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 "euomphaliform" 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 or ambiguity of apertural outline. More specimens could be included in analysis of apertural area because this measurement is less sensitive to complete preservation of the apertural (whorl 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 $100\% \cdot (A_1 - A_2)/A_2$) 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 cephalopedal 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
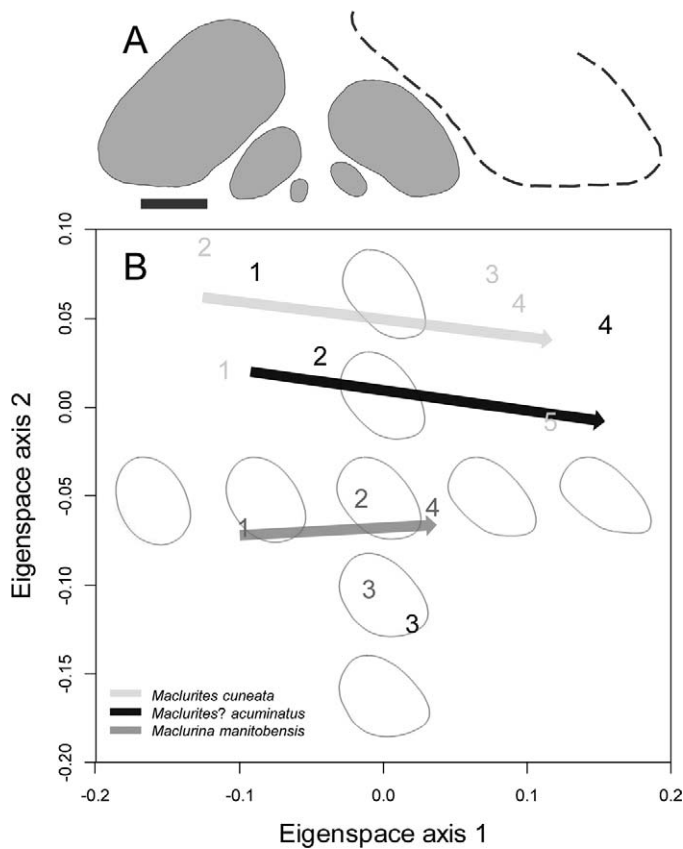
FIGURE *1*—Ontogenetic trends in apertural shape of Ordovician macluritid gastropod species. *A*, whorl cross-sections of *Maclurina cuneata* (Whitfield, 1878) (FMNH specimen PE 61202A) illustrating typical ontogenetic change in aperture size and shape; ontogeny progresses from small, ellipsoidal apertures to larger, angulate apertures, coincident with flattening of basal surface; dashed outline illustrates final incomplete aperture; the same specimen is illustrated in light gray in *B*; scale bar=1.0 cm; *B*, graph of first two eigenshape axes illustrates that apertures in three macluritid species all become progressively less round and more angular during ontogeny; numbers denote position of aperture in eigenshape space, setting smallest measurable aperture as 1 and progressing to largest measurable aperture; first two eigenshape axes account for 62% of variance in data (Table 3); species ontogenetic trends are calculated as least-squares regression lines.

apertural margin. Photographs of alternating apertures were rotated computationally so that all apertures were positioned in the same orientation, facing adaperturally with the coiling axis to the left. The shell radius for each aperture was measured as the distance perpendicular from the coiling axis to the outermost point along the apertural margin. Use of the innermost point generally does not alter results, but is less informative as a proxy for overall shell size because of the wide variation among species in the angle of the apical cavity. Analysis of ontogenetic trends in apertural area was conducted using least-squares regression analysis, fitting logistic (non-linear, sigmoidal) and power (linear when potted on log-log graph) functions, calling the functions lm () and nls () in the statistical language R (R Development Core Team, 2011). Model selection was evaluated employing maximum-likelihood methods with small-sample-corrected Akaike information criterion (AIC_C), and Akaike weights (Burnham and Anderson, 2002).

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 (Frýda 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 circle-normalized angular deviation (phi, 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.

| Species	Specimen identifier	Notes
Maclurina manitobensis (Whiteaves, 1890)	PE 61201A	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 Mount, Frobisher Bay, Baffinland, S.K. Roy." Morphology agrees well with description and figures in Roy (1941; fig. 81a–81c, p. 116).
Maclurina manitobensis (Whiteaves, 1890)	PE 61201B	Smaller half from cross-section of specimen PE 61201A
Maclurites cuneata (Whitfield, 1878)	PE 61202	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.
Maclurites magnus Le Sueur, 1818	PE 61203	Label states "*Maclurea magna* LeSeur, Chazy Ls." 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 *Monitorella crenulata* and the apical cavity shape also resembles that of *Maclurites? acuminatus* (cf. Rohr and Measures, 2001), although the aperture of this specimen is significantly wider, with a more circular outer apertural margin.
Maclurites ponderosus (Billings, 1865)	Rohr and Measures (2001, fig. 4)	Rohr and Measures (2001; fig. 4).
Maclurites? acuminatus (Billings, 1865)	Rohr and Measures (2001, fig. 5.21) GSC 117456.	Rohr and Measures (2001; fig. 5.21). These authors note that a lack of diagnostic criteria renders uncertainty in whether this specimen should be classified in the genus *Maclurites* or *Maclurina*.
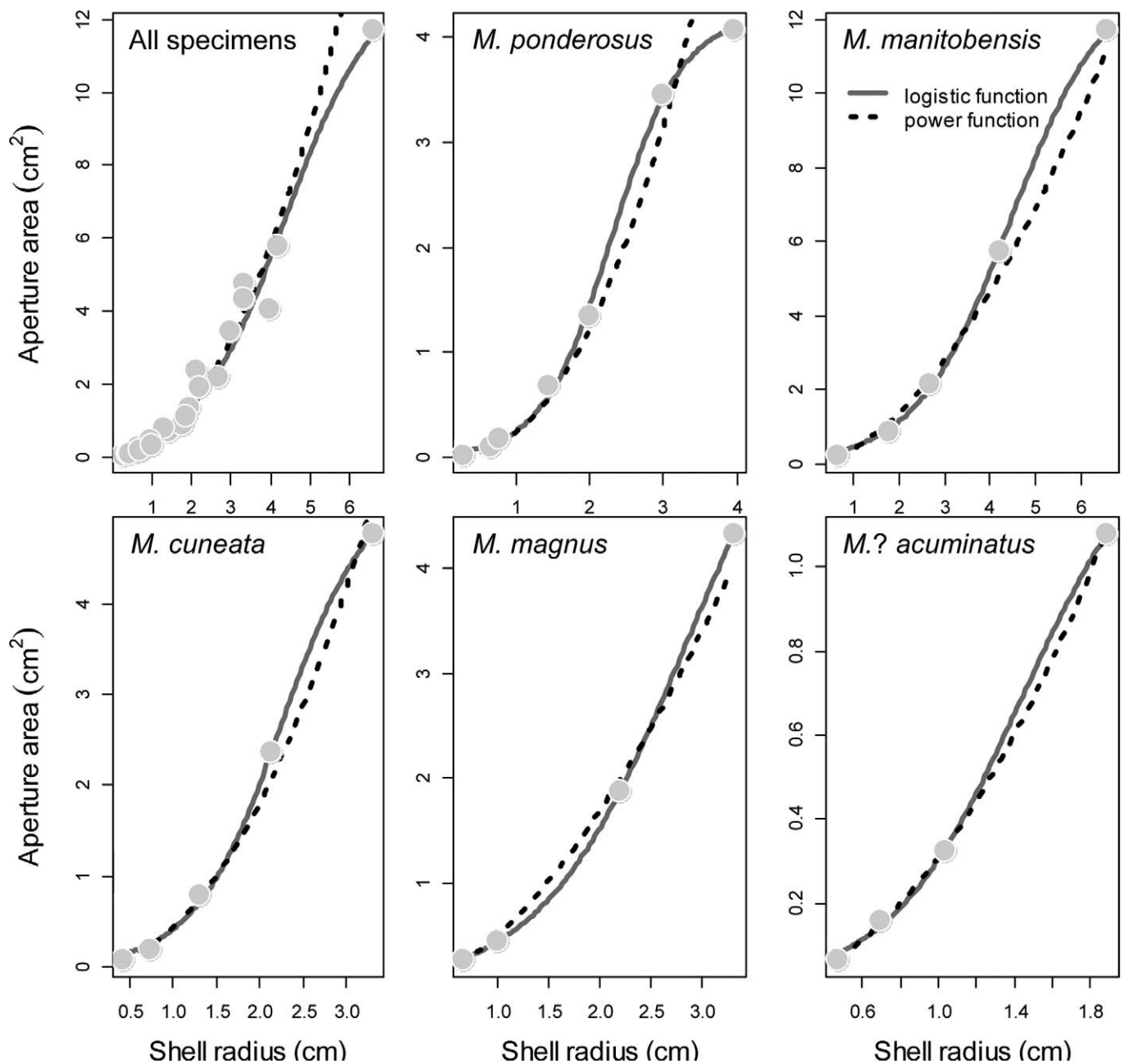
FIGURE 2—Trends in apertural size (units cm^2) during ontogeny for five macluritid gastropod species, with best-fit least-squares regression curves for logistic and power functions; ontogeny is measured as shell radius (distance from coiling axis to outer apertural margin); taxonomic information is found in Table 1; the top-left graph juxtaposes the measured apertures for all five specimens.

RESULTS

An inflection point occurs in the apertural size trend (Fig. 2) of five *Maclurites* and *Maclurina* species, approximately one volution 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 least-squares regression models, respectively. The logistic function model has four parameters (k=4): K=asymptotic size (in units cm²), r=instantaneous rate of increase (area cm²/radius cm), and a_0=initial apertural area (cm², the intercept); the linear model has three parameters (k=3): β=slope (or scaling coefficient, area cm²/radius cm) and α=intercept (cm²); both models also have a parameter for the root-mean-square error (RMSE); ℓ=log-likelihood for each model, AICc=small-sample unbiased Akaike Information Criterion, and Akaike weight is the relative support for each model. The model with lower AICc values is better supported than the alternative, given the likelihood and number of model parameters; Akaike weights greater than 0.900 (in bold) have substantially better support than the alternative model. The final row combines the whorls of all specimens (using the larger specimen FMNH PE 61201A of M. manitobensis). Specimens A and B of M. manitobensis are counterpart cross-sections of the same fossil.

Species	Specimen	Logistic model							Power model							Scaling coefficient 95% CI
		RSE	df	K	r	a_0	ℓ	AIC$_C$	Akaike weight	RSE	df	β	α	ℓ	AIC$_C$	Akaike weight	
M. manitobensis	FMNH PE 61201A	0.129	2	13.24	0.953	0.186	5.452	Inf	0.000	0.179	3	1.753	−0.889	2.786	24.428	**1.000**	(1.434–2.071)
M. manitobensis	FMNH PE 61201B	0.193	1	5.877	2.008	0.020	3.672	−39.344	**1.000**	0.392	2	1.652	−0.886	−0.544	Inf	0.000	(0.401–2.903)
M. cuneata	FMNH PE 61202	0.077	2	5.351	1.977	0.061	7.988	Inf	0.000	0.137	3	2.067	−0.844	4.136	21.728	**1.000**	(1.805–2.329)
M. magnus	FMNH PE 61203	0.015	1	6.468	1.409	0.117	13.818	−59.636	**1.000**	0.113	2	1.712	−0.662	4.435	Inf	0.000	(1.330–2.094)
M. ponderosus	Rohr and Measures (2001, fig. 4)	0.073	4	4.205	2.109	0.033	10.375	7.250	**0.952**	0.271	5	2.309	−1.388	0.397	13.206	0.048	(2.007–2.612)
M.? acuminatus	Rohr and Measures (2001, fig. 5.21)	0.019	1	1.369	2.881	0.022	12.963	−57.926	**1.000**	0.046	2	1.979	−1.176	8.016	Inf	0.000	(1.786–2.172)
All specimens		0.500	22	13.170	0.894	0.255	−16.541	43.082	0.000	0.330	23	2.045	−1.084	−6.688	20.519	**1.000**	(1.877–2.213)

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 excurrent 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).

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

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.

	ES1	ES2	ES3	ES4	ES5	ES6	ES7	ES8	ES9	ES10	ES11	ES12
Eigenvalues	0.10	0.06	0.03	0.02	0.01	0.01	0.01	0.01	0.00	0.00	0.00	0.00
Total variance (%)	38.1	23.5	11.6	8.2	5.3	3.6	2.5	2.0	1.9	1.8	1.1	0.5
Cumulative variance (%)	38.1	61.6	73.1	81.4	86.7	90.3	92.7	94.8	96.6	98.4	99.5	100.0

suggested by the high frequency of morphological transitions between "euomphaliform" and "trochiform" gastropods (Wagner, 2002; Wagner and Erwin, 2006). Although suspension feeding is relatively uncommon among extant gastropods—estimated to have evolved five to twelve times independently among 17 extant families and subfamilies representing a wide gamut across the gastropod phylogeny (Declerck, 1995)—nearly all extant suspension-feeding gastropods also bear a single ctenidium (Declerck, 1995). Using biomechanical models, Morris (1991) demonstrated that *Maclurites* would have been able to generate robust water currents with a single ctenidium, bringing water into the mantle cavity basally, passing upward by the enlarged ctenidium, and exiting at the apical angulation (sinus) where the anus was likely located.

A broadly similar mantle-cavity flow pattern occurs in the extant suspension-feeding gastropod *Crepidula* (Chaparro et al., 2002; Navarro and Chaparro, 2002), which also undergoes similar feeding changes during its protandric ontogeny. Juvenile *Crepidula* males are mobile, scraping algae with their radula; they supplement their diet with suspension-feeding as their single ctenidium develops in late juvenile stages, and they are primarily suspension-feeders when maturing as sedentary, sexually mature females, using their radula both to supplement their diet and to transfer captured algae from their ctenidium to their mouth. Based on this comparison, it may even be possible that juvenile, still-mobile macluritids supplemented their feeding in part or in whole with suspension feeding, as do the small intertidal gastropod *Lirularia* (McLean, 1986) and late juveniles of *Crepidula* (Chaparro et al., 2002; Navarro and Chaparro, 2002).

Consideration of broader phylogenetic patterns allows these life habits to be generalized across additional macluritoid and euomphaloid lineages. Wagner (2002) observed that the basic ontogenetic trend quantified here was typical of all advanced macluritids, and that primitive members of this clade retain rounded, lenticular apertures into adulthood. The evolution of macluritids likely records a peramorphic trend in which advanced macluritid juveniles retained apertural morphologies typical of their adult ancestors. It is possible, therefore, that the evolutionary diversification of macluritids is associated with increasing specialization toward suspension-feeding. The importance of this life habit is emphasized by the work of Wagner and Erwin (2006), who concluded that the "euomphaliform" morphotype evolved five times independently from ancestral pleurotomariiform and trochiform morphotypes typically interpreted as mobile algae-grazers. They also concluded that "open-coiled euomphaloids," likely sharing the sedentary suspension-feeding habit, evolved independently four times from the same ancestors. The ontogenetic trends documented above using morphometrics suggest that sedentary suspension feeding was an important and recurrent feeding strategy throughout the evolution of the macluritoids and, by extension, other euomphaloid Paleozoic gastropods.

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