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The significance of pelvic fin flexibility for tree climbing fish

Adhityo Wicaksono^a, Saifullah Hidayat^b, Yudithia Damayanti^{a,b}, Desmond Soo Mun Jin^c,
Erly Sintya^a, Bambang Retnoaji^{b,*}, Parvez Alam^{a,*}

^a Laboratory of Paper Coating and Converting, Centre for Functional Materials, Abo Akademi University, Porthaninkatu 3, 20500 Turku, Finland

^b Laboratory of Animal Embryology, Faculty of Biology, Universitas Gadjah Mada, Yogyakarta, Indonesia

^c Rapid Gain Global Corporation, Singapore

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ABSTRACT

In this article, we compare the characteristics of biomechanical attachment exhibited by two morphologically different mudskipper species, *Boleophthalmus boddarti* (with fused pelvic fins) and *Periophthalmus variabilis* (with unfused pelvic fins). *P. variabilis* is a tree and rock climber while *B. boddarti* dwells in the muddy shallows and is unable to climb. Our aim in this article is to determine whether it is predominantly chemical or morphological properties of the pelvic fins from each species that may allow *P. variabilis* to climb trees whilst preventing *B. boddarti* from doing the same. To fulfil our objective we perform friction and suction resistance tests, Fourier transform infrared spectroscopy of the mucosal secretions under the fins, direct geometrical measurements and finite element modelling. We find that *B. boddarti* has considerable resistance to pull-off forces, while *P. variabilis* has greater frictional resistance. Both species produce mucopolysaccharides that we suggest aid Stefan adhesion to different substrates. *P. variabilis* fins are, nevertheless, considerably more flexible than those of *B. boddarti* and we conclude that *P. variabilis* is consequently able to maintain a more intimate surface area of contact with underlying material, which aids Stefan adhesion, increases frictional resistance, and helps it to climb trees.

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1. Introduction

Mudskippers (Teleostei: Gobiidae: Oxudercinae) are extraordinary land walking fish that reside outside of water for most of their lives. They are most typically found in the estuarial muddy tidal zones from the Indo-Pacific to Oceania (Takita et al., 1999) and are able to breathe on land by (a) carrying water in large gill chambers that act as temporary reservoirs, (b) strengthened gill filaments that are short and sturdy and able to resist collapse under dry conditions (Piper, 2007), (c) cutaneous respiration through highly vascularised skin (Park, 2002) and (d) water movement within the gill chambers, allowing for superior aeration. These fish are unique since they are able to propel themselves on land using primarily their pectoral fins (Pace and Gibb, 2009), and some species additionally climb steep inclines like trees and rock faces (Fig. 1). They are stabilised by pelvic fins, which exhibit differential morphological characteristics between the genera (Jaafar et al., 2006; Budney and Hall, 2010). Two common characteristic differences of pelvic fins include fused

fins, which are concave-shaped and unsplit, lying underneath the body; and unfused fins, which are split pelvic fins with the appearance of a fin-like leg that also begins underneath the fish, but which then protrudes either side of the fish (Larson and Lim, 2005).

Here, we consider the attachment characteristics of pelvic fins from two morphologically different Indonesian mudskipper species, *Boleophthalmus boddarti* (the blue-spotted mudskipper) (Chen et al., 2014; Martin, 2013) and *Periophthalmus variabilis* (the slender mudskipper) (Jaafar and Larson, 2008; Jaafar et al., 2009). *B. boddarti* is a large, heavy species of mudskipper with fused pelvic fins, while *P. variabilis* is a smaller, lighter mudskipper with unfused pelvic fins (Fig. 2). Unlike *B. boddarti*, *P. variabilis* is able to climb very steep, sometimes vertical inclines such as trees and rocks. *B. boddarti* lacks the versatile motion of *P. variabilis*, but is nevertheless able to walk and leap with relative ease in its estuarial habitat.

P. variabilis is abundant in mangrove ecosystems from both the low and high forest zones (Polgar and Bartolino, 2010). These mudskippers need to live in hot and humid habitats in order to breathe. Typically their habitats range in temperature from 24 to 30 °C and have a relative humidity between 60 and 80% (Clayton and Wells, 1994; Al-Behbehani and Ebrahim, 2010). To maintain its temperature requirement, *P. variabilis* will sunbathe on rocks or on tree branches or trunks. It can be presumed that their ability

* Corresponding authors.

E-mail addresses: bambang.retnoaji@ugm.ac.id (B. Retnoaji), parvez.alam@abo.fi, shantanou@gmail.com (P. Alam).

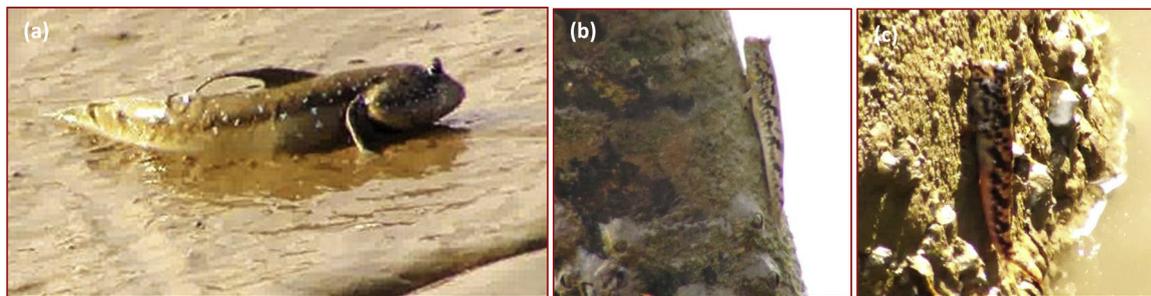


Fig. 1. Examples of mudskippers in their native environments: (a) *Boleophthalmus boddarti* lying flat in mud; (b and c) *Periophthalmus variabilis* climbing near-vertical terrain on (b) a mangrove tree and (c) igneous rock.

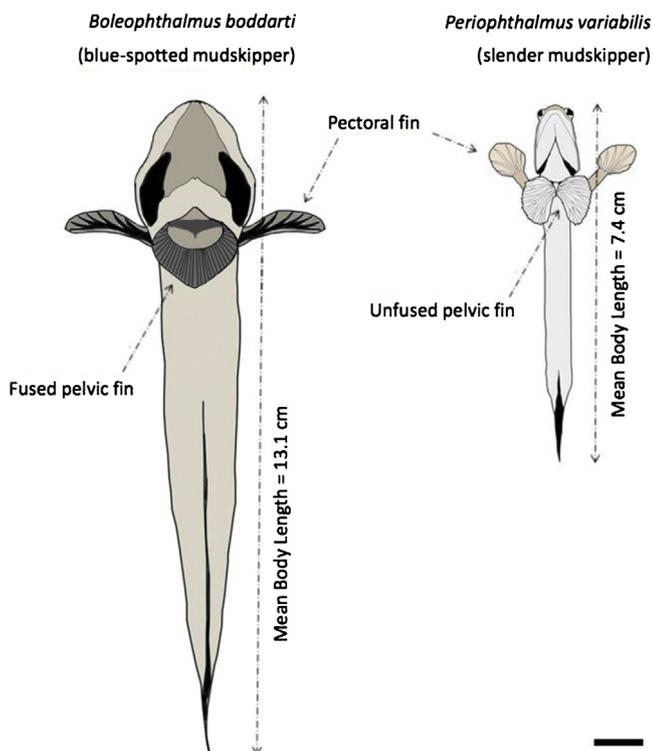


Fig. 2. Schematics of *Boleophthalmus boddarti* and *Periophthalmus variabilis* showing the positions of the fused and unfused pelvic fins, respectively. The relative size difference between the fish images shown in this figure is representative of actual size differentials between the two species. Scale bar = 1 cm.

to climb mangrove trees has evolved from at least a need to maintain high body temperatures by using the heat from direct sunlight. *P. variabilis*, living in the most terrestrial habitats (Khaironizam and Norma-Rashid, 2003), exhibits a somewhat different size and external morphology to other mudskippers (Murdy, 1989). A quantitative analysis of a mudskipper community made in Peninsular Malaysia (Polgar and Bartolino, 2010) elucidated a decrease in the size of mudskipper species from sea to land. The smaller size of mudskippers can be considered selectively more beneficial in terrestrial habitats. This may be due to either synecological or autoecological factors, or both. Parallels can be drawn to the research of Tracy et al. (2010), where frogs with smaller body size were found to exhibit superior thermoregulation that is of benefit in dry terrestrial conditions. The morphological development of their pelvic fins is perhaps an eco-ethological adaptation to their amphibious lifestyles. With these specialised pelvic fins, they can adhere to rocks and exposed roots, and are able to climb the stems of mangroves (Ming-Chih, 2013). A secondary reason for climbing mangrove trees may be related to feeding habits and diet, which for

P. variabilis typically consists of crustaceans and insects (Swennen et al., 1995).

We hypothesise that the unfused pelvic fins of *P. variabilis* are morphologically more advantageous for tree climbing than the fused pelvic fins of *B. boddarti*. The objectives of the present paper are to physically, chemically and mechanically characterise the pelvic fin structures of both *P. variabilis* and *B. boddarti* to determine the validity of our hypothesis.

2. Materials and methods

2.1. Fish sampling

The two species of mudskipper under investigation, *B. boddarti* and *P. variabilis*, were collected in the coastal area of Central Java between October and December 2014. The specimens were caught using a fish net and placed into separate aerated aquaria. Adult male fish were collected from both species and their selection was based on an abundance of their availability during all collection periods. Fish underside geometries were characterised, by direct measurement and by using a segmented measuring grid placed under each fish. A total of six fish from each species were physically characterised with respect to body length, contact area of the fish on a flat surface (excluding the total surface area of the central fins), surface area of the central fins and weight. Video footage and pictures were taken of *P. variabilis* to characterise pectoral/pelvic fin kinematics during a vertical climb. This was done by placing a fish inside a glass container and gently coercing it to climb vertically, whilst filming from the other side.

2.2. Biomechanical testing of attachment strength

Calibrated tension gauges (based on spring load deflection) were used to determine the suction and static friction forces for each mudskipper species. Suction forces were measured by lifting mudskippers off a varnished surface perpendicular to the surface. Friction was measured by pulling the mudskipper parallel to the surface. The surface was not banked at any angle. In each case, the gauges were attached to the body just below the pelvic fins. In total, four measurements were made for *P. variabilis* and six for *B. boddarti*.

2.3. Fourier transform infrared spectroscopy and molecular modelling of mucus secretions

Mucus secretions on the underside of each mudskipper species may have adhesive properties, thus serving to decrease slip during climbing and improve suction when mounted on an object such as a rock or a branch (Maie et al., 2012). To determine the constituents of mudskipper mucus in each species, we collected mucus samples from each fish species using a small plastic scraper together

with a micropipette (10 μl tip) to remove the mucus. We use this method to avoid scarring and damage to the fish epidermal tissues. We sourced mucus from different parts of the main body of the fish and also from the pelvic fin regions. Samples were refrigerated prior to Fourier transform infrared (FTIR) analysis, which was conducted in ATR mode.

After identifying the chemical compounds present in the mucus, we built these compounds in Ascalaph Designer software and performed *ab initio* simulations using the Firefly/PC GAMESS package. For the quantum mechanical *ab initio* simulations, we used an electrostatic MP2/6–311+G(2d,p) method. Substrate materials (i.e., water, cellulose, lignin, hemicellulose, calcium carbonate and silica structures) were also built and *ab initio* simulations were performed using the same procedure. Molecular dynamics simulations were then conducted between the mudskipper mucopolymers and each of the substrate materials. The substrate materials cellulose, lignin and hemicellulose were chosen because they constitute the primary component of trees, which unfused fin mudskippers regularly climb or sit on. Similarly, calcium carbonate and silica are primary components of igneous rocks to which mudskippers often attach (see Fig. 1) and as such were used in our simulations as substrate materials. We simulated the interaction of single mucopolymer molecules identified in the mudskipper slime with the surfaces of each substrate within an implicit Sheffield water condition (Grant et al., 2007). All simulations were conducted with a time step of 2.5 fs in a vacuum. The united-atom force field is optimized for the analysis of intermolecular and intramolecular interactions (Case et al., 2005) and includes (Yang et al., 2006) harmonic potentials to model angle terms, Fourier series to represent the torsion terms, 6–12 potentials for the van der Waals terms and Coulomb's law in respect of the electrostatic terms:

$$E_{\text{total}} = \sum_{\text{bonds}} [K_b \cdot (b - b_{\text{eq}})^2] + \sum_{\text{angles}} [K_\theta \cdot (\theta - \theta_{\text{eq}})^2] + \sum_{\text{dihedrals}} \frac{V_n}{2} [1 - \cos(n\phi - \gamma)] + \sum_{i < j} \left[\frac{A_{ij}}{(R_{ij})^{12}} - \frac{B_{ij}}{(R_{ij})^6} + \frac{q_i q_j}{\epsilon (R_{ij})^{12}} \right] \quad (1)$$

The terms in Eq. (1) for bond stretching are the force constant (K_b), bond length (b) and equilibrium value (b_{eq}). For the angle bending, the terms are the force constant (K_θ), bond angle (θ) and equilibrium value (θ_{eq}). The torsion terms considered include periodicity (n), the force constant (V_n), torsion angle (ϕ) and phase angle (γ). Finally, the non-bonded interactions between the i and j atom pairings include A_{ij} and B_{ij} as van der Waals parameters; also, q_i and q_j for the atomic charges, R for the non-bonded interaction length and ϵ as the dielectric constant including the effect of the medium.

2.4. Finite element analyses of pelvic fin displacement

Pelvic fins were built and geometrically approximated in three dimensions for each mudskipper species by direct measurement of the mudskipper fin rays and fin webs. The thickness of *B. boddarti* fin webs was 0.1 mm while the fin rays and the stem were modelled with a thickness of 0.2 mm. For *P. variabilis* the fin webs were 0.1 mm, the fin rays were 0.16 mm and the stem was modelled with a thickness of 0.13 mm. Table 1 provides further geometrical details on the fin ray lengths for each species modelled (further details on mudskipper geometries are provided in the supplementary online Appendix). Both cartilaginous fin rays and webbed connective tissues were modelled as elastic isotropic materials, each with a Young's modulus of 50 MPa (Balaban et al., 2015) and a near-incompressible solid Poisson's ratio of 0.49. These values of Young's modulus and Poisson's ratio correspond well to fish cartilage with low levels of cartilage mineralization. The models were

Table 1

Geometrical idealisations used for pelvic fin components of the two studied mudskipper species, *Boleophthalmus boddarti* and *Periophthalmus variabilis*. The idealisations are based on direct measurements of mudskipper pelvic fins, fin rays and fin webs.

Fin ray	Length [mm] (<i>B. boddarti</i>)	Length [mm] (<i>P. variabilis</i>)
Innermost ray	11	4
Second ray	10	3.5
Third ray	7	2
Outermost ray	5.5	1.1

Table 2

Average morphological values for the two studied mudskipper species (\pm standard error in parentheses, sample number $n = 6$). The complete library of measurements for each species is provided in Tables S1 and S2 in the supplementary online Appendix.

	<i>B. boddarti</i>	<i>P. variabilis</i>
Body mass [g]	18.5 (± 0.90)	3.7 (± 0.26)
Body length [mm]	131 (± 2.5)	74 (± 1.8)
Underbody surface area (UA) [mm ²]	1365 (± 26)	637 (± 15)
Pelvic fin surface area (PA) [mm ²]	226 (± 4.2)	119 (± 2.9)
Ratio of PA:UA	0.166 ($\pm 6.5 \times 10^{-9}$)	0.187 ($\pm 5.1 \times 10^{-18}$)

used to simulate the effects of friction upon single pelvic fin displacement and were loaded with 1 N/m of force from front to back on the underside of the fin. The stem connects the pelvic fins to the body and this was fixed with zero degrees of freedom ($U = 0$).

3. Results and discussion

3.1. Physical and biomechanical characterisation

The measured body lengths, weights, lower body surface areas and pelvic fin areas of six individuals from each mudskipper species are provided in Table 2 (more detailed physical characterizations are provided in Tables S1 and S2 in the supplementary online Appendix). From Table 2 it becomes apparent that the mass, body length and surface areas are considerably higher in *B. boddarti* than in *P. variabilis*. The ratio of the area of the pelvic fins to the underbody area is different between the species as *P. variabilis* appears to have a slightly greater pelvic fin area with respect to its underbody area than *B. boddarti*. To statistically validate the difference, the Mann–Whitney U -test (two-tailed, $\alpha = 0.05$) was conducted (see Tables S1 and S2). The test shows there is a significant difference ($P = 0.0022$) between the species with respect to the ratio of the area of the pelvic fins and the underbody area between the species. Mean static friction, F_s , and suction, S , resistances were measured for *B. boddarti* at 99 MPa and 114 MPa, respectively. For *P. variabilis*, the mean static friction and suction resistances were 256 MPa and 32 MPa, respectively. The mudskipper with fused fins, *B. boddarti*, has a higher suction resistance as compared to its friction resistance ($F_s/S = 0.9$), while the opposite is true for the mudskipper with unfused fins, *P. variabilis* ($F_s/S = 8.0$). *P. variabilis* has a friction resistance that is approx. 2.5 times higher than that of *B. boddarti*, while its suction resistance is approx. 3.5 times lower. We suggest that *P. variabilis* requires greater friction resistance than *B. boddarti* since, unlike *B. boddarti*, *P. variabilis* climbs trees and rocks (sometimes vertically) and therefore requires stronger attachment parallel to its direction of movement. Contrarily, *B. boddarti* has greater suction resistance, perhaps due partially to its greater weight, but perhaps also partly because it attaches laterally to rock faces where a degree of resistance to wave-induced push-off forces is needed.

During vertical climbs, *P. variabilis* propels itself forwards using its pectoral fins, during which time the pelvic fins are in an unextended form. Once the pectoral fins reach the limit of terminal extension (approximately perpendicular to the axis of the fish

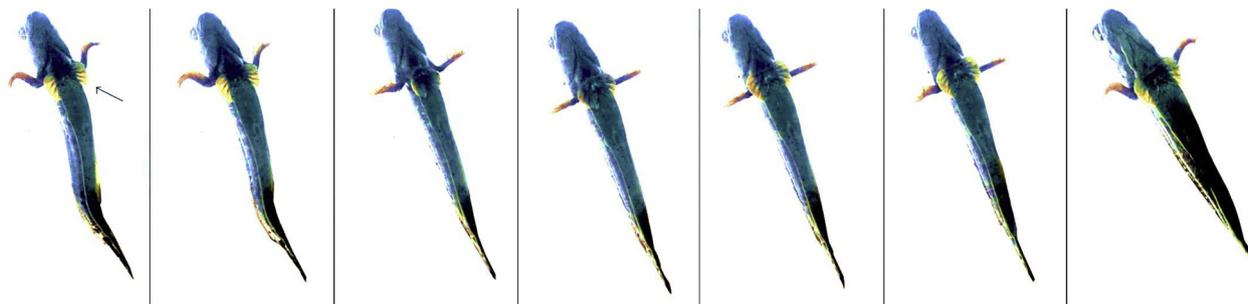


Fig. 3. Sequential antagonistic movements of *P. variabilis* pectoral and pelvic fins during a vertical climb.

body), the pelvic fins spread out and essentially flatten to the surface upon which it climbs. During the stage of pelvic fin attachment, the pectoral fins return to a position from where they are once again able to propel the fish forwards, and this cycle repeats during vertical climbs. The antagonistic movement of pectoral and pelvic fins can be seen in Fig. 3, which shows individual frames from a video of *P. variabilis* during a vertical climb upon a glass surface. This mode of forward propulsive motion has also been reported for the lump-sucker (Davenport and Thorsteinsson, 1990), which briefly unpeels its sucker prior to moving forwards.

3.2. FTIR characterisation

We hypothesise that the mudskippers exhibit a type of Stefan adhesion (Stefan, 1874), whereby attachment is a coupled function of suction and the close-range effects of mucosal secretions (Shephard, 1994; Smith, 2002). This type of adhesion is ubiquitous in many marine organisms (e.g. limpets; Smith, 1991) and resistance is primarily to interfacial shearing, though it has the additional effect of improving tensile pull-off (Vogel, 2003). To confirm our hypothesis, we begin by characterising the mucous secretions underneath each mudskipper species by FTIR analysis. Fig. 4 shows typical FTIR spectra for both the fused fins and unfused fins of the two investigated mudskipper species. Both spectra are identified as representing predominantly hyaluronic acid (HA) (see chemical structure insert in Fig. 4) (Alkrad et al., 2003; Park et al., 2003; De Hoog et al., 2010; Panagos et al., 2014), which is a glucosaminoglycan polysaccharide composed of monomers of 1,4-glucuronic acid and 1,3-N-acetyl glucosamine. In a study by Alkrad et al. (2003), slight shifts in IR spectral peaks of HA are noted to arise as a function of its molecular weight. In our spectra, strong peaks can be detected at 3386 cm^{-1} (N-H and O-H stretches), 1631 cm^{-1} (C=O carboxyl amide I) and 1110 cm^{-1} (C-O-C, C-O, C-O-H stretch). The peak at 1110 cm^{-1} is indicative of pyranose rings in either an α or β conformation, and the associated C-O stretch comes from either β -1-4 or β -1-3 glycosidic linkages between individual pyranose rings (Kovalev and Litvinenko, 1965). Shoulder peaks at 3244 cm^{-1} and 2897 cm^{-1} indicate N-H/O-H stretches and C-H stretches, respectively.

3.3. Molecular dynamics simulations of mucosal biopolymer to climbing substrates

Based on that our spectra are very similar to previously reported HA FTIR spectra (Alkrad et al., 2003; De Hoog et al., 2010), we modelled the molecular adhesion of HA to water, mangrove constituents (cellulose, hemicellulose, lignin) and to igneous rock constituents (calcium carbonate and silica). Table 3 shows the interaction energies between HA and our different simulated substrates. Water is an ever present fluid in mudskipper environments and in mudskipper slime. From our simulation results, water is shown to form strong interaction energies with HA and consequently, we can deduce that

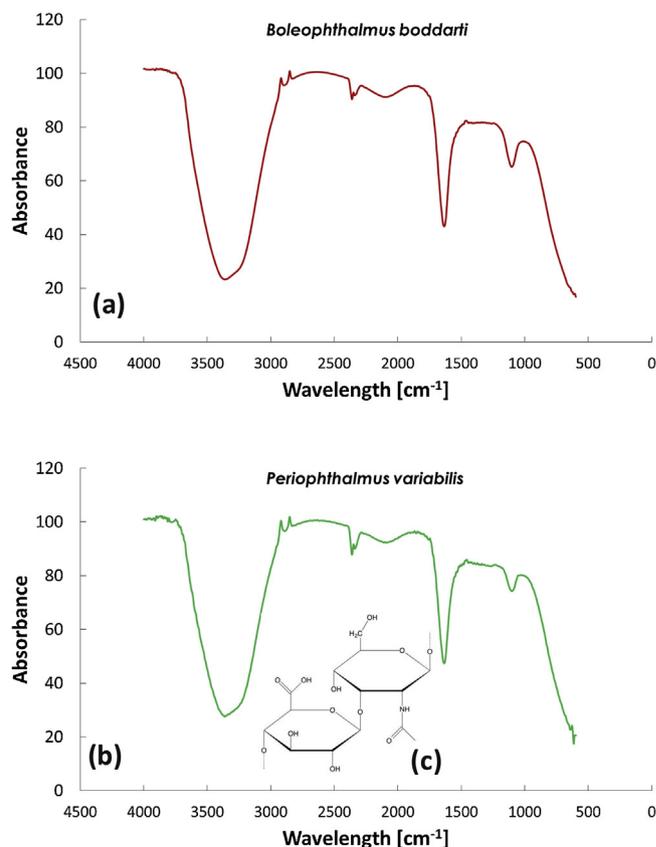


Fig. 4. FTIR spectra for the pelvic fins of (a) *Boleophthalmus boddarti* (fused fins) and (b) *Periophthalmus variabilis* (unfused fins). The spectra indicate the presence of hyaluronic acid, the chemical structure of which is shown in (c).

it plays an important role in the success of mudskipper adhesion. The strongest interaction energies are with calcium carbonates followed by silica. Of the typical woody materials, HA attaches most strongly to hemicellulose. We infer from our results that when climbing trees or rocks, *P. variabilis* might in fact benefit from a degree of wetness that may be present as a thin fluid layer, or which is present in the mucopolysaccharide (Park et al., 2003) slime itself. Moreover, from our simulation results, we deduce that it is easier for these mudskippers to ascend native igneous rocks than to climb trees at equal angles. Though *B. boddarti* does not climb steeply inclined rocks or trees, it may still serve to benefit in view of lateral stability when subjected to currents, waves and during movement.

3.4. Finite element modelling of pelvic fin flexibility

Another factor of importance for mudskipper attachment is the contacting areas of the pelvic fins to a surface under loading. The

Table 3
 Interaction energies of hyaluronic acid (HA) with regard to typical substrates that mudskippers will attach to.

	Van der Waals [kcal/mol]	Electrostatic [kcal/mol]	Total interaction energy [kcal/mol]
HA–Water	–10.4	–53.4	–63.8
HA–CaCO ₃	+30.7	–297.6	–266.9
HA–Silica	–117.3	–43.4	–160.6
HA–Cellulose	–39.8	–10.2	–50.0
HA–Hemicellulose	–43.5	–27.8	–71.3
HA–Lignin	–16.9	+9.6	–7.3

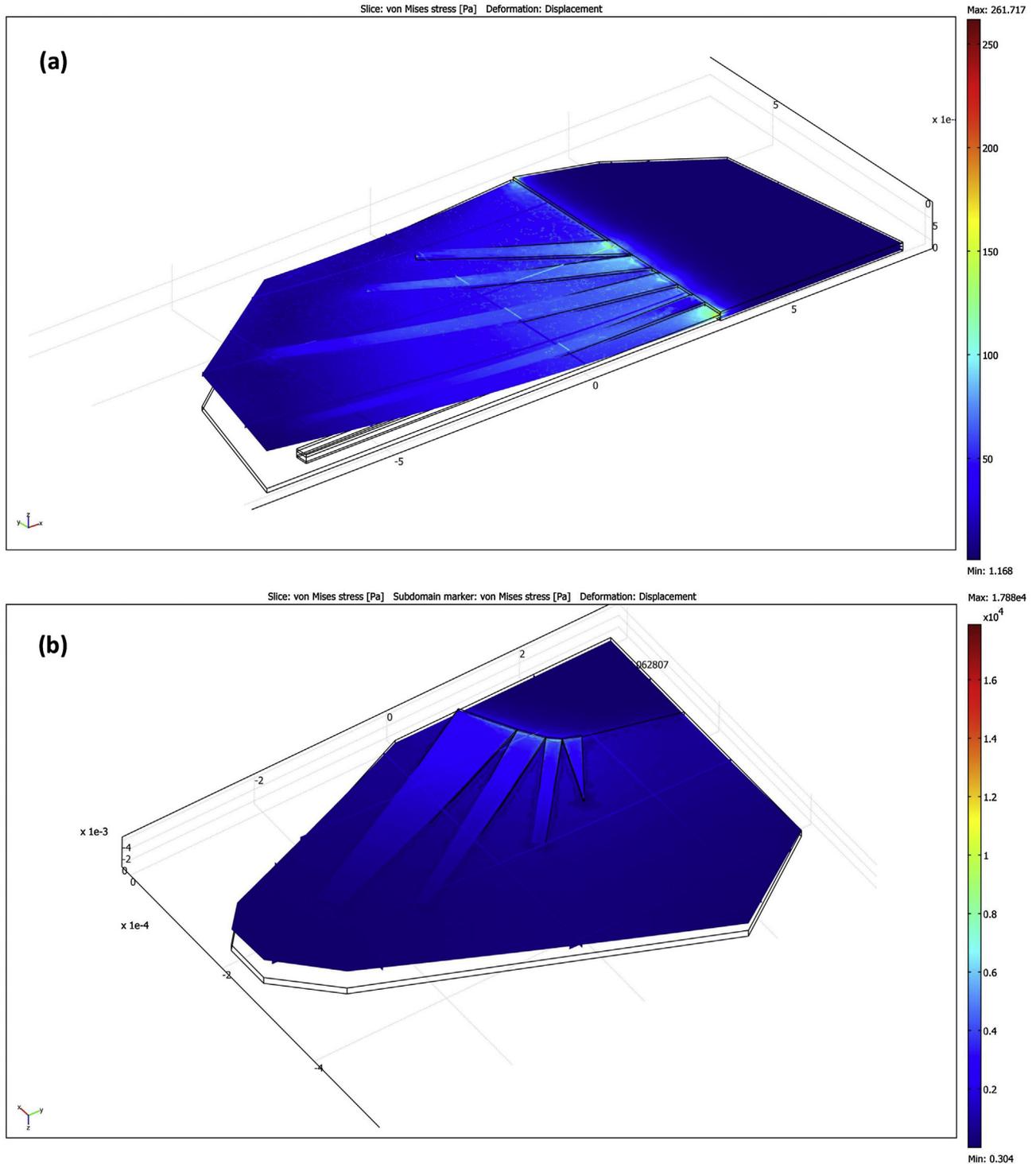


Fig. 5. Finite element models showing von Mises stress distributions on loading for (a) the *Boleophthalmus boddarti* fin and (b) the *Periophthalmus variabilis* fin. The stresses are highest in both species at the base of the fin rays.

Table 4
Distribution of displacements, δ , under equal loading conditions for *B. boddarti* and *P. variabilis* as predicted by our finite element models. The innermost ray is the longest fin ray and the length of each ray decreases from the innermost to the outermost ray, which is the shortest.

Fin ray	δ [μm] (<i>B. boddarti</i>)	δ [μm] (<i>P. variabilis</i>)
Innermost ray	1.6	5.9
Second ray	1.29	5.1
Third ray	0.49	2.2
Outermost ray	0.22	0.8

surface area ratios of the thin flexible web-like material of the fin to the thicker fin rays are determined as 2.97 and 3.88 for *B. boddarti* and *P. variabilis*, respectively, as calculated from the model geometries. Since there is a higher ratio of web to ray material in the unfused-fins species, it will naturally exhibit a lower rigidity as compared to the fins from the fused-fins species. Additionally, our finite element analyses (Fig. 5) reveal that under the same conditions of loading (1 N/m), the unfused fins of *P. variabilis* are able to flex by more than four times that of the fused fins of *B. boddarti* (8.7 μm as compared to 2.0 μm). The geometrical construct of the pelvic fins of *B. boddarti*, therefore, has a greater rigidity than the pelvic fins of *P. variabilis*. The fin rays of *B. boddarti* are spread across the entirety of the web material and stabilise the web more effectively than the fin rays of *P. variabilis*, which are confined to more localised regions of individual fins. We deduce, therefore, that it is global fin rigidity that prevents *B. boddarti* from gaining intimate contact with adjacent material, and thus, the ability to adhere to materials at steeper inclines. Contrarily, the high level of fin flexibility exhibited by *P. variabilis* implies that during movement, the fins can more intimately spread upon a surface and it is perhaps also this quality of the fins of *P. variabilis*, coupled to its inherent mucopolysaccharide-based Stefan adhesion, that aids this species of mudskipper during vertical and near-vertical climbs of trees and rocks. A high level of flexion, nevertheless, also means that the fins of *P. variabilis* experience higher localised stresses than those of *B. boddarti* under higher loads (485 Pa as compared to 61 Pa at the tip of the longest fin-ray for each species, respectively). These are, nevertheless, relatively low stresses and the cartilaginous material making up the foot is highly elastic. Table 4 provides further details on the displacements, δ , experienced by each fin ray for both species under the conditions of loading at 1 N/m. Since there is a progressive reduction in the extent of displacement from the innermost to the outermost fin ray in each species, the global deformational character of each fin is non-linear. The displacements are considerably higher in *P. variabilis* than in *B. boddarti*, which clarifies that *P. variabilis* has a deformational versatility that does not exist in *B. boddarti*.

In summary, we can stipulate that both mudskipper species are capable of Stefan adhesion with their pelvic fins, which is itself a function of the strength of attraction of secreted mucopolysaccharides (primarily hyaluronic acid) to a specific substrate. However, since the pelvic fins of *P. variabilis* are more malleable than those of *B. boddarti*, its fins can more intimately contact a surface and Stefan adhesion is thus more effective for *P. variabilis*. We suggest that with the combined properties of high fin flexibility, light weight and optimised Stefan adhesion through improved intimacy of contact, the pelvic fins of *P. variabilis* are in fact an essential tool used by this species of mudskipper for tree climbing.

4. Conclusions

In the present study, we compared the chemical, physical and mechanical characteristics of fused pelvic fins (*B. boddarti*) and unfused pelvic fins (*P. variabilis*) of mudskippers. Mudskipper species with unfused pelvic fins are able to climb trees whereas

species with fused pelvic fins do not have this capability. Both species have pectoral fins that can be used for movement on land; however, since the pelvic fins of each species are discernibly different, we compared the pelvic fins of each species to elucidate the differences and thus hypothesise on how these differences influence the ability or inability to climb trees. *B. boddarti* are almost twice as long as, and almost five times heavier than, *P. variabilis*. Using FTIR spectroscopy, we found that both species of mudskipper secrete mucopolysaccharides and using molecular dynamics methods we found that these mucopolysaccharides are likely to aid Stefan adhesion in both species. Subsequent geometrical and mechanical characterisations (using the finite element method) nevertheless made it clear that *P. variabilis* has considerably more flexible pelvic fins than *B. boddarti*. We suggest that this helps *P. variabilis* gain greater intimacy of contact with surfaces, improving Stefan adhesion and frictional resistance, which when combined with its lighter weight allows it to climb with relative ease. To date, there are no reports on the physico-chemical functionality of mudskipper pelvic fins. Research efforts have rather focused on the role of pectoral fins in mudskipper locomotion. The research herein therefore presents a new concept, which is that good pelvic fin design benefits the tree climbing activities of certain fish. Our research results additionally provide insights by which soft-body robotic materials can be optimized in view of locomotion over steep inclines.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.zool.2016.06.007>.

References

- Al-Behbehani, B.E., Ebrahim, H.M.A., 2010. Environmental studies on the mudskippers in the intertidal zone of Kuwait bay. *Nature and Science* 8, 79–89.
- Alkrad, J.A., Mrestani, Y., Stroehli, D., Wartewig, S., Neubert, R., 2003. Characterization of enzymatically digested hyaluronic acid using NMR, Raman, IR and UV-vis spectroscopies. *J. Pharmaceut. Biomed. Anal.* 31, 545–550.
- Balaban, J.P., Summers, A.P., Wilga, C.A., 2015. Mechanical properties of the hyomandibula in four shark species. *J. Exp. Zool.* 323, 1–9.
- Budney, L.A., Hall, B.K., 2010. Comparative morphology and osteology of pelvic fin-derived midline suckers in lumpfishes, snailfishes and gobies. *J. Appl. Ichthyol.* 26, 167–175.
- Case, D.A., Cheatham, T.E., Darden, T., Gohlke, H., Luo, R., Merz, K.M., Onufriev, A., Simmerling, C., Wang, B., Woods, R.J., 2005. The amber biomolecular simulation programs. *J. Comp. Chem.* 26, 1668–1688.
- Chen, H., Polgar, G., Yin, W., Fu, C.Z., 2014. Cryptic species and evolutionary history of the *Boleophthalmus pectinirostris* complex along the northwestern Pacific coast. *Acta Hydrobiol. Sin.* 38, 75–86.
- Clayton, D.A., Wells, K., 1994. *Discovering Kuwait's Wildlife*. Fahad Al Marzouq Printing and Publishing, Kuwait.
- Davenport, J., Thorsteinsson, V., 1990. Sucker action in the lumpsucker *Cyclopterus lumpus* L. *Sarsia* 75, 33–42.
- De Hoog, H.P.M., Arends, I.W.C.E., Rowan, A.E., Cornelissen, J.J.L.M., Nolet, R.J.M., 2010. A hydrogel-based enzyme-loaded polymersome reactor. *Nanoscale* 2, 706–716.
- Grant, J.A., Pickup, B.T., Sykes, M.J., Kitchen, C.A., Nicholls, A., 2007. A simple formula for dielectric polarisation energies: the Sheffield Solvation Model. *Chem. Phys. Lett.* 441, 163–166.
- Jaafar, Z., Larson, H.K., 2008. A new species of mudskipper, *Periophthalmus takita* (Teleostei: Gobiidae: Oxudercinae), from Australia, with a key to the genus. *Zool. Sci.* 25, 946–952.
- Jaafar, Z., Lim, K.K.P., Chou, L.M., 2006. Taxonomical and morphological notes on two species of mudskippers, *Periophthalmus walailakae* and *Periophthalmodon schlosseri* (Teleostei: Gobiidae) from Singapore. *Zool. Sci.* 23, 1043–1047.
- Jaafar, Z., Perrig, M., Chou, L.M., 2009. *Periophthalmus variabilis* (Teleostei: Gobiidae: Oxudercinae), a valid species of mudskipper, and a re-diagnosis of *Periophthalmus novemradiatus*. *Zool. Sci.* 26, 309–314.
- Khaironizam, M.Z., Norma-Rashid, Y., 2003. First record of the mudskipper, *Periophthalmodon septemradiatus* (Hamilton) (Teleostei: Gobiidae) from Peninsular Malaysia. *Raffles Bull. Zool.* 51, 97–100.
- Kovalev, I.P., Litvinenko, V.I., 1965. Investigation of flavonoid glycosides. *Chem. Nat. Comp.* 1, 178–184.
- Larson, H.K., Lim, K.K.P., 2005. *A Guide to Gobies of Singapore*. Singapore Science Centre, Singapore.

- Maie, T., Schoenfuss, H.L., Blob, R.W., 2012. Performance and scaling of a novel locomotor structure: adhesive capacity of climbing gobiid fishes. *J. Exp. Biol.* 215, 3925–3936.
- Martin, K.L., 2013. Theme and variations: amphibious air-breathing intertidal fishes. *J. Fish Biol.* 84, 577–602.
- Ming-Chih, H., 2013. Mudskippers in Tainan: the ecology and lifestyle of mudskipper *Periophthalmus modestus* in Tainan coastal wetland. *Int. J. Sci. Eng.* 3, 37–43.
- Murdy, E.O., 1989. A taxonomic revision and cladistic analysis of the oxudercine gobies (Gobiidae: Oxudercinae). *Rec. Austral. Mus. Suppl.* 11, 1–93.
- Pace, C.M., Gibb, A.C., 2009. Mudskipper pectoral fin kinematics in aquatic and terrestrial environments. *J. Exp. Biol.* 212, 2279–2286.
- Panagos, C.G., Thomson, D., Moss, C., Bavington, C.D., Olafsson, H.G., Uhrin, D., 2014. Characterisation of hyaluronic acid and chondroitin/dermatan sulfate from the lumpsucker fish, *C. lumpus*. *Carbohydr. Polym.* 106, 25–33.
- Park, J.Y., 2002. Structure of the skin of an air-breathing mudskipper, *Periophthalmus magnuspinnatus*. *J. Fish Biol.* 60, 1543–1550.
- Park, J.Y., Lee, Y.J., Kim, I.S., Kim, S.Y., 2003. A comparative study of the regional epidermis of an amphibious mudskipper fish, *Boleophthalmus pectinirostris* (Gobiidae, Pisces). *Folia Zool.* 52, 431–440.
- Piper, R., 2007. *Extraordinary Animals: An Encyclopedia of Curious and Unusual Animals*. Greenwood Publication, Connecticut.
- Polgar, G., Bartolino, V., 2010. Size variation of six species of oxudercine gobies along the intertidal zone in a Malayan coastal swamp. *Mar. Ecol. Progr. Ser.* 409, 199–212.
- Shephard, K.L., 1994. Functions for fish mucus. *Rev. Fish Biol. Fish.* 4, 401–429.
- Smith, A.M., 1991. The role of suction in the adhesion of limpets. *J. Exp. Biol.* 161, 151–169.
- Smith, A.M., 2002. The structure and function of adhesive gels from invertebrates. *Integr. Comp. Biol.* 42, 1164–1171.
- Stefan, J., 1874. Versuche über die scheinbare Adhäsion. *Sitz.-Ber. Akad. Wiss. Wien (Abt. II Math.-Phys.)* 69, 713–735 (in German).
- Swennen, C., Ruttanadaku, N., Haver, M., Piummongkol, S., Prasertsongscum, S., Intanai, I., Chaipakdi, W., Yeesin, P., Horpet, P., Detsathit, S., 1995. The five sympatric mudskippers (Teleostei: Gobiidae) of Pattani area, Southern Thailand. *Nat. Hist. Bull. SIAM Soc.* 42, 109–129.
- Takita, T., Agusnimar, Ali, A.B., 1999. Distribution and habitat requirements of oxudercine gobies (Gobiidae: Oxudercinae) along the Straits of Malacca. *Ichthyol. Res.* 46, 131–138.
- Tracy, C.R., Christian, K.A., Tracy, C.R., 2010. Not just small, wet, and cold: effects of body size and skin resistance on thermoregulation and arboreality of frogs. *Ecology* 91, 1477–1484.
- Vogel, S., 2003. *Comparative Biomechanics: Life's Physical World*. Princeton University Press, Princeton.
- Yang, L., Tan, C.-H., Hsieh, M.-J., Wang, J., Duan, Y., Cieplak, P., Caldwell, J., Kollman, P.A., Luo, R., 2006. New-generation amber united-atom force field. *J. Phys. Chem. B* 110, 13166–13176.