ventral interarea differs from *Eochonetes* in its anacline orientation. One individual appears to have 2 or 3 dorsal fossettes, but fossettes were not observed in other disarticulated specimens. The interior of *T. nubila* closely resembles that of *T. convexa*; accessory dentition is either poorly preserved or poorly developed and a true median ridge is absent. Thus, this species likely belongs within *Plectodonta*.

*Eochonetes maeorum* new species  
Figure 7.12–7.15

- 1957 *Thaerodonta* sp.; Ross, p. 457, pl. 40, fig. 22.  
1970 *Thaerodonta* aff. *T. clarksvillensis*; Macomber, p. 439, pl. 78, fig. 7a–d.

*Type specimens*.—FMNH PE 11072 (holotype), FMNH PE 11070 and 11071 (paratypes), USNM 124834 (paratype) from the Rock Creek Beds of the upper Bighorn Formation, Johnson County, Wyoming.

*Diagnosis*.—Angular to slightly acute cardinal extremities; wide delthyrium covered apically by short rounded pseudodeltidium; ventral interior unknown; denticles numerous (7), present on each cardinal extremity concentrated in center of hinge line; brachial process small, rounded; median septa faint,

lacking elevation; lateral ridges and bema faint; bema extending outward from tips of brachial process.

*Occurrence*.—Upper Katian Rock Creek Beds of the upper Bighorn Formation in Johnson County, Wyoming.

*Description*.—Outline semicircular. Hinge line straight; cardinal extremities angular to slightly acute. Ventral interarea apsacline. Delthyrium wide, covered apically by short rounded pseudodeltidium. Ventral interior unknown. Dorsal interarea hypercline. Denticles numerous, 7 on each cardinal extremity, concentrated in center of hinge line. Cardinal process small, slightly elevated; chilidial plates steep; brachial process small, rounded, extending anteriorly into median ridges; no true median septa; two ridges do not touch. Sockets wide, shallow. Muscle scar wide, lobe-shaped, separated by two median ridges that extend for two-thirds of valve; adductor scars equal in size with lateral ridges in center; lateral ridges faint, not extending as far as median ridges. Bema faint; anterior extension from brachial process.

*Etymology*.—Named for Betty Mae Bauer and Elsie Mae Shimanek.

*Remarks*.—Concentration of denticles in the center of the hinge line is unique to this species. In other *Eochonetes* species, denticles begin in the center and extend to the end of the cardinal extremity. The cardinal extremities of this species are angular rather than acute as is more common among *Eochonetes* species. The external surface of each ventral valve is swollen anteriorly. This swelling includes excess shell material built up along the commissure.

The small size of *Eochonetes maeorum* n. sp. is similar to that of *E. dignata*. However, the dorsal lateral septa of *E. maeorum* n. sp. are less well developed and the bema is fainter than that of *E. dignata*. The brachial process is similar in size and shape to that of *E. johnsonella*. The median ridge separation is also very similar to that of *E. johnsonella*; the two ridges connect with the brachial process and do not ever touch. Notably, *E. maeorum* n. sp. has centrally located, less-numerous denticles, whereas denticles are pronounced along the entire hinge length of both *E. dignata* and *E. johnsonella*.

Macomber (1970) previously described *Eochonetes maeorum* n. sp. as having an affinity to *E. clarksvillensis* based on internal and external characters, i.e., shape and size range. However, the dorsal muscle field of *E. clarksvillensis* is much more deeply incised than that of *E. maeorum* n. sp. The size and shape of the denticles of *E. maeorum* n. sp. are similar to those of *E. clarksvillensis*, but the denticles of *E. maeorum* n. sp. are more evenly spaced and sized. Those of *E. clarksvillensis* increase in size with lateral extent.

*Eochonetes minerva* new species  
Figure 9.1, 9.4

- 1965 *Thaerodonta* cf. *T. recedens*; Howe, p. 649, pl. 81, figs. 13–17.

*Type specimens.*—USNM 145043 (holotype) from the Aleman Limestone, Montoya Group, west-facing escarpment 3 mi east of Helms West Well, Hudspath County, Texas; USNM 145042 (paratype) from the Baylor Mountains east-facing escarpment, 1.6 mi N50°W of Watson Ranch House, Culberson County, Texas; USNM 145044 (paratype) from the H-2 Hueco Mountains west-facing escarpment, 3 mi east of Helms West Wall, Hudspath County, Texas; USNM 145045 (paratype) from the Franklin Mountains east-facing escarpment, 1.1 mi south of state line, El Paso County, Texas.

*Diagnosis.*—Acute to alate cardinal extremities; ventral median septum extending one-third of shell length, then bifurcating; primary teeth large, one or two accessory teeth present with that adjacent to primary tooth more pronounced than other; primary sockets ae wide followed by two adjacent accessory sockets; denticles beginning immediately after sockets and persisting to cardinal extremity tip; low short median septum on dorsal valve between branched median ridges.

*Occurrence.*—Upper Katian in the Aleman and Cutter formations of the Montoya Group of Texas.

*Description.*—Outline semicircular to subquadrate; cardinal extremities acute to alate. Ventral valve evenly gently convex; interarea apsacline. Delthyrium moderately wide; pseudodeltidium very small, rounded. Median septum extending one-third of length then bifurcateing. Adductor muscle scars subcircular, located posteriorly; diductor muscle scars elongate, extending two-thirds of shell length. Primary teeth strong; one or two accessory teeth with first stronger than second; fossettes (5–10) developed few millimeters from accessory teeth and extending to end of cardinal extremity. Dental plates extending anteriorly into strong lateral ridges. Dorsal valve slightly concave; interarea hypercline. Cardinal process stout, elevated posteriorly; brachial process short, rounded. Median septum bifurcating posteriorly; small short ridge appearing briefly anteriorly between two median ridges. Adductor muscle scars weakly impressed, wide, with lateral ridges; lateral ridges beginning posteriorly, elevating, continuing anteriorly. Bema faint but elevated slightly, outlining muscle scar field. Primary sockets wide, with two accessory sockets adjacent; denticles occurring immediately adjacent, extending to tip of cardinal extremity.

*Etymology.*—Named for the Roman goddess of wisdom.

*Remarks.*—Dentition is well-developed but not as pronounced as in the other two *Eochonetes* species in the southern midcontinental region (*E. magna* and *E. mucronata*). The median septum that reappears anteriorly between the two median ridges is unique to this species and was not observed in the other species examined. The ventral valve exterior is worn, whereas the interior of *E. minerva* n. sp. is similar to that of *E. magna* but lacks the well-defined accessory teeth of the latter. The cardinalia region of the dorsal valve is characterized by a brief median ridge prior to the bifurcation, which is similar in shape to those of *E. magna* and *E. mucronata*. The ventral valve is similar in outline to that of *E. recedens*, but the muscle scars are more deeply impressed and at more acute angle in *E. minerva* n.

sp. The internal dorsal muscle scars are lightly impressed, which is similar to those of the species of *Eochonetes* found in the Maquoketa Group of the midcontinental region, but this species differs in the presence of a faint, true median septum occurring between the two median ridges. In morphospace, *E. minerva* n. sp. plots (Fig. 3) within the *E. magna* and *E. clarksvillensis* occupied space for the dorsal valve and adjacent to, but not overlapping, the *E. clarksvillensis* morphospace field for the ventral valve. In the phylogenetic analyses, *E. minerva* n. sp. is hypothesized to be in a sister relationship with *E. vaurealensis* and *E. recedens* rather than creating a polytomy with *E. recedens*, which would be expected if the species were synonymous.

*Eochonetes mucronata* (Howe, 1965)

Figure 8.12–8.14

- 1965 *Thaerodonta mucronata* Howe, p. 648, pl. 81, figs. 18–24.  
1965 *Thaerodonta mucronata scabra* Howe, p. 648, pl. 82, figs. 9–11.

*Type specimens.*—USNM 145035 (holotype), USNM 145036–145039 (paratype series) from the Aleman Limestone, Montoya Group, west-facing escarpment 3 mi east of Helms West Well, Hudspath County, Texas; USNM 145040–145041 (paratype series) from the Cutter Limestone, Montoya Group, small ridge, 0.7 mi S55°W of Sugarloaf Mount, El Paso County, Texas.

*Diagnosis.*—Cardinal extremities very acute, mucronate; anterior margin truncate to gently rounded. Exterior roughly lamellose on some specimens. Two accessory teeth (ventral valve) with corresponding sockets (dorsal valve) nearly equal in size to primary teeth; denticles/fossettes numerous (15+), beginning after accessory teeth, terminating prior to cardinal extremity tip. Teeth curving slightly toward cardinal extremities. Dorsal adductor muscle scars subcircular, persisting for most of shell length, divided by strongly elevated lateral ridges.

*Occurrence.*—Upper Katian in the Aleman and Cutter formations of the Montoya Group of Texas.

*Remarks.*—Howe (1965) differentiated *Eochonetes mucronata scabra* as a subspecies of *E. mucronata* on the basis of possessing a rough lamellose exterior. No preserved valve interiors of *E. mucronata scabra* were recognized from the strata. The rough lamellose exterior has been observed in occasional specimens of other species (e.g., *E. magna*, *E. recedens*), and thus it is more likely caused by depositional or taphonomic conditions rather than reflecting a specific and discrete genotype. Consequently, this feature is not considered to be of taxonomic importance, and *E. mucronata scabra* is synonymized with *E. mucronata* herein. The teeth and accessory dentition of *E. mucronata* resemble those of *E. magna* in the curvature toward the cardinal extremities; however, the overall angles of the ventral muscle scars in *E. magna* exceeds those of *E. mucronata*.

*Eochonetes recedens* (Sardeson, 1892)

Figure 9.7–9.13

- 1892 *Leptaena recedens* Sardeson, p. 330, pl. 4, figs. 29–32.

- 1892 *Leptaena saxea* Sardeson, p. 330, pl. 4, figs. 33–35.  
 1949 *Thaerodonta recedens*; Wang, p. 20, pl. 11A, figs. 1–3.  
 1949 *Thaerodonta saxea*; Wang, p. 21, pl. 11B, figs. 1–5.  
 1988 *Thaerodonta recedens*; Howe, p. 214, figs. 2.9–2.12, 2.14–2.17, 10, 11.

*Syntypes*.—YPM IP 027652–027654 and 201725 from the Elgin Member, Maquoketa Group, Minnesota.

*Diagnosis*.—Lateral margins acute to gently sloping; anterior margin truncate. Ventral anterior margin occasionally forming broad sulcus. Accessory teeth subdued if present. Cardinal fossettes/denticles originating in center of hinge line; averaging 5–9 per cardinal extremity, evenly spaced along hinge line, typically increasing in size laterally.

*Occurrence*.—Upper Katian of Iowa, Missouri, Minnesota, and Illinois in the Maquoketa Group.

*Materials*.—SUI 1881–1884; USNM 145046, 418151, 418152–418156, and 418158. For a complete list of nonfigured examined specimens examined, see Supplemental Data 1.

*Remarks*.—Wang (1949) suggested that the comparatively larger size, narrower sulcus, stronger accessory teeth, and weaker denticles justified distinguishing *Eochonetes saxea* from *E. recedens*. However, Howe (1965) noted that when examining large populations, differences between the two species are not consistently expressed. The morphometric analyses presented herein recovered nearly complete overlap in morphospace occupation of *E. saxea* and *E. recedens* in all analyses. No other consistent morphological differences were present in the additional characters coded within the phylogenetic analysis. Due to the high level of morphological similarity exhibited by these two taxa, *E. recedens* and *E. saxea* are synonymized herein.

The ventral lateral ridges, which extend from the dental plates, are rounded with a slight bend in them, which is unique to this species (Fig. 9.10, 9.11). Denticle number varies among specimens, but the location is invariant; the denticles consistently originate in the center of the shell and extend laterally prior to terminating ~1–2 mm from the tip of the cardinal extremity.

*Eochonetes recedens* specimens exhibit subequal shell width and length. Individuals found in the northern midcontinental region have acute cardinal extremities compared to the more alate specimens found in the Central Basin. The shell outline is similar to that of *E. aspera*, but *E. recedens* is distinguished by its more angular cardinal extremities. The anterior portion of *E. recedens* exhibits a truncated to gently rounded shape similar to that of *E. johnsonella*, but *E. recedens* can be distinguished by less-divergent dorsal median ridges and a more-elongated ventral muscle scar field.

*Eochonetes voldemortus* new species  
 Figure 7.21–7.23

- 1959 *Thaerodonta* sp.; Ross, p. 458, pl. 55, figs. 40–43.

*Type specimens*.—USNM 133257 (holotype) and USNM 133258 (paratype) from the Saturday Mountain Formation, on ridge between Black Canyon and South Creek, just north of divide, South Lemhi Ridge, Idaho.

*Diagnosis*.—Length commonly less than half the width; lateral margins gently sloping; ventral interior unknown; denticles numerous, 9 or 10 on one cardinal extremity, originating in center of hinge, terminating 1 mm from cardinal extremity tip; bulbous median ridge prior to bifurcation; very faint bema.

*Occurrence*.—Upper Katian Saturday Mountain Formation of Idaho.

*Description*.—Outline semicircular. Hinge line straight; cardinal extremities acute. Ventral interarea aplanate. Delthyrium small, covered apically by rounded pseudodeltidium. Ventral interior unknown. Dorsal interarea hypercline. Denticles numerous, 9 or 10 on one cardinal extremity, originating in center of hinge, terminating 1 mm from cardinal extremity tip. Cardinal process stout; chilidial plates steep; brachial process short, pointed; sockets wide, deep. Muscle scar field short, narrow; median ridges extending from central portion of brachial process, one-half shell length; lateral ridges elevated, terminating early. Bema faint, extending directly from tip of brachial process; median ridges extending anterior to extent of bema.

*Etymology*.—Named after the fictional antagonist, Voldemort, of J.K. Rowling's Harry Potter series.

*Remarks*.—Shell width to length ratio is low (0.48–0.49). Dorsal valve muscle scars are very faint and lateral septa originate near brachial process but do not extend as far as the median ridges. Typically, the muscle scar field of *Eochonetes* extends for approximately two-thirds of the shell, whereas in this species is approximately one-half. The median ridges split after a very brief bulbous median ridge.

The small size of *Eochonetes voldemortus* n. sp. is similar to that of *E. dignata* and *E. maeorum* n. sp., but the width to length ratio is smaller (0.49) than in the other species (0.55–0.65). The bema is the faintest of all the species compared. Rather than having a brief median septum as seen in *E. magna* and *E. mucronata*, there is a rounded connection of the two ridges, ~0.5 mm in length.

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### Accessibility of Supplemental Data

Data are available from the Dryad Digital Repository: <http://doi.org/10.5061/dryad.62h0b>.

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