Influence of atrypid morphological shape on Devonian episkeletobiont assemblages from the lower Genshaw formation of the Traverse Group of Michigan: A geometric morphometric approach

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ABSTRACT

Atrypids examined from the lower Genshaw Formation of the Middle Devonian (early middle Givetian) Traverse Group include a large assemblage of *Pseudoatrypa* bearing a rich fauna of episkeletobionts. We identified two species of *Pseudoatrypa* – *Pseudoatrypa lineata* and *Pseudoatrypa* sp. A based on ornamentation and shell shape. Qualitative examination suggested that the former had fine-medium size ribbing, narrow hinge line, widened anterior, gentle to steep mid-anterior fold, a more domal shaped dorsal valve, and an inflated ventral valve in contrast to the coarse ribbing, widened hinge line, narrow anterior, gentle mid-anterior fold, arched shape dorsal valve, and flat ventral valve of the latter. Geometric morphometric analysis supported two statistically different shapes ($p<0.01$) for the two distinct species.

This study further examined these atrypids to investigate the influence of morphology on episkeletobiont settlement on the two *Pseudoatrypa* species. Among the 343 atrypid hosts examined, nearly 50% were encrusted by episkeletobionts. Common encrusters included microconchids, bryozoan sheets, and hederellids. Less common encrusters included auloporid corals, cornulitids, tabulate corals, *Ascodictyon*, craniid brachiopods, and fenestrate bryozoans. Hederellids, auloporid corals, cornulitids, and tabulate corals encrusted a few living *Pseudoatrypa* hosts, but determination of pre- or post-mortem encrustation by the majority of episkeletobionts is equivocal. In a very few cases, episkeletobionts crossed the commissure indicating the death of the host.

Some episkeletobionts, microconchids and the sheet bryozoans, were more common on *Pseudoatrypa lineata*, which exhibited more dorsal-ventral convexity than *Pseudoatrypa* sp. A. Perhaps, *P. lineata* may have provided a larger surface area for episkeletobiont settlement relative to *Pseudoatrypa* sp. A.

In both the host species, encrustation was heaviest on the convex dorsal valve. This suggests that most of the encrustation occurred in a reclining, dorsal-valve-up life orientation of both species, in which the convex dorsal valve was exposed in the water column and the ventral valve remained in contact with the substrate. However, life orientations of these atrypid species could not be confidently predicted simply from the location preferences of episkeletobionts alone, as the life orientation of the host would also have been a hydrodynamically stable orientation of the articulated shell after death.

Most episkeletobionts encrusted the posterior region of both dorsal and ventral valves of the two species, which suggests that the inflated areas of these valves, when exposed, favored the settlement of most episkeletobiont larvae.

1. Introduction

Pseudoatrypa is a common brachiopod from the Givetian to late Frasnian of North America. This genus occurs throughout much of the Traverse Group in the Michigan Basin, including the Genshaw Formation (Kelly and Smith, 1947; Koch, 1978). Here we focus on material from the lower Genshaw Formation to: 1) analyze morpho-logical shape patterns in two *Pseudoatrypa* species, and, 2) investigate episkeletobiont interactions with these species to determine how the distinct morphological shapes of the two species may have influenced their settlement.

Pseudoatrypa is frequently encountered in Devonian Midcontinent basins. Webster (1921) first described the taxon as *Atrypa devoniana* from the late Frasnian Independence Shale of Iowa; his specimens were later designated as the type species of the new genus *Pseudoatrypa* (Copper, 1973; Day and Copper, 1998). *Pseudoatrypa* also occurs in the Traverse Group of the Michigan Basin (Stumm, 1951; Copper, 1973; Koch, 1978) and in the Silica Formation of Ohio

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and equivalent rocks from northern Indiana (Wiedman, 1985). Webster (1921) described the species *Atrypa lineata* from the late Middle Devonian (late Givetian) upper Osage Springs Member of the Lithograph City Formation of the Upper Cedar Valley Group of Iowa, which was later included in *Pseudoatrypa* by Day and Copper (1998). Fenton and Fenton (1935) described a subspecies and growth variant forms of this species from the late Givetian Cedar Valley of Illinois. Herein we test both qualitatively and quantitatively whether distinct species exist within *Pseudoatrypa* from the Lower Genshaw Formation of Michigan, and whether these external morphology influences episkeletobiont assemblages.

Episkeletobionts are organisms that adhere to, or encrust, the surface of a shell (Taylor and Wilson, 2002). Episkeletobionts are useful as ecological and life status indicators of their hosts—whether the host was living at the time of encrustation or was dead (Watkins, 1981; Anderson and Megivern, 1982; Brezinski, 1984; Gibson, 1992; Lescinsky, 1995; Sandy, 1996; Sumrall, 2000; Morris and Felton, 2003; Schneider, 2003, 2009a; Zhan and Vinn, 2007; Rodrigues et al., 2008). Episkeletobionts have been used to infer the life orientation of brachiopods (Rudwick, 1962; Hurst, 1974; Pitrat and Rogers, 1978; Kesling et al., 1980; Spjeldnaes, 1984; Lescinsky, 1995), the preferred orientation of host water currents (e.g., Kesling et al., 1980), potential camouflage for hosts (Schneider, 2003, 2009a), the attracting or antifouling nature of ornamentation (Richards and Shabica, 1969; Richards, 1972; Carrera, 2000; Schneider, 2003, 2009a; Schneider and Leighton, 2007), and the function of the valve punctae (Thayer, 1974; Curry, 1983; Bordeaux and Brett, 1990). Brachiopod hosts are useful for investigating host influences on episkeletobiont preferences such as shell texture (Schneider and Webb, 2004; Rodland et al., 2004; Schneider and Leighton, 2007), size of host (Ager, 1961; Kesling et al., 1980), and antifouling strategies (Schneider and Leighton, 2007). Although other Paleozoic marine organisms were frequently encrusted, brachiopods remain one of the best understood hosts for Paleozoic episkeletobionts.

In the present study, the settlement of a live episkeletobiont during the life of the host is called a live–live association (pre-mortem encrustation) and the settlement of a live encruster on a dead host is called a live-dead association (post-mortem encrustation). Taylor and Wilson (2003) provided the following criteria for distinguishing between pre- and post-mortem associations: (a) If the episkeletobiont fossil overgrows (crosses) the commissural margin, or if there is evidence of internal valve encrustation, then the brachiopod host was dead when the organism overgrew the commissure - this is evidence of a live-dead association; (b) if the episkeletobiont and the host both have a similar degree of preservation, and if there is evidence of scars representing the repair of damage inflicted by episkeletobionts, then the brachiopod host was alive during encrustation - this is evidence of live-live association; and (c) if certain episkeletobionts repeatedly encrust specific locations on host shells, e.g., if branching fossils, like auloporid corals or hederellids, branch towards or are aligned parallel to the commissure or if solitary organisms, such as cornulitids, grow with their apertures pointing towards the commissure, then hosts and their episkeletobionts experienced live-live associations. In other cases, there is no way to tell for certain whether the host was alive or dead at the time of encrustation.

Our purpose herein is twofold: (1) to quantitatively assess putatively distinct species of *Pseudoatrypa* from the Genshaw Formation, herein described as *Pseudoatrypa lineata* and *Pseudoatrypa* sp. A; and (2) to examine the influence of species morphology on encrustation by episkeletobionts. We structured the study by testing the following hypotheses:

1) two species of *Pseudoatrypa* - *Pseudoatrypa lineata* and *Pseudoatrypa* sp. A, previously distinguished on qualitative features, must have statistically distinct shell shapes and are validly different species; if not they will be considered growth variants of the same species;

2) episkeletobionts are influenced by morphology and will preferentially encrust the two species differently; and

3) given the preferred orientation of atrypid adult shells—convex dorsal valve raised into the water column and flat ventral valve in contact with the substrate (as inferred by Fenton and Fenton (1932)) —the extent of encrustation coverage on the ventral valve will be limited by physical contact with the substrate and thus statistically less than on the dorsal valve.

These hypotheses were tested using geometric morphometric assessment of shell shape and statistical analysis of the location of encrusting organisms.

2. Geologic setting

Pseudoatrypa brachiopods were collected from the lower Genshaw Formation of the Middle Devonian Traverse Group. The Traverse Group ranges in thickness from ~25.0–169.5 meters (Ehlers and Kesling, 1970; Wylie and Huntoon, 2003), with depositional environments ranging from shallow water carbonate lagoons with coral-stromatoporoid reefs to storm-dominated mixed carbonate-siliciclastic shelf deposits and offshore muddy shelf to slope environments (Ehlers and Kesling, 1970). The Genshaw Formation was named by Warthin and Cooper (1935) for strata overlying their Ferron Point Formation and underlying their Killians Limestone, later revised by the same stratigraphers to include the Killians Limestone as the upper member of the Genshaw Formation (Warthin and Cooper, 1943). Warthin and Cooper (1943) placed the new upper contact at the base of the overlying Newton Creek Limestone. The Genshaw Formation remained one of the least studied units of the lower Traverse Group until recently, when the LaFarge Quarry in the Alpena area began to mine into this unit and exposed nearly the entire Formation (Bartholomew, 2006). The Genshaw Formation accumulated during the highstand of a third-order sea level sequence (Wylie and Huntoon, 2003; Brett et al., 2010).

The Genshaw Formation, which is ~30.0 meters thick (Fig. 1), is subdivided into informal lower, middle, and upper (formerly Killians Member) portions (Wylie and Huntoon, 2003). The lower unit of the Genshaw Formation begins with a 0.5 m-thick crinoidal grainstone, which locally contains burrows on its lower surface. Overlying this basal bed of the Genshaw Formation is a thin, argillaceous succession capped by a limestone-rich interval to the top of the lower Genshaw. The brachiopods used in this study were collected from the argillaceous beds of this lower unit (Fig. 1).

3. Materials and methods

3.1. Sampling

Samples examined were collected by A. Bartholomew of State University of New York, New Paltz from the northeastern outcrop of the Lafarge Alpena Quarry, Alpena County, Michigan (Fig. 1). He extensively sampled all brachiopods from a shale bed of the lower Genshaw Formation. The 185 well-preserved atrypids examined for encrustation in this study have been deposited in the Indiana University Paleontology Collection (IU 100059 – IU 100243). Use of ammonium chloride spray in a dry environment helped distinguish morphological features of the species.

3.2. Species recognition

The atrypid sample was first divided into two populations based on the qualitative traits examined in this study. The two populations are similar in that they have an apical foramen, hinge line with incurved extremities, orbicular to subquadrate shell outline, ribbing with implantations and bifurcations, and somewhat similar spacing
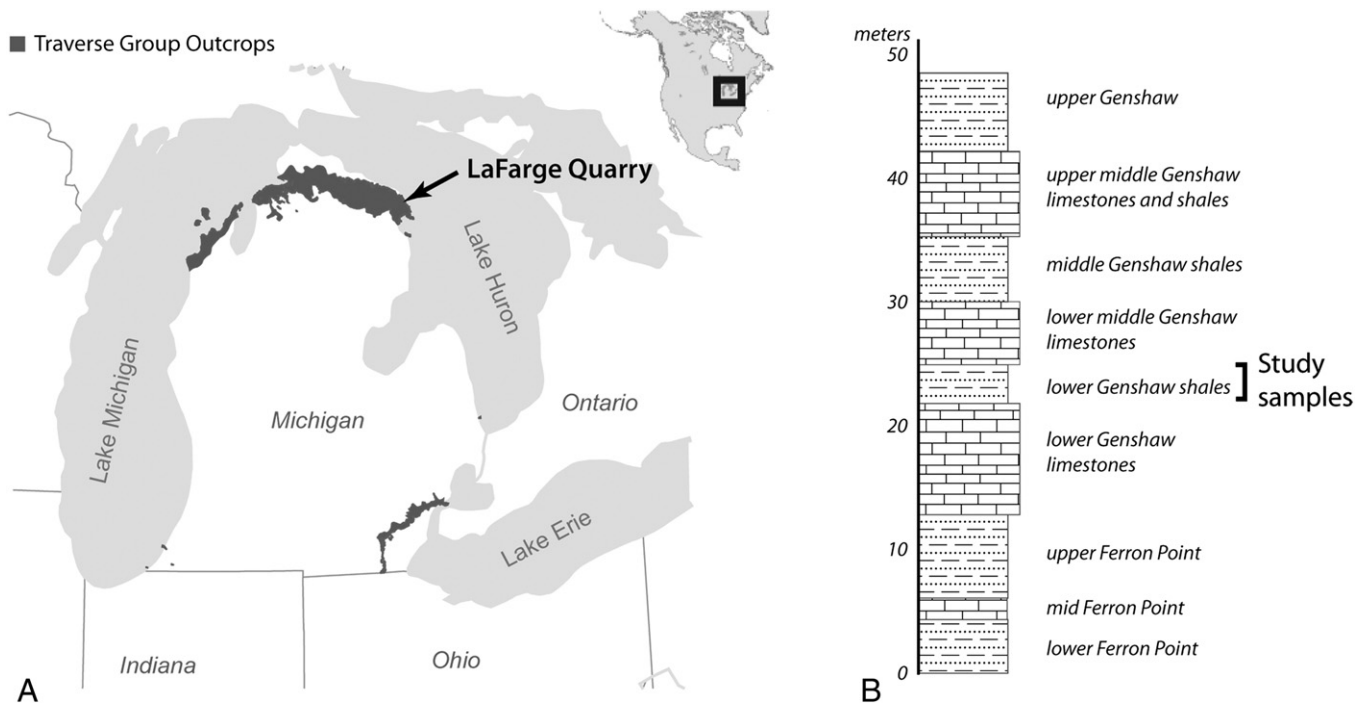
Fig. 1. A) Map showing Michigan surface exposures of the Middle Devonian Traverse Group and the location of the La Farge Quarry, Alpena area, from which the samples used in this study were collected, B) Simplified stratigraphic section of the Traverse Group at La Farge Quarry showing the horizons of the Genshaw Formation where the specimens used in this study were collected (after Bartholomew, 2006).

between growth lamellae or frills, with frills crowding more at the anterior. However, *Pseudoatrypa lineata* is different from *Pseudoatrypa* sp. A in having a) a smooth, arcuate, domal curvature to the dorsal valve as opposed to the arched shape in the latter, b) slightly inflated ventral valve with an inflation near the umbo as opposed to a more flattened ventral valve in the latter, c) relatively lower dorsal valve curvature height, d) fine to medium closely spaced ribs in contrast to coarse ribs in the latter, e) angular to subrounded hinge line as opposed to the widened hinge in the latter, f) widened median deflection (fold and sulcus) on the commissure as opposed to the narrow deflection in the latter, and g) gentle to steep mid-anterior fold as opposed to the gentler fold in the latter.

3.3. Morphometrics

We performed geometric morphometric analysis to determine morphological variation within and between the two qualitatively distinguished populations assigned to *Pseudoatrypa lineata* and *Pseudoatrypa* sp. A. No crushed specimens were used for morphometrics.

Geometric morphometrics is the analysis of geometric landmark coordinates points on specific parts of an organism (Bookstein, 1991; MacLeod and Forey, 2002; Zelditch et al., 2004). We based our morphometric analysis on the use of landmarks to capture shape (Rohlf and Marcus, 1993); landmarks represent discrete geometric points on each specimen that correspond among forms (*sensu* Bookstein, 1991). In this study, we used 10 two-dimensional landmark points on the external shell to capture the most meaningful shape differences (Fig. 2). When selecting landmarks for analyses, we selected points that not only characterized body shape accurately, but also represented some aspect of the inferred ecological niche. All landmarks were defined by geometric position on host shells (1 = beak tip on brachial valve; 2 and 8 = intersection points of the commissure and the hingeline; also region for food intake from inhalant currents; 3 and 7 = length midpoint projected onto the commissure; these points are perpendicular to, and crosses the midline of the shell; 4 and 6 = lowest point of median deflection (fold and sulcus) on the commissure; 5 = middle point of commissure; 9 = tip of umbo on pedicle valve; 10 = maximum height

on brachial valve). These landmarks are appropriate for analyses attempting to capture shape changes or function. For this study, we conducted four different analyses operating on ten landmarks in four different orientations of the shell. Two analyses were conducted in the x-y plane of the dorsal and ventral valves; these analyses capture only the view in that plane (Fig. 2A-B). These analyses of the dorsal and ventral valve views, included nine landmarks, which were selected to encompass the outline of the entire specimen in the x-y plane. Although brachiopods are bilaterally symmetrical, landmarks were included from both the left and right sides of the specimens to record the functional response of these hosts to the then existing ecological conditions and to encrusting episkeletobionts. Capturing both the postero-lateral distal extremities of the hingeline and the lowest points of median deflection on the commissure, even of a bilaterally symmetrical organism may be important for determining shape changes in the host species, as each of these locations may possess unique specific abundances of distinct episkeletobiont assemblages (Bookstein, 1991; Kesling et al., 1980). Two separate analyses operating on landmarks in the y-z plane were conducted from the anterior and posterior views of the shells (Fig. 2C-D). For posterior and anterior regions of the shell, landmark measurements (four landmarks on posterior and three landmarks on anterior) were taken only on half of the specimen (anterior/posterior view left or right) (Fig. 2C-D). Overall, these two orientations measure not only the shape of the valves, but also capture the shape of the brachiopod lophophore support, the spiralia (Bookstein, 1991; Haney et al., 2001). The four views (dorsal, vental, anterior, and posterior) were analyzed separately.

Procrustes analysis (Rohlf, 1990; Rohlf and Slice, 1990; Rohlf, 1999; Slice, 2001) was performed on original shape data, rotating, translating and scaling all landmarks to remove all size effects, while maintaining their geometric relationships (Procrustes superimposition). Principal component analysis of the covariance matrix of the residuals of the Procrustes superimposed coordinates was performed to determine the morphological variation of the two species along their major principal component axes (1 and 2) in the shape morphospace (Fig. 2) and to provide a set of uncorrelated shape variables for further statistical analysis. Procrustes distances, which are the sum of
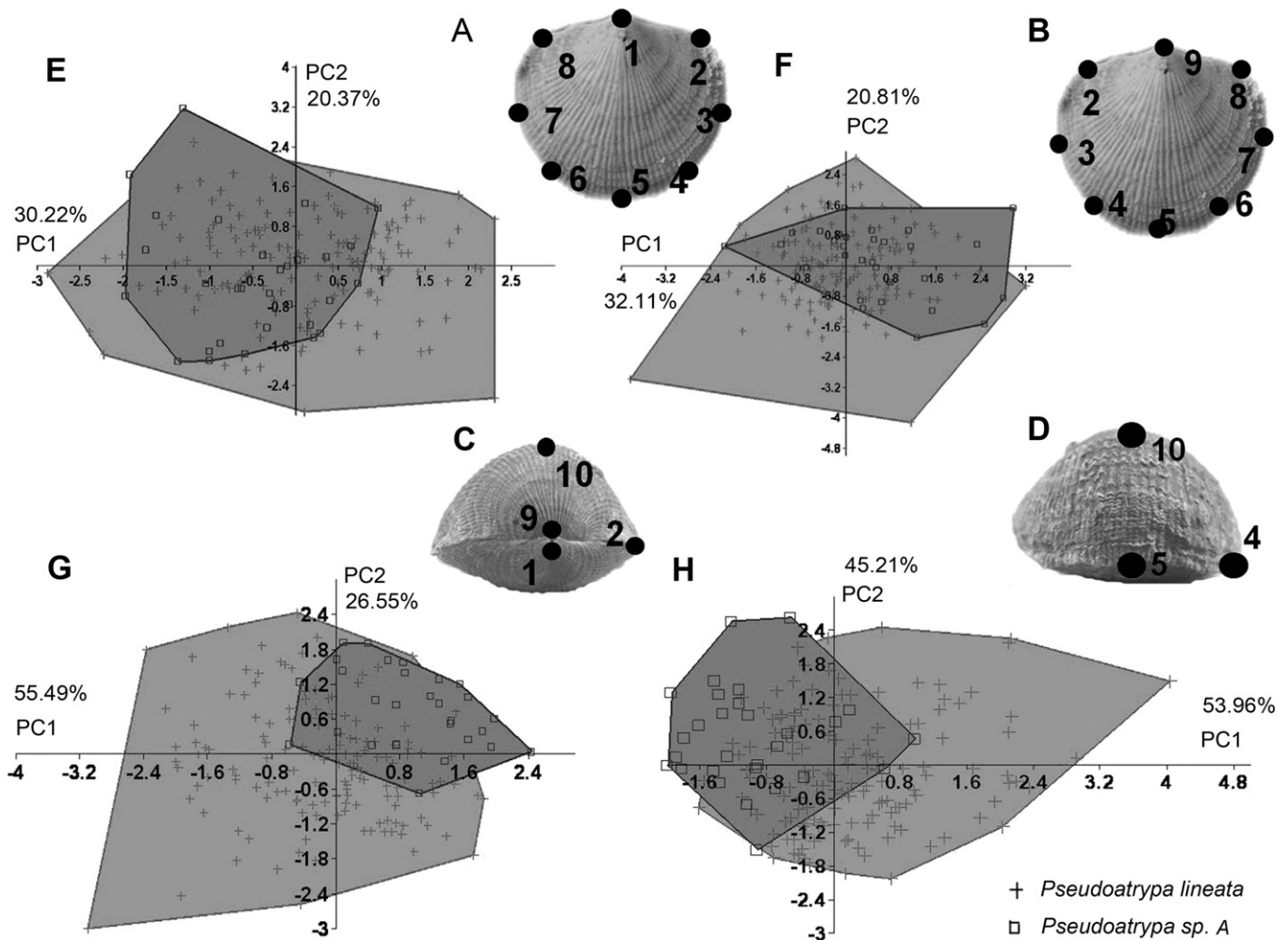
Fig. 2. A) Location of eight landmark points on dorsal valves of host species, B) location of eight landmark points on ventral valves of host species, C) location of four landmark points on posterior region of host species, D) location of three landmark points on anterior region of host species; morphological shape variation between the two host species *Pseudoatrypa lineata* and *Pseudoatrypa* sp. A along E) dorsal vales, F) ventral valves, G) posterior region, and H) anterior region.

the distances between corresponding landmarks of Procrustes superimposed objects (equal to their Euclidean distance in the principal components space if all axes are used), were calculated as a measure of difference between mean morphological shapes of the dorsal valves, ventral valves, posterior and anterior regions of *Pseudoatrypa lineata* and *Pseudoatrypa* sp. A and thin plate spline plots (Bookstein, 1989) were used to visualize those differences. Multivariate analysis of variance (MANOVA) and discriminant function analysis (DFA) of the shape variables was used to test for significant shell shape differences between the two species along the dorsal, ventral, anterior and posterior regions of the shells (Hammer and Harper, 2005). Multivariate analysis of variance (MANOVA) was performed to test shape variation between the two species. Adult shells of the two species, larger than 1.9 cm in size, were used for geometric morphometric analyses to avoid any misinterpretation in comparative shape study between the two species that could have resulted from not controlling for ontogenic development.

3.4. Episkeletobiont analysis

Brachiopods were first examined microscopically for encrustation data (100x magnification). Episkeletobiont distribution was tabulated for each species, for valve preference within each species, and for position on each valve. The relationship between these episkeletobionts and the host atrypids were investigated based on their placement on the host shell. The *Chi-square* test was used to determine whether

differences in most abundant episkeletobiont assemblages were significant between the two host species and between the dorsal and ventral valves of each species. Furthermore, species and valve preference by episkeletobionts was reconstructed based on the abundance and location of episkeletobionts, as described below.

Mean encrustation frequency per species was determined to compare encrustation abundance on the dorsal and ventral valves of the two species as

$$A_C = [(\textstyle\sum E_T / \sum V_E)]*100, \tag{1}$$

where A_C is the mean encrustation frequency with respect to episkeletobiont count, E_T is the total number of episkeletobiont colonies, and V_E is the total number of valves encrusted.

The total area of the valve that was encrusted was measured on each individual host, and the proportion of the valve that was encrusted was calculated using the equation:

$$A_A = A_E / A_V *100, \tag{2}$$

where A_A is the encrustation area per valve (A_E) with respect to total valve area (A_V).

Relationship between encrustation area (A_A) and principal component (PC axis 1) scores of the shape co-ordinates of the valve morphology was tested using the product-moment correlation (r). A

p-value was also reported for this correlation method to determine if 'r' was significantly different from 0.0.

Following the methods previously established by Bose et al. (2010), each valve of the atrypid hosts was divided into six regions (Fig. 3). The six regions were defined as postero-left lateral (PLL), posteromedial (PM), postero-right lateral (PRL), antero-left lateral (ALL), anteromedial (AM), and antero-right lateral (ARL). These six divisions, i.e., six different surface areas of host, were selected such that they represent biologically functional grids for both the host and the episkeletobiont. The PLL and PRL regions were selected based on the idea that host inhalant currents in those regions may attract episkeletobionts, and these currents may also partially influence episkeletobiont settling along the PM region. Similarly, the AM region was selected based on the host exhalant current criteria, which may also partially influence the ALL and ARL regions. Thus, selecting these six regions and recording the frequency of episkeletobionts on each of these regions will help infer host-episkeletobiont relationships in live-live associations.

Area ratios for each region of the shell was determined using the following equation (Fig. 3):

$$\mathbf{R} = A_R / A_T, \qquad (3)$$

where R is the area ratio, A_R is the area of each region, and A_T is the total area.

The frequency of encrustation in each region was recorded by counting individual colonies as one occurrence and then summing for all atrypid hosts. For comparison with the actual frequency of episkeleto-biosis, expected episkeletobiosis for each region was calculated by:

$$\mathbf{E} = NR_i, \qquad (4)$$

in which the expected number of episkeletobionts (E) is calculated by multiplying the total number of episkeletobionts (N) for all *Pseudoatrypa* specimens by the area ratio (R) for a given region on the atrypid shell (i). The null hypothesis used here for developing the expected value is as follows: Given that we have six regions for one valve, and each region has a chance of being encrusted based on their proportion of available surface area (assuming as a null hypothesis a random distribution of encrusters), then if one region accounts for x% of the surface area on the valve, then the expected value for that region is x% of the total number of episkeletobionts encrusting that valve (all six regions) for that species. The same approach is used to determine the expected value for the other regions. Colonial episkeletobionts—sheet-like and branching—posed a problem for calculations because these specimens often crossed borders into adjacent regions. For these specimens, colonization of an episkeleto-biont that extended into two or more regions was divided among the total number of regions it inhabited. For example, branching auloporid corals and hederellids that were observed in all the three anterior regions were counted as 1/3 for each region.

We then quantified common episkeletobionts (i.e., microconchids, bryozoans sheets, and hederellids) for their distribution on six regions of the shell of both dorsal and ventral valves of each host, using Equation 2 above. Distribution of rare episkeletobionts on host shells was also examined, but only for dorsal valves, as episkeletobiont abundance of rare encrusters is negligible on ventral valves. A *chi-square* test was also performed for the total observed and expected episkeletobiont activity along the six regions to determine the episkeletobiont location preference on the atrypid valve within each species.

4. Results

4.1. Morphology and morphometrics

Two-hundred and thirty two specimens of atrypids were assigned to *Pseudoatrypa lineata* and 111 specimens of atrypids were assigned to *Pseudoatrypa* sp. A. Representatives of the two species from this study are shown in Fig. 4. The first two principal component axes (axes 1 and 2) explained a total of 50.2% of the variation in dorsal valves, 52.9% of the variation in ventral valves, 82.0% of the variation in the posterior region and 98.0% of the variation in the anterior region (Fig. 2). Principal component analysis of dorsal and ventral valves indicates that there is considerable shape variation within each species and that the two species overlap considerably in the morphology of both valves in the x-y plane (Fig. 2E-F). Procrustes distances between the mean shape of the two species are 0.023 for the dorsal valves and 0.028 for ventral valves, suggesting that ventral valves show slightly greater morphological differentiation than dorsal valves. Principal component analysis of posterior and anterior regions also indicates that there is considerable variation in morphology between the two species in the y-z plane (Fig. 2G-H). Procrustes distances between the mean shape of the two species are 1.69 for the posterior region and 1.53 for anterior region.. MANOVA detects a small significant difference in mean shape of dorsal, ventral, posterior and anterior regions ($p < 0.01$). DFA detects a small but significant difference in mean shape of dorsal and ventral valves ($p < 0.01$) and a large significant difference in mean shape of the posterior and anterior regions ($p << 0.01$) (Fig. 5). The significance of the MANOVA and the DFA demonstrates that the two populations can be distinguished as separate species, based on shell shape.

Thin plate spline visualisation plots show the mean morphological shapes of these two species are different (Fig. 6). Dorsal valves show a difference in the shape of the posterior hinge line and anterior commissure. The distances between the umbo tip and the posterior left and right lateral margins in the dorsal valve plots are less in *Pseudoatrypa lineata* than in *Pseudoatrypa* sp. A, confirming the observation of a more widened hinge line in the latter. Similarly, the distances between the middle point of commissure and the lowest point of the median deflection (fold and sulcus) on both halves of the
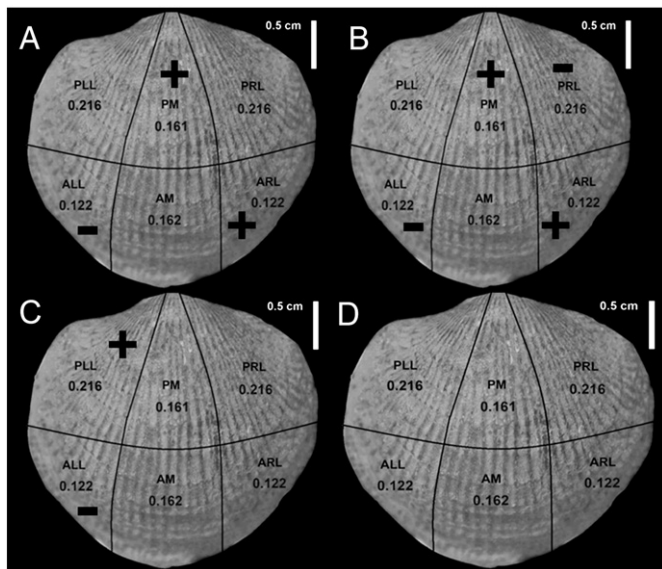

Fig. 3. *Pseudoatrypa* specimen divided into six regions for episkeletobiont frequency study; PLL = postero-left lateral, PM = posteromedial; PRL = postero-right lateral; ALL = antero-left lateral, AM = anteromedial; and ARL = antero-right lateral. Numbers represent the area ratios of each grid across the *Pseudoatrypa lineata* and *Pseudoatrypa* sp. A host valve. Scale bar 0.5 cm. Note that the area ratios are slightly different for *P. lineata* host species which are as follows: PLL = 0.18, PM = 0.138, PRL = 0.18, ALL = 0.147, AM = 0.208, ARL = 0.147. Significantly greater observed episkeletobiont frequency than expected is denoted by a plus symbol and smaller observed episkeletobiont frequency than expected is denoted by a minus symbol across the six regions of the valve; this is described for A) dorsal valve of *P. lineata*, B) dorsal valve of *Pseudoatrypa* sp. A, C) ventral valve of *P. lineata*, and D) ventral valve of *Pseudoatrypa* sp. A.
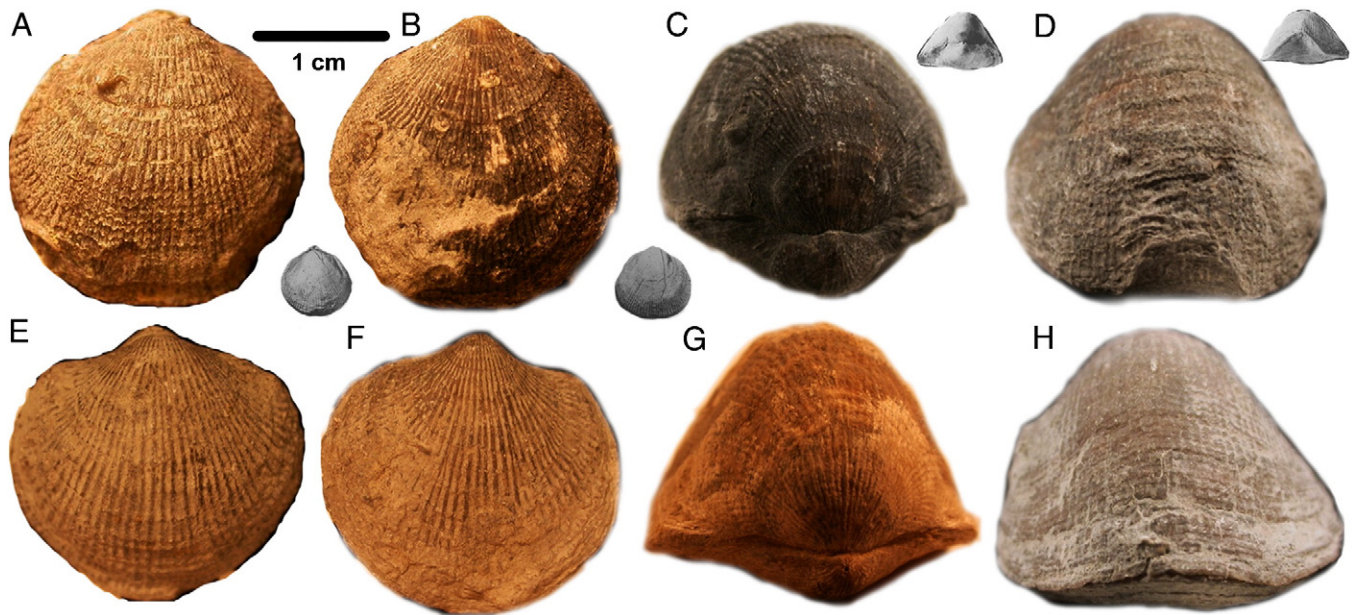
Fig. 4. *Pseudoatrypa lineata* A) Dorsal view, B) ventral view, C) posterior view, D) anterior view (IU#100069); *Pseudoatrypa* sp. A E) dorsal view, F) ventral view, G) posterior view and H) anterior view (IU#100220). The small inset illustrations next to dorsal and ventral views of *P. lineata* represent the type specimen of *Atrypa lineata var. inflata* as described in Fenton and Fenton, 1935 and the posterior and anterior views represent the type specimen of *Atrypa lineata* as described in Day and Copper, 1998.

specimen suggesting a widening of the deflection in *Pseudoatrypa lineata* and narrowing in *Pseudoatrypa* sp. A. Ventral valves, however, do not show much significant difference in shape, except for the widened hinge line in *Pseudoatrypa* sp. A relative to the narrow hinge line in *Pseudoatrypa lineata*. The posterior region plots show greater distance

between the dorsal umbo and ventral beak tip and lesser distance between dorsal umbo and maximum curvature point in *P. lineata* than in *Pseudoatrypa* sp. A, consistent with the visual observation of a domal, relatively shallower dorsal valve and inflated ventral valve in *P. lineata* and arched, relatively deeper dorsal valve and flattened ventral valve in
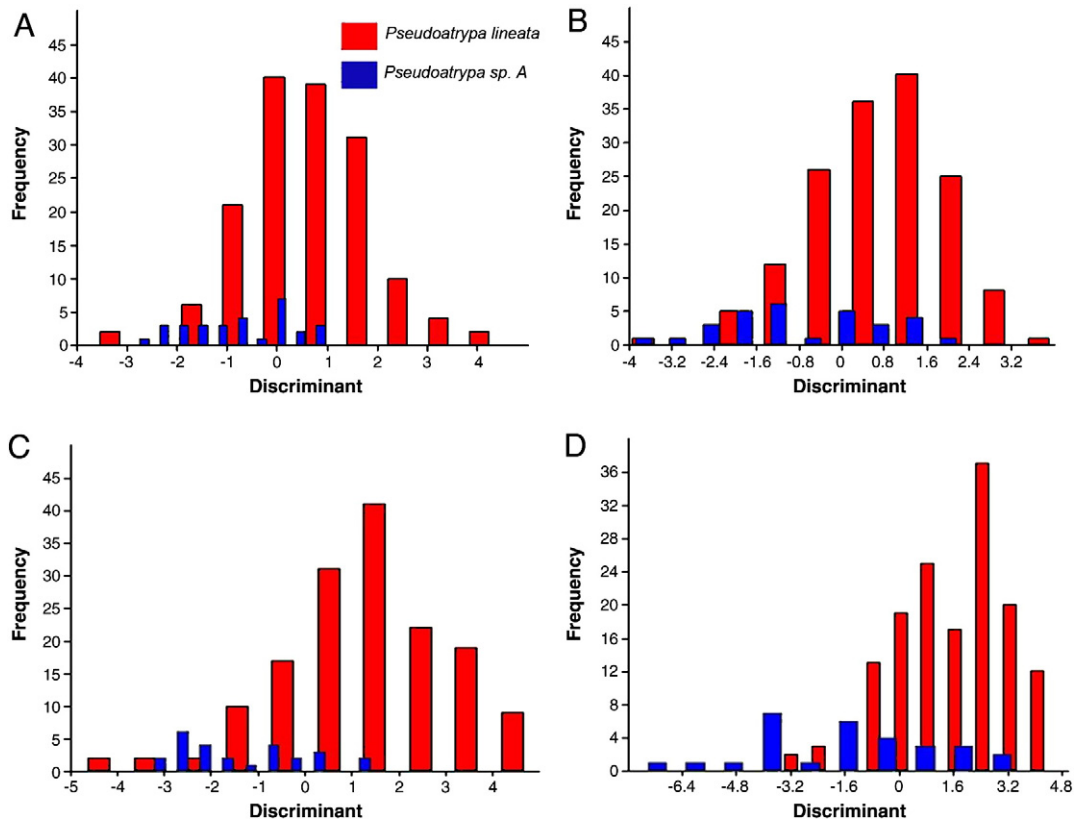

Fig. 5. Discriminant function analysis showing the morphological distinctness between *P. lineata* and *Pseudoatrypa* sp. A for A) dorsal valves: Hotelling's t^2 P = **0.00759** (Dorsal valves DFA) B) ventral valves: Hotelling's t^2 P = **0.002113** (ventral valves DFA), C) posterior region: Hotelling's t^2 P = **6.304 × 10^{-9}** (posterior region DFA), and D) anterior region: Hotelling's t^2 P = **1.973 × 10^{-12}** (anterior region DFA).
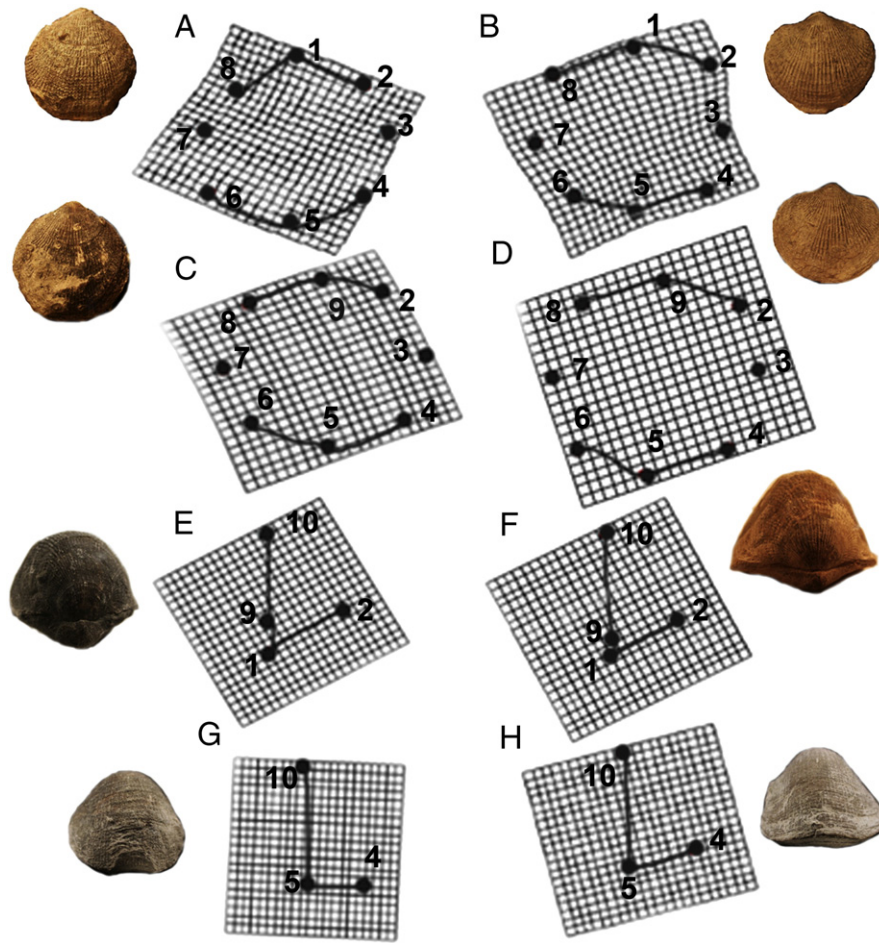
Fig. 6. Thin Plate Spline visualisation plots for mean morphological shape of A) dorsal valves of *P. lineata*, B) dorsal valves of *Pseudoatrypa* sp. A, C) ventral valves of *P. lineata*, D) ventral valves of *Pseudoatrypa* sp. A, E) posterior region of *P. lineata*, F) posterior region of *Pseudoatrypa* sp. A, G) anterior region of *P. lineata* and H) anterior region of *Pseudoatrypa* sp. A.

Pseudoatrypa sp. A. The mean shape plots for the anterior region show less distance between the mid-anterior and right anterior margin in *P. lineata* than *Pseudoatrypa* sp. A and the lateral margin is higher in *Pseudoatrypa* sp. A than in *P. lineata*. This demonstrates that the two species are substantially different in morphological shape (Fig. 6).

4.2. Frequency of episkeletobionts

Pseudoatrypa lineata and *Pseudoatrypa* sp. A are hosts to many colonial episkeletobionts – hederellids, sheet-like bryozoans, tabulate corals, fenestrate bryozoans and *Ascodictyon* – as well as many solitary episkeletobionts - microconchids, craniid brachiopods, and *Cornulites* (Fig. 7). Episkeletobionts encrusted 155 specimens (out of 232 total specimens) of *Pseudoatrypa lineata* and 30 specimens (out of 111 total specimens) of *Pseudoatrypa* sp. A, for a total of 185 encrusted specimens. Episkeletobionts encrusted more frequently on *Pseudoatrypa lineata* than *Pseudoatrypa* sp. A. On *Pseudoatrypa lineata*, 125 dorsal valves (81%) and 65 ventral valves (42%) out of 155 encrusted specimens were encrusted, compared with 30 dorsal valves (100%) and 22 ventral valves (74%) out of 30 encrusted specimens of *Pseudoatrypa* sp. A.

A total of 354 episkeletobionts encrusted *Pseudoatrypa lineata* dorsal valves ($A_C = 2.83\%$) and 74 episkeletobionts encrusted ventral valves ($A_C = 1.14\%$). On *Pseudoatrypa* sp. A, 152 episkeletobionts encrusted dorsal valves ($A_C = 5.07\%$) and 61 encrusted ventral valves ($A_C = 2.77\%$). Dorsal valves are more heavily encrusted for both species (Fig. 8; Table 1). However, average encrustation frequency (A_A) was only weakly correlated with the principal component (PC1) scores for both *Pseudoatrypa lineata* (dorsal view: r = −0.08, p = 0.36; posterior view: r = 0.08, p = 0.40; anterior view: r = 0.01, p = 0.87) and *Pseudoatrypa* sp. A (dorsal view: r = 0.09, p = 0.63; posterior view: r = −0.06, p = 0.75; anterior view: r = −0.10, p = 0.62), implying that episkeletobionts did not have a strict preference for shape.

Microconchids, hederellids and sheet bryozoans were the most abundant epizoans, while tabulate corals, auloporid corals, craniid brachiopods, fenestrate bryozoans, *Cornulites* and *Ascodictyon* were present but rarer. Overall, dorsal valves of both species were encrusted more frequently by microconchids, sheet bryozoans and hederellid colonies (Chi-square test, *p<0.05*) (Table 2). Frequencies of each episkeletobiont taxon on both valves of the two species are illustrated in Table 2 and Fig. 8. For each episkeletobiont taxon, mean frequency based on encrustation count (A_C) is presented in Table 1.

4.3. Location of episkeletobionts

The frequency of biotic interactions varies among the six regions on both valves of the *Pseudoatrypa lineata* and *Pseudoatrypa* sp. A hosts; dorsal valves of each are illustrated in Fig. 9 and 10. Dorsal valves are more heavily encrusted than the ventral valves with relatively greater episkeletobiont concentration on all the grids (*p<0.01*).

4.3.1. Dorsal valves

In dorsal valves, the posteromedial region contains the most frequent occurrence of episkeletobionts on both *Pseudoatrypa lineata* and *Pseudoatrypa* sp. A. Microconchids, the most frequent episkeletobiont, is noticeably abundant on all of the six shell regions of both species (Fig. 9).
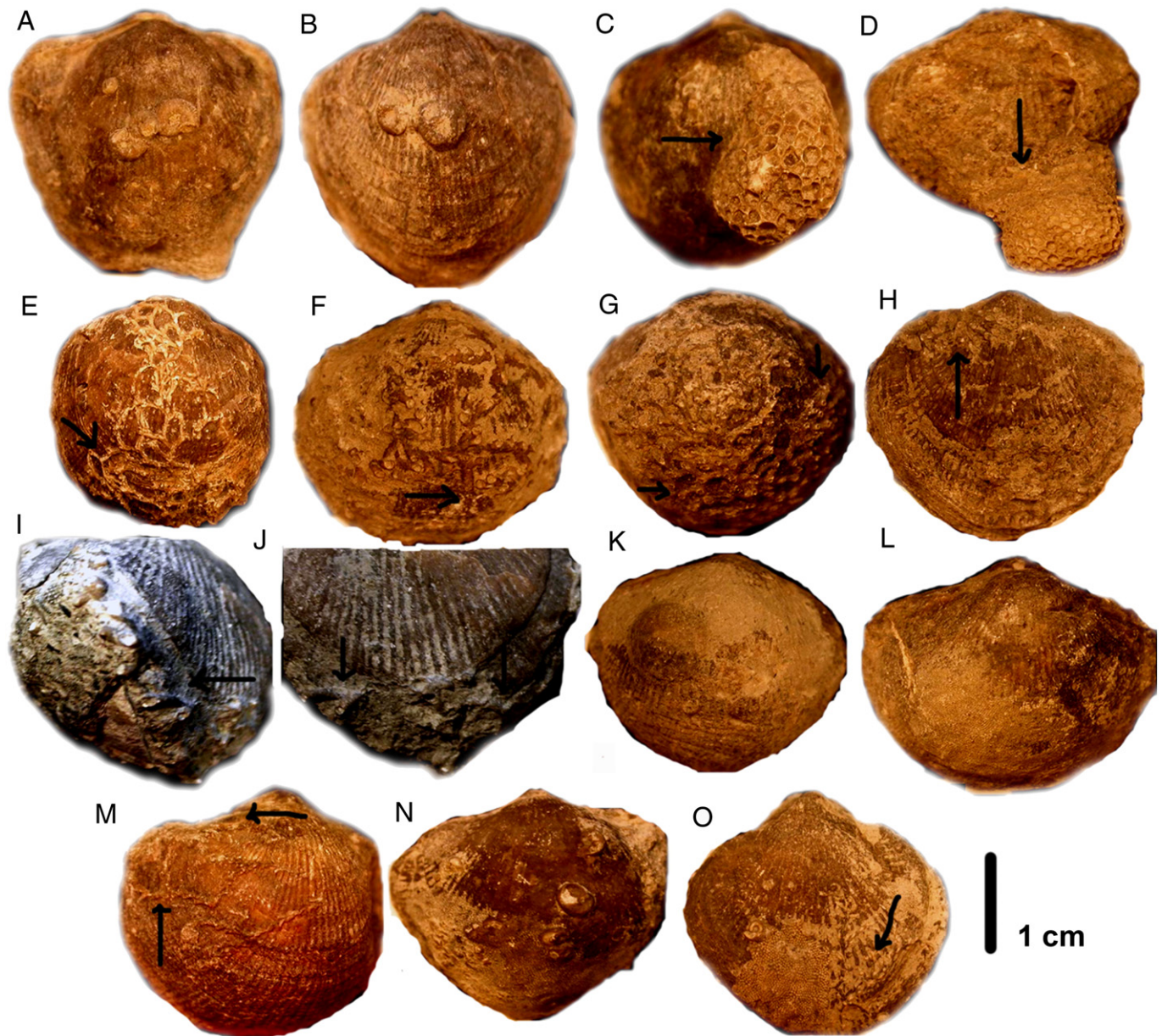
Fig. 7. Different types of episkeletobionts on *P. lineata* and *Pseudoatrypa* sp. A hosts – A-B) (IU#100196, IU#100211) Microconchid tube-worms; C-D) (IU#100179, IU#100122) tabulate sheet corals; E-J) (IU#100061, IU#100109, IU#100164, IU#100177, IU#100241) auloporid coral colonies; K) (IU#100222) craniid brachiopod; L) (IU#100174) bryozoans sheet; M) (IU#100077) hederellid colony; N-O) (IU#100138, IU#100226) mutual co-occurrences of hederellid, bryozoan sheet and microconchid tube worms. Black arrows indicate the episkeletobiont extension to the posterior or anterior edges of the host valve.

The episkeletobiont distribution was non-random on dorsal valves. The observed frequency of total episkeletobionts across all regions of the two *Pseudoatrypa* species is significantly different than expected if episkeletobionts randomly encrusted any portion of the shell (*Chi-square*; $p \ll 0.01$) (Table 3). Specifically, the antero-left lateral region of *P. lineata* was encrusted at a lower rate than expected (*Chi-square*, $p \ll 0.01$) whereas the postero-right lateral and antero-left lateral regions were encrusted at a lower than expected rate on *Pseudoatrypa* sp. A (*Chi-square*, $p = 0.04$, $p \ll 0.01$) respectively (Table 4; Fig. 3). Conversely, the diagonally opposite posteromedial and antero-right lateral regions were encrusted at a greater frequency than expected in both the species (*Chi-square*, $p = 0.015$ and $p < 0.027$ in *P. lineata*; $p \ll 0.01$ and $p = 0.08$ in *Pseudoatrypa* sp. A) (Table 4; Fig. 3). The remaining regions do not show any significant difference between expected and observed episkeletobiont frequency (Table 4; Fig. 10).

4.3.2. Ventral valves

On ventral valves, the postero-left lateral region bears abundant episkeletobionts on both species. Microconchids are common to all of the six shell regions of *P. lineata*, but absent in postero-right lateral and antero-right lateral regions of *Pseudoatrypa* sp. A.

The ventral valve episkeletobiont distribution was too low to infer whether the distribution was random or non-random in the six regions. The observed frequency of total episkeletobionts across all regions of the two *Pseudoatrypa* species for ventral valves is not significantly different than expected (*Chi-square*, *P. lineata*, $p = 0.13$ and *Pseudoatrypa* sp. A, $p = 0.29$) (Table 3). However, the postero-left lateral region of *P. lineata* was encrusted at a greater rate than expected (*Chi-square*, $p = 0.03$) and the antero-left lateral region was encrusted at a lower rate than expected rate on *P. lineata* (*Chi-square*, $p = 0.03$) (Table 4; Fig. 3). The remaining regions do not show any
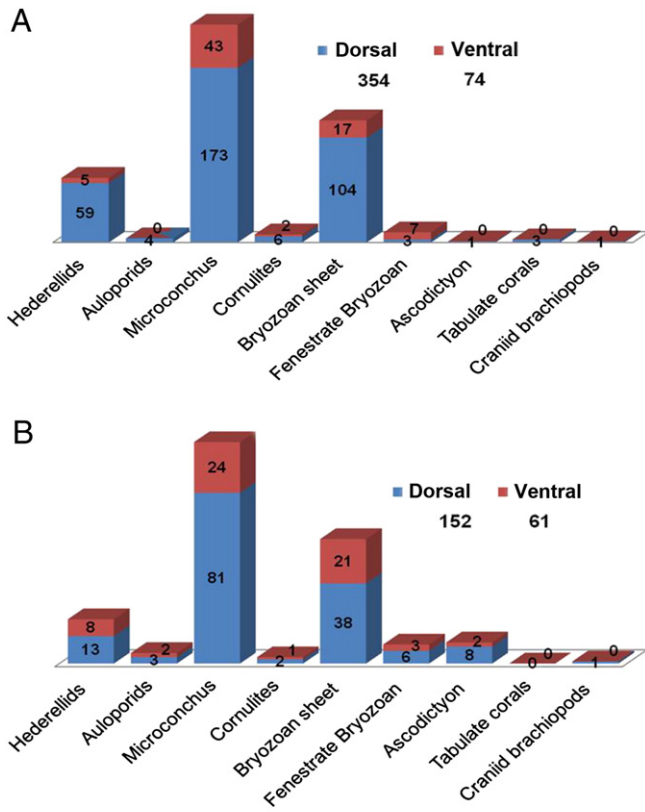
Fig. 8. Total episkeletobiont count on A) *P. lineata* and B) *Pseudoatrypa* sp. A.

significant difference between expected and observed episkeletobiont frequency on *P. lineata* (Table 4). None of the six regions of the ventral valve show any significant difference between expected and observed episkeletobiont activity in *Pseudoatrypa* sp. A (Table 4).

5. Discussion

5.1. Morphology of Pseudoatrypa lineata and Pseudoatrypa sp. A

The two species *Psueudoatrypa lineata* and *Pseudoatrypa* sp. are different enough to warrant splitting into separate species. These samples show significant morphological differences, especially in their dorsal convexity, that are sufficient to designate them as two distinct species based on qualitative traits and significant morphometric shape. Thus, in addition to the visually distinguishing characteristic differences in shell shape, morphometric results suggest that the two morphotypes deserve species-level distinction. In this

Table 1
Mean encrustation frequency (A_C) results of each episkeletobiont type on *Pseudoatrypa lineata* and *Pseudoatrypa* sp. A.

Episkeletobiont type	*Pseudoatrypa lineata* (dorsal)	*Pseudoatrypa lineata* (ventral)	*Pseudoatrypa* sp. A (dorsal)	*Pseudoatrypa* sp. A (ventral)
Hederellids	**0.3**	0.05	**1.44**	1.21
Auloporids	0.02	0	0.33	0.3
Microconchus	**0.89**	0.43	**9.00**	3.64
Cornulites	0.03	0.02	0.22	0.15
Bryozoan sheet	**0.54**	0.17	**4.22**	3.18
Fenestrate Bryozoan	0.02	0.07	0.67	0.45
Ascodictyon	0.01	0	0.89	0.3
Tabulate corals	0.02	0	0	0
Craniid brachiopods	0.01	0	0.11	0

study, morphological shape variation exists within each species. Principal component analysis indicates morphologies of the two species overlap when dorsal and ventral valves are considered. However, the morphological differences between the two species is best observed in the posterior and anterior views, which is also observed in overall qualitative traits of these species (Figs. 2, 4, 5). The morphological differences between the two species are clearly visible in the thin plate spline plots and the differences in mean are significant using MANOVA, when the posterior and anterior regions are assessed. The two species are separable by DFA (Fig. 5). These differences were in the shape of the hinge line and commissure, height of dorsal valve curvature, and ventral valve inflation (Figs. 4 and 5). Thus, we consider the two morphotypes to be different species.

Pseudoatrypa lineata (Webster, 1921), was described by Fenton and Fenton (1935) and Day and Copper (1998) as a medium-large sized atrypide with dorsibiconvex to convexoplanar shells with inflated dome-like dorsal valves. *Pseudoatrypa lineata* from Cedar Valley of Iowa possessed fine radial, subtubular to tubular rib structure (1-2/1 mm at anterior margin), irregularly spaced concentric growth lamellae (more like wrinkles or lines) crowding towards the anterior and lateral margins in larger adults (20 mm length), with very short projecting frills or almost absent. Day and Copper (1998) grouped *Atrypa lineata*, a growth variant form of *A. lineata* and a subspecies of this species, *Atrypa lineata* var. *inflata* (described earlier by Fenton and Fenton (1935)), all under *Pseudoatrypa lineata*. In our study, one of the species sampled from the Givetian age Traverse Group resemble the overall shape and morphology of *P. lineata* described previously from the late Givetian Cedar Valley of Iowa by Fenton and Fenton (1935) and hence are called *P. lineata* for the purpose of this study.

In contrast, the other species do not resemble *P. lineata* type specimens in that they possess a highly arched dorsal valve in contrast to the dome shaped dorsal valve, a flat ventral valve in contrast to the slightly inflated ventral valve, coarser ribs in contrast to the fine-medium ribs, and a subquadrate shell outline in contrast to the rounded outline of *P. lineata*. *P. devoniana* has an elongated shell outline and is Late Frasnian in age (Day and Copper, 1998). *P. witzkei* has a rounded shell outline, a shallow dorsal valve profile and is middle Frasnian in age (Day and Copper, 1998). *Desquamatia (Independatrypa) scutiformis* has a subrounded shell outline, shallow dorsal valve and highly imbricate tubular ribs in contrast to the subtubular ribs in this species. Thus, the species described in this study is referred to *Pseudoatrypa* sp. A, as it does not resemble *P. lineata* or other species of late Givetian time.

P. lineata diagnosed in this study clearly resembles *A. lineata* var. *inflata* of Fenton and Fenton (1935) in having similar shell size (2.1-2.4 ± 0.2 cm), shell thickness and convexity (slightly convex ventral valve), ribs with implantations and bifurcations, and numerous growth lines crowding at the anterior. However, *Pseudoatrypa* sp. A resembles *A. lineata* described by Fenton and Fenton (1935) in having larger sized shells (2.3-3.3 ± 0.2 cm), flattened ventral valve, etc. but is significantly different from *A. lineata* in its dorsal valve shape. Thus, both *P. lineata* and *Pseudoatrypa* sp. A in this study are described as two distinct species of *Pseudoatrypa* (Fig. 4) based on ornamentation and overall shell shape differences (Figs. 4–6).

Several studies have speculated possible causes (e.g., sedimentation rates, current stimuli, oxygen level, substrate conditions, etc.) behind the observed morphologies for brachiopod shell shape (Lamont, 1934; Bowen, 1966; Copper, 1967; Alexander, 1975; Richards, 1969, 1972; Leighton, 1998). Copper (1973) suggested *Pseudoatrypa* was a soft muddy bottom inhabitant favoring quieter water, though in later studies (Day, 1998; Day and Copper, 1998), *Pseudoatrypa* has been reported from carbonate environments of the Upper Devonian Cedar Valley group of Iowa. In this study, the samples of the two species were collected from a thin succession of argillaceous shales representing middle shelf environments. These argillaceous beds

Table 2
Summary of encrustation by episkeletobiont type. The number of brachiopods encrusted by each episkeletobiont (shells encrusted) and the percentage of encrusted shells that had that particular episkeletobiont (%) are reported. The total number of encrusters of each episkeletobiont are reported for each valve. p values report the probability that the rate of encrustation is the same on dorsal and ventral valves. Grand totals give the total number of shells encrusted by each episkeletobiont in both species and the total number of encrustations by each episkeletobiont.

Episkeletobiont	Pseudoatrypa lineata					Pseudoatrypa sp. A					Grand Totals	
	Shells encrusted	%	Dorsal encrusters	Ventral encrusters	P	Shells encrusted	%	Dorsal encrusters	Ventral encrusters	P	Shells	Encrusters
Hederellids	23	14.8	59	5	<**0.05**	5	16.7	13	8	<**0.05**	28	85
Auloporids	4	2.6	4	0		2	6.7	3	2		6	9
Microconchus	55	35.5	173	43	<**0.05**	9	30.0	81	24	<**0.05**	64	321
Cornulites	2	1.3	6	2		2	6.7	2	1		4	11
Bryozoan sheet	64	41.3	104	17	<**0.05**	6	20.0	38	21	<**0.05**	70	180
Fenestrate Bryozoan	3	1.9	3	7		2	6.7	6	3		5	19
Ascodictyon	1	0.7	1	0		2	6.7	8	2		3	11
Tabulate corals	2	1.3	3	0		1	3.3	0	0		3	3
Craniid brachiopods	1	0.7	1	0		1	3.3	1	0		2	2
Total	155		354	74		30		152	61		185	641

contained large atrypids with encrusters attached on both valves, which suggests that these shells might have been subject to agitated currents from time to time that were capable of occasionally flipping the shells over in a moderate-low water energy conditions, thus enabling the growth of encrusters on both sides. Thus, as the *P. lineata* and *Pseudoatrypa* sp. A both existed in the same sedimentological regime and were exposed to similar environmental conditions (similar oxygen-level, energy, and substrate conditions), the causes of the difference in shape of the two species are more likely genetic rather than ecomorphic.

5.2. Species preference of episkeletobionts

Episkeletobionts more frequently encrusted *Pseudoatrypa lineata* over *Pseudoatrypa* sp. A (Tables 1–2). In particular, microconchids and sheet bryozoans, the two most abundant episkeletobionts, were more
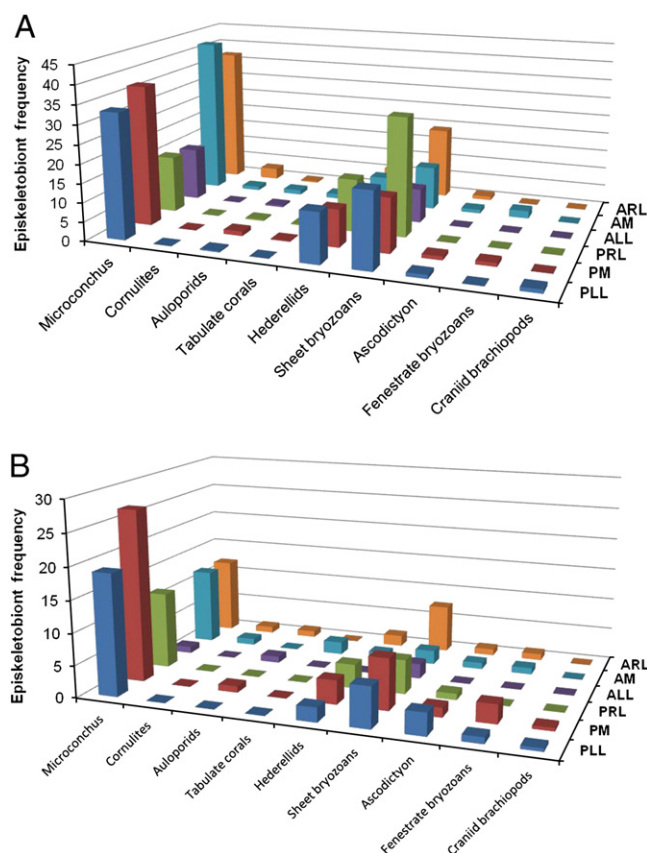

Fig. 9. Total standardized frequency of each episkeletobiont activity on dorsal valves across each region for A) 125 *P. lineata* and B) 30 *Pseudoatrypa* sp. A hosts. (Note: Standardized frequency = Frequency of colonized episkeletobionts on host species). The six regions are as follows: PLL = postero–left lateral region; PM = posteromedial region; PRL = postero–right lateral region; ALL = antero–left lateral region; AM = anteromedial region; and ARL = antero–right lateral region.
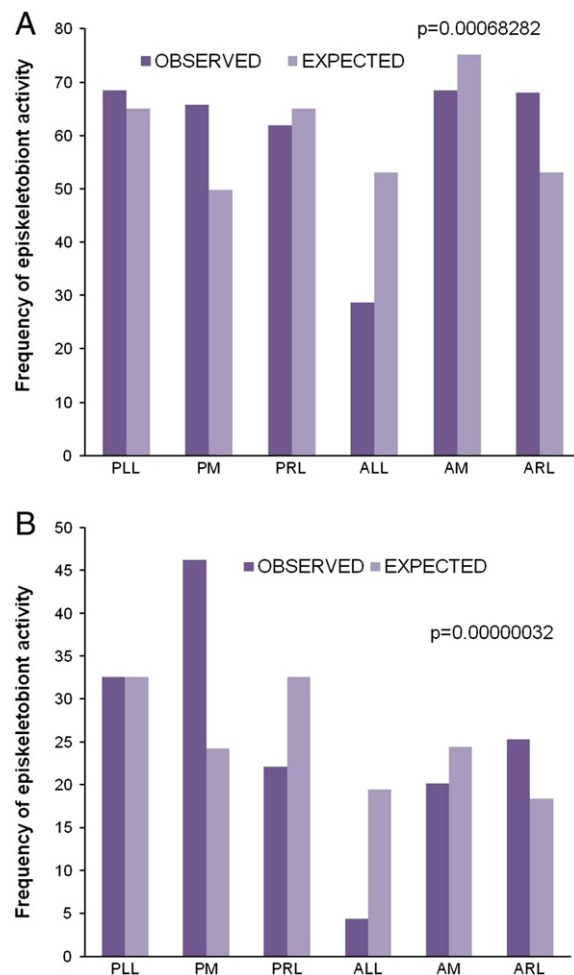

Fig. 10. Observed versus expected episkeletobiont activity in dorsal valves across each region. Observed values are the actual frequency of encrustation for each region of the shell; expected values are calculated as described in the text. A) 125 count *P. lineata* hosts and B) 30 count *Pseudoatrypa* sp. A hosts. The six regions are as follows: PLL = postero–left lateral region; PM = posteromedial region; PRL = postero–right lateral region; ALL = antero–left lateral region; AM = anteromedial region; and ARL = antero–right lateral region.

Table 3

Sum of the observed and expected number of episkeletobiont activity across six shell regions of a) dorsal valves and b) ventral valves of *Pseudoatrypa lineata* and *Pseudoatrypa* sp. A. The six regions are as follows: PLL postero–left lateral region; PM posteromedial region; PRL postero–right lateral region; ALL antero–left lateral region; AM anteromedial region; ARL antero–right lateral region. Note that in ventral valves, many rare episkeletobionts were absent, so only the most abundant episkeletobionts is considered.

Regions	*Pseudoatrypa lineata*		*Pseudoatrypa* sp. A	
	Observed	Expected	Observed	Expected
DORSAL				
PLL	68.4	65.0	32.584	32.544
PM	65.7	49.8	46.25	24.26
PRL	61.9	65.0	22.08	32.54
ALL	28.7	53.1	4.333	19.43
AM	68.4	75.1	20.17	24.41
ARL	68.0	53.1	25.25	18.38
SUM	361.1	361.1	150.667	151.564
VENTRAL				
PLL	15	9.18	11	6.696
PM	6	7.038	7	5.006
PRL	10	9.18	4	6.696
ALL	2	7.497	2	3.782
AM	9	10.608	4.83	5.022
ARL	9	7.497	2.17	3.782
SUM	51	51	31	30.984

common on *P. lineata* than *Pseudoatrypa* sp. A. No strict species preference was observed for the third-most abundant taxon, hederellids, or for any of the rarer episkeletobionts (*Cornulites*, auloporid corals, tabulate corals, fenestrate bryozoans, *Ascodictyon*, craniid brachiopods).

Among the abundant episkeletobionts, the greatest episkeletobiont activity on the two species can be attributed to the calcareous

Table 4

Results of *Chi-square* test of observed versus expected episkeletobiont activity for *Pseudoatrypa lineata* and *Pseudoatrypa* sp. A a) dorsal and b) ventral valves. A *p-value* < 0.05 indicates either more or less biological activity in that shell region than expected, as indicated.

	p values	Observed is — than expected
A) Pseudoatrypa lineata		
PLL vs. sum of other areas	0.6410	
PM vs. sum of other areas	0.0150	MORE
PRL vs. sum of other areas	0.6710	
ALL vs. sum of other areas	0.0003	LESS
AM vs. sum of other areas	0.3850	
ARL vs. sum of other areas	0.0270	MORE
A) Pseudoatrypa sp. A		
PLL vs. sum of other areas	0.9300	
PM vs. sum of other areas	9.4×10^{-7}	MORE
PRL vs. sum of other areas	0.042	LESS
ALL vs. sum of other areas	0.0003	LESS
AM vs. sum of other areas	0.3639	
ARL vs. sum of other areas	0.0822	MORE
B) Pseudoatrypa lineata		
PLL vs. sum of other areas	0.0300	MORE
PM vs. sum of other areas	0.6700	
PRL vs. sum of other areas	0.5400	
ALL vs. sum of other areas	0.0300	LESS
AM vs. sum of other areas	0.5800	
ARL vs. sum of other areas	0.5500	
B) Pseudoatrypa sp. A		
PLL vs. sum of other areas	0.0600	
PM vs. sum of other areas	0.3300	
PRL vs. sum of other areas	0.2400	
ALL vs. sum of other areas	0.3200	
AM vs. sum of other areas	0.9200	
ARL vs. sum of other areas	0.3700	

spirorbiform microconchid tube worms. These spiral worm tubes (0.5-5.0 mm) on *Pseudoatrypa* hosts resemble those encrusting the Middle Devonian Hamilton Group brachiopod hosts (Bordeaux and Brett, 1990: Fig. 2). A few tube worms, as shown in Fig. 7, were very large (>3 mm).

Bryozoan sheets, the second most abundant episkeletobiont, generally encrusted *Pseudoatrypa* hosts over large surface areas (Fig. 7L, N, O). They were more common on *P. lineata* than *Pseudoatrypa* sp. A. The surface covering patterns and colonial morphology of the trepostome bryozoans was similar to those encrusting Middle Devonian brachiopods from the Kashong Shale (Bordeaux and Brett, 1990). In a few instances, bryozoans even overgrew spirorbiform microconchids and hederellids (Fig. 7N-O).

Hederellids, the third most abundant episkeletobiont, were common on both species and did not show a strict preference for either host. Hederellids, originally defined as suborder Hederolloidea (Bassler, 1939), are characterized by tubular, calcitic branches. Hederellids have been traditionally referred to bryozoans, but the true affinity of hederelloids has been called into question by some recent workers (Wilson and Taylor, 2001; Taylor and Wilson, 2008). These Genshaw Formation hederellids (Fig. 7M, O) resemble the hederellid species *Hederella canadensis* that encrusted brachiopods from the Devonian Silica Formation of northwestern Ohio (Hoare and Steller, 1967; Pl. 1), brachiopods from the Middle Devonian Kashong Shale of New York (Bordeaux and Brett, 1990, Fig. 2) and *Paraspirifer bownockeri* from the Michigan Basin (Sparks et al., 1980).

Coarse ribs and spines on brachiopod shells have been considered anti-predatory and anti-fouling tools (Richards and Shabica, 1969; Vermeij, 1977; Alexander, 1990; Leighton, 1999, 2003; Carrera, 2000; Dietl and Kelley, 2001; Schneider, 2003, 2009a; Schneider and Leighton, 2007; Voros, 2010) and in some cases have been avoided by epizoans (Richards, 1972). Consistent with this hypothesis, finer ribbed taxa in modern (Rodland et al., 2004) and Devonian (Hurst, 1974; Thayer, 1974; Anderson and Megivern, 1982; Schneider and Webb, 2004; Zhan and Vinn, 2007; Schneider, 2009b) brachiopod assemblages experienced greater encrustation frequency than more coarsely ribbed taxa. . In this study, there may be a similar preference for finer ribs. As there is no relationship between shell shape and encrustation, but episkeletobionts did prefer *P. lineata*, the data suggest that ornamentation may have been the determining factor in encruster preference for hosts. The fine-medium rib structure of *P. lineata* may have attracted more episkeletobionts than the coarsely ribbed *Pseudoatrypa* sp. A specimens.

Thus, although most episkeletobionts do not exhibit a preference for one of the species, the microconchids, and sheet bryozoans clearly exhibited a preference for *P. lineata*. Surprisingly, *Pseudoatrypa* sp. A, which possesses a relatively larger shell size than *P. lineata*, is less preferred by the most abundant episkeletobionts. One possible explanation for this could be the greater surface area provided by the inflated geometry of the dorsal valve of *P. lineata*, despite its smaller overall shell size. In other words, *P. lineata* may have facilitated heavier encrustation by providing a larger surface area for settlement.

5.3. Live-dead and live-live associations

Both live and dead hosts could be used as a substrate for episkeletobiont settlement. While live hosts might attract encrusters through their feeding currents, dead hosts, obviously, can only be used as a substrate for encrustation.

For some episkeletobionts, hosts would serve merely as hard substrates. In an epizoan ecology study performed by Watkins (1981), it was observed that some epizoans had a very weak preference for live hosts. There is evidence of hederellids and sheet bryozoa encrusting dead hosts or wood (Thayer, 1974). There is also evidence of microconchids encrusting dead brachiopod hosts from the Upper Devonian Cerro Gordo Member of the Lime Creek Formation of Iowa

(Anderson and Megivern, 1982). In contrast, in other studies (e.g., Ager, 1961; Hoare and Steller, 1967; Richards, 1974; Kesling and Chilman, 1975; Morris and Felton, 1993), auloporids, hederellids and cornulitids frequently displayed preferential growth along or toward the commissure, particularly on Devonian alate spiriferides and large atrypides, possibly in order to take advantage of feeding and respiration currents actively generated by the host's lophophore.

Because post-mortem encrustation cannot be ruled out, it is critical to interpret whether the brachiopod host was alive concurrently with the episkeletobionts. We observed that in rare cases, episkeletobionts oriented themselves on the brachiopod host in specific directions or encrusted particular regions to benefit from feeding currents (Fig. 7). These instances may indicate live-live associations.

Sparks et al. (1980), suggested a commensal relation between *Paraspirifer bownockeri* hosts and the spirorbiform microconchids, whereas Barringer (2008) noted no preferred location or orientation of microconchids on host valves, and suggested that they simply infested the hard substrates of the brachiopods. In the present study, microconchids randomly encrusted both valves (Fig. 7A-B), with no particular concentration along the commissure area nor any particular orientation of their apertures, thus leaving the host-episkeletobiont relationship ambiguous. Their random orientation on the host valves may indicate that they fed from ambient water currents, rather than requiring currents induced by live brachiopods, a result consistent with other studies (Ager, 1961; Pitrat and Rogers, 1978; Hurst, 1974; Kesling et al., 1980; Fagerstrom, 1996). Encrusting bryozoans rarely indicate live-live episkeletobiont-host interactions (Fagerstrom, 1996). Microconchids or sheet bryozoa in this study could have encrusted the two species whether live or dead, possibly because of the availability of their hard substrate.

Hederellid colonies that encrusted brachiopods with their apertures oriented towards the anterolateral commissure may have been in that position to benefit from host exhalant currents as described by Bordeaux and Brett (1990). *Hederella* has been reported to have a commensal relationship with its host by Sparks et al. (1980), whereby the episkeletobiont benefited from the hard surface for attachment and from the elevation above the soft substrate but this would be also true for a dead host. In our study, orientation of the apertures of hederellid colonies towards the postero-left lateral end of the host and their termination towards the lateral margin could indicate that the hederellid was taking advantage of host-induced currents (Fig. 7M). Such an orientation of hederellids indicates that these organisms may have either benefited from host's feeding inhalant currents, and possibly may have harmed the host by taking in too much of the host's food supply, thus implying a commensal, or parasitic relationship. In one particular instance, however, hederellid colonies were found to parallel the anterior commissure, which would support a commensal relation with the host (Fig. 7O). Thus, some of these associations of hederellids and host brachiopods provide evidence of a real, biological interaction.

Some of the rare episkeletobionts also possibly encrusted live hosts. Although auloporid corals were rare, four colonies grew from the medial region of the host towards the anterior commissure suggesting the possibility of mutualism in which corals would benefit from the host feeding currents and protect the host from predators by using possible stinging cells (Fig. 7E). Another colony grew parallel to its host's commissure, suggesting a commensal relationship in which the encruster may have benefited from host feeding currents (Fig. 7G). On another specimen (Fig. 7H), the hinge-proximal location of the corallites with their termination towards the postero-left lateral end of the host suggests possible live-live association with a mutualistic relation between the host and the episkeletobiont. In one instance, the tabulate coral colony, located along the anterior commissure and extending upright suggests a possible live-live association (commensal relation) between the host and the episkeletobiont, where the encruster may have benefited from host exhalant

currents (Fig. 7D). *Cornulites* attached along the anterior commissure of one host, suggesting encrustation of a live host. Based on the encruster location preference, these instances suggest a live-live association between the host and the episkeletobiont, thus providing further evidence of real, biological interactions. For other host-encruster associations (*Ascodictyon*, fenestrate bryozoans, craniid brachiopods), the live or dead status of the host remains unknown.

Overall, the preferred location of the most abundant episkeletobionts (microconchids, sheet bryozoans and hederellids) and the rare episkeletobionts that show possible evidence of live-live associations (*Cornulites*, auloporid corals, and tabulate corals) is for the posterior region of both dorsal and ventral valves, regardless of host species (described in next section), suggesting that larval settlement of the episkeletobionts may have occurred at the highest point of inflation on brachiopod valves, regardless of whether the brachiopod was dead or alive.

5.4. Distribution of episkeletobionts on P. lineata and Pseudoatrypa sp. A

Distribution of episkeletobionts has assisted in interpretations of life orientation of brachiopod hosts in the past (Hurst, 1974). Encrustation frequency (A_C) on hosts assessed from encrustation count (Table 2) were preferentially greater for dorsal valves than ventral valves for both species. This suggests that the dorsal valves probably facilitated greater encrustation due to their domal shell geometry relative to the flattened ventral valve, or possibly because the dorsal valve was "up" and so more exposed to settlement by encrusters.

Episkeletobionts may have settled randomly or non-randomly on the host surface of both valves. In this study, episkeletobiont occurrence varies among the six regions sampled on the dorsal valve of the hosts of the two species (Fig. 10). On dorsal valves, microconchids had no preference for posterior or anterior, sheet bryozoans preferred the posterior region over the anterior, and hederellids also preferred the posterior region. Microconchids had a high preference for postero-medial and second-most preference for the antero-medial region on dorsal valves of both species and a high preference for postero-left lateral region and secondmost preference for postero-medial region on ventral valves. Sheet bryozoans frequently encrusted the postero-right lateral region of the dorsal valve of both species with a secondary coverage on postero-left lateral, postero-right lateral and antero-right lateral regions (Fig. 9). Sheet bryozoans frequented the postero-left and postero-right lateral regions and secondarily encrusted the anteromedial and antero-right lateral regions of the ventral valves. Hederellids often occupied a vast area along the brachiopod host, often along the posterior edge (Fig. 7M, O) in both hosts. Although the ventral valve had a comparatively lower concentration of episkeletobionts as compared to dorsal valves, the most abundant episkeletobionts showed similar preferences for posterior versus anterior regions on both valves.

The rare episkeletobionts, *Cornulites*, auloporids and tabulate corals, preferred the anterior regions while *Ascodictyon*, fenestrate bryozoans and craniid brachiopods had no strict preference for anterior or posterior regions of dorsal valves. Tabulate corals and craniid brachiopods were absent on ventral valves, and *Ascodictyon*, fenestrate bryozoans, *Cornulites* and auloporid corals were too low in abundance to determine their preference for a specific region on the valve. Cornulitids, where present, dominated the anterior (antero-medial and antero-right lateral) commissural margin of the host valves with their aperture pointing away from the hinge margin. Auloporid corals most frequently grew their branching colonies along the anterior commissure (antero-left lateral and antero-right lateral) of dorsal valves od both host species with some occurrences in the postero-medial region (Fig. 9); the same pattern is also observed for ventral valves. This could simply be a preference of auloporids for settling and growing near their hosts' exhalant currents, a suggested phenomenon for other brachiopod-auloporid associations (e.g., Shou-Hsin, 1959; Pitrat and Rogers, 1978; Alvarez and Taylor, 1987; Taylor and Wilson, 2003; Zapalski, 2005).

Tabulate sheet-like corals, craniid brachiopod, *Ascodictyon*, and fenestrate bryozoans were too low in abundance to determine whether they were random or non-randomly distributed along the grids of the dorsal valve of the two species. Overall, the greater abundance of episkeletobionts on the posterior region of dorsal and ventral valves may have been due to the greater chances of encruster larval settlement on the highest point of the shell geometry, simply because they are higher above the substrate and so more likely to be encountered first by settling larvae. Alternatively, episkeletobiont settlers possibly selected those regions to benefit from host feeding currents. This pattern held true for both hederellid colonies and sheet bryozoans. In addition, hederellids may have selected the posterior edges of the host to benefit from host feeding currents. Although fewer in abundance, the preference of auloporid corals, tabulate corals and cornulitids along the anterior region of the hosts suggest that these episkeletobionts may have selected that region possibly to benefit from the host feeding (exhalant) currents. In general, most episkeletobionts preferred margins of posterior and anterior areas of the valves, an encrustation pattern worth noting. Thus, this nonrandom distribution of episkeletobionts on *Pseudoatrypa* is a real, biological signal.

5.5. Inference of life orientation in P. lineata and Pseudoatrypa sp. A.

Atrypids that were dorsibiconvex (dorsal valve more convex than the ventral valve) to planoconvex (dorsal valve flat and ventral valve convex), lived attached by a pedicle in their early stages of life in an almost reclining life orientation, probably with the dorsal valve closest to the substrate and ventral valve facing upwards (Alexander, 1984), and later with increasing convexity of the dorsal valve through ontogeny, they attained an inclined or a vertically upright life orientation (Fenton and Fenton, 1932) (Fig. 11A-C). When the pedicle later atrophied in their adult stage, they attained a hydrodynamically stable resting life position (Fenton and Fenton, 1932) by falling on their relatively flattened ventral valve with their convex dorsal valves facing upright into the water column (Fig. 11D), such that the commissure was subparallel to the substrate. In this resting life position, the roughly domal shape of the shell would provide an optimally streamlined condition for receiving currents from potentially any direction (Copper, 1967). Problematically for interpretation

of live-live episkeletobiont-host interactions, this last orientation was also the most likely orientation for the brachiopod after death. In this study, encrustation distribution patterns and frequency suggest that, at the time when most encrustation occurred, these hosts were oriented with their dorsal valves up after pedicle atrophy. Whether these species were alive or dead at the time of encrustation cannot be discerned. Thus, our results from location preference of episkeletobionts on host species alone cannot suggest if these host species were encrusted pre- or post-mortem. In addition, these shells preserved no frills, which would have provided stability to the organism in a particular orientation. Frills, characteristic of atrypid brachiopods, are large growth lamellae that can project beyond the contour of the valves and can assist as anchors in high energy, mobile substrates (Copper, 1967). Thus predicting their life orientation without such evidence is difficult based on encrustation distribution pattern alone.

The difference in morphology of the two species poses the question of whether they had similar life orientations. If these species were living in soft substrates, then the shape difference in *P. lineata* (inflated pedicle valve) and *Pseudoatrypa* sp. A (flattened pedicle valve) would have had little or almost no effect in their stability patterns in life or in availability of cryptic surface area, once the brachiopod was in its dorsal-valve-up orientation. However, if these species were resting on hard substrates in the same orientation, then the inflated ventral valves in *P. lineata* would have had a greater surface area exposed along the umbo region for encruster settlement than *Pseudoatrypa* sp. A. Both species would not have had much difference in stability though because of their relatively flattened ventral valve. Given that both these species lived in similar environments, life orientations may also have been similar regardless of whether they lived on soft or hard substrates. Thus, encrustation may have occurred on the shell surface of these species specific to each of their multiple life or death orientations.

6. Conclusions

Pseudoatrypa lineata and *Pseudoatrypa* sp. A (Variatrypinae) dominated the atrypide assemblage recovered from the Lower Genshaw Formation of the Middle Devonian Traverse Group of Michigan. The two species were identified based on differences in
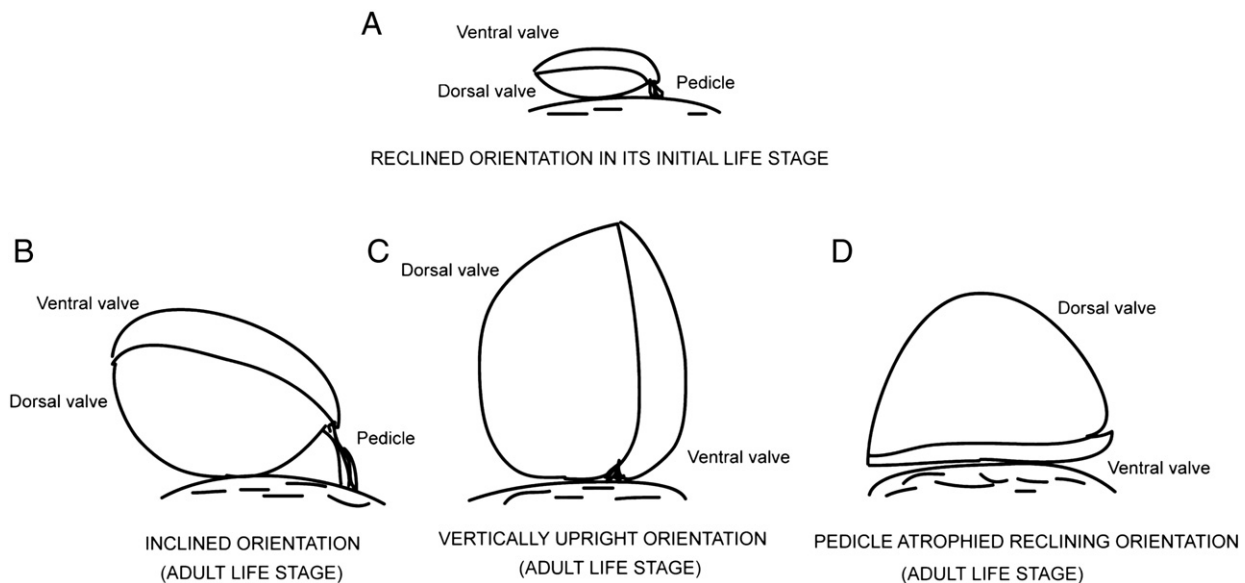

Fig. 11. Possible stages of life and death orientation in *P. lineata* and *Pseudoatrypa* sp. A – A) initial immature life stage where the host remain attached by its pedicle to the substrate in a reclining orientation with the ventral valve up and dorsal valve down, B) mature adult life stage where the host remain attached by its pedicle to the substrate in an inclined orientation with the increasingly convex dorsal valve facing the substrate and the ventral valve facing up, C) mature adult life stage where the host remain attached by its pedicle to the substrate in a vertically upright orientation, D) mature adult stage with a reclining orientation with dorsal valve up and ventral valve down after the pedicle has atrophied – this could represent both life and death orientations in atrypids.

qualitative traits and statistical shape analysis. *Pseudoatrypa lineata* differs from *Pseudoatrypa* sp. A in having a relatively smaller shell size, domal shape with a relatively shallower dorsal valve curvature, slightly convex ventral valve with inflation near the umbo, narrower hinge line, wider commissure with a pronounced gentle to steep fold, and fine-medium sized closely spaced ribs. Statistically significant shape values and large morphological distances between the two species, supports the distinct shapes of the two species identified.

Of the 343 *Pseudoatrypa* hosts examined from both species, 185 of them bore episkeletobionts. The most abundant episkeletobionts were the microconchids, hederellids and the sheet bryozoans. Auloporid corals, *Cornulites*, tabulate corals, *Ascodictyon*, craniid brachiopods, and fenestrate bryozoans were very rare. Several episkeletobionts in this study provide evidence of encrusting a live host based on the location preference of the episkeletobionts. Hederellids, auloporid corals, tabulate corals, and *Cornulites* had a live-live episkeletobiont-host relationship. The majority of other episkeletobionts, notably micro-conchids, sheet bryozoans, and *Ascodictyon,* were enigmatic in determining whether their relationship was with a live or a dead host. Very few epizoans crossed the commissure of the host after the host's death.

Most episkeletobionts (microconchids and sheet bryozoans) preferred *P. lineata*, despite the fact that this species is generally smaller. This differential effect in epibiosis could be due to the nature of ribbing structure (fine to medium) and greater exposed area facilitated by the shell shape of *P. lineata*. Overall, the episkeletobiont preference for one species over another strongly suggests that the overall episkeletobiont distribution was influenced by shape and ornamentation variation in atrypid samples. Abundant encrusting organisms – microconchids, sheet bryozoans and hederellids, had a preference for *P. lineata* dorsal valves. This greater abundance of episkeletobionts on dorsal valves and lower abundance on ventral valves is suggestive of most of the encrustation occurring when the host species were oriented with their convex dorsal valves up and ventral valves down with most of the ventral valve surface in contact with the sediment substrate. Whether encrustation was pre- or post-mortem was challenging to discern for the majority of host-episkeletobiont associations as life orientation of the host would also be a hydrodynamically stable orientation of the articulated shell after death. Additionally, the most abundant episkeletobionts showed a preference for the posterior region on both dorsal and ventral valves of both species. This suggests that the posterior umbonal region may have provided an inflated surface that remained exposed, thus, favoring the settlement of most episkeletobiont larvae in that region.

The present study of the Genshaw Formation documents epibiosis on two species of atrypids, which significantly enhances our understanding of morphological influence on episkeletobiont distribution.

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