MORPHOMETRICS INDICATES GIANT ORDOVICIAN MACLURITID GASTROPODS SWITCHED LIFE HABIT DURING ONTOGENY

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ABSTRACT—Paleontologists have long speculated that the bizarre, giant Ordovician gastropods Maclurites Le Sueur, 1818 and Maclurina Ulrich and Scofield, 1897 lived more like suspension-feeding oysters than typical algivorous snails. Geometric and eigenshape morphometrics demonstrate the plausibility of this lifestyle, but with a twist. The apertures of these gastropods were small ellipsoids when young, transitioning rapidly to polygonal morphologies at maturity, with angulations (sinuses) occurring in regions associated with development of mature ctenidia (gills) and enhanced stability on the seafloor. Combined with knowledge of extant suspension-feeding gastropods and functional and phylogenetic analysis of the anatomy of other fossil relatives, this ontogenetic pattern suggests these snails began life as typical mobile algae-grazers, but switched to sedentary suspension-feeders as they aged.

INTRODUCTION

INFERRING THE ecology of extinct animals is a challenge, but especially so for strange fossils. With their flat bottom, heavily thickened shell, massive operculum, idiosyncratic hyperstrophic coiling, and enormous size up to 26 cm in diameter (Rohr et al., 1992), Maclurites Le Sueur, 1818 and Maclurina Ulrich and Scofield, 1897 are perhaps the most bizarre Ordovician gastropods (Fig. 1A). Their ecology was first suggested by Salter in 1859, who concluded, based on their non-abraded flat bottom and encrusting stromatoporoid sponges above, that they lay sedentary on the seafloor. This inference remains unchanged today, anchored by the work of Linsley (1977, 1978) who further speculated that these snails were suspension-feeders based on functional interpretations of shell mobility and stability. Wagner and Erwin (2006), drawing on similar functional analyses, also argued macluritidoids and other Paleozoic gastropods with “eumphaliform” morphotypes were sedentary suspension-feeders based on the correlated decline in both this morphotype and feeding habit across the Phanerozoic. Although this feeding habit is rare among extant gastropods, the argument is based on a rational interpretation of macluritid functional morphology, albeit one formed more by lack of options than by direct evidence: suspension-feeding is the only possible heterotrophic feeding mode available to such an enormous, immobile mollusk. Analyses of extant suspension-feeding gastropods (Declerck, 1995; Chaparro et al., 2002; Navarro and Chaparro, 2002) provide valuable insight because such gastropods typically begin life grazing algae (or deposit feeding), only switching to suspension-feeding after ctenidia (gills) are sufficiently mature to have suitable filtration surfaces and flow rates. Therefore, if macluritids were typical suspension-feeding gastropods, their aperture—a snail’s most important shell feature functionally related to respiration, excretion, reproduction, sensation, defense, and, in the case of suspension feeders, feeding within the mantle cavity—might exhibit an ontogenetic switch in morphology during growth. Here we use morphometrics of cross-sectioned macluritid fossils to demonstrate that such a morphological transition in apertural size and shape does occur, and that it substantiates the hypothesis that macluritids underwent a transition from a typical mobile snail when young, switching to life as a sedentary suspension feeder when mature.

METHODS

Specimens.—Specimens of Maclurites and Maclurina that were cross-sectioned through the coiling axis were obtained from the Field Museum of Natural History (FMNH) and from published figures (Rohr and Measures, 2001) (Fig. 1A, Table 1). Not all specimens were able to be subjected to both apertural size analysis and eigenshape analysis due to partial preservation and also where the angulation (sinus) develops along the apical cross-section (margin). For the specimen of Maclurina manitobensis, both halves of the cross-sectioned specimen were available, with specimen FMNH PE 61201A used in measurement of apertural area and specimen FMNH PE 61201B used for apertural shape, although the counterpart was used in some cases to visually confirm the shape of certain apertures. As an estimate of measurement error, the separately measured counterparts had negligible sampling errors. Apertural area (A) had a mean percent error of 0.65% across both apertures (mean of 100% (A1−A2)/A2) whereas radius measurements had a mean percent error of 3.3%. For eigenshape analysis, the mean Euclidean distance along eigenshape axes 1 and 2 between paired apertures was 0.029; divided by the maximum (diagonal) range (\sqrt{range_{axis1}^2 + range_{axis2}^2}) across the two-dimensional eigenshape space, this is equal to a 6.2% error in apertural shape. Similar measurement error values were obtained on replicate measurements of individual specimens.

Because macluritids have slow, log-linear whorl expansion rates (Banks and Johnson, 1957), these cross sections spanned the entire teleoconch (post-larval) ontogeny, revealing between four and seven apertures at one-half volutions (180° revolutions) around the coiling axis, with the earliest aperture in each specimen designated 1, progressing incrementally to later apertures. The interior apertural margin was digitized because it is functionally related to the relevant anatomy of the mantle cavity and cephalopodal mass, and because several specimens were preserved as steinkerns (internal molds).

Apertural area methods.—Interior apertural margins were digitized using tpsDig (Rohlf, 2010) (Fig. 1A), setting the first Cartesian (x,y) coordinate at a constant landmark near the point of uppermost whorl contact corresponding to maximum inflection—and also where the angulation (sinus) develops along the apical whorl margin—and then continuing clockwise around the
Eigenshape axes account for 62% of variance in data (Table 3); species numbers denote position of aperture in eigenshape space, setting smallest measurable aperture to larger, angulate apertures, coincident with flattening of basal margin. Inclusion of larval protoconchs was not possible owing to lack of preservation, as is true for all other known macluritids (Fryda and Rohr, 2006). Digitized apertural outlines were interpolated in tpsDig to 100 equally spaced coordinates along a closed curve; this number of interpolated coordinates was sufficient to characterize the entire shape of macluritid apertures, even those with substantial angulations. The online software Morpho-tools.net (Krieger, 2012) was employed to conduct subsequent analyses. Standard eigenshape analysis (MacLeod, 1999) calculates the net circular-normalized angular deviation (phil, φ) between each adjacent apertural coordinate within each apertural curve and subjects these shape functions to a mean-centered singular value decomposition (using the covariance matrix). In addition to identifying those eigenshape axes that explain the greatest proportion of variance in the apertural shape data, the resulting output allows the ability to model how apertures change shape during macluritid ontogeny within the resulting eigenspace shape-space.

**Eigenshape analyses.**—To study trends in apertural shape, eigenshape analysis was used (MacLeod, 1999), which enables quantitative modeling of the entire apertural morphology, independent of its size, and is useful for specimens lacking discernible landmarks. We were only able to conduct eigenshape analysis on thirteen apertures from the three best-preserved specimens (three species) that had completely preserved apertural margins spanning the teleoconch ontogeny. Inclusion of larval protoconchs was not possible owing to lack of preservation, as is true for all other known macluritids (Fryda and Rohr, 2006). Digitized apertural outlines were interpolated in tpsDig to 100 equally spaced coordinates along a closed curve; this number of interpolated coordinates was sufficient to characterize the entire shape of macluritid apertures, even those with substantial angulations. The online software Morpho-tools.net (Krieger, 2012) was employed to conduct subsequent analyses. Standard eigenshape analysis (MacLeod, 1999) calculates the net circular-normalized angular deviation (phil, φ) between each adjacent apertural coordinate within each apertural curve and subjects these shape functions to a mean-centered singular value decomposition (using the covariance matrix). In addition to identifying those eigenshape axes that explain the greatest proportion of variance in the apertural shape data, the resulting output allows the ability to model how apertures change shape during macluritid ontogeny within the resulting eigenspace shape-space.

**Table 1**—Specimens used in study, with notes on taxonomy. Specimen numbers are those of the Field Museum of Natural History (FMNH, Chicago, IL) Fossil Invertebrate collections.

<table>
<thead>
<tr>
<th>Species</th>
<th>Specimen identifier</th>
<th>Notes</th>
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<tbody>
<tr>
<td><em>Maclurina manitobensis</em></td>
<td>PE 61201A</td>
<td>Steinkern displaying remnants of recrystallized shell around portions of steinkern. Larger half of cross-section of specimen PE 61201B. Label states “Maclurites sp., Silliman’s Fossil Mt., Frobisher Bay, Baffinland, S.K. Roy.” Morphology agrees well with description and figures in Roy (1941; fig. 81a–81c, p. 116).</td>
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<td>(Whiteaves, 1890)</td>
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<tr>
<td><em>Maclurina manitobensis</em></td>
<td>PE 61201B</td>
<td>Smaller half from cross-section of specimen PE 61201A. Steinkern displaying remnants of recrystallized shell around portions of steinkern. Label states “Silliman’s Fossil Mt., Frobisher Bay, S.K. Roy.” Morphology, especially narrow apical cavity and shape of apertures, agrees well with description and figures in Roy (1941; fig. 83a–83d, p. 118). However, the earliest apertures in this specimen are elliptical and not subtriangular as drawn in Roy’s figure.</td>
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<tr>
<td>(Whiteaves, 1890)</td>
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<tr>
<td><em>Maclurites cuneata</em></td>
<td>PE 61202</td>
<td>Steinkern displaying remnants of recrystallized shell around portions of steinkern. Label states “Silliman’s Fossil Mt., Frobisher Bay, S.K. Roy.” Morphology, especially narrow apical cavity and shape of apertures, agrees well with description and figures in Roy (1941; fig. 83a–83d, p. 118). However, the earliest apertures in this specimen are elliptical and not subtriangular as drawn in Roy’s figure.</td>
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<tr>
<td>(Whitfield, 1878)</td>
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<tr>
<td><em>Maclurites magnus</em></td>
<td>PE 61203</td>
<td>Label states “Maclura magna LeSeur, Chazy L.” A cross-sectioned specimen displaying recrystallized (possibly silicified) shell. Apertural margin displays faint, opisthocline growth lines. Apical cavity has nearly vertical apertural margins. The growth lines and apical cavity shape resemble that of <em>M. crenulata</em> and the apical cavity shape also resembles that of <em>Maclurites? acuminatus</em> (cf. Rohr and Measures, 2001), although the aperture of this specimen is significantly wider, with a more circular outer apertural margin.</td>
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<tr>
<td>Le Sueur, 1818</td>
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<td><em>Maclurites ponderosus</em></td>
<td>Rohr and Measures (2001, fig. 4)</td>
<td>Rohr and Measures (2001; fig. 4). These authors note that a lack of diagnostic criteria renders uncertainty in whether this specimen should be classified in the genus <em>Maclurites</em> or <em>Maclurina</em>.</td>
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<tr>
<td>(Billings, 1865)</td>
<td></td>
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<tr>
<td><em>Maclurites? acuminatus</em></td>
<td>Rohr and Measures (2001, fig. 5.21) GSC 117456.</td>
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<td>(Billings, 1865)</td>
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RESULTS

An inflection point occurs in the apertural size trend (Fig. 2) of five *Maclurites* and *Maclurina* species, approximately one volition before each specimen achieved mature size. Trends were analyzed statistically using least-squares regression analysis, fitting both logistic (sigmoidal) and power (linear on log-log graph) functions. Although both best-fit lines visually approximate the data, maximum-likelihood methods identify that the logistic (sigmoidal) growth model has greater support than the isometric power model in three (or four, depending on which cross-section is used for *M. manitobensis*) of five species (Table 2). Given the limited number of measurable apertures (an inherent constraint when dealing with slowly growing gastropods), such methods are most powerful for the ontogenetically nearly complete specimen of *M. ponderosus* (Rohr and Measures, 2001). Each of these five species grows according to distinct growth trajectories, evident by the heterogeneity of best-fit parameters (Table 2) and when all specimens are juxtaposed in a single analysis (Fig. 2). The interspecific growth trajectory is best-fit by a power function (even when removing the largest outlying aperture: Akaike weight equals 0.953 for power and 0.047 for logistic). For growth relationships involving two-dimensional area and linear radii, inter- and intra-specific scaling coefficients overlap the expected value of 2.0 (Table 2). However, the best-preserved specimen, *M. ponderosis*, has a scaling coefficient that is significantly larger than this expected value, lending additional support that the growth trajectory of individual species follows a non-isometric,
TABLE 2—Logistic and power function model-fitting statistics for ontogenetic increase in apertural size. Ontogenetic age is measured as shell radius (units cm), the distance from the coiling axis to the outer margin of successive apertures. Apertural size is measured as apertural area (units cm²). RSE and d.f. are the residual standard error and degrees of freedom for the best-fit logistic function and power (log-log) function. The instantaneous rate of increase (area cm²/radius cm), and a₀ is the intercept (cm²); both models also have a parameter for the root-mean-square error (RMSE); the log-likelihood for each model, AICc; the small-sample unbiased Akaike Information Criterion, and Akaike weight is the relative support for each model. The model with lower AICc values was selected, with associated Akaike weights. The table shows logistic model fit statistics for individual species (FMNH PE) and a single species pool (All specimens). The logistic model fit statistics for individual species are shown in bold, and the species pool is shown in italics.

| Species     | Specimen | RSE | df | K    | a₀    | b₀ | AICc | RSE | df | K    | a₀    | b₀ | AICc | RSE | df | K    | a₀    | b₀ | AICc |
|-------------|----------|-----|----|------|-------|----|-----|-----|----|------|-------|----|-----|-----|----|------|-------|----|-----|-----|----|-----|
| M. manitobensis | FMNH PE 61201A | 0.129 | 2 | 13.24 | 0.035 | 6.52 | 2.796 | 0.999 | 0.179 | 0.089 | 17.53 | 0.998 | 0.186 | 6.25 | 2.796 | 0.999 | 0.179 | 0.089 | 17.53 | 0.998 | 0.186 |
| M. magnus | FMNH PE 61203 | 0.015 | 1 | 6.468 | 0.006 | 5.351 | 1.977 | 1.000 | 0.111 | 0.076 | 9.308 | 1.000 | 0.107 | 6.468 | 0.006 | 5.351 | 1.977 | 1.000 | 0.111 | 0.076 | 9.308 | 1.000 | 0.107 |
| M. ponderosus | FMNH PE 61201B | 0.073 | 2 | 4.265 | 0.010 | 0.005 | 0.064 | 1.000 | 0.137 | 0.005 | 0.064 | 1.000 | 0.137 | 0.005 | 0.064 | 1.000 | 0.137 | 0.005 | 0.064 | 1.000 | 0.137 | 0.005 |
| M. attenuatus | FMNH PE 61201A | 0.129 | 2 | 13.24 | 0.035 | 6.52 | 2.796 | 0.999 | 0.179 | 0.089 | 17.53 | 0.998 | 0.186 | 6.25 | 2.796 | 0.999 | 0.179 | 0.089 | 17.53 | 0.998 | 0.186 |
| All species  |          | 0.090 | 22 | 13.170 | 0.004 | 0.253 | 6.581 | 1.000 | 0.137 | 0.005 | 0.064 | 1.000 | 0.137 | 0.005 | 0.064 | 1.000 | 0.137 | 0.005 | 0.064 | 1.000 | 0.137 | 0.005 |

DISCUSSION

These results demonstrate that Ordovician macluritid gastropods underwent a substantial and rapid morphological transition in apertural morphology during ontogeny, a transition suggestive of an associated switch in their ecological life habit. Juvenile snails had small, smoothly ellipsoidal apertures; their overall shell size, apertural shape, and the lack of a flat basal surface suggest the life habit of typical mobile, algae-grazing vetigastropods. As the snails grew, and presumably as maturing ctenidia became larger and generated sufficient feeding currents in the mantle cavity (Declerck, 1995; Chaparro et al., 2002; Navarro and Chaparro, 2002), the aperture changed to accommodate flattening of the basal surface and buttressing where the aperture abutted prior whorls and progressive development of an upper angulation (sinus) to accommodate modified flow within the mantle cavity. The limited number of shell volutions, typically no more than four in even the largest macluritid teleoconchs, and the shift in apertural area and shape preceding production of the final whorl volution may further suggest a reduction in growth rate coincident with this ecological transition. These observations—combined with the thickened shell, stabilizing infilling of whorls in advanced macluritid species (Rohr and Measures, 2001; Wagner, 2002), massive and potentially anchoring operculum (Rohr and Yochelson, 1999), and occurrence within productive, shallow-subtidal carbonate-bank depositional environments (Nelson, 1959; Rohr et al., 1992; Gubanov and Rohr, 1995; Rohr and Measures, 2001)—all suggest a transition to a sedentary, suspension-feeding lifestyle for these now-giant snails.

Additional lines of evidence also support this lifestyle for these taxa. Functional interpretations of macluritid apertures (Morris, 1991; Wagner, 2002; Wagner and Erwin, 2006) suggest that derived macluritids with asymmetrical apertures and weak sinuses, including those studied here, had a reduced-to-absent ctenidium on the apical (post-torsional right) side and an enlarged ctenidium on the outermost side. This anatomy is also logistic allometry when the complete growth sequence is available.

Eigenshape analysis (Fig. 1B, Table 3) demonstrates that macluritid apertures also changed shape during ontogeny, becoming progressively less round and more angular. This morphological trend, which occurs in tandem across species, occurs primarily along eigenshape axis 1, which records a gradient increasing from ellipsoidal to polygonal apertural morphologies. Species are differentiated somewhat along axis 2, recording a gradient increasing from (slightly bloated) spherical to oblong-oval morphologies. Similar parallel trends, from rounded to variously polygonal morphologies, are recorded on higher eigenshape axes, typically focusing on the location of individual angulations. Within gastropod apertures, such angulations are typically associated with regions of mantle cavity water flow (Linsley, 1977), although soft mantle tissue also plays an important role (Voltzow et al., 2004) in regulating water flow. Based on the eigenshape gradients, the most pronounced angulations developed in four apertural regions: an upper angulation corresponding to a weak sinus functioning as an excavent region associated with ctenidia (Wagner, 2002; Wagner and Erwin, 2006); along the inner apical surface, which abuts the previous whorl; and along both edges of the basal surface, which allow progressive flattening with maturation. There is a notable shift in the eigenspace between earlier apertures (having negative values along axis 1) and later ones (with positive values), which tends to coincide in ontogeny with the inflection point visible in apertural area (Fig. 1B).
Table 3—Variance accounted for by each eigenshape axis (ES) in the eigenshape analysis. Although meaningful shape information is explained on several of the first axes, only the first two axes are discussed.

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<th>ES1</th>
<th>ES2</th>
<th>ES3</th>
<th>ES4</th>
<th>ES5</th>
<th>ES6</th>
<th>ES7</th>
<th>ES8</th>
<th>ES9</th>
<th>ES10</th>
<th>ES11</th>
<th>ES12</th>
</tr>
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<tr>
<td>Eigenvalues</td>
<td>0.10</td>
<td>0.06</td>
<td>0.03</td>
<td>0.02</td>
<td>0.01</td>
<td>0.01</td>
<td>0.01</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
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<tr>
<td>Total variance (%)</td>
<td>38.1</td>
<td>23.5</td>
<td>11.6</td>
<td>8.2</td>
<td>5.3</td>
<td>3.6</td>
<td>2.5</td>
<td>2.0</td>
<td>1.9</td>
<td>1.8</td>
<td>1.1</td>
<td>0.5</td>
</tr>
<tr>
<td>Cumulative variance (%)</td>
<td>90.3</td>
<td>92.7</td>
<td>94.8</td>
<td>96.6</td>
<td>98.4</td>
<td>99.5</td>
<td>100.0</td>
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NOVACK-GOTTSHALL AND BURTON—ONTOGENETIC CHANGES IN MACLURITID GASTROPODS


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