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# ASYMMETRY IN *THECIDELLINA* (BRACHIOPODA) FROM THE PLIOCENE-PLEISTOCENE OF CURAÇAO, NETHERLANDS ANTILLES: PHENOTYPIC NOT GENOTYPIC

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*Abstract*. Shape analysis of a large sample of the thecideid brachiopod *Thecidellina* from the Pliocene and Pleistocene rocks on the Caribbean island of Curaçao highlights asymmetry within the population. However, the 30 analysed specimens display a lack of a consistent asymmetry. The brachiopods were cemented to substrates by a cicatrix, accommodated by a change in shell structure. The plastic morphology of *Thecidellina* may have been due to overcrowding and competition for resources on limited substrates.

## INTRODUCTION

Thecideid brachiopods are morphologically unusual invertebrates with a distinctive lifestyle. The main sites for living species in, for example the Caribbean (Jackson et al. 1971) and Canary islands (Logan 2004), are in shallow-water and cryptic settings where they occur in great numbers although it is possible that populations exist on isolated patches of hard substrate in deeper water. They have a stratigraphic range from the Triassic to the Holocene and were the last brachiopod order to appear in the fossil record. Nevertheless, the phylogenetic affinities of this distinctive group remain equivocal and it is still unclear if the order is descended from a progenitor in the strophomenates (such as the davidsonioids), spiriferides, or the terebratulides (Baker 2006). Thecideides are generally rare in the Caribbean fossil record (Harper 2002); however the thecidid genus *Thecidellina* is abundant in the Pliocene-Pleistocene rocks of Curaçao in the Netherlands Antilles. The island of Curaçao is situ-

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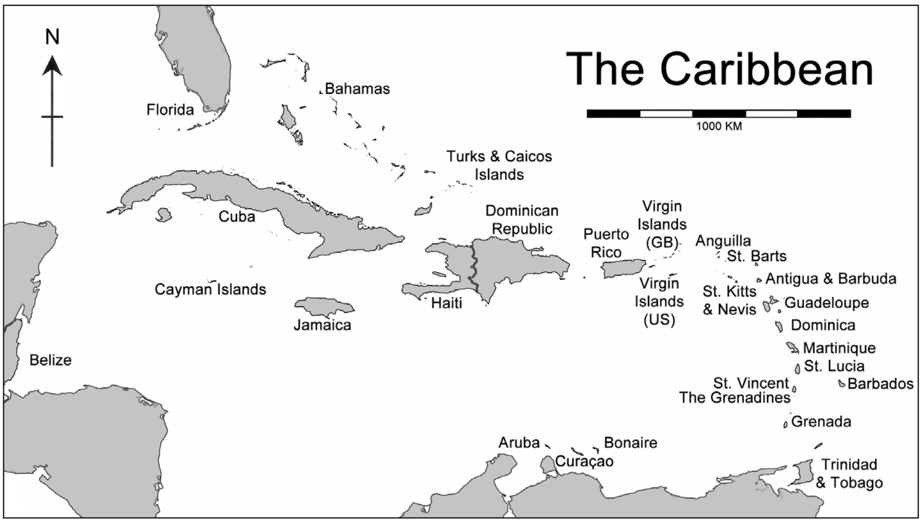

Fig. 1 - Location of Curaçao within the Caribbean Sea.

ated in the southern Caribbean Sea approximately 70 km from the northern coast of Venezuela (Fig. 1). It is an east-west orientated island about 60 km long with well-exposed Cenozoic rocks particularly around the coast. Within the upper part of the successions the Seroe Domi Formation crops out along the leeward coast of the island (Fig. 2) as well as on the adjacent islands of Aruba and Bonaire together comprising the ABC Islands. The three islands are part of the Aruba-La Blanquilla island archipelago extending for approximately 500 km.

Asymmetry in living and fossil brachiopods is well documented. Usually this condition is restricted to the commissures and associated with nutrient gathering (Fürsich & Palmer 1984; Afanasjeva 2014) although the latter author noted closeness of settlement and uneven substrates as contributing factors. Over 50 brachiopod species are known to exhibit commissural asymmetry (Fürsich & Palmer 1984). The nature of asymmetry in brachiopods is variable and may be confined to the shell exterior, to the soft parts, or both caused by congenital defects together with the life mode of the species (Asgaard 1968; Baliński & Biernat 2003), environment constraints (Ager 1967), or as a genetic non-adaptive feature (see Schrøder et al. 2016 2018 together with Berorocal-Casero & Garcia Jorel 2023 for comprehensive reviews).

The specimens of *Thecidellina* described, illustrated and analyzed here are characterised by total-shell asymmetry. It is hypothesized to be associated with a cemented lifestyle and a growth strategy in a confined space.

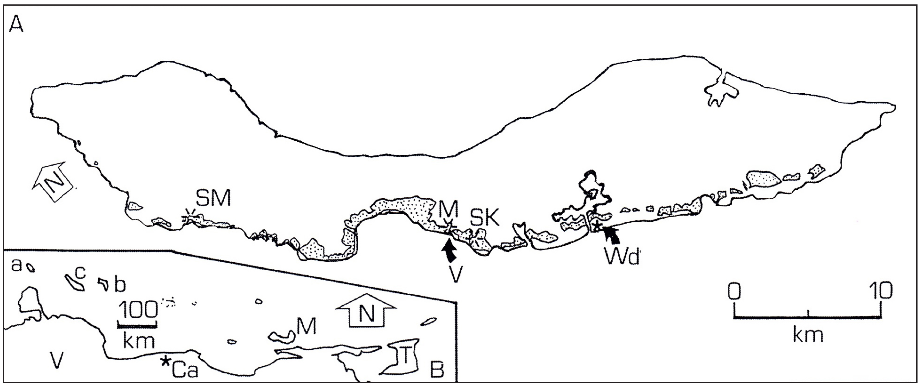

Fig. 2 - A) Outline map of Curaçao showing the outcrop of the Miocene-Lower Pleistocene Seroe Domi Formation (open stipple) (simplified after Herweijer 1979 pls. 1 2; see also Helmers and Beets 1977 pl. 4; Jackson and Robinson 1994 fig. 14.3(a)). The approximate positions of important fossil localities including those mentioned in the text are indicated thus: M = Seroe Kabritoe near Malpais; SK = Seroe Kabrita north-west of Saliña Sint Michiel; SM = Santa Maftabaai; V = Vaersenbaai. Key: Wd = Willenstad; dense stipple = coastline. B) Inset map of the south-east Caribbean region. Key: a = Aruba; b = Bonaire; c = Curaçao; Ca = Caracas; M = Islade Margarita; T = Trinidad; V = Venezuela. After Donovan and Hensley (2006, fig. 1).

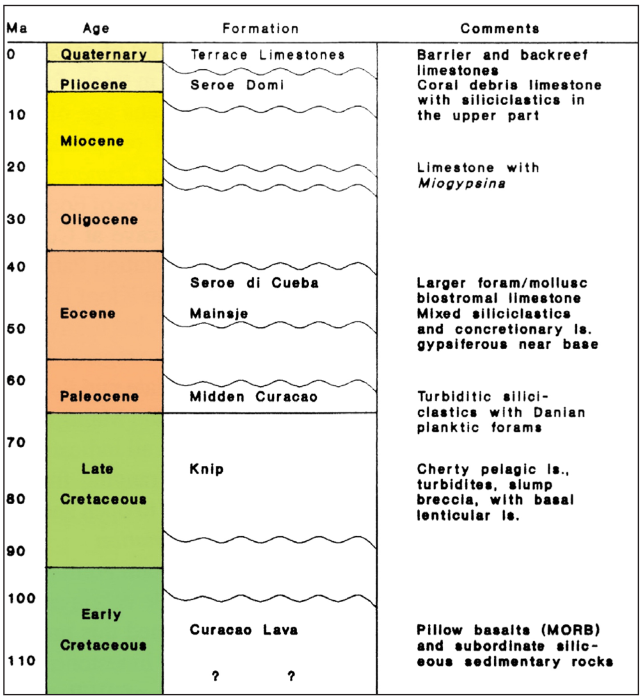

Fig. 3 - The Cretaceous and Cenozoic stratigraphy of the ABC islands (modified after Jackson & Robinson 1994, fig. 14.3b).

## LOCATION AND STRATIGRAPHY

The Netherlands Antilles is part of the Caribbean Mountain system formed by a broad east-west trending Mesozoic and Cenozoic orogenic belt which marks the boundary zone between South America and the Caribbean (Donovan & Jackson 1994). The older part of the Cenozoic succession is only exposed in the southeastern part of the island (Jackson & Robinson 1994 p. 255) including the Seroe Domi Formation (Fig. 3) which ranges in age from Late Miocene to Early Pleistocene. The exposure at Saliña Sint Michiel, north of the settlement of Dorp Sint Michiel south-west coast of central Curaçao (GPS 12.1511° -68.9952 ° WGS84), is correlated with the Pliocene (Fig. 3). It consists of brown-weathering calcareous medium- to coarse-grained sandstones with abundant skeletal material rich in pectinids and *Spondylus* with rarer decapods, balanid barnacles, the common micromorphic brachiopod *Thecidellina,* echinoids and an asteroid (Harper et al. 2003). *Thecidellina* is abundant, disarticulated, and dispersed across shell pavements in the formation (Fig. 4a b).

More recent studies have focused on echinoderms (Harper et al. 2003; Donovan & Schelfhorst 2012), decapod crustaceans (Collins et al. 2009; Sload et al. 2018), and trace fossils (Donovan and Hensley 2006; Donovan 2015).

A second collection was made from the same formation in the Port area uphill below the storage tanks on the north side of the bridge (see Fouke 1994 pp. 32–34 GPS 12.112883$^{0}$ -68.933167$^{0}$ WGS84) referred to here as the Pecten Bed. The rocks are part of Fouke's upper subunit 2 lithofacies 7 (Pliocene to Lower Pleistocene) and comprise coral packstones grainstones and boundstones. *Thecidellina* (recorded as *T. barretti*) has been previously reported *in situ* attached to fronds of the coral *Leptoseris* (Fouke 1994). The unit has undergone some dolomitization but not all the formation has been diagenetically altered (Fouke 1994; Fouke et al. 1996).

## TAXONOMY AND SHELL STRUCTURE OF *THECIDELLINA*

*Thecidellina* is a small brachiopod usually cemented to a substrate with cyrtomatodont dentition and characterized by tubercles internally. The genus is distinguished from other members of the Thecidellinidae in having a long dorsal median septum elongate brachial lobes and a fibrous shell fabric suppressed in both valves.

The fossil material from the Seroe Domi Formation (Figs 5, 6) is identified with the living species *Thecidellina meyeri* Hoffmann & Lüter, 2009 described from the Caribbean Sea around the islands of Aruba, Bonaire, and Curaçao. This species is relatively large for the genus with an inter-brachial ridge and a massive, but short, cardinal process. The ventral valve is elongate. The hemispondylium is not connected to the valve floor and median ridge is generally lacking. The fossil specimens are large ventral valves reaching 7 mm in length and compare well with the living material. However, the brachial bridge is not well developed or more likely broken in the Seroe Domi dorsal valves.

The shell structure of the Curaçao *Thecidellina* has been recently investigated within the context of the history of the order (Simonet Roda et al. 2021). The mode of attachment and shell structure of the order has evolved through time. The attachment scar on the ventral valve in some Triassic and Cretaceous thecideides became obsolete in

Fig. 4 - Field exposures of the Seroe Domi Formation at Saliña Sint Michiel. a) Bedding surface crowded with disarticulated shells of *Thecidellina* (more prominent specimens indicated by a white arrow head). b) Beds of calcareous sandstone packed with fossil debris.

larger specimens while the ventral valve increased in convexity and the dorsal valve in concavity, hinting that such individuals were secondarily free-lying in maturity. In contrast late Cenozoic forms such as *Thecidellina meyeri* and living thecideides are permanently cemented to substrates. The gradual shift from fibrous to acicular shell structures associated with the cicatrix in these species seems to coincide with an overall change in the living strategy of thecideides towards permanent attachment (Simonet Roda et al. 2021).

## Shape analysis

Geometric morphometric techniques, based on the analysis of homologous points or (pseudo) landmarks, have been used to study morphological patterns in many types of both fossil and living organisms (see Hammer & Harper 2024). With their ability to provide a method for systematic identification and differentiation of characters, these techniques have been used for analysis of species discrimination and morphological change in many

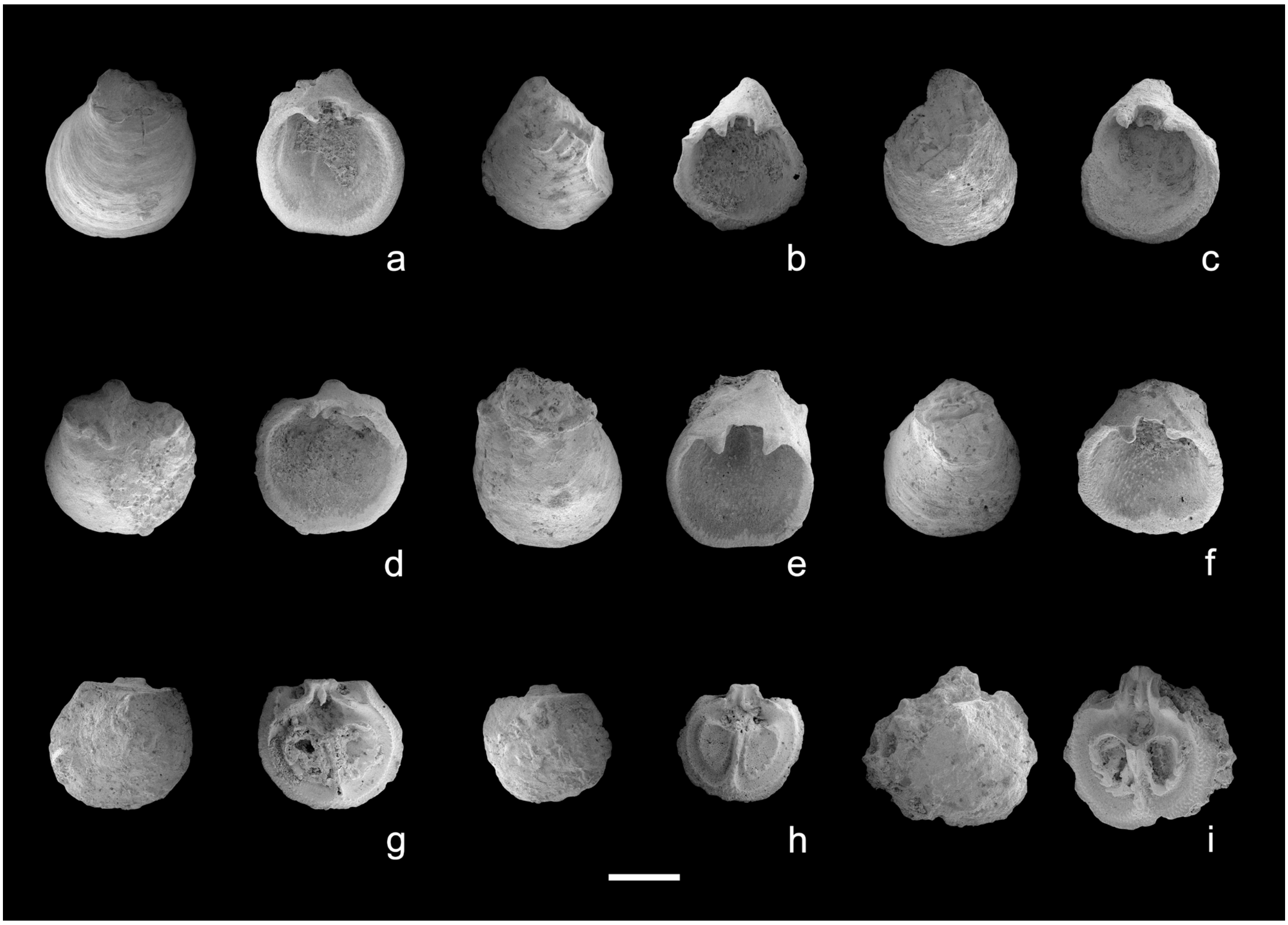

Fig. 5 - *Thecidellina meyeri* specimens indicating the shape variation especially the asymmetry in part of the sample from the Seroe Domi Formation. The valve exteriors are the left of the pairs. The ventral exteriors show variation in the posteriorly-situated cicatrix for attachment to a hard substrate. a) Ventral exterior and interior UF 280234; b) ventral exterior and interior UF 280228; c) ventral exterior and interior UF 280229; d) ventral exterior and interior UF 280230; e) ventral exterior and interior UF 280232; f) ventral exterior and interior UF 280231; g) dorsal exterior and interior UF 280227; h) dorsal exterior and interior UF 280226; i) dorsal exterior and interior UF 280236. Scale bars are 1 mm. Specimens figured herein are reposited in the Invertebrate Paleontology Division, Florida Museum of Natural History, University of Florida and indicated by the acronym UF followed by a unique catalogue number.

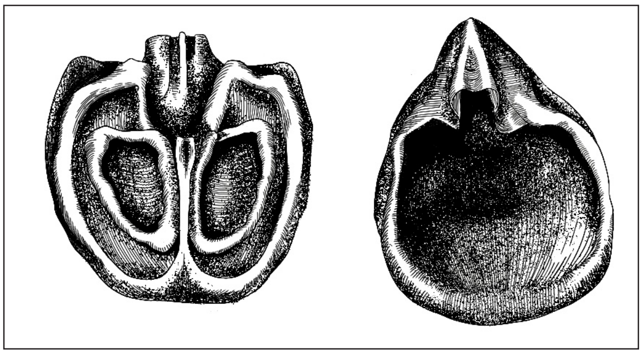

Fig. 6 - Reconstructions of dorsal (left) and ventral (right) interiors of *Thecidellina meyeri*.

types of organisms including brachiopods (e.g. Colmenar et al. 2014; Huang & Harper 2013).

About 30 unprepared specimens were cleaned and some matrix removed before being photographed and landmark data generated. Care was taken that the rim of each valve was perpendicular to the camera lens to ensure that specimens were photographed at a uniform angle. As most specimens were in the form of well-preserved individual valves, it was possible to use interiors for this study. To allow a detailed representation of variation in both internal structures and general morphology 14 landmarks were used for dorsal valves and 10 for ventral valves (Fig. 7a b).

Data sets were initially prepared and analysed using the geometric morphometric methods described in Colmenar et al. (2014) with Procrustes-

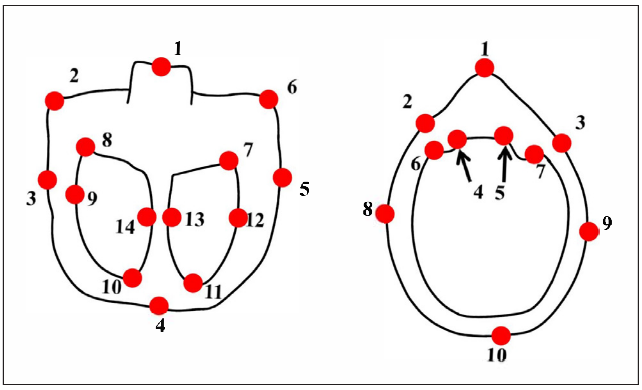

Fig. 7 - Landmarks on dorsal (left) and ventral (right) valves of *Thecidellina meyeri.*

fitting transformations being performed on all landmark data to remove the effect of variations in the size orientation and position of each specimen on coordinate locations. Principal component analysis (PCA) and thin-plate spline (TPS) methods were then used to examine variations between the samples of *Thecidellina*. The use of these methods in morphological analysis is detailed in Hammer & Harper (2024) and the software package PAST was used to calculate them (Hammer et al. 2001). Details of genus specific analyses are given below. Samples of *Thecidellina* were available from two locations on the island of Curaçao – the Pecten Bed and the salina (salt pan) near the town of Sint Michiel. The shells were analysed to identify any morphological variation between the two populations and any morphological groupings within the collections. Data from indicative single individuals of three Holocene (living) species, *T. barretti* (Davidson, 1864), *T. bahamiensis* Lüter & Logan, 2008 (in Lüter et al. 2008) and *T. williamsi* Lüter & Logan, 2008 (in Lüter et al. 2008); all three figured in the latter publication were also included in the PCA to allow comparison of this collection with other species.

| Dorsal | | |
|---|---|---|
| PC | Eigenvalue | % variance |
| 1 | 0.005469 | 32.78 |
| 2 | 0.002124 | 12.733 |
| 3 | 0.001875 | 11.24 |
| 4 | 0.001424 | 8.5379 |
| 5 | 0.001107 | 6.6349 |
| 6 | 0.000913 | 5.4701 |
| 7 | 0.00077 | 4.6133 |
| 8 | 0.000649 | 3.8896 |
| 9 | 0.000441 | 2.6458 |
| 10 | 0.000408 | 2.447 |

| Ventral | | |
|---|---|---|
| PC | Eigenvalue | % variance |
| 1 | 0.006082 | 38.774 |
| 2 | 0.002328 | 14.842 |
| 3 | 0.001988 | 12.677 |
| 4 | 0.001243 | 7.9253 |
| 5 | 0.000909 | 5.7979 |
| 6 | 0.000773 | 4.929 |
| 7 | 0.000484 | 3.0831 |
| 8 | 0.000416 | 2.6525 |
| 9 | 0.000355 | 2.2645 |
| 10 | 0.000318 | 2.025 |

Tab. 1 - Variance percentages for principal components 1–10 from the PCA of *Thecidellina* dorsal and ventral valves.

The PCA calculated the percentage variance of the first ten components is shown in Table 1. Figure 8 shows scatter plots of values from all specimens for components 1–4.

The PC1 accounts for 32.78% of variation in shape in the dorsal valve and 38.77% in the ventral valve. For the dorsal valve those variables related to landmarks 5, 6, and 7 (all in the posterior right quadrant of the shell) have some of the largest weightings while for the ventral valve landmarks 1 and 5 have the greatest influence (see Fig. 9 for loadings and Fig. 7 for landmark positions). The PC2 accounts for 12.73% of variance in the shape of the dorsal valve and 14.84% in the ventral with dorsal landmarks 2 and 6 and ventral landmarks 1, 8, and 9 having the largest weightings.

On both dorsal and ventral PC1/2 graphs, the samples of the two locations group closely together (Fig. 8). On the graph of ventral data all specimens of the smaller Pecten Bed population as well as the *T. barretti, T. bahamiensis,* and *T. williamsi* specimens plot inside the convex hull polygon of the Sint Michiel sample. On the graph 3/6 Pecten Bed specimens plot outside of this polygon, but are still in close proximity. However, on this graph, the three living species show a very clearly marked separation (primarily on the PC1 axis) from both Curaçao populations indicating marked morphological differences. These Holocene species show much less separation on the PC3/4 graphs for both dorsal and ventral data sets with all specimens plotting within the Sint Michiel polygon on the graph for ventral specimens and in close proximity to it on that for dorsal valves.

## Ventral Warps

Figure 10a displays warps of ventral valve components 1–4. For the ventral valves, PC1 shows a strong anterior-posterior divide (which is symmetrical across the median axis) with positive values indicating expansion in the lower two thirds of the valve and compression in the upper third (Colmenar et al. 2014) centred around the three anterior most landmarks. Most specimens show positive values for this component, but in those which do plot

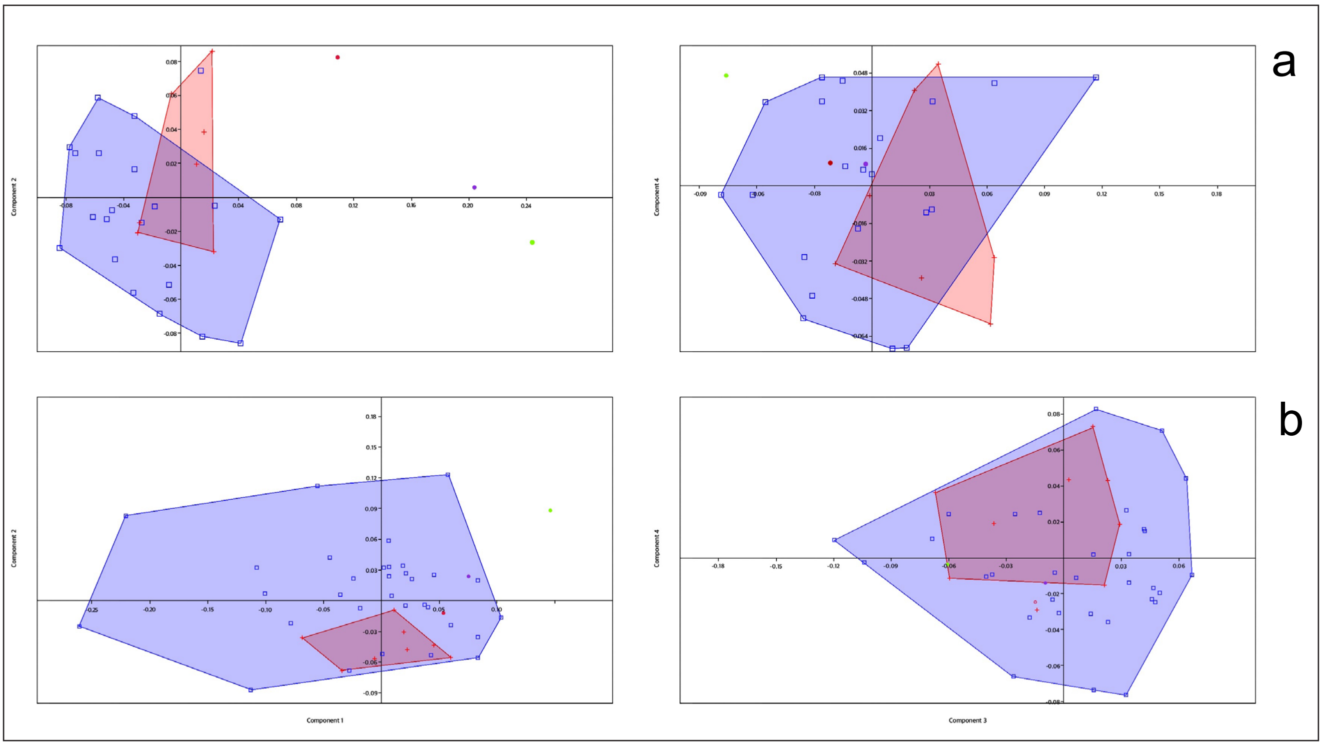

Fig. 8 - Principal Components scatter plots of specimen scores of the first four components. a) Scores for the ventral valves on the PC1 and PC2 (left), and PC3 and PC4 (right). b) Scores for the dorsal valves on the PC1 and PC2 (left), and PC3 and PC4 (right). On both dorsal and ventral PC1/2 graphs the samples of the two locations group closely together.

in the negative half of the graph there is a greater range of values.

Further PC2 shows a pattern of asymmetrical deformation with, for positive values, both the upper and lower extremities of the warp grid moving to the right. Most Sint Michiel specimens show positive values while all Pecten Bed specimens show negative ones. This indicates general contraction with maximum width landmarks 8 and 9 showing a movement down and towards the centre as well as an expansion in the area between teeth.

For PC3 both the Pecten Bed and Sint Michiel populations show a relatively even distribution across positive and negative values while all three living specimens have negative values. Also, PC3 shows an asymmetrical pattern of distortion with – for positive values – expansion being concentrated around landmarks 3, 5 and 7 (left tooth), and compression between L6 and L8 which skews the valve towards the left.

With the fourth principal component, Sint Michiel specimens show a negative average value with a greater number plotting in the lower half of the PC3/4 graph. Pecten Bed specimens are distributed mostly in the positive half of the of the PC4 axis while all three living species show negative values. Positive values indicate an expansion in the lower half of the valve between L8–10 with compression in the area of the teeth which is strongest on the right.

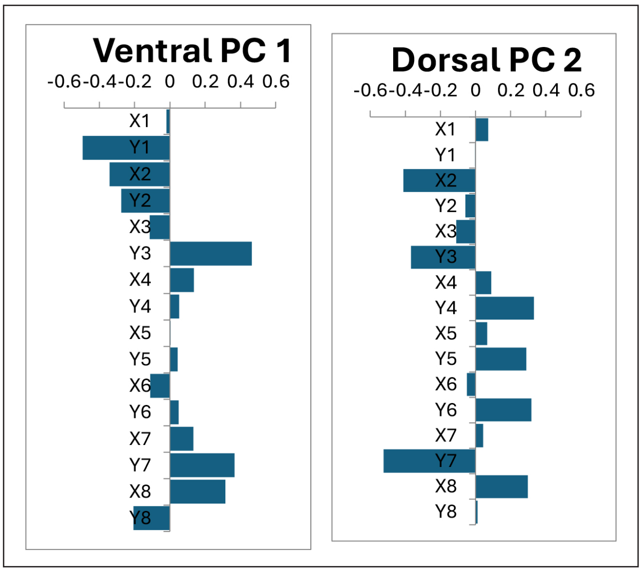

Fig. 9 - Loadings of landmarks on the first two Principal Components (Eigenvectors) for ventral and dorsal valves.

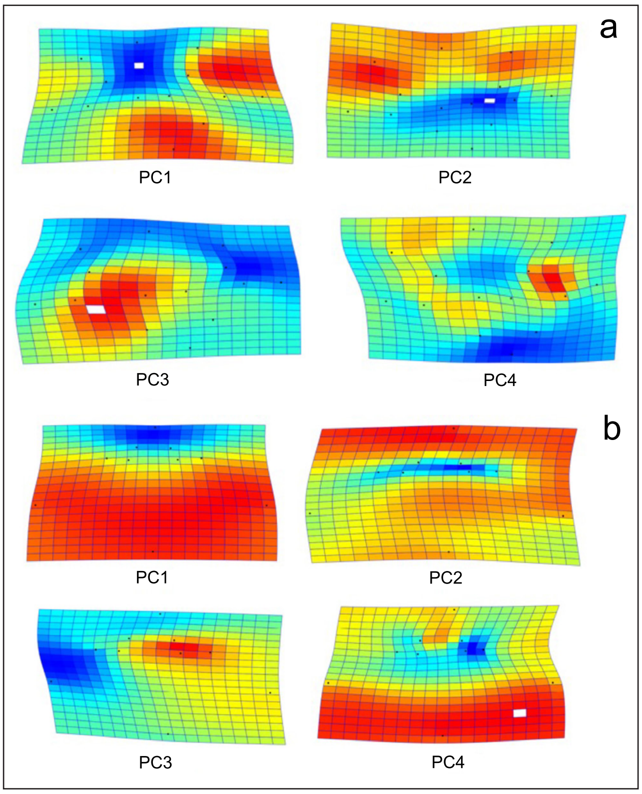

Fig. 10 - Warps for first four Principal Components for ventral and dorsal valves. a) Warps for the ventral principal components (left). b) Warps for the ventral principal components (right). Dorsal valve PC1 shows the clearest trend with the majority of Curaçao specimens with values indicating a right-hand skew; however, a significant proportion of specimens display an opposite skew. Ventral valves have a slight preference for left-hand compression (mirroring the compression of the dorsal valve).

### Dorsal Warps

Figure 10b shows dorsal warps (relative to the mean) for components 1–4, all with a deformation score of 0.10 and coloured according to expansion factor. The dorsal PC1 warp shows a strong skew which, for negative values (such as those shown by the majority of Curaçao specimens), compresses the shell on the right-hand side. The three living species show a large separation with the Curaçao specimens on the PC1 axis, all showing strongly positive values indicating expansion on the right side of the valve giving a skew in the opposite direction.

The Curaçao specimens are far more evenly distributed on the PC2 axis with the Pecten Bed population tending to show positive values while the average Sint Michiel specimen shows a negative one. The PC2 shows differing deformation trends in the posterior and anterior half of the valve with positive values indicating expansion in the upper half and contraction in the lower half which is concentrated in the middle of the valve.

For Pecten Bed specimens, PC3 values tend to be positive with 5/7 specimens plotting in this area of the graph, the majority of Sint Michiel specimens show negative values as do all three living specimens. For positive values PC3 shows compression around the three posterior-most landmarks while expansion centred around the left brachial lobe. The distribution of Curaçao specimens along the PC4 axis shows no clear pattern, but all three living species show negative values. Positive PC4 values indicate compression around the three anterior-most landmarks and expansion around both brachial lobes which is stronger on the right side.

## Summary of morphometric analyses

The two fossil populations from Curaçao do not appear to show any significant separation on either dorsal or ventral principal component graphs with the greater majority of the smaller Pecten Bed population plotting within the convex hull polygon surrounding all the points of the larger Sint Michiel population. This indicates that these populations are part of a single morphological group suggesting that they represent a single species. Separations between the Holocene (living) species is often less than that of individuals within the Curaçao population – even on the dorsal PC1/2 graph where the Pliocene-Pleistocene species show the most differentiation, the level of this differentiation between separate species is still smaller than between individuals at the extremes of the Curaçao population. Further study (especially of the brachial loop characteristics which based on the Pliocene-Pleistocene examples appear to be some of the most distinctive differences between *Thecidellina* species) is therefore needed to confirm the integrity of this group.

Several principal components show morphological patterns which are asymmetrical, a reflection of the skewed asymmetric shapes of many of the specimens. However, distribution of the values of specimens for these components does not show any strong trend. Dorsal valve PC1 shows the clearest trend with the majority of Curaçao specimens having values which indicate a right-hand skew, but dominance of this trend is not strong with a significant proportion of specimens showing an opposite skew. Ventral valves show a slightly increased incidence of left-hand compression (mirroring the compression of the dorsal valve), but this trend is again not a strong one.

The lack of a strong preference for a particular pattern of asymmetry suggests that its cause is not a constant universal factor governing the growth of all *Thecidellina,* for example, such as might be produced if the shell asymmetry were to have a genetic component – where it would be expected that there would be at least an overall preference for a particular form.

This asymmetry is likely related to the unusual method by which *Thecidellina* attaches itself to the substrate – cementation of the ventral valve – and its cryptic space-restricted habitat (Lüter et al. 2007). The attitude of the cemented shell varies according to the angle of the attachment surface, likely due to the need for an elevated commissure to provide a measure of protection against overgrowth by organisms such as encrusting sponges (Lüter et al. 2007; Jackson et al. 1971).

However, the presence of a weak preference for asymmetry in a particular direction – particularly shown by the more variable dorsal valves – suggests that its source is not entirely random, indicating that there may be some factor other than simple chance which governs shell asymmetry. With the importance of attachment orientation to the shape of the shell, a preference for attachment in a particular relationship with a non-random factor such as mean fluid flow or illumination direction might be expected; the distribution of *Argyrotheca johnsoni* Cooper, 1934 specimens which are found in association with living *Thecidellina* over a single coral, has been suggested to be related to light intensity (Jackson et al. 1971). This would likely lead to many individuals being attached in the same orientation and thereby developing similar asymmetries.

If specimens from a particular location were collected mainly from the remains of a single reef face, this could lead to a dominance of individuals which had been attached in a particular orientation. With the relatively small sample sizes which originate from only two locations, the effect of this collection bias could result in the appearance of the trend which was found in this analysis. The validity of the proposed connection between asymmetry pattern and attachment position could be tested by comparison of asymmetry patterns between populations – each from a homogenous environment – which have been collected from different locations.

## PALAEOECOLOGY

Thecideid brachiopods have an unusual morphology and within the rhynchonelliforms a distinctive lifestyle. Most fossil brachiopods were rooted to the substrate by a variety of pedicle types (e.g., Bromley & Heinberg 2006) and cementation to a hard substrate is more typical for the craniiforms (Harper & Moran 1997). Ventral valves of *Thecidellina* are attached directly to a substrate. Elsewhere in the Caribbean, fossil record thecideid brachiopods are found encrusting heart urchins in the Oligocene strata of Antigua (Donovan et al. 2017) although evidence of cementation is lacking. Similarly, the older *Praelacazella* from the Cretaceous of western Australia displays a similar encrusting life mode (Schrøder et al. 2024).

Direct attachment suggests parallels to the life habits with other cemented encrusters such as balanid barnacles. These are typically gregarious through necessity. Reproduction is by copulation rather than release of gametes into the water column in synchronisation with external stimuli as is the case of, for example, sessile cnidarians (e.g., Neufeld & Palmer 2008; Siebert & Juliano 2017). The gregarious habit of balanids is determined by the secretion of species-specific enzymes into the water column which attract conspecific larvae before settlement (Crisp & Meadows 1962). *Thecidellina* species on the other hand were considered to be hermaphroditic containing both ovaries and testes brooding larvae in their mantle cavities (Williams et al. 2000), but more recently a dioecious mode of reproduction has been indicated (Hoffmann & Lüter 2009). The fossil taxon formed a gregarious association on hard substrates similar to concentrations observed in living *T. meyeri* from around the ABC Islands (Hoffmann & Lüter 2009).

**CRediT authorship contribution statement**

David Harper: Conceptualization, Field investigation, Methodology, Writing – original draft, Writing – review and editing, Formal analysis, Visualization.

Mabel la Turner: Lab investigation, Methodology Data curation.

Stephen Donovan: Field investigation, Methodology, Writing – original draft, Writing – review and editing.

Roger Portell: Field investigation, Methodology, Writing – original draft, Writing – review and editing. Specimen curation.

Harper, Donovan and Portell acquired funds for the field work.

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