Evaluating paedomorphic heterochrony in trilobites: the case of the diminutive trilobite *Flexicalymene retrorsa minuens* from the Cincinnatian Series (Upper Ordovician), Cincinnati region

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SUMMARY *Flexicalymene retrorsa minuens* from the upper-most 3 m of the Waynesville Formation of the Cincinnatian Series (Upper Ordovician) of North America lived approximately 445 Ma and exhibited marked reduction in maximum size relative to its stratigraphically subjacent sister subspecies, *Flexicalymene retrorsa retrorsa*. Phylogenetic analysis is consistent with the notion that *F. retrorsa retrorsa* was the ancestor of *F. retrorsa minuens*. *F. retrorsa minuens* has been claimed to differ from *F. retrorsa retrorsa* "in size alone," and thus presents a plausible example of global paedomorphic evolution in trilobites. Despite strong similarity in the overall form of the two subspecies, *F. retrorsa minuens* is neither a dwarf nor a simple progenetic descendant of *F. retrorsa retrorsa*. More complex patterns of global hetero-chronic paedomorphosis, such as a neotonic decrease in the rate of progress along a common ontogenetic trajectory with respect to size, coupled with growth cessation at a small size, "sequential" progenesis, or non-uniform changes in the rate of progress along a shared ontogenetic trajectory with respect to size, can also be rejected. Rather, differences between these subspecies are more consistent with localized changes in rates of character development than with a global hetero-chronic modification of the ancestral ontogeny. The evolution of *F. retrorsa minuens* from *F. retrorsa retrorsa* was largely dominated by modifications of the development of characters already evident in the ancestral ontogeny, not by the origin of novel structures. Factors promoting size reduction in *F. retrorsa minuens* appear to have been specific to this subspecies, because other co-occurring taxa, including other trilobite species, do not show marked differences in mean size.

INTRODUCTION

Trilobite ontogeny displayed progressive modifications of morphology expressed over an extended series of instars (e.g., Barrande 1852; Hughes et al. 2006). Ontogenies of this kind permit exploration of the ways in which subtle differences in mature form developed, and evolutionary change among tri-lobite taxa has commonly been attributed to heterochrony (e.g., Jaekel 1901; Stubblefield 1936; Fortey and Rushton 1980; McNamara 1983, 1986; Ramsköld 1988; Chatterton et al. 1990; Clarkson and Ahlberg 2002). Although evolutionary change in Trilobita invariably involved the modification of ontogeny, a review of putative cases of heterochronic change among trilobite species considered few to be securely founded (Chatterton and Speyer 1997, p. 204). These authors argued that most and possibly all studies lacked the detailed docu-mentation of comparative developmental patterns and phylo-genetic relationships needed to support heterochronic interpretations. Recent analyses have begun detailed tests of heterochronic explanations for differences between species

pairs in which ancestor–descendant relationships are strongly supported (e.g., Webster et al. 2001; Webster and Zelditch 2005; Webster in press). An apparently peramorphic pattern of evolution from the early Cambrian trilobite *Nephrolenellus multinodus* to its descendent species *Nephrolenellus geniculatus* was achieved by subtle allometric repatterning (Webster and Zelditch 2005) rather than a global or localized pattern of heterochrony in which the ancestral ontogenetic trajectory was maintained in the descendant.

The most striking putative examples of heterochrony in trilobites invoke paedomorphosis, a pattern in which fea-tures of the early ontogenetic stages of ancestors are re-tained in the mature forms of descendants (McNamara 1986). Paedomorphosis is commonly considered easier to detect than peramorphosis because the descendant ontog-eny is encompassed within the ontogeny of the ancestor. However, although many cases of trilobite paedomorphosis have been suggested, the conservation of an ontogenetic trajectory in both the ancestor and descendant required in order to satisfy a testable definition of heterochrony

(Zelditch and Fink 1996) has yet to be demonstrated. In this paper, we discuss a case that fulfills stringent requirements for examination of morphological evolution in the fossil record (see Jablonski 2000, p. 29), as part of a larger study of morphological evolution within a well-represented species lineage in an exceptionally refined stratigraphic context. This study concerns the relationship between the diminutive Upper Ordovician trilobite *Flexicalymene retrorsa minuens* (Foerste 1919) and its putative ancestor *Flexicalymene retrorsa retrorsa* (Foerste 1910). The two subspecies closely resemble one another and the original description of *F. retrorsa minuens* (Foerste 1919, p. 76) stated explicitly that the diminutive *retrorsa minuens* differed from *F. retrorsa retrorsa* "by size alone" (Fig. 1), thus implying a simple pattern of paedomorphic evolution.

If Foerste's (1919) interpretation was correct, several heterochronic possibilities might account for this observation. Dwarfism is defined as a negative perturbation in growth rate that produces a descendant that has the same shape as the ancestor but is of a smaller size (Alberch et al. 1979). This implies that the ancestor and descendant shared a common trajectory of shape change but that size was decoupled from shape such that the descendant completed the same degree and manner of shape change as the ancestor but accomplished this over a smaller size range (Fig. 2). This model predicts that the largest forms of both species should share similar shapes, provided that they are sampling an equivalent portion of ontogeny. A second possibility is "pure" or "terminal" progenesis (McNamara 1983), in which the ancestor and descendant shared a common pattern of shape change and size change, but the descendant terminated its development at a smaller

size, that is at an earlier point along the developmental trajectory of the ancestor. This model predicts that the mature descendant was of similar shape to similarly sized growth stages of the ancestor. A third possibility is a more complex pattern in which the rate of progress along a conserved ontogenetic trajectory with respect to size neither increased uniformly (as in dwarfism) nor was conserved (as in progenesis). Possible examples could include a decrease in the rate of progress along a common ontogenetic trajectory with respect to size (as in neoteny) coupled with progenetic cessation of growth at a small size, or non-uniform changes in the rate of progress with respect to size along a shared ontogenetic trajectory. Another possible example of this kind of change is "sequential progenesis" (*sensu* McNamara 1983, not to be confused with "sequential heterochrony" of Smith 2001), in which shortening of the intermolt interval diminished progress along the common ontogenetic trajectory of all characters other than trunk segment generation. Predicting the morphological consequences of such heterochronic models is less straightforward, but all require conservation of allometric trajectory and that the mature shape of the descendant equals that of the ancestor at some point in its ontogeny. This paper evaluates these and other possibilities.

GEOLOGICAL SETTING

The Cincinnatian Series (Upper Ordovician) in the tri-state area of Indiana, Kentucky, and Ohio, North America, is an excellent natural laboratory for the analysis of microevolutionary change within well-represented macroinvertebrates
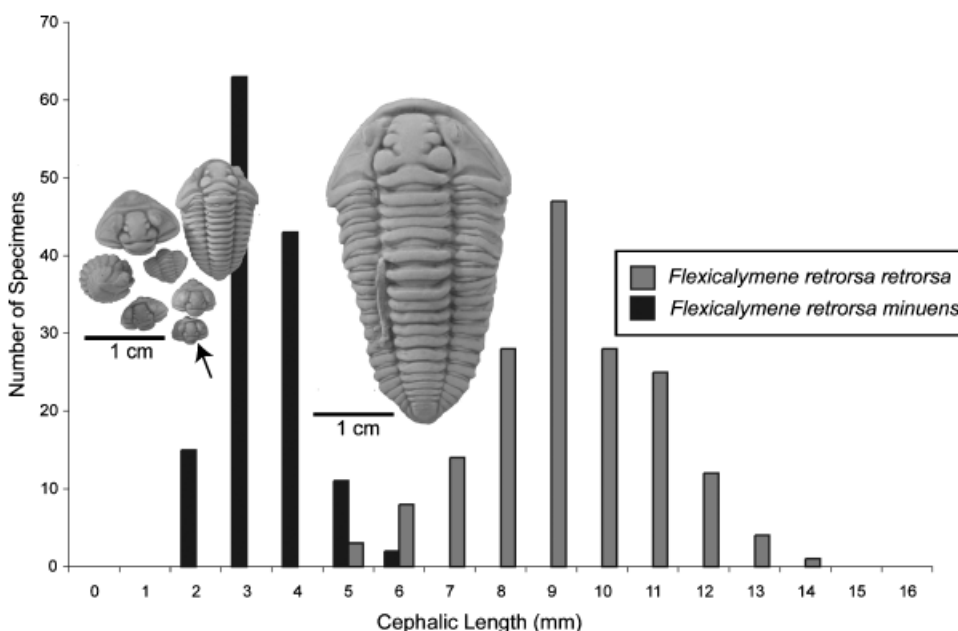
Fig. 1. Size–frequency relationships for *Flexicalymene retrorsa retrorsa* from the lower Blanchester Member of the Waynesville Formation and for the miniaturized *Flexicalymene retrorsa minuens* from the uppermost Blanchester Member of the Waynesville Formation. All specimens of *F. retrorsa minuens* are holaspid, except for the specimen indicated by the arrow, which is an ultimate degree meraspid with 12 thoracic segments.
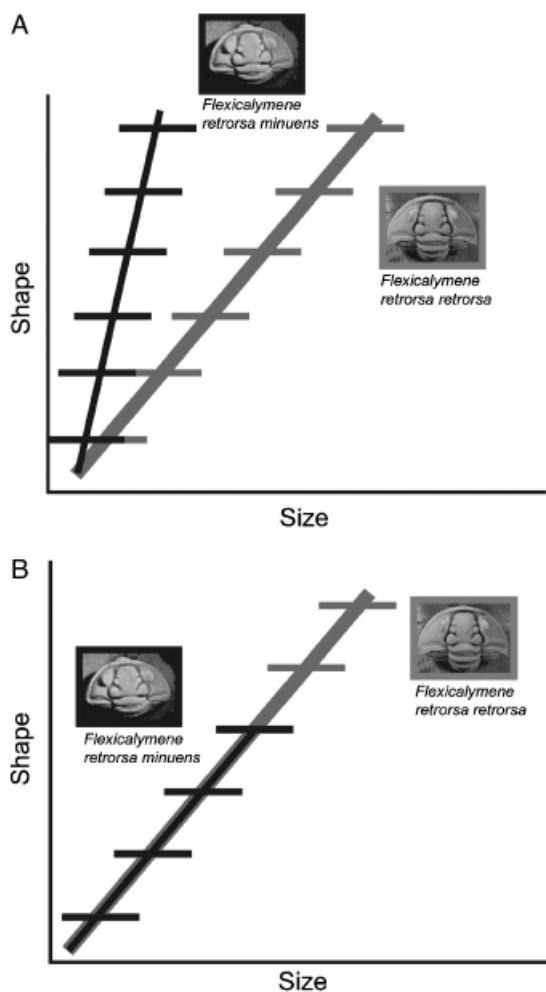
Fig. 2. Contrast between the dwarfism and progenesis. (A) In dwarfism, the descendant follows the same ontogenetic pattern of shape change as the ancestor, resulting in mature forms with similar shapes in both the ancestor and descendant, but a reduction in the rate of size increase results in a smaller-sized descendant. (B) In a "pure" progenetic descendant, precocious maturation at an early stage in development results in a mature descendant that retains the shape of a juvenile form of the ancestor. Horizontal lines symbolize instars.

such as the trilobite genus *Flexicalymene*. Recent sequence stratigraphic analyses have placed documented morphological trends within a high-resolution temporal and spatial context (Jennette and Pryor 1993; Holland et al. 1997; Holland et al. 2000; Brett and Algeo 2001; Miller et al. 2001). Deposits within the Cincinnatian Series are known world wide for their abundant and exceptionally well-preserved fossils. *Flexicalymene* is extremely numerous, commonly represented by articulated exoskeletons, and is represented in a variety of environments throughout the Cincinnatian Series. Complete specimens commonly show excellent preservation with little to no deformation (Hunda et al. 2006), a requirement for

detailed morphometric analyses of shape and shape change. These trilobites have a complex morphology offering multiple shapes and discrete characters for morphometric analysis. A limitation of this analysis is that only portions of the holaspid ontogenies of both subspecies are represented in our sample. Although this restricts our ability to resolve among alternative explanations for the patterns seen, it does not preclude us from testing Foerste's (1919) key claim about the differences between the subspecies.

Specimens assigned to *F. retrorsa minuens* are confined to the upper three meters of the Blanchester Member of the Waynesville Formation, whereas those of *F. retrorsa retrorsa* occur throughout the underlying Arnheim Formation and in the Waynesville Formation below that level. The two subspecies are not known to co-occur at any locality or stratigraphic level, but the lowest occurrence of *F. retrorsa minuens* is within 2 m of the highest occurrence of *F. retrorsa retrorsa* at the Route 1 section.

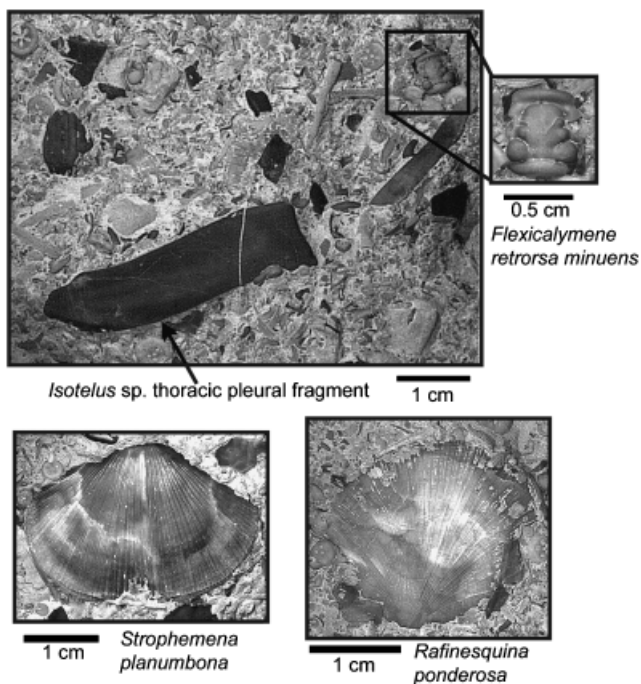## PHYSICAL OR BEHAVIORAL INFLUENCES ON SIZE IN *FLEXICALYMENE*

A consideration of the significance of the size range present within any given bed is particularly important in trilobites due to the molting habit: a smaller average size does not necessarily imply that the individuals that produced it never grew to larger sizes. Hence, it must be established that the occurrence of *F. retrorsa minuens* was not the result of size-selective physical processes associated with deposition (see Speyer 1987 for a more complete discussion) or the result of biological aggregations of individuals at particular size classes (Speyer and Brett 1985; Hughes and Cooper 1999).

The reworking and winnowing of sediments and bioclasts often associated with tempestite deposition can result in a size-specific taphonomic bias in storm-dominated strata (Brett and Allison 1998). Because in the Cincinnatian Series the various bed types have been interpreted to be deposited by storm-related processes (Ettensohn 1992; Holland 1993; Jennette and Pryor 1993), it is possible that the predominance of small specimens of *Flexicalymene* in the strata of the upper Blanchester Member of the Waynesville Formation (herein referred to as uppermost Waynesville) was the result of size sorting due to physical processes. However, several lines of evidence indicate that this explanation does not apply in this case.

Firstly, all mature *Flexicalymene* in these strata are small regardless of whether they occur in limestones or mudstones, whereas all mature *Flexicalymene* in the subjacent Waynesville strata are larger, regardless of lithology. This suggests that the size decrease was a general feature of the uppermost Waynesville *Flexicalymene* and was not related to particular lithology.

Secondly, Cincinnatian mudstones have been shown to consist of numerous event beds deposited by distal storm processes (Schumacher and Shrake 1997; Hughes and Cooper 1999; Hunda et al. 2006), resulting in the rapid burial of organic remains and the preservation of articulated trilobites. Hydrodynamic size sorting of individuals is uncommon in such mudstones due to the relatively low energy of deposition associated with such beds. Rather, such assemblages appear to be commonly in situ or involve locally derived individuals, many of which were alive at the start of the immediate sequence of events that led to their final burial (Hunda et al. 2006).

Thirdly, size sorting is more common in limestone beds that are made up of concentrated skeletonized remains subject to repeated reworking in turbulent events (Brett and Allison 1998). Although limestone packstones of the uppermost Waynesville Formation may have undergone an increased degree of reworking compared with the mudstones, fauna contained within these beds nevertheless exhibits a wide variety of sizes, including large sclerites of the large trilobite *Isotelus* (Fig. 3). This suggests that size sorting by physical

Table 1. Character and character states used in the cladistic analysis of species of *Flexicalymene*

1. Position of palpebral lobe (0) opposite L2 (1) opposite S2
2. Length (exsag.) of palpebral lobe (0) 1/5 sagittal length of glabella (1) 1/4 (2) 1/3
3. Shape of glabella (0) bell-shaped (1) parabolic
4. Preglabellar furrow width (sag.) versus glabellar length (sag.) (0) 0.1, (1) 0.06, (2) 0.05, (3) 0.04
5. Frontal lobe outline (0) subquadrate (1) anteriorly rounded
6. L1 shape (0) subquadrate (1) subcircular
7. L1/L2 ratio (exsag. Width) (0) 1.5, (1) 1.7, (2) 2.0
8. Anterior cephalic margin (0) strongly rounded (1) moderately rounded (2) straight
9. Inclination of anterior cephalic border (0) shallow (1) moderately inclined (2) steeply inclined
10. Lateral portion of anterior border furrow (0) anteriorly migrating (1) straight
11. Posterior facial suture (0) travels laterally from palpebral lobe (1) travels posteriorly then laterally from palpebral lobe
12. Cephalic ornamentation (0) tubercles and pustules, (1) tubercles and granules, (2) densely packed coarse granules, (3) densely packed fine granules
13. Genal angle at maturity (0) genal spine present, (1) pointed genal angle, (2) rounded genal angle
14. Width of thorax versus width of axis (0) 3.0x, (1) 2.5x
15. Interpleural furrows (pygidium) (0) moderately incised, (1) weakly incised, (2) perceptible only at pygidial border
16. Width of pygidium (tr.) versus sagittal length (0) 1.6x, (1) 1.8x, (2) 1.4x
17. Terminal piece of pygidium (sag. length) versus length (sag.) of pygidium (0) 3.5x, (1) 3.0x, (2) 2.5x
18. Number of pygidial rings (0) six with faint 7th, (1) five with faint 6th, (2) four with faint fifth
19. Slope of pygidial pleural region (0) shallow, (1) moderately steep, (2) very steep

Fig. 3. Packstone bed from the uppermost Waynesville Formation with various skeletal elements of the enclosed fauna. Crinoid ossicles, *Strophemena planumbona*, *Rafinesquina ponderosa,* and *Isotelus* thoracic fragments are comparable in size to those found throughout their ranges in the Cincinnatian Series. Specimens of *Flexicalymene retrorsa minuens* (inset of cranidium) are dramatically and consistently smaller than those of other *Flexicalymene* from the Cincinnatian Series, and is the only member of this fauna that exhibits miniaturization.

processes was not a general aspect of these beds. Similarly, depositional processes associated with the strata of the uppermost Waynesville Formation apparently operated at numerous horizons within the Cincinnatian Series, and these beds are the only ones known to contain specimens of *Flexicalymene* with a consistently smaller size. Hence, there is no indication that physical processes associated with size sorting were responsible for the small size of the *retrorsa minuens* in the uppermost Waynesville Formation.

Size segregation in trilobites has often been associated with specific behavioral aggregates associated with molting and/or copulation (Speyer and Brett 1985; Hughes and Cooper 1999; Karim and Westrop 2002; Paterson et al. 2007). Size segregation has been documented in *Flexicalymene* in the Cincinnatian Series (Hughes and Cooper 1999), and interpreted to represent a biological association rather than the product of mechanical sorting. Trilobite clusters of this nature are often found on a single bedding plane, are spatially restricted, and represent a snapshot of trilobite behavior in time.

However, specimens of *Flexicalymene* are consistently small throughout the uppermost Waynesville Formation and thus are neither temporally nor spatially restricted, occurring in both limestone and shale beds in the last few meters of the formation, and distributed along individual beds that can be traced over 100 km across the paleoramp. These consistent features indicate that the dramatic size decrease exhibited within these beds was a general phenomenon and was not related to either physical sorting or specific aggregation.

With regard to the samples compared morphometrically in the analysis below, both came from well-localized, separate "butter shale" intervals each characterized by numerous articulated, complete exoskeletons, commonly enrolled. The enrolled posture suggests that these individuals were alive immediately before events leading to their burial. Detailed analyses of similar beds (Schumacher and Shrake 1997; Hunda et al. 2006) suggest that the individuals represented in such beds, although possibly preserved in a series of burial

events, probably accumulated over an interval of <1000 years in both cases (Hunda et al. 2006).

PHYLOGENETIC PLACEMENT

Assessment of the pattern of evolutionary change between *retrorsa retrorsa* and *retrorsa minuens* requires that they are immediate sister taxa. A cladistic analysis of 19 characters (Table A1; Appendix A) was used to investigate the phylogenetic relationships of 16 North American and European calymenid species. These taxa were selected as the putative in-group because they have been assigned previously to *Flexicalymene* and are the plausible closest relatives of *F. retrorsa retrorsa* and *F. retrorsa minuens*. The results show that *F. retrorsa minuens* is more closely related to *F. retrorsa retrorsa* than to any other species (Fig. 4). The order of the stratigraphic appearance of species occurring in the type
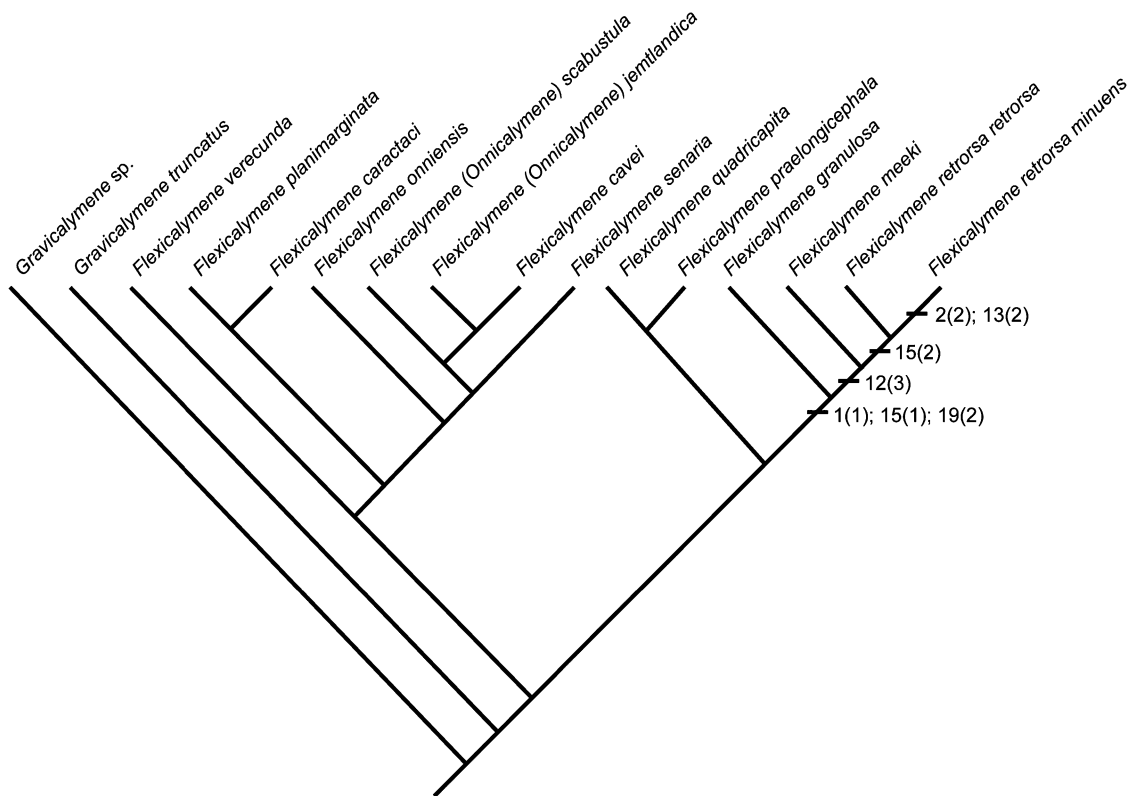
Fig. 4. One of 76 most parsimonious cladograms depicting the hypothesized phylogenetic relationships of 16 calymenid species from North America and Europe. In all 76 cladograms, the relationships between species of Cincinnatian *Flexicalymene* are supported. Disagreement of relationships occurs within clades of non-Cincinnatian taxa. Synapomorphies are shown only for the Cincinnatian clade as these are consistent across all cladograms. In all cladograms, *Flexicalymene retrorsa minuens* and *Flexicalymene retrorsa retrorsa* are most closely related to each other and zero length branches posit an ancestor–descendant relationship (for a discussion of zero length branches, see Smith 1994). *Gravicalymene* sp. and *Gravicalymene truncatus* were chosen as outgroup taxa because they occur in the same region (Ohio, Indiana, Kentucky) and in the Cincinnatian Series (Edenian, Kope Formation). Cladistic analysis was conducting using Paup 4.0b (Swofford 2002). A heuristic search was used with simple addition sequence and branch-swapping (tree-bisection-reconnection TBR) search parameters. (Tree length = 58; CI = 0.58; RI = 0.68). Refer to Table 1 for a description of the characters and character states and Appendix A for the cladistic matrix.
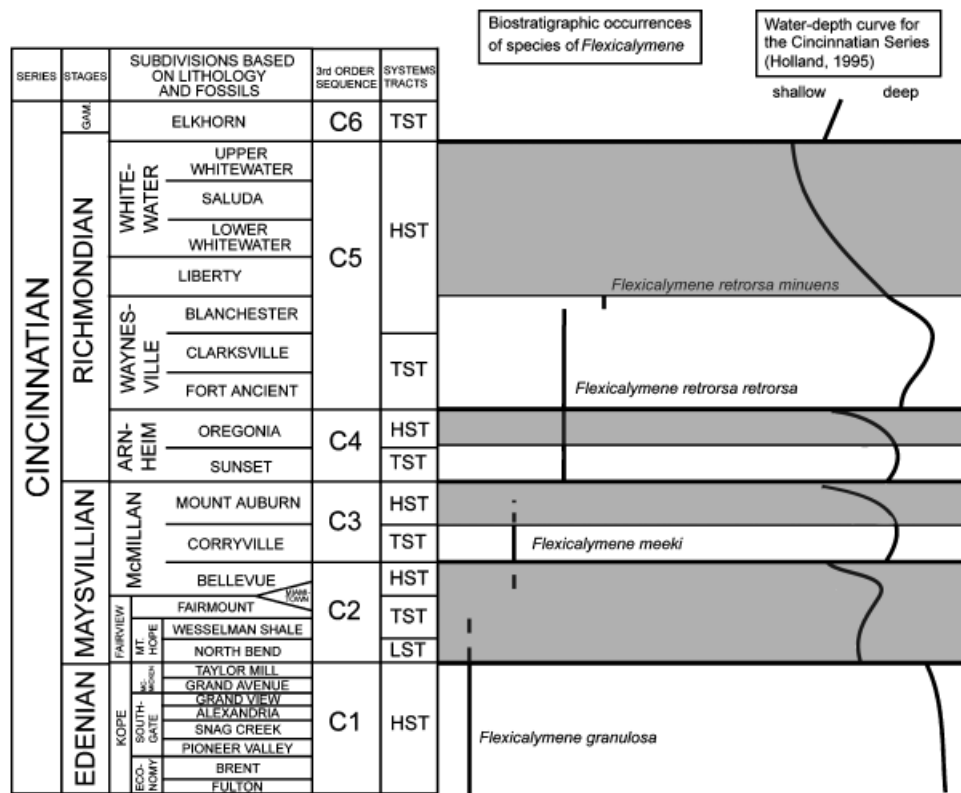
Fig. 5. Biostratigraphic range chart of Cincinnatian species of *Flexicalymene*. Stratigraphic occurrence is independent of sequence stratigraphic architecture (third-order cycles, sequence tracts, and sequence boundaries) and lithofacies, as defined by Holland (1993). Species occurrence in the Bellevue Member is unknown due to the difficulty in sampling this shallow water interval. However, *Flexicalymene meeki* is known to occur in the Miamitown Shale. Upper Richmondian strata are dominated by stacked limestone beds, representing another shallow water interval. Collection of material is difficult above the Waynesville Formation; therefore, species occurrence is also unknown for this interval.

Cincinnatian Series is consistent with this clade structure (Fig. 5), and suggests that *F. retrorsa retrorsa* may have been ancestral to *F. retrorsa minuens*. This is supported by the observation that *F. retrorsa retrorsa* has no distinctive autapomorphies of its own.

The analysis suggests that *F. retrorsa minuens* differs from *F. retrorsa retrorsa* by the possession of a rounded genal angle and by its relatively larger palpebral lobe. The different states of these characters between the two species relate to differences in the ontogenetic expression of characters common to both taxa: there are no novel characters seen in *F. retrorsa minuens* that are not evident in *F. retrorsa retrorsa*.

MATERIALS AND METHODS

One hundred and seventy-seven specimens of *F. retrorsa retrorsa* were collected from a single 43-cm-thick shale bed from a locality near Oldenburg, Indiana (Fig. 6), from the lower Blanchester Member of the Waynesville Formation (Fig. 7). One hundred and seventeen specimens of *F. retrorsa minuens* were collected from a single 54-cm-thick shale bed from the Caesar Creek locality,

Ohio (Fig. 6), from the uppermost Blanchester Member of the Waynesville Formation (Fig. 7). Specimens from both localities are completely articulated, and occur in both prone and enrolled positions. All specimens used in this analysis were holaspid, with the mature complement of 13 thoracic segments, and were apparently also in the epimorphic phase of development (Hughes et al. 2006). An additional 22 disarticulated cranidia of *F. retrorsa minuens* were collected from a locality along the Route 1 highway, Indiana, from the uppermost Blanchester Member of the Waynesville Formation (Figs. 6 and 7). The cranidial lengths of these specimens were within the holaspid size range from the Caesar Creek locality and these specimens were therefore considered holaspids. Two latest stage meraspids (each with 12 thoracic segments) were collected from the Caesar Creek locality but were not used in this analysis due to their rarity.

Specimens were prepared using an air abrasive with sodium bicarbonate abrasive powder for shale specimens and a 50/50 mixture of sodium bicarbonate and dolomite abrasive powder for limestone specimens. Specimens were imaged in dorsal view with the palpebral lobe horizontal, following the recommendation of Shaw (1957). Specimens that showed deformation were eliminated from the analysis, although this was a rare circumstance. Data on nominal (presence/absence) and ordinal (states assessed along a
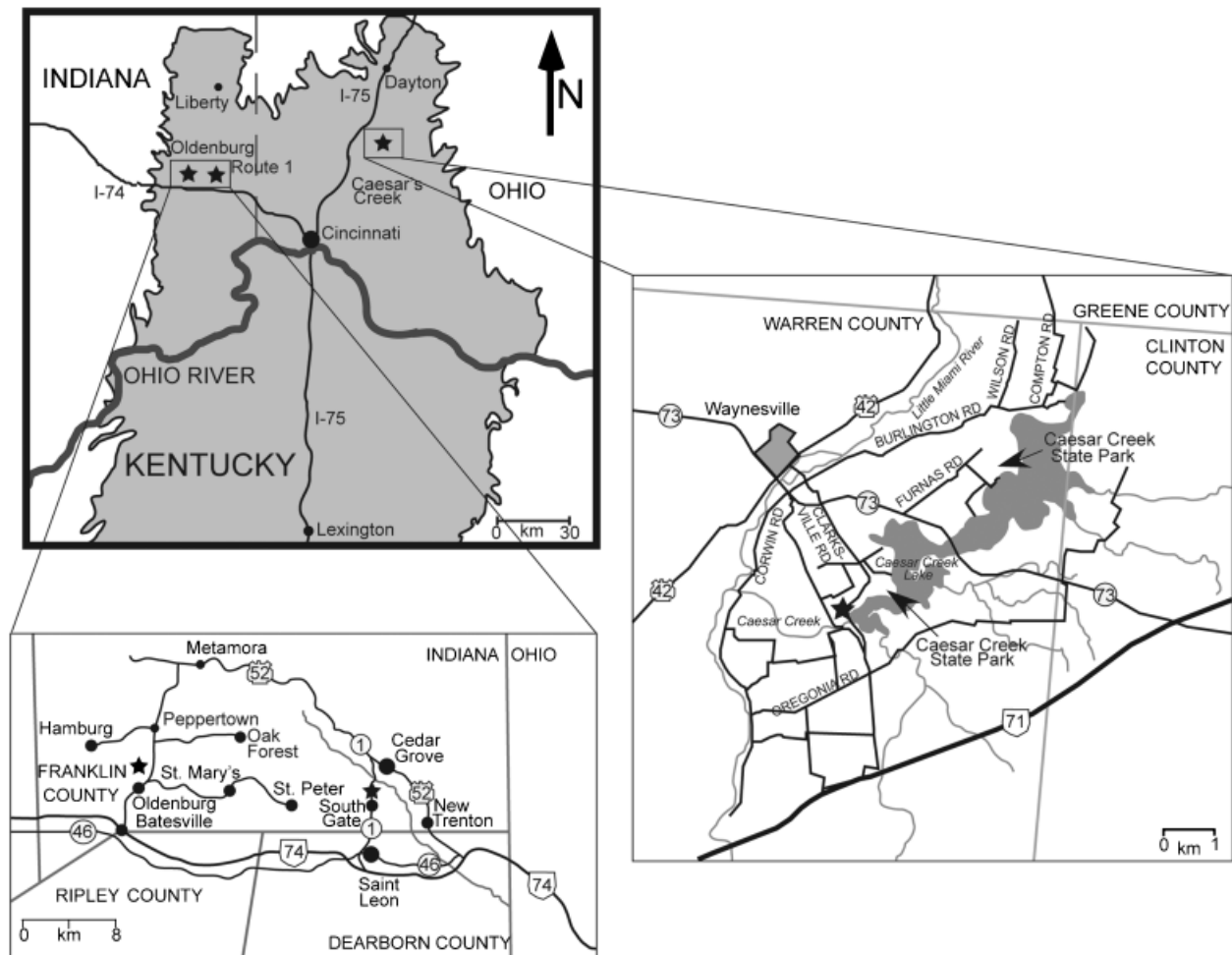
Fig. 6. Locality maps for the Oldenburg locality, Route 1 locality, and Caesar Creek locality. Specimens of *Flexicalymene retrorsa retrorsa* were collected from a single shale bed at the Oldenburg locality, Indiana, of the Blanchester Member of the Waynesville Formation. Specimens of *Flexicalymene retrorsa minuens* were collected from a single shale bed from the Caesar Creek locality, Ohio, and a packstone bed from the Route 1 locality, Indiana, of the uppermost Blanchester Member of the Waynesville Formation.

ranked scale) characters, such as glabellar ornament and the development of the genal spine, were recorded. Cartesian X and Y coordinates of a series of morphological landmarks were recorded for each specimen on a Macintosh computer using the public domain NIH Image program (developed at the United States National Institutes of Health and available on the Internet at http://rsb.info.nih.gov/nih-image/). In addition to morphometric analysis, the condition of the genal spine was visually assessed (condition documented as either present, absent, or vestigial) as this character often exhibits changes in its expression related to ontogenetic development in trilobites.

Measurement error of landmark placement was assessed by taking replicate measurements of all landmarks on a single specimen. This specimen was removed and reoriented 20 times over the period of a day. Landmark configurations from these 20 images were then analyzed for measurement error. Single group analysis of variance with 900 bootstraps (DisparityBox6h; Sheets 2003) was used to calculate the proportion of variance contributed by mea-

surement error to the observed variance measured in all specimens of *F. retrorsa* from a single bed. Analysis indicates that 9.69% of the total variation may have resulted from measurement error (95% confidence interval of 7.35–10.87%).

Morphometric analysis concentrated on the cranidia of these trilobites for several reasons: (1) the variety of enrollment positions make it difficult to find a standard orientation for measurement and obscures the thoracic and pygidial margins, (2) trilobites within limestones are disarticulated, with cranidia the most commonly represented sclerite, and (3) previous taxonomic assignments of calymenids have focused on the morphological features of the cranidium. A suite of 33 landmarks distributed over the cranidium of *Flexicalymene* provided coverage of all the distinctly identifiable homologous points (Fig. 8; Table 2). Bilaterally symmetrical landmarks on the left and right side of the cranidium were reflected across the sagittal axis, as defined by landmarks 3 and 5, and an average value for each pair was calculated. Landmark configurations of each specimen were then superimposed,
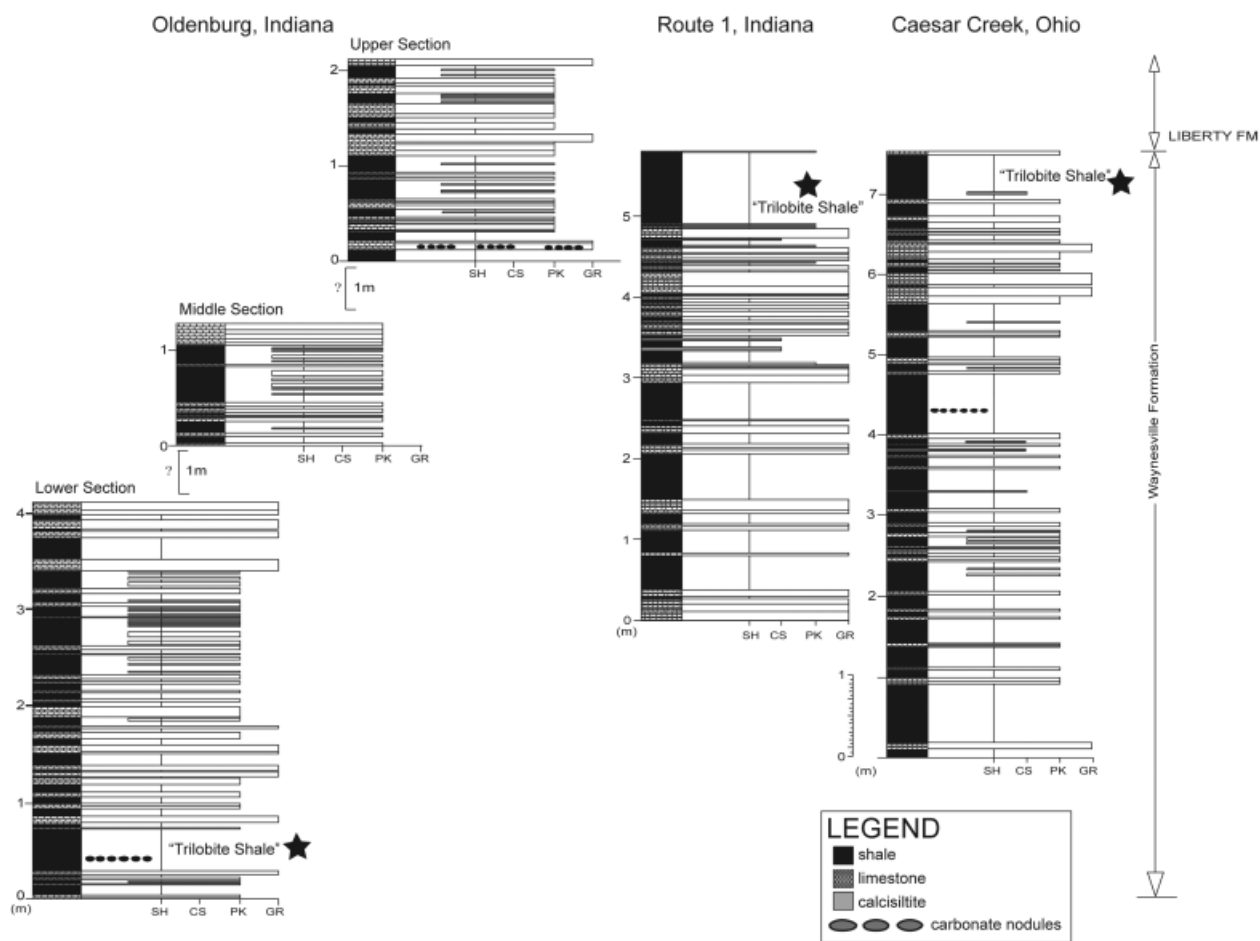
Fig. 7. Correlated stratigraphic sections of the Oldenburg locality, Caeser Creek locality, and Route 1 locality. Star symbol indicates the stratigraphic position of the samples. Specimens analyzed are confined to individual beds or sets of mudstone beds that likely represent a series of stacked event beds, each representing rapid deposition from a flow-bearing fine-grained sediment associated with distal storm processes below the storm-wave base. SH, shale; CS, calcisiltite; PK, packstone; GR, grainstone.

using three superimposition techniques: Procrustes superimposition (Bookstein 1991), Bookstein registration (Dryden and Mardia 1998), and sliding baseline registration (SBR) (for a discussion of these superimposition techniques, see Webster et al. 2001). All analyses were conducted using Procrustes landmark coordinates, but plots of landmark superimposition are shown in SBR configuration because this approach provides the most convenient visual summary of important morphological trends. Centroid size (Bookstein 1991) was utilized as the measure of overall size in all morphometric analyses. Although size did not necessarily equate with ontogenetic age (the amount of growth attained by each individual per molt not necessarily being identical), a multivariate size measure is acceptable for identifying whether heterochrony is operating or not (Webster et al. 2001). The IMP morphometrics package written by Dr. David Sheets (http://www3.canisius.edu/ ∼ sheets/morphsoft.html) was used to perform all analyses.

Static comparisons of sample shape were achieved by superimposition of the reflected and averaged landmark configurations.

The Procrustes landmark coordinates were then calculated and compared using Goodall's F-test with 400 bootstraps, which compares the within-group variance with the between-group variance in order to test for statistically significant differences in morphology between the two groups. The lack of abundant juveniles (protaspid and meraspid stages) in this analysis restricts comparison to mature (holaspid stage) growth trajectories. Vectors of growth summarizing patterns of cranidial shape change during the holaspid phase of ontogeny were constructed using thin-plate spline analysis (Bookstein 1991). In an initial analysis used to test for significant allometric growth within each species, mathematical decomposition of shape changes from a reference form (here the consensus of the five smallest specimens for each species) resulted in the generation of partial warps scores that represent the magnitude and direction of shape change in that species (for a discussion of these techniques, see Zelditch et al. 1992; Webster et al. 2001; Zelditch et al. 2004). These partial warp scores were then regressed against log centroid size to determine whether size-dependent shape change occurred within the available portions of the ontogenies of *F. retrorsa*
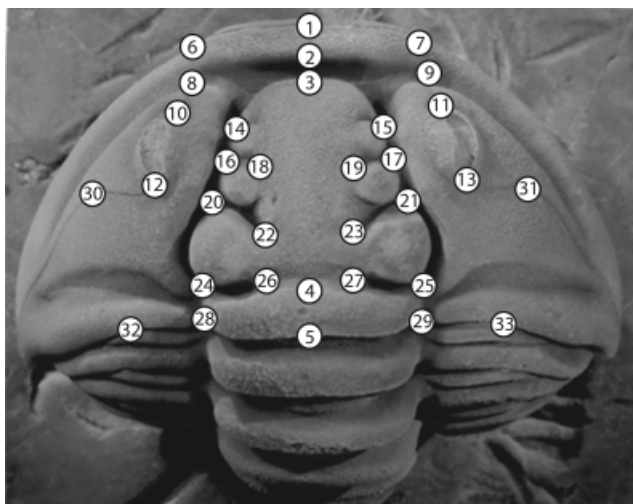
Fig. 8. Locations of cephalic landmarks for *Flexicalymene*. A total of 33 landmarks were digitized and homologous landmarks on the left and right side were averaged after reflection across the sagittal axis, defined by landmark #3 and #5.

retrorsa and *F. retrorsa minuens*. Shape changes associated with size were then displayed as vectors of landmark migration and as thin-plate splines depicting shape changes as bending motions within a grid (see Fig. 11).

In order to compare the growth patterns in the two species, growth vectors were calculated for available ontogenies of each species using a common reference form, the generalized least squares Procrustes consensus form of all specimens in the analysis. In this analysis, vectors were calculated using raw landmark coordinates from Bookstein registration and SBR, in addition to the partial warp scores generated from TPS analysis, in order to provide a more comprehensive comparison of growth patterns (Webster et al. 2001). Angles between the holaspid ontogenetic growth trajectories of *F. retrorsa retrorsa* and *F. retrorsa minuens* were calculated using each of these methods. The angle between holaspid ontogenies is statistically compared with the range of angles of each species in order to assess the extent to which we can be confident that the between-species growth trajectories are significantly different (Webster et al. 2001; Zelditch et al. 2003). Four hundred bootstraps of within-species variance in ontogenetic trajectories were run for each species. Within species variance was computed from 95%, 90%, and 80% confidence limits. The angle between ontogenies is considered to be significant if it exceeds the bootstrapped within species variance at 95% confidence (Zelditch et al. 2003).

RESULTS

Analysis of nominal and ordinal characters reveals that both *F. retrorsa retrorsa* and *F. retrorsa minuens* displayed an allometric relationship between genal spine condition and overall body size (Fig. 12). Small specimens of *F. retrorsa retrorsa* have either entire (pointed) or vestigial (nubin-like) genal spines on the fixigena (Fig. 12b). The relative size of the fixigenal spines reduced with increasing size such that

Table 2. Landmarks corresponding to Fig. 8

Landmark	Type	Description
1	2	Intersection of anterior border with midline
2	2	Intersection of the anterior border furrow with the midline
3	2	Intersection of the anterior margin of the frontal lobe with the midline
4	2	Intersection of the anterior margin of the occipital ring with the midline
5	2	Intersection of the posterior margin of the occipital ring with the midline
6, 7	1	Intersection of anterior facial suture with anterior cephalic border
8, 9	1	Intersection of anterior facial suture with anterior border furrow
10, 11	2	Anterior limit of palpebral lobe
12, 13	2	Posterior limit of palpebral lobe
14, 15	1	Intersection of axial glabellar furrow with S3
16, 17	1	Intersection of axial glabellar furrow with S2
18, 19	3	Medial termination of S2
20, 21	1	Intersection of axial glabellar furrow with S1
22, 23	3	Medial termination of S1
24, 25	1	Intersection of axial furrow with antero-lateral termination of occipital ring
26, 27	3	Medial termination of S0
28, 29	1	Intersection of axial glabellar furrow and posterior margin
30, 31	2	Maximum curvature of posterior facial suture
32, 33	2	Maximum change in curvature ("kink") in posterior margin

Type 1, discrete juxtapositions of tissues; three or more structures meet, that is intersection of axial glabellar furrow and posterior margin; Type 2, maxima of curvature, that is maximum curvature of posterior facial suture; Type 3, extremal points; endpoints of a feature, that is medial termination of a glabellar furrow. Landmark types after Bookstein (1991).
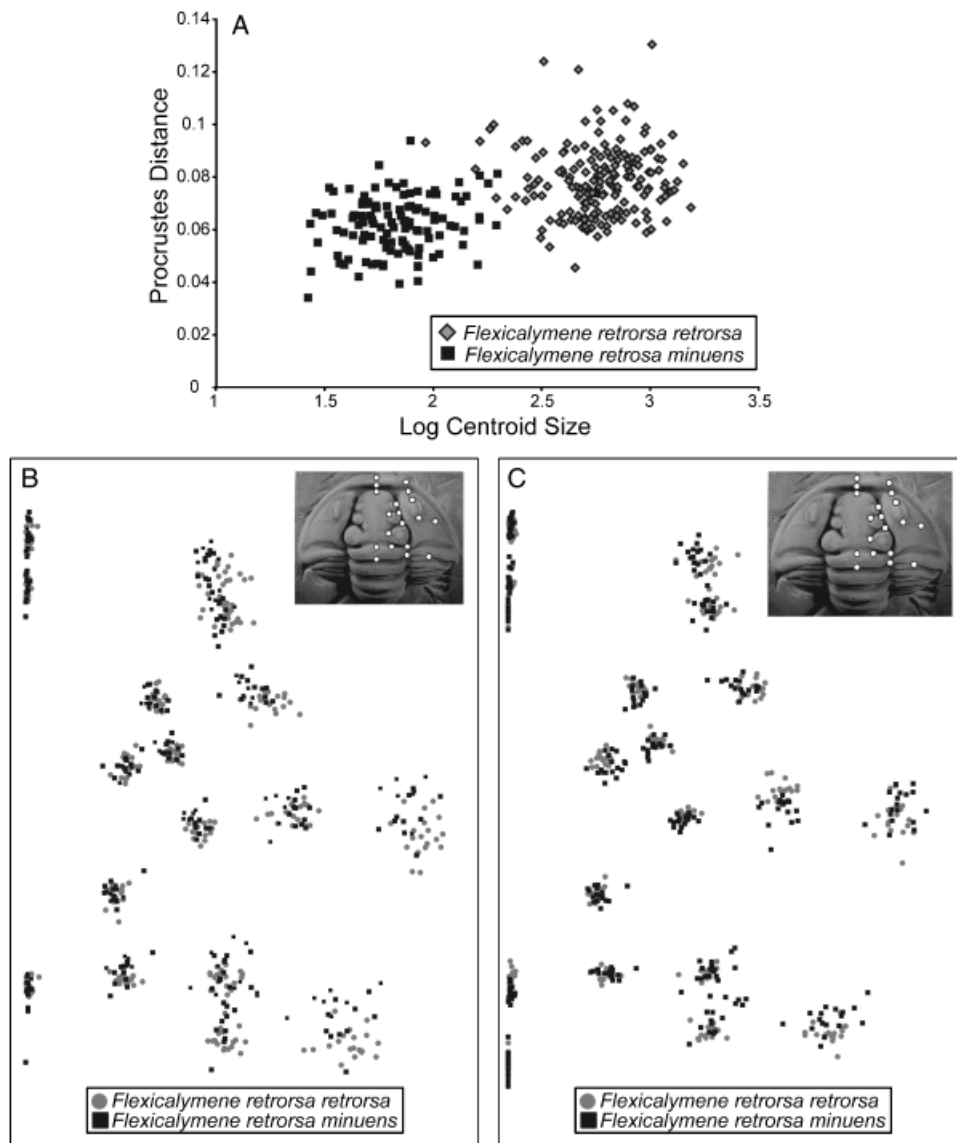
Fig. 9. Comparison of *Flexicalymene retrorsa retrorsa* and *Flexicalymene retrorsa minuens* cranidial shape. (A) Plot of Procrustes distance (a univariate metric for assessing differences in multivariate shape space) against log centroid size suggests that *F. retrorsa minuens* had a different cranidial shape than *Flexicalymene retrorsa retrorsa*. (B) Superimposition of cranidial landmarks of the 17 largest specimens of both subspecies shows differences in shape. Interpretations of morphological patterns are consistent across multiple registrations (Bookstein, Procrustes, and Sliding Baseline Registration [SBR]). SBR is used for illustrative purposes. Goodall's *F*-test with 400 bootstraps confirms a statistically significant difference in shape between the two species ($P = 0.0025$). (C) Superimposition of cranidial landmarks of specimens with size overlap (17 largest specimens of *F. retrorsa minuens* and 17 smallest specimens of *F. retrorsa retrorsa*) shows a statistically significant difference in cranidial shape (Goodall's *F*-test; 400 bootstraps; $P = 0.0025$) despite a similar size.

intermediate-sized specimens (7–10 mm in cephalic length) have vestigial spines only and larger specimens (>10 mm in cephalic length) lack fixigenal spines, yielding a rounded genal angle. In contrast, the genal angle of *F. retrorsa minuens* is consistently rounded, and lacked fixigenal spines at all observed sizes (Fig. 12a). Specimens of *F. retrorsa minuens* that lack genal spines are of a size similar to those of *F. retrorsa retrorsa* that have fixigenal spines at their most prominent

degree of expression (within the size range of 4–7 mm in cephalic length, Fig. 12). This result suggests that, with respect to the genal spine allometry, *F. retrorsa minuens* cannot have evolved from *F. retrorsa retrorsa* by "terminal" progenesis because, even assuming a common ontogenetic trajectory, individuals of the same size show different character states.

Comparison of cranidial shape of the largest specimens of *F. retrorsa retrorsa* (size range of 20.18–22.27 centroid size)
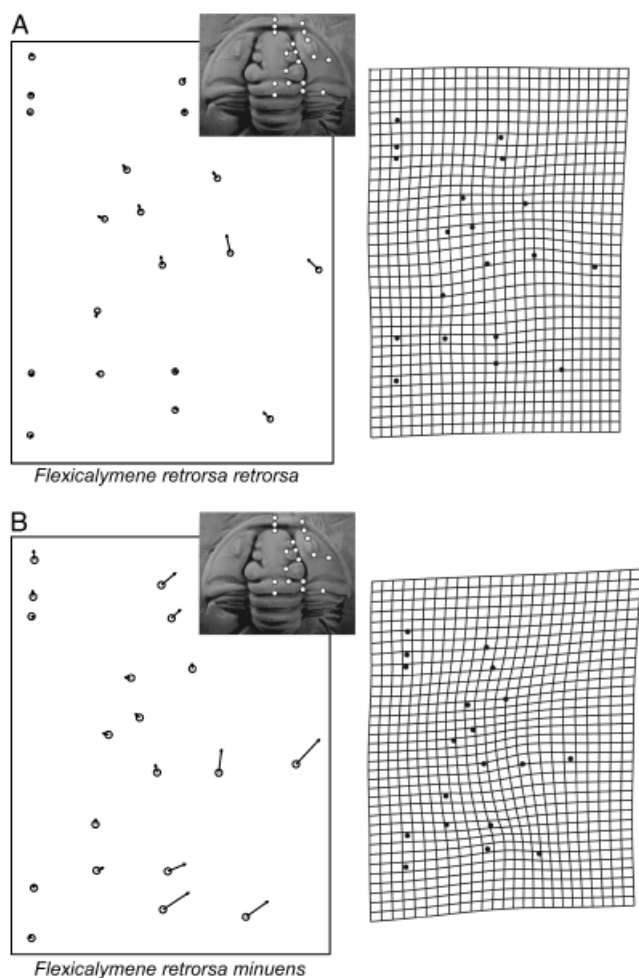
Fig. 10. Holaspid allometry in *Flexicalymene retrorsa retrorsa* and *Flexicalymene retrorsa minuens*. Ontogenetic shape changes are depicted as vector diagrams and thin-plate spline projections. Vectors are calculated using the Procrustes superimposition method. Arrows indicate the direction of shape change from small to large specimens. (A) Size-related shape change contributes 2.0% of shape variance within specimens of *F. retrorsa retrorsa*. (B) Size-related shape change contributes 7.16% of shape variance within specimens of *F. retrorsa minuens*.

and the largest specimens of *F. retrorsa minuens* (size range of 7.43–9.87 centroid size) indicates that the cranidial shape of these two groups is significantly different, based on Goodall's *F* test (Fig. 9). If it is valid to assume that the specimens analyzed represent similar portions of mature ontogeny (both samples containing the largest individuals in each bed), this result argues against dwarfism as an explanation for the evolution of *F. retrorsa minuens* from *F. retrorsa retrorsa*. This is because if *F. retrorsa minuens* is a dwarf of *F. retrorsa retrorsa,* we would expect it to have attained at the same ultimate shape as its ancestor but at a smaller maximum size.

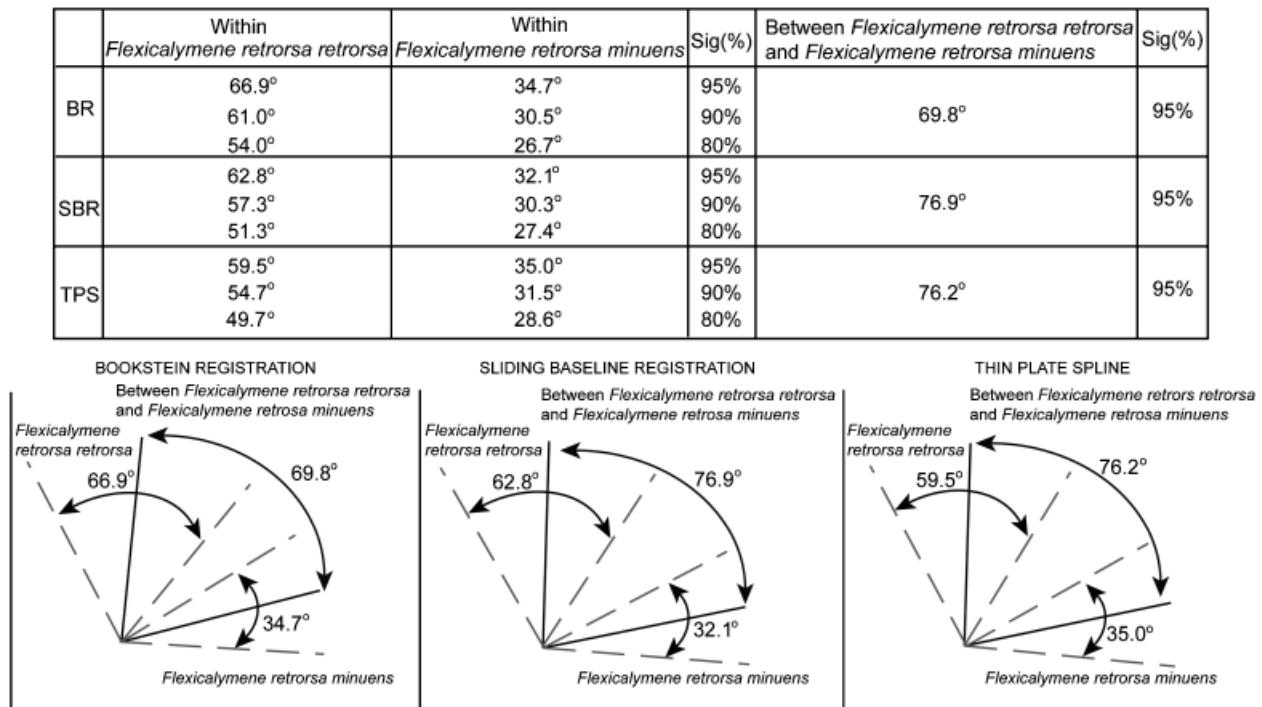A comparison of all individuals of both species in the interval 8.91–13.14 centroid size shows that the two species

differed significantly in shape at the same size. This argues against a "terminal" progenetic explanation, which requires that the ancestor and descendant shared both a common trajectory and a common degree of size change, and hence would be predicted to share the same shape at the same size.

The regression of shape change with size shows statistically significant allometry in both species (Fig. 10). In the *F. retrorsa retrorsa* sample, 2% of the shape change is dependent upon centroid size. Allometry is expressed as a slight forward expansion of the anterior glabella relative to the posterior portion of the cranidium, as well as a slight anterior movement of the palpebral lobe, resulting in a smaller palpebral lobe in larger specimens. In *F. retrorsa minuens* specimens, 7.2% of the variance is explained by the dependence of shape on size. In these specimens, shape transition from small to large specimens is expressed as an expansion and outward movement of the lateral cephalic landmarks, resulting in a wider cranidium. Changes in the shape of the palpebral lobe with size are similar to the allometric pattern observed in *F. retrorsa retrorsa*, with the anterior edge of the palpebral lobe occupying a stable position and an anteriorly migrating posterior palpebral margin, resulting in a relatively smaller palpebral lobe as the overall size increased.

The results suggest that holaspid/epimorphic ontogenetic change in *Flexicalymene* departs relatively little from isometry, which is typical of many trilobites (Hughes and Chapman 1995; Hughes et al. 1999). However, even small departures from isometry, if statistically significant, permit comparisons of ontogenetic trajectories in order to test the presence of heterochrony or allometric repatterning. Differences in ontogenetic trajectories expressed at the 95% confidence level were found when ontogenetic vectors between the two species were compared using both the TPS method and using both raw BR and SBR coordinates (Fig. 11). This suggests that the pattern of shape change in the intervals of ontogeny sampled between the two species was different, and provides a further argument against "terminal" progenesis because, according to that explanation, similar size ranges should show similar patterns of shape change. It may also argue against dwarfism, provided that the portions of ontogeny available in both subspecies are directly comparable.

DISCUSSION

The different patterns of genal spine development and shape differences at common size permit the rejection of "terminal" or "pure" progenesis (*sensu* McNamara 1983) as the pattern by which *retrorsa minuens* evolved from *retrorsa retrorsa*. The rejection of dwarfism requires further consideration because we cannot be sure that the samples represent the same portions of the ontogenies in both species. However, the samples differ not only in mean shape but also in the way in which the

	Within Flexicalymene retrorsa retrorsa	Within Flexicalymene retrorsa minuens	Sig(%)	Between Flexicalymene retrorsa retrorsa and Flexicalymene retrorsa minuens	Sig(%)
BR	66.9° 61.0° 54.0°	34.7° 30.5° 26.7°	95% 90% 80%	69.8°	95%
SBR	62.8° 57.3° 51.3°	32.1° 30.3° 27.4°	95% 90% 80%	76.9°	95%
TPS	59.5° 54.7° 49.7°	35.0° 31.5° 28.6°	95% 90% 80%	76.2°	95%

Fig. 11. Within- and between-species comparison of pattern of shape change during development. Comparisons based on vectors calculated using Bookstein registration, sliding baseline registration, and thin-plate spline analysis of landmark data. Within-species angles calculated from 400 bootstraps, given at 95%, 90%, and 80% confidence limits. Between-species angles considered statistically significant if the angle between ontogenies exceeds within-species angles at 95% confidence. In all cases, between-species angles exceed within-species angles of ontogenetic trajectories.

shape changed with increasing size. If *retrorsa minuens* was a dwarf of *retrorsa retrorsa*, then at any given holaspid size *retrorsa minuens* are expected to be further along the common ontogenetic trajectory than those of *retrorsa retrorsa*. Hence, in the region of overlapping size ranges observed, we should expect to see in *retrorsa minuens* features characteristic of the later development of *retrorsa retrorsa*. Whereas this is the case with respect to the development of the genal spine, it is not the case with respect to characters that vary allometrically. Most importantly, whereas the allometries of both species show a decrease in the relative size of the palpebral lobe, at common size, the relative size of the lobe in *retrorsa minuens* is larger than that of *retrorsa retrorsa* (see landmark configuration in Fig. 9). This is opposite of what would be expected if *retrorsa minuens* is a dwarf, unless larger *retrorsa retrorsa* than those in our sample showed a pattern of late stage holaspid-positive allometry of the palpebral lobe. Such a pattern would be most unusual in trilobites, in which palpebral lobe allometries in the holaspid phase, if significant, are almost invariably negative (Hughes 1994). Furthermore, as the degree of allometry in trilobites commonly declined in later ontogenetic stages (Hughes 1994), the greater amount of allometry within the *retrorsa minuens* sample compared with that of *retrorsa retrorsa* is in conflict with the expectation that the *retrorsa*

minuens sample represents a more mature portion of ontogeny than the *retrorsa retrorsa* sample. These observations confirm that *retrorsa minuens* is not a dwarf of *retrorsa retrorsa*.

The contrast between the conditions of the genal spine and palpebral lobes at the common size in both species is particularly important because whereas the genal spine condition in *retrorsa minuens* appears mature with respect to the condition in *retrorsa retrorsa*, the palpebral lobe size appears immature (Fig. 12C). This implies a disassociation in the ontogenetic pathways of these different characters during the evolution of *retrorsa minuens* from *retrorsa retrorsa*. Hence, any global heterochronic model, all of which require parallel patterns of ontogenetic shape change in both the ancestor and descendent, can be rejected in this case. This includes a case in which a decrease in the rate of progress along a common ontogenetic trajectory (as in neoteny) was coupled with cessation of development at small size (as in progenesis) in *retrorsa minuens* with respect to *retrorsa retrorsa*. Other global descriptions, such as "sequential progenesis," can be rejected on the same grounds.

Although no global pattern of heterochrony was operative in the evolution of *retrorsa minuens* from *retrorsa retrorsa*, the character transitions could be consistent with a pattern of "local" heterochrony (e.g., Edgecombe and Chatterton 1987),

in which changes in developmental timing affect various characters independently. This explanation could pertain in this case to the contrasting patterns seen in the ontogenies of the genal spine and other aspects of cranidial shape. However, such local heterochrony is not favored by the observation that with respect to cephalic shape, the two species differed significantly in the degree and pattern of ontogenetic change within the holaspid phase. The restricted portions of ontogeny available limit the value of detailed further investigation of this issue.

The transition from *retrorsa retrorsa* to *retrorsa minuens* was apparently accompanied by relatively minor modifications to existing developmental patterning mechanisms involving the rate of development. These could have included changes to the relative timing of events such as cellular or tissue differentiation or apoptosis, but could also have included changes in the spatial patterning over which particular developmental modules exerted an influence. Whatever the cause, the evolutionary changes chronicled in the exoskeletons

of the two species apparently required only a minor modification of the patterning mechanisms operative in the ancestor. We see little evidence for the operation of other kinds of evolutionary modifications of ontogeny, such as those discussed by Webster and Zelditch (2005).

The catalyst for the reduction in size and associated shape changes in *retrorsa minuens* is not known. Dramatic size decreases in taxa are commonly coincident with marked shifts in ambient environmental parameters such as temperature (Hunt and Roy 2006), decreasing pH (Scott 1948) associated with higher levels of hydrogen sulfide as a result of decaying organic matter (Cloud 1948), hypersalinity (Gerdes and Krumbein 1984), reduced levels of primary production (Girard and Renaud 1996; Fraiser and Bottjer 2004), and dysaerobic conditions (Savrda et al. 1984). However, the presence of other faunal elements such as brachiopods, molluscs, echinoderms, and trilobites such as *Isotelus,* all of which displayed sizes similar to those in beds bearing *retrorsa retrorsa,* questions the generality of any causal factors. Rather, the widespread occurrence of this diminutive species across the Cincinnatian paleoshelf, and the lack of incidence of similar miniaturized forms elsewhere in the recurrent lithofacies and repeated cycles of water depth through the Cincinnatian Series argue against the size difference as being a response to a broad environmental shift. It appears more likely that selec-
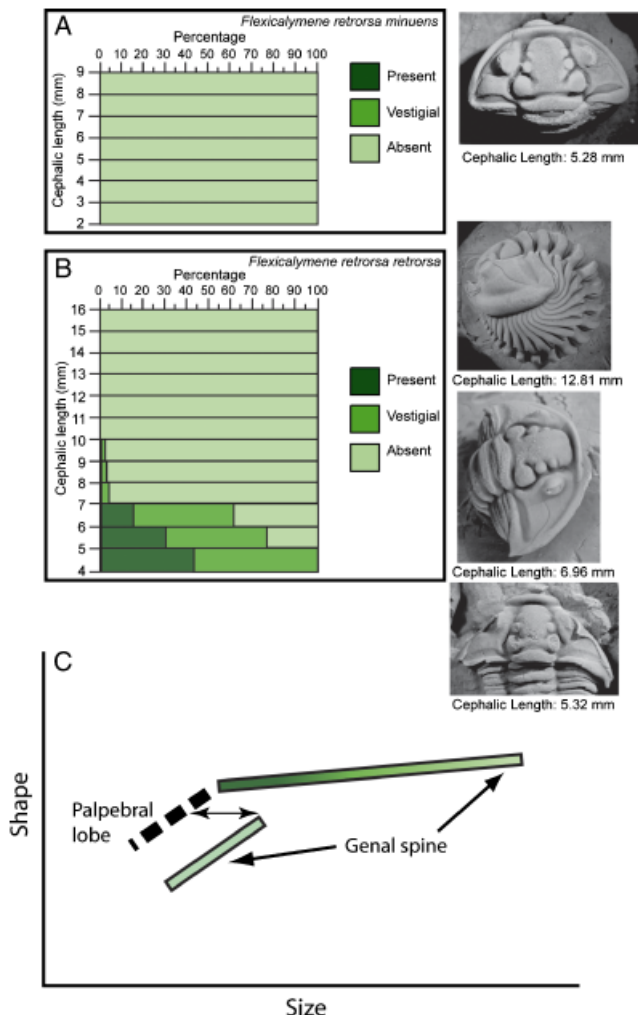
Fig. 12. Comparison of the occurrence of genal spines in *Flexicalymene retrorsa retrorsa* and *Flexicalymene retrorsa minuens.* (A) *F. retrorsa minuens* never has fixigenal spines regardless of size. This condition is similar to that of large specimens of *Flexicalymene retrorsa*; yet, the size of the specimen (cephalic length) is similar to the specimen of *Flexicalymene retrorsa* with full-fixigenal spines. (B) *F. retrorsa retrorsa* exhibits a size-related pattern in genal spine occurrence. Small specimens have both full and vestigial (pointed) spines on the fixigena. The size and occurrence of fixigenal spines are reduced with increasing size such that intermediate-sized specimens either have vestigial spines or have lost them while larger specimens (>10 mm in sagittal cephalic length) have lost the genal spines altogether. (C) Cartoon summarizing ontogenetic differences between *retrorsa retrorsa* and *retrorsa minuens*. Bars represent the sampled ontogenetic trajectories of the two subspecies, which followed different patterns of shape change (degree of allometry indicated approximately by the slope of the bars), and yielded different shapes at common size. It is possible that *retrorsa retrorsa* followed the same pattern of shape change seen in the sampled *retrorsa minuens* but at a size smaller than that represented (projected ontogeny indicated by the dashed black line), and this could explain why *retrorsa minuens* appears juvenilized compared with similarly sized *retrorsa retrorsa* in a manner consistent with global heterochrony. However, this cannot have been the case because all *retrorsa minuens*, regardless of size, displayed the mature, spine-absent state (box infill light green) with respect to genal spine development, whereas equivalently sized *retrorsa retrorsa* possessed either a spine (box infill dark green) or a nubbin (box infill medium green) at the genal angle. Such a result demonstrates that *retrorsa minuens* does not differ from *retrorsa retrorsa* "by size alone" and is not a pure paedomorph.

tion favored the size reduction for reasons specific to the ecology of this species. The fact that the miniaturized morphotype appears only once during the approximately 6.5 Ma history of a *Flexicalymene* species lineage within the Cincinnatian Series of the Cincinnati region also argues against *retrorsa minuens* being an ecophenotype of *retrorsa retrorsa*, as does its consistent occurrence and size throughout the uppermost Waynesville Formation.

CONCLUSIONS

Analysis of the sister species pair *F. retrorsa retrorsa* and *F. retrorsa minuens* indicates that the unusually small subspecies *retrorsa minuens* did not evolve from *retrorsa retrorsa* by global heterochronic dwarfism, progenesis, or neoteny. Rather, the results suggest a more complex pattern of rate modification along varied ontogenetic trajectories. This result is significant in that *retrorsa minuens* had previously been interpreted to differ from *retrorsa retrorsa* "by size alone," and thus presented a likely case of global paedomorphic evolution in trilobites. Consideration of the geological setting of the two species suggests that ecological factors specific to *retrorsa minuens*, rather than taphonomic bias or a general environmental change affecting all taxa, was the cause.

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APPENDIX A

Table A1

Table A1. Character data used in phylogenetic analysis of calymenid trilobites

Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Gravicalymene sp. (Ross 1967)	0	1	0	1	0	1	2	0	0	0	0	0	?	?	0	?	?	?	0
Gravicalymene truncatus (Ross 1979)	0	1	0	0	0	1	1	0	0	0	0	0	1	?	0	0	0	2	0
F. verecunda (Dean 1979)	0	1	1	1	1	1	0	1	0	0	0	1	0	?	0	2	?	0	?
F. onniensis (Shirley 1936)	?	?	1	1	1	1	1	1	?	0	1	1	?	?	0	1	2	1	1
F. (Onnicalymene) scabustula (Thorslund 1940)	0	1	1	2	1	0	2	1	0	0	0	1	1	?	0	2	1	1	1
F. (Onnicalymene) jemtlandica (Siveter 1976)	0	0	1	2	1	0	2	1	0	0	0	1	1	?	0	1	0	1	1
F. cavei (Price 1974)	0	0	1	2	0	0	2	1	0	0	0	2	1	0	?	0	1	1	1
F. planimarginata (Reed 1906)	0	0	1	1	0	1	0	1	?	0	0	?	1	?	0	?	1	0	?
F. caractaci (Salter 1865)	0	0	1	1	1	1	0	1	1	0	0	1	1	1	0	0	1	1	1

Table A1. (Contd.)

Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
F. senaria (Conrad 1841)	0	0	1	2	1	1	2	1	1	1	0	1	1	1	0	1	1	2	1
F. praelongicephala (Stumm and Kauffman 1958)	0	0	0	1	0	1	2	1	2	1	?	1	?	?	0	0	2	0	1
F. quadricapita (Stumm and Kauffman 1958)	0	1	0	1	0	1	0	2	2	0	1	1	1	?	0	0	2	0	1
F. granulosa (Foerste 1910)	1	1	0	1	1	1	2	2	2	1	1	2	1	1	1	1	2	2	2
F. meeki (Foerste 1910)	1	1	0	1	1	1	1	1	1	1	1	1	3	0	1	2	0	2	2	2
F. retrorsa retrorsa (Foerste 1910)	1	1	0	1	1	1	1	1	2	1	1	3	1	1	2	0	2	2	2
F. retrorsa minuens (Foerste 1919)	1	2	0	3	1	1	1	1	2	1	1	3	2	1	2	2	2	2	2

Refer to Table 1 for characters and character states. Coding sources are the following: Salter (1865), Foerste (1910, 1919), Shirley (1936), Stumm and Kauffman (1958), Ross (1967, 1979), Price (1974), Siveter (1976), and Dean (1979).