The evolution of conspicuous facultative mimicry in octopuses: an example of secondary adaptation?

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The 'Mimic Octopus' *Thaumoctopus mimicus* Norman & Hochberg, 2005 exhibits a conspicuous primary defence mechanism (high-contrast colour pattern during 'flatfish swimming') that may involve facultative imperfect mimicry of conspicuous and/or inconspicuous models, both toxic and non-toxic (Soleidae and Bothidae). Here, we examine relationships between behavioural and morphological elements of conspicuous flatfish swimming in extant octopodids (Cephalopoda: Octopodidae), and reconstructed ancestral states, to examine potential influences on the evolution of this rare defence mechanism. We address the order of trait distribution to explore whether conspicuous flatfish swimming may be an exaptation that usurps a previously evolved form of locomotion for a new purpose. Contrary to our predictions, based on the relationships we examined, flatfish swimming appears to have evolved concurrently with extremely long arms, in a clade of sand-dwelling species. The conspicuous body colour pattern displayed by swimming *T. mimicus* may represent a secondary adaptation potentially allowing for mimicry of a toxic sole, improved disruptive coloration, and/or aposematic coloration.   © 2010 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2010, **101**, 68–77.

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INTRODUCTION

The survival of highly visible individuals, and especially the subsequent diversification of their descendents into lineages with successful conspicuous defence behaviours, remains a puzzling topic in evolutionary biology (Sword, 2002). Few animals exemplify this issue better than the 'Mimic' octopus (*Thaumoctopus mimicus* Norman & Hochberg, 2005). Even among a group of animals for which instant shape-changes and apparent disappearing acts are par for the course, the protean abilities of *T. mimicus* stand out. Like its relatives, this octopus is capable of demonstrating excellent crypsis and polyphenism; however, *T. mimicus* frequently increases its conspicuousness through the intensification of a high-contrast body colour pattern (Hanlon, Conroy & Forsythe, 2008), a behaviour believed to represent facultative imperfect (low-fidelity) mimicry of a visually conspicuous venomous sea snake [*Laticauda* spp.], visually conspicuous toxic flatfish [*Pardachirus pavoninus* (Lacepède 1802); *Zebrias* spp.], and/or a suite of drably coloured non-toxic flounders and soles (Norman, Finn & Tregenza, 2001; Hanlon *et al.*, 2008). A lack of standardized photographs precluded our ability to examine the degree of possible mimicry with statistical analysis of flatfish/octopus morphometrics and colour

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patterns. Although the toxicity of *T. mimicus* is unknown, it may be unpalatable (Norman & Hochberg, 2006), and potentially displays honest warning coloration. These behaviours are neurally controlled rather than anatomically fixed. *Thaumoctopus mimicus* can regulate conspicuousness while imitating animals (mobile and sessile) or inanimate objects, and frequently challenges the distinction between mimicry and crypsis (Endler, 1981; Hanlon *et al.*, 2008). By incorporating conspicuousness and possibly mimicry, rather than crypsis, into its primary defence, the ancestors of these octopuses experienced a behavioural shift from a situation in which 'the operator does not perceive the mimic and therefore makes no decision', to one based on the predator detecting the mimic and subsequently being deceived (Endler, 1981), or receiving honest warning.

Visual defences in Cephalopods

Crypsis and polyphenism are the most common primary defences (behaviours that decrease the predator's chances of encountering and detecting an animal as a prey item; Edmunds, 1974) in shallow-water octopodids (hereafter referred to as octopuses; Hanlon & Messenger, 1996). Although octopuses are functionally colour-blind (Marshall & Messenger, 1996; Mäthger *et al.*, 2006), many species have evolved through selective predation pressure the means to match their background shape, skin pattern, texture, and colour almost instantly (Packard, 1972). When motionless, some cephalopods can attain such excellent camouflage that public forums have incorrectly questioned the authenticity of videotaped examples, such as one described recently by Hanlon (2007; contested in http://www.metacafe.com/watch/1001148/amazing_camouflage/). In addition to crypsis achieved by the skin, their flexible bodies also allow them a tremendous diversity of body postures (Huffard, 2006). By changing shape frequently (polyphenism) octopuses may impair their predators' formation and use of a search image (Hanlon, Forsythe & Joneschild, 1999).

Crypsis is compromised each time an octopus moves to forage or escape predators (Hanlon *et al.*, 1999; Huffard, Boneka & Full, 2005; Huffard, 2006). Species that live on rocky reefs can duck into crevices and camouflage themselves against habitat irregularities when they traverse terrain and risk drawing attention to themselves (Hanlon, 2007). By contrast, octopuses living in homogeneous low-relief habitats like sand plains have few opportunities for concealment, and are especially vulnerable to exposure while away from their dens. These octopuses sometimes incorporate deceptive resemblance into locomotion (plant matter, Hanlon & Messenger, 1996; Huffard *et al.*, 2005; flatfish, Hoover, 1998; Hanlon *et al.*, 2008;

Hanlon, Watson & Barbosa, 2010), thereby sidestepping the need to hide per se. However, in most of these examples octopuses still imitate other cryptic objects or animals.

Visually conspicuous primary defences appear to be rare in cephalopods. In all known cases they occur in octopuses that can otherwise exhibit excellent camouflage. The tiny blue-ringed octopuses (*Hapalochlaena* spp.) flash iridescent aposomatic body patterns to warn of a tetrodotoxin-laced bite (Hanlon & Messenger, 1996); these rings can also be visible when the animal is resting. Examples of conspicuous mimicry consist of octopuses imitating visually obvious fish. The large *Octopus cyanea* Gray, 1849 (French Polynesia) can resemble the shape and body-colour pattern of a non-cryptic parrotfish when swimming well above complex reef structures (Hanlon *et al.*, 1999). *Octopus insularis* Leite, *et al.* 2008 has been reported to exhibit facultative social mimicry by temporarily imitating the fish with which it happens to be associated at the time (Krajewski *et al.*, 2009).

Perhaps the most widely publicized though insufficiently analysed example of conspicuous defence in octopuses is conspicuous 'flatfish swimming' by *T. mimicus*, found on sand plains throughout the Indo-West Pacific (Norman *et al.*, 2001). 'Flatfish swimming' comprises the following behavioural elements: similar swimming durations and speeds to that of flatfish, arms positioned to attain flatfish shape, both eyes positioned prominently as flatfish eyes, and undulating movements of arms during swimming that resemble fin movements of flatfish (Hanlon *et al.*, 2008). Thus far it has been reported for *T. mimicus*, *Macrotritopus defilippi* (Verany, 1851), 'White V' octopus, and the 'Hawaiian Long-Armed Sand Octopus' (Hoover, 1998; Hanlon *et al.*, 2008; Hanlon *et al.*, 2010). Unlike the latter three octopuses, which remain camouflaged during flatfish swimming, *T. mimicus* consistently incorporates conspicuousness, with a high-contrast dark brown and light cream body-colour pattern (Hanlon *et al.*, 2008). Whereas all of the octopuses mentioned here are capable of acute crypsis, at times *T. mimicus* utilizes a primary defence that makes no attempt at camouflage, and may actually aim to draw attention.

Towards an evolutionary understanding of a conspicuous primary defence in *T. mimicus*

Here we report patterns of behavioural trait distribution in extant octopuses and reconstructed ancestral states to explore possible scenarios for the evolution of conspicuous flatfish swimming in *T. mimicus*. Relationships among species, traits, and their reconstructed ancestral states can provide a highly informative framework for understanding changes in

both behaviour and morphology through time (Winter-bottom & McLennan, 1993). Central to this investigation is the well-documented fact that many behaviours, including visual defences and their associated body colour patterns (e.g. Brodie III, 1989), are heritable traits. Supporting the idea that flatfish swimming is inherited is the observation of this behaviour in a laboratory-reared octopus (the behaviourally, ecologically, and morphological similar *M. defilippi*) that had never seen a flatfish (Hanlon *et al*., 2010). Given the widespread use of flatfish swimming in *T. mimicus*, 'White V', *M. defilippi*, and the Hawaiian Long-Armed Sand Octopus, and its absence in other observed species that are also sympatric with flatfish, we assume that the ability to express this behaviour is a genetically determined presence/absence trait. However, recent reports of possible social mimicry (Krajewski *et al*., 2009) and conditional learning (Hvorecny *et al*., 2007) in octopuses point to the possibility that environmental cues and learning may also influence the expression of the traits examined here.

We address the order of trait distribution to explore whether conspicuous flatfish swimming may incorporate an exaptation that usurps a previously evolved form of locomotion for new purpose, as previously hypothesized (Huffard, 2006), or if it may be an adaptation. With adaptation, anatomical changes and corresponding behavioural uses evolve at the same time (Blackburn, 2002). Exaptations, by contrast, are traits that 'are fit for their current role . . . but were not designed for it' (Gould & Vrba, 1982), having evolved originally either as adaptations for other uses, or when inextricably linked to other selected traits (Andrews, Gangestad & Matthews, 2002). Once established, exaptations can then be followed by secondary adaptations related to the new use (Gould & Vrba, 1982). Specifically, we consider the onsets of: (1) activity during daylight hours (either diurnal or crepuscular); (2) the use of 'dorsoventrally compressed' swimming (DVC; swimming with the head and mantle lowered and the arms spread laterally; Fig. 1D; Video S1); (3) high-contrast dark-brown and light/white body (HCDL) patterns in the deimatic ('bluff') display; (4) expression of flatfish swimming; and (5) HCDL visible at rest, including high-contrast arm bands. All of these traits are considered essential to the use of conspicuous flatfish swimming as a visual defence. The presence of very long arms (here considered to be ≥ 6.5 times the mantle length) is examined as a potential morphological correlate to flatfish swimming because it may allow the better imitation of undulating flatfish fins.

Potential visibility to predators, whether via exposed habitat or daytime activity, can influence the evolution of visual defences (Martins, Marquez & Sazima, 2008). We predict that diurnal activity was an evolutionary precursor to conspicuous flatfish swimming, enabling generations of visual predators to select against poor mimics. The HCDL body patterns, in particular in the form of distinct arm bands, impart conspicuousness in this defence. In many octopus species the deimatic display during secondary defence involves high-contrast disruptive body patterns involving light and dark components (Fig. 1; Messenger, 2001). Thus HCDL is likely to have evolved early in this lineage.

Dorsoventrally compressed swimming is an essential aspect of flatfish swimming. In form, these two modes of locomotion are similar, but DVC does not necessarily incorporate the imitation of flatfish: the entire head and mantle may be raised rather than just the eyes, and the arms need not undulate like flatfish fins. For example, both *Abdopus aculeatus* (d'Orbigny, 1834) and *Wunderpus photogenicus* Hochberg, Norman & Finn, 2006 (Video S1) employ DVC, but not flatfish swimming.

The DVC mode of swimming may also be an efficient way for long-armed octopuses to swim. This streamlined mode of locomotion may incorporate lift, to increase biomechanic efficiency (Huffard, 2006) and combat the known physiological inefficiencies of jet-propelled locomotion in octopuses (Wells *et al*., 1987; Wells, 1990). DVC may be particularly important to octopuses with high mass relative to their jet-propulsive abilities, such as very large octopuses or those with disproportionally long arms. Heavier octopuses swim relatively slower (body lengths/time) than octopuses with less mass (as in *A. aculeatus*; Huffard, 2006). All else being equal, arm mass would be higher in long-armed octopuses than in their shorter-armed relatives. Yet without a corresponding increase in mantle size and volume, long-armed octopuses are likely to exhibit disproportionally weaker jet-propulsive abilities, and may need to rely more on lift during swimming.

MATERIAL AND METHODS

To examine the relationships of shallow water octopuses (Table S1) we estimated genealogical relationships among mitochondrial DNA (mtDNA) lineages using Bayesian and maximum-likelihood (ML) methods, as implemented in MrBayes MPI v3.1.2 (Appendix S1; Huelsenbeck *et al*., 2001; Ronquist & Huelsenbeck, 2003; Altekar *et al*., 2004) and PAUP* v4.0b10 (Swofford, 2002), respectively. The specific model chosen was the 'best-fit model' (SYM + I + G) selected by Akaike's information criterion (AIC) in MrModeltest 2.3 (Nylander, 2004). For the Bayesian analyses, the alignment was partitioned into four blocks: *16S* and the three codon positions for *cytochrome c oxidase subunit I* (*COI*). These genes were
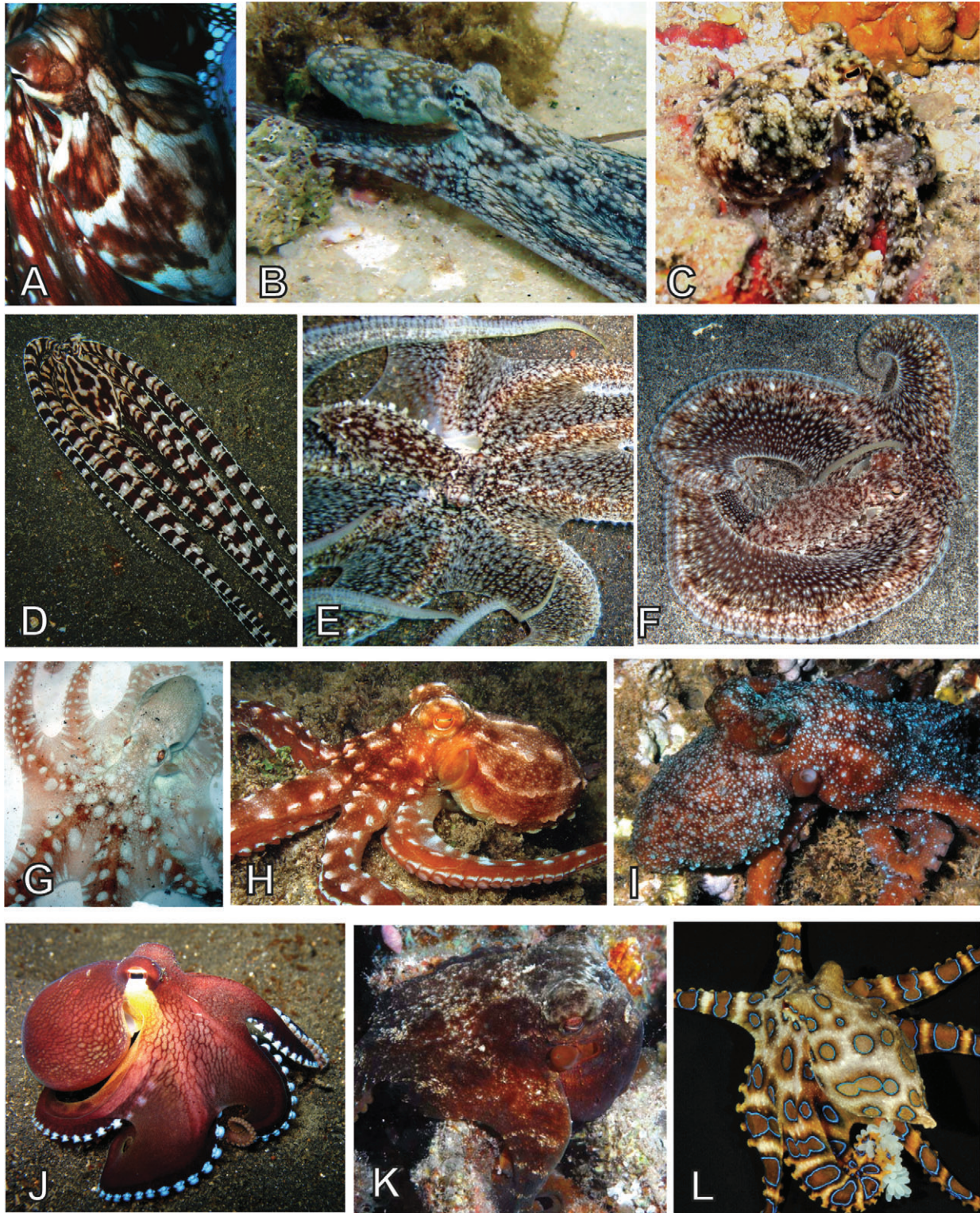
Figure 1. Example deimatic displays in some of the shallow-water octopuses examined here. A, *Octopus cyanea* (Palmyra Atoll); B, *Abdopus aculeatus*; C, *Abdopus* sp. 1; D, *Thaumoctopus mimicus*; E, 'White V'; F, Hawaiian Long-Armed Sand Octopus (photo by John Hoover); G, *Callistoctopus aspilosomatis*; H, *Callistoctopus ornatus*; I, *Callistoctopus luteus* (Sasaki, 1929) (photo by John Hoover); J, *Amphioctopus marginatus* (Taki, 1964); K, *Octopus* sp. 1 (photo by John Hoover); L, *Hapalochlaena lunulata* (Quoy & Gaimard, 1832) (photo by Roy L. Caldwell); remaining photos by C. L. Huffard.

chosen because they are well represented for octopo-dids in GenBank, allowing for a broad sampling of taxa. MrModeltest was independently applied to each partition. Three different models were assigned to the four partitions (for *16S* and the first *COI* codon position we used nst = 6 rates = invgamma GTR + G + I; for the third *COI* codon position we used nst = 6 rates = gamma GTR + Gamma; and for the second *COI* codon position we used HKY + I). The MrBayes analysis (Appendix S2) ran for 50 000 000 generations, and we sampled every 1000 trees. We determined a burn-in value by examining the sample parameter values using Tracer v1.4. The distribution of parameter values reached stationarity by 12 500 trees. For ML analyses, trees were rooted using the out-group species noted above. The specific model chosen was the best-fit model (SYM + I + G) selected by AIC in MrModeltest 2.3: the concatenated *COI* and *16S* alignment length is 1216 base pairs; transition/transversion ratio = 2.9925; nucleotide frequencies, A = 0.2638, C = 0.2675, G = 0.2404, and T = 0.2282; rates = gamma; shape parameter for a gamma distribution = 0.5625; and Pinvar = 0.4712. ML analyses were conducted using the heuristic search mode with 'as is' addition and TBR branch-swapping. ML Bootstrap analyses (1000 replicates) used the same model and search options as above. All analyses were performed on an 88-core Apple Xserve Xeon cluster, using the iNquiry bioinformatics cluster tool (v2.0, build 755). Specimens were collected from localities throughout the tropical Pacific, and we compared these taxa with existing samples deposited in GenBank (Table S1). Out-groups were specimens of *Vampyropteuthis* and *Argonauta* following the results of previous investigations into cephalopod phylogeny (Carlini, Young & Vecchione, 2001; Lindgren, Giribet & Nishiguchi, 2004).

To our knowledge, the resulting tree (Fig. 2) is currently the only reconstruction of Octopodid relationships that includes Thaumoctopus and its relatives, onto which we could map behavioral characters. Onto this tree we mapped arm lengths and behavioural traits based on published literature, the first author's own experiences observing these animals, and unpublished data from cephalopod biologists (Fig. 3; Table S2). In the event of discrepancies between our observations and published accounts we followed our own observations, as these were typically made on the animal that was the source of examined DNA. Ancestral states were reconstructed following unordered parsimony (Mesquite 2.5).

RESULTS AND DISCUSSION

PHYLOGENETIC RELATIONSHIPS

Thaumoctopus mimicus appears most closely related to the crepuscular *W. photogenicus*. These two octopuses appear closely related to the 'White V' octopus, which overlaps both species (at least partially) in geographic range, habitat, and activity patterns. The ecologically similar but geographically distant 'Hawaiian Long-Armed Sand Octopus' is also found in this clade. We recommend that these latter octopuses be placed in the genus *Thaumoctopus* (with the genus *Wunderpus* treated as a synonym) when described, because of nominal seniority. Because the *Thaumoctopus* + *Wunderpus* clade does not reflect a unified taxonomic grouping, we refer to this as the 'Long-Armed Sand Octopus' clade (LASO). Tissue for the behaviourally, ecologically, and morphologically similar *M. defilippi* was not available. LASO appears sister to the highly cryptic and primarily diurnal *Abdopus* clade, found in intertidal and subtidal reef flats throughout the tropical Pacific. The clade formed by LASO + *Abdopus* is sister to the *O. cyanea* clade of large but cryptic reef-dwelling octopuses. Morphological, genetic, and behavioural affinities among these octopuses have been noted previously (Norman & Finn, 2001; Guzik, Norman Mark & Crozier, 2005; Huffard, 2007). *Octopus cyanea* Gray, 1849, described as one single species from Australia, is commercially important throughout its range (Norman, 1992), and represents at least three distinct populations (Hawaii, the Line Islands, and Indonesia).

PATTERNS OF TRAIT DISTRIBUTION

Contrary to a previous prediction (Huffard, 2006), flatfish swimming by LASO does not appear to be an exaptation. Rather, both DVC and flatfish swimming may have evolved in conjunction with exceptionally long arms in their most recent common ancestor. In this case, it appears that corresponding behavioural and morphological traits emerge concurrently, following the definition of 'adaptation' (Blackburn, 2002). This potential adaptation may have yielded selective advantages via possible flatfish mimicry, improved biomechanic efficiency, or both. Because some gape predators of LASO may not be able to fit an adult flatfish into their mouth quickly, flatfish mimicry without imitation of a toxic model may still provide survival and fitness advantages (Huffard, 2006). LASO + *A. aculeatus* species all have long arms and exhibit DVC. This mode of locomotion may have evolved to combat the inefficiencies of forward (eyes or arms-first) swimming by octopuses with long arms. *Octopus kaurna* Stranks, 1990 and *Callistoctopus ornatus* (Gould, 1852) also have long arms, but unlike LASO + *Abdopus* species, their dorsal arms are disproportionally robust compared with their ventral arms. This morphology may impose unique locomotory constraints on forward swimming that may have precluded the evolution of DVC.
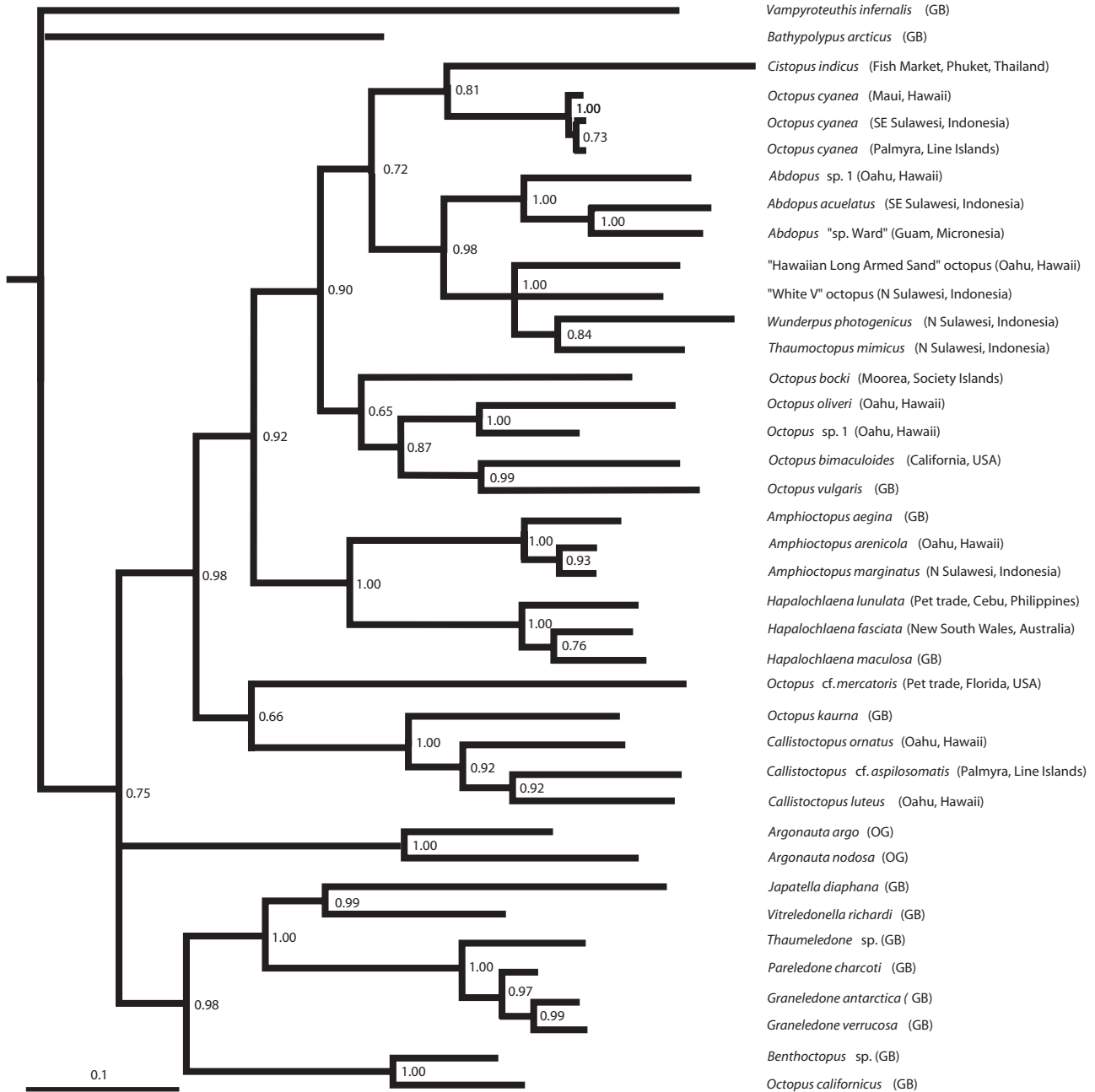
Figure 2. Phylogenetic relationships (location given in parentheses). Numeric values represent Bayesian posterior probabilities.

The conspicuous use of HCDL during primary defence appears unique to *T. mimicus* and *W. photogenicus*. The increased expression of this body pattern may represent a secondary adaptation for possible mimicry of conspicuous models, a form of disruptive coloration, or possibly honest signalling of unpalatability. The use of HCDL in the deimatic display appears concurrently with diurnal activity in the most recent common ancestor of *LASO* +

Abdopus + *O. cyanea* + *Cistopus indicus* (d'Orbigny, 1840), and again in the most recent common ancestor of *O. bimaculoides* and *O. vulgaris*. However, this colour pattern is evident in the resting coloration of *T. mimicus* and *W. photogenicus* only. For all other octopuses in this study, the HCDL pattern is apparent only in the deimatic display (when disturbed). Conspicuously bold arm bands may enable the mimicry of banded sea kraits and lionfish by these two octopuses,
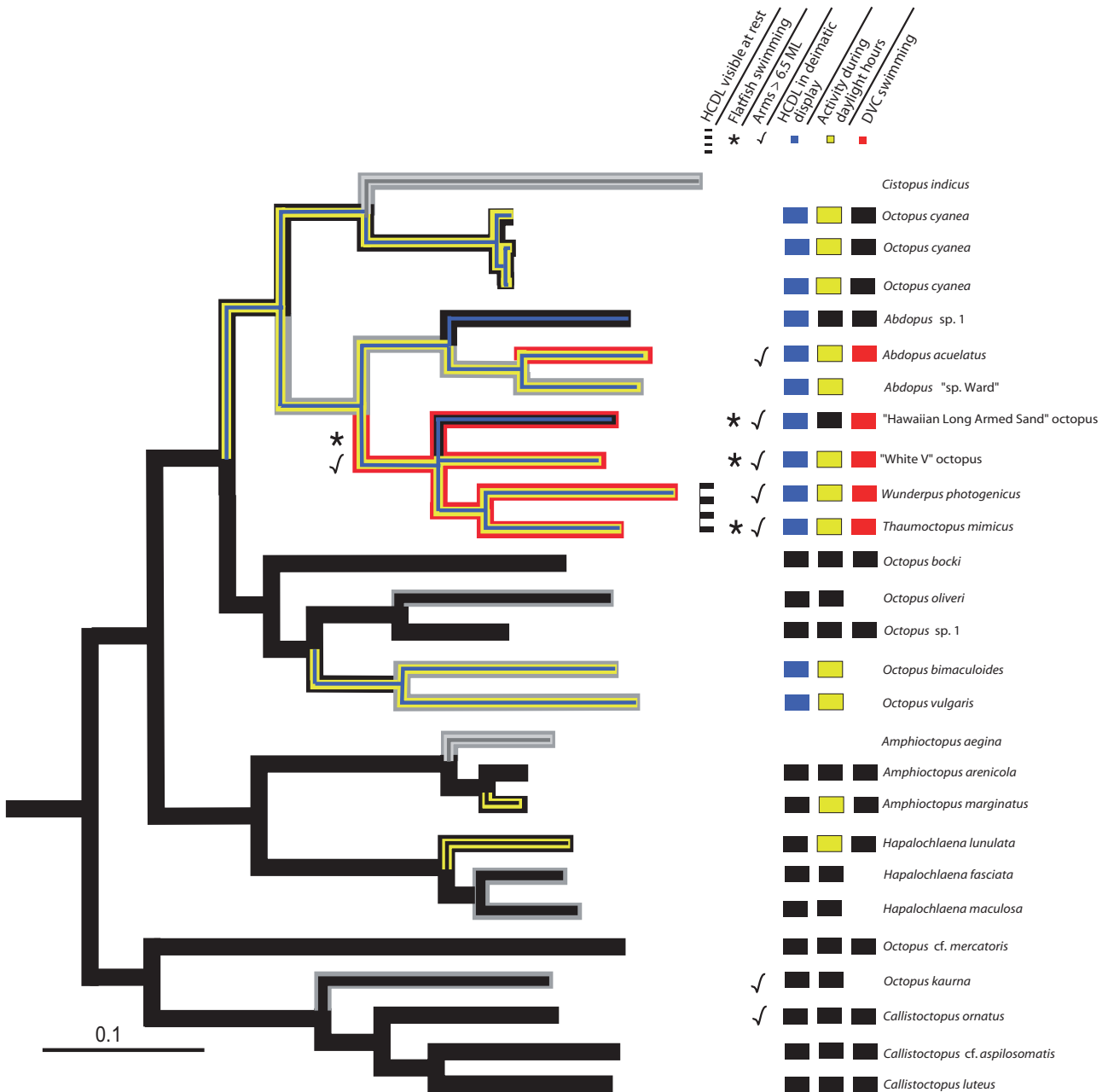
Figure 3. Trait distribution and character reconstruction of extant and ancestral benthic octopodids in Figure 2. Grey bars represent unknown values. Data sources for traits are given in Table S2.

and toxic soles by *T. mimicus* (Norman *et al.*, 2001). Alternatively, this disruptive pattern may inhibit the ability of predators to detect *T. mimicus* and *W. photogenicus* body outlines in their natural habitat: black sand substrate flecked with white shell fragments. Correspondence in white component size for HDCL and the substrate should be analysed (as was carried out for disruptive coloration in cuttlefish; Hanlon *et al.*, 2009) to assess this possibility. Finally, the intake and subsequent rejection of *T. mimicus* as prey

by a flounder suggests this octopus may be unpalatable (Norman & Hochberg, 2006), and that it uses conspicuousness as a warning coloration.

IMPERFECT MIMICRY

Mimics that use multiple models may evolve imperfect mimicry of an intermediate form, rather than multiple strong resemblances (Sherratt, 2002). *Thaumoctopus mimicus*, 'White V', and the 'Hawaiian

Long-Armed Sand Octopus' appear to resemble a suite of flatfish rather than a single species [although 'White V' has been suggested to be a high-fidelity mimic of *Bothus mancus* (Broussonet, 1782); Hanlon *et al*. 2010]. These octopuses inhabit areas of very high teleost biodiversity, the former two overlapping with what appears to be the global epicentre (Roberts *et al*., 2002), with numerous potential models and predators. All three octopuses overlap in range with the common and similarly coloured *B. mancus* and *Bothus pantherinus* (Rüppell, 1830). According to http://www.fishbase.org, an additional 30 nominal Bothid and Soleidid taxa overlap *T. mimicus* and 'White V' in approximate size (> 11 cm total length), depth (< 50 m), habitat (sand), and possible geographic range within Indonesia. These fishes span from conspicuous to cryptic, and include both toxic (e.g. *P. pavoninus* and potentially *Zebrias* spp.) and non-toxic lineages. Although the lack of a conclusive flatfish model has generally been identified as a weakness in the cephalopod mimicry literature (Hanlon *et al*., 2008), we feel it reflects imperfect mimicry of multiple models in regions of high biodiversity.

Visual defences can be maintained if they are 'good enough' to cause pause during the speed-versus-accuracy decisions of predators: this applies to imperfect mimicry with or without conspicuous coloration (Edmunds, 2000; Chittka & Osorio, 2007). These decisions may cause enough confusion to allow 'mimic' octopuses to escape predation. In *T. mimicus*, even minor resemblance to rare toxic models may further slow reactions and benefit survival. We do not know how potential unpalatability (Norman & Hochberg, 2006), perhaps in conjunction with arm autotomy (exhibited by LASO + *Abdopus*; Norman & Hochberg, 2006; C. L. Huffard, unpubl. data) may further contribute to predator confusion, learning, and/or future avoidance (Maginnis, 2006). Although the toxicity of *T. mimicus* (and thus 'honesty' of a potentially aposematic signal) remains to be tested, conspicuous flatfish swimming appears to be a secondary adaptation that: (1) follows the concurrent appearance of very long arms and a unique mode of locomotion; (2) represents a shift towards predator detection rather than predator avoidance during primary defence in an otherwise cryptic lineage; and (3) may be reinforced if predators can learn from similar (though cryptically coloured) behaviours in sympatric relatives (e.g. Dafni, 1984).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. GenBank accession numbers, collection localities (newly analysed), and references (previous studies) for the samples used in this study.

Table S2. Behavioural and morphological traits for samples species. Order reflects top-bottom order of these taxa in Figure 3. A = Absent, D = Activity during daylight reported, N = Nocturnal, P = Present; U = Unknown; Very long-arms ($> 6.5 \times$ ML) in bold. Sources: 1) Norman and Sweeney (1997); 2) Hanlon and Messenger (1996); 3) Yarnall, 1969; 4) Forsythe and Hanlon (1997); 5) CLH unpublished data; 6) CLH personal observations in situ; 7) Norman and Finn (2001); 8) Huffard (2007); 9) Huffard (2006); 10) Ward, 1998; 11) Hoover, 1998; 12) Hanlon *et al*., 2008; 13) Norman, 2000; 14) Hochberg *et al*., 2006; 15) Norman and Hochberg, 2005; 16) CLH personal observations in aquaria; 17) Cheng, 1996; 18) Packard and Sanders, 1971; 19) Kayes, 1974; 20) Huffard and Hochberg 2005; 21) Norman, 1993; 22) Norman and Hochberg unpublished data. 23) Roy Caldwell personal observations in aquaria; 24) Toll, 1998.

Video S1. Dorsoventrally compressed swimming, but not flatfish swimming, by *Wunderpus photogenicus*.

Appendix S1. DNA isolation, amplification, and sequencing.

Appendix S2. MrBayes command blocks.

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