

# Biodiversity and Evolutionary Ecology of Extinct Organisms

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# Chapter 2

## Testing the Taxonomy and Phylogeny of Eastern North American Atrypid Brachiopods: A Geometric Morphometric Approach

### 2.1 Introduction

#### 2.1.1 Taxonomy

All atrypide brachiopods in North America were once referred to a single collective species, *Atrypa reticularis* (e.g., Fenton and Fenton 1930). *Atrypa reticularis sensu stricto* is now recognized only from the Silurian of Gotland (Copper 2004). The group has been radically revised in the last three decades and the understanding of the evolutionary relationships between genera is still in flux. The brachiopods that were once referred to one species are now distributed among 38 genera in five subfamilies within the family Atrypidae (Copper 1973, 1996, 2001a, 2002, 2004; Day 1998; Day and Copper 1998; Williams et al. 2002). Although the taxonomy of Copper's (1973) phylogeny is now partially out of date, having been revised again by Copper (2001a) based on differences in shell size, shell shape, surface ornamentation and internal morphological features, his phylogenetic hypothesis remains the only one for atrypides. To date, no one has attempted to quantify the morphological characters of these genera to test whether shell shape evolution is consistent with the phylogenetic arrangement. In this study, genera from the Atrypinae, Variatrypinae and Spinatrypinae are studied based on external morphological characters.

The genus *Atrypa* has been revised extensively since 1965 and has been split into several genera (Alvarez 2006). *Atrypa* was most closely related to *Desquamatia* and *Spinatrypa* (Boucot 1964) which were then all referred to Atrypinae (Williams and Rowell 1965). The phylogenetic relationships of *Atrypa*, *Gotatrypa*, *Kyrtatrypa* and many other atrypids were later studied by Copper (1973) who suggested that *Atrypa* is more closely related to *Gotatrypa* than to *Spinatrypa* or *Pseudoatrypa*. Based on that phylogeny and subsequent work, *Desquamatia* is today referred to Variatrypinae and *Spinatrypa* is referred to Spinatrypinae (Copper 2002).

Atrypid individuals that have been measured for this study belong to the Atrypinae, Variatrypinae and Spinatrypinae subfamilies, which have similar dorsally to dorso-medially directed spiralia (Copper 1996, 2002), distinct jugal processes, and distinct types of pedicle collar attachments to deltidial plates (Copper 1967, 1977). These three subfamilies were selected for this study as representatives of the family Atrypidae as they represent the longest stratigraphic ranges within the Silurian and Devonian time periods.

Atrypin adults have wavelike, overlapping or imbricate growth lamellae extended as frills, with loss of pedicle opening during ontogeny in most shells; while variatrypins have widely separated growth lamellae extended as expansive frills or alternatively have reduced growth lamellae but with simple tubular ribs, with most forms retaining the pedicle foramen. Spinatrypinae have commonly spinose, short growth lamellae with ribs disrupted into waves, producing nodular surface macro-ornament, with all forms retaining the pedicle foramen (Copper 2001a, 2002).

Copper (1973) used rib structure, pedicle structure, structure of jugal processes and dentition type to construct his phylogeny of four atrypide families. Shell shape was not considered as a criterion in his (1973) phylogenetic reconstruction. In our study, atrypid shell shape was evaluated using geometric morphometrics on nine genera representing three subfamilies of Atrypidae recognized by Copper's taxonomy and phylogeny. Our data from the Early Silurian to Early Devonian samples consist of individuals that belong to the Atrypinae while the Middle Devonian to Late Devonian samples consist of those from the Variatrypinae and Spinatrypinae subfamilies (Table 2.1). We analyzed shell shape to see if the patterns of differentiation are consistent with the taxonomic and phylogenetic structure proposed by Copper. A complete phylogenetic analysis based on internal morphological characters of these diverse atrypid genera in the Atrypinae, Variatrypinae and Spinatrypinae subfamilies from the eastern North American region awaits future analysis. Overall, this study tests whether the differences in shell shape between genera are consistent with Copper's classification and whether the quantitative results support the phylogeny of the atrypid brachiopods.

### ***2.1.2 Hypotheses***

Six hypotheses were tested in this study: (1) if the Atrypinae, Variatrypinae and Spinatrypinae are distinct subfamilies, as proposed by Copper (1973) and Williams et al. (2002), then the average morphology of these subfamilies should show significant differences between them; (2) likewise, if the genera within subfamilies are truly distinct, then the average shell shape between these genera should show morphometric differences; (3) furthermore, if genera are correctly referred to subfamilies, then average morphological distance between genera in different subfamilies should be greater than that from within one subfamily; (4) If evolutionary stasis is predominant in the P3 evolutionary ecological unit (EEU, see below) caused by ecological interlocking or other environmental influences, then,

**Table 2.1** Geographic locations for atrypid taxa with specific information on time interval and stage, EE subunit, and depositional environment

| Nos. | Locality                      | Sample size | Taxonomy  | Formation  | Period            | Stage                              | EE Unit (duration in my) | Basin  | Environment   |
|------|-------------------------------|-------------|---|--|-------------------|------------------------------------|--------------------------|--|---|
| 18   | North-central Iowa, USA       | 123         | <i>Pseudotrypa</i> , Variatrypinae                                      | Cerro Gordo Member, Lime Creek Shale, Hackberry Grove      | Devonian (Late)   | Frasnian                           | Genesee (5–6)            | Southern margin of the Iowa Basin                          | Mid-outer carbonate shelf; restricted and open marine oxic facies |
| 17   | NE Michigan, USA              | 210         | <i>Pseudotrypa</i> , Variatrypinae                                      | Traverse Group   | Devonian (Middle) | Late Eifelian-Middle Late Givetian | Hamilton-Tully (6–7)     | Flanks of the northeastern part of Michigan Basin          | Mixed setting (siliciclastics and carbonates)                     |
| 16   | Western New York, USA         | 134<br>23   | <i>Pseudotrypa</i> , Variatrypinae<br><i>Spinatrypa</i> , Spinatrypinae | Hamilton Group   | Devonian (Middle) | Late Eifelian-Middle Late Givetian | Hamilton-Tully (6–7)     | Folded ridge valley province of northern Appalachian Basin | Siliciclastics bordered by carbonate shelf                        |
| 15   | Southeastern Indiana, USA     | 63          | <i>Pseudotrypa</i> , Variatrypinae                                      | Hamilton Silver Creek member of the North Vernon limestone | Devonian (Middle) | Late Eifelian-Middle Late Givetian | Hamilton-Tully (6–7)     | Cincinnati Arch between Illinois and Michigan Basin        | Carbonate   |
| 14   | Fulton, Central Missouri, USA | 33          | <i>Pseudotrypa</i> , Variatrypinae                                      | Callaway Limestone   | Devonian (Middle) | Late Eifelian-Middle Late Givetian | Hamilton-Tully (6–7)     | Southern Iowa Basin  | Carbonate   |
| 13   | Ohio, USA                     | 9           | <i>Pseudotrypa</i> , Variatrypinae                                      | Dundee Limestone   | Devonian (Middle) | Lower-Mid Eifelian                 | Onondaga (5–6)           | Northwestern flank of the Findlay Arch                     | Carbonate   |
| 12   | Central New York, USA         | 34          | <i>Spinatrypa</i> , Spinatrypinae                                       | Onondaga Limestone   | Devonian (Middle) | Lower-Mid Eifelian                 | Onondaga (5–6)           | Ridge and valley province of central Appalachian Basin     | Carbonate   |

Table 2.1 (continued)

| Nos. | Locality                   | Sample size   | Taxonomy  | Formation  | Period           | Stage      | EE Unit (duration in my) | Basin  | Environment                            |
|------|----------------------------|---------------|---|--|------------------|------------|--------------------------|--|--|
| 11   | Eastern Tennessee, USA     | 151           | <i>Atrypa</i> ,<br>Atrypinae  | Birdsong Shale?,<br>Linden Group,<br>Helderbergian               | Devonian (Early) | Emsian     | Schoharie (5)            | On the east along flanks of the Nashville Dome   | Siliciclastics                         |
| 10   | Central-east New York, USA | 33<br>1       | <i>Atrypa</i> , Atrypinae<br><i>Kyriatrypa</i> , Atrypinae                                    | Schoharie Grit, New Scotland<br>Limestone of Helderbergian Group | Devonian (Early) | Emsian     | Schoharie (5)            | Northeast-trending folds in the Valley and Ridge Province of the central Appalachian Basin | Shallow carbonates and siliciclastics. |
| 9    | West Virginia, USA         | 46<br>4       | <i>Atrypa</i> ,<br>Atrypinae<br><i>Kyriatrypa</i> ,<br>Atrypinae                              | Keyser Limestone   | Devonian (Early) | Lockhovian | Helderberg (6)           | On a carbonate ramp in the valley and ridge province of the central Appalachian Basin      | Carbonate                              |
| 8    | Maryland, USA              | 11<br>17      | <i>Atrypa</i> ,<br>Atrypinae<br><i>Kyriatrypa</i> ,<br>Atrypinae                              | Keyser Limestone   | Devonian (Early) | Lockhovian | Helderberg (6)           | On a carbonate ramp in the valley and ridge province of the central Appalachian Basin      | Carbonate                              |
| 7    | Central-east New York, USA | 34<br>28      | <i>Atrypa</i> ,<br>Atrypinae<br><i>Kyriatrypa</i> ,<br>Atrypinae                              | Lower Helderberg Group   | Devonian (Early) | Lockhovian | Helderberg (6)           | Northeast-trending folds in the Valley and Ridge Province of the central Appalachian Basin | Carbonate                              |
| 6    | Oklahoma, USA              | 76<br>13<br>2 | <i>Atrypa</i> , Atrypinae<br><i>Kyriatrypa</i> ,<br>Atrypinae<br><i>Endrea</i> ,<br>Atrypinae | Hunton (Haragan) Limestone<br>(Yellow shale below limestone)     | Devonian (Early) | Lockhovian | Helderberg (6)           | 'Hunton Ramp' on the margin of the Oklahoma Aulacogen and Ouachita Trough                  | Carbonate ramp                         |

Table 2.1 (continued)

| Nos. | Locality                    | Sample size         | Taxonomy  | Formation                            | Period            | Stage      | EE Unit (duration in my)     | Basin  | Environment  |
|------|-----------------------------|---------------------|---|--------------------------------------|-------------------|------------|------------------------------|--|--|
| 5    | Oklahoma, USA               | 79<br>10<br>3       | <i>Atrypa</i> ,<br><i>Atrypinae</i><br><i>Gotatrypa</i> ,<br><i>Atrypinae</i><br><i>Oglapetes?</i> ,<br><i>Atrypinae</i>  | Henryhouse Limestone, Hunton Group   | Silurian (Late)   | Ludlow     | Keyser (2)                   | Surface of Anadarko Basin                                      | Carbonate  |
| 4    | West-Central Tennessee, USA | 64<br>81<br>5       | <i>Atrypa</i> ,<br><i>Atrypinae</i><br><i>Gotatrypa</i> ,<br><i>Atrypinae</i><br><i>Endrea</i> ,<br><i>Atrypinae</i>  | Waldron Clay member, Wayne Formation | Silurian (Middle) | Wenlock    | Upper Clinton-Lockport (7-8) | Northern and western margins of the Central Basin of Tennessee | Siliciclastics in the thick limestone sequence                           |
| 3    | Indiana, USA                | 18<br>43<br>8       | <i>Atrypinae</i><br><i>Atrypa</i> ,<br><i>Atrypinae</i><br><i>Endrea</i> ,<br><i>Atrypinae</i><br><i>Oglapetes?</i> ,<br><i>Atrypinae</i>   | Niagara Group                        | Silurian (Middle) | Wenlock    | Upper Clinton-Lockport (7-8) | Cincinnati Arch between Illinois and Michigan Basin            | Carbonates   |
| 2    | Western New York, USA       | 41<br>54<br>3<br>1  | <i>Atrypinae</i><br><i>Atrypa</i> ,<br><i>Atrypinae</i><br><i>Gotatrypa</i> ,<br><i>Atrypinae</i><br><i>Endrea</i> ,<br><i>Atrypinae</i><br><i>Oglapetes?</i> ,<br><i>Atrypinae</i> | Lockport Formation                   | Silurian (Middle) | Wenlock    | Upper Clinton-Lockport (7-8) | Thrusts along ridge and valleys of central Appalachian Basin   | Siliciclastics   |
| 1    | Quebec, Canada              | 2<br>111<br>18<br>7 | <i>Atrypa</i> ,<br><i>Atrypinae</i><br><i>Gotatrypa</i> ,<br><i>Atrypinae</i><br><i>Joviatrypa</i> ,<br><i>Atrypinae</i><br><i>Dihelictiera</i> ,<br><i>Atrypinae</i>               | Jupiter Formation                    | Silurian (Early)  | Llandovery | Lower Clinton (4)            | Anticosti Basin  | Shallow water shelly packstones to middle-outer shelf micritic mudstones |

despite taxonomic replacement, morphology is expected to remain the same with substantial overlap between genera through time; (5) If evolutionary stasis is predominant in the P3 EEU, then minor morphological change is expected within each genus through time; (6) If biogeographic differences in shell shape among geographic locations are due to provinciality, then at a given time, genera from the same paleogeographic locations are expected to cluster and morphological distances among paleogeographic locations are expected to be similar to those observed between genera.

### ***2.1.3 Ecological Evolutionary Units and Subunits***

The Silurian and Devonian have been classified into a single Paleozoic Ecological Evolutionary Units (EEU) (designated as P3), which was a time marked by periods of stability (designated as subunits or Ecological Evolutionary Subunits (EESUs)) (Boucot 1983, 1986, 1990a, b, c; Sheehan 1991, 1996; Holterhoff 1996; Brett et al. 2009) interspersed by periods of minor reorganization and extinction (Brett et al. 1990; Brett and Baird 1995; Holterhoff 1996; Sheehan 1996; Ivany et al. 2009). The major extinction events of the end-Ordovician and Late Devonian mark the P3 EEU boundaries (Sheehan 1996). The eight P3 EESUs included in the present study are shown in Fig. 2.1, Table 2.1. The P3 EESUs have been well studied (Brett and Baird 1995; Brett et al. 2009) in the Appalachian Basin with respect to community stability patterns, but studies involving morphological shape change or stasis within brachiopod species lineages from these EESUs are lacking excepting Lieberman et al. (1995) who studied two brachiopod species lineages for stasis. In general, brachiopods were abundant, diverse and well-preserved during this time interval, providing plentiful data for morphological shape study. Morphological shape change patterns in P3 EEU atrypid subfamilies and genera are described here to trace both temporal and spatial variation within these brachiopod genera. Thus, this study is designed to determine comparative morphological shape patterns within the atrypid brachiopods belonging to the Atrypinae, Variatrypinae and Spinatrypinae from the strata making up the P3 EEU from the Appalachian Basin and their stratigraphic equivalents within the Eastern American biogeographic Realm, spanning the entire 64 Myr of the Silurian-Devonian (441–376 Myr) rock record.

## **2.2 Materials**

### ***2.2.1 Paleogeography***

During the Silurian-Devonian time, the Eastern American Realm was relatively isolated from other biogeographic realms and was indeed a realm of its own. Though these realms had established connections between them in this long

interval of time during major transgressive events of the transgressive-regressive sea level cycles, much of the evolution of these atrypide lineages possibly occurred within the basin. Boucot (1975) and Boucot and Blodgett (2001) referred to the Eastern American Realm as a warm or hot unit with lower to mid latitudinal strata rich in evaporites, redbeds, carbonate rocks and reef developments. Thus, Silurian and Devonian of Eastern North America, representing high taxic diversity at all taxonomic levels, make an important biogeographic realm for taxonomic investigation.

The Silurian was a period of marked provincialism for the brachiopod faunas (Boucot and Blodgett 2001) during which the Acadian orogeny occurred (Van der Pluijm 1993) and shallow marine carbonate deposition was widespread (Berry and Boucot 1970). During the Llandovery (early Silurian), sea levels were low and a comparatively cool climate was indicative from the less extensive reef deposits (Copper 2001b) and thus, evolution of some endemic atrypide genera were possibly restricted in their small environmental regimes. Climates warmed up and sea levels started rising during the Wenlock (middle Silurian) as evidenced by the onset of reef growth (Copper 1973, 2004). Abundant patch reefs occurred in parts of Michigan, Ontario, Ohio and Indiana (Cumings and Shrock 1928; Lowenstam 1957). A shallow marine environmental setting is suggested by the presence of mid-platform carbonates in eastern North America during this time. Thus, our samples (*Atrypa*, *Gotatrypa*, *Endrea*) from the Middle Silurian of Appalachian basin, Cincinnati Arch and central Tennessee basins were somewhat similar during this time. Some of the Early Silurian genera (*Joviatrypa*, *Dihelictera*) remained restricted to the Hudson Bay lowlands. Some genera (*Atrypa*, *Gotatrypa*) in Anadarko basin of Oklahoma localities still persisted in the carbonate platforms during the Ludlow time. By the Pridoli time (late Silurian), sea level dropped leading to evaporitic conditions in some basins and closure of many sea connections between basins, including between eastern North America and Europe. This provincialization continued during much of the Early Devonian (Copper 1973) of Eastern North America, which gave rise to some endemic genera (*Kyrtatrypa*) in the margins of Oklahoma aulacogen, central Appalachian basin (central-east New York, West Virginia and Maryland) and the eastern Tennessee Nashville Dome localities with continued persistence of the *Atrypa* lineage in these localities. During the Early Devonian and early Middle Devonian (Lockhovian-early Eifelian), sea level was low and most genera (*Atrypa*, *Kyrtatrypa*) from the Appalachian, Michigan, Iowa and Anadarko basins were most likely separated by geographic barriers (Findley, Kankakee and Cincinnati Arches) which persisted through the Middle Devonian, thus, giving rise to new evolutionary lineages (*Pseudoatrypa*, *Spinatrypa*) in some early Eifelian localities (Ohio and central New York). All of these intracratonic arches served as barriers to shallow marine dispersal during the Devonian (Koch and Day 1995; Rode and Lieberman 2005). Later in the Middle Devonian (late Eifelian to early Givetian), sea levels had risen again and climates warmed up with widespread carbonate deposition in this region. This marked sea-level rise during this time possibly breached the Ozark dome, Wisconsin, Findley, Kankakee, Cincinnati Arches and Acadian



Highlands of Eastern North America further facilitating mixing of faunas within all geographic localities in the Eastern American biogeographic realm. The late Givetian, or early Frasnian (Late Devonian) was thus, a marked period of cosmopolitanism when Appalachian sea lanes were connected all over again and thus similar genera (*Pseudoatrypa*) persisted across various geographic localities (Michigan Basin, Iowa and Missouri localities in Iowa Basin, northern Appalachian Basin and Cincinnati Arch) during this time. At the end of the Frasnian time, black shales or disconformities were produced locally with sea levels continuing to rise. Eventually, the muddy bottom dwelling and stenohaline atrypides went extinct at the end of the Frasnian more likely due to ecological replacement of these faunas by other higher order organisms (Copper 1973). Thus, this varied biogeographic setting makes it all the more interesting to investigate the taxonomic composition in atrypides during the Silurian-Devonian time period in eastern North America.

Of the eighteen sampled geographic localities in this study, samples from Hudson Bay lowlands represent inner shelf environments, those from Appalachian (New York, Maryland, West Virginia) localities represent inner to middle shelf environments, Tennessee localities represent inner shelf environment with some derived clastics in the north, Michigan locality represents middle shelf environment, Cincinnati Arch (Indiana) locality represents middle shelf environment, Ohio locality represent environments dominated by eastern derived clastics, Missouri locality represent inner shelf environments, Iowa locality represents inner shelf environments with presence of evaporite beds, and Oklahoma localities represent environments that ranged from inner to middle shelves (Day 1998).

Thus, for this study, geographic variation was examined in a few genera from the Middle Silurian, Early Devonian and Middle Devonian Eastern North American localities. The stratigraphic, lithologic and paleogeographic settings for the sampled atrypids from Silurian-Devonian of Eastern North America in this study are given in Table 2.1.

## 2.3 Methods

### 2.3.1 Data Set

We tested morphological variation using a total of 1593 dorsal and ventral valves (Table 2.1) of well preserved atrypid brachiopods. Of those specimens, 1300 specimens were used to test morphological evolution within *Atrypa*, *Gotatrypa* and *Pseudoatrypa*; and 904 specimens were used to assess geographic variation within *Atrypa* from the Middle Silurian and Early Devonian localities, *Kyrtatrypa* from the Early Devonian localities, and *Pseudoatrypa* from the Middle Devonian localities in eastern North America. Specimens were identified to genus level and grouped within their respective subfamilies (Atrypinae = 964, Variatrypinae = 572, and Spinatrypinae = 57). The geographic location and respective

|   | Geologic time scale | Sheehan's 9 EEUs | EE subunits (EESUs) Brett and Baird (1995) | Time span (my) |
|---|---------------------|------------------|--|----------------|
| → | Tertiary            | M3               | <b>Genessee (11.)</b>                      | 5-6            |
|   | Cretaceous          | M2               | <b>Hamilton</b>                            | 6-7            |
| → | Jurassic            |                  | <b>Onondaga</b>                            | 5-6            |
| → | Triassic            | M1               | <b>Schoharie</b>                           | 5              |
|   | Permian             |                  | Oriskany                                   | 2-3            |
|   | Carboniferous       | P4               | <b>Helderberg</b>                          | 6              |
|   | Devonian            | <b>P3</b>        | <b>Keyser</b>                              | 2              |
|   | Silurian            |                  | Salina                                     | 3-4            |
| → | Ordovician          | P2               | <b>Upper Clinton-Lockport</b>              | 7-8            |
|   |                     | P1               | <b>Lower Clinton</b>                       | 4              |
| → | Cambrian            | C2               | Medina                                     | 5              |
|   |                     | C1               |  |                |

**Fig. 2.1** Ecological evolutionary unit P3 (*circled*) showing the major subdivided 11 EE subunits in the Silurian and Devonian (data sampled from the 8 EESUs are marked in *bold*). (after Brett and Baird 1995)

sample sizes are reported on the map in Fig. 2.2 and in Table 2.1. All specimens were identified based on external morphological characters and ornamentation (Fig. 2.3). The material we used is housed in the Invertebrate Paleontology Collections of the American Museum of Natural History, Yale Peabody Museum, New York State Museum and Indiana University Paleontology Collections.

2.3.2 Geometric Morphometrics

Geometric morphometrics is the analysis of geometric landmark coordinate points on specific parts of an organism (Bookstein 1991; MacLeod 2002; Zelditch et al. 2004; Webster 2011). Morphometric analysis is based on the use of landmarks to capture shape (Rohlf and Marcus 1993); landmarks are points representing the same location on each specimen. In this study, we used 9 two-dimensional landmark points to capture the most meaningful shape differences (Fig. 2.4). Landmarks were digitized from image files using Thin Plate Spline Dig software (Rohlf 2004). When selecting landmarks for analyses, we chose points that not only characterized body shape accurately, but also represented some aspect of the

inferred ecological niche. These landmarks represent discrete points that correspond among forms (sensu Bookstein 1991) and are appropriate for analyses attempting to capture shape changes or function. These points are at the intersection of articulation of both valves except landmarks 1 and 9 (1 = umbo tip on dorsal valve on the plane of symmetry; 2 and 8 = left and right posterior marginal tips of the hingeline; also region for food intake from inhalant currents; 3 and 7 = mid shell tips along the widest region of the shell; 4 and 6 = anterior commissure marginal ends; 5 = anterior margin of commissure on the plane of symmetry; 9 = beak tip on ventral valve on the plane of symmetry). The same eight landmarks (1–8 on dorsal valves and 2–9 on ventral valves) were used to compare both dorsal and ventral valves (Fig. 2.4).

Procrustes analysis (Rohlf 1990; Rohlf and Slice 1990; Rohlf 1999; Slice 2001) was performed on original shape data, rotating, translating and scaling all landmarks to remove size effects while maintaining their geometric relationships. Pairwise Procrustes distances were calculated between the mean shapes of genera both within Atrypinae and between Atrypinae, Variatrypinae and Spinatrypinae (Fig. 2.5). Procrustes distances were also calculated between mean shell shapes within each genus from different time units and between mean shell shapes of different geographic localities in the Middle Silurian, Early and Middle Devonian. These distances were all measured in Procrustes units. Procrustes units are measures of shape difference in multivariate space, whose units are arbitrarily derived from the landmark data, but they are comparable across objects with the same number of landmarks (Rohlf 1990; Rohlf and Slice 1990). Principal component analysis was performed on the covariance matrix of Procrustes residuals to determine the morphological variation between the Atrypinae, Variatrypinae and Spinatrypinae and among genera within Atrypinae. Principal component analysis was also performed to determine within genus variation in time and space units.

### 2.3.3 *Morphometric Divergence*

Evolutionary rate and mode in morphological divergence were assessed using the maximum-likelihood method of Polly (2008). This method estimates the mean per-step evolutionary rate and the degree of stabilizing or diversifying selection from a matrix of pairwise morphological distances and divergence times. Morphological distance was calculated as pairwise Procrustes distances among genera (Fig. 2.5) and divergence time was calculated using the patristic distance in millions of years on phylogenetic tree of Copper (1973) (Fig. 2.6), which is an estimate of the total time in millions of years that the two genera have been diverging independently since they last shared a common ancestor. The method uses the following equation to estimate rate and mode simultaneously,

$$D = rt^{\wedge} a, \quad (2.1)$$

where  $D$  is morphological divergence (procrustes distance),  $r$  is the mean rate of morphological divergence,  $t$  is divergence time, and  $a$  is a coefficient that ranges from 0 to 1, where 0 represents complete stabilizing selection (stasis), 0.5 represents perfect random divergence (brownian motion) and 1 represents perfect diversifying (directional) selection (Polly 2008). Maximum-likelihood is used to find the parameters  $r$  and  $a$  that maximize the likelihood of the data, and are thus the best estimates for rate and mode. The data were bootstrapped 1000 times to generate standard errors for these estimates. This method is derived directly from the work presented by Polly (2004) and is mathematically related to other methods in evolutionary genetics (Lande 1976; Felsenstein 1988; Gingerich 1993; Roonarine 2003; Hunt 2007).

Lastly, a few atrypid genera (*Atrypa*, *Gotatrypa*, *Endrea*, *Pseudoatrypa*) were tested for morphological shape differences in specimens from shale and carbonate lithologic settings. For example, *Atrypa* specimens were tested for differences between Lower Devonian Linden Group of Tennessee (siliciclastic) and Keyser Limestone of Maryland (carbonate). Similar tests were performed for other genera.

### 2.3.4 Statistical Analysis

We performed several statistical tests to assess morphological distinctness between atrypin genera, between atrypid subfamilies and to investigate the correctness of the phylogenetic relatedness between these genera. Multivariate analysis of variance (MANOVA) was performed to test for significant morphological shape difference (a) between three subfamilies, (b) between genera within one subfamily, (c) within genera between time and space units, and (d) within genera between shale and carbonate environments. Discriminant function analysis (DFA) was also performed to highlight the morphological differentiation within and between subfamilies. Pairwise distance between genera from within a subfamily was then compared with those between subfamilies. A bootstrap test was performed to draw statistical inference regarding the frequency (out of 1000 iterations) of randomly observing the difference in mean sample morphology between time units. The trend in mean shape through time was constructed for individual genera from Principal component scores. Euclidean cluster analysis (UPGMA) was performed to identify similarities in individual genera sampled from different time intervals, and from geographic intervals at a given time. Average Euclidean distances in time and space were also compared to assess whether the temporal distances are similar to what one would expect from the replacement of one population by a geographically distinct one (Polly 2003).

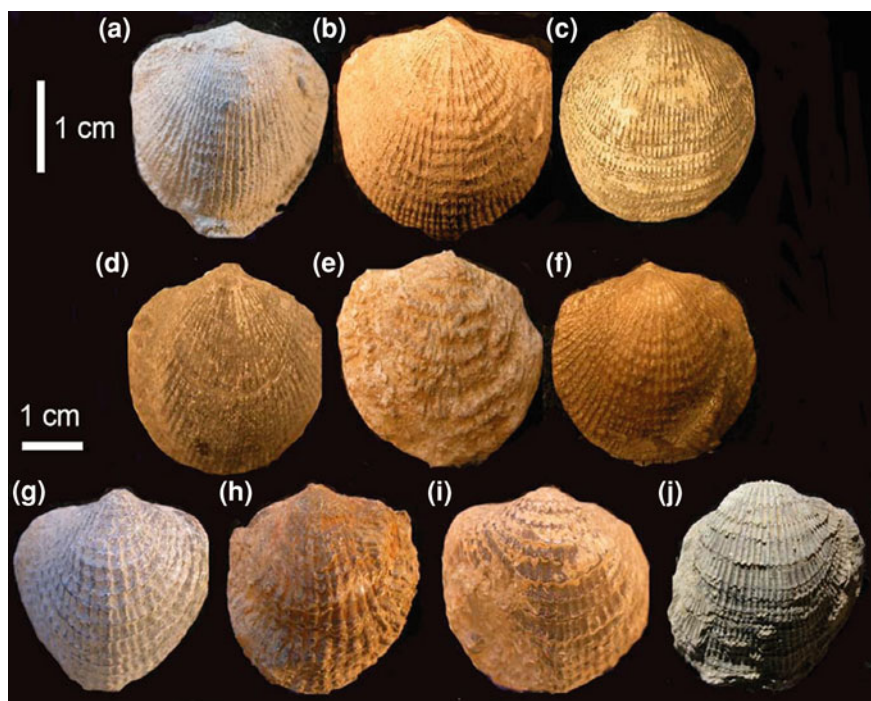


**Fig. 2.2** Sampled localities for atrypid brachiopods in eastern North America. Filled triangle in black indicates Silurian localities. Filled square in black indicates Devonian localities. Numbers 1–18 indicate 18 different localities from where samples were collected. For detailed locality information see Table 2.1

## 2.4 Results

### 2.4.1 Taxonomic Differentiation

Based on qualitative phenotypic traits, the specimens were identified to genus level (Fig. 2.3, Table 2.1). Atrypin genera were distinguished from other genera by their characteristic closely spaced growth lamellae and loss of the pedicle opening. The most distinguishable phenotypic characters of the variatrypin genera included the long, tubular rib structure, pedicle opening and wide spacing between growth lamellae; while spinatrypin genera possessed spinose growth lamellae with highly imbricated tubular rib structure. Frills were not preserved in most atrypides, so it could not be utilized in distinguishing the atrypid members in various subfamilies. Our sample includes the following genera: Atrypinae—*Atrypa*, *Gotatrypa*, *Endrea*,

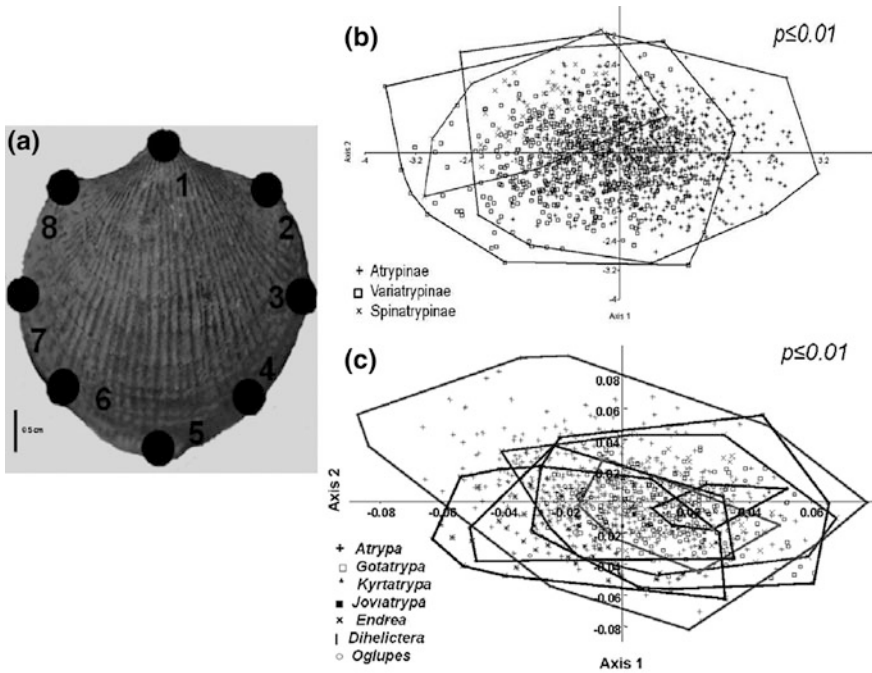


**Fig. 2.3** Dorsal views of genera from Atrypinae, Variatrypinae, and Spinatrypinae subfamilies: **a** YPM 224604, *Atrypa*; **b** YPM 224444, *Gotatrypa*; **c** NYSM E2341 62-5, *Kyratrypa*; **d** YPM 224240, *Joviatrypa*; **e** YPM 224522, *Endrea*; **f** YPM 224450, *Dihelictera*; **g** YPM 225957, *Spinatrypa*; **h** YPM 226001, *Spinatrypa*; **i** YPM 226006, *Spinatrypa* (note the spinose imbricated lamellae in lower right area of the shell in **h**, and widened spaces between growth lamellae in **i**; **j** YPM 225921, *Pseudoatrypa*. Note: the scale bar is the upper vertical line 1 cm for specimens **a–f** and the lower horizontal line 1 cm for specimens **g–j**

*Joviatrypa*, *Kyratrypa*, *Dihelictera*, *Oglupes?*, *Protatrypa*, and *Rugosatrypa*; Variatrypinae—*Pseudoatrypa*, and *Desquamatia* (*Independatrypa*); Spinatrypinae—*Spinatrypa*. Note that *Protatrypa*, *Rugosatrypa* and *Desquamatia* (*Independatrypa*) were not included in the morphometric analysis because of their small sample sizes.

Principal component analysis showed significant overlap between the subfamilies and genera. MANOVA found significant differences between mean shell shape in the three subfamilies for dorsal valves ( $F = 30.7$ ,  $df1 = 24$ ,  $df2 = 3130$ ,  $p < 0.01$ ) (Fig. 2.4b). MANOVA (post hoc pairwise tests with Bonferroni correction) also found significant differences among mean shape in the following genera within Atrypinae for dorsal valves ( $F = 4.389$ ,  $df1 = 72$ ,  $df2 = 5060$ ,  $p < 0.01$ ) and ventral valves ( $F = 3.628$ ,  $df1 = 72$ ,  $df2 = 5027$ ,  $p < 0.01$ ) (Fig. 2.4c, Table 2.2): *Atrypa*-*Gotatrypa*, *Atrypa*-*Endrea*, *Atrypa*-*Kyratrypa*, *Endrea*-*Kyratrypa*, *Gotatrypa*-*Kyratrypa*, *Kyratrypa*-*Joviatrypa*, and *Oglupes?*-*Gotatrypa*. Significant differences in mean shape were also found between

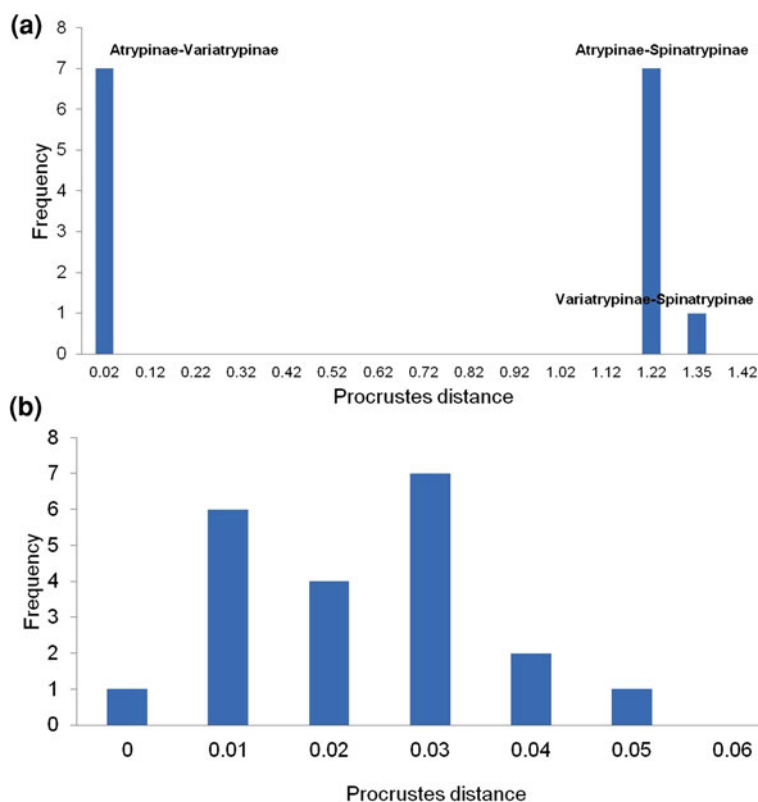




**Fig. 2.4** **a** Location of eight landmarks on the pedicle valve of an atrypid sample for geometric morphometric analysis; **b** CVA plot showing morphometric differences between Atrypinae, Variatrypinae, and Spinatrypinae subfamilies ( $p < 0.01$ ); **c** CVA plot showing morphological differentiation between genera within Atrypinae subfamily ( $p < 0.01$ ). Note that *Rugosatrypa* and *Protatrypa* have been removed from analysis as these were only one member from each genus

*Pseudoatrypa-Spinatrypa*, from Variatrypinae and Spinatrypinae respectively ( $p < 0.01$ ). On average, the mean shape difference between subfamilies ranged from 0.1 to 1.3 Procrustes units, and the difference between genera within the Atrypinae subfamily ranged from 0.01–0.05 Procrustes units (Fig. 2.5).

Maximum-likelihood estimation of the rate and mode of evolution given phylogeny of (Copper 1973) (Fig. 2.6) yielded a rate of  $0.012 \pm 0.12$  Procrustes units per million years and a mode coefficient  $a$  of  $0.97 \pm 0.15$ , indicating that diversifying selection has made the means of these atrypid genera more different than one would expect by random evolution (Fig. 2.7). In random evolution or Brownian motion, the direction and intensity of selection would have caused change in morphology over time but with changeable conditions (Polly 2004). A general observation suggests that morphometric shape differences between pairs of genera increases with phylogenetic distance with some discrepancy in *Pseudoatrypa* (Variatrypinae) (Table 2.3), which appears to be morphologically closer to the atrypins, more similar to what one would expect for genus-level than sub-family level differentiation.

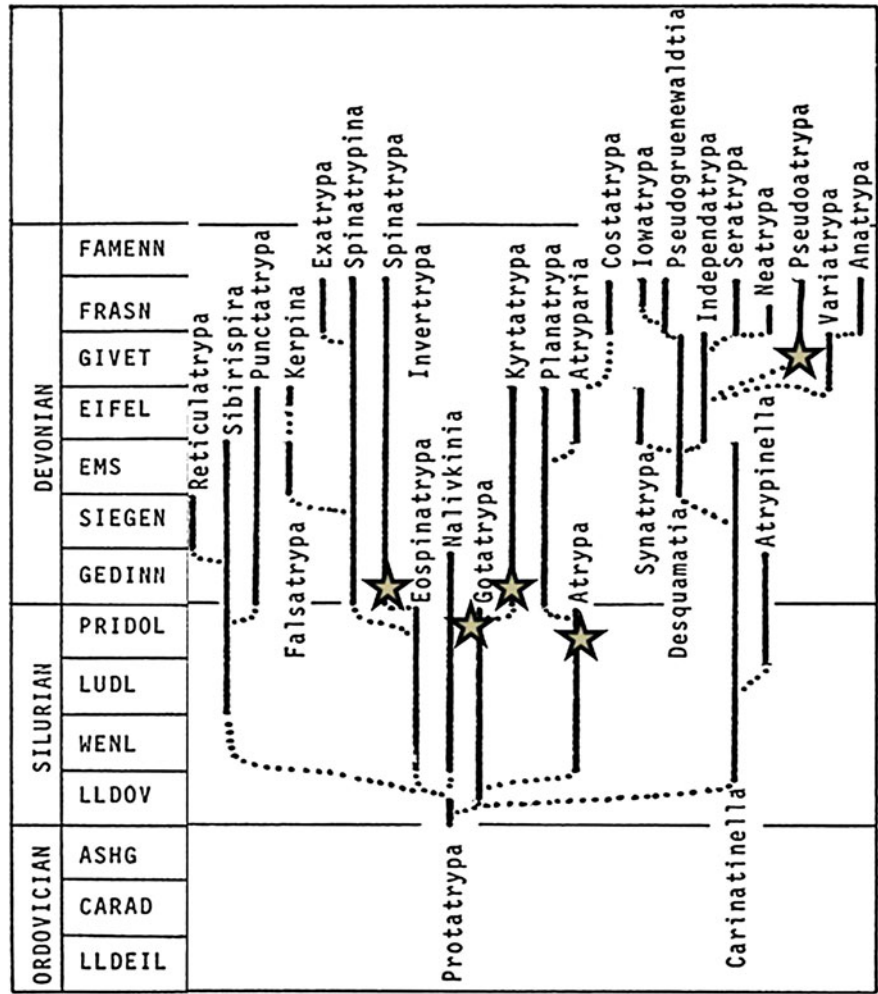


**Fig. 2.5** **a** Histogram for Procrustes distance between genera from three subfamilies. All genera from Atrypinae nearly maintain a small distance with Variatrypinae (0.12) while a large distance with Spinatrypinae (1.22–1.25). A large procrustes distance (1.345) between Variatrypinae and Spinatrypinae; **b** Small procrustes distance between genera within Atrypinae subfamily (0.01–0.05)

### 2.4.2 Temporal Variation

Principal component analysis of atrypid individuals shows morphological variation within each group with considerable morphological overlap among the six clustered groups of atrypids based on six coarse scale time units (Fig. 2.8). MANOVA found significant shape differences in dorsal valves for individual genus between different time horizons (*Atrypa*:  $F = 4.09$ ,  $df1 = 24$ ,  $df2 = 1008$ ,  $p < 0.01$ ; *Gotatrypa*:  $F = 4.475$ ,  $df1 = 24$ ,  $df2 = 484$ ,  $p < 0.01$ ; and *Pseudootrypa*:  $F = 10.43$ ,  $df1 = 12$ ,  $df2 = 510$ ,  $p < 0.01$ ), suggesting short term changes within a lineage. On average, the difference between Early, Middle and Late Silurian time units in *Gotatrypa* shell shape ranges from 1.1 to 1.8 Procrustes units, the difference between Middle Silurian, Late Silurian and Early Devonian





**Fig. 2.6** Copper's phylogenetic chart from his 1973 paper that was used to calculate evolutionary divergence times (m.y.) between atrypid genera. The five genera used in this study are marked in the figure as star symbols

time units in *Atrypa* shell shape ranged from 0.7 to 1.1 Procrustes units, and the difference between Middle and Late Devonian time units in *Pseudoatrypa* shell shape was 1.0 Procrustes units (Table 2.4). Overall, these distances were larger than those observed between genera within a subfamily and were comparable to those observed between genera from distinct subfamilies.

### 2.4.3 Spatial Variation

MANOVA indicated significant geographic shell shape differences among mean shape in individual genera (Middle Silurian *Atrypa*:  $F = 10.48$ ,  $df_1 = 24$ ,  $df_2 = 214$ ,  $p < 0.01$ ; Early Devonian *Atrypa*:  $F = 4.18$ ,  $df_1 = 48$ ,  $df_2 = 1165$ ,  $p < 0.01$ ; Early Devonian *Kyrtatrypa*:  $F = 2.109$ ,  $df_1 = 36$ ,  $df_2 = 136.6$ ,  $p < 0.01$ ; and Middle Devonian *Pseudoatrypa*:  $F = 5.191$ ,  $df_1 = 48$ ,  $df_2 = 1481$ ,  $p < 0.01$ ).

Dendograms illustrated in Fig. 2.9 depict the similarity in mean valve shape between different geographic localities from the eastern North America region during the three time intervals sampled. Valve morphological shape in the Middle Silurian *Atrypa* shells shows a greater similarity between Tennessee and New York than either region with Indiana (Table 2.5, Fig. 2.9).

During the Early Devonian, *Atrypa* shells from Tennessee and Oklahoma form a close cluster with less morphological distance to the Maryland sample than to the New York and West Virginia samples, which form a cluster with almost similar distance with Maryland (Table 2.5, Fig. 2.9). During the Early Devonian, *Kyrtatrypa* shells from Maryland and New York form a closer cluster with Oklahoma than with West Virginia (Table 2.5, Fig. 2.9). During the Middle Devonian, Missouri samples are more closely linked to those from Michigan and New York than with those from Indiana and Ohio (Table 2.5, Fig. 2.9). Thus, only the Early Devonian *Atrypa* shells show some biogeographic signal.

On average, the shape difference between Middle Silurian *Atrypa* from different geographic regions ranged from 1.7 to 2.3 Procrustes units and the difference between *Atrypa* from different regions in the Early Devonian ranged from 1.0 to 2.0 Procrustes units. The shape difference between *Kyrtatrypa* from different regions in the Early Devonian ranged from 1.4 to 2.8 Procrustes units. The shape difference between *Pseudoatrypa* samples from different Middle Devonian geographic regions ranged from 0.6 to 2.3 Procrustes units. Overall, geographic variation within genera is greater than temporal variation.

Average Procrustes distance over time suggests that the magnitude of morphological shape change was similar in the dorsal and ventral valves (0.025 and 0.028 Procrustes units respectively). Likewise, average Procrustes distance was similar in the two valves between geographic regions (0.030 and 0.029 for Middle Silurian, 0.027 and 0.029 for Early Devonian, and 0.040 and 0.037 Procrustes units for Middle Devonian respectively). However, geographic variation was slightly greater than temporal variation within these samples as suggested from the range of Procrustes distances within these units (time: 0.025–0.028; space: 0.027–0.040). Geographic variation (0.6–2.3) was also greater than temporal variation (0.7–1.8) when tested for individual genera (Tables 2.4, 2.5).

Lastly, significant statistical differences were observed within each genus between shale and carbonate environments ( $p < 0.01$ ).

**Table 2.2** ‘p’ values show distinctness between the genera within Atrypinae subfamily<sup>a</sup>

|                    | <i>Atrypa</i> | <i>Dihelictera</i> | <i>Endrea</i> | <i>Gotatrypa</i> | <i>Joviatrypa</i> | <i>Kyrtatrypa</i> | <i>Oglupes</i> |
|--------------------|---------------|--------------------|---------------|------------------|-------------------|-------------------|----------------|
| <i>Atrypa</i>      | 0             | 0.262              | <b>0.000</b>  | <b>0.000</b>     | 0.088             | <b>0.000</b>      | 0.184          |
| <i>Dihelictera</i> | 1             | 0                  | 0.616         | 0.685            | 0.950             | 0.031             | 0.780          |
| <i>Endrea</i>      | <b>0.000</b>  | 1                  | 0             | 0.084            | 0.827             | <b>0.000</b>      | 0.242          |
| <i>Gotatrypa</i>   | <b>0.000</b>  | 1                  | 1             | 0                | 0.655             | <b>0.000</b>      | 0.011          |
| <i>Joviatrypa</i>  | 1             | 1                  | 1             | 1                | 0                 | <b>0.004</b>      | 0.444          |
| <i>Kyrtatrypa</i>  | <b>0.000</b>  | 0.647              | <b>0.000</b>  | <b>0.000</b>     | 0.076             | 0                 | 0.658          |
| <i>Oglupes</i>     | 1             | 1                  | 1             | 0.229            | 1                 | 1                 | 0              |

<sup>a</sup>  $p < 0.01$ 

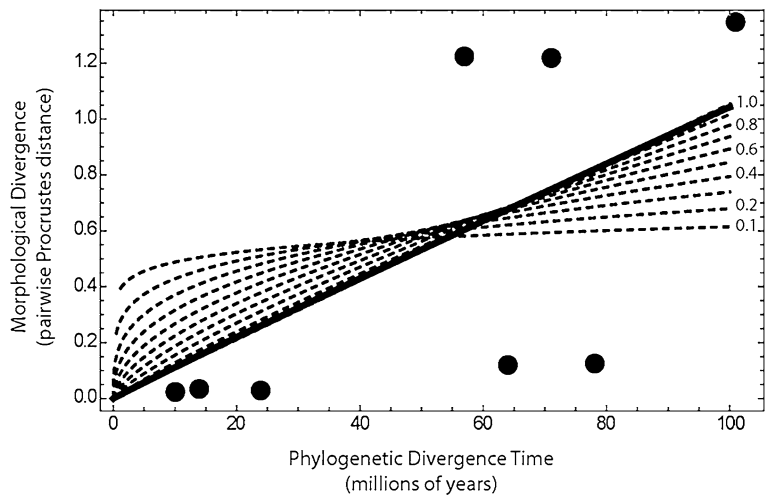
## 2.5 Discussion

### 2.5.1 Taxonomy

In this study, various atrypid genera from the Silurian-Devonian atrypid subfamilies were identified based on phenotypic characters other than shell shape. Overall, significant morphometric differences exist in the shells between subfamilies, thus supporting suggestions put forward by Copper (1973) that these groups are distinct. Significant morphometric differences also exist in the shells between genera within Atrypinae subfamily, also supporting his (Copper 1973) suggestion that they are distinct. However, the differences in external shell morphology and shell shape among subfamilies and genera are small, further evidenced from smaller morphological distances, with considerable shape overlap at all levels. Thus, this suggests that genera would be difficult to distinguish based on shell shape alone. Overall, morphological distance is greater between subfamilies than between genera from the same subfamily, thereby supporting phylogenetic patterns and taxonomic differentiation proposed by Copper (1973).

Though morphometric differences are statistically significant between the shape means of subfamilies and genera, their overall morphological variation overlaps at all levels. This study determined the morphological distances between genera from atrypid subfamilies under investigation and evaluated its relationship with the evolutionary divergence time intervals between genera worked out from the phylogenetic chart proposed by Copper in 1973. His (Copper 1973) phylogeny was the most recent study performed in terms of understanding the generic relationships in atrypides, and so this was used in testing the taxonomy and phylogeny of a few atrypid genera of interest in terms of morphological shape.

The results of the analysis of evolutionary rate and mode indicate that diversifying selection has probably been acting on these atrypid genera, despite the very small morphological divergences among them (Fig. 2.7). Based on the principal component plots (Fig. 2.4), the large degree of morphometric overlap among genera might be interpreted to represent stasis, since none of the atrypid genera have unambiguously diverged from each other. However, the statistical definition

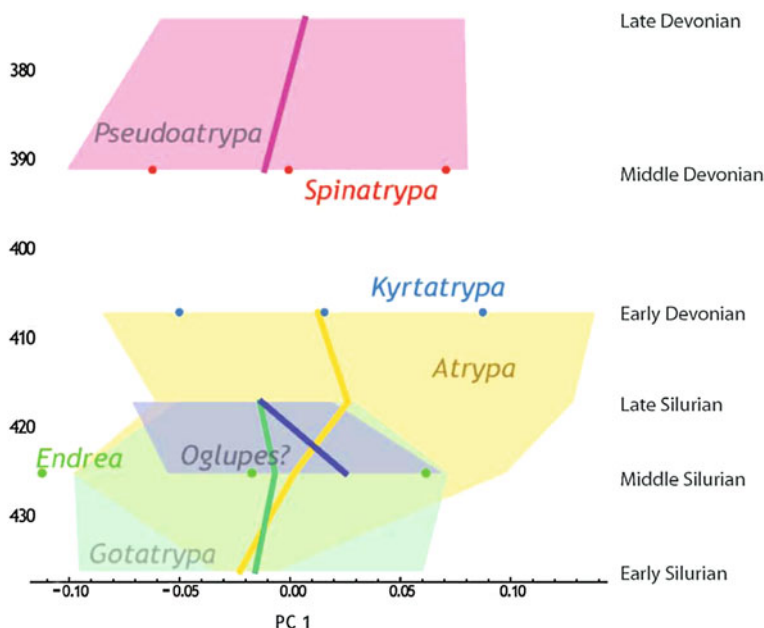


**Fig. 2.7** Graph showing morphometric divergence (pairwise Procrustes distances) and phylogenetic divergence (millions of years). The series of *dashed lines* show the expected relationship between morphological and phylogenetic divergence time from strong stabilizing selection (0.1), through random divergence (0.5), to diversifying (directional) selection (1.0). The maximum-likelihood estimate of this relationship, shown by the *dark line*, suggests that these atrypids have experienced diversifying selection

**Table 2.3** Procrustes distances between genera within three subfamilies (Atrypinae: *Atrypa*, *Gotatrypa*, *Kyrtatrypa*, Variatrypinae: *Pseudoatrypa* and Spinatrypinae: *Spinatrypa*) and evolutionary time between genera calculated from Copper’s (1973) phylogenetic chart

| Atrypide taxa                           | Phylogenetic distance (m.y.) | Morphological distance (Procrustes units) |
|---|------------------------------|---|
| <i>Atrypa</i> - <i>Gotatrypa</i>        | 10                           | 0.023                                     |
| <i>Atrypa</i> - <i>Kyrtatrypa</i>       | 24                           | 0.026                                     |
| <i>Gotatrypa</i> - <i>Kyrtatrypa</i>    | 14                           | 0.032                                     |
| <i>Atrypa</i> - <i>Pseudoatrypa</i>     | 64                           | 0.121                                     |
| <i>Gotatrypa</i> - <i>Pseudoatrypa</i>  | 64                           | 0.122                                     |
| <i>Kyrtatrypa</i> - <i>Pseudoatrypa</i> | 78                           | 0.127                                     |
| <i>Atrypa</i> - <i>Spinatrypa</i>       | 57                           | 1.223                                     |
| <i>Gotatrypa</i> - <i>Spinatrypa</i>    | 57                           | 1.224                                     |
| <i>Kyrtatrypa</i> - <i>Spinatrypa</i>   | 71                           | 1.22                                      |
| <i>Pseudoatrypa</i> - <i>Spinatrypa</i> | 101                          | 1.345                                     |

of stasis, or stabilizing selection, is that less divergence has occurred than expected under a random-walk (Brownian motion) model of evolution given the amount of time since divergence and the degree of within-taxon variation (Bookstein 1987; Gingerich 1993; Roopnarine 2001). For these atrypide genera, the changes in mean shape are greater than expected given time since divergence and the amount of within-genus variation—the most likely estimate of *a* in Eq. 2.1 given the data



**Fig. 2.8** Morphological shape trend for dorsal valves with a minimum, mean and maximum PC scores for seven atrypid genera (*Atrypa*, *Gotatrypa*, *Endrea*, *Oglupes?*, *Kyratrypa*, *Pseudoatrypa*, *Spinatrypa*) distributed in the six time units (early Silurian, middle Silurian, Late Silurian, early Devonian, middle Devonian, late Devonian)

presented in Fig. 2.7 is near 1.0 (dark line). Stasis would produce a pattern where the best fit would have a value near 0.0 for parameter  $a$ , which is decidedly not the case for these data, even when bootstrapped to account for the small sample size and seemingly outlying data points. The best interpretation of shape evolution in these genera given the data is that they were diversifying from one another, but at a rate slow enough that they still overlapped considerably through the time period covered in our study. Our morphometric data are thus consistent with the divisions of taxonomy and the broad strokes of phylogenetic arrangement proposed by Copper (1973), but they indicate that divergences among these genera are very small compared to their within-genus variation, so much so that it is impossible to refer single individuals to a genus on the basis of their geometric shell shape alone. Overall, the scaling between morphological distance and phylogenetic interval generally supports his (Copper 1973) phylogenetic arrangement.

Some general observations noted for a few genera that were included for the test of evolutionary rates and modes are also described. Morphological relatedness between *Pseudoatrypa* and other genera (*Atrypa*, *Kyratrypa*, *Gotatrypa*) from Atrypinae shows a discrepancy with the evolutionary divergence time proposed by Copper (1973). The lesser morphological shape distance between atrypin and variatrypin members retrieved from our analysis suggests the possibility of a generic level difference rather than one at the subfamily-level; however, it also

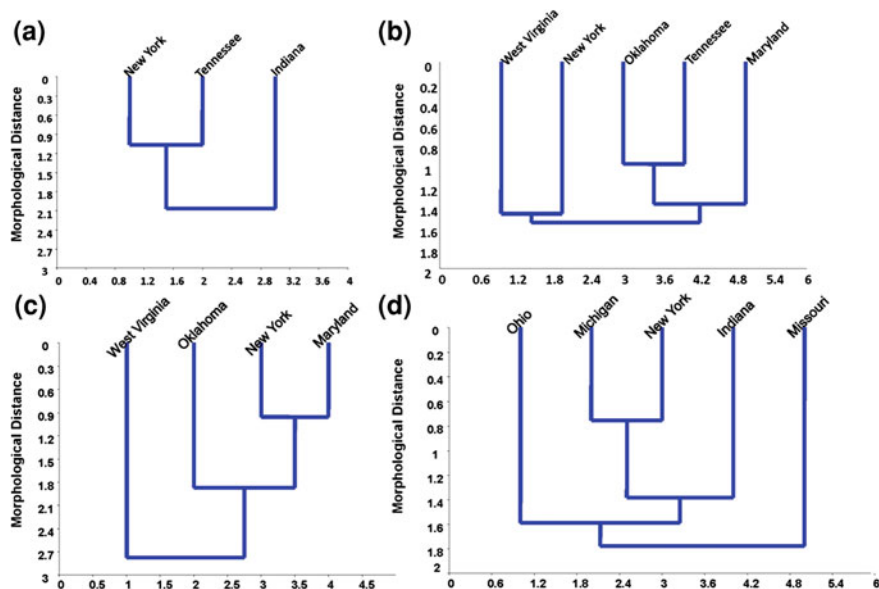
**Table 2.4** Procrustes distance in *Atrypa*, *Gotatrypa*, and *Pseudoatrypa* between time units

| <i>Gotatrypa</i>    | Early Silurian  | Middle Silurian | Late Silurian  |
|---------------------|-----------------|-----------------|----------------|
| Early Silurian      | 0               | 1.1262          | 1.7833         |
| Middle Silurian     | 1.1262          | 0               | 1.6767         |
| Late Silurian       | 1.7833          | 1.6767          | 0              |
| <i>Atrypa</i>       | Middle Silurian | Late Silurian   | Early Devonian |
| Middle Silurian     | 0               | 1.0888          | 0.70276        |
| Late Silurian       | 1.0888          | 0               | 0.86955        |
| Early Devonian      | 0.70276         | 0.86955         | 0              |
| <i>Pseudoatrypa</i> | Middle Devonian | Late Devonian   |                |
| Middle Devonian     | 0               | 0.992           |                |
| Late Devonian       | 0.992           | 0               |                |

confirms that these two subfamilies are closely related. Also, the greater phylogenetic distance between atrypin genera and *Pseudoatrypa* than between atrypin genera and *Spinatrypa* may raise doubts about their phylogenetic arrangement with respect to atrypin genera as retrieved from the phylogenetic chart proposed by Copper (1973). His (Copper 1973) distinctions were made on characters other than shell shape, such as morphology of the pedicle, rib structure and internal features, which may be more diagnostic than simple shell shape. Indeed, the differences in mean shell shape that we found are largely congruent with his (Copper 1973) divisions. In other words, shape analysis has partial bearing on classification, and without including other morphological characters into the morphometric analysis, it is challenging to firmly support the correctness of the phylogeny proposed by Copper (1973). Nevertheless, while the atrypid genera might not have been taxonomically oversplit, the large morphological overlap in shell shape raises questions about the level of distinction among the genera. Overall, though morphometric shell shape is a simple morphological measure, it involves multivariate phenotypic traits that can model complex parts of morphologies in genera, further capturing functional constraints among them, thus proving their usefulness in taxonomic studies (Webster and Zelditch 2009).

### 2.5.2 Temporal Variation

Phenotypic traits have been studied in the paleontological fossil record, both qualitatively and quantitatively, in terms of long-term and short-term geologic intervals. No one has quantified morphological characters to study atrypids in long term intervals using geometric morphometrics. Our current understanding is that atrypids originated in the late Middle Ordovician (Llandeilo) and increased in generic diversity and abundance during the Early Silurian (upper Llandovery to Wenlockian), after which they declined in diversity during the Late Silurian (Pridoli) through the Early Devonian (Lockhovian), followed by another peak in diversity during the Emsian-Givetian when many of these genera had worldwide distributions



**Fig. 2.9** Morphological links for dorsal valves of atrypids in various eastern North America biogeographic locations—**a** *Atrypa* in Middle Silurian; **b** *Atrypa* in Early Devonian; **c** *Kyratrypa* in Early Devonian; **d** *Pseudoatrypa* in Middle Devonian

(Copper 2001a, b). Thus, abundant and well preserved atrypids in the Silurian-Devonian geologic interval comprise a great case study to test temporal change.

Our data include atrypid subfamilies and the genera within those subfamilies available for investigation from a 64 Myr (Silurian-Devonian) time period. Using geometric morphometrics, in studying temporal variation patterns, besides solving taxonomic and phylogenetic problems in Silurian-Devonian well preserved, abundant atrypids, is an entirely novel approach. While morphometric differences existed between atrypid subfamilies and genera and for genera between successive time intervals corresponding to the EE subunits ( $p < 0.01$ ; Figs. 2.4, 2.8; Table 2.2), considerable morphological overlap between lowermost and uppermost mean morphological shape occurrences is exhibited with short term changes within lineages in the intermediate time intervals (Fig. 2.8). Overall, smaller morphological distances between atrypids show that the three subfamilies, Atrypinae, Variatrypinae and Spinatrypinae did not differ much based on morphological shape. However, the statistically significant valve shapes differences within these subfamilies over time (Fig. 2.4) could have been in response to their adapting to changing paleoenvironmental conditions prevailing in those time periods. On average, atrypids show smaller average morphological distances in time (0.025–0.028), which is representative of little or no morphological change, as expected in an EEU.

The small magnitude of morphological distance between subfamilies (0.12–1.35), although relatively greater than those between genera within Atrypinae (0.01–0.05), concurs with the current classification system in atrypides.

**Table 2.5** Procrustes distance in *Atrypa* from middle Silurian and early Devonian localities, *Kyrtatrypa* from early Devonian localities, and *Pseudoatrypa* from middle Devonian localities within the Eastern North American province

| <i>Atrypa</i><br>(Middle Silurian)       | Indiana  | New York |          | Tennessee     |               |
|--|----------|----------|----------|---------------|---------------|
| Indiana                                  | 0        | 2.2978   |          | 1.7388        |               |
| New York                                 | 2.2978   | 0        |          | 1.78          |               |
| Tennessee                                | 1.7388   | 1.78     |          | 0             |               |
| <i>Atrypa</i><br>(Early Devonian)        | Maryland | New York | Oklahoma | Tennessee     | West Virginia |
| Maryland                                 | 0        | 1.8611   | 1.4005   | 1.3523        | 2.0355        |
| New York                                 | 1.8611   | 0        | 1.2749   | 1.5206        | 1.8178        |
| Oklahoma                                 | 1.4005   | 1.2749   | 0        | 0.99102       | 1.5379        |
| Tennessee                                | 1.3523   | 1.5206   | 0.99102  | 0             | 1.2561        |
| West Virginia                            | 2.0355   | 1.8178   | 1.5379   | 1.2561        | 0             |
| <i>Kyrtatrypa</i><br>(Early Devonian)    | Maryland | New York | Oklahoma | West Virginia |               |
| Maryland                                 | 0        | 1.4029   | 2.0997   | 2.4742        |               |
| New York                                 | 1.4029   | 0        | 1.5751   | 2.8275        |               |
| Oklahoma                                 | 2.0997   | 1.5751   | 0        | 2.8087        |               |
| West Virginia                            | 2.4742   | 2.8275   | 2.8087   | 0             |               |
| <i>Pseudoatrypa</i><br>(Middle Devonian) | Indiana  | Michigan | Missouri | New York      | Ohio          |
| Indiana                                  | 0        | 1.463    | 2.2745   | 1.6567        | 1.7556        |
| Michigan                                 | 1.463    | 0        | 1.4886   | 0.64741       | 1.5887        |
| Missouri                                 | 2.2745   | 1.4886   | 0        | 1.3663        | 2.0634        |
| New York                                 | 1.6567   | 0.64741  | 1.3663   | 0             | 1.4282        |
| Ohio                                     | 1.7556   | 1.5887   | 2.0634   | 1.4282        | 0             |

Surprisingly, the morphological shape distances within *Atrypa*, *Gotatrypa* and *Pseudoatrypa* in time (0.7–1.8) are similar or greater than those measured between subfamilies (Table 2.4). This suggests that this difference may be either due to differences in sample size (as the between-genera distances are based on several samples of the same family, whereas the distances through time are based on sub-samples of the same genus), or it may be due to numerous real short-term changes within the lineages, which get averaged out when comparisons are made between genera. This observed pattern is consistent with stasis. This further suggests that within group variation was greater than between group variation.

### 2.5.3 Spatial Variation

Morphological distances and range of these distances between geographic localities within *Atrypa* (Middle Silurian and Early Devonian), *Kyrtatrypa* (Early



Devonian) and *Pseudoatrypa* (Middle Devonian) (0.6–2.8) are similar to greater than those observed for individual genus (*Atrypa*, *Gotatrypa* and *Pseudoatrypa*) in time (0.7–1.8) (Tables 2.4, 2.5), thus, further confirming greater amount of within-group variation in atrypids. The distances for all these genera also tend to overlap, but the random clustering of geographic localities for each genus and all genera, do not provide a strong biogeographic signal. On average, the smaller average morphological distances in space units (0.027–0.040), suggest little or no morphological change in atrypids spatially.

### 2.5.4 Environmental Effect

Atrypin, variatrypin and spinatrypin genera lived in broad depositional settings ranging from siliciclastics to carbonates to mixed siliciclastic-carbonate settings (Jodry 1957; Droste and Shaver 1975; Cuffey et al. 1995). For example, *Joviatrypa* preferred quiet, relatively deeper water, muddy substrate assemblage, *Dihelictera* are known to have been derived from a patch reef assemblage, and *Endrea* are derived from biostromal to reefal units (Copper 1995, 1997), while many smooth to tubular ribbed atrypids preferred high energy reefal settings (Copper 1973). *Spinatrypa* have been commonly found in high energy sandy environments (Leighton 2000), though they have also been accounted from low energy muddy environments (Copper 1973). Some of the atrypids of the Genshaw Formation of Traverse Group lived in the full range of rough to quieter energy conditions (McIntosh and Schreiber 1971). Thus, there is a wide variation in preference of substrates and energy conditions for atrypid genera to thrive.

Atrypides expanded in diversity and abundance through Emsian to Givetian, and the expansion of reef growth both equatorially and latitudinally could explain their distribution along the shallow water (<100 m deep) tropical shelf environments (Copper 2001a, b). Overall, atrypin genera preferred nearshore to slope habitats (Zhang and Barnes 2002; Copper 2001a, b), variatrypin genera preferred middle to outer platform habitats (Day 1995) and spinatrypins preferred outer platform to platform margin habitats (Leighton 2000).

While it is probable that the variation observed within individual atrypid genera in time and space suggests some short term changes and within group variation, it is also important to take into account the paleoenvironmental settings from which these genera were derived that may have caused this variation. Testing for preference of habitats, sedimentology, grain size, and lithology and their correlation with respective atrypid genera may provide a clue for the causes behind the morphological variation observed both within a genus and between the genera in time and space. However, this study mainly focuses on testing the taxonomy and phylogeny using geometric morphometrics, and thus the environmental parameters that may have caused this morphological shape change is the scope of a future study.

Results from one test performed were analysed to determine the morphological shape response to lithologic settings. The same genus (*Atrypa*, *Gotatrypa*, *Endrea*,

*Pseudoatrypa*) tested for morphometric shape from shale and carbonate lithologic settings show statistically significant results ( $p < 0.01$ ). However, the temporal patterns observed in genera from three pairs of distinct lithologic settings, Early Silurian packstones and mudstones and Middle Silurian carbonate-siliciclastics, Early Silurian packstones and mudstones and Late Silurian carbonate-siliciclastics, Middle Devonian carbonate-siliciclastic and Late Devonian carbonates show a slightly higher range of morphological distances (0.99–1.78 Procrustes units) as compared to those from three pairs of similar lithologic settings, Middle and Late Silurian carbonate-siliciclastics, Middle Silurian and Early Devonian carbonate-siliciclastics, and Late Silurian and Early Devonian carbonate-siliciclastics which show a relatively smaller range of morphological distances (0.70–1.09 Procrustes units). Overall, there appears to be no significant relationship between the temporal patterns and lithologic settings, as similar magnitudes (1.1 Procrustes units) of morphological distances result when both overlapping (Middle and Late Silurian carbonate-siliciclastics) and distinct (early Silurian packstones to mudstones and middle Silurian carbonate-siliciclastics) lithologic settings were compared in time. Thus, lithological distribution does not explain for the greater similarity in certain time intervals (middle Silurian-early Devonian: 0.70 Procrustes units, late Silurian-early Devonian: 0.87 Procrustes units) than other intervals (middle Silurian-late Silurian: 1.09 Procrustes units). Similarly, spatial patterns and lithologic settings for genera from the Middle Silurian, Early and Late Devonian time periods exhibit no significant relationship. Magnitudes of morphological distances are similar for both overlapping and distinct lithologies in spatial units. In terms of biogeographic setting, only Early Devonian *Atrypa* genus shows biogeographic signal in that Tennessee and Oklahoma samples are closely linked with more resemblance to Maryland samples than to New York and West Virginia samples. However biogeographically closely spaced Maryland and West Virginia, and Maryland and New York samples from Early Devonian show less similarity. Other genera from Middle Silurian, Early and Middle Devonian (*Atrypa*, *Kyrtatrypa*, *Pseudoatrypa*), show no biogeographic signal. For instance, the greater morphological distances between the Middle Devonian closely spaced Missouri and Indiana-Ohio samples as compared to smaller distances between the distantly spaced Missouri and West Virginia-New York samples, suggest that these derived morphological links cannot be explained by biogeographical setting. Neither can these discrepancies be explained by environmental parameters like lithologic settings. Thus, given that the relationship between change in morphological shape and change in other environmental parameters remain unravelled, the morphometric differences in shape observed within genera, between genera, and between subfamilies in time and space could be attributed to their adaptability to other changing environmental conditions or their differential life habits. An overall morphological shape overlap within these groups in the Silurian and Devonian time intervals suggests a close relationship among the genera and subfamilies.

Considerable mean morphological shape overlap between Lower Clinton and Genesee EESU (both relatively close to the P3 EEU boundaries), is indicative of similar climatic settings during this time, such as lowering of the sea level, and the

onset of cold climate. However, it is noteworthy that these were different genera in the respective EESUs (*Atrypa*, *Gotatrypa* represent Lower Clinton and *Pseudotrypa* represent Genesee) and that they still show considerable overlap, which was probably because they belonged to closely related subfamilies.

If the hypothesis of ecological locking (Morris 1995; Morris et al. 1995) within EEU is correct, then morphological stability is expected within these atrypids as these were sampled from the P3 EEU of the Phanerozoic rock record. Atrypides, most likely, maintained their evolutionary stability through ecological interactions within the unit and as there were no major extinction events within that period, the ecosystem must have remained stable throughout with the exception of minor extinction events that separated the EESUs within the P3 EEU. In this study, overall morphological shape overlap observed between atrypid genera in time, though new taxonomic entities replace each time unit, can be referred to as a case of loose stasis. However, individual genera show large amount of distances between time units and thus, evolutionary rates and modes of each genus in time need to be further investigated to confirm whether loose stasis was really the case.

Morphological evolutionary patterns tested in a few atrypid genera (*Atrypa*, *Gotatrypa*, *Pseudotrypa*) suggest morphological change observed within each lineage is not dramatic as they show some change around the mean which get averaged out in time when compared to other generic pair distances, a pattern similar to stasis. In contrast, these short term changes may be a causal effect of ecophenotypic variation. A few atrypid genera (*Atrypa*, *Kyrtatrypa*, *Pseudotrypa*) tested in space, also show variation within the same group in space units, and no strong biogeographic signal can be derived from the pattern of clustering observed in eastern North American geographic localities. Overall, atrypids are phenotypically plastic, and often distinguishing one genus from another may be very challenging based on morphological shape alone.

## 2.6 Conclusion

Morphological distances between subfamilies were greater than those between genera within a subfamily, thus suggesting the correct reference of these genera to their respective subfamilies. Evolutionary divergence times among genera retrieved from the phylogenetic tree proposed by Copper (1973) are consistent with the pairwise distances calculated from our morphological shape data, which further supports the taxonomic arrangement and phylogenetic patterns reported in his (Copper 1973) research article. Evolutionary rate and mode indicate that diversifying selection has probably been acting on these atrypid genera at a very slow rate, despite the very small morphological divergences among them. However, some discrepancy arises, and so further evaluation of phylogenetic distances between atrypin genera with that of *Pseudotrypa* and *Spinatrypa* as a test of relatedness is necessary. Moreover, the morphological shape distances between variatrypin and atrypin genera were so small that these are more like the generic level differences

than subfamily level differences. Thus, these discrepancies need to be further examined through a phylogenetic analysis using the combination of internal morphological features and quantified morphological shape.

Morphological shape analysis shows considerable overlap in Silurian–Devonian atrypid members within the P3 EEU, representing a case of loose stasis. Moreover, large morphological distances between time units within the same genus suggest the possibility of short term changes within a lineage being averaged out when compared with generic pair distances, representing a pattern similar to stasis. Results from several geometric morphometric techniques (including Procrustes analysis and principal component analysis) suggest a certain degree of morphological variability between subfamilies and genera in time and space, which can be attributed to changing paleoenvironmental conditions. Temporal change with some constraints within individual genus (*Atrypa*, *Gotatrypa* and *Pseudotrypa*) and geographic variation within some genera (*Atrypa*, *Kyrtatrypa* and *Pseudotrypa*) suggest within group variation was greater than between group variation. Geographic differentiation in morphological shape within atrypids appears to be greater than temporal variation.

Overall, morphological shape change pattern and morphometric divergence in atrypid genera is consistent with the phylogeny proposed by Copper in 1973. Thus, in the 64 myr time scale within the P3 EEU, atrypids in general reflect a high degree of morphological shape conservation in the Silurian–Devonian time interval, regardless of their distinct taxonomic entities.

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