

**SYSTEMATIC, BIOGEOGRAPHIC AND MICROHABITAT-BASED MORPHOMETRIC
VARIATION OF THE BIVALVE *ANOMALOCARDIA SQUAMOSA*
(BIVALVIA: VENERIDAE: CHIONINAE) IN THAILAND**

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ABSTRACT. – The venerid genus *Anomalocardia* is tropical American in origin, yet has a distribution spanning the tropical western Atlantic to western Pacific oceans. This distribution makes it the most widespread genus of the monophyletic, tropical American Chioninae. Other tropical American chionine genera have either remained restricted to American waters since their originations at various times during the early Neogene, or have sparse fossil or relict Recent distributions in the northwestern Pacific. This is in spite of tremendous diversification throughout Atlantic and Pacific American waters. Here we analyze the morphologic variation of *A. squamosa* (Linnaeus, 1758) from Thailand, focusing specifically on the correspondence between morphological variability and microhabitat variation, with the eventual goal of uncovering possible adaptive advantages of *Anomalocardia* relative to other chionine genera. Significant variation was found among sites, characterized by differences in the shape of valve commissures and siphonal regions. The variation corresponds qualitatively with differences in sediment and water energy. We further compare *A. squamosa* to the congeneric, western Atlantic *A. brasiliana* (Gmelin, 1791), and the related eastern Pacific species, *Ilioichione subrugosa* (Wood, 1828), establishing *A. squamosa* as a geographically widespread species, and finding all the taxa to be morphologically distinct. Finally, the analysis of *A. brasiliana* reveals that individuals from the Caribbean are morphologically distinct from Brazilian individuals.

KEYWORDS. – Geometric morphometrics, distribution, adaptation, shell characters.

INTRODUCTION

The genus *Anomalocardia* presents an anomalous biogeographic distribution among the tropical and subtropical American members of the venerid subfamily Chioninae, the genera of which form a distinct monophyletic clade within the Veneridae (Kappner & Bieler, 2006). The clade first occurs in the Early Oligocene of the southeastern United States (Dockery, 1982), being represented abundantly by the genera *Lirophora* Conrad, 1863, and *Chionopsis* Olsson, 1932 (see Roopnarine, 1996). The phylogenetic histories of subsequent radiations remain unknown, but resulted in the origination of additional genera in the tropical western Atlantic during the Miocene, most notably the type genus *Chione* Mühlfeld,

1811, as well as *Anomalocardia* Schumacher, 1817, and *Liromissus* Roopnarine, 1997. Eventual invasion of the tropical eastern Pacific during the Miocene and Pliocene resulted in further diversification of these genera (Roopnarine, 2001), accompanied by additional generic originations, for example *Ilioichione* Olsson, 1961, and perhaps *Chionista* Keen, 1958. The latter is currently ranked as a subgenus of *Chione*, but morphological distinctiveness (Roopnarine, 2001) and recent molecular studies suggest a closer relationship to *Chionopsis* (see Kappner & Bieler, 2006; those authors represent *Chionopsis* subgenerically in their analyses with *Puberella* Fischer-Piette & Vukadinovic, 1977). The subfamily also radiated successfully into temperate waters, being represented in the western Atlantic by various species

of *Mercenaria* Schumacher, 1817, during the Neogene and Recent, and in the eastern Pacific today by *Protothaca* Dall, 1902, and *Humilaria* Grant & Gale, 1931. There was also radiation into the southern ocean, where *Ameghinomya* Ihering, 1907 (Oligocene-Miocene) (designated a synonym of *Protothaca* by Rios, 1994, but of uncertain subfamily assignment based on Kappner & Bieler, 2006) occurred in Argentina and Chile, and could represent one of the few genus-level extinctions within the Chioninae. Furthermore, the eastern Pacific genus *Securella* Parker, 1949, which first occurs in the Late Oligocene and is potentially a sister-taxon of *Chionopsis* (see Anderson & Roopnarine, 2001), successfully invaded the northern Pacific during warm periods of the Miocene, subsequently became extinct in the Americas, but is today represented by a single species, *S. stimpsoni* Gould, 1861, in the Sea of Japan (Amano et al., 2000). Likewise, *Humilaria* also migrated to the northern Pacific and Japan during the Miocene (Amano, 1998), but is represented today only in the cold temperate eastern Pacific by *H. kennerleyi* Reeve, 1863. Significant Late Pliocene and Plio-Pleistocene extinctions affected the tropical western Atlantic more severely than the tropical eastern Pacific, and chionine diversity today is much higher in the latter region (Roopnarine, 1996).

Therefore, almost without exception, members of the American Chioninae have remained restricted to the Americas since the subfamily's origination, or are restricted there today. The westwardmost area of distribution is the Galapagos Islands, where the genera *Chione* and *Chionopsis* are represented by *Chione undatella* (Sowerby, 1835) and *Chionopsis amathusia* (Philippi, 1844), respectively. *Anomalocardia* is a notable exception to this pattern. The genus first occurs in the Miocene, and is potentially a sister-taxon of *Lirophora* (Roopnarine, 1996), although recent molecular analyses assign it various relationships within the American Chioninae (Kappner & Bieler, 2006). *Anomalocardia* must have invaded the eastern Pacific by at least the Lower Pliocene, if the monospecific *Ilioichione* (Pliocene-Recent) is indeed the sister-taxon and therefore likely derived from a species of *Anomalocardia* (Roopnarine, 1996). Today the genus is represented in the western Atlantic by the species *A. brasiliiana* (Gmelin, 1791) and *A. cuneimeris* (Conrad, 1846). Surprisingly, the genus also radiated into the western Pacific and Indo-Pacific, being represented today in those regions by the species *A. producta* (Kuroda & Habe, 1951) and *A. squamosa* (Linnaeus, 1758), respectively. There is no paleontological evidence to shed light on the timing of the westward invasion(s), nor are there phylogenetic hypotheses (morphological or molecular) of the relationships between the western Atlantic and western Pacific species.

The anomalous nature of *Anomalocardia*'s biogeographic distribution represents an opportunity to understand the favourable circumstances, constraints, and processes associated with biogeographic and evolutionary radiation. This paper takes a first step towards this goal by examining the conchological distinction and morphological relationships among members of the genus, focusing on the species *A.*

squamosa. Conchological variability within the species is examined with morphometric analyses of samples collected from different microhabitats in the Gulf of Thailand and the Philippines, and conchological distinctiveness is examined by morphometric comparison to samples of the Caribbean species *A. brasiliiana*, and the eastern Pacific *Ilioichione subrugosa* (Wood, 1828).

MATERIALS AND METHODS

Specimen collection. – Specimens of *Anomalocardia squamosa* were collected from the intertidal and shallow subtidal zones of Kungkrabaen Bay (KKB), located in Chantaburi Province, Thailand (Fig. 1). KKB is an oval lagoon, 4.6 km long and 2.6 km wide, covering approximately 640 ha (6.4 km²) (Hambrey et al., 1999). Most of the bay is fringed with mangroves. The level of the ground rises noticeably along the central shoreline, and could represent gradual uplift of the bay on its eastern side.

Sampling stations were chosen randomly to have representative samples from different microhabitats present in the area (Table 1), the main habitat variables being sediment type and water energy. In this way, four main stations were defined in the bay and one outside the bay (Fig. 1). Specimens were placed in one of three categories: live-collected, empty shells of presumably Recent dead individuals, and subfossil specimens. Recent empty shells were collected on mangrove-fringed, open mud flats at the southern end of KKB (KKB-01, KKB-02), in close proximity to stations with abundant living individuals. Subfossil specimens were collected from dry sediments exposed by channels running through the mangroves that fringe the central region of the bay (KKB-04-L1, KKB-04-L4). These sediments are above the intertidal zone, and whereas they contain a diversity of marine molluscan shells, they are inhabited by terrestrial plants, insects, and molluscs. Living specimens were collected at several stations within the bay, representing

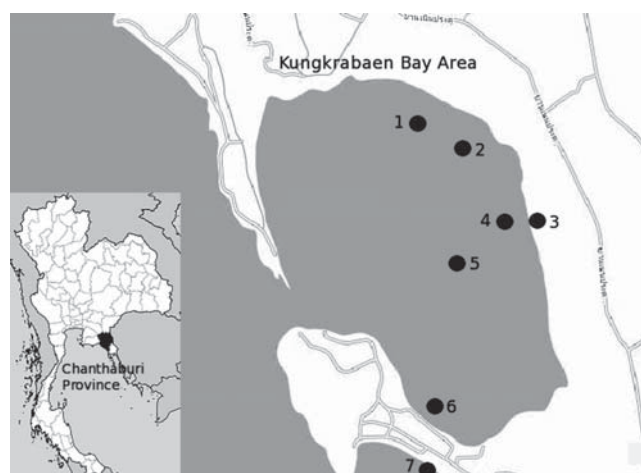


Fig. 1. Map of Thailand showing the location of Kungkrabaen Bay, and sampling localities. Locality numbers: 1, KKB-04-station 3; 2, KKB-04-station 2; 3, KKB-04-L1 and -L4; 4, KKB-04-station 1; 5, KKB-04-seagrass; 6, KKB-01, -02, and -03; 7, KKB-16. See text and Table 1 for additional locality details.

Table 1. Sample designations and locations in Kungkabaen Bay, with microhabitat summaries. See Fig. 1 for additional details.

Sample	Microhabitat and location
KKB-01	“boardwalk location”, southern part of Kungkabaen Bay, mud surrounding mangrove fringe, 12°34.42'N 101°54.25'E, dry at low tide
KKB-02	“boardwalk location”, southern part of Kungkabaen Bay, shelly mudflat with <i>Isognomon</i> oyster bar, 12°34.50'N 101°54.24'E, dry at low tide with water channels
KKB-03	“middle of bay station”, eastern part of Kungkabaen Bay, mud surrounding isolated mangroves, 12°35.16'N 101°54.40'E, dry at low tide
KKB-04	“middle of bay station”, eastern part of Kungkabaen Bay, mud in mangrove hammock, 12°35.31'N 101°54.29'E, dry at low tide
KKB-16	Pak Nam Khem Nu, ocean-side beach at side of road below bridge, 12°32.331'N 101°57.012'E

fine mud, sandy mud, and mixed shellhash and seagrass microhabitats (KKB-03, KKB-04). A sample was also collected at Pak Nam Khem Nu (KKB-16), an open-coast sandy beach, south of the bay. All living specimens were fixed in 70% ethanol. Soft tissues were removed from some shells for morphometric analysis of the shells, but all tissue and shell material were preserved and are deposited in the Invertebrate Zoology collections of the California Academy of Sciences (CASIZ).

Additional samples of *Anomalocardia squamosa* from the Philippines (CASIZ 731) were analyzed, along with samples of *A. brasiliana* from Jamaica (CASIZ 175394), Colombia (CASIZ 092096, CASIZ 088665), and Brazil (CASIZ 43265), and *Ilioichione subrugosa* from Ecuador (CASIZ 175393) (Fig. 2; Table 2). Microhabitat data were less specific for these materials compared to data for the Thai samples.

Laboratory work. – Specimens were selected randomly from each location, cleaned of soft tissues if necessary, and the shells photographed with a Konica-Minolta DiIMAGE 1A

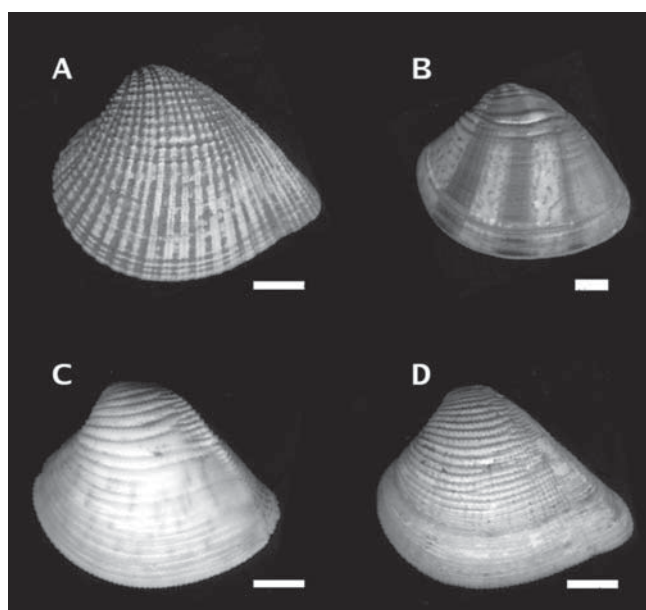


Fig. 2. Example specimens of species analyzed morphometrically: A, *Anomalocardia squamosa*, KKB-03; B, *Ilioichione subrugosa*, Ecuador; C, *A. brasiliana*, Colombia; D, *A. brasiliana*, Brazil. Scale bars = 5 mm.

digital camera or scanned with an Epson Perfection 4870 Pro flatbed scanner. The numbers of specimens selected from each sample are presented in Table 2. Nineteen Type I or II geometrically homologous landmarks (Rohlf, 1996; Roopnarine & Vermeij, 2000) were identified on the interior of each left valve and used to archive the shape of that specimen (Fig. 3). Left valves only were used in the analyses because of the inequivalve hinge morphology between left and right valves. Landmark coordinates were captured digitally from specimen images using the software Tnimage for Linux (<http://entropy.brneurosci.org/tnimage.html>).

Raw landmark data were used for both the calculation of specimen size and the description of shape. Size was calculated as Centroid Size, the square root of the summed squared distances of a specimen's landmarks to their geometric centroid:

$$S = [\sum(d_i)^2]^{1/2}$$

where S is centroid size, and d_i represents a landmark's distance to the geometric centroid. S has the advantage over other measures of size employed in morphometric analyses of being independent of shape measured in the absence of allometry (Bookstein, 1991). Shape was described using the method of principal warp analysis (Bookstein, 1991),

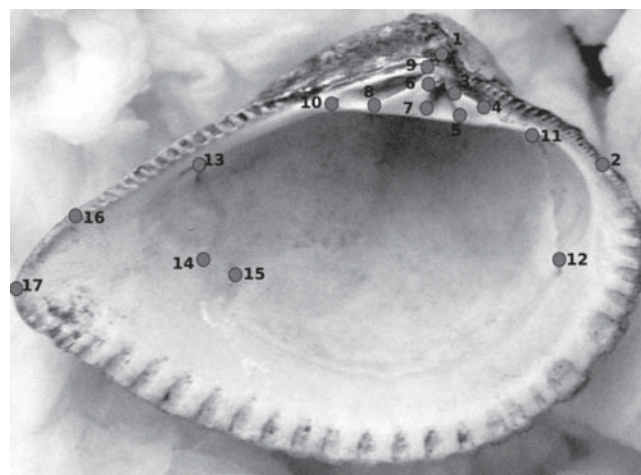


Fig. 3. Internal view of left valve of *Anomalocardia squamosa*, showing location of Type I and II geometrically homologous landmarks. This is the view and orientation used for digitization of the landmarks.

Table 2. Samples and sample sizes used for morphometric analyses. KKB designations correspond to those listed in Table 1 and illustrated in Fig. 1. All samples are of *Anomalocardia squamosa*, except for those from Jamaica, Colombia and Brazil (*A. brasiliana*), and Ecuador (*Ilioichione subrugosa*).

Species	Sample	N
<i>A. squamosa</i>	KKB-01	12
	KKB-02	10
	KKB-03	32
	KKB-04-seagrass	13
	KKB-04-station 1	20
	KKB-04-station 2	10
	KKB-04-station 3	20
	KKB-04-L1	8
	KKB-04-L4	24
	KKB-16	15
	Philippines, Manila Bay, CASIZ 731	23
<i>A. brasiliana</i>	Jamaica, Kingston, CASIZ 175394	27
	Colombia, Cartagena Bay, CASIZ 092096, 088665	55
	Brazil, Rio de Janeiro, CASIZ 43265	13
<i>I. subrugosa</i>	Ecuador, CASIZ 175393	19

which essentially summarizes a specimen's shape as a transformation relative to a common reference form. The major dimensions of shape variation are summarized by specimen distributions on principal warps in a Kendall shape space, and specimen coordinates on these axes (partial warp scores) summarize specimen shape completely and can be used as ordinary variables in parametric statistical analyses. Principal warp analyses were performed with tpsRelw (Rohlf, 2002). Among-sample shape variation was tested with multivariate analysis of variance (MANOVA) of partial warp scores and subsequent classification performed using canonical variates analysis (CVA). Statistical analyses were performed with Stata 9.0 for Linux (<http://www.stata.com/>).

RESULTS

Multivariate analysis of variance (MANOVA) and subsequent canonical variates analysis (CVA) of the pooled partial warp scores for all digitized specimens from the Kungkrabaen collection revealed significant differentiation among samples (Wilks' $\lambda = 0.00005$; $p < 0.0001$) (Fig. 4). CVA resulted in the recognition of four major morphological groups. The largest group comprised the majority of the samples, including samples from muddy substrata within Kungkrabaen Bay itself. These included both living specimens and dead-collected shells. This major group also included subfossil specimens collected from the fringing mangrove region. The three smaller groups represent single sample collections, namely specimens collected from a seagrass bed area in central KKB, a sandy-mud substratum area near the middle of the bay's shoreline, and the outer shore, beach-collected sample. Reliability of the CVA was 97.5%, reflecting this major delineation of samples along sediment type.

A relative warps analysis (RWA) was performed to interpret the morphological differences revealed by the CVA. Relative warps analysis is essentially a principal components analysis of scaled partial warp scores. This analysis summarizes the individual descriptions of specimen shape (partial warp scores) as linear combinations, in the same way that principal components analysis treats traditional morphometric distance

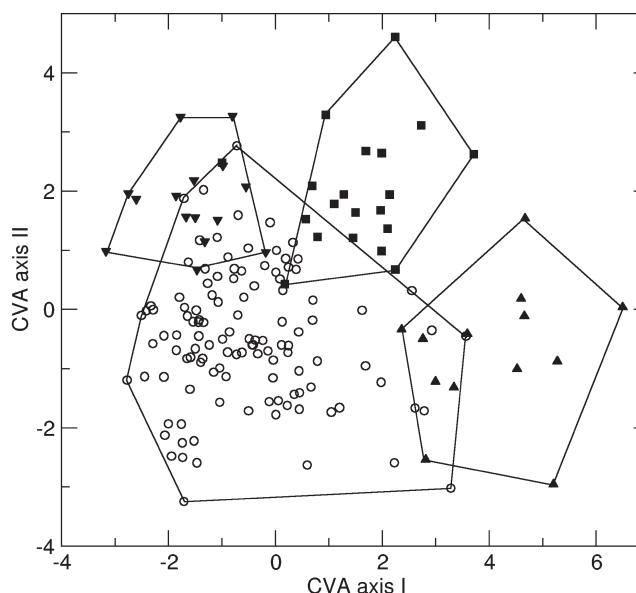


Fig. 4. Canonical variates analysis of all Kungkrabaen Bay samples (see Table 1), illustrating discrimination into four major morphological groups. The apparent overlap among samples is the result of showing only the first two canonical axes. Lines joining symbols (specimens) outline the range of variation of each group. Circles, KKB-01, KKB-02, KKB-03, KKB-04-station 1, KKB-04-station 2, KKB-04-L1, KKB-04-L4; inverted triangles, KKB-16; solid squares, KKB-04-station 3; solid triangles, KKB-04-seagrass.

Table 3. Centroid sizes of four major morphological groups (see Figs. 4 & 6). Mean values and standard deviations are reported.

Sample	Centroid size
KKB-01, fine mud along fringing mangroves, southern end of KKB	28.70 ± 5.99
KKB-04-seagrass	16.99 ± 2.32
KKB-16, sandy beach on the open coast	33.53 ± 3.99
KKB-04-station 3, sandy mud along fringing mangroves near the middle of the KKB shoreline	25.59 ± 3.79

measures. RWA produced morphologically interpretable differences among the four major morphological groups. Specimens from the seagrass and station 3 sites have obviously rounded posterior margins, perhaps the result of growing in coarser sediment grain size (Fig. 5). Specimens from muddy substrata within KKB, and those from the outer beach, tend to have straighter posterior margins, but the dorsoventral posterior junction of the margin, the elongation of which is characteristic of all species of *Anomalocardia*, is noticeably broader in specimens from within the bay. This results in a broader siphonal area in the shells of those specimens, although it cannot be confirmed at present whether this corresponds with relatively wider siphons. Furthermore, although soft-tissue material was preserved in 70% ethanol for all specimens, post-preservation distortion prevents the testing of siphon width differences among the morphological groups.

The possibility exists that differences among samples result purely from size-related or allometric variation, and this was tested first with the relationships between relative warps and centroid size, and second by examination of thin plate spline models of those relationships. The morphological groups discriminated by the CVA – muddy substratum within the bay, sand substratum within the bay, seagrass, and the open coast beach sample – differ significantly in centroid size

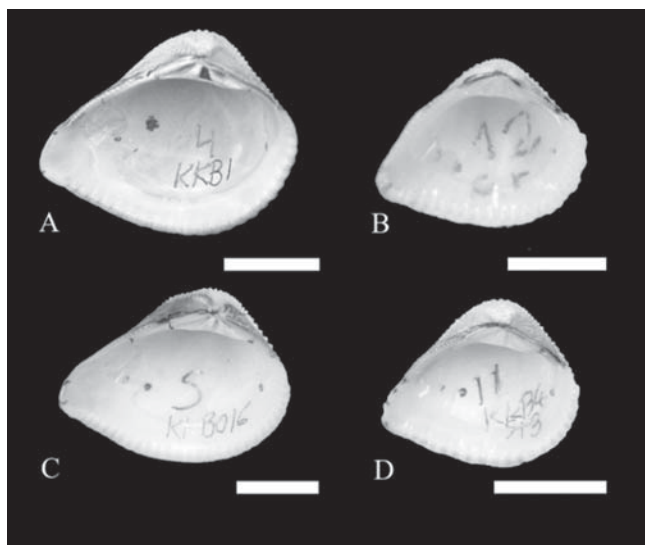


Fig. 5. Example specimens of the four microhabitat-correspondent morphological groups uncovered by relative warps analysis and canonical variates analysis of morphometric data: A, KKB-01, fine mud along fringing mangroves, southern end of KKB; B, KKB-04-seagrass; C, KKB-16, sandy beach on the open coast; D, KKB-04-station 3, sandy mud along fringing mangroves near the middle of the KKB shoreline (see Fig. 1). Scale bars = 10 mm.

distributions (ANOVA, $F = 25.02$, $p < 0.0001$), with the seagrass sample comprising on average smaller individuals (Table 3). Relative warp I (RW I, 21.57% of total variance) was the only factor significantly correlated with centroid size (Pearson's $r^2 = 0.498$, $p < 0.0001$) for the pooled samples, but there was significant among-sample variation of the relationship (ANCOVA, $F = 15.84$, $p < 0.0001$). All groups discriminated by the CVA, with the exception of the open coast beach sample, exhibited significant allometry between RW I and centroid size (linear regressions: muddy substratum, $r^2 = 0.1751$, $p < 0.0001$; sandy substratum, $r^2 = 0.2090$, $p < 0.0427$; seagrass, $r^2 = 0.3293$, $p < 0.0403$; beach, $r^2 = 0.2260$, $p < 0.0733$) (Fig. 6). The three allometric relationships within the bay – muddy substratum, sandy substratum, and seagrass – all differed significantly (ANCOVA, $F = 4.63$, $p = 0.0112$).

The morphological significance of the allometric variation was assessed by examining thin plate splines of predicted shell shape of the largest specimen within each category (Fig. 6). It is obvious that allometry does not account for shape differences among any of the morphological groups (splines are relatively uniform), with the exception of the seagrass specimens. Allometry in that group is responsible for the rounded nature of the posterior margin. This also implies that the similarity in margin shape between this group and those from the sandy substratum locality (Station 3) does not arise from similar patterns of growth.

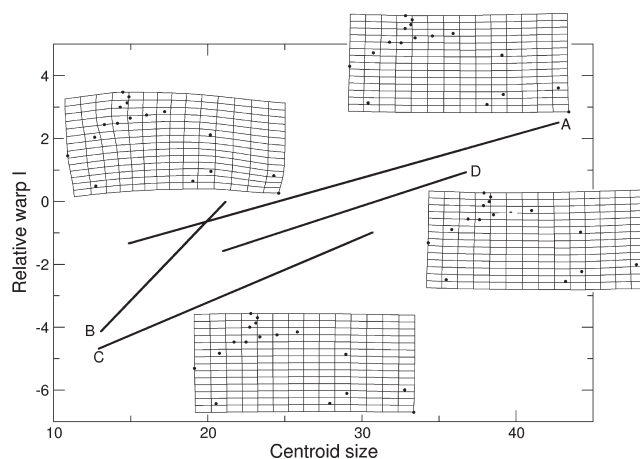


Fig. 6. Allometric curves derived from relative warps analysis of pooled samples and centroid size: A KKB-01, fine mud along fringing mangroves, southern end of KKB; B, KKB-04-seagrass; C, KKB-16, sandy beach on the open coast; D, KKB-04-station 3, sandy mud along fringing mangroves near the middle of the KKB shoreline. Thin plate spline diagrams are of specimen shape predicted, at maximum centroid size for each group, on the basis of the allometric relationships.

Comparison of all samples of *Anomalocardia*, including the Philippine *A. squamosa* and western Atlantic samples of *A. brasiliiana*, as well as the eastern Pacific *Ilioichione subrugosa*, yielded significant interspecific discrimination (Fig. 7). The intraspecific variation among KKB microhabitats described above was overwhelmed by interspecific differences. There is some indication of geographic differentiation within *A. squamosa*, between the Thai and Philippine specimens, but it is statistically equivocal. More interestingly, however, is the significant difference between Brazilian and Caribbean specimens of *A. brasiliiana*. The morphological discrimination is enough to warrant further investigation of the status of these samples as comprising a single species, and is in keeping with additional circumstantial evidence of differentiation between Brazilian and Caribbean individuals assigned to the same chionine species (Roopnarine & Vermeij, 2000).

DISCUSSION

The terminal morphology of any bivalve shell is the combined result of genotype, induced environmental influences on valve phenotype, and genotype-environment interactions. Intraspecific variation of shell morphology is often ascribed to ecophenotypic processes, yet this assumption is rarely tested. Furthermore, genotypic bases of morphological plasticity vary among species, and in combination with historical contingency, are likely responsible for considerable intertaxon differences in geographic range and variation. *Anomalocardia* is exceptional in the clade of tropical American chionine venerids in being the only member of that clade to have successfully established itself in the Indo-Pacific region. Recall that the tropical American chionine clade originated in the western Atlantic, and that multiple lineages invaded the eastern Pacific successfully during the Neogene (Roopnarine, 1996, 2001), yet only three have ever extended their ranges to the western Pacific, and only two persist there today. Whereas accidents of history might explain this anomaly,

the failure of other members of the Chioninae to extend their ranges similarly presents an opportunity to question whether *Anomalocardia* is better suited for such extensions, and if so, which characteristics confer this ability.

This study approached the question by examining the range of variation of *Anomalocardia* in a small geographic area encompassing heterogeneous environments. The use of geometric morphometrics as both a morphological descriptor and analytical tool is well suited for this type of study. Geometric morphometrics has been well established as capable of high resolution, reliable discrimination of inter- and intraspecific morphological variation in bivalves and other molluscs, and has been used for conchological developmental studies in gastropods and bivalves (Guralnick & Kurpius, 2001; Roopnarine, 2001), microhabitat-based differentiation in gastropods (Tang & Roopnarine, 2003), species discrimination (Roopnarine & Vermeij, 2000), and the description of macroevolutionary patterns (Anderson & Roopnarine, 2005). Analysis of multiple samples of *A. squamosa* from the Kungkabaen Bay area revealed an interesting pattern of variation related to microhabitat differences, most notably sediment type. Samples collected from fine mud substrata within the bay formed a fairly homogeneous set, regardless of whether the specimens were live-collected or collected as dead and possibly transported shells, or represent subfossil individuals deposited at some time in the recent geological past. The three samples that were not assignable to this large set were collected from coarser-grained, sandy substrata. One sample (KKB-04-Station 3) collected in the bay was found in fairly close proximity to “mud” samples and the mangrove fringe, but the sediment was sandy (calcareous) mud. Another sample, also collected in the bay, consisted of a coarse, carbonate-rich (shellhash) sediment with abundant seagrasses. The final sample was collected from the open coast, with a more siliceous sandy sediment and presumably greater wave energy.

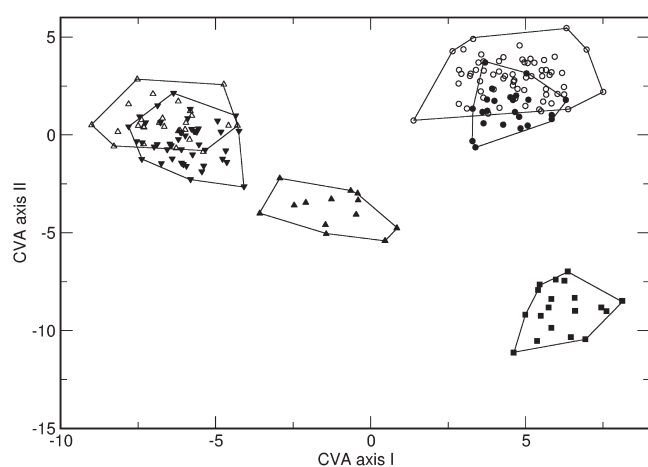


Fig. 7. Canonical variates analysis of morphometric data of *Anomalocardia squamosa*, *A. brasiliiana*, and *Ilioichione subrugosa*. Open circles, *A. squamosa*, Thailand; solid circles, *A. squamosa*, the Philippines; open triangles, *A. brasiliiana*, Jamaica; solid inverted triangles, *A. brasiliiana*, Colombia; solid triangles, *A. brasiliiana*, Brazil; solid squares, *I. subrugosa*, Ecuador.

It is reasonable to assume that the intraspecific variation of the KKB samples and specimens is ecophenotypic, given both the clear correspondence to sediment type, as well as the likelihood that all samples comprise individuals drawn from common regional gene and larval pools. Nevertheless, variation of shell form suggests that individuals are either growing very differently among these localities because of differences in microenvironment, or that selection is operating at very fine geographic scales to filter recruitment from the common pools, pre- or post-settlement. Morphometric assessments cannot resolve these issues, but do highlight the fact that *Anomalocardia squamosa* is capable of very high levels of morphological variation and perhaps adaptation. The sampling protocols used in this project will allow future application of sclerochronological techniques (Schöne et al., 2002) for the analysis of growth patterns and strategies, and molecular analyses for the elucidation of patterns of relationship among the KKB microhabitats.

The interspecific comparisons of *Anomalocardia squamosa* to *A. brasiliiana* and *Ilioichione subrugosa* rescale the level of variation among the KKB samples. There is considerable

overlap between specimens of *A. squamosa* from Thailand and the Philippines, and the species differs significantly from *A. brasiliensis* and *I. subrugosa*. The morphometric analysis therefore confirms the definition of *A. squamosa* as a single, widespread species. Qualitative morphological differences among the three species are obvious (Fig. 2), and whereas a phylogenetic analysis of the genus has not yet been performed, *A. squamosa* is morphologically more similar to *A. brasiliensis* than either is to *I. subrugosa*. A phylogenetic revision of the entire genus, including *I. subrugosa*, will be required to determine the pattern of relationships among the western Atlantic *Anomalocardia*, the Indo-Pacific species and the eastern Pacific *Ilioichione*. The resulting hypotheses, in combination with any fossil data from the eastern and western Pacific that might become available, will help to elucidate the pathway by which *Anomalocardia* invaded the western Pacific. They could also shed some light on the underlying basis for disparity of geographic range between *Anomalocardia* and the other tropical American chionine lineages.

Finally, one unexpected result of the present analysis is the obvious differentiation between samples of *Anomalocardia brasiliensis* from the Caribbean (Colombia and Jamaica) and those from Brazil. Roopnarine & Vermeij (2000) noted differences between Brazilian material assigned to the Caribbean species *Chione cancellata* (Linnaeus, 1767) compared to accurately assigned Caribbean specimens. Furthermore, the same study highlighted a geologically old provincial separation between the Caribbean and the subtropical region to the north, a separation that persists to this day at the congeneric and subspecific levels. That particular division originated as early as the Pliocene, most likely a result of changing oceanographic and ecosystem conditions associated with restriction and closure of the Panama Seaway (Coates et al., 2004). It would therefore be of great interest to learn if a similar separation exists south of the Caribbean. This would assist in determining the systematic status of Caribbean and Brazilian *A. brasiliensis* for inclusion in the unusual biogeographic history of *Anomalocardia*.

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THAI ABSTRACT

หอยสองฝาวงศ์เวเนอริดีในสกุล *Anomalocardia* มีต้นกำเนิดจากเขตร้อนของทวีปอเมริกา แต่กลับมีการแพร่กระจายครอบคลุมเขตร้อนของมหาสมุทรแอตแลนติกและแปซิฟิกตะวันตก การแพร่กระจายดังกล่าวทำให้หอยสองฝาสกุลนี้มีเขตการแพร่กระจายกว้างขวางมากที่สุดสำหรับหอยสองฝาในวงศ์ย่อยไคโอนินีย์ หอยสองฝาไคโอนินีย์ที่มีกำเนิดจากเขตร้อนของทวีปอเมริกากุ่มอื่นมีการแพร่กระจายจำกัดอยู่ในน่านน้ำของทวีปอเมริกาตั้งแต่กลุ่มเริ่มมีกำเนิดมาในยุคนีโอจีน โดยมีฟอสซิลกระจัดกระจายและหาได้ไม่มากนัก หรือมีการแพร่กระจายในรัศมีแคบๆ ในปัจจุบันอยู่เฉพาะในเขตมหาสมุทรแปซิฟิกเขตร้อนถึงเหนือ ทั้งนี้แม้ว่าหอยกลุ่มดังกล่าวมีการแบ่งแยกเป็นหอยหลากหลายชนิดทั่วมหาสมุทรแอตแลนติกและแปซิฟิกในเขตทวีปอเมริกา ในการวิจัยครั้งนี้เราได้ทำการวิเคราะห์ความแตกต่างทางสัณฐานวิทยาของ *A. squamosa* (Linnaeus, 1758) จากประเทศไทย โดยเน้นความสัมพันธ์ระหว่างรูปร่างของเปลือกกับสิ่งแวดล้อมที่พบประชากรหอย โดยมีวัตถุประสงค์เพื่อเปรียบเทียบความสามารถในการปรับตัวของหอยสกุล *Anomalocardia* เทียบกับหอยสกุลอื่นในกลุ่มเดียวกัน ผลจากการศึกษาพบว่า มีความแตกต่างของรูปร่างลักษณะของเปลือกค่อนข้างสูงในแต่ละพื้นที่ โดยเห็นได้ชัดจากรอยหยักบริเวณตำแหน่งขอบเปลือก และบริเวณตำแหน่งท่อน้ำสัมพันธ์กับ ลักษณะของตะกอนและความเร็วของกระแสน้ำ เราได้ทำการเปรียบเทียบ *A. squamosa* กับหอยสกุลเดียวกันคือ *A. brasiliensis* (Gmelin, 1791) รวมทั้งหอยที่มีความใกล้เคียงกันทางสายพันธุ์จากมหาสมุทรแปซิฟิกฝั่งตะวันออกคือ *Ilioichione subrugosa* (Wood, 1828) และสรุปว่า *A. squamosa* เป็นหอยที่มีการแพร่กระจายกว้าง และมีความแตกต่างทางสัณฐานวิทยาจากหอยสองฝานิดที่ทำการศึกษายเปรียบเทียบ ท้ายสุดการวิเคราะห์สัณฐานวิทยาของ *A. brasiliensis* แสดงให้เห็นว่าหอยชนิดดังกล่าวจากทะเลแคริบเบียนมีรูปร่างแตกต่างจากหอยชนิดเดียวกันที่มาจากประเทศบราซิล

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