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COMPARATIVE ECOLOGY OF TWO PARAPATRIC POPULATIONS OF *ISOGNOMON* (BIVALVIA: ISOGNOMONIDAE) OF KUNGKRABAEN BAY, THAILAND

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ABSTRACT. – This study provides a detailed comparison of the ecology of two parapatric populations of the bivalve genus *Isognomon* inhabiting the adjacent mangrove forest and mudflat zones of the mangrove ecosystem of Kungkrabaen Bay, northeastern Thailand. Separated initially by habitat, the two populations display substantial morphological differences and are clearly distinguished by morphometric analyses, suggesting that they are distinct species. The marked differences in shell shape, thickness, and the morphology of the byssus are hypothesized to be adaptations to different attachment substrata of mudflat and mangrove environments, and are related to differences in the pattern and relative success of predation and fouling. Quantitative analyses of relative frequencies and success of predation, and the spatial structure of the mangrove and mudflat communities of *Isognomon* suggest that there is a tradeoff between success of the defense against predators and fouling, and the efficiency of physical stabilisation. The associations formed by conspecific individuals of *Isognomon* spp. in both habitats create microhabitats for different suites of epibionts by providing attachment sites and sheltered environments. The results of this analysis suggest that ecological criteria are important in identifying potential cryptic species and indicate the need for a taxonomic revision of *Isognomon*.

KEYWORDS. – Mangroves, predation, functional morphology, adaptive compromise, ecology.

INTRODUCTION

Mangrove forests are unique intertidal ecosystems dominated by specialised plants adapted to high salinity and frequent tidal inundation. They occupy the interface of salt and fresh waters and frequently penetrate into river estuaries (Macnae, 1968). Mangrove forests are nutrient-rich environments that fuel a variety of food chains acting as feeding and nursery grounds for a large number of species. Mudflat communities are part of the estuarine component of mangrove ecosystems, which, for the most part, lies within the intertidal zone exposing broad expanses of slit and clay at low tide (Morton & Morton, 1983). These environments house a great diversity of primary producers, bacteria, and invertebrates (Macnae, 1968; Wells, 1984; Hogarth, 1999). Molluscs are one of the most abundant groups of invertebrates in the mangrove communities inhabiting both forest and mudflat habitats (Morton, 1983; Hogarth, 1999).

Species of the bivalve genus *Isognomon* Lightfoot, 1786, are amongst the most numerous and common bivalves found in mangroves of tropical and subtropical shallow waters and intertidal communities around the world (Morton & Morton, 1983; Harper & Morton, 1994). In the Indo-Pacific region, *Isognomon isognomum* (Linnaeus, 1758) and *I. ephippium* (Linnaeus, 1758) have frequently been reported in the mangroves (Yonge, 1968; Berry, 1975; Way & Purchon, 1981; Morton, 1983; Reid, 1985; Frith et al., 1976; Ng & Sivasothi, 1999; Ashton et al., 2003; Lee & Chao, 2004). Both species are epifaunal filter feeders, typically attached to clefts of prop roots or larger stones in a substratum consisting largely of gravelly clay covered with silt of the muddy estuarine environments.

Literature on mangrove-associated isognomonids is very limited, and studies on their ecology are almost nonexistent. Yonge's (1968) extensive functional morphological study, which focused on comparisons amongst various Indo-Pacific species of the genera *Isognomon* and *Malleus* Lamarck, 1799, contained a brief account of the ecology of the *I. isognomum* mudflat beds. Stanley (1970) and Reid (1985) discussed functional morphology of western Atlantic and Indo-Pacific species of *Isognomon*, respectively, and mentioned the ecological settings and the association of these bivalves with their substrata. Siung (1980) provided a brief account of biology and ecology of western Atlantic *I. alatus* (Gmelin, 1791), and Frith et al. (1976) studied density and abundance of *I. ephippium* in the mangroves of Thailand. Lazareth et al. (2003) analysed trace elements in the shells in Kenyan populations of *I. ephippium*.

In Thailand, only *Isognomon ephippium* has been reported from mangroves in the southern part of the country (Frith et al., 1976; Tantanasiriwong, 1979; Swennen et al., 2001; Printrakoon et al., 2005). Occasionally, these animals were found on the banks of wide channels in mangroves with a high (25–150 cm) vertical range of distribution along the prop roots of *Rhizophora apiculata* Blume, 1827 (Frith et al., 1976).

This work focused on the ecology of two populations of *Isognomon* inhabiting adjacent mudflat and mangrove zones of Kungkrabaen Bay on the eastern coast of the Gulf of Thailand. Multiple ecological parameters pertaining to abiotic (salinity, acidity, etc.) and biotic factors associated with spatial structure of *Isognomon* community (biofouling and predator-prey interactions), as well as distribution, density, biomass, and substratum preference were evaluated for the two isognomonid populations. The ecological characteristics were associated with particular aspects of shell and byssal morphology, providing grounds for functional morphological interpretations and possible adaptive scenarios. The study is pertinent to the urgent conservation effort to protect fragile mangrove communities from ever-growing destruction by the expanding shrimp-farming industry.

MATERIALS AND METHODS

***Study sites.* –** The study was conducted in the southeastern part of Kungkrabaen Bay located on the coastline of Thamai District, Chantaburi Province, on the eastern coast of the Gulf of Thailand (Fig. 1). Nine canals pass through the mangrove forest to an oval-shaped estuary that is approximately 4.6 km long and 2.6 km wide. The inner half of the periphery of the bay is covered by 264 ha of mangrove forest surrounded by extensively developed shrimp farmlands (Thimdee et al., 2004). The mangrove forest is dominated by Rhizophoraceae [*Rhizophora apiculata, R. mucronata* Lamarck, 1804*, Ceriops decandra* (Griffith) Ding Hou, 1958], Combretaceae [*Lumnitzera littorea* (Jack) Voigt, 1845*, L. racemosa* Willdenow, 1803], and Sterculiaceae (*Heritiera littoralis* Dryander ex Aiton, 1789) (Nakasone et al., 1985).

The study area (station KKB-01; 12º34.42'N 101º 54. 25'E) was divided into two sites: the mangrove forest and mudflat zones (Figs. 1–2). The sites were square areas of 100 m^2 and approximately 200 m apart from each other. The fieldwork was conducted at low tide on 25 and 30 Aug.2006. The voucher specimens were deposited in the malacological collections of Mahidol University (Bangkok, Thailand) and the American Museum of Natural History (New York, USA).

***Physical characteristics of the environment.* –** Measurements of salinity, acidity, and water temperature were obtained directly in the field in three replicates at each site using a digital detector. Sediment samples (approximately 500 g) were collected from three non-overlapping areas within each site. The particle composition of the sediment samples was analysed at the Department of Soil Science, Faculty of Agriculture, Kasetsart University.

***Shell and byssus measurements.* –** Fifty living individuals of *Isognomon* were collected from each site (Fig. 3). The shells were used for morphometric analysis, and the soft tissue was

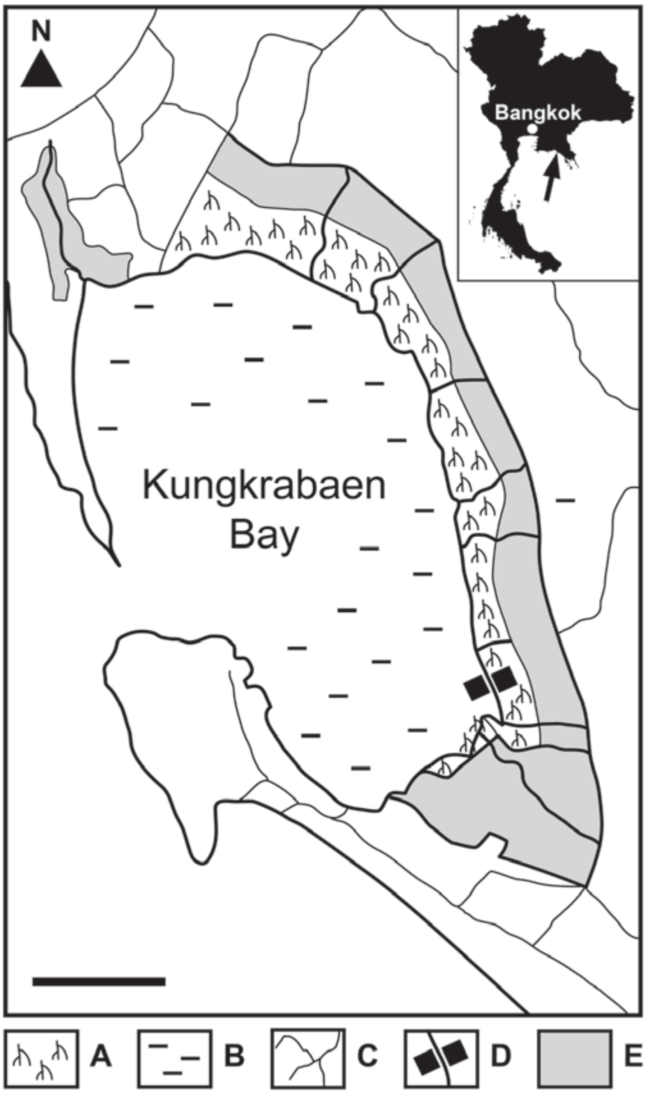

Fig. 1. Map of Kungkrabaen Bay, Chantaburi Province, Thailand, showing the location of the study sites (inset = map of Thailand showing the location of the bay (arrow): A, the mangrove zone; B, the mudflat zone; C, canals; D, the two study sites (station KKB-01); E, shrimp farming area. Scale bar = 1 km. Based on Thimdee et al. (2004).

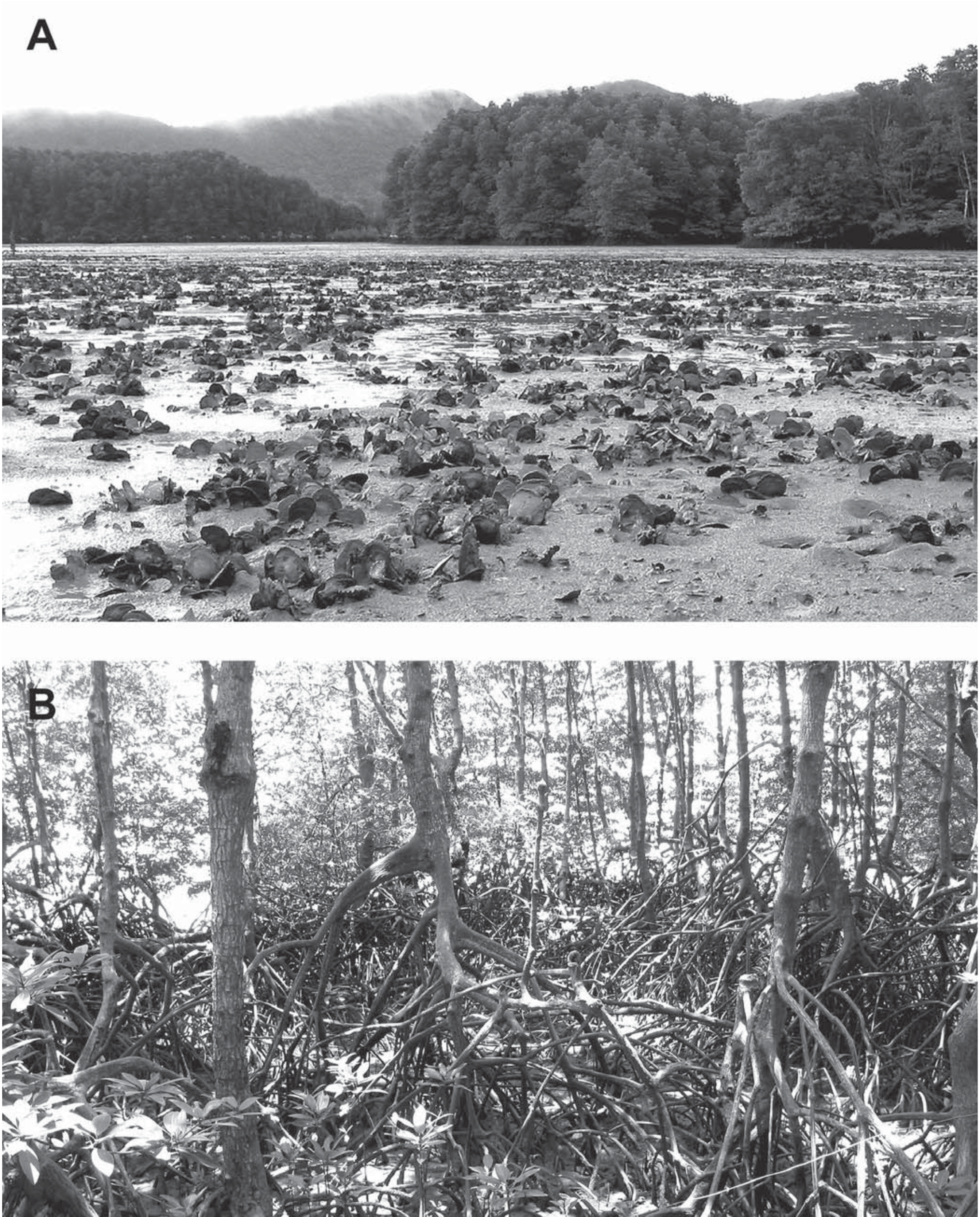

Fig. 2. The mudflat (A) and mangrove (B) zones of Kungkrabaen Bay mangrove ecosystem inhabited by *Isognomon* spp. as seen at low tide.

used for measuring biomass (see below). Maximum shell height (HS), shell length (LS), and hinge length (LH) of each right valve were measured with a digital caliper to the nearest 0.01 mm (Fig. 4). Shell size is expressed as maximum shell length unless otherwise noted. LS is the dimension between the most distant extremities of the anterior and posterior shell margins measured parallel to the hinge axis; HS is the longest dimension between the ventralmost extremity of the shell margin to the hinge line as measured perpendicular to the latter; LH is the extent of the hinge line measured along the hinge axis. Shell thickness was measured with a micrometer to the nearest 0.01 mm at two locations: (1) the site of the insertion of the accessory pedo-byssal retractor muscle (AM); and (2) the middle part of the anterior surface of the posterior pedo-byssal retractor muscle (PRM) (Fig. 4). These sites were chosen because: (1) the attachment areas of homologous muscles are considered to be homologous to each other (and, therefore, comparable); and (2) they represent the regions of maximum (at AM) and average (at PRM) thickness of the valves.

The byssus was isolated from 30 individuals from each study site. The byssus was excised from the visceral mass and cut from its root at the point of its emergence from the visceral mass. The following measurements were taken (Fig. 5): (1) the stem length (BSL; the length of the proximal fused portion of the byssus); (2) the length of the most extensive thread (BTL; measured from its origin proximal to the common stem to the distalmost adhesive disc); (3) the byssus breadth (BB; the length of the widest area of the fan of the byssus measured perpendicular to the stem); and (4) the diameter ratio (BDR, the ratio of the longest and shortest dimensions of the cross section of the byssal stem).

Microscopy and imaging. – Initial observations on shell morphology, and predation and fouling markings were made using a stereo dissection microscope at a laboratory of the Burapha University, Chantaburi campus. For scanning electron microscopy (SEM), dried shells were sputter-coated with gold-palladium using a Denton Vacuum, and were viewed on a Zeiss DSM-950 scanning electron microscope at the American Museum of Natural History. Most observations were made at the following settings: Vacc 7.0 kV, Ie 7.0 μA, and Vext (extraction voltage) 4.7 kV. All SEM samples were stored in a silica-gel desiccator. All habitat, in situ, and laboratory photographs were made with a Canon G2 (4 megapixels) digital camera.

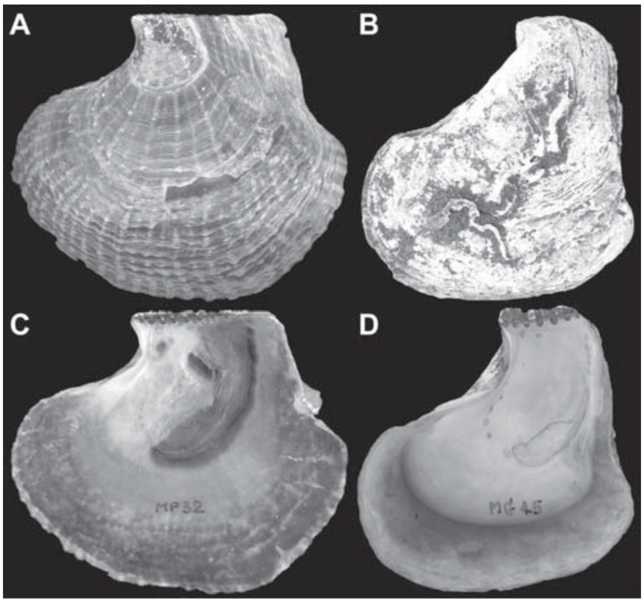

Fig. 3. Representative specimens of mudflat *Isognomon* (A, C; 66.5 mm) and mangrove *Isognomon* (B, D; 50.0 mm): A–B, lateral views of the exterior surfaces of left valves; C–D, lateral views of the interior surfaces of right valves.

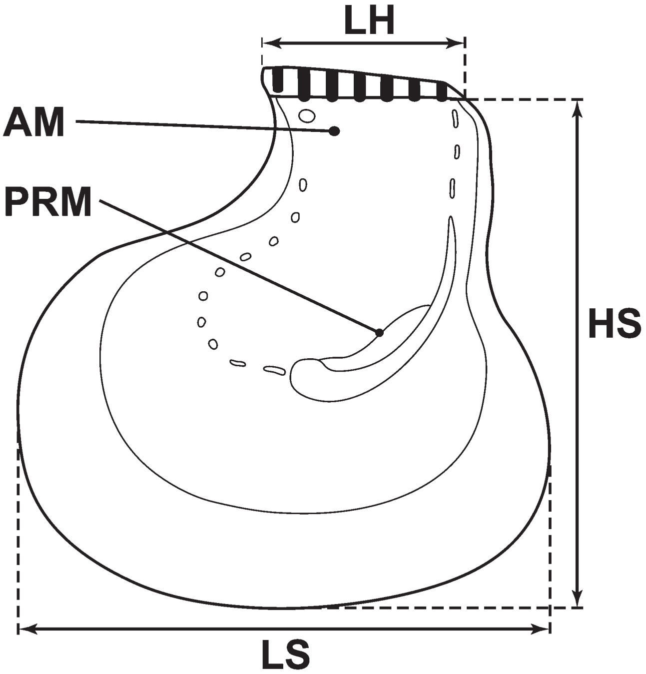

Fig. 4. Diagrammatic view of the interior surface of the right valve of a generalised *Isognomon* shell showing shell measurements. AM, site of insertion of the accessory pedo-byssal retractor muscle; HS, maximum shell height; LH, maximum hinge length; LS, maximum shell length; PRM, middle part of anterior surface of the posterior pedo-byssal retractor muscle.

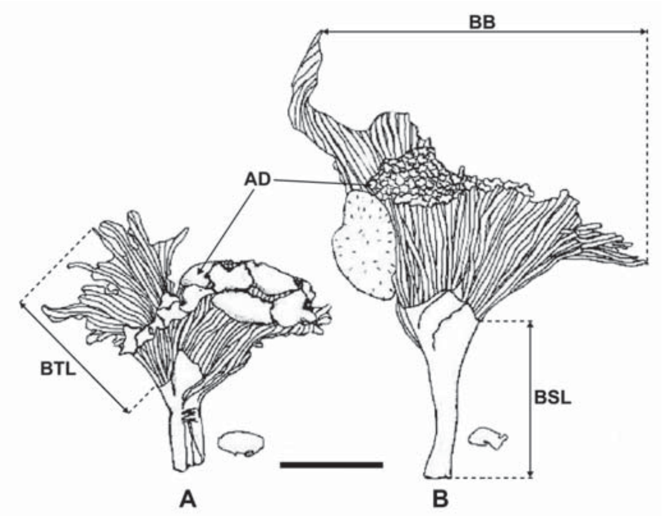

Fig. 5. Diagrammatic views of byssi showing lateral and cross-sectional views of the mangrove: A, and mudflat; B, *Isognomon*. AD, adhesive disc; BB, byssus breadth; BSL, byssal stem length; BTL, maximum byssal thread length.

Biomass. **–** Fifty tissue samples of *Isognomon* individuals (the same specimens for which the shells were used for the morphometric analysis) from each zone were used for determining biomass. The soft tissue was separated from the shell and the byssus was excised at the point of its emergence from the visceral mass. The soft tissues of the individuals obtained from each site were placed in foil containers, weighed prior to placing into an oven at 80°C, and reweighed after three days upon complete desiccation. To minimise experimental error, the tissue samples were divided, so that the weights were obtained for individual subsamples, and combined subsequently.

Population density and distribution. **–** Due to the qualitatively different nature of the physical environments in mangrove and mudflat ecosystems, population density and distribution of individuals were estimated in somewhat different ways that, nevertheless, provided an adequate basis for comparison between the sites.

Mangrove: Eight individual trees of *Rhizophora apiculata* were randomly selected. For each *R. apiculata*, all individuals of *Isognomon*, either attached to the tree or lying on the ground within the periphery of the expanse of the tree's prop roots, were counted, noting the number of living, dead, and juvenile (< 20 mm) individuals. The following additional measurements were made: (1) the numbers of *Isognomon* clusters and solitary individuals; (2) the number of individuals in a cluster; (3) the elevation of individual or clustered *Isognomon* (distance from the surface of the substratum to a solitary individual or the lowest individual of the cluster measured along a straight line perpendicular to the substratum; eight measurements per replicate); (4) the distance between the most closely located clusters on the same tree (four measurements per replicate); and (5) the distance between most closely located trees (four measurements per replicate).

Mudflat: Eight 1 m^2 areas were randomly selected and all individuals of *Isognomon*, either on the surface or submerged in the mud, were counted, noting the number of living, dead, and juvenile (< 20 mm) individuals. The following additional measurements were made: (1) the numbers of *Isognomon* clusters and solitary individuals; (2) the number of individuals in a cluster; and (3) the distance between most closely located clusters (four measurements per replicate).

Attachment to substrata. **–** The orientations of *Isognomon* individuals relative to the substratum (individual-substratum angle, IS) and neighbouring individuals within a cluster (individual-individual angle, II) were recorded (Figs. 6E, 7F). The angle formed by the valves of laterally adjacent individuals was measured as the angle formed by an imaginary line passing through the shell commissure when viewed along an anteroposterior axis. The angle between each valve and its substratum was measured as the angle formed by an imaginary line passing through the shell commissure and a line parallel to the surface of the substratum. In total, 34 measurements (17 IS angles plus 17 II angles) were taken for ten clusters for each of the two habitats. The respective views were obtained with the digital camera and the angles measured using the computer program tpsDig version 2.05 (Rohlf, 2005).

Associated biota. **–** Associated fauna refers to co-occurring macroinvertebrate species irrespective of their association with *Isognomon* individuals. They include potential predators, fouling organisms, parasites, mutualists and commensals. Their occurrences in the mudflat and mangrove zones were documented in the field and representative samples were collected for identification in the laboratory.

A limited quantitative analysis was performed on the fouling organisms and a more comprehensive analysis was conducted on the drilling predation (see below). Samples of 50 living individuals from the mangrove and mudflat *Isognomon* were examined for the incidence of fouling organisms, noting to which valve (left or right) they were attached. Only the presence or absence of fouling organisms was scored. The degree of fouling (ranging from zero to complete encrustation of the entire valve) was not evaluated. In addition, the interior surfaces of the valves were inspected for the marks of fouling organisms, namely the blisters caused by boring epibionts. Measurements were taken for both mangrove and mudflat *Isognomon* individuals and the differences were evaluated for statistical significance.

Analysis of predation. **–** Actual instances of predation were actively sought and documented in the field. For a quantitative analysis, 50 dead and 50 living individuals were collected at six randomly chosen areas from each study site (200 individuals total) for the analysis of traces of predation. Predator damage here refers to the drill hole (borehole) morphology and the frequency of drill hole per valve associated with the activity of predatory gastropods. (See Discussion for the reasons for excluding other forms of predation from the analysis.) The incidence of drilling and its relative success were compared between the mangrove and mudflat zones. The incidence of drilling was calculated as the number of drill holes (complete and incomplete) divided by the number of individuals (valve pairs). The relative success of predation was estimated as the proportion of incomplete drill holes in a sample to the total number of drill holes. In addition, the following observations were made: (1) the positions of incomplete and complete drill holes on the valve surfaces; and (2) the distribution of drill holes between right and left valves. The relationship of drilling to the physical orientation of the prey was calculated as the proportion of drill holes in right and left valves. The association of drilling and mortality was calculated as the proportion of complete drill holes in living vs. dead individuals. These measurements were taken for both mangrove and mudflat *Isognomon* individuals and the differences were evaluated for statistical significance.

Statistical analysis. **–** Standard statistical analyses of variance (ANOVA) were performed using the computer program SPSS (Version 11.5, SPSS Inc., Chicago, Illinois, USA). Statistical significance for bivariate tabular analysis was evaluated using a χ^2-test. The significance of measurement differences between populations is reported at minimum 95% confidence level.

RESULTS

Abiotic factors. – Water temperature, acidity, and salinity did not differ significantly between the mangrove and mudflat habitats, although the latter was generally more saline. On the other hand, the sediment composition differed between the habitats. Sandy loam, characteristic of the mudflat, contained the highest percentage of sand content, whereas in the mangroves, loam and sand were present in approximately equal proportions. Moreover, the substratum of the mangrove contained proportionally twice as much clay as the substratum of the mudflat (Table 1). The difference in the sediment

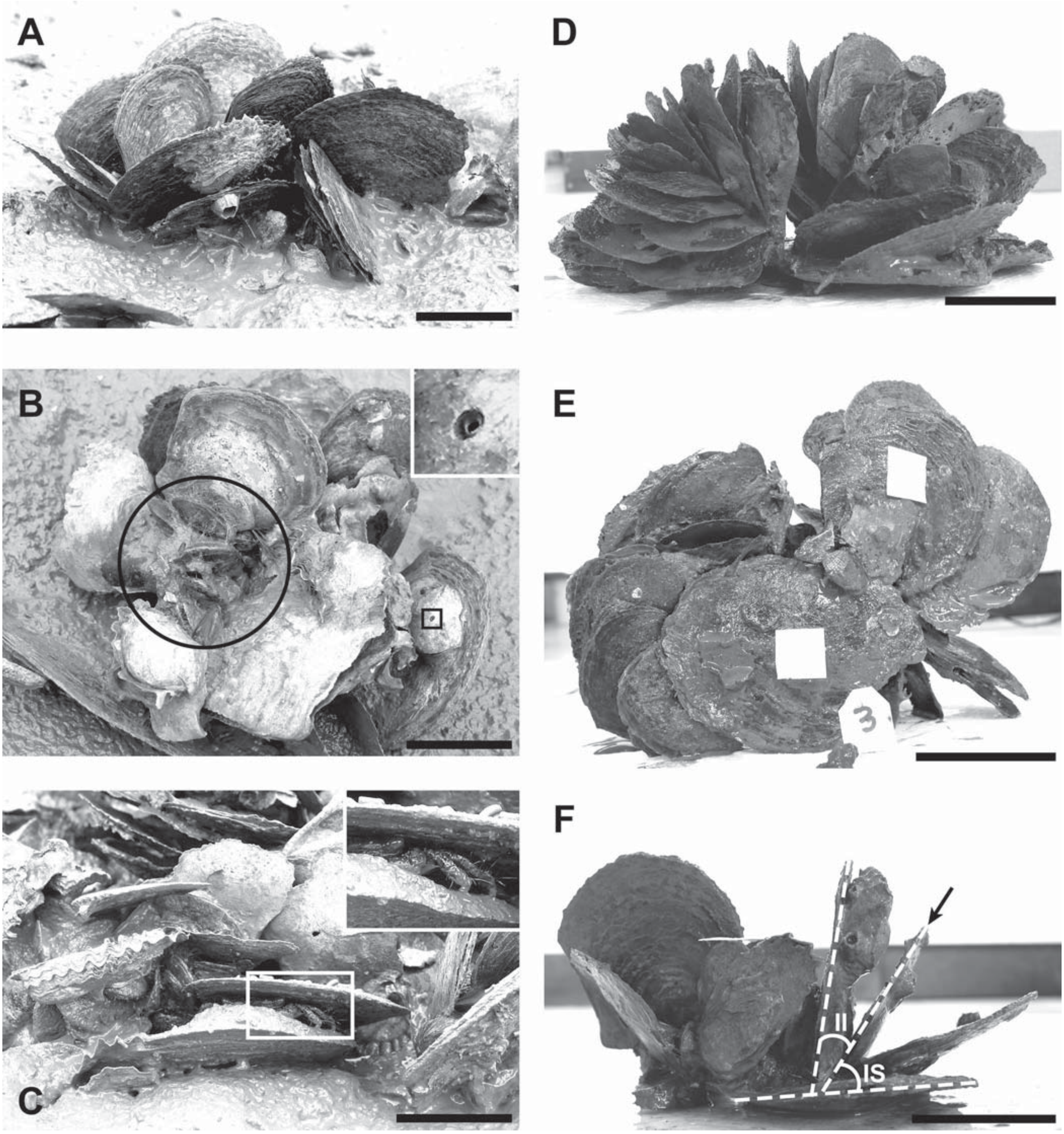

Fig. 6. Mudflat *Isognomon*: A, Characteristic cluster ("clump") showing orientation of the shells in situ; B, top view of the clump pulled apart to show the lattice of byssal attachments formed by mytilids (circle) [inset = magnified muricid drill hole (square) on the exterior surface of an *Isognomon* shell]; C, side view of a clump showing crevices (formed by *Isognomon* shells arranged in parallel) inhabited by a crab (square; see also inset); D, side view an isolated and cleaned clump, showing the arrangement of isognomonid shells; E, ventral view of same sample as D, showing two large dead shells (white squares) that form the base of the clump; F, posterior view of an individual (arrow) illustrating the method of measuring the angle of inclination relative to the basal shell (IS) and to a neighbouring individual (II). Scale bars ca. 50 mm.

Table 1. Physical parameters of the environment of the mudflat and mangrove habitats of Kungkrabaen Bay (n = 3).

Physical factor	**Mudflat** (Mean ± SD)	**Mangrove** (Mean ± SD)
pH of water	6.7 ± 0.5	6.3 ± 0.3
Water temperature (ºC)	28.3 ± 1.0	29.5 ± 0.1
Salinity (‰)	24.7 ± 0.6	21.0 ± 1.0
Sediment composition	sandy loam	loam
Sand (%)	55.7 ± 4.2	41.7 ± 1.2
Loam (%)	36.0 ± 3.5	43.3 ± 3.1
Clay (%)	8.3 ± 1.2	15.0 ± 2.0

Table 2. Shell measurements and orientation of *Isognomon* on right valve in different habitats. * = significant difference, p < 0.05. AM, site of insertion of the accessory pedo-byssal retractor muscle; HS, maximum shell height; IS, individual-substrate angle; II, individual-individual angle, II; LH, maximum hinge length; LS, maximum shell length; PRM, middle part of anterior surface of the posterior pedo-byssal retractor muscle.

Shell characteristics	**Habitat**	
	Mudflat (Mean ± SD)	**Mangrove** (Mean ± SD)
Shell size		
HS (mm) *	74.2 ± 12.3	58.9 ± 5.9
LS (mm) *	71.5 ± 9.1	56.0 ± 5.8
LH (mm) *	33.1 ± 5.8	22.0 ± 2.5
Shell thickness		
AM (mm) *	1.28 ± 0.68	2.17 ± 0.56
PRM (mm) *	0.91 ± 0.36	1.85 ± 0.39
Orientation		
II (°) *	23.3 ± 8.5	32.5 ± 13.0
IS (°) *	6.7 ± 4.9	39.4 ± 12.2

composition accounts for higher density of the substratum in the mangrove than in the mudflat.

Species discrimination. **–** Isognomonid bivalves were the most abundant molluscan species of both the forest and mudflat zones of the mangrove ecosystem of Kungkrabaen Bay (Figs. 1–2). Separated initially by habitat, the two populations displayed substantial morphological differences and were definitively quantitatively distinguished based on the robust results of the morphometric analysis of linear shell measurements of the shell. All measured parameters showed statistically significant differences (Table 2). These data indicated that the individuals of the mudflat population were significantly larger (by about 1.5 times) but nearly twice as thin as their mangrove neighbours. Importantly, there were no instances of shells of the mudflat morphotype being found in the mangrove zone (either attached to the trees or on the substratum) and vice versa.

The structure and the organisation of the byssus – a distally widening fan of discrete byssal fibers terminating in flat adhesive discs – were essentially similar in the mudflat and mangrove individuals but in the former the fan was much wider and more laterally compressed (Fig. 5). Although the number of byssal threads was not counted, the byssal characteristics (diameter ratio and stem length) significantly differed between the two populations (Table 3, Fig. 5).

Consistent discrete differences in features of soft anatomy, including the stomach and the mantle edge, were also detected between the two populations (Tëmkin & Printrakoon, unpubl. data), a fact that, together with the evidence discussed above, provides grounds for provisionally distinguishing the two morphotypes as distinct species. For the sake of convenience and to avoid hurried taxonomic decisions, in the foregoing discussion the species are referred to here as the "mudflat" and the "mangrove" *Isognomon*. Because each morphotype was restricted to its habitat and there were no other isognomonid species in the surveyed area, such indiscriminate usage of "*Isognomon*" is not going to cause confusion when applied to both species. A detailed treatment of anatomy and taxonomy is beyond the scope of this work and will be presented elsewhere (Tëmkin & Printrakoon, in prep.).

Spatial structure of the communities. **–** (Table 4) This section subsumes the discussion of substratum attachment and spatial organisation because these two aspects are intimately interrelated.

Mudflat (Fig. 6): On the mudflat, all *Isognomon* individuals were aggregated into tightly packed clusters maintained

Table 3. Byssal characteristics of mudflat and mangrove *Isognomon* (n = 50). BB, byssal breadth; BDR, byssal diameter ratio [ratio of the longest (L) and shortest (W) dimensions of cross-sections of the byssal stem]; BTL, length of the most extensive byssal thread; BSL, byssal stem length; L, length; W, width. * = significant difference, p < 0.05.

Byssal characteristic	**Mudflat** **Mean ± SD (min–max)**	**Mangrove** **Mean ± SD (min–max)**
Stem length (cm) *	1.92 ± 0.15 (1.80–2.20)	0.92 ± 0.32 (0.63–1.67)
BB (cm) *	4.03 ± 0.65 (3.71–4.60)	2.94 ± 0.26 (2.60–3.40)
Byssal length (cm) *	1.69 ± 0.43 (1.03–2.65)	0.97 ± 0.28 (0.57–0.14)
BDR L (mm); W (mm)	2.0 ± 0.65 (0.26–0.37; 0.10–0.23)	1.6 ± 0.23 (0.26–0.43; 0.17–0.27)

by byssal attachments as individual clumps. On average, there were ten (mean 10.63 ± 4.4 individuals, n = 27) *Isognomon* individuals per clump but this number ranged from 4 to 24 individuals. The clumps had a particular, albeit not fixed, structure. Typically a single large shell or a few dead shells (83–113 mm shell height; Fig. 6E) lying horizontally formed the base upon which a core of several other individuals positioned themselves side by side with their shell commissures parallel to each other (Fig. 6D). Other individuals in a clump were frequently placed at angles up to 90° relative to the core individuals. Few clumps showed a regular, fan-wise arrangement of isognomonid shells because other shells (including those of other species) were attached more or less irregularly to the periphery of the clump and within the crevices formed by the core shells (Figs. 6A–B, F). The isognomonid shells within the clump were densely packed: the neighbouring shells were placed at a sharp average angle of 23° (mean 23.3 ± 8.5°, range 14.5–39.4°, n = 17). The shells on the periphery of the clumps were nearly horizontal to the substratum (mean 6.7 ± 4.9°, range 0–14.7°, n = 17). Occasional juveniles were always pleurothetic on the right valve attached to larger individuals. The entire structure, amalgamated by the network of byssal attachments (or isognomonids themselves and, particularly, of small mytilids wedged between; Fig. 6B), cementing ostreids, and compacted sediment, composed an integrated whole that could easily be isolated in its entirety. The clumps were positioned at the surface of the muddy substratum, so that the individuals were largely at or above the water-sediment interface, the exception being the basal (typically dead) individuals that were completely or partially buried in the mud.

Mangrove (Fig. 7): In the mangroves, most individuals formed small clusters (mean 3.9 ± 3.0 individuals, n = 71), ranging from 2 to 17 individuals attached (sequentially with their shell commissures parallel to each other) to prop roots of *Rhizophora apiculata* or wedged into the crevices formed by the upside-down forks of the prop roots (Figs. 7A, D). On average, the clusters were separated by 30 cm (mean 29.0 ± 17.9 cm, range 9–88 cm, n = 20). The average angle formed by two neighbouring individuals was 32.5° (mean 32.5 ± 13.0°, range 13.5–53.8°, n = 17). Individuals of the mangrove *Isognomon* attached to the prop roots at variable heights ranging from the level of the substratum to a maximum height of 35 cm (mean 16.3 ± 7.9 cm, range 0–35 cm, n = 77). Solitary individuals typically attached with the plane of commissure at a low angle, averaging 39.4° (mean 39.4 ± 12.2°, range 13.5–53.8°, n = 17) and reclining exclusively on the right valve (Fig. 7C). Occasional juveniles were always pleurothetic on the right valve attached either to the larger shells or the surface of prop roots (Fig. 7D, inset). Occasional single individuals were found attached by the byssus to the dead shells lying in the sediment underlying the mangrove trees. In no cases did individuals in the mangrove zone form clumps on the substratum.

Population density and biomass. – (Table 4) Comparison of the measurements of density between total density (mean 105.0 ± 43.65 individuals/m^2, range 48–192 individuals/m^2) and the density of dead individuals alone (mean 37.6 ± 21.6 individuals/m^2, range 6.67–76.00 individuals/m^2) on the mudflat showed that nearly half of the individuals of *Isognomon* in a clump were dead. That is, their shells remained attached, retained as structural components of the clump. The clumps were relatively densely distributed (mean 10.5 ± 1.5 clumps/m^2, range 4–12 clumps/m^2) at an average shortest distance of 23.5 cm (mean 23.5 ± 7.9 cm, range 10–38 cm) from each other. The high population density of living individuals (mean 57.5 ± 50.2 individuals/m^2, range 9–168 individuals/m^2, n = 8) accounted for a substantial measure of the biomass (mean 358.9 ± 37.0 g/m^2, range 337.0–411.0 g/m^2, n = 8) on the mudflat.

The comparison of the measurements of density between total density (mean 15.0 ± 11.15 individuals/m^2, range 4.9–36.5 individuals/m^2) and the density of dead individuals alone (mean 2.8 ± 1.9 individuals/m^2, range 0.8–6.7 individuals/m^2) in the mangroves showed that the proportion of dead individuals was extremely high. The shells of dead individuals concentrated on the substratum and no empty (dead) shells were found attached to the prop roots. This contrasted sharply with the situation on the mudflat, where dead shells were retained in the cluster. The relatively low density of living individuals (mean 12.2 ± 11.7 individuals/m^2, range 3.77–35.7 individuals/m^2) accounted for the comparatively low measure of biomass (mean 20.9 ± 5.3 g/m^2, range 14.91–21.28 g/m^2, n = 8).

The number of individuals per cluster, density (of both living and dead individuals), and biomass of the mudflat *Isognomon* greatly exceeded those of the mangrove *Isognomon*, the difference being statistically significant. With regard to the distribution of the two populations, it is noteworthy that no co-occurring living or dead individuals of the mudflat

Table 4. Ecological characteristics of mudflat and mangrove *Isognomon*. * = significant difference, $p < 0.05$.

Ecological characteristic	**Mudflat** **Mean ± SD (min–max)**	**Mangrove** **Mean ± SD (min–max)**
Total density (individuals/m^2)* (n = 8)	105.0 ± 43.7 (48–192)	15.0 ± 11.5 (4.9–36.5)
Density of living individuals (individuals/m^2)* (n = 8)	57.48 ± 50.2 (9.3–168.0)	12.22 ± 11.65 (3.8–35.7)
Density of dead individuals (individuals/m^2)* (n = 8)	37.6 ± 21.6 (6.7–76)	2.8 ± 1.9 (0.9–6.7)
Density of clusters (clusters/m^2) (n = 8)	10.5 ± 1.5 (4–12)	8.9 ± 5.0 (6–20)
Biomass (g/m2)* (n = 8)	358.9 ± 37.0 (337.0–411.0)	20.9 ± 5.3 (14.91–21.28)
Individuals/cluster *	10.6 ± 4.4 (4–24) (n = 27)	3.9 ± 3.2 (1–17) (n = 102)
Distance between clusters (cm)	23.5 ± 7.9 (10–38) (n = 20)	29.0 ± 18.0 (9–88) (n = 24)
Distance from ground (cm)	0	16.3 ± 7.9 (0–35) (n = 77)

and mangrove *Isognomon* (distinguished by morphological criteria as discussed above) were observed.

It must be noted that the observations on the population density of *Isognomon* individuals in the two study sites cannot be extrapolated to the entire mangrove ecosystem of Kungkrabaen Bay without reservations. Although no quantitative assessment of large-scale distribution of *Isognomon* was attempted in this study, we noted that the distribution of *Isognomon* clumps in the mudflat zone was patchy. Potential reasons for such non-uniform distribution include topography of the substratum, and direction of currents and tidal waves. No apparent patchiness in the distribution of the mangrove *Isognomon* was noted but, admittedly, this is more difficult to evaluate without a quantitative study.

Associated fauna. **–** (Table 5) The macroinvertebrate faunas associated with the *Isognomon*-dominated habitats are listed in Table 5. Seven gastropod species were found in total. Of these, *Nerita lineata* Gmelin, 1791*, Littoraria pallescens* (Philippi, 1846)*, L. articulata* (Philippi, 1846), and *Cerithidea obtusa* (Lamarck, 1822) were attached to the trunks or prop roots of *Rhizophora* sp., whereas *Clypeomorus pellucida* (Hombron & Jacquinot, 1852) and *Assiminea* sp. were found on the substratum beneath the mangrove trees. On mudflats, three species were identified: *Cerithidea cingulata* (Gmelin, 1791)*, Nassarius* sp., and *Chicoreus capucinus* (Lamarck, 1822). *Chicoreus capucinus* was the only gastropod species inhabiting both microhabitats.

Infaunal bivalves underlying the *Isognomon* clumps in the mudflats consisted of the venerids *Anomalocardia squamosa* (Linnaeus, 1758) and *Gafrarium pectinatum* (Linnaeus, 1758). The dominant epifaunal bivalves byssally attached to the surfaces and invading the crevices formed by *Isognomon* shells in the clumps were the mytilids *Brachidontes pharaonis* (P. Fischer, 1870), *B. striatularis* (Lamarck, 1819)*, Modiolus* sp., and *Xenostrobus* sp. Other sympatric mudflat bivalves included *Placuna sella* (Gmelin, 1791), typically reclining on one valve or partially buried in the mud, and various ostreids, cemented to the exterior shell surface of *Isognomon* (Fig. 12B).

The mangrove crab and mangrove hermit crab (*Diogenes* spp.) were found actively moving in both habitats (Fig. 6C). The barnacle *Euraphia* sp. (Fig. 6A) was frequently found attached to the exterior surface of the mudflat *Isognomon*, whereas the tube worm *Pomatoleios* sp. formed large colonies encrusting the surface of the shells of the mangrove *Isognomon* (Figs 7B, 8).

Overall, 48% of the associated macroinvertebrate species were present in both the mangrove and mudflat zones.

Predation. **–** Drill-hole morphology: Two types of drill holes were observed in the present study. The first type was characterised by a relatively large (approximate outer diameter 1.8 mm, n = 5) opening, circular or oval in cross section, with cylindrical or slightly conical (decreasing in diameter down the bore axis, perpendicular to the external shell surface) sides, and the outer edge frequently beveled (Figs. 6B, 8, 10D). The edges of the drill holes typically appeared bleached (lighter coloured relative to the shell surface) and smooth at the macroscopic level. This morphology is consistent with the drill-hole characteristics documented for muricid and naticid gastropods (Carriker & Yochelson, 1968; Kowalewski, 1993, 2004; Jonkers, 2000).

The second type of drill hole was characterised by a branched network of small (approximate outer diameter 5 µm, n = 10) tunnels, circular to crescent-shaped in cross section, extending in various directions relative to shell surface and frequently parallel to it (Fig. 9). The interior surfaces of these holes

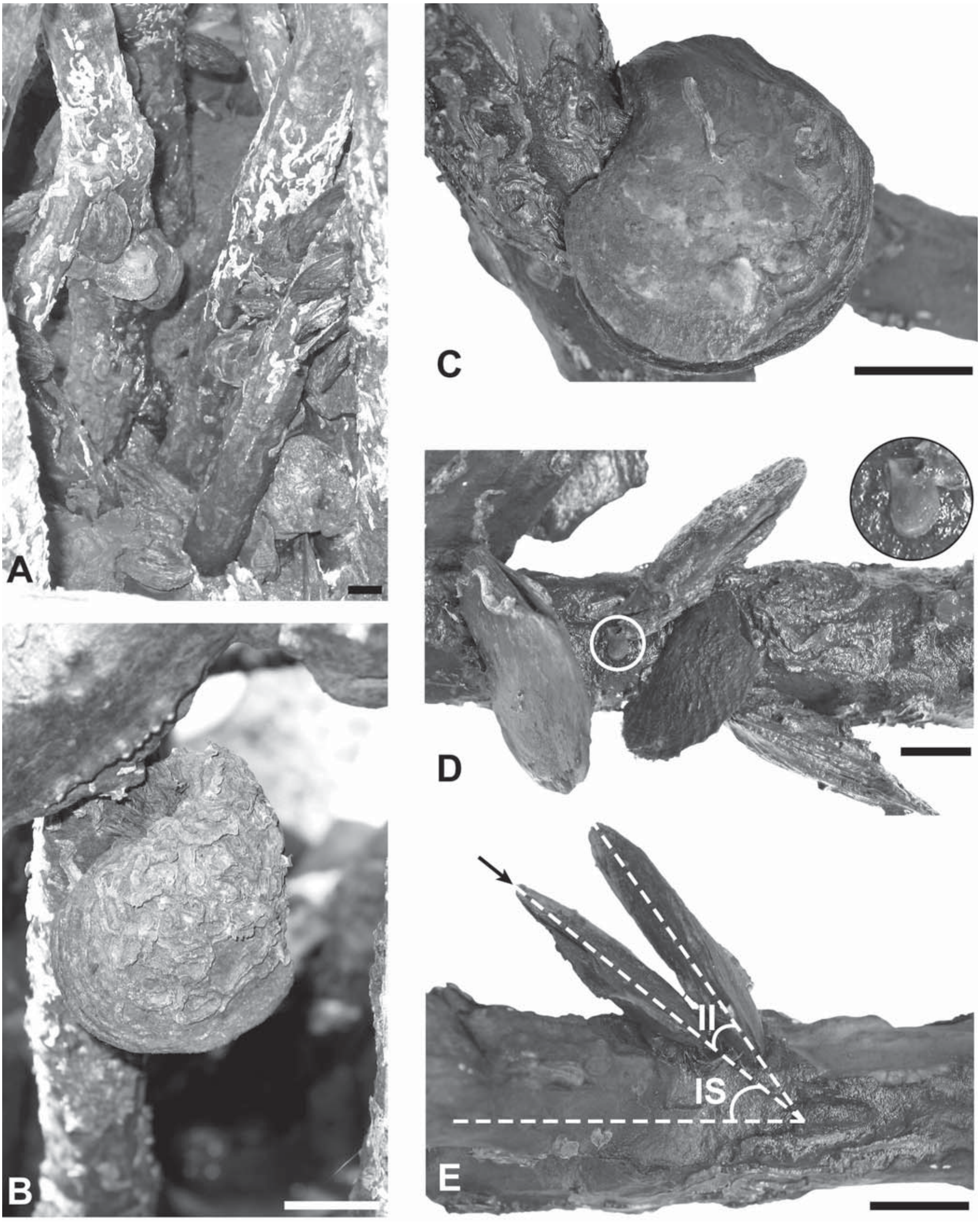

Fig. 7. Mangrove *Isognomon*: A, Characteristic distribution of colonial individuals in crevices formed by forks of prop roots of *Rhizophora apiculata* in situ; B, a solitary individual; C, view of attachment showing the fit of the convex surface of the prop root and the concave anterior margin of the shell; D, lateral view of a prop root showing the pleurothetic position of the shells [inset = juvenile individual (circle) completely pleurothetic on the right valve]; E, anterior view of an individual (arrow) illustrating the method of measuring the angle of inclination relative to the prop root (IS), and to a neighbouring individual (II). Scale bars ca. 20 mm.

Table 5. Most abundant macroinvertebrate species associated with mangrove and mudflat habitats of Kungkrabaen Bay. +, present; –, absent.

Family	Species	Mudflat	Mangrove
Gastropoda			
Potamididae	*Cerithidea cingulata* (Gmelin, 1791)	+	–
Muricidae	*Chicoreus capucinus* (Lamarck, 1822)	+	+
Nassariidae	*Nassarius* sp.	+	–
Neritidae	*Nerita lineata* Gmelin, 1791	–	+
Littorinidae	*Littoraria pallescens* (Philippi, 1846)	–	+
Littorinidae	*L. articulata* (Philippi, 1846)	–	+
Potamididae	*Cerithidea obtusa* (Lamarck, 1822)	–	+
Cerithiidae	*Clypeomorus pellucida* (Hombron & Jacquinot, 1852)	–	+
Assimineidae	*Assiminea* sp.	–	+
Bivalvia			
Veneridae	*Anomalocardia squamosa* (Linnaeus, 1758)	+	–
Veneridae	*Gafrarium pectinatum* (Linnaeus, 1758)	+	–
Mytilidae	*Brachidontes pharaonis* (P. Fischer, 1870)	+	+
Mytilidae	*Braciodontes striatularis* (Lamarck, 1819)	+	+
Mytilidae	*Modiolus* sp.	+	–
Mytilidae	*Xenostrobus* sp.	+	+
Placunidae	*Placuna sella* (Gmelin, 1791)	+	+
Crustacea			
Diogenidae	*Diogenes* sp.	+	+
Balanidae	*Euraphia* sp.	+	–
Polychaeta			
Serpulidae	*Pomatoleios* sp.	–	+

appeared to have a smooth lining, possibly secreted by the burrower. When such drill holes penetrated the isognomonid shells completely, they frequently caused elongated blisters of various sizes on the interior surface of the host valves, affecting both nacreous and prismatic areas (Fig. 9). This drill-hole morphology and associated blisters correspond to boring by polychaete worms or sponges (Dharmaraj et al., 1987), but in the present study the identity of the burrower was not verified. Shell drilling by polychaetes and sponges, although detrimental to the host, is not predatory and, therefore, is excluded from the analysis of predation but is discussed in the section on fouling.

Observations of predation in situ (Fig. 10): The muricid gastropod *Chicoreus capucinus* was the only predator observed in the process of feeding on both mangrove and mudflat *Isognomon*. The fact that the attachment of the gastropod to a bivalve shell was not merely co-occurrence was verified by removing the gastropod and detecting a completely drilled hole underneath (Fig. 10C, D).

Predation frequency (Table 6): Predation here refers exclusively to the drilling associated with the activity of predatory gastropods and excludes morphologically distinct drilling by polychaetes. The incidence of drilling predation was significantly higher in the mangrove *Isognomon* than in the mudflat *Isognomon* ($\chi^2 = 16.45$, $p < 0.001$). The relative success of predation, however, was significantly lower in mangroves compared to that in the mudflats ($\chi^2 = 7.90$, $p < 0.01$). The incidence of predation did not show a significant

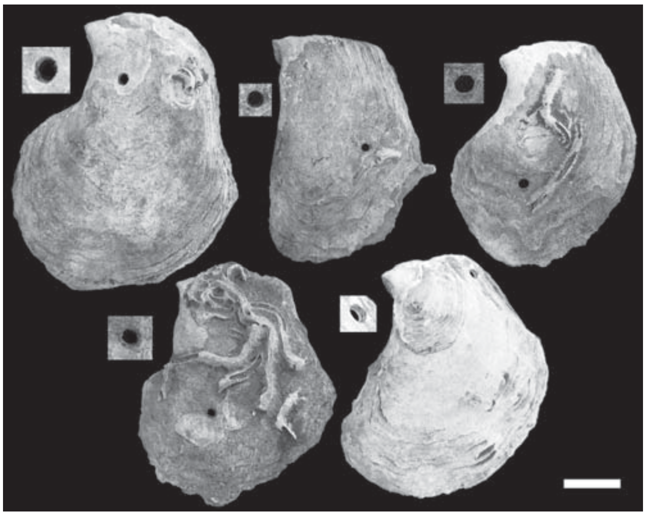

Fig. 8. Muricid drill holes in a sample of left valves of mangrove *Isognomon*, with magnified views of the exterior openings of the drill holes. Scale bar = 1 cm.

Table 6. Incidence of complete and incomplete drilling in mudflat and mangrove *Isognomon*. Predation success was measured as incidence of complete (C) and incomplete (I) drill holes, scored for random samples of equal sizes for living and dead individuals, and noting whether they occurred in the right (RV) and left (LV) valves. n = number of individuals (pairs of valves).

Mudflat

Predation success	Living (n = 50)		Dead (n = 50)		Total (%)
	LV	RV	LV	RV	
I	0	0	1	1	2 (2%)
C	1	0	5	5	11 (11%)
Total	1	0	6	6	13 (13%)

Mangrove

Predation success	Living (n = 50)		Dead (n = 50)		Total (%)
	LV	RV	LV	RV	
I	8	9	3	3	23 (23%)
C	0	0	13	2	15 (15%)
Total	8	9	16	5	38 (38%)

difference between the right and left valves for either population, but there was a bias towards higher frequency of drill holes in the left valve in the sample of dead shells of the mangrove *Isognomon*.

No single prominent pattern of drill-hole distribution on the surfaces of the valves was detected (neither complete nor incomplete), except for a low incidence of drill holes along the ventral margins. This pattern of preferential drilling away from the ventral shell margins is corroborated by previously reported observations on *Isognomon legumen* (Gmelin, 1791) (Harper & Morton, 1994) and other bivalves (Guerrero & Reyment, 1988; Jonkers, 2000). Most drill holes were distributed in the area overlying the visceral mass, the gills, and attachment areas of the adjacent posterior adductor and posterior pedo-byssal retractor muscles. Also, in the mangrove sample, complete drill holes were located more centrally, away from valve margins, whereas incomplete drill holes were predominantly distributed along the periphery of the shell, particularly along the curve of the byssal notch in the right valve (Fig. 11). A maximum of one drill hole per valve was present in the mudflat *Isognomon*, whereas up to three holes per valve were detected in the mangrove *Isognomon*. In cases when multiple holes were present in a single valve, only one was complete. No edge drilling was detected. The concentration of drill holes in the region of the shell overlaying the soft tissues and the typical presence of a single hole per valve suggest selection of a drilling position on the part of the gastropod predator, an observation consistent with previous laboratory studies (reviewed by Carriker & Yochelson, 1968).

The presence of complete drill holes showed a statistically significant association with mortality ($\chi^2 = 22.97$, $p < 0.001$) for the entire sample. There was no significant difference between the mangrove and mudflat samples in that respect.

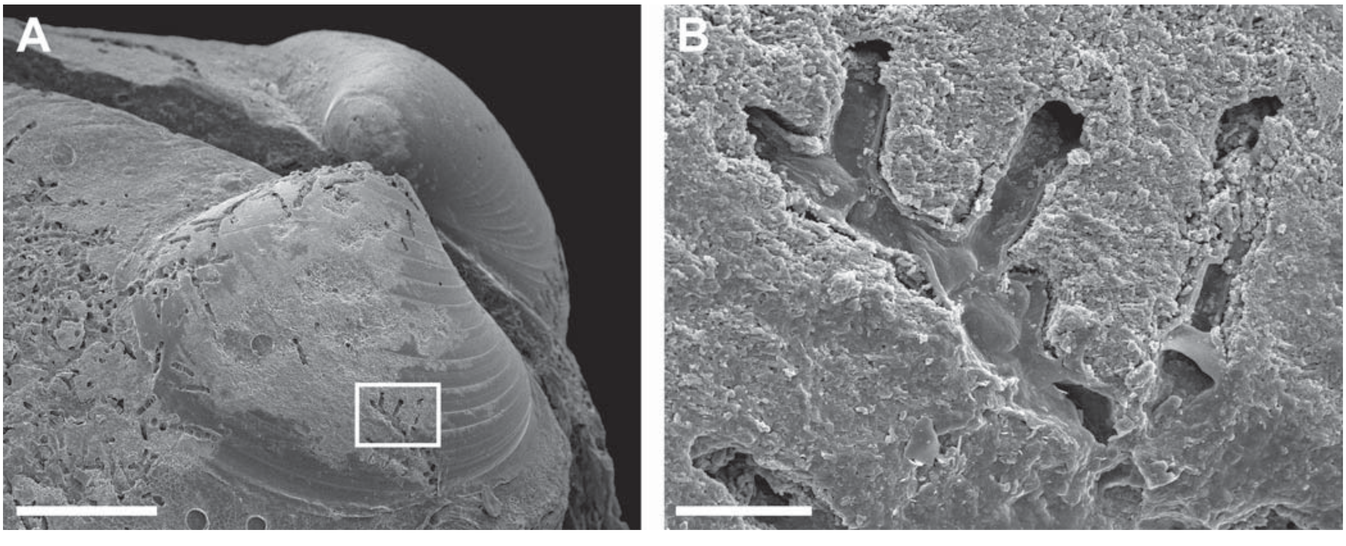

Fig. 9. Drill holes of unidentified borer in the prodissoconch and surrounding area of the right valve of an individual mudflat *Isognomon* (SEM): A, lateral view showing the density of perforations and the varying direction of the tunnels; B, close-up of square area in A showing the branching drill hole lined with possibly secreted organic matrix. Scale bars: A = 100 µm; B = 10 µm.

Table 7. Incidence of major fouling organisms on mudflat and mangrove *Isognomon* and the incidence of blisters (presumably resulting from the activity of boring polychaetes or sponges) observed on the inner surfaces of *Isognomon* valves. n = number of living individuals (articulated valves).

Type of Fouling	**Mangrove (n = 50)**		**Total (%)**	**Mudflat (n = 50)**		**Total (%)**
	LV	RV		LV	RV	
Cementing ostreids	3	4	7 (7%)	20	14	34 (34%)
Tubicolous polychaetes	46	47	93 (93%)	2	3	5 (5%)
Barnacles	0	1	1 (1%)	2	5	7 (7%)
Blisters	7	9	16 (16%)	18	18	36 (36%)

Fouling. **–** The differences in the incidence of fouling by cementing ostreids, serpulid polychaetes, and barnacles between mangrove and mudflat *Isognomon* were all statistically significant (Table 7). Fouling by bryozoans and sponges was noted in only a few instances. The most predominant fouling organisms in the mangrove *Isognomon* were serpulid polychaetes, the tubes of which were cemented to 93% of the valves scored. In comparison, the proportion of *Isognomon* valves with serpulid attachment in mudflats (5%) was negligible. On the other hand, the incidence of cementing ostreids was substantially higher in the mudflats. The difference in the incidence of barnacle fouling, although it did not differ greatly, was nevertheless statistically significant, being more frequent in the mudflat *Isognomon*. The incidence of blisters (whether ruptured or not; Fig. 12A) on the interior of valves and attributed to the activity of unidentified polychaetes, was significantly higher in the mudflats.

DISCUSSION

Our study clearly demonstrated that the adjacent mudflat and forest zones of the mangrove ecosystem Kungkrabaen Bay provide mutually exclusive habitats for two previously unrecognized, totally parapatric, morphologically distinct populations of isognomonid bivalves. The mangrove and mudflat *Isognomon* populations showed significant differences in spatial community structure, adaptive strategies for physical stabilisation, and response to predation and fouling. Alternative solutions to the problem of co-optimisation of physical stabilisation and defense against predation illustrate a complex interplay of ecological opportunity and constraints on phenotypic expression.

Abiotic factors. **–** Amongst examined abiotic factors, only the sediment composition significantly differed between the mangrove and mudflat habitats. This difference is responsible for the dissimilarity in density of the underlying substrata: due to the presence of a higher percentage of clay, a denser substratum provides sufficient support for anchoring prop roots of the mangrove trees, which, in turn, form the principal attachment substratum for the mangrove population of *Isognomon*. The softer substratum of the mudflat provides a considerably different environment for epifauna and demands a different suite of morphological adaptations for physical stabilisation than the more compacted substratum of the mangroves.

Physical stabilization. **–** Many aspects of shell morphology in epifaunal bivalves are associated with attachment and physical stabilisation in diverse ecological settings (Stanley, 1970, 1972; Seilacher, 1984). The differences in shell morphology between the mangrove and mudflat isognomonids can readily be interpreted in functional morphological terms of optimising attachment and stabilisation to their respective substrata.

The absence of siphons exerts a major constraint on the ecological opportunities of *Isognomon*, confining members of the genus (as well as the entire superfamily Pterioidea J. E. Gray, 1847 [1820]) to epifaunal habitats. Remaining at or above the water-sediment interface is critical to this group of bivalves for efficient filtration. Expansion of the surface area of the valves in pleurothetic bivalves (including isognomonids) to form ballast has previously been considered to be a stabilisation mechanism in soft sediment with low sedimentation rates (Seilacher, 1984). This strategy ("stable reclining" combined with orthothetic vertical recliners) is amongst the most widespread adaptations for stabilisation that has evolved polyphyletically in a number of secondary soft-bottom dwelling invertebrates (Seilacher, 2005).

The extreme flatness and thinness (and, consequently, low weight), and significantly larger surface area in the mudflat *Isognomon* provide sufficient stability to prevent sinking into the soft sediment. These characteristics also facilitate the assembly of the cluster: the large shell size provides a large surface area for attachment of conspecifics and other epibionts, whereas the thinness allows for denser packing of individuals within a clump. Each cluster examined contained one (rarely two) basal "founder" individual(s), typically a large dead shell lying flat on the surface of the mud or slightly buried beneath. Other shells were attached to it in orthothetic orientation, so that the incurrent and excurrent gapes were elevated as dorsally as physically possible. Stability was maintained by tight packaging of neighbouring individuals, which is most effective when valves are oriented parallel to each other. Other epibionts, particularly ostreid and mytilid bivalves, contributed further to maintenance of the cluster integrity by, respectively, cementing to the shells and binding them together by a lattice of byssal threads. Thus, the aggregation of multiple individuals into larger clumps further enhanced the ability of these bivalves to stay at the surface by providing a stable, non-sinking, horizontal attachment site for a physiologically beneficial pleurothetic orientation.

Individuals of the mangrove *Isognomon* are characterised by a broadly rounded and wide concavity of the anterodorsal margin of the expanded anterodorsal portion of the shell with a wide and nearly symmetrical byssal gape that fits the convex surface of mangrove prop roots. Such shell morphology maximises the surface of the contact area between the anterior portion of the shell and the byssus on one hand, and the limited area of the prop root surface on the other. The short byssus ensures a rigid attachment to the prop root. The forks of prop roots provide particularly stable attachments sites and were nearly always filled by one or several individuals. The somewhat more inflated and significantly thicker shell of the mangrove *Isognomon* enhances the contact area between the shell and the substratum but, at the same time, precludes the formation of tightly packed clusters, as evidenced by significantly larger angles formed by the valves of adjacent individuals.

Spatial structure of the communities. – The difference in spatial structure of the mangrove and mudflat environments exerts a major influence upon the pattern of distribution and population density of associated biota. In the mudflats, the distribution of individuals of *Isognomon* is limited to the two-dimensional surface of the substratum. In the mangroves, on the other hand, the prop roots of mangrove trees create a three-dimensional space, where vertical distribution was constrained by the surface area of prop roots and the extent of high tides. Despite this major difference, the shortest distances between neighbouring clusters in the two habitats were not significantly different. Population density, on the other hand, was nearly ten-fold higher in the mudflats than in the mangroves. There are several interrelated reasons that might collectively account for the observed difference. With rare exceptions, most living individuals of the mangrove *Isognomon* were found attached to the prop roots, suggesting

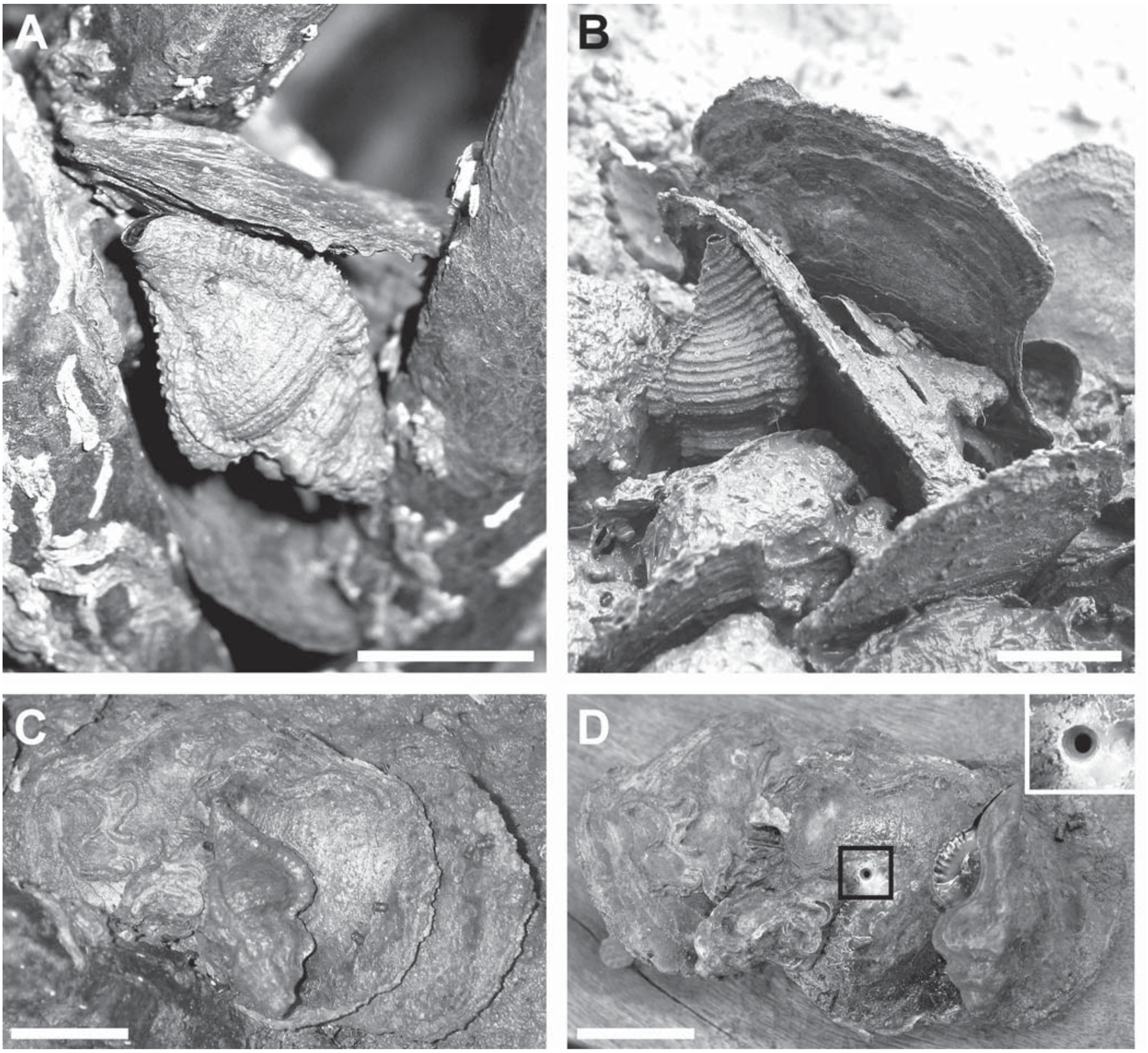

Fig. 10. Predation by the muricid gastropod *Chicoreus capucinus* on *Isognomon* in situ in mangrove (A, C) and mudflat (B) habitats; D, Same specimen as C with predator removed, showing the complete drill hole (square), magnified in inset. Scale bars ca. 25 mm.

that their habitat is largely restricted to the limited surface of prop roots. Moreover, one of the most suitable areas for attachment were the clefts of prop roots, which are too narrow to accommodate a large number of individuals, thus being another factor limiting the size of the clusters. This hypothesis is supported by the fact that the number of individuals in clusters attached to prop roots was significantly smaller than the number of individuals comprising a clump on the mudflat. In addition, the thinner and somewhat more flattened shells of mudflat *Isognomon* allowed for tighter packaging of individuals within a clump (and, hence, population density) as evidenced by statistically significantly lower angles formed

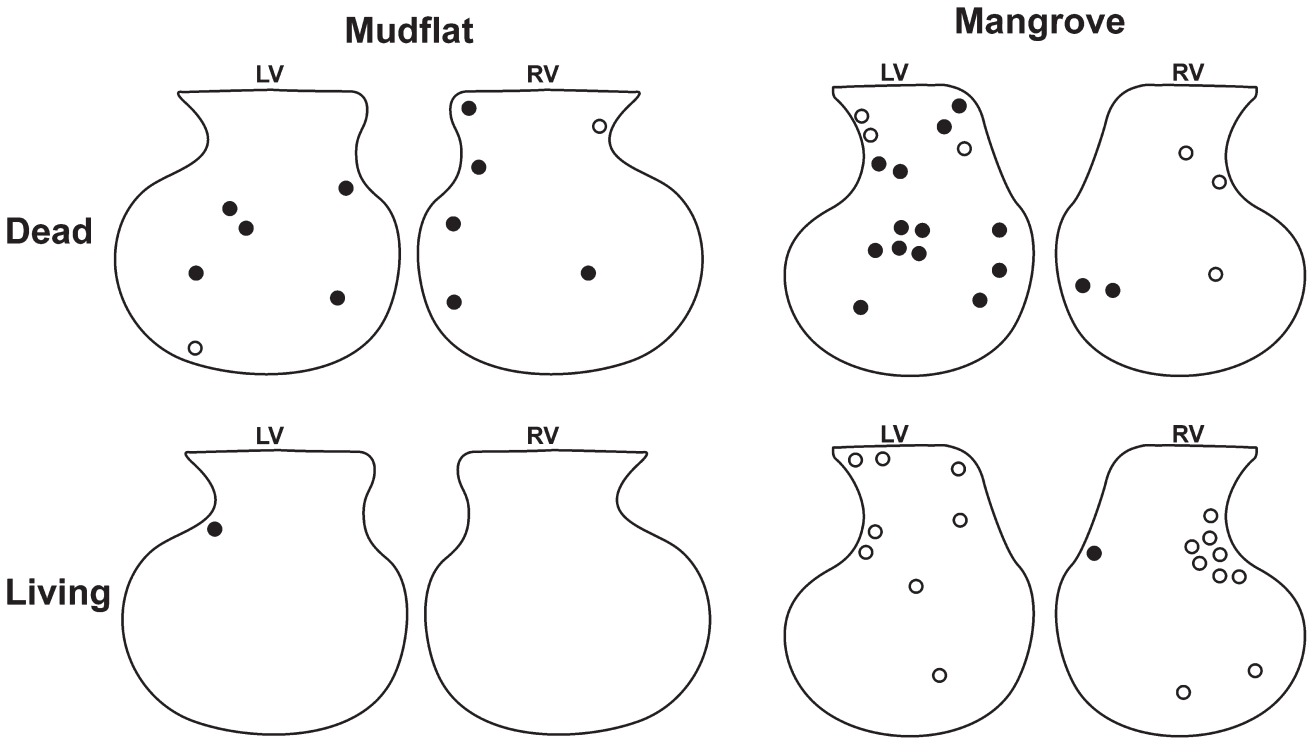

Fig. 11. Diagrammatic views of the generalized exterior surfaces of right (RV) and left (LV) valves showing muricid drill hole locations in living and dead individuals of mudflat and mangrove *Isognomon*. Filled circles represent complete drill holes; empty circles represent incomplete drill holes.

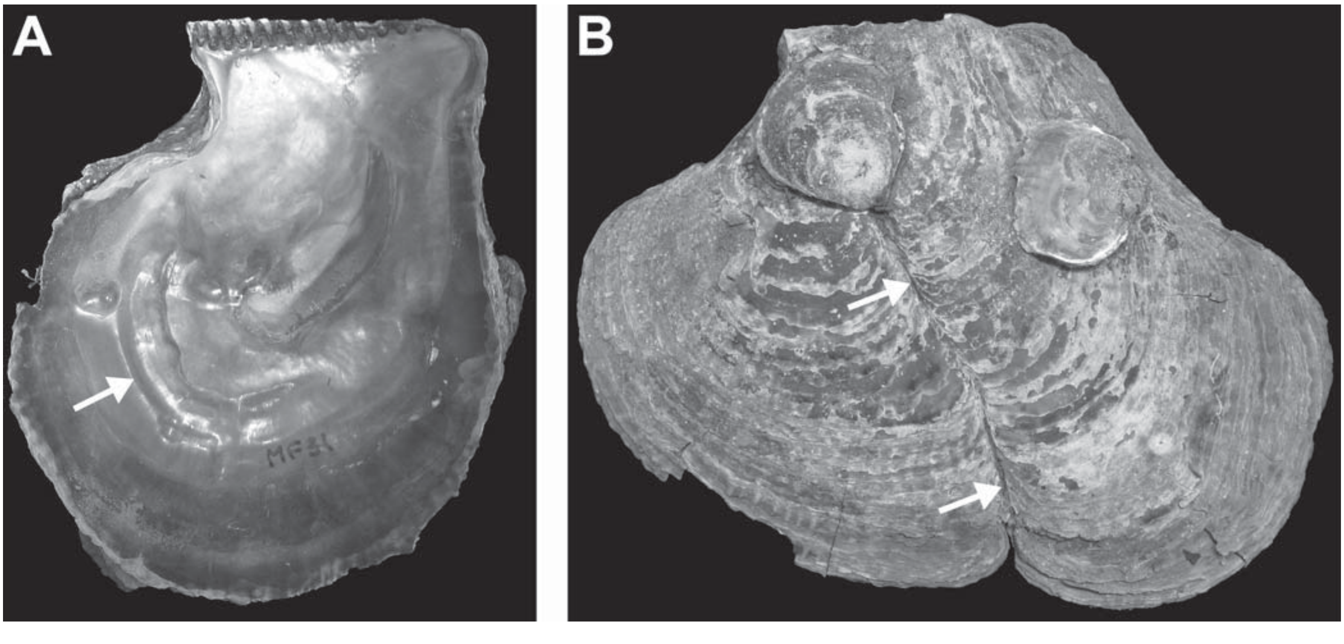

Fig. 12. Examples of teratologies in mudflat *Isognomon*: A, Interior surface of a right valve showing an extensive blister (arrow) underlying the nacreous layer that developed as a result of the activity of boring polychaetes (62 mm); B, exterior surface of a left valve showing remarkable recovery from extensive damage (arrows), which potentially represents an instance of crushing predation (156 mm). Also note two cemented ostreids attached to the valve.

by adjacent individuals. Although it is difficult to compare quantitatively the areas suitable for attachment between the prop roots and mudflats, it is certainly more limited in the mangroves. Additionally, the number of *Isognomon* individuals attached to the shells of other *Isognomon* individuals in a cluster in the mangroves was smaller because a large number of shells attached to each other would likely be too heavy and fall off the tree (especially upon periodic agitation by tidal waves), a situation further aggravated by thicker and heavier shells of the mangrove *Isognomon*. In fact, upon death of an individual in the mangroves, its shell falls under its own weight, accumulating under the tree, whereas the shells of dead individuals in the mudflats are maintained incorporated into the clump rather than being scattered by tidal waves.

The large-scale organisation of a similar mudflat community from Darvel Bay, Sabah (Borneo), was briefly described by Yonge (1968). This ecosystem, situated on the bottom of a shallow channel with a mud-covered rocky substratum, was dominated by sympatric, very dense populations of the pterioid species *Isognomon isognomum* and *Malleus regula* (Forsskål, 1775). Like the mudflat ecosystem of Kungkrabaen Bay, the aggregation of pterioid shells provided protected habitats for a rich invertebrate fauna (Yonge, 1968), but no particular spatial arrangement of isognomonid shells was reported. It must be noted that the shell morphology of *I. isognomum* (similar to that of *M. regula*) differs substantially from the shells of the *Isognomon* species studied herein, being very narrow to irregularly shaped, and greatly dorsoventrally elongated. It is plausible that species-level morphological differences prevented clump formation in one case but facilitated it in the other.

Physiological consequences. – Reid (1985) suggested that the extreme lateral flattening of *Isognomon ephippium* (found in mudflat areas adjacent to the mangrove forest) is an adaptation for physical stabilisation in an agitated environment that offers a lower resistance to strong currents (given that the shells are oriented with the hinge axis parallel to the flow). He also linked the expansion of the ventral shell margins and the elongation of the shell along the sagittal axis to the increasing area of the gills, thereby enlarging the area of filtration and particle collection. Thus, if the shells are positioned with the hinge axis perpendicular to the shoreline, i.e., in the direction of onshore wave action, this would maximise filtration efficiency as well as minimise drag under the normal conditions of slow longshore drift. The results of the present study are in partial agreement with Reid's conclusions but provide the basis for an alternative hypothesis linking the flatness of *Isognomon* with physical stabilisation and physiological efficiency. The differences are largely due to the fact that the interpretation advanced here incorporates the spatial structure of the mudflat community, whereas Reid's (1985) experiments and observations were conducted on single, isolated individuals of *Isognomon*.

Reid's (1985) hypothesis relies on the particular orientation of *Isognomon* individuals relative to wave action. In the present study, no bias for shell position relative to the shoreline or wave action was observed. Instead, the orientation of the shells appeared to be determined by the arrangement of the shells in an individual clump that maximised the tightness of the packing. Moreover, incorporated in a clump, an *Isognomon* individual is unable to change its position. As discussed above, the clump assembly is a considered here as a means for physical stabilisation. These relatively large structures are unlikely to be disturbed by normal wave action that can present stress for a solitary individual. Thus, the same physical characteristic of the mudflat *Isognomon* shell, namely its extreme flatness, ensures physical stabilisation for both colonial and solitary individuals, albeit by different mechanisms.

Reid (1985) experimentally demonstrated that form drag, created when a shell is positioned at a right angle to the flow (such as longshore drift), maximises turbulence that results in particle resuspension, prolonging food availability to the organism, thereby maximising filtration efficiency. The effectiveness of this strategy also depends upon a specific orientation of the shell. However, as noted by Reid (1985), animals downstream of an individual with its shell oriented normal to the current could benefit from the turbulence regardless of their own placement. In colonial mudflat *Isognomon*, this is likely to be the rule. Because of its three-dimensionality, the clump as a whole presents an impediment to water flow regardless of the direction of the current, so that all of the constituent individuals (regardless of their position) benefit from turbulence. Taking advantage of turbulence is consistent with raising the filtering mechanism above the level of the substratum. It reduces the amount of indigestible slit and provides an opportunity to feed on phytoplankton higher in the water column (Reid, 1985).

Associated biota. – Most invertebrates surveyed in this study can be interpreted as mutualists or commensals relative to the two species of *Isognomon*, transiently or permanently inhabiting the protective microhabitats created by isognomonid clusters. The cursory analysis of sympatric macroinvertebrates revealed that the faunas of the mangrove and mudflat were largely overlapping (48% of associated species were shared by the two habitats). The gastropod fauna was more diverse in the mangroves, whereas the bivalve fauna was more varied on the mudflat. *Isognomon* individuals in both habitats were subject to extensive biofouling by the same organisms, but at significantly different frequencies: in the mudflats, the fouling organisms were mainly cementing ostreids and barnacles, and in the mangroves, largely tubicolous serpulid polychaetes. Although most fouling organisms do not kill their host directly, they negatively affect its growth rate and mortality indirectly by reducing plankton availability, physically interfering with opening and closing of the valves, and exhausting the host's energy, inducing it to secrete additional layers of nacre to seal off the irritant (Dhamaraj et al., 1987; Gervis & Sims, 1992).

The frequency of drilling by polychaete worms was significantly more widespread in the mudflat *Isognomon* species. Although this type of drilling is not directly linked to predation, serving primarily as shelter or, possibly, for deriving shell material (Carriker & Yochelson, 1968), studies on other pterioids of the genus *Pinctada* Röding, 1798 (the shell structure and life mode of which is similar to that of shallow-water isognomonid species) suggest that this type of boring causes considerable damage to the shell, making it more fragile and susceptible to other invaders (Dhamaraj et al., 1987; Gervis & Sims, 1992). Consistent with their extreme thinness, the shells of the mudflat *Isognomon* showed significantly higher incidence of shell damage (in the form of blisters that were frequently ruptured).

Predation. – Predation is amongst the most significant of ecological interactions. The drilling (boring) mode of predation leaves unambiguously identifiable holes in the valves of bivalve molluscs, living and dead, and is arguably the most studied and best understood kind of predation on bivalves (reviewed by Carriker & Yochelson, 1968; Vermeij, 1983). In addition, drill holes can either be complete (perforating the shell) or incomplete, the latter representing unsuccessful attempts. Previous authors (Vermeij, 1980, 1983; Vermeij et al., 1989; Kowalewski, 2004) used the frequency of predation marks to gauge the level of predation intensity by recording the relative proportion of drilled and undrilled valves collected at a given site. Harper & Morton (1994), however, noted that this measure of predation pressure can be misleading because it assumes equal transportability of both perforated and non-perforated valves and to a small degree of breakage by both premortem (crushing by other predators) and postmortem (transport) processes. The study of Harper & Morton (1994) focused on *Isognomon legumen*, a much smaller (> 30 mm) and thin-shelled bivalve, inhabiting exposed rocky shores. The authors assumed that the shells of this species were prone to postmortem breakage and transport, but did not evaluate whether these confounding factors were actually at play. In the present analysis, no evidence of transport was observed: despite the vigorous tidal regime; no shells of the mangrove *Isognomon* were found on mudflats and vice versa. Potential obstacles for shell transport included the soft sediment (dead shells were typically fully or partially buried in the mud) and the relatively heavy weight of the shells.

In addition to drilling predation, bivalves show marks of crushing predation, primarily by fish and crustaceans. No attempt to analyse the effect of crushing predation was made in the present study for the following reasons: (1) no potential crushing predators were identified; (2) shell crushing is difficult to distinguish from postmortem breakage (Vermeij, 1983; Harper, 2005); (3) shell margins of dried *Isognomon* shells are easily damaged, making it difficult to distinguish post- from premortem crushing; (4) marginal damage, even if resulting from predation, is unlikely to be lethal because the gills and mantle margins can withdraw deep inside the mantle cavity (Reid, 1985; present obs.); (5) shell repair is relatively difficult to interpret unequivocally (Vermeij, 1983), (6) apart from marginal damage, a negligible number of markings that could be interpreted as crushing predation was observed, and (7) the fact that few living individuals with very extensive injuries showed remarkably successful repair suggests that even substantial crushing damage is not necessarily lethal (Fig. 12B). Admittedly, non-lethal damage to the shell might indirectly lead to mortality by weakening the shell, redirecting its resources to repair, providing easier access of the soft tissues to other predators and parasites, and/or preventing sufficiently tight closure leading to desiccation at low tide. These effects, however, are difficult to evaluate in the field. Little evidence for crushing predation suggests that it was not a significant factor contributing to mortality of either the mangrove or mudflat *Isognomon* of Kungkrabaen Bay.

The survey of associated biota reveals that only one species, a muricid gastropod *Chicoreus capucinus*, was a potential predator. This agrees perfectly with the in situ observations of this gastropod preying on both populations of *Isognomon* (Fig. 10). Furthermore, these findings are consistent with the observed drill-hole morphology, characteristic of muricid gastropods. Additional, albeit limited, observations of similar drill holes in individuals of other species of bivalves suggested that the dietary requirements of *C. capucinus* are broad and that there is no specialisation in feeding on isognomonids, consistent with previous reports (Nielsen, 1986; Middelfart, 1996; Gribsholt, 1997; Tan, 1999; Wells et al., 2001).

The fact that the incidence of drilling predation was significantly higher in the mangrove *Isognomon* but its success was lower, suggests that, on one hand, access to the valve surfaces of the mangrove *Isognomon* was easier but the defense against the actual attack was more effective compared to those of the mudflat *Isognomon*. This hypothesis is corroborated by the following factors pertaining to the differences in shell morphology, spatial organisation, and physical stabilisation between the mangrove and mudflat *Isognomon*. In the mudflat, the *Isognomon* individuals were consolidated in tightly packed clumps that prevented the predator from easy access to the surface of the valves. This arrangement of shells was possible because of the extreme thinness and flatness of the valves of the mudflat *Isognomon*. (However, this did not prevent access by much smaller drilling predators, as evidenced by a high incidence of blisters.) In cases when individuals in a cluster were not packaged tightly (i.e., when the angle between the valves of adjacent individuals was large (exceeding approximately 25°) enough to allow for the access of a gastropod predator), the shells, because of the valves' thinness, were easily perforated by a gastropod, consistent with the significantly high success of predation and the observation of a maximum of one drill hole per valve. Previous studies reported that clumping of bivalves reduces predation by shell-crushing crustaceans (Okamura, 1986; Lin, 1991). To our knowledge, the present analysis is the first report demonstrating that clumping reduces drilling predation as well.

A different pattern of drilling predation was observed in the mangrove *Isognomon*. Tighter fixation to mangrove roots is achieved by thicker shells and higher valve convexity. This, in turn, prevents the shells from tight packaging, making them more readily accessible to the predator, but, at the same time, more difficult to penetrate. The considerable thickness of mangrove *Isognomon* shells is likely to be responsible for relatively low incidence of non-predatory (polychaete or sponge) drilling. This is also consistent with the fact that only in the mangrove *Isognomon* were multiple drilling attempts documented per valve. In such cases, only one of the holes was complete (presumably lethal), whereas the rest were incomplete (non-lethal). The distribution of individuals on the surface of prop roots is likely another factor contributing to the elevated incidence of muricid predation in this habitat. Because of the limited surface area of the prop roots, locating prey becomes an easy task: just crawling along the roots would certainly bring a predator in contact with prey. Also, the study of Wells et al. (2001), which focused on population ecology and feeding of *Chicoreus capucinus* at Ang-Sila, showed that population density of the muricid was significantly higher in the mangroves than on the sand.

Evolutionary implications. **–** This comparative ecological study of two presumably closely related species of *Isognomon* presents a remarkable example of complex interaction between adaptations for physical stabilisation and defense against predation and fouling. The organism-level properties, namely, the physical characteristics of shell morphology, are here hypothesised to have a profound effect on the effectiveness of physical stabilisation and predation intensity, both being essential factors influencing survival in the physiologically difficult intertidal environment. The most significant finding that emerged in this analysis was the fact that the demands for physical stabilisation and defense against predation require conflicting morphological adaptations that could not be simultaneously realised in a given ecological situation. The failure to optimise diverse demands of the active environment necessarily entailed a tradeoff between the effectiveness of defense against predators and fouling organisms on one hand and the strength of physical stabilisation on the other. Such an "adaptive compromise" (Rasnitsyn, 1987, 2002) is conceptualised to result from the intrinsic constraints (ontogenetic, phylogenetic, and constructional) on potential phenotypic expressions and conflicting requirements of multiple extrinsic (biotic and abiotic) ecological factors.

The present study has established a comparative quantitative framework that allowed independent evaluation of the effects of widely differing ecologies on channeling morphological variation and the ensuing differences in: (1) the mechanisms of spatial organisation at the level of the individual and the entire community; and (2) the dynamics of fouling and predator-prey interactions. In addition, the discovery of two morphologically distinct populations (potential cryptic species) suggests that the biodiversity of the seemingly well-known mangrove macrofauna is likely to be underestimated. Faced with the current decline of mangroves, this work highlights the need for a concerted effort in ecology and taxonomy that has an immediate relevance to conservation of these fragile ecosystems.

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THAI ABSTRACT

ผลงานวิจัยเรื่องนี้เป็นการเปรียบเทียบนิเวศวิทยาของประชากรหอยแฉลบ *Isognomon* สองประชากรที่อาศัยอยู่ในพื้นที่ติดกัน โดยประชากรหนึ่งอยู่ภายในป่าชายเลน อีกประชากรหนึ่งอยู่ในเขตหาดโคลนภายในอ่าวคุ้งกระเบน ในประเทศไทย ประชากรหอยสองฝาทั้งสองมีความแตกต่างกันของรูปร่างอย่างเห็นได้ชัดเจน เมื่ออาศัยการวิเคราะห์สัณฐานวิทยาทำให้คาดว่าประชากรหอยแฉลบทั้งสองน่าจะเป็นหอยคนละชนิดกัน โดยสิ่งที่เห็นเด่นชัดคือ หอยทั้งสองประชากรมีรูปร่างของเปลือก ความหนาของเปลือก และโครงสร้างของเส้นใยยึดเกาะที่แตกต่างกัน ผู้วิจัยตั้งข้อสมมติฐานว่าความแตกต่างดังกล่าวอาจเกิดขึ้นจากการอาศัยอยู่ในพื้นที่ที่แตกต่างกันทำให้ประชากรทั้งสองอยู่ภายใต้ความกดดันทางธรรมชาติที่แตกต่างกันในเรื่องของผู้ล่าและการถูกปกคลุมโดยสิ่งมีชีวิตอื่นๆ การวิเคราะห์เชิงปริมาณเกี่ยวกับความถี่ในการถูกผู้ล่าคุกคาม รวมทั้งสภาพทางกายภาพของตะกอนที่หอยอาศัยอยู่แสดงให้เห็นว่าประชากรหอยทั้งสองมีการปรับตัวเพื่อรองรับสภาพแวดล้อมที่ต่างกัน การอยู่ร่วมกันของหอยชนิดเดียวกันในสิ่งแวดล้อมที่ต่างกันทั้งสองแห่ง ทำให้เกิดความแตกต่างกันในรายละเอียดของสิ่งมีชีวิตที่มาเกาะ การสร้างเส้นใยยึดเกาะ และการปกป้องตนเองจากสภาวะแวดล้อมที่ไม่เหมาะสม ผลจากการวิเคราะห์ในครั้งนี้ทำให้เห็นว่าข้อมูลในเชิงนิเวศวิทยามีความสำคัญในการใช้จำแนกชนิดของหอย และแสดงให้เห็นถึงความจำเป็นในการทบทวนอนุกรมวิธานของหอยสองฝาในสกุล *Isognomon*

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