Fossil tip-dating reveals novelties on evolutionary and diversification trends in three Late Ordovician brachiopod genera (Atrypida, Anazygidae)

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Abstract

During the Ordovician, the brachiopod order Atrypida originated and diversified. However, speciation patterns and evolutionary drivers within three atrypide Laurentian genera, *Anazyga*, *Catazyga*, and *Zygospira*, remain poorly known. Herein, we propose a Bayesian phylogenetic framework for these clades. Morphological character data, including 34 internal and external characters, were collected for 20 species, including seven species assigned to *Zygospira*, six species previously assigned to *Anazyga*, and seven species previously assigned to *Catazyga*. Morphological data were analyzed in BEAST2.5 via an Mk Model of morphological character evolution implementing the fossilized birth–death (FBD) model. In addition, FBD-based rates of extinction, origination, and fossil sampling were estimated across four Late Ordovician time intervals. Primary results include: (1) each genus was polyphyletic as traditionally established; (2) proposed transfer of all *Anazyga* and two *Catazyga* species to *Zygospira* based on reconstructed evolutionary relationships; (3) recognition of one new species, *Zygospira idahoensis* Vilela-Andrade n. sp., and the elevation of *Z. multicostata* Howe, 1965, originally a subspecies, to species status; and (4) updated understanding of clade origination and speciation. The origination age for the clade is calibrated to be 453 Ma (Sandbian 2). Recovered biodiversification rates indicate that the highest speciation and extinction rates occurred in the Katian 3 stage slice, when the number of species in the clade peaked. Subsequently, a decline in biodiversification led to an extinction episode in the Katian 4 for all lineages. *Catazyga* and *Zygospira* are interpreted as early Late Ordovician atrypids that experienced both rapid radiation and extinction during the Katian.

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Non-technical Summary

The Late Ordovician was a time of rapid diversification and biodiversity accumulation for brachiopods, a key component of the Paleozoic Evolutionary Fauna, composed predominantly of filter-feeding benthic organisms. In this paper, we reconstruct the evolutionary relationship and biodiversity dynamics of a key group of atrypide brachiopods in the family Anazygidae, including the genera *Anazyga*, *Catazyga*, and *Zygospira*. Analysis of multiple potential datasets of internal and external characters using Bayesian phylogenetic methods under the fossilized birth–death model recovered topologies that were most robust when incorporating only external characters. Moreover, all recovered topologies indicate that species previously assigned to *Anazyga* and *Zygospira* do not separate into discrete clades but are intermixed within a single monophyletic group. Consequently, we propose a systematic revision based on external characters that recognizes two monophyletic genera: *Catazyga*, which includes most species historically assigned to *Catazyga*, and *Zygospira*, which includes most species historically assigned to *Zygospira* and *Anazyga*. One new species, *Zygospira idahoensis* is described, and one former subspecies is elevated to species status as *Zygospira multicostata*. The Anazygidae is estimated to have originated around 453 million years ago in the Sandbian Stage. Recovered diversification rates indicate that the highest speciation and extinction rates occurred in the late Katian (Katian 3) state, when the total number of species in the clade reached its peak. This was followed by an abrupt decline in biodiversification rates that led to an extinction episode in the Katian 4 Stage for all lineages. Therefore, *Catazyga* and *Zygospira* are interpreted as early Late Ordovician atrypids that experienced both rapid radiation and extinction during the last phase of the Ordovician Radiation in the Katian Stage.

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Introduction

The order Atrypida originated and diversified in the Middle Ordovician (Darriwilian), flourished during the Late Ordovician, and persisted through the early Silurian until its extinction in the Late Devonian (Harper et al., 2017). Anazygidae Davidson, 1882 is an early, geographically widespread brachiopod family within the order Atrypida that ranges from the Middle to Late Ordovician (Copper, 1977; Baarli et al., 2022). Anazygidae species are stratigraphically important taxa that substantially impacted community structures and ecosystems (Copper, 1977; Patzkowsky and Holland, 1999; Sproat and McLeod, 2023). Typical species within the Anazygidae are small (5–15 mm), oval-shaped, with fine-ribbed shells characterized by brachidia with "the apex of their vertical spiral cones directed towards the bottom of the dorsal valve" (i.e., coiling toward the margins of the dorsal valve; Davidson, 1882, p. 4). Their interior morphology consists of a calcified, whorled spiralia, which has historically played an important role in atrypide taxonomy (Sproat and McLeod, 2023).

This study focuses on *Anazyga* Davidson, 1882, *Catazyga* Hall and Clarke, 1894, and *Zygospira* Hall, 1862, which are paleoecologically significant taxa in Late Ordovician communities of (mainly) Laurentia (Copper, 1977; Patzkowsky and Holland, 1999). A parsimony analysis conducted by Baarli et al. (2022) that included 40 characters and 71 atrypide genera recovered these genera as forming a monophyletic group with the Silurian non-Laurentian genera *Zygatrypa* and *Pentlandella*; however, the geographic and stratigraphic relations among these five genera remain unclear and require reevaluation. Four *Zygospira* species were recently systematically revised by Sproat and McLeod (2023); however, no previous studies have explored species-level evolutionary relationships of Late Ordovician anazygid species. The goal of this study is to reconstruct species-level relationships and evolutionary rates within this group in the Late Ordovician. In addition, this analysis investigates the relative importance of incorporating internal and external characters versus only external characters into tip-dated Bayesian phylogenetic analyses implementing a fossilized birth–death (FBD) model.

Background

The atrypide genus *Zygospira* Hall, 1862 ranges from the late Sandbian to the late Katian Age (Late Ordovician) throughout North America (Foerste, 1924; Wang, 1949; Howe, 1965; Copper, 1977; Jin et al., 1997; Sproat and McLeod, 2023), although species have also been reported from Australia (Percival, 1991) and Wales (Cowper Reed, 1905). *Zygospira* was erected by Hall (1862), who defined *Zygospira* as being externally distinct from other atrypids due to its size, circular to oval shape, number of ribs, and discrete combination of internal structures, specifically five to eight spiralium whorls that coil laterally. *Anazyga* was described 20 years later by Davidson (1882) as a genus similar to *Zygospira*, which was characterized as being longitudinally oval and having one to three spiralium whorls. Later, Copper (1977) characterized *Anazyga* as the earliest known wholly ribbed atrypide and described it as being coarsely ribbed. The earliest species attributed to *Anazyga* are Sandbian 2 in age whereas most species previously attributed to *Zygospira* are Katian in age. This has led various authors to interpret these as time-stratigraphic lineages (e.g., Copper, 1977). *Anazyga* species are commonly found in North America, although they have also been reported from Laurentian terranes in the United Kingdom and in Baltoscandia (Copper, 1977).

Similarities in the internal structures of *Zygospira* and *Anazyga* suggest very close evolutionary affinities, with the primary difference between the two being the location and orientation of the jugum that connects the spiralia and differences in the orientation of the spiralia (Copper, 1977). Species have been transferred between *Anazyga* and *Zygospira* by various authors over the past 140 years. For example, a total of 10 *Zygospira* species were transferred to *Anazyga* (Copper, 1977) on the basis of stratigraphic ranges, the presence of teeth cavities, and jugum position. Baarli et al. (2022) inferred *Zygospira* + *Anazyga* as a monophyletic group, but it is possible each genus may be paraphyletic as historically defined.

The third anazygid genus, *Catazyga* Hall and Clarke, 1894, was assigned in addition with the Silurian genus *Pentalandella* Boucot, 1964 to the subfamily Catazyginae by Baarli et al. (2022), although Baarli et al. (2022) noted a significant stratigraphic gap between these genera. *Catazyga* is diagnosed as a rotund costellate brachiopod with an elliptical outline. *Catazyga* is recorded from eastern North America and Europe and assumed to have originated during the early Katian, making it younger than both *Anazyga* and *Zygospira*. From the literature, there is no apparent doubt about the division between *Catazyga* and its related genera due to its unique rotund profile and abundance of prominent costellae. There are, however, uncertainties in the phylogenetic position of *Anazyga* within the clade. Externally, *Anazyga* appears most closely related to *Zygospira*, but internally, it shares multiple morphological features with both *Catazyga* and *Zygospira*, such as the dorsal spiralia with fewer whorls (Copper, 1977).

Internal characters have historically been given substantial taxonomic importance in differentiating *Anazyga* and *Zygospira*; however, the internal morphology of most species within the clade has not been well characterized. In total, only three species have well-documented brachidia, *Anazyga recurvirostra* (Hall, 1847), *Zygospira modesta* Say in Hall, 1847, and *Z. kentuckiensis* Nettelroth, 1889 (Hall, 1862; Davidson, 1882; Copper, 1977; Sproat and McLeod, 2023). Due to variable preservation of internal structures and the labor- and time-intensive process of serial sectioning required to examine the spiralia morphology in anazygids, little is known about species-specific internal anatomy. Generalizations from these three well-constrained species are frequently made when describing species and genera (Ross and Dutro, 1966), or internal morphology is not discussed at all (Cowper Reed, 1905; Fenton and Fenton, 1922; Cooper, 1956). These biases in species' descriptions make it difficult to fully account for the importance of internal morphology in evolutionary history of anazygid taxa. In this study, analyses were conducted with both internal (when available) and external characters and with exclusively external characters to reconstruct relationships among *Anazyga*, *Catazyga*, and *Zygospira*. We aim to explore the importance of utilizing internal characters to describe the broadly distributed family and to clarify the taxonomy within the family on the basis of a holistic framework combining both internal and external morphology.

This study presents the first species-level phylogeny for the atrypide genera *Anazyga*, *Catazyga*, and *Zygospira*. The relative importance of internal versus external characteristics to phylogeny estimation is examined, and the monophyly of each named genus is assessed and systematically revised as needed. In addition, extinction and speciation rates were inferred for the group across the Late Ordovician to quantify biodiversification trends during this interval. Thus, this analysis provides a framework for evaluating macroevolutionary patterns in these lineages during the globally recorded rise in Late Ordovician brachiopod diversity.

Materials and methods

Studied taxa. All available Late Ordovician Laurentian species of *Zygospira*, *Anazyga*, and *Catazyga* were examined and morphologically characterized. In total, 147 specimens representing 20 anazygid species (Table 1) were included within the morphological dataset. *Zygospira* species diagnoses follow recent revisions of Sproat and McLeod (2023). *Anazyga* and *Catazyga* species were identified following the original descriptions and subsequent revisions by Copper (1977). *Protozyga exigua* Hall, 1847 was included as the outgroup for comparison. This species was chosen because earlier phylogenetic analyses by Baarli et al. (2022) recovered *Protozyga* as a sister group to Anazygidae.

The subspecies *Zygospira resupinata multicostata* Howe, 1965 from the Montoya Group in Texas is poorly understood, and its placement within *Zygospira resupinata* Wang, 1949 was suggested by Sproat and McLeod (2023) to possibly indicate an early lineage split between *Anazyga* and *Zygospira*. Because of that, *Z. resupinata multicostata* was added to the dataset as a separate operational taxonomic unit (OTU) to elucidate its phylogenetic position within the clade. Two *Catazyga* species from Scoto-Avalonia, *Catazyga arcana* Williams, 1962 and *Catazyga hicksi* (Cowper Reed, 1905), were also included in the analysis as this region has close paleoenvironmental and tectonic affinities with Laurentia (Harper et al., 2023). Similarly, *Catazyga homeospiroides* Ross and Dutro, 1966 from Alaska was included within the dataset given its geographical proximity with Laurentia and tectonic displacement from Laurentian subterranes (Servais et al., 2023).

Characters and coding. A total of 34 characters, including external and internal traits, were coded for the measured specimens (Fig. 1; Table 2; Supplementary Data 1). Character traits were selected on the basis of the assessment of the published literature on the group (Copper, 1977; Baarli et al., 2022; Sproat and McLeod, 2023). Atrypida was the first brachiopod order to evolve the spiralia as a helical structure with ribbons of calcite (Copper, 2001). Within Anazygidae, the number and directionality of the spiralia whorls is considered a diagnostic trait and significant for systematics and classification. *Zygospira* spp. comprise species ranging from 4 to 10 mm in length, and the lophophore has five to eight whorls bearing a lateral orientation (Hall, 1862; Copper, 1977). *Anazyga* spp. are similar in size, ranging from 4 to 6 mm, and are described as typically possessing one to three whorls in their lophophore (Davidson, 1882; Copper, 1977). *Catazyga* spp. typically have larger valves than the other genera, with lengths ranging from 10 to 19 mm and bear three to 10 lophophore whorls (Hall and Clarke, 1894; Copper, 1977). Traits that have traditionally been used to differentiate species within these clades (e.g., spiralia characteristics, shell size, number of ribs) were combined with characters newly developed from empirical assessment of analyzed specimens (e.g., rib spacing, deflection rate) to generate a comprehensive character set. Many of the incorporated traits are continuous characters. However, the incorporation of continuous traits in morphological phylogenetics has long been challenging (Rae, 1998; Goloboff et al., 2006; Parins-Fukuchi, 2018; Wright and Hopkins, 2024) due to the mathematical limitations of incorporating continuous values into analyses. Consequently, the 10 characters within this dataset that

Table 1. Species included in the phylogenetic analysis. Names in the first and second columns indicate original taxonomic assignment and current taxonomic nomenclature, respectively. *Anazyga* species are transferred to *Zygospira* herein; therefore, names in the third column indicate the updated nomenclature (this study). *Indicates outgroup species

Original nomenclature	Current nomenclature	This study
*Protozyga exigua** Hall, 1847	*Protozyga exigua** Hall, 1847	*Protozyga exigua** Hall, 1847
Anazyga calhounensis Fenton and Fenton, 1922	*Anazyga calhounensis* Fenton and Fenton, 1922	*Zygospira calhounensis* (Fenton and Fenton, 1922)
Zygospira circularis Cooper, 1956	*Anazyga circularis* (Cooper, 1956)	*Zygospira circularis* Cooper, 1956
Zygospira lebanonensis Cooper, 1956	*Anazyga lebanonensis* (Cooper, 1956)	*Zygospira lebanonensis* Cooper, 1956
Atrypa recurvirostra Hall, 1847	*Anazyga recurvirostra* (Hall, 1847)	*Zygospira recurvirostra* (Hall, 1847)
Zygospira variabilis Fenton and Fenton, 1922	*Anazyga variabilis* (Fenton and Fenton, 1922)	*Zygospira variabilis* Fenton and Fenton, 1922
Zygospira anticostiensis Billings, 1862	*Catazyga anticostiensis* (Billings, 1862)	*Catazyga anticostiensis* (Billings, 1862)
Catazyga arcana Williams, 1962	*Catazyga arcana* Williams, 1962	*Catazyga arcana* Williams, 1962
Catazyga cartieri Cooper and Kindle, 1936	*Catazyga cartieri* Cooper and Kindle, 1936	*Catazyga cartieri* Cooper and Kindle, 1936
Athyris headi Billings, 1862	*Catazyga headi* (Billings, 1862)	*Catazyga headi* (Billings, 1862)
Zygospira hicksi Cowper Reed, 1905	*Catazyga hicksi* (Cowper Reed, 1905)	*Zygospira hicksi* Cowper Reed, 1905
Catazyga homeospiroides Ross and Dutro, 1966	*Catazyga homeospiroides* Ross and Dutro, 1966	*Catazyga homeospiroides* Ross and Dutro, 1966
Zygospira uphami Winchell and Schuchert, 1892	*Catazyga uphami* (Winchell and Schuchert, 1892)	*Zygospira uphami* Winchell and Schuchert, 1892
Zygospira cincinnatiensis James in Meek, 1873	*Zygospira cincinnatiensis* James in Meek, 1873	*Zygospira cincinnatiensis* James in Meek, 1873
Zygospira concentrica Ulrich, 1879	*Zygospira concentrica* Ulrich, 1879	*Zygospira concentrica* Ulrich, 1879
Zygospira kentuckiensis Nettelroth, 1889	*Zygospira kentuckiensis* Nettelroth, 1889	*Zygospira kentuckiensis* Nettelroth, 1889
Zygospira modesta Say in Hall, 1847	*Zygospira modesta* Say in Hall, 1847	*Zygospira modesta* Say in Hall, 1847
Zygospira aff. *Z. putilla* Ross, 1959	*Zygospira* aff. *Z. putilla* Ross, 1959	*Zygospira idahoensis* new sp.
Zygospira resupinata Wang, 1949	*Zygospira resupinata* Wang, 1949	*Zygospira resupinata* Wang, 1949
Zygospira resupinata multicostata Howe, 1965	*Zygospira resupinata multicostata* Howe, 1965	*Zygospira multicostata* new sp.
Zygospira sulcata Howe, 1965	*Zygospira sulcata* Howe, 1965	*Zygospira sulcata* Howe, 1965
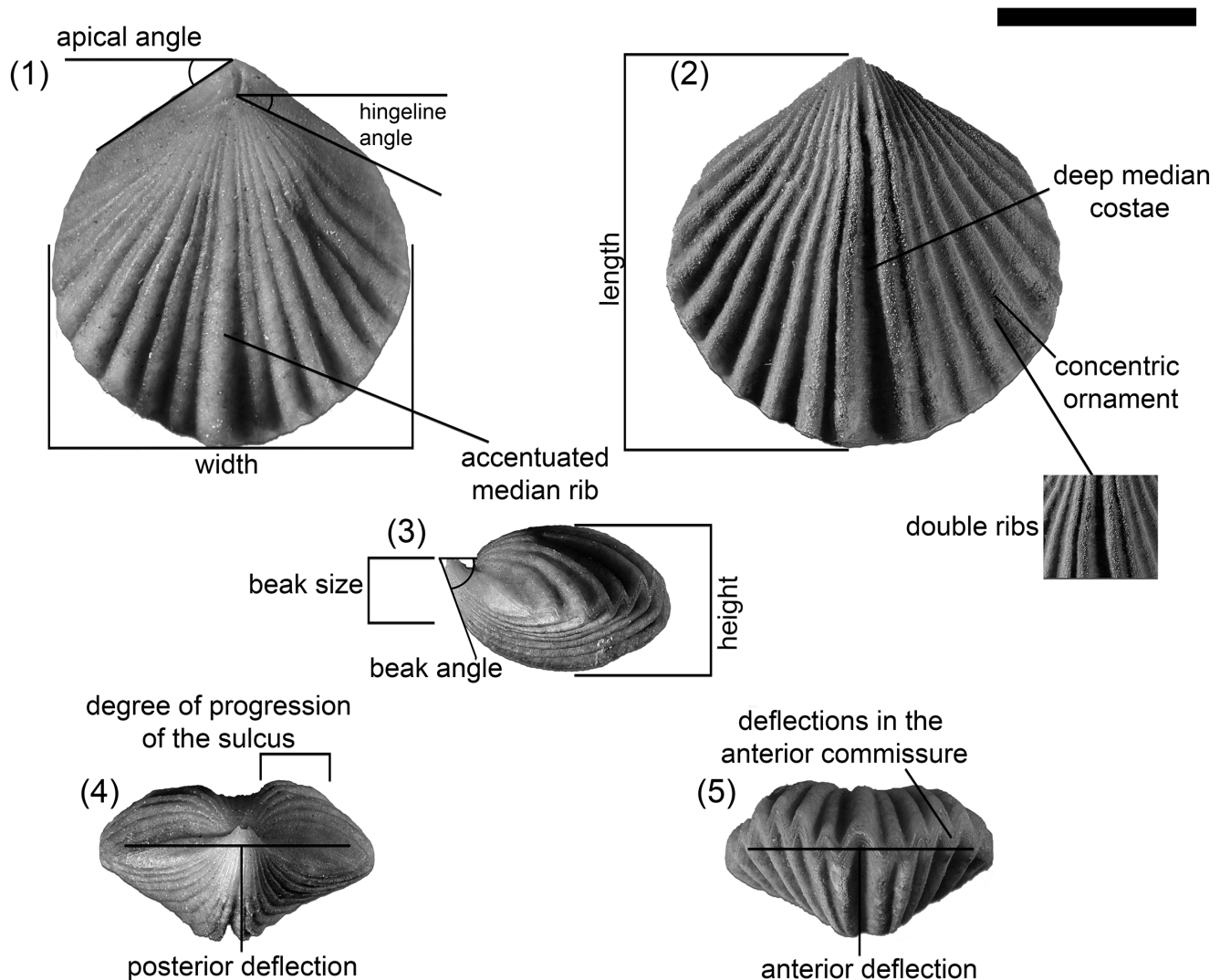
Figure 1. Explanation of key morphological characters indicated in Table 2. *Zygospira modesta* Say in Hall, 1847 specimen from the Arnheim Formation of Brookville, Indiana. (**1**) Dorsal view. (**2**) Ventral view. (**3**) Lateral view. (**4**) Posterior view (hinge line). (**5**) Anterior view (commissure opening). Scale bar = 2 mm.

represent continuous traits (e.g., maximum shell length, maximum shell width, and maximum shell height) were converted into categorical character states for analysis. The categorization was initially graphically executed, by looking for natural breaks in the slopes in a plot as is typical for phylogenetic analyses of similar clades (Stigall Rode, 2005; Wright and Stigall, 2013, 2014; Bauer and Stigall, 2016). After manual identification of character state ranges, an analysis of variance (ANOVA) was conducted in R to ascertain whether the proposed character states were statistically distinct. If the bins were statistically distinct, they were accepted as valid states. If not, the process was repeated until statistically distinct character states were identified. In general, continuous traits were divided into multistate characters. Conversely, categorical traits were mainly binary characters (such as presence or absence). Polymorphism was commonly observed in anazygids and, therefore, incorporated into the final character matrix as well. See Supplementary Data 1 for additional details on character definition and coding. Some characters, notably internal characters, are not available for many in-group taxa, resulting in "?" within the character matrix (Table 2). Anazygid taxa rarely disarticulate owing to their tightly fitting cyrtomatodont teeth and sockets; thus, internal characters are known mainly from serial sections, which are available for only a few species. Nevertheless, incorporating characters with missing data has been demonstrated to improve phylogenetic resolution and accuracy in general and within Bayesian inference in particular (e.g., Wiens, 2003; Wiens and Moen, 2008; Roure et al., 2013; Khakurel et al., 2024), so we retain these characters herein.

Phylogenetic analysis. Phylogenetic analysis was conducted using a Bayesian "tip-dated" phylogenetic approach implementing the FBD process in BEAST 2.5 v2.7.6 (Bouckaert et al., 2019; Wright et al., 2021). Bayesian phylogenetic analyses incorporating the FBD model facilitate the joint inference of evolutionary relationships, divergence times, and diversification dynamics (Stadler, 2010; Heath et al., 2014; Wright, 2017; Wright et al., 2021). First proposed by Stadler (2010), the FBD model is a stochastic model that simulates rates of birth (λ) and death (μ) for individuals sampled in the past at a rate (ψ). When applied to paleontological data, λ is considered as the rate of species' origination (speciation, i.e., lineage-splitting events), μ is the extinction rate, and ψ is the fossil sampling and recovery rate (Stadler et al., 2018). Bayesian tip-dating approaches incorporating the FBD model can be viewed as a Bayesian hierarchical

Table 2. Morphological characters included in phylogenetic analysis. *Indicates internal characters

Character	Character states
1. Maximum length (mm)	(0) 0–5, (1) 5–10, (2) 10–15, (3) +15
2. Maximum width (mm)	(0) 0–5, (1) 5–10, (2) 10–15, (3) +15
3. Maximum height (mm)	(0) 0–5, (1) 5–10, (2) 10–15, (3) +15
4. Length/width ratio	(0) 0–1, (1) 1–2
5. Shell outline	(0) Quadrate, (1) Rectangular, (2) Transverse, (3) Elliptical, (4) Elongate, (5) Pentagonal
6. Number of ribs ventral valve	(0) 0–10, (1) 10–20, (2) 20–30, (3) +30
7. Number of ribs dorsal valve	(0) 0–10, (1) 10–20, (2) 20–30, (3) +30
8. Concentric ornament	(0) Absent, (1) Growth lines
9. Ribs appearance	(0) Weak, (1) Strong, (2) Very fine
10. Profile	(0) Biconvex, (1) Dorsibiconvex, and (2) Ventribiconvex
11. Beak angle (°)	(0) 0–20, (1) 20–40, (2) 40–60, (3) +60
12. Beak size (mm)	(0) 0–5, (1) +5
13. Position fold/sulcus	(0) Not developed, (1) Originating near the umbo and extending to the anterior margin, (2) Originating anterior to the umbo
14. Apical angle (°)	(0) 0–40, (1) 40–60, (2) +60
15. Hinge line angle (°)	(0) 0–40, (1) 40–60, (2) +60
16. Accentuated median rib	(0) Absent, (1) Present
17. Sinuosity of the anterior commissure	(0) Rectimarginate, (1) Parasulcate, (2) Paraplicate, (3) Unisulcate, (4) Sulciplicate, (5) Bisulcate
18. Magnitude of anterior deflection relative to the commissure (mm)	(0) 0–3, (1) 3–5, (2) +6
19. Magnitude of posterior deflection relative to the hingeline (mm)	(0) 0–2, (1) 2–6, (2) +6
20. Indentation in the median costae	(0) Absent, (1) Present
21. Deflections in the anterior commissure	(0) Absent, (1) Zig-zag
22. Double ribs to side of dorsal fold	(0) Absent, (1) Present
23. Degree later progression of the sulcus (mm)	(0) 0–2, (1) 2–4, (2) 4–6, (3) +6
24. Accentuated median rib (ventral)	(0) Absent, (1) Present
25. Degree of deflection of fold and sulcus relative to commissure	(0) Flat or weakly folded, (1) Strongly pronounced
26. Ribs spacing (number of ribs dorsal valve/maximum width)	(0) 0–2, (1) 2–4, (2) 4–6, (3) +6
27. Anterior deflection rate (maximum height/fold anterior deflection)	(0) 0–2, (1) 2–4, (2) +4
28. Posterior deflection rate (maximum height/fold posterior deflection)	(0) 0–2, (1) 2–4, (2) +4
29. Number of whorls*	(0) 0–5, (1) 5–10, (2) +10
30. Jugum position*	(0) Absent, (1) Short, (2) Posteroventral, (3) Mediodorsal
31. Cardinal processes*	(0) Absent, (1) Present
32. Teeth*	(0) Absent, (1) Weak, (2) Strong
33. Jugum shape*	(0) D-shaped, (1) V-shaped, (2) W-shaped
34. Hinge plates*	(0) Absent, (1) Present

model composed of three parts: (1) a tree model (e.g., the FBD); (2) a model of morphological character evolution; (3) a clock model describing how rates vary across the tree (Warnock and Wright, 2020; Wright et al., 2021). The principal strength of tip-dating approaches is that they infer time-calibrated phylogenetic trees, allowing inference of divergence times (Wright et al.,

2021), and potentially lead to improved phylogenetic inferences compared with undated approaches (Barido-Sottani et al., 2020; Mongiardino Koch et al., 2021).

Empirically informed prior distributions were placed on FBD parameters using values calculated from clade-wide fossil occurrence data (Wright et al., 2021; Thuy et al., 2022). Empirical

estimates for extinction and origination rates were obtained from the Paleobiology Database (PBDB; paleobiodb.org) platform on the basis of generalized rates obtained for the Rhynchonelliformea clade (= all articulated brachiopods). A total of 21,242 occurrences of Ordovician rhynchonelliform taxa were extracted from the PBDB and the mean per capita rates were calculated for each of the seven Ordovician Ages (i.e., Tremadocian, Floian, Dapingian, Darriwilian, Sandbian, Katian, and Hirnantian). Equations for per capita rates are from Foote (2000), which considers the time interval duration and the number of boundary crossers. The distribution of per capita rates and the total number of occurrences were then analyzed in R to place priors on diversification, turnover, and fossil sampling (Wright et al., 2021).

Chronostratigraphic ranges were created for each individual species on the basis of data obtained from oldest and earliest-known occurrences from museum specimens augmented with data from the PBDB (Table 3). To avoid regional synonyms and outdated nomenclature, all geologic formations and unit names were revised and adapted to the recently revised Cincinnatian Series sequence stratigraphy (Brett et al., 2020). Absolute ages follow the Ordovician timescale of Goldman et al. (2020).

The substitution model for morphologic character evolution was set to follow the Mk Model (Lewis, 2001), with a gamma distribution accounting for rate variation among characters. Per-branch rate variation was modeled using an uncorrelated, log-normal relaxed

Table 3. Chronostratigraphic data for the 21 analyzed species in millions of years (Ma). Taxonomic nomenclature correlates with the second column on Table 1. Age range is from Middle Ordovician (453.5 Ma) to the Ordovician–Silurian boundary (443.07 Ma) following dates within Goldman et al. (2020). First appearance (FA), and last appearance (LA) are given for all analyzed species. *Indicates outgroup species

Taxon	FA	LA
*Protozyga exigua**	453.5	450
Zygospira modesta	450.5	446.04
Zygospira sulcata	451	450.5
Zygospira resupinata	450	450
Zygospira cincinnatiensis	451	450
Zygospira kentuckiensis	451	448
Zygospira concentrica	451	450.5
Zygospira resupinata multicostata	451	450.5
Anazyga circularis	453.5	451
Anazyga lebanonensis	453.5	451
Anazyga aff. *A. putilla*	453.5	451
Anazyga recurvirostra	453.5	450
Anazyga variabilis	453.5	451
Anazyga calhounensis	451	450
Catazyga headi	448	443.07
Catazyga cartieri	451	450
Catazyga homeospiroides	451	450
Catazyga anticostiensis	450	445.5
Catazyga arcana	453.5	451
Catazyga hicksi	450.5	450
Catazyga uphami	451	450

clock model. The log-normal clock model predicts that the evolutionary rate in branches is generally low but can vary sporadically over time and/or throughout the tree (Ho and Phillips, 2009; Wright et al., 2021). For more details about the application of these models to paleontological data, please see Wright et al. (2021). Markov-chain Monte Carlo (MCMC) was conducted in BEAST2 (Bouckaert et al., 2019) to infer phylogenies and evolutionary parameters. MCMC was run for 2,000,000 iterations. The burn-in value was set to 10,000 initial generations.

To assess the effects of the internal versus external traits on anazygid phylogeny, we used the model configuration described in the preceding to analyze four potential scenarios: (1) an analysis including external + internal traits with no phylogenetic constraints; (2) an analysis including only external traits with no phylogenetic constraints; (3) an analysis including only external traits but implementing a Catazyginae constraint, which requires *Catazyga* species (exclusive of *Catazyga hicksi* and *C. uphami* [Winchell and Schuchert, 1892]) to resolve as a clade (see Barido-Sottani et al., 2023); and (4) an analysis including only external traits with clade constraints forcing the monophyly of all three genera.

To assess the MCMC convergence and posterior probability of each scenario modeled, the software TRACER was used (Rambaut et al., 2018). Convergence and model diagnostics were assessed according to Nascimento et al. (2017) and Wright et al. (2021) (i.e., trace plots, estimated sample size (ESS) values, MCMC mixing, etc.). In addition, tree topologies for alternative scenarios were compared using maximum clade credibility (MCC) trees with the median node heights in TreeAnnotator (distributed with BEAST2). An MCC represents a point estimate of phylogeny and is found by identifying the tree in the MCMC sample with the largest product of clade posterior probabilities (Heled and Bouckaert, 2013).

To infer diversification dynamics over the Late Ordovician, we ran a subsequent analysis implementing a skyline FBD model using the MCC tree obtained from scenario 3 (our preferred phylogeny; see Results). The advantage of a skyline model is that it allows inferences of time-varying (piecewise constant) FBD parameters for discrete time intervals (Gavryushkina et al., 2014; Wright et al., 2021). Therefore, considering previous interpretations of anazygid evolution and diversification throughout the Late Ordovician (Copper, 1977), four time intervals were considered for the skyline model. The intervals were based on North American Ordovician stages: Interval 1: Chatfieldian (Sandbian 2 and Katian 1 stage slices); Interval 2: Edenian (Katian 2); Interval 3: Maysvillian (Katian 3); and Interval 4: Richmondian (Katian 4) and Gamachian (Hirnantian) stages. Exponential priors were placed on each estimated rate: birth (speciation), death (extinction), and sampling rate. MCMC was run for 5,000,000 generations to estimate FBD parameters for each interval, with a set burn-in of 500,000 runs.

Repositories and institutional abbreviations. Specimens from the type series for each species were analyzed when available. In addition, or when types were not available, non-type museum specimens and specimens illustrated in the literature were coded to incorporate a wide range of morphological and geographical variation within each species. For all specimens, both the dorsal and ventral valves were analyzed. Specimens displaying internal characters were limited; therefore, internal characters were coded mainly from literature sources (Davidson, 1882; Cowper Reed, 1905; Foerste, 1910; Williams, 1962; Copper, 1977, 1986).

Types, figures, and other specimens examined in this study are reposited in the following institutions: Smithsonian National Museum of Natural History (NMNH), Washington D.C, USA;

Cincinnati Museum Center (CMC), Cincinnati, OH, USA; Field Museum of Natural History (FMNH), Chicago, IL, USA; Minnesota Geological Survey (MGS), Saint Paul, MN, USA; University of Iowa Museum of Natural History (UIMNH), Iowa City, IA, USA; Sedgwick Museum at Cambridge University (SMCU), Cambridge, UK; and Walker Museum, Chicago, IL, USA (WM).

Results

Among the four scenarios analyzed, our preferred model was scenario 3: the model constructed using only external traits and a phylogenetic constraint that required topologies to resolve a monophyletic Catazyginae with exception of *C. hicksi* and *C. uphami*. The inferred MCC for scenario 3 is shown in Figure 2 (log posterior probability mean −323.38). In all four scenarios (Fig. 2; Supplementary Data 2), the Bayesian framework recovered paraphyly among the subfamilies Anazyginae and Catazyginae. In the first scenario (internal + external characters, no taxonomic constraints), the estimated topology was similar to Figure 2: Anazyginae includes two distinct clades, and Catazyginae contains all previously assigned *Catazyga* species + *Zygospira kentuckiensis* (log posterior probability −327.56; Supplementary Data 2). In the second scenario (external characters only, no taxonomic constraints, log posterior probability −318.77), *Catazyga* species + *Zygospira kentuckiensis* were also estimated as a group. *Anazyga recurvirostra* recovered as a basal taxon and as the sister taxon to the derived zygospirinids, and *C. hicksi* + *Z. resupinata* + *A. calhounensis* Fenton and Fenton, 1922 resolved as a polytomy (Supplementary Data 2). The fourth scenario (external characters only, constrained to monophyletic traditional genera) recovered the lowest log posterior probability (−342.19) among all runs, and internal relationships observed in previous scenarios were not maintained (Supplementary Data 2).

Although scenario 2 recovered a slightly higher posterior probability than our preferred model (−318.77 versus −323.38), the recovery of *Z. kentuckiensis* in the Catazyginae group does not reflect a biologically reasonable topology. The placement of *Zygospira kentuckiensis* within *Zygospira* has never been questioned

within the literature. *Zygospira kentuckiensis* is the largest zygospirinid known (Sproat and McLeod, 2023), and the fact that this species was estimated to belong within Catazyginae in scenarios 1 and 2 suggests that the size of the shell (Table 2) may have been overly influential in resolving this topology in these models. Consequently, our preferred phylogenetic framework for *Anazyga* is scenario 3, which imposes a phylogenetic constraint of a monophyletic Catazyginae (scenario 3; see Fig. 2). With this constraint imposed, *Z, kentuckiensis* groups appropriately with other *Zygospira* species, and thus this is our preferred topology for systematic revision.

There were no scenarios in which the set of species attributed to *Catazyga, Anazyga*, or *Zygospira* in the recent revisions (e.g., the middle column of Table 2) resolved as monophyletic groups. *Catazyga* would form a monophyletic assemblage if *C. hicksi* and *C. uphami* are excluded from the genus. In all scenarios, anazygid clades included a mix of species previously assigned to *Anazyga* and *Zygospira*. Therefore, the validity of *Anazyga* and *Zygospira* as discrete monophyletic entities is not supported. Consequently, the best supported systematic interpretation transfers *Anazyga* species to *Zygospira*, as indicated in Figure 3.

The predicted highest mean posterior probability estimate for the clade's origination was during the late Sandbian Stage, around 453.48 Ma. The origin of both subfamilies was estimated to have occurred in the Katian Stage Slice 1 while the Anazyginae group is estimated to have originated 452.68 Ma, which is slightly before the Catazyginae estimate of 452.25 Ma. The predicted diversification rate for the entire family was relatively low (mean 0.16); whereas the turnover rate was higher (mean 0.82).

Skyline model (Fig. 4; Table 4) predicted higher speciation and extinction rates for intermediate stage slices (Katian 2 and Katian 3). Katian 4 exhibited the lowest speciation and extinction rates, indicating a decline in speciation within the clade. Biodiversity (the counted number of lineages) was estimated to be the highest at Katian 3 and early Katian 4.

Discussion

Recognition of clades. Phylogenetic analysis resolved the genera into two clades that coincide with the two subfamilies proposed by Davidson (1882), Copper (1977), and Baarli et al. (2022): (1) Catazyginae (Fig. 2), encompassing a monophyletic group of *Catazyga* species, and (2) Anazyginae (Fig. 2), including the species historically assigned to *Anazyga* and *Zygospira* plus two species formerly assigned to *Catazyga*: *Catazyga hicksi* and *C. uphami*. Catazyginae comprises all other known *Catazyga* species and is supported by finely ribbed, biconvex, pentagonal shells. Within all phylogenetic scenarios analyzed, Catazyginae was clearly distinct from Anazyginae. Anazyginae includes both *Anazyga* and *Zygospira* species that have strong costae, plicated outline, and prominent fold and sulcus. In all analyzed scenarios, the group was largely monophyletic (Fig. 2; Supplementary Data 2). In the most probable scenario, two sister groups were recovered within Anazyginae, one including the type species of *Anazyga*, *A. recurvirostra*, and the other including the type species of *Zygospira*, *Z. modesta* (Fig. 2). However, both clades within Anazyginae included a mix of species assigned to both *Anazyga* and *Zygospira*, rendering both genera polyphyletic as recently circumscribed. Therefore, a systematic revision is proposed in which *Anazyga* is synonymized with *Zygospira*, with revised species assignments indicated in Figure 3 and Table 1. Previous phylogenetic (Baarli et al., 2022) and early
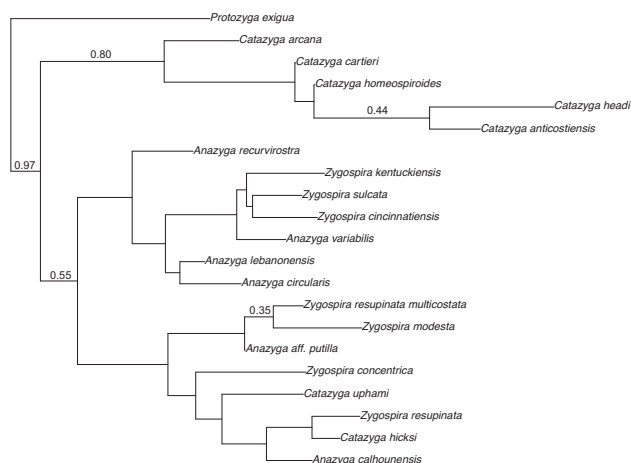
Figure 2. MCC tree Bayesian phylogeny estimated using external data and with the partial *Catazyga* clade constraint (scenario 3) for the subfamily Anazygidae under the fossilized birth–death model. Log posterior probability: −323.38. Posterior probabilities higher than 0.30 are labeled. Taxonomic nomenclature correlates with the second column on Table 1.
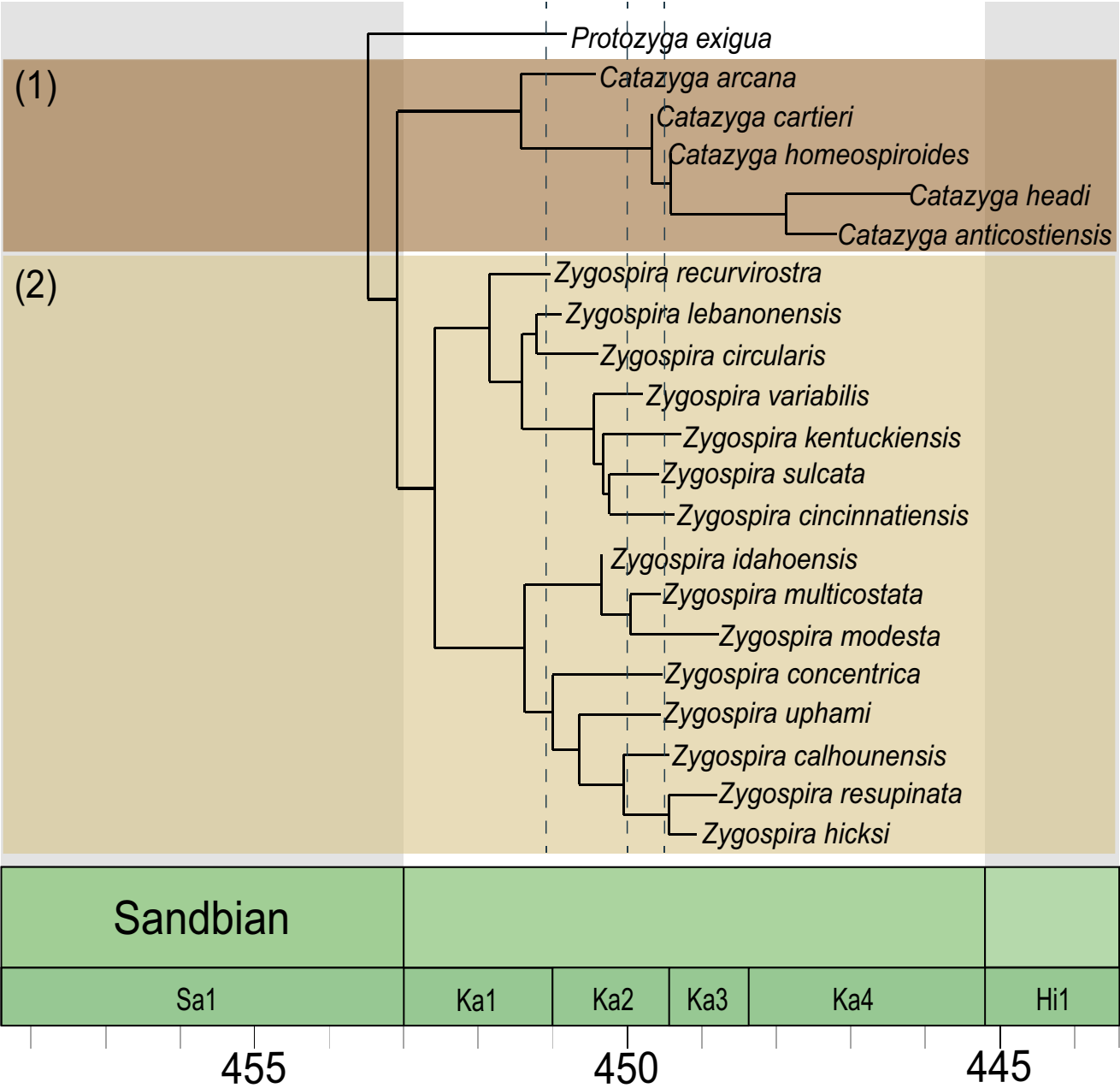
Figure 3. Time-calibrated phylogeny of the Anazygidae based on results of Bayesian phylogenetic analysis with revised systematic interpretation. Evolutionary relationships and branch lengths are scaled to geologic time. X-axis reflects units of time in millions of years (Myr). (**1**) Represents the Catazyginae group. (**2**) Represents the Anazyginae group. Taxonomic nomenclature correlates with the third column on Table 1.

systematic studies (Hall, 1862; Hall and Clarke, 1894; Copper, 1977) also expressed concerns about the validity of *Anazyga* and *Zygospira* as discrete evolutionary entities. Our results suggest that some species previously assigned to *Anazyga* may be ancestral to later forms of *Zygospira*, as predicted by Copper (1977).

The overlapping evolutionary signal within Anazyginae is interpreted as a response to the typical external anatomy shared by all anazyginid species related to the size, folding, and striae in the shells. However, some species previously assigned to *Anazyga* share internal traits with catazyginid species, specifically the directionality of the jugum relative to the spiralia (Hall and Clarke, 1894; Copper, 1977). This internal similarity likely represents the pleisiomorphic condition of Anazygidae in general as it is expressed in the oldest

members of both subfamilies (Figs. 2 and 3). The close and sometimes overlapping relationship among the three traditional genera indicates that the division of the family into three monophyletic genera is not supported by evolutionary relationships among the species.

The incorporation of internal traits in the phylogeny does not improve resolution of the evolutionary relationships in the group in our analysis (Supplementary Data 2). Instead, tree support is reduced and resolution declines. In fact, one noticeable outcome is the positioning of *Zygospira kentuckiensis* among the Catazyginae clade, an outcome highly inconsistent with overall shell morphology that appears to be influenced primarily by the larger size of the shell. When internal traits are excluded from the data matrix,
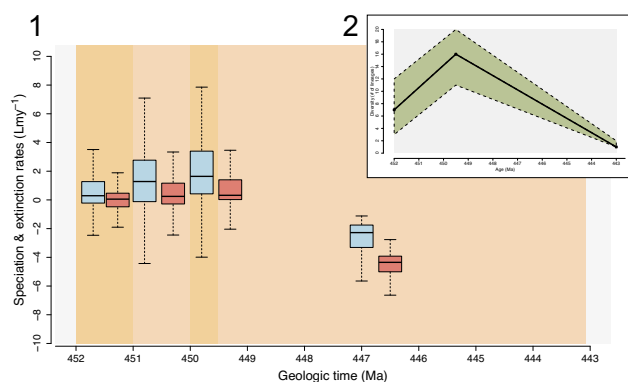
Figure 4. (**1**) Boxplot of estimated birth (speciation) and death (extinction) rates in lineages per million years (Lmy^{-1}). Speciation rates are shown in blue boxes, and extinction rates in red. Thick horizontal lines indicate median values. The four analyzed time intervals are highlighted by the tan and light tan rectangles. 452–451 Ma (Chatfieldian, Sandbian 2–Katian 1); 451–450 (Katian 2, Edenian); 450–449.7 (Katian 3, Maysvillian); 449.7–443 (Katian 4–Hirnantian, Richmondian and Gamachian). (**2**) Diversity through time, counts represent the number of branches (lineages) during three Late Ordovician stages: Sandbian (452 Ma), Katian (449.7 Ma), and Hirnantian (443 Ma).

Table 4. Estimated Skyline median speciation and extinction rates for the four analyzed time intervals. Interval 1: Chatfieldian (Sandbian 2 and Katian 1 stage slices); Interval 2: Edenian (Katian 2); Interval 3: Maysvillian (Katian 3); Interval 4: Richmondian (Katian 4) and Gamachian (Hirnantian) Stage.

Estimated rate	Interval 1	Interval 2	Interval 3	Interval 4
Mean speciation rate	1.725	0.946	4.716	−0.330
Mean extinction rate	1.006	−0.375	3.149	−2.132
Mean preservation rate	−0.210	0.081	0.641	−0.525

the analysis recovers a more resolved phylogenetic tree with stronger tree support (Supplementary Data 2). In the latter case, the monophyly in Catazyginae is still maintained (posterior probability −318.77). Taking that into account, our preferred phylogenetic tree includes a clade constraint in Catazyginae, which consists of five *Catazyga* species: *C. arcana*, *C. cartieri* Cooper and Kindle, 1936, *C. homeospiroides*, *C. anticostiensis* (Billings, 1862), and *C. headi* Billings, 1862. Two species previously assigned to *Catazyga*, *Catazyga hicksi* and *Catazyga uphami*, are also not included in Catazyginae; these two species were, in fact, first described as *Zygospira* spp. and exhibit the diagnostic size and ornamentation characters of *Zygospira* (Winchell and Schuchert, 1892; Cowper Reed, 1905). Hence, they are transferred to *Zygospira* herein.

Evolutionary patterns. Clade origination is inferred to have occurred around 453 Ma, during the late Sandbian Age (Fig. 3). Results indicate that anazygids underwent a basal division into the two subfamilies during the early Katian. Within Anazyginae, the clade including *Zygospira recurvirostra* diversified first, becoming more abundant and widespread in the Katian 1 and Katian 2 stage slices (Chatfieldian to Edenian). The clade including *Zygospira modesta* diversified mainly during the Katian 2 slices (Edenian to basal Maysvillian). Catazyginae was less diverse, but cladogenetic events extended from the late Chatfieldian through Richmondian (stage slices Katian 1 through 4). *Catazyga* and *Zygospira* became abundant, sometimes forming shell pavements across the basins at

specific horizons (Copper, 1977; Harper et al., 2017), such as those observed by Bretsky (1969) and Copper (1982).

Anazygid speciation and extinction rates indicate a biodiversification event during the middle Katian Stage, followed by a decline in both speciation and extinction rates (Fig. 4). Rates reached their maximum during the Maysvillian (Katian 3), causing a biodiversity accumulation by the early late Katian (Fig. 4). The diversity decline observed during the Richmondian and later (Katian 4 and Hirnantian Stage) is explained by a decline in speciation rates; reducing the number of origination events led to the clade's downfall (Fig. 4). The radiation of *Zygospira* and *Catazyga* reached its peak during the Katian 3 Stage (Fig. 4). This finding is coordinated with higher speciation rates present at the last peak of diversification of the latest part of the Ordovician Radiation before the diversity decline by the late Katian (Rasmussen et al., 2019). Anazygid biodiversification has been previously examined (Copper, 1977, 2001; Sproat and McLeod, 2023), and these results documenting their rapid but brief radiation conform to the diversification patterns predicted by earlier studies (Copper, 1977, 2001; Harper et al., 2017).

Model implications. Previous studies have interpreted *Anazyga* as an earlier genus and *Zygospira* to have occurred temporally later (Davidson, 1882; Hall and Clarke, 1894; Copper, 1977, 2001; Sproat and McLeod, 2023). However, these results do not conform with that perspective. Instead, *Zygospira* is reconstructed as a diverse clade with an ancestor–descendent relationship among species previously assigned to *Anazyga*, such as *A. recurvirostra*, and other anazyginids. Anazygid species are predominantly present from the late Sandbian to early Katian Stage, and *Catazyga* is the only genus that persisted throughout and beyond Katian 4 (Fig. 3).

Internal characters, such as lophophore support structures have historically been given strong evolutionary significance in atrypide brachiopods (Hall, 1862; Hall and Clarke, 1894; Copper, 1977). Unfortunately, data on the internal morphology of anazygid species, notably their brachidia, are scarce (Sproat and McLeod, 2023). Serial sections of shell interiors for *Zygospira modesta*, *Z. kentuckiensis*, *Anazyga recurvirostra*, and *Catazyga headi* are the only ones available at the present (Copper, 1977; Sproat and McLeod, 2023), limiting the potential for incorporation of brachidia into phylogenetic analyses. Because interior data are unknown for most of the focal species, anazygid species have been classified by most previous authors primarily by their external morphology (such as shell size, outline, beak size and angle, and costae appearance) and their stratigraphic range in the early Paleozoic (e.g., Copper, 1977) coupled with assumptions about interior morphology. In our analyzed scenarios, incorporation of limited internal character data resulted in lower tree support, but further studies on the interior of this lineage are needed for a comprehensive view of the range of internal shell features that it contains. Therefore, the following systematic revision is based on external-character-only phylogenetic framework.

Conclusions

The Anazygidae were a widespread and diverse clade in the Late Ordovician, and its species played an important role in ecological communities. Indeed, there are no stratigraphic units among the Edenian to Richmondian strata of eastern North America in which this clade is absent. The increase in diversification and speciation right at the end of the Ordovician Radiation suggest that anazygids might have been one of the last clades to benefit from the environmental cooling and increase in oxygenation during the interval

Table 5. Specimens examined for species that do not require taxonomic revision. *Indicates non-type specimen

Species	Museum/publication	Catalog number	Type
C. anticostiensis	USNM	PAL 94413a	*
C. anticostiensis	USNM	PAL 94413b	*
C. anticostiensis	CMNH	22638b	*
C. anticostiensis	CMNH	22538b	*
C. arcana	Williams (1962)	BB 26733	Holotype
C. headi	USNM	PAL 87052	Plesiotype
C. headi	Copper (1977)	GS 45398	*
C. headi	FMNH	PE 89339	*
C. headi	CMNH	95342	*
C. headi	CMNH	89904	*
C. headi	CMNH	89538	*
C. headi	CMNH	6182	*
C. headi	FMNH	PE 89341a	*
C. headi	FMNH	PE 89341b	*
Z. cincinnatiensis	CMNH	PE 9509	*
Z. cincinnatiensis	CMNH	28127	*
Z. cincinnatiensis	CMNH	69136	*
Z. cincinnatiensis	CMNH	19064	*
Z. cincinnatiensis	CMNH	18946	*
Z. concentrica	CMNH	19027a	*
Z. concentrica	CMNH	19027b	*
Z. concentrica	CMNH	33583	*
Z. concentrica	CMNH	18969	*
Z. kentuckiensis	USNM	PAL 511871	Plesiotype
Z. kentuckiensis	USNM	PAL 511872	Plesiotype
Z. kentuckiensis	USNM	PAL 97596	Plesiotype
Z. kentuckiensis	USNM	PAL 9748a	*
Z. kentuckiensis	USNM	PAL 9748b	*
Z. kentuckiensis	CMNH	19062a	*
Z. kentuckiensis	CMNH	19062b	*
Z. kentuckiensis	CMNH	54470a	*
Z. kentuckiensis	CMNH	54470b	*
Z. kentuckiensis	CMNH	33663a	*
Z. kentuckiensis	CMNH	33663b	*
Z. modesta	USNM	PAL 40485	Plesiotype
Z. modesta	USNM	PAL 418150	Plesiotype
Z. modesta	USNM	PAL 418149	Plesiotype
Z. modesta	USNM	ACC 175438a	*
Z. modesta	USNM	ACC 175438b	*
Z. modesta	USNM	PAL 1.22F1	*
Z. modesta	USNM	PAL 1356a	Lectotype
Z. modesta	Foerste (1910)	1356–1	*
Z. modesta	FMNH	6460	*

(*Continued*)

Table 5. (*Continued*)

Species	Museum/publication	Catalog number	Type
Z. modesta	FMNH	1496	*
Z. modesta	CMNH	64207a	*
Z. modesta	CMNH	64207b	*
Z. modesta	CMNH	69130a	*
Z. modesta	CMNH	69130b	*
Z. recurvirostra	USNM	PAL 87057	Plesiotype
Z. recurvirostra	USNM	PAL 97609	Plesiotype
Z. recurvirostra	USNM	PAL 78460	Holotype
Z. recurvirostra	USNM	PAL 24869	*
Z. recurvirostra	USNM	PAL 24871	*
Z. recurvirostra	USNM	PAL 124826	Plesiotype
Z. recurvirostra	USNM	PAL 705.3	Holotype
Z. recurvirostra	FMNH	P9509	*
Z. resupinata	USNM	PAL 2.6G5c	*
Z. resupinata	USNM	ACC 306219	*
Z. resupinata	USNM	PAL 175438	*
Z. resupinata	SUI	1874	Holotype
Z. resupinata	SUI	1873	Paratype
Z. sulcata	USNM	PAL 145059	Paratype

(Rasmussen et al., 2019; Stigall et al., 2019). The two genera within this revised classification, *Zygospira* and *Catazyga*, are shown to be monophyletic groups using Bayesian phylogenetic methods. However, species within the former genus concepts of *Anazyga* and *Zygospira* do not segregate as clades. Therefore, species previously assigned to these genera are reassigned to *Zygospira*. Some species previously ascribed to *Anazyga*, such as *Z. calhounensis*, occur basally within the clade and include more plesiomorphic features. *Catazyga* is reconstructed as a monophyletic genus, spanning almost the entire Late Ordovician. Although likelihoods calculated from different datasets cannot readily be compared in a model-fitting framework (e.g., Bayes Factors), it is interesting to note the phylogenetic trees with the highest posterior probability recovered were those constructed without internal traits. However, further work in examining the internal morphology of species within this lineage may result in a more detailed and finer scaled framework. In addition to difficulty imposed by the small size, many shared traits among members of the clade such as the position of the spiralia, overall shape of the spirals, and valve outline are extremely variable (Hall and Clarke, 1894) and often poorly documented. This makes it more complex to fully reconstruct evolutionary relationships and establish a taxonomic framework with confidence. Nevertheless, phylogenetic estimation of evolutionary relationships is the first step to understanding how ecological and biogeographical factors might have impacted the apparent evolutionary convergence in the clade.

Systematic paleontology

The original description and later revisions are sufficient to characterize some anazygid species; species that do not require additional revision or description are listed in Table 5. The original and subsequent descriptions of these species may be combined with the character data in Supplementary Materials to provide enhanced diagnoses. Revised generic descriptions for all genera and species descriptions for seven species are presented in the following. The genera *Anazyga* and *Zygospira* are synonymized as *Zygospira*. *Zygospira* aff. *Z. putilla* Ross, 1959 is recognized as a new species, *Zygospira idahoensis* Vilela-Andrade n. sp. The subspecies *Zygospira resupinata multicostata* Howe, 1965 is elevated in the taxonomic rank to an independent species, *Zygospira multicostata* Howe, 1965.

Class **Rhynchonellata** Williams et al., 1996
Order **Atrypida** Rzhonsnitskaya, 1960
Family **Anazygidae** Davidson, 1882
Subfamily **Anazyginae** Davidson, 1882

Genus ***Zygospira*** Hall, 1862
Figures 1, 5, 6

Type species. *Producta (Atrypa) modesta* Say in Hall, 1847. Katian, Cincinnati, Ohio, and Nashville, Tennessee, regions, U.S.A.

Other species. The type horizon and locality of *Anazyga calhounensis* Fenton and Fenton, 1922 is unknown, neotype from the Kimmswick Limestone in Batchtown, Illinois, U.S.A; *Zygospira circularis* Cooper, 1956 from the upper Carters Formation, Franklin, Tennessee, U.S.A., and Saturday Mountain Formation, Lemhi Range, Idaho, U.S.A; *Zygospira lebanonensis* Cooper, 1956 from the Lebanon Formation, Shelbyville, Tennessee, U.S.A, and Saturday Mountain Formation, Lemhi Range, Idaho, U.S.A; *Zygospira* aff. *Z. putilla* Ross, 1959 = *Zygospira idahoensis* n. sp. from the Saturday Mountain Formation in Lemhi Range, Idaho, U.S.A; *Atrypa recurvirostra* Hall, 1847 from the Trenton Group, Minnesota, New Jersey, New York, and Virginia, U.S.A, Red River Formation,
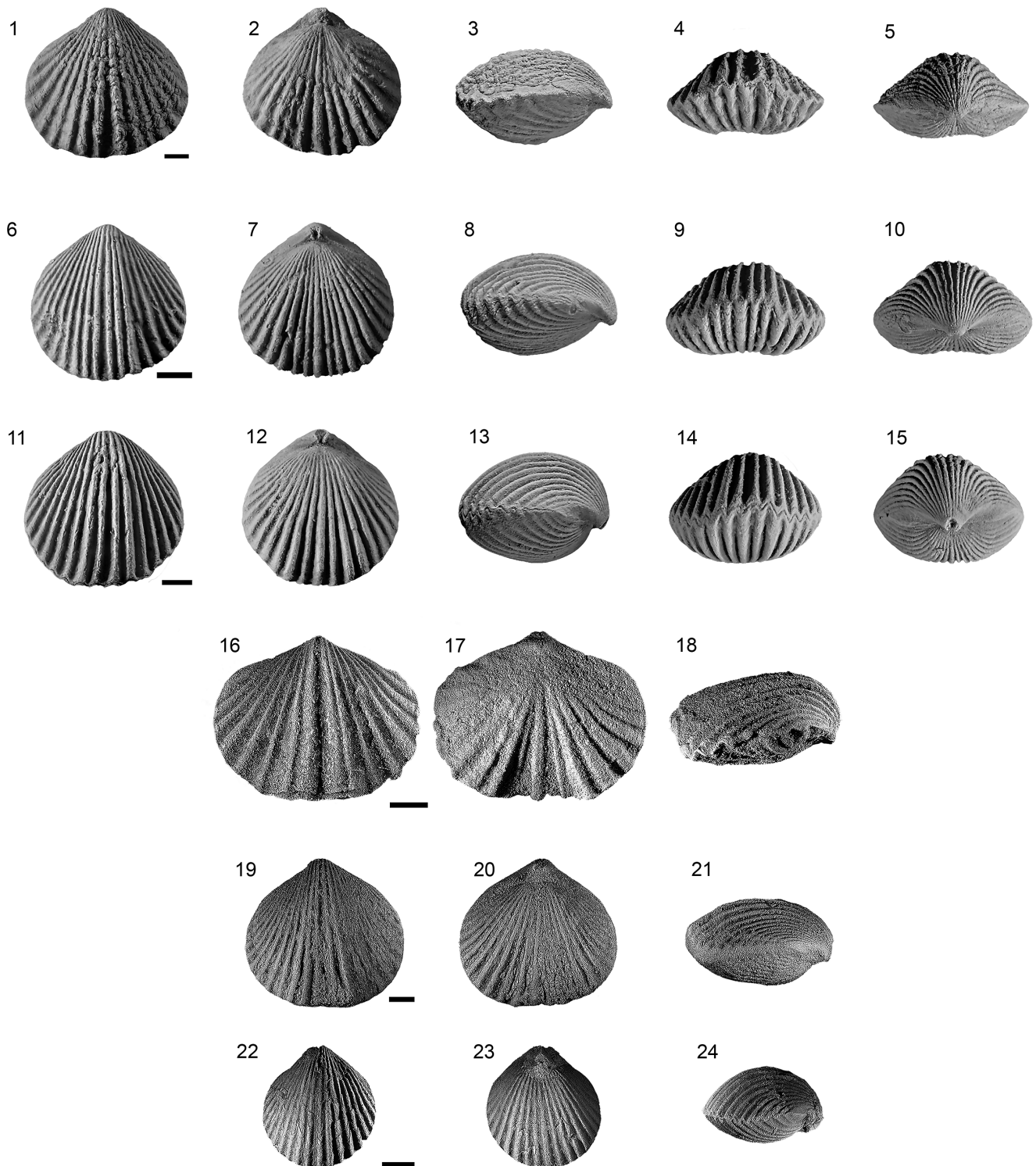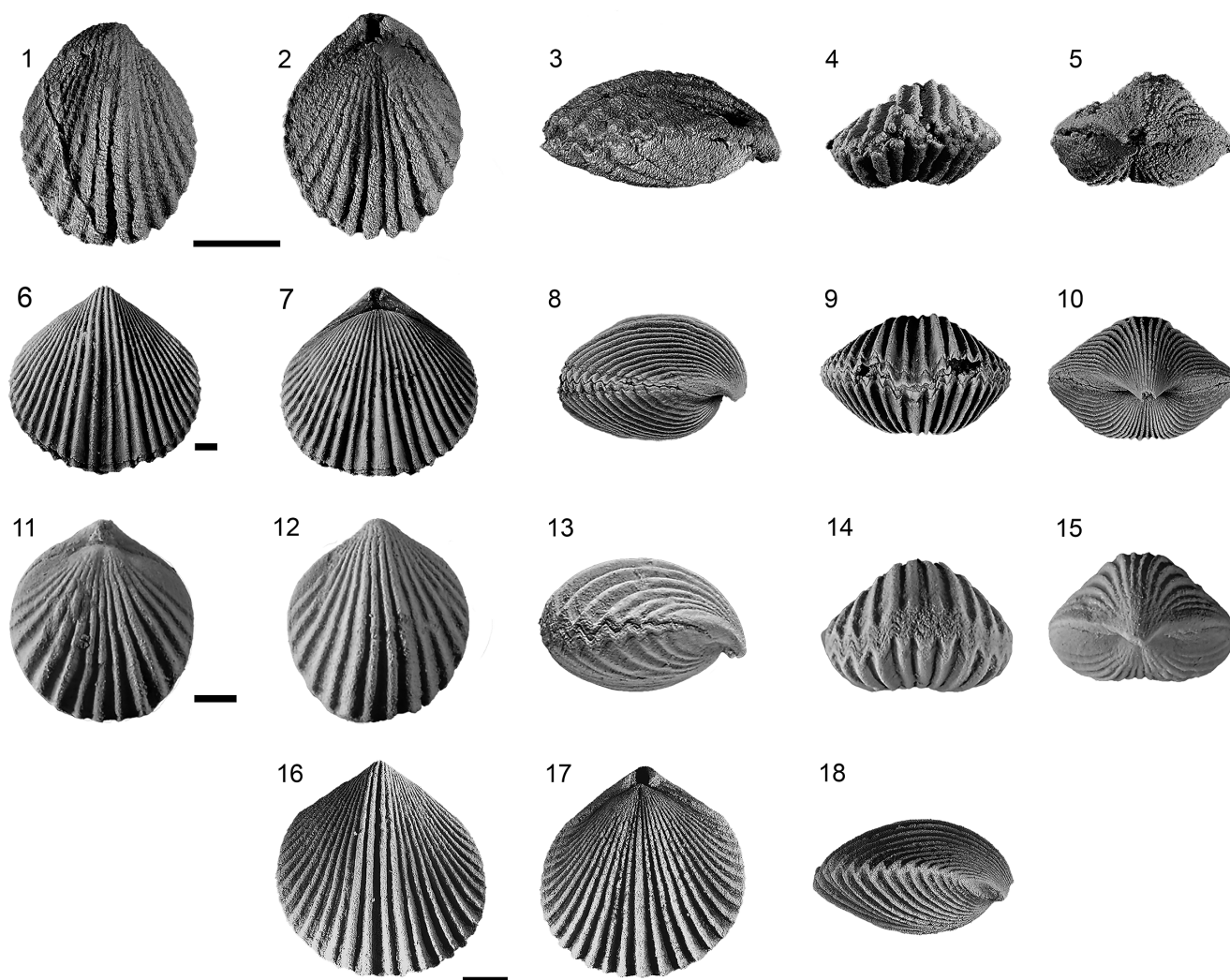
Figure 5. (**1–5**) *Zygospira variabilis* Fenton and Fenton, 1922 (holotype) FMNH UC25861. (**1**) Ventral, (**2**) dorsal, (**3**) lateral, (**4**) anterior, and (**5**) posterior views. (**6–15**) *Zygospira variabilis fountainensis* Fenton and Fenton, 1922. (**6–10**) (Cotype) FMNH UC27455A. (**6**) Ventral, (**7**) dorsal, (**8**) lateral, (**9**) anterior, and (**10**) posterior views. (**11–15**) (Cotype) FMNH UC27455B. (**11**) Ventral, (**12**) dorsal, (**13**) lateral, (**14**) anterior, and (**15**) posterior views. (**16–18**) *Zygospira cincinnatiensis* James in Meek, 1873 (plesiotype) CMC19064. (**16**) Ventral, (**17**) dorsal, and (**18**) lateral views. (**19–21**) *Zygospira kentuckiensis* Nettelroth, 1889 (plesiotype) CMC54470. (**19**) Ventral, (**20**) dorsal, and (**21**) lateral views. (**22–24**) *Zygospira recurvirostra* Hall, 1847 (plesiotype) FMNH20757a. (**22**) Ventral, (**23**) dorsal, and (**24**) lateral views. Scale bars = 1 mm.

Montana, U.S.A, and Cynthiana Formation, Kentucky, U.S.A; *Zygospira variabilis* Fenton and Fenton, 1922 from the Plattin Formation of Missouri, and Decorah Formation, Minnesota, U.S.A; *Zygospira cincinnatiensis* James in Meek, 1873 from the Hudson River Group, Kope, Fairview (Fairmount Member), and Mt. Auburn formations in Cincinnati, Ohio, U.S.A; *Zygospira concentrica* Ulrich, 1879 from the Kope, Lorraine, and Bellevue formations in Cincinnati, Ohio, U.S.A; *Zygospira kentuckiensis*

Figure 6. (**1–5**) *Zygospira idahoensis* n. sp. (holotype) USNM PAL 133263. (**1**) Ventral, (**2**) dorsal, (**3**) lateral, (**4**) anterior, and (**5**) posterior views. (**6–10**) *Zygospira multicostata* Howe, 1965 (holotype) USNM PAL 145054. (**6**) Ventral, (**7**) dorsal, (**8**) lateral, (**9**) anterior, and (**10**) posterior views. (**11–15**) *Zygospira calhounensis* Fenton and Fenton, 1922 (neotype) FMNH UC27458A. (**11**) Ventral, (**12**) dorsal, (**13**) lateral, (**14**) anterior, and (**15**) posterior views. (**16–18**) *Zygospira resupinata* Wang, 1949 (holotype) SUI1874. (**16**) Ventral, (**17**) dorsal, and (**18**) lateral views. Scale bars = 1 mm.

Nettelroth, 1889 from the Waynesville Formation in Jefferson, Marion, and Oldham counties, Kentucky, U.S.A, Reedsville Formation near Ewing, Virginia, U.S.A, and Manitoulin Island in Canada; *Zygospira modesta* Hall, 1847 from the Hudson River Group, Fairmount, and Corryville formations in Cincinnati, Ohio, U.S.A, Liberty Formation in Oxford, Ohio, U.S.A, Arnheim Formation in Nashville, Tennessee, and Waynesville, Ohio, U.S.A, and Whitewater Formation in South Gate, Indiana, U.S.A; *Zygospira resupinata multicostata* Howe, 1965 = *Zygospira multicostata* Howe, 1965 from the Montoya Group, El Paso, Texas, U.S.A; *Zygospira resupinata* Wang, 1949 from the Maquoketa Formation, Jackson County, Iowa, U.S.A, Elkhorn Formation, in Hamburg, Indiana, and Eaton, Ohio, U.S.A; *Zygospira sulcata* Howe, 1965 from the Montoya Group, El Paso, Texas, U.S.A; *Zygospira uphami* from the Galena Group in Weisebach's Dam, Spring Valley, and Wykoff and Fountain, Minnesota, U.S.A; and *Zygospira hicksi* Cowper Reed, 1905 from the Slade Formation, Haverfordwest, Wales. For discussion of additional species, see Copper (1977) and Sproat and McLeod (2023).

Diagnosis. Small biconvex shells. Outline subcircular to elliptical. Surface plicated with fine to strong ribs. Ventral valves often have an accentuated median costa, fewer ribs, and elevated marginal ridges from the sulcus. Dorsal valves composed of double radiating ribs and a deep median costa. Concentric growth lines usually absent. Distinct and curved beak, often with an acute angle from the ventral shell. Usually prominent fold and sulcus, resulting in a wide commissure. Acute dorsal apical area, narrow and prominent ventral umbo, associated with a small and triangular delthyrium. Crura are oppositely long, extending anteriorly toward a dorsally oriented spiralia. The number and shape of whorls vary, and the presence of dental cavities is observed.

Occurrence. Early Late Ordovician (Sandbian 2–Katian 4 stages), mostly abundant in the strata of central to eastern North America, with possible occurrences reported in Wales and Australia. In the United States, *Zygospira* is abundant and diverse in rocks from the Katian 2 to early Katian 4 stages (Edenian to early Richmondian stages in North American nomenclature).

Remarks. Zygospira was proposed by Hall (1862) and externally defined as "shell bivalve, equilateral, inequivalve, surface plicate in the typical species; a sinus in the dorsal valve" (Hall, 1862, p. 24)

with the typical form being *Zygospira modesta.* The internal morphology of *Zygospira* was described as being similar to *Atrypa,* another atrypide genus, that had similar spiralia. *Anazyga* was proposed as a distinct genus by Davidson (1882) on the basis of its smaller size, oval outline, and whorls positioned in the same direction as observed in *Zygospira.* However, shortly thereafter, Hall and Clarke (1894) noted that the morphological features of *Zygospira,* especially the jugum position, supported synonymizing *Anazyga* with the older *Zygospira* (Hall and Clarke, 1894; Sproat and McLeod, 2023).

Eighty years later, uncertainties regarding Anazygidae came back into debate. Copper (1977) restored *Anazyga* Davidson, 1882 as a discrete genus on the basis of size, the direction of the spiralia, and rib appearance. Copper (1977, p. 24) reassigned basal zygospirid forms to *Anazyga* Davidson, 1882 on the basis of *Zygospira* "having coarser ribs, more strongly carinated shells, with differentiated mid and lateral ribs, and planoconvex-ventribiconvex shells." Williams et al. (1996) analyzed zygospirid specimens and showed that biconvexity and accentuated costae are predominant in both *Anazyga* and *Zygospira,* and argued that these features should not be used to distinguish the two genera.

Sproat and McLeod (2023) recently recharacterized *Zygospira* on the basis of its coarse external ribs and its mediodorsally directed spiralia according to serial section data. The studies of both Copper (1977) and Sproat and McLeod (2023) constrained the genus *Zygospira* to comprise stratigraphically younger species but also noted that the lack of data on the internal characters for most species was problematic. However, these species do not optimize as clades in the phylogenetic analyses presented herein, which suggests *Anazyga* and *Zygospira* are not discrete evolutionary entities.

Copper (1977) also pointed to differences in internal morphology of the type species of *Anazyga* and *Zygospira* such as having a larger number of whorls and the jugum being positioned posterodorsally. Nonetheless, the availability of internal data is not sufficient to show a phylogenetic signal separating the clades (see Discussion). Thus, although the type species of *Anazyga recurvirostra* and *Zygospira modesta* show distinct jugal processes, the variability observed within *Zygospira* itself (Hall and Clarke, 1894; Howe, 1965; Sproat and McLeod, 2023) and external morphological features indicate that the two type species may be variations of the same lineage.

Notably, in the current study, neither genus optimizes as a clade within the best supported phylogenetic reconstruction, and tree support is reduced when constraints are emplaced to force the species into monophyletic groups reflecting historical species associations (Scenario 4). Consequently, our analyses strongly support synonymy of *Anazyga* with *Zygospira.* Therefore, all valid species previously attributed to *Anazyga* are transferred to the genus *Zygospira* herein.

Zygospira idahoensis Vilela-Andrade new species
Figure 6.1–6.5

1913 *Atrypa putilla* Savage, p. 85, pl 4, fig. 25.
1959 *Zygospira aff. putilla* Ross, p. 457, pl. 56, figs 11, 12.

Holotype. USNM PAL 133263 (figured), from the Late Ordovician Saturday Formation, Lemhi Range, Idaho, U.S.A.

Diagnosis. Elongate, dorso-biconvex, rectimarginate, strongly sulcate shells. Few homogenous ribs, strongly carinated. Dorsal valve covered by the umbo, strong shell convexity on each side of the sulcus, and growth lines sometimes present. Short and curved beak. Large, distinct, and round delthyrium.

Occurrence. Sandbian, Late Ordovician (Mohawkian Series) of the United States. Hudson River Group in Missouri, U.S.A; Saturday Mountain Formation (Sandbian 2) in Lemhi Range, Idaho, U.S.A.

Description. Average length of 3.7 mm, width of 3.31 mm, and height of 1.94 mm. Biconvex, elongate shells, average number of costae is 14 in the ventral valve and 12 in the dorsal valve. Strong and distinct simple costae radiating anterior to the umbo, lack of concentric ornamentation. Prominent curved umbo, projecting in a 55° angle from the dorsal shell. Interior not examined.

Etymology. The specific name *idahoensis* comes from Latin. The name is derived from the toponym in which the specimen was found, Idaho, U.S.A. followed by the suffix *ensis,* meaning "place" or "location."

Additional materials. USNM PAL 133262, USNM PAL 133263.

Remarks. Hall and Clarke (1894) erected *Zygospira putilla* for Silurian specimens that shared morphological similarities, notably plications on the valves and the posteriorly directed spiralia, with the genus *Zygospira.* Amsden (1974) synonymized *Zygospira putilla* and *Atrypa praemarginalis* Savage, 1913 and assigned this species to *Eospirigerina* on the basis of ontogenetic variation apparent in studied specimens and overall shell size. *Eospirigerina* is a member of the subfamily Spirigerininae, which is not closely related to the Anazyginae, which includes *Zygospira* (Baarli et al., 2022). Thus *Z. putilla* Hall and Clarke, 1894 is now included within *Eosprigerina praemarginalis* and is excluded from the monophyletic concept of *Zygospira* developed herein. The specimens examined by Amsden (1974) and Ross (1959) from the Edgewood Formation are also eospirigerinid forms (see plate 18, figs. 1a–j and plate 19, figs. 1a–h in Amsden, 1974) and members of a clade exclusive of the Anazygidae.

Separately, Ross (1959) identified *Z. putilla*-like specimens from the Saturday Mountain Formation (Sandbian 2 Stage) in Idaho as atypical *Z. putilla* specimens. These atypical specimens were identified as *Zygospira aff. Z. putilla* Hall and Clarke, 1894. Morphological affinities shared between the Saturday Mountain specimens and *Zygospira recurvirostra, Z. circularis,* and *Z. lebanonensis* were noted.

The *Zygospira aff. Z. putilla* specimens described by Ross (1959) differ from typical *Z. putilla* Hall and Clarke 1894 forms by their unusual elongate outline, small size, strong ribs, lack of concentric ornamentation, presence of double-ribbed valves, and occurrence in Late Ordovician (Mohawkian) strata. *Zygospira aff. Z. putilla* differs from eospirigerinids in not having radial growth lines, having small sizes (3–5 mm), and being found in older rocks (down to the Sandbian 2 Stage Slice) than is typical of the Spirigerininae clade that becomes more common in the latest Ordovician (Hirnantian) (Baarli et al., 2022). Therefore, the *Zygospira* aff. *Z. putilla* specimens described by Ross (1959) do not fit within the genus concept of *Eospirigerina* but rather fit within the current genus concept of *Zygospira.* In our phylogenetic analysis, *Zygospira* aff. *Z. putilla* specimens resolved as a sister taxon to *Zygospira multicostata* and *Zygospira modesta.* Given that the name *Zygospira putilla* still refers to other unrelated specimens, we herein erect a new taxon, *Zygospira idahoensis,* to include the species assigned to *Zygospira* aff. *Z. putilla* by Ross (1959).

Zygospira multicostata Howe, 1965
Figure 6.6–6.10

1965 *Zygospira resupinata multicostata* Howe, p. 653, pl. 81, figs. 1–8.
1997 *Zygospira resupinata multicostata* Jin et al., p. 40, pl. 30, figs. 1–21.

Type specimens. USNM PAL 145054 (holotype) and USNM PAL 145055, USNM PAL 145056, and USNM PAL 145057 (paratypes) from the Aleman Limestone of the Late Ordovician Montoya Group (Katian 2 Stage Slice, Cincinnatian, Edenian), Hueco Mountains, El Paso, Texas, U.S.A.

Diagnosis. Elliptical in outline, biconvex in lateral profile, parasulcate, gently folded shells. Numerous strong ribs, presence of double ribs, and ventral accentuated median costae. Remarkable resupination on the dorsal and ventral shells, i.e., ventral folding and dorsal sulcation. Short and curved beak. Small delthyrium and palintrope area, mostly covered by the curved, accentuated umbo.

Occurrence. Aleman Limestone (Katian 2) of the Montoya Group in the Hueco and Franklin Mountains, New Mexico, U.S.A; Surprise Creek (Katian 3, Maysvillian Stage) and Caution Creek (Katian 4, early Richmondian Stage) formations in the Hudson Bay Lowlands of Manitoba, Canada.

Description. Average length of 7.05 mm, width of 6.75, and height of 4.74 mm. Costae numerous, average dorsal costae number of 28.73. Costae originating anterior to the umbo. In the dorsal valve, deep median costae and double ribs are often observed. The ventral valve has accentuated median costae and very gentle sulcus. Shell resupinate. Internal characters unknown.

Etymology. Following the description of *Zygospira resupinata multicostata* (Howe, 1965), the subspecific name *multicostata* comes from Latin and refers to the numerous costae of this species, the prefix *multi* meaning "many" and the adjective *costatus* meaning "ribbed."

Remarks. Howe (1965) described this taxon as a subspecies of *Zygospira resupinata*. However, *Z. multicostata* is morphologically distinct and resolves in a distant position from *Z. resupinata* in the phylogenetic analysis. Thus, *Z. multicostata* is raised to species level herein. *Zygospira multicostata* is distinguishable from *Zygospira resupinata* Wang, 1949 by its larger number of ventral and dorsal costae (27–28 to 16–19, respectively), greater resupination, larger size, and thicker shells as discussed by Howe (1965) and Sproat and McLeod (2023). When compared with the two most common contemporaneous zygospirinids from the Cincinnati basin, *Zygospira modesta* and *Z. kentuckiensis*, *Z. multicostata* shows gentler fold and sulcus, resupination, and more ribs (>25). Jin et al. (1997) noted that Canadian forms of the species are more elongate and have a larger number of ribs (25–35). *Zygospira multicostata* is placed within *Zygospira* because of its plicate shells, small size, double-ribbed costae, and distinct apical region. On the basis of a single specimen, illustrated by Jin et al. (1997, pl. 30, fig. 21) from the Hudson Bay Lowlands, Sproat and McLeod (2023) noted that the calcified spiralia of *Z. multicostata* has a dorsomedial directionality, which is consistent with *Zygospira* (Hall, 1847; Davidson, 1882).

Zygospira calhounensis Fenton and Fenton, 1922
Figure 6.11–6.15

1922 *Zygospira calhounensis* Fenton and Fenton, p. 76, pl. 2, figs. 4–6.
1977 *Anazyga calhounensis* Copper, p. 305.

Type specimens. The original holotype (FMNH UC27457) is now lost. FMNH UC27458A, a complete, articulated specimen from the type series, is herein designated as the neotype. The neotype and paratype specimens, including FMNH UC27458B, are from the Kimmswick Limestone in Batchtown, Illinois

Diagnosis. Shell size varying in length and width from 4 to 6 mm, oval outline (length > width), no evident median costae or prominent rib, medium to fine parallel ribs originating near the umbo. Concave umbo projecting on top of the dorsal valve, round delthyrium, distinct palintrope area. Weak fold and sulcus, dorsal valve almost flat, with no clear prominent costae. Shell wider toward anterior, very rotund anterior area.

Occurrence. Maysvillian, Late Ordovician (Cincinnatian Series, Katian Stage) in the United States. Type specimens collected from the Kimmswick Limestone (Katian 2 Stage) in Batchtown, Illinois, U.S.A.

Description. Average length of 5.04 mm, width of 4.57 mm, and height of 3.68 mm. Elliptical (or oval) shell, unisulcate anterior commissure. Average number of costae on the dorsal valve is 18.25. Medium fine ribs originating near the umbo, overall biconvex valves. Absence of apparent growth lines, high angled umbo, with round delthyrium opening. No evident dorsal median costae, absence of double ribbing on the dorsal valve. Fold and sulcus very weak. Internal characters are unknown.

Remarks. Although similar in rib orientation and appearance, *Zygospira calhounensis* is distinguished from *Z. circularis* by the overall outline, which is longer than wide, and by the rotundity of the anterior area (see Fig. 5.3–5.8). The commissure deflection is not influenced by the folding but is, nonetheless, significantly wider than the rest of the shell.

Zygospira circularis Cooper, 1956

1956 *Zygospira circularis* Cooper, p. 670, pl. 141C, figs. 18–21.
1977 *Anazyga circularis* Copper, p. 305.

Type specimens. USNM PAL 111374a (holotype) from the Carters Formation in Tennessee, U.S.A; USNM PAL 133267 and 133268 (plesiotypes) from the Saturday Mountain Formation, Idaho, U.S.A.

Diagnosis. Shell size varying in length and width, semi-circular shell, very short in height (depth), inconspicuous ribs, unusually large number of ribs for genus, ribs spacing distance is continuous throughout the valves. No apparent median costae, ribs uniform in size and appearance. Gentle ventral fold and sulcus, almost flattened toward maximum convexity in dorsal valve.

Occurrence. Sandbian and Katian stages, Late Ordovician in the United States. Specimens found in the Carters Formation (Katian 1) in Tennessee, U.S.A (holotypes) and in the Saturday Mountain Formation (Sandbian 2) in Idaho, U.S.A (plesiotypes).

Description. Dorso-biconvex semicircular to quadrate shells ranging from 3.0 to 4.5 mm in length and width. An average of 22 distinctive but not prominent ribs on the dorsal and ventral valves. Absence in growth lines, weak fold and sulcus originating anterior to the umbo, parasulcate anterior commissure, dorsally flattened shells, with anterior and posterior fold deflection of 0.80 and 0.10 mm, respectively. Small, low-angled umbo, barely covering the dorsal valve. Internal characters unknown and not examined herein.

Remarks. Zygospira circularis differs from other zygospirinids in its almost completely circular outline and the lack of a prominent median costa on the dorsal valve. In the original description, Cooper (1956, p. 33) differentiated *Z. circularis* from other species as "resembling *Z. variabilis* Fenton and Fenton but differs in its more rounded outline and indistinctness of the fold and sulcus." However, *Z. circularis* is not as rotund as *Z. variabilis*, it has more numerous and weaker ribs, and the umbo is not as well developed and projected. Otherwise, *Zygospira variabilis* has a more typical *Zygospira* shape, with stronger and well-spaced ribs, and fold and sulcus. Ross (1959) described *Z. circularis* as being similar to *Z. resupinata* Wang, 1949 by also having clear, distinct ribs. *Zygospira circularis* has a typical morphology (outline, overall rib morphology, and size) observed in basal anazyginids, such as *Z. sulcata* Howe, 1965 and *Z. concentrica* Ulrich, 1879 from the Upham Limestone in New Mexico and the Kope Formation in Ohio, respectively.

Zygospira hicksi Cowper Reed, 1905

1905 *Zygospira hicksi* Cowper Reed, p. 452, pl. 23, figs. 17–19.
1977 *Catazyga hicksi* Copper, p. 312.

Type specimens. SMCU A30861 (paralectotype), SMCU A30862 (lectotype) from the Slade and Redhill formations in Cuckoo Grove Lane, Haverfordwest, Wales.

Diagnosis. Large shells with slight fold and sulcus on dorsal valve. Elliptical outline, simple radiating ribs, double ribs absent, weak deep median costae, growth lines present. Short teeth, adductor muscle fields divided by median ridge. Brachidia morphology unknown.

Occurrence. Katian Stage, Late Ordovician in Wales. Specimens found in the Slade and Redhill formations (Katian 4) in Cuckoo Grove Lane, Haverfordwest, Wales.

Description. Average length and width of 10 mm; 25–30 ribs; short, curved beak.

Remarks. Zygospira hicksi was erected by Cowper Reed (1905), who noted its circular outline and the numerous fine ribs. *Zygospira hicksi* was the second known atrypide brachiopod in the Ordovician exposures in Britain. Cowper Reed (1905) identified overall outline similarities with *Zygospira (Catazyga) headi. Zygospira hicksi* however, differs from this early catazyginid by bearing fewer ribs and having a more quadrate outline. Similar to *Z. kentuckiensis*, *Z. hicksi* is a larger zygospirinid with numerous ribs.

Zygospira lebanonensis Cooper, 1956

1892 *Hallina saffordi* Winchell and Schuchert, p. 292, pl. 34, figs. 55–58.

1894 *Zygospira saffordi* Hall and Clarke, p. 151, pl. 84, figs. 36–38.
1956 *Zygospira lebanonensis* Cooper, p. 671, pl. 142C, figs. 11–15.
1977 *Anazyga lebanonensis* Copper, p. 306.

Type specimens. USNM PAL 111377a (holotype) from the Lebanon Formation in Tennessee, U.S.A; USNM PAL 133270 (plesiotype) from the Saturday Mountain Formation in Lemhi Range, Idaho, U.S.A.

Diagnosis. Overall small shell, variable length and width. Rectangular to semicircular and biconvex valves. Ventral and dorsal valves are characterized by having strong simple, rounded costae. Small umbo and palintrope area. Strong ventral sulcus originating approximately two-thirds toward anterior of valve, containing three deep median costae and deformation progressing approximately 1 mm from the sulcus.

Occurrence. Sandbian (Late Ordovician, Mohawkian Series) stages in the United States. Lebanon Limestone (Sandbian 1) at Shelbyville, Tennessee, U.S.A; Moccasin Formation in Tennessee, U.S.A; Camp Nelson Formation in Kentucky, U.S.A; Barnhart Formation in Missouri, U.S.A; Saturday Mountain Formation (Sandbian 2) in Lemhi Range, Idaho, U.S.A.

Description. Average length of 4.2 mm, width of 4.2 mm, and height of 2.4 mm. Parasulcate anterior commissure, no prominent median costa on either valve.

Additional materials. Plesiotypes: USNM PAL 133269, USNM PAL 133270.

Remarks. Zygospira lebanonensis was first identified by Winchell and Schuchert (1892) as a terebratulid species rather than an atrypid, although the authors have highlighted the external morphological similarities between *Z. lebanonensis* and *Z. recurvirostra*. Hall and Clarke (1894) identified similarities with zygospirinids, including the development of spiral cones and lophophore's loops and an inward inclination of the apices, which are typical of *Zygospira*.

Zygospira uphami Winchell and Schuchert, 1892

1892 *Zygospira uphami* Winchell and Schuchert, p. 291.
1895 *Zygospira uphami* Winchell and Schuchert, p. 468, pl. 34, figs. 45–48.
1977 *Catazyga uphami* Copper, p. 312.

Type specimens. Neotype: MGS 8227 from the Late Ordovician Galena Formation, Weisebach Dam, Spring Valley, Minnesota.

Diagnosis. Large, pentagonal, biconvex shells. Strong and numerous ribs, radiating anteriorly to the umbo and extending to the anterior margins, growth lines, and double ribs sometimes present, absent accentuated and deep median costae. Weak fold and sulcus, thick umbo.

Occurrence. Sandbian 2 and Katian 1, Late Ordovician (Mohawkian Series). Present in the fine-grained horizons in the Galena Group (Edenian) in Weisebach Dam, Spring Valley, and Wykoff and Fountain, Minnesota, U.S.A.

Description. Average length of 7.8 mm, width of 7.1, and height of 4.7 mm. Biconvex to dorso-biconvex, pentagonal shells, average number of costae in the ventral valve of 36.2 and dorsal of 37.5.
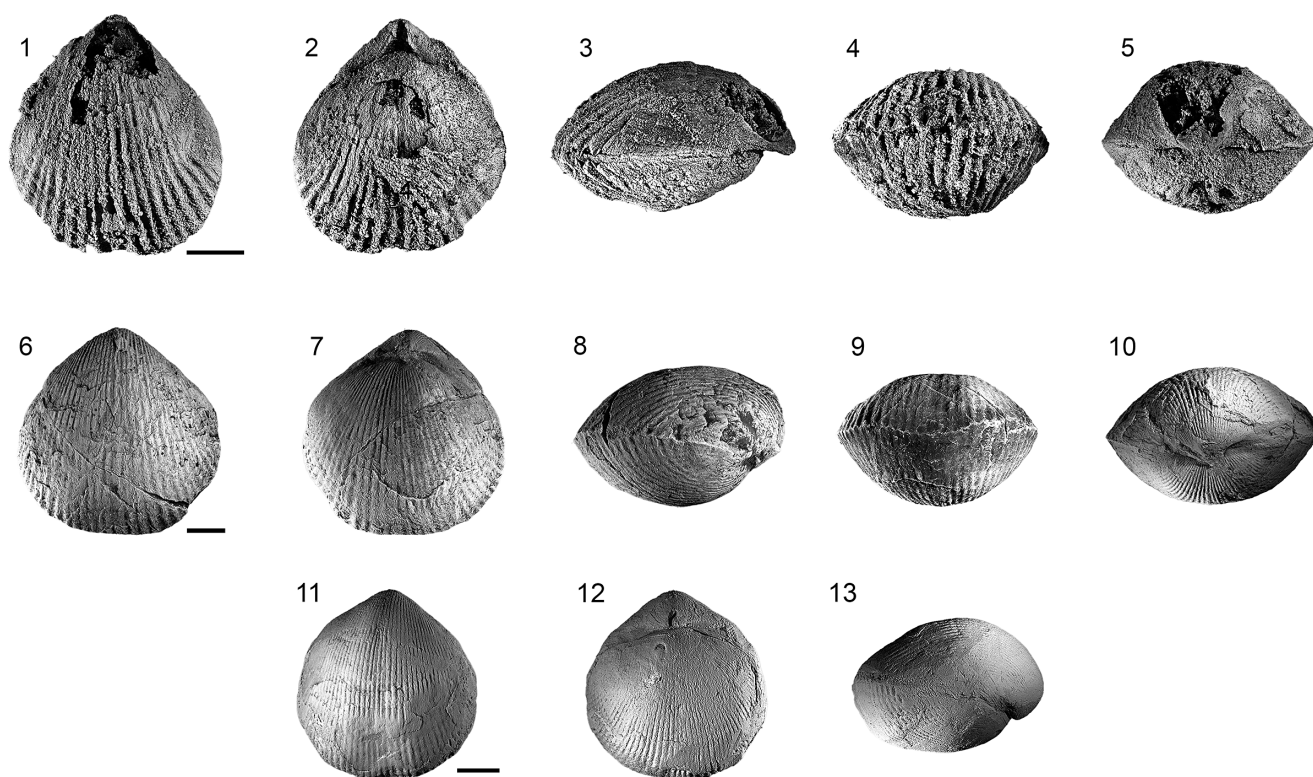
Figure 7. (**1–5**) *Catazyga homeospiroides* Ross and Dutro, 1966 (holotype) USNM PAL 145327. (**1**) Ventral, (**2**) dorsal, (**3**) lateral, (**4**) anterior, and (**5**) posterior views. (**6–10**) *Catazyga cartieri* Cooper and Kindle, 1936 (holotype) USNM PAL 91786E. (**6**) Ventral, (**7**) dorsal, (**8**) lateral, (**9**) anterior, and (**10**) posterior views. (**11–13**) *Catazyga headi* Billings, 1862 (plesiotype) FMNH PE89341. (**11**) Ventral, (**12**) dorsal, and (**13**) lateral views. Scale bars = 2 mm.

Dorsal costae radiating near the umbo. Parasulcate zigzagged anterior. Thick and curved umbo (average size of 2.4 mm), partially covering the dorsal valve (ventrally apsacline). Internal characters are unknown.

Remarks. Copper (1977) reassigned *Zygospira uphami* Winchell and Schuchert, 1892 to *Catazyga* without further reasoning. The internal morphology of *Catazyga uphami* was neither examined herein nor described by either Copper (1977) or Winchell and Schuchert (1892, 1895). Bayesian phylogenetic inference in this study indicates a placement within *Zygospira* rather than *Catazyga* on the basis of external characteristics. *Zygospira uphami* is distinguished from *Catazyga*-form species by its smaller size, less numerous but more accentuated costae, stronger fold in the dorsal valve, lack of concentric ornament, and double ribs. These morphological attributes, and the evolutionary placement of *Z. uphami* as a sister taxon to *Z. calhounensis* and *Z. resupinata* support transferring this species back into *Zygospira*.

Zygospira variabilis Fenton and Fenton, 1922
Figure 5.1–5.5

1922 *Zygospira variabilis* Fenton and Fenton, p. 75, pl 2, figs. 7–9.
1922 *Zygospira variabilis fountainensis* Fenton and Fenton, p. 76, pl 2, figs. 1–3.
1977 *Anazyga variabilis* Copper, p. 305.

Type specimens. FMNH UC25861 (holotype) and USNM PAL 111387a (plesiotype) from the Late Ordovician Plattin Formation, St. Genevieve County, Missouri, U.S.A.

Diagnosis. Strongly biconvex, rectangular shells. Poorly developed fold and sulcus. Sulcus on the ventral valve separated from shell flanks by two accentuated lateral ridges. Strong ribs originating near the umbo. Absence of growth lines. Very distinct apsacline ventral valve, resulting in a large, high-angled prominent umbo.

Occurrence. Sandbian, Late Ordovician (Mohawkian Series) in the United States. Plattin Formation in Missouri, U.S.A; Decorah Formation in Missouri, U.S.A.; Black River Formation in Kentucky, U.S.A.

Description. Average length of 5.3 mm, width of 5.6 mm, and height of 3.6 mm. Biconvex, rectangular shells, average number of costae in the dorsal valve of 15.5 and dorsal of 17. Dorsal costae radiating near the umbo. Parasulcate anterior commissure. Sharp and curved dorsal umbo (average size of 1.7 mm), partially covering the ventral valve (ventrally apsacline). Internal characters are unknown.

Additional materials. USNM PAL 111387a-b, USNM PAL 111388a-b. *Z. variabilis fountainensis* Fenton and Fenton, 1922 cotypes: FMNH UC27455A, FMNH UC7455B.

Remarks. As noted by Fenton and Fenton (1922), *Zygospira variabilis* can be distinguished from *Z. recurvirostra* by its overall greater size but less convex lateral profile and its stronger and fewer ribs in both valves. Analysis of internal morphology of a silicified specimen (USNM PAL 111387d) indicates a resemblance of the crura of *Z. variabilis* with those documented from *Z. modesta* Hall,

1862 and *Z. recurvirostra* Davidson, 1882. In this case, both stems are parallel to each other for a short distance before the start of the loops, which were not preserved well enough to describe further. In the same paper, Fenton and Fenton (1922) erected a subspecies, *Zygospira variabilis fountainensis*, remarking the specimens as almost identical to *Z. variabilis* except for a larger number of fine costae and a rounder outline. We consider these differences to fall within the range of variation for *Z. variabilis* as circumscribed herein.

<div align="center">Subfamily Catazyginae Copper, 1977</div>

<div align="center">Genus <i>Catazyga</i> Hall and Clarke, 1894
Figure 7</div>

Type species. *Athyris headi* Billings, 1862, p. 147, from the Pontgravé River Formation, Bécancour, Quebec, Canada, by original designation.

Other species. *Zygospira anticostiensis* Billings, 1862 from the Hudson River Formation in Anticosti Island, Quebec, Canada; *Catazyga arcana* Williams, 1962 from the Kiln Mudstone in the Craighead Formation in Ayrshire, Girvan district, Scotland; *Catazyga cartieri* Cooper and Kindle, 1936 from the Whitehead Formation in Percé, Quebec; *Athryis headi* Billings, 1862 from the Pontgravé River Formation in Bécancour, Quebec, Canada, and from the Waynesville Formation in Madison and Weisburg, Indiana, U.S.A, Oxford, Woodville, Waynesville, and Blanchester, Ohio, U.S.A; *Athyris headi borealis* Billings, 1862 from the Hudson River Formation in Lake St. John, Quebec, Canada; *Catazyga headi filistriata* Sproule, 1936 from the Cobourg Formation, Georgian Bay, Ontario, Canada; *Catazyga homeospiroides* Ross and Dutro, 1966 from the Jones Ridge Formation near the Tatonduk River, Alaska, U.S.A. For discussion of additional species, see Copper (1977).

Diagnosis. Moderate to large, elongate, fine-ribbed shells. Strongly biconvex shells. Numerous ribs, rarely bifurcating double ribs, concentric ornamentation frequently present at the margins. Rectinomarginate to unisulcate anterior commissure. Weak fold and sulcus, lack of distinct deep or accentuated median costae. Thick umbo, projecting upward and covering most of the ventral valve. Discrete pedicle openings. Deep, thick adductor area, small teeth socket cavities. Narrow and poorly defined diductor muscle field. Jugum located posterior to midline of spiralia, directly inclined toward whorls apices, three to 10 whorls.

Occurrence. Early to middle Late Ordovician (Sandbian 2 to Katian 4). The oldest specimens are found in Sandbian 2 to Katian 1 exposures in Wales and Scotland. In North America, *Catazyga* is more abundant and commonly found in exposures from the Katian 4 Stage (Richmondian) in the eastern basins, such as the Cincinnati Arch and on Anticosti Island, Québec (Canada).

Remarks. *Catazyga* was erected by Hall and Clarke (1894) on the basis of its rotundity, weak fold and sulcus, and great number of costae. Internally, *Catazyga* is distinguished from *Zygospira* by having spiralia that have apices oriented dorsal medially but toward the posterior, comprising three to 10 whorls, which is larger than the five to eight whorls of known *Zygospira* spiralia. Copper (1977) described additional details of *Catazyga* muscle fields and hinge structures; the genus is recognized by having a broad ventral adductor muscle area and irregular, small, teeth sockets.

<div align="center"><i>Catazyga homeospiroides</i> Ross and Dutro, 1966
Figure 7.1–7.5</div>

1966 *Catazyga homeospiroides* Ross and Dutro, p. 8, pl. 2, figs. 8, 11, 13.
1977 *Catazyga homeospiroides* Copper, p. 315.

Holotype. USNM PAL 14532 from the Jones Ridge Formation in Alaska, U.S.A.

Diagnosis. Thick, elliptical biconvex shells, protruding umbo, and well-defined delthyrium. Poorly developed fold and sulcus. Distinct and well-spaced costae radiating anterior to the umbo, occasional presence of growth lines. Rectimarginate and marginally deflected anterior commissure.

Occurrence. Katian 1 Stage, Late Ordovician (Edenian, Cincinnatian Series) in the United States. Trenton Formation in Alaska, U.S.A.

Description. Overall large specimens, average length of 11.8 mm, width of 11.0 mm, and height of 8.20 mm. Elliptical shells, average number of costae in the dorsal valve of 13 and 19.5 strong ribs in the dorsal valve. Growth lines occasionally present, absence of double ribs and median costae. Interior morphology unknown.

Additional materials. Holotype: SNM145327; paratypes: USNM PAL 145331 and USNM PAL 145329.

Remarks. In the original description, Ross and Dutro (1966) were hesitant to unambiguously place *Catazyga homeospiroides* within *Catazyga*. Copper (1977) further indicated that the placement required additional confirmation. On the basis of these analyses, the higher number of costae (>10), rotundity, poor development of the fold and sulcus, and ovoid outline present in the analyzed specimens are consistent with the placement of this species within the genus *Catazyga*. Phylogenetic analysis conducted herein additionally supports the inclusion of *C. homeospiroides* within *Catazyga*, although the internal morphology of this species remains unknown.

Overall, *C. homeospiroides* is a typical *Catazyga* form, but with coarser costae as a derived trait. The species can be distinguished from other Catazyginae forms by its coarser costae, weak fold and sulcus, larger but not curved umbo, and extreme biconvexity. Ross and Dutro (1966) noted that *Catazyga homeospiroides* closely resembles *C. cartieri* in outline and number of growth lines. Furthermore, the costae in *C. homeospiroides* are coarser than *C. cartieri*. *Catazyga arcana*, another related species from the Scoto-Avalonia terrane (Girvan) differs from *C. homeospiroides* by having a highly convex dorsal shell, whereas *C. homeospiroides* is characterized by its more equal biconvexity. Finally, Ross and Dutro (1966) compared *C. homeospiroides* with the typical Catazyginae form, *C. headi*, which can be differentiated by finer costae and a more rotund outline.

<div align="center"><i>Catazyga cartieri</i> Cooper and Kindle, 1936
Figure 7.6–7.10</div>

1936 *Catazyga cartieri* Cooper and Kindle, p. 359, pl. 52, figs. 8–13, 18.
1977 *Catazyga cartieri* Copper, p. 315.

Type specimens. USNM PAL 91786a–e (holotypes); USNM PAL 91786a (paratype) from the Whitehead Formation in Percé, Quebec, Canada.

Diagnosis. Biconvex, elliptical shells. Numerous fine costae originating near the short, thick umbo. Absence of growth lines and median costae. Short delthyrium. Rectimarginate commissure opening. Fold and sulcus typically absent or weak when present.

Occurrence. Katian 1 Stage, Late Ordovician (Edenian in the Cincinnatian Series) in Canada. Whitehead Formation, northwest Percé, Gaspé Peninsula, Quebec, Canada.

Description. Average length of 16.6 mm, width of 15.8, and height of 10.3 mm. Average number of fine costae in the dorsal valve of 30.5 and of 32 in the dorsal valve, lack of double ribs and growth lines. High angled umbo (59°) and average umbo size of 5.0 mm. Interior not examined.

Remarks. As noted by Cooper and Kindle (1936), *Catazyga cartieri* differs from other Catazyginae forms in its sharp umbo and convex valves. *Catazyga cartieri* shows an unusual rotundity in its outline and profile, and costae are evenly and homogenously distributed throughout the valves.

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