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# A unique form of light reflector and the evolution of signalling in *Ovalipes* (Crustacea: Decapoda: Portunidae)

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The first demonstration, to our knowledge, of an evolutionary shift in communication mode in animals is presented. Some species of *Ovalipes* display spectacular iridescence resulting from multilayer reflectors in the cuticle. This reflector is unique in animals because each layer is corrugated and slightly out of phase with adjacent layers. Solid layers are separated from fluid layers in the reflector by side branches acting as support struts. An effect of this reflector is that blue light is reflected over a 'broad' angle around a plane parallel to the sea floor when the host crab is resting. Species of *Ovalipes* all possess stridulatory structures. The shallow-water species with the best developed stridulatory structures are non-iridescent and use sound as a signal. Deep-water species possess poorly developed stridulatory structures and display iridescence from most regions of the body. In deep water, where incident light is blue, light display is highly directional in contrast to sound produced via stridulation. Sound and light display probably perform the same function of sexual signalling in *Ovalipes*, although the directional signal is less likely to attract predators. Deep-water species of *Ovalipes* appear to have evolved towards using light in conspecific signalling. This change from using sound to using light reflects the change in habitat light properties, perhaps the hunting mechanisms of cohabitees, and its progression is an indicator of phylogeny. The changes in sexual signalling mechanisms, following spatial–geographical isolation, may have promoted speciation in *Ovalipes*.

**Keywords:** *Ovalipes*; evolution; sound; animal iridescence; corrugated multilayer reflector; signalling

## 1. *OVALIPES* AND ITS ADAPTATION TO SOUND AND LIGHT

The genus *Ovalipes* is one of six swimming crab genera in the portunid subfamily Polybiinae. The genus includes 11 species of relatively large swimming crabs with both Indo-Pacific and western Atlantic representatives. Each species has one of two depth ranges: 0–60 m ('shallow') or 80–500 m ('deep'). Adult *Ovalipes* are principally benthic and are aggressive, opportunistic carnivores. *Ovalipes floridanus*, *O. stephensoni* and *O. australiensis* have been observed to be extremely aggressive with conspecifics and other portunids (Williams 1984; S. T. Ahyong, personal observation). Crabs probably possess dichromatic colour vision, which is known in other crustaceans, and typically have well-developed compound eyes (Land 1984). Likewise, species of *Ovalipes* all have well-developed eyes (approximately twice the width in deep-water species compared with that of shallow-water species) and many possess some red pigmentation. The main predators of *Ovalipes catharus* are generalist demersal fish (McLay 1988) and this is likely to be the case for most other species of the genus. For example, *O. catharus* is consumed by over 30 species of commercially taken fish that are known to feed on a variety of animals (McLay 1988).

The genus comprises two clades (groups A and B), each with two subgroups (A1, A2, B1, B2), some of which show iridescence to varying degrees (see table 1). The iridescence displayed by some species is highly conspicuous, to a degree which is unique among decapod Crustacea, and comparable to the extensively studied sapphirinid copepods (see, for example, Chae & Nishida 1994, 1995). However, the mechanism behind the iridescence in *Ovalipes* has so far not been studied. Multilayer reflectors are the commonest cause of iridescence in animals. Those studied to date always possess flat, parallel layers, often as a quarter-wave stack (Land 1972; Chae & Nishida 1994).

All species of *Ovalipes* are capable of sound production via stridulation, though these stridulatory structures vary in development with species group (Stephenson 1969). In group A species, stridulatory carinae (forming a 'file') are principally located along the lower margin of the chelae. These carinae are engaged by the modified dactyl of the first walking leg for which at least 29 different stridulatory repertoires are possible (Stephenson 1969). Group B species bear stridulatory carinae along the lower, lateral margin of the carapace, and these are engaged by the merus of the walking legs. The carinae of subgroup B2 species are better developed (in terms of precise arrangement and number and height of ridges) than those of subgroup B1 species. Consequently *O. ocellatus* (B2) is capable of a louder and more diverse (at least 20 different stridulatory repertoires) repertoire than *O. iridescens* (B1; at least 13

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Table 1. *Species groups within* Ovalipes (*based on Stephenson & Rees 1968; Williams 1984*), *and their geographical distributions*
(Depths quoted from Stephenson & Rees (1968) and Wenner & Read (1982).)

| species | depth | distribution |
|---|---|---|
| group A1 (non-iridescent) | | |
| *O. punctatus* | shallow | Japan, China |
| *O. trimaculatus* | shallow | eastern and western South America, eastern and western South Africa, Indian Ocean |
| *O. catharus* | shallow | New Zealand, southern Australia |
| *O. australiensis* | 0–55 m | Australia |
| *O. elongatus* | shallow | Lord Howe Island, Kermadec Islands (South Pacific Ocean) |
| group A2 (non-iridescent) | | |
| *O. georgei* | shallow | western Australia |
| group B1 (extensive iridescence) | | |
| *O. iridescens* | 80–204 m | South Africa, Indonesia, Japan, southern Australia |
| *O. molleri* | 135–475 m | southeastern Australia |
| group B2 (limited iridescence) | | |
| *O. ocellatus* | shallow | eastern North America |
| *O. floridanus* | 13–46 m | eastern North America, Gulf of Mexico |
| *O. stephensoni* | 0–227 m<br>(usually $< 50$ m) | eastern North America |

different stridulatory repertoires) (Stephenson 1969). However, stridulatory carinae are most strongly developed in group A species, where the ridges and the length of the file itself are much longer and occupy the largest proportion of body surface (see Fletcher 1992, p. 240). Hence *O. australiensis* (A) is capable of a more diverse and louder repertoire than *O. ocellatus* (B2) (Stephenson 1969). Consequently, we term stridulatory structures in group A species as 'well-developed', group B1 species as 'reduced', and group B2 species as 'moderately developed'. Males, females and juveniles all bear stridulatory structures, and these are often best developed in adult males (Stephenson 1969). Proposed functions for such sound production include mate attraction, aggregation signals, aggressive–territorial signals and other information signals such as predator warning (Busnel 1963; Stephenson 1969). Male *O. catharus,* however, have been observed to stridulate in the presence of females before and during mating (McLay 1988). This, coupled with the sexual dimorphism in stridulatory structures observed by Stephenson (1969) strongly supports the use of sound as a sexual signal.

Light–colour signalling systems have been extensively studied in various groups including birds (see, for example, Bleiweiss 1992), fish (see, for example, Verrell 1991) and insects (see Silberglied 1984). Only recently has the evolution of such systems been considered in a phylogenetic context (see Harvey & Pagel 1991; Brooks & McLennan 1991). Variation in signalling has often been considered an important factor in speciation (Verrell 1991), although previous studies in this field have involved only one mode of signalling. The study of signalling in *Ovalipes* in a phylogenetic context is unusual, therefore, because at least two modes of signalling are involved (omnidirectional sound production and/or directional iridescent display). These signals differ in their potential to conceal information.

The aims of this study are (i) to determine the mechanism behind the iridescence in *Ovalipes* and its advantages in the crab's environment; and (ii) to test whether iridescent display has evolved independently in different lineages within *Ovalipes*, and investigate its relation to sound production.

## 2. CAUSE OF IRIDESCENCE IN *OVALIPES*

The fifth pereopods in *Ovalipes* are modified for swimming and form a terminal paddle. The paddle is flat, comprehensively iridescent in subgroup B1 species, and therefore ideal for studying internal reflecting structures and taking reflectance measurements.

The reflectance of a paddle of *Ovalipes molleri* was measured using an integrating sphere, and was found to peak at 0.58 for all wavelengths between 380 and 570 nm. This measurement is actually made up of reflections at all angles. When viewed at one angle, the surface showed strong iridescence, with colour varying with the viewing angle. At normal incidence, the structure appears yellow, whereas at angles of approximately 45° from the surface normal, the structure appears blue. The latter observation was confirmed using a laser beam and measurement table where it was found that blue (wavelength 460 nm) reflectance was only obtained where the angles of incidence and reflectance were between 45° and 55° from the normal.

The mechanism behind cuticular iridescence in *Ovalipes* was examined using electron microscopy. The paddles of the non-iridescent *O. australiensis* and the comprehensively iridescent *O. molleri* were cleaned using five half-second ultrasound exposures. Part of a paddle from each species was critical point dried, coated with gold, and examined in a scanning electron microscope for surface ornamentation.

Different parts of the above paddles were fixed overnight in 2.5% glutaldehyde with 2% paraformaldehyde in 0.1 M sodium cacodylate buffer, then washed in 0.1 M sodium cacodylate buffer. Specimens were subsequently

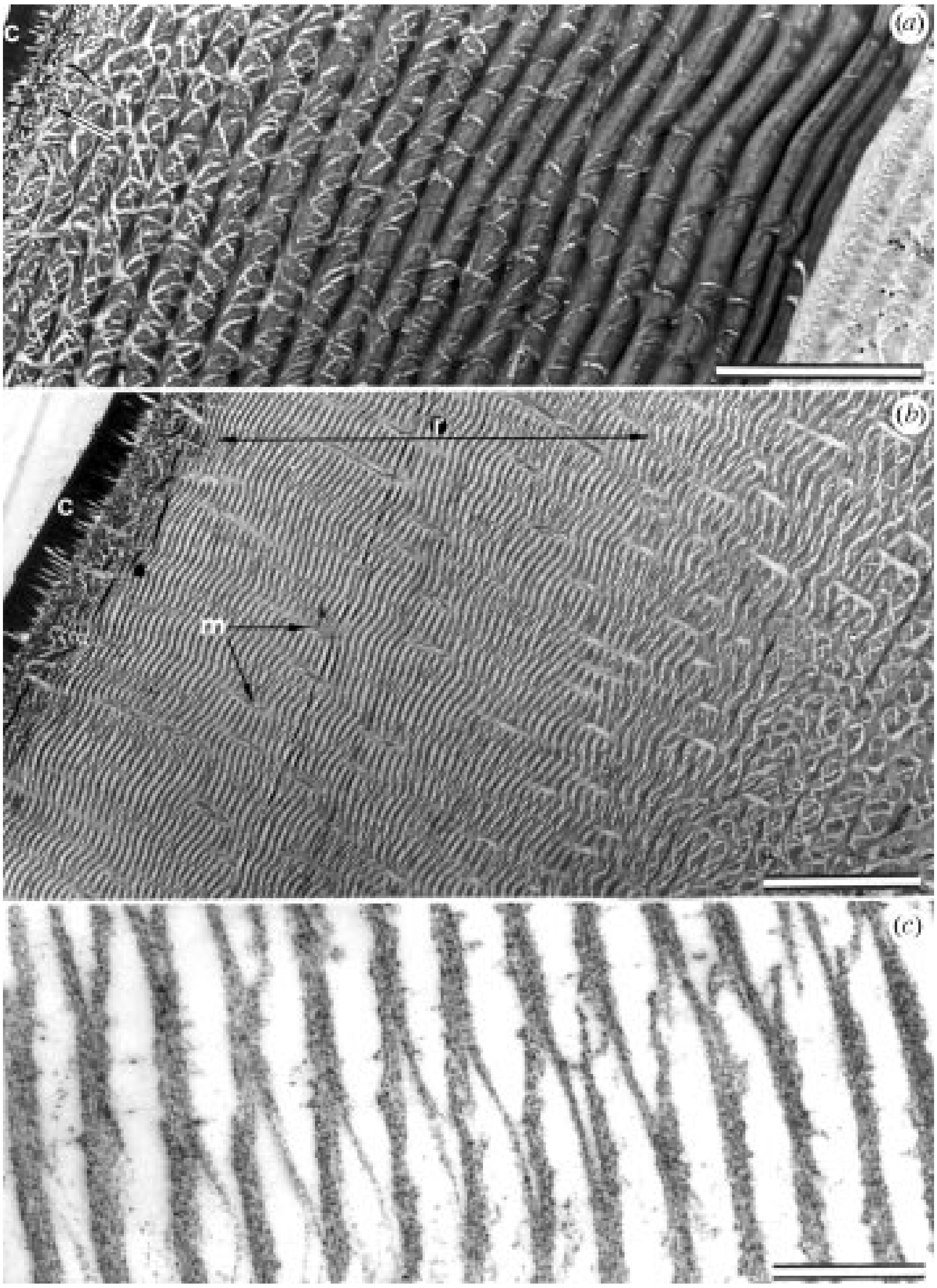

Figure 1. Transmission electron micrographs of the cuticle of swimming paddles of adult *Ovalipes*; c represents epicuticle (external layer). (*a*) *Ovalipes australiensis* (non-iridescent); multilayer reflector for crab-visible light is absent (the periodicity in this structure is *ca.* 1 µm, which would reflect wavelengths in the infrared). (*b*) *Ovalipes molleri* (iridescent), bearing a multilayer reflector (area r) in the position arrowed in (*a*); m represents examples of pore canals. (*c*) Close-up of a section of the multilayer reflector of *O. molleri*, from area r in (*b*). (*a*, *b*) Scale, 5 µm; (*c*) scale, 500 nm.

postfixed in 1% osmium tetroxide, and then dehydrated through an alcohol series and finally 100% acetone. Specimens were then embedded in Spurr resin, and 60 nm sections were cut. Sections were stained using lead citrate and uranyl acetate, then examined in a transmission electron microscope (TEM).

In *O. molleri*, the cuticular surface was devoid of periodic structures. However, the iridescence displayed by the surfaces of the body and appendages of *O. molleri* is the result of multilayer reflectors. These are intracuticular structures, which appear as numerous, alternating light and dark layers in the TEM (figure 1*b*,*c*). The refractive indices of the layers are assumed to be 1.34 for the low index layer, which is probably essentially water, and 1.52 for the high index layer (see Land 1972), consisting of chitin (see Stevenson 1985). The chitin layers are separated within a liquid matrix in a unique manner. Each layer is composed of about eight (dependent on position in stack), thin, tightly packed chitin sheets. At intervals of 2–4 µm, three sheets branch off at an angle of *ca.* 20°, alternating branches diverging in opposite directions, to join the layer below, forming 'trapezoid' shapes and thus acting as structural supports (like a girder system). Approximately five sheets remain in the complete layer for a relatively short lateral distance of about 0.5 µm. However, three chitin sheets from the layer above then join with the layer to reform the original eight or so sheets (figure 1*c*). Therefore, the number of sheets in each layer is constant for most of the layer length. This is important because the total thickness of the chitin layer is about a quarter of the wavelength of light, and the composite of layers forms a multilayer reflector. Furthermore, the branches leaving each layer contain only three chitin sheets and are too thin to alter the optical effect of the multilayer reflector significantly. The branches impart rigidity to the chitin component of the reflector, thus preventing the chitin layers from collapsing.

The multilayer reflector in *O. molleri* deviates from the theoretically optimal quarter-wave stack (see Land 1972) in that each layer is corrugated and there is a small, progressive change in the thickness of the layers with depth in the structure. The corrugations are non-conformal throughout the structure, i.e. the crests of adjacent layers do not line up along a perpendicular (surface normal) transect through the reflector. This removes the diffraction effects which would otherwise occur, as the phases of the diffracted beams are then randomized. The reflector, therefore, behaves purely as the multilayer type (see Land 1972).

To simulate the colour of the *O. molleri* reflector, a multilayer structural model was used where the structure was viewed as consisting of tilted 'blocks' of multilayers (figure 2*a*). The watery layers were assumed to have constant thickness throughout, but the thickness of the chitin layers was assumed to increase with depth in two stages, approximately in accordance with the micrograph of figure 1*b*. The typical size of a coherent block of layers near the top was taken to be ten chitin layers. The top layer in the simulated structure was therefore taken to consist of ten chitin layers 75 nm thick. Beneath this block were placed two additional coherent blocks, each containing five chitin layers, of thickness 87 nm and 94 nm, respectively. The calculated reflectance curve of this structure at 45° incident angle is shown in figure 2*b*. The colour of the resultant reflection was determined to be a well-saturated blue (maximum wavelength 440 nm) with CIE coordinates $x = 0.166$, $y = 0.091$, and luminosity 0.822. The principal effect of tilting the multilayer into blocks is to broaden the range of setting angles of the reflector that reflect a particular wavelength in one direction. When incident light is in the vertical plane, a missetting of the reflector by up to 14° each side of the 45° from the horizontal position will still produce the horizontal reflection of blue light. The corrugated form of the layers in the reflector of *O. molleri* is unique among animals. In contrast to the condition of *O. molleri*, the cuticle of *O. australiensis* lacks a multilayer reflector for crab-visible light (figure 1*a*).

## 3. THE FUNCTION OF IRIDESCENCE IN *OVALIPES*

In *Ovalipes*, iridescent light display may play a similar role to sound production, but because the reflectance resulting from the multilayer reflector under blue light is restricted to an angular range of 28°, the crab may be able to achieve some degree of signal directionality in contrast to the omnidirectional sound produced via stridulation. The use of light display as a means of intraspecific signalling, and in particular, courtship display, is known in several marine taxa including myodocopid ostracods (Parker 1995), sapphirinid copepods (Chae & Nishida 1994, 1995) and some fish (Denton & Rowe 1994). The degree of iridescent display in *Ovalipes* group B1 is sexually dimorphic as a consequence of general sexual dimorphism. For example, the iridescent chelipeds are larger in males than in females of *O. molleri*.

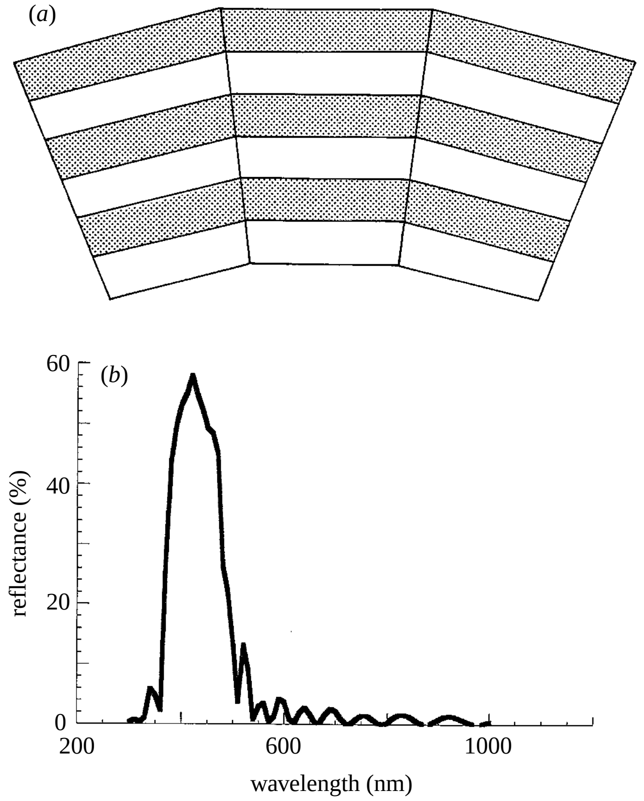

Figure 2. (*a*) Tilted blocks of multilayer reflectors which combine to approximate the effect of corrugations as in the reflector of *Ovalipes molleri*. (*b*) The reflectance wavelength curve calculated for the reflector of *Ovalipes molleri* at an angle of incidence of 45°. The structure assumed watery layers 116 nm thick and three sets of thicknesses for the chitin layers: from top to bottom there are ten chitin layers 75 nm thick, five layers 87 nm thick, and five layers 94 nm thick.

The advantage of broadening the angular reflectance profile of *Ovalipes* iridescence by tilting is apparent considering the distribution of light in the sea. It was found that in one body of water, at depths greater than *ca.* 40 m, the light distribution with respect to the angle to the vertical reaches an asymptotic form with a strong predominance of downward-travelling light to a depth of at least 500 m (Preisendorfer 1959; Tyler 1960; Denton & Nicol 1965). For each 10–20° increase in angle to the vertical, the light radiance is approximately halved (see Lythgoe 1979; Denton & Rowe 1994). At depths exceeding about 200 m, daylight becomes exclusively blue (Denton 1990). The effective limit of sunlight penetration in the sea is about 1000 m (Denton 1990). When at rest on the sea floor, with the carapace inclined at an angle of around 45°, blue light is therefore reflected laterally from the iridescent species of *Ovalipes* (i.e. parallel to the sea floor). Because the blue reflection is not highly sensitive to the angle of incidence as a result of the structure of the reflector, the carapace and appendages may be positioned over a 28° angular

Table 2. *Contingency table testing correlation between presence of extensive iridescence and habitat depth using Sillen–Tullberg (1993) independent states test (including outgroups,* Polybius henslowii *and* Liocarcinus holsatus)

(Shallow water (0), deep water (1). Fisher exact test $p < 0.05$ shows significant correlation between habitat depth and extensive dorsal iridescence in *Ovalipes*.)

| | habitat depth<br>shallow<br>0→0 | deep<br>0→1 | total |
|---|---|---|---|
| iridescence absent or minimal | 22 | 0 | 22 |
| iridescence extensive | 0 | 1 | 1 |
| total | 22 | 1 | 23 |

range even in a parallel illumination and still maintain lateral reflection (at the expense, however, of reduced maximum reflectance). If the layers of the reflector were flat, and the optical thickness constant, then the blue reflection may be too precise or angle-dependent to be practically employed by the crab. Thus, the crab may effectively display light laterally without drawing unnecessary attention from above, i.e. the risk of predation is reduced.

In shallow water, the *Ovalipes* reflector is probably a disadvantage. If the crab is in the open, yellow light (present in shallow water) will be reflected vertically into the water column. Such displays may attract the attention of predatory fish, for example, which often possess excellent vision in shallow water (see Land 1990). A compromise in iridescent display is present in some species of *Ovalipes* (group B2), which often live in relatively shallow water. In these species, iridescence is restricted to body areas that are slanted at *ca.* 45° when the crab is horizontal on the sea floor, thereby retaining blue reflectance parallel to the sea floor, albeit from relatively small areas. If other colours are reflected into the water column, the crab would appear as a series of small patches of light, acting as disruptive coloration. Hence, the crabs may escape predation.

## 4. EVOLUTION OF LIGHT DISPLAY IN *OVALIPES*

The fossil record for *Ovalipes* is relatively poor. The earliest known fossils of the genus, however, are from the Upper Pliocene of New Zealand (Glaessner 1960) and attributable to group A. The most parsimonious interpretation of the cladogram (figure 3) indicates that *Ovalipes* originated in shallow water and bore stridulatory structures. Group A species are principally Indo-West Pacific, whereas Group B species occur in both the western Atlantic (B2) and Indo-West Pacific (B1) (table 1).

In *Ovalipes*, the degree of iridescence inversely correlates with development of the stridulatory carinae. Group A species, with ‘well-developed’ stridulatory carinae, lack dorsal iridescence. The shallow-water B2 species, with ‘moderately developed’ stridulatory carinae, have sparsely distributed iridescence. Conversely, B1 species, with ‘reduced’ stridulatory carinae, bear extensive iridescence. These extensively iridescent species exclusively inhabit ‘deep’ waters, between about 80 and 475 m. Here, light intensity and spectral composition is very reduced. This enables deep-water *Ovalipes* to only reflect light ‘laterally’ and could explain the confinement of extensive iridescence in *Ovalipes* to deep water. Such directionality of light display is of course not possible in shallow water under ‘full’ spectrum light owing to the nature of the reflector. Therefore, in shallow water, light display may have no advantage for signalling over sound production, if the directional component is as important as implied in the literature (for examples, see Magnhagen 1991; Verrell 1991).

If the degree of development of stridulatory carinae corresponds to complexity or efficiency of the stridulatory repertoire, then it is likely that the deep-water species have shifted towards increased use of iridescent display as a means of sexual signalling. Although we have no direct evidence of this, our results show a significant ($p < 0.05$) relation between habitat depth and extensive dorsal iridescence (see figure 3). In fact, when ‘light’ characters are included in the phylogenetic analysis, the inferred evolutionary relationships are strengthened (in terms of topological robustness). This therefore resembles the evolution of light display in myodocopid ostracods (Parker 1995).

Verrell (1991) places the concept of ‘illegitimate’ receivers (i.e. predators and parasites) of sexual signals between other, ‘exploited’ species in an evolutionary context. The arms-race created among ‘exploited’ and ‘exploiter’ may promote divergence of sexual-signalling systems in the former. Such a divergence may generate sufficient sexual isolation among populations to lead to speciation (Verrell 1991). Predation may have been the main selection pressure in the evolution of the genus *Ovalipes*, where light display is ultimately a divergence from sound production as a means of intraspecific signalling, because of its increased species-targeting properties; the transition from sound production to light display therefore correlates with phylogeny. It is well-known that the evolution of visual and auditory signals is affected by predation (Endler 1978, 1983; Tuttle & Ryan 1982). ‘In general, the signal evolves as a local balance between the relative strengths of sexual selection and predation’ (Endler 1992, p. S127). Behavioural data involving deep-sea animals, however, are generally scarce and there are presently none available for the predators of deep-water *Ovalipes*. Nonetheless, this study of *Ovalipes* appears to be the first demonstration of an evolutionary shift in communication mode in animals.

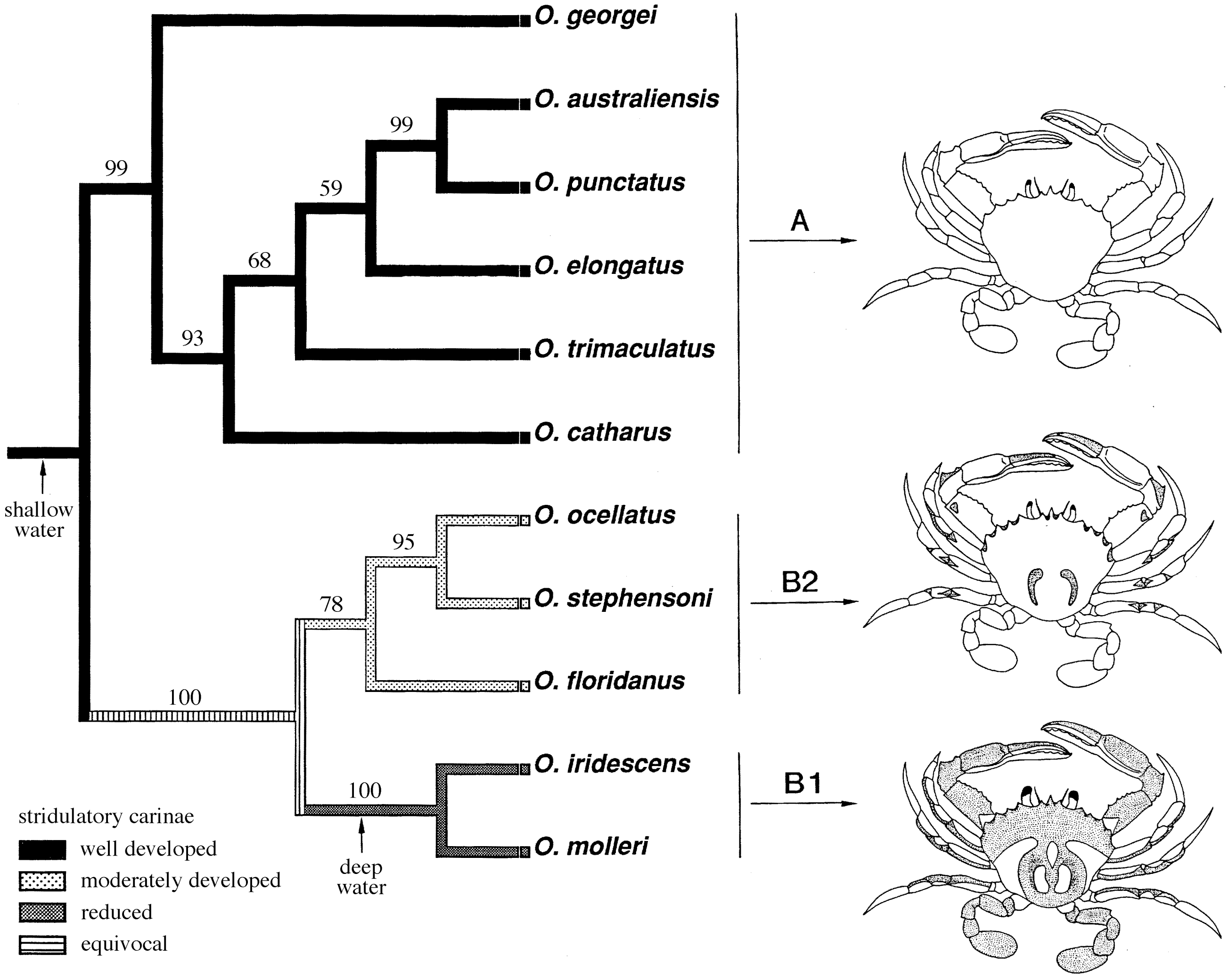

Figure 3. Single most parsimonious cladogram of *Ovalipes* based on 55 morphological characters, excluding iridescence (tree length 92, consistency index 0.837, homoplasy index 0.163, retention index 0.916). Character states were unordered and equally weighted. The input data matrix was produced in MacClade 3.0, and the cladogram was generated under the heuristic search option (TBR, MULPARS, DELTRAN, ten replicates) in PAUP 3.11. Outgroups (not shown) comprised two other polybiine species: *Liocarcinus holsatus* and *Polybius henslowii*. Bootstrap percentages, based on 100 randomized replicates, indicate robust cladistic structure (data available on request). The degree of development of stridulatory carinae is illustrated on the cladogram against generalized representatives from each clade (shading indicates distribution of iridescence).

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