Evolutionary variation in the expression of phenotypically

plastic color vision in Caribbean mantis shrimps, genus *Neogonodactylus*.

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Summary

Many animals have color vision systems that are well suited to their local environments.

Changes in color vision can occur over long periods (evolutionary time), or over relatively short periods such as during development. A select few animals, including stomatopod crustaceans, are able to adjust their systems of color vision directly in response to varying environmental stimuli. Recently, it has been shown that juveniles of some stomatopod species that inhabit a range of depths can spectrally tune their color vision to local light conditions through spectral changes in filters contained in specialized photoreceptors. The present study quantifies the potential for spectral tuning in adults of three species of Caribbean *Neogonodactylus* stomatopods that differ in their depth ranges to assess how ecology and evolutionary history influence the expression of phenotypically plastic color vision in adult stomatopods. After 12 weeks in either a full-spectrum "white" or a narrow-spectrum "blue" light treatment, each of the three species evidenced distinctive tuning abilities with respect to the light environment that could be related to its natural depth range.   A molecular phylogeny generated using mitochondrial cytochrome oxidase C subunit 1 (CO-1) was used to determine whether tuning abilities were phylogenetically or ecologically constrained. Although the sister taxa *N. wennerae* and *N. bredini* both exhibited spectral tuning, their ecology (i.e. preferred depth range) strongly influenced the expression of the phenotypically plastic color vision trait. Our results indicate that adult stomatopods have evolved the ability to undergo habitat-specific spectral tuning, allowing rapid facultative physiological modification to suit ecological constraints.

Introduction

There are many examples of visual systems adapted to local environmental conditions in aquatic environments (Lythgoe and Partridge 1989; Lythgoe 1990; Partridge and Cummings 1999). For example, in temperate communities, sympatric species of surfperch that occupy different microhabitats have spectral sensitivity variation correlated with illumination characteristics of each environment type (Cummings and Partridge 2001). Scotopic spectral sensitivity can vary among populations of sand gobies (*Pomatoschistus minutus*) living under different light conditions (Jokela et al. 2003). Coral reef lutjanids (snapper fish) also have maximal photopigment absorbances (i.e. λmax) well-correlated with differing light conditions in the areas they inhabit (Lythgoe et al. 1994). In cichlid fishes living in photically different habitats in Lake Malawi, long-wavelength shifted and UV-shifted clades exist, produced by interspecific variation in gene expression of subsets of cone opsin genes (Carleton and Kocher 2001). The feeding ecology and habitat preferences of these fishes are hypothesized to have induced an adaptive radiation in nuptial coloration as well (Allender et al. 2003). Invertebrate examples also are abundant, ranging from crustaceans to cephalopods (Morris et al. 1993; Cronin et al. 1994b; Marshall et al. 1999). It is thought that changes in the sensitivities of visual systems with varying photic conditions act to increase visual contrast (McFarland and Munz 1975), improving visual performance in given light environments.

Stomatopod crustaceans have a complex color vision system, often adapted to local photic conditions using an unusual response that involves plastic changes in photoreceptor filtering (Cronin et al. 2000). Stomatopods make up a group of moderate-sized, benthic marine predators that branched off from other Malacostracans approximately 400 million years ago. Modern stomatopods (also known as mantis shrimp) are placed in seven superfamilies with over

450 species that occur mostly in coral reef environments (Ahyong and Harling 2000; Ahyong and Lowry 2001onwards). Many species in the superfamilies Gonodactyloidea and Lysiosquilloidea have an intricate color vision system with up to ten photoreceptor classes in the "visible" spectrum (Manning et al. 1984; Cronin and Marshall 1989b; Cronin et al. 1994c; Cronin et al. 1994d; Marshall and Oberwinkler 1999; Harling 2000) as well as four or more classes of ultraviolet-sensitive receptors (Schiff 1963; Cronin et al. 1994d; Marshall and Oberwinkler 1999). Some retinal classes of ommatidia contain colored intrarhabdomal filters that narrowly tune the sensitivities of underlying photoreceptors (Marshall et al. 1991; Cronin et al. 1994a). Particular species that inhabit a wide depth range (from shallow intertidal to > 20 m) have evidenced phenotypically plastic modification of their color vision system, produced by changes in the colored filters in response to varying light environments (Cronin et al. 2001; Cronin and Caldwell 2002; Cheroske et al. 2003). Stomatopod post-larvae maintained in laboratory lighting approximating shallow water (full-spectrum, white) or deep water (narrow-spectrum, blue) shift their spectral sensitivities to improve the match to surrounding light conditions in as little as a few weeks (Ibid.).

Although previous work has only involved postlarvae, adult mantis shrimp of individual species can occur in different depth/light environments as well. The genus *Neogonodactylus* consists of approximately 20 species with typical ecology for gonodactyloids, occurring over a range of depths on coral reefs in the tropical eastern Pacific, western tropical Atlantic, Caribbean and Gulf of Mexico (Manning 1995). Some of the western Atlantic species of *Neogonodactylus* occur parapatrically segregated by habitat depth. Along the shores of the southeastern United States, *N. wennerae* is most common at depths from 10-30 meters (Manning 1969; Manning and Heard 1997). As such, this taxon should experience large fluctuations in light environments and

would be a likely species in which spectral tuning would evolve. In contrast, *N. oerstedii* commonly occurs in waters less than 5 meters and rarely down to 29 m, and *N. bredini* is most common in the intertidal in 2 meters or less of water. These species would therefore experience relatively homogenous light environments and the evolution of spectral tuning would be unlikely in such taxa. However, until 1997, *N. wennerae* was incorporated into *N. bredini* when Manning and Heard (1997) separated *N. bredini* into two species based on two minor morphological differences and their different depth ranges. Thus, if spectral tuning does exist in adults, the expression of this trait may be influenced by phylogenetic affinity as well as habitat.

Given what is currently known about how light environments can influence visual systems in stomatopods and about the ecology of closely-related *Neogonodactylus* species, the research reported here explores whether the visual system in adult stomatopods is labile and whether this physiologically-adaptive sensory system relates to features of stomatopod habitats or phylogeny. Using laboratory light treatments, we examined the abilities of three closely-related species to express phenotypically plastic color vision changes. The physiologically-adaptive color vision trait of these three species was mapped onto a molecular phylogeny to assess how quickly this trait can evolve in recently diverged species and the degree to which spectral tuning is a function of ecology or shared evolutionary history.   Currently, only two distantly-related stomatopod species (both Pacific species, from different superfamilies) have been reported to have phenotypically plastic color-vision (Cronin et al. 2001; Cheroske et al. 2003). If this physiological tuning is an inherent trait to all stomatopods with complex color vision, then environmentally induced spectral changes in sensitivity should be exhibited in many species regardless of habitat. In contrast, if expression of the trait is influenced by the ecology of each species, only those occurring over a wide depth range (>10 m) should show spectral acclimation

to different light conditions.

Materials and Methods

Adult individuals (35-50 mm in length) of *N. oerstedii* Hansen 1895 and *N. wennerae* Marshall and Heard 1997 were purchased from tropical fish suppliers in Florida. *N. oerstedii* also were collected in nearshore, shallow water (<5 meters) off Key Largo in September 2001 (n=8) and March 2002 (n=6). Additional *N. wennerae* (n=9) were collected from a "live rock" mount at approximately 7 m depth in the Gulf of Mexico near Tampa. We hand-collected adult *N. bredini* Manning 1969 (29-45 mm, n=10) from intertidal coral rubble (<1 meter) at two sites in Bermuda during July of 2003. All animals were transported to the aquarium facility at University of Maryland, Baltimore County (U.M.B.C.) in Baltimore, Maryland.

Animals were assigned randomly to individual 10-gallon saltwater aquaria, each with an Aqua-Clear Mini side-mounted water filter, 50W submersible heater and 18W fluorescent light source. Aquaria in the "white" light treatment were illuminated by GE Aquarays full-spectrum tubes, while "blue" light aquaria were illuminated by GE Aqua-Blue tubes surrounded by three layers of "Lagoon Blue" (HT 186) plastic stage lighting filter material (Lee Filters, Burbank CA) that absorbed wavelengths >550 nm. Animals were fed frozen shrimp two times per week, and 25% water changes were made once a month. Stomatopods were maintained under light treatments for 12 weeks before their visual systems were examined as described next.

We assessed spectral changes of intrarhabdomal filters in the two sets of ommatidia where they occur (Row 2 and Row 3 of the midband; see Marshall et al. 1991) using microspectrophotometry. Our methods are explained in detail elsewhere (Cronin and Marshall 1989a) but are described briefly here. Eyes were cryosectioned to 14 μm at -30º C and sections

mounted between microscope coverslips in mineral oil. Each section then was placed on a microscope stage and a circular, linearly polarized, 1.5 μm diameter, monochromatic beam of light was passed through a clear area of the preparation. The beam was scanned from 400-700 nm at 1 nm intervals to create a reference scan. It then was moved to pass through an intrarhabdomal filter and again spectrally scanned to measure the absorbance of the filter. In histological sections that were parallel to the long axis of the photoreceptors, intrarhabdomal filter lengths were estimated to the nearest ocular unit (± 0.5 μm) along the longitudinal axis using a calibrated ocular micrometer. Three to five replicate spectral scans and also length measurements (=sampling units) of each of the four filter classes were recorded and averaged per animal and then averaged for all animals (=experimental units) within a treatment. Spectral absorbances of all intrarhabdomal filter classes were compared using the wavelength of 50% absorbance (with peak absorbance normalized to 100%) on the long wavelength limb of each curve. Spectral and filter length data were analyzed statistically using a one-way ANOVA with a significance level of $p < 0.05$.

Mitochondrial cytochrome oxidase C subunit 1 (CO-1) was sequenced from seven Caribbean *Neogonodactylus* species as well as four other species from the Gonodactylidae identified by Barber and Erdmann (2000) as members of the sister clade to the *Neogonodactylus*. PCR amplifications were done using primers HCO and LCO (Folmer et al. 1994) following the methods of Barber and Erdmann (2000). Five microliters of PCR product were prepared for sequencing through digestion with 0.5 units of Shrimp Alkaline Phosphatase and 5 units of Exonuclease for 30 minutes at 37 ºC, followed by an inactivation step at 80 ºC for 15 minutes. PCR products were then sequenced using Big Dye (Ver 3.1, Applied Biosystems Corp.) chemistry and visualized with an ABI 377 automated DNA sequencer. Forward and reverse

sequences were compiled and proofread in Sequencher 4.2, and then aligned by eye.

Phylogenetic relationships were determined by maximum likelihood in PAUP (Swofford 2002) using model parameters determined by ModelTest 3.0 (Posada and Crandall 1998). The optimal topology was determined through a heuristic search, using 1000 random addition replicates, and 1000 bootstrap replicates were performed with 10 random addition replicates to determine robustness of the topology.

Results

No changes in Row 2 intrarhabdomal filter classes were observed in response to variation in light environment (Figure 1), a result consistent with previous studies (Cronin et al. 2001; Cronin and Caldwell 2002; Cheroske et al. 2003). The plastic response of Row 3 filters to different photic conditions varied among the three *Neogonodactylus* species used in this study. Both the proximal and distal Row 3 filters in *N. wennerae* were short-wavelength shifted in blue-light treated animals compared to white-light treated (Figure 1). Distal filters were shifted by approximately 15 nm, while proximal filters differed by approximately 8 nm (Table 1). Proximal filters in blue-treated animals also were significantly shorter in length relative to those of white-light treated animals (Figure 2, $F_{1,5} = 36.03$, $p < 0.005$). In *N. bredini*, distal Row 3 filters spectrally differed by approximately 16 nm (absorbing at shorter wavelengths in blue-treated animals), but there were no significant spectral differences in Row 3 proximal filters between light treatments (Figure 1, Table 1). Significant variation in filter length also was found in *N. bredini* Row 3 proximal filters between light treatments (Figure 2, $F_{1,8} = 15.19$, $p < 0.005$); proximal filters in blue-light treated animals were approximately 30% shorter in length compared to filters in white-light treated animals. There was no significant difference in spectral properties

or in length of either class of Row 3 filter in *N. oerstedii* (Figure 1 & 2, Table 1).

To examine how evolution and ecology influence the expression of this phenoptyically-plastic color vision trait, we constructed a molecular phylogeny using representatives from the three *Neogonodactylus* species of these experiments as well as other Caribbean stomatopod species. A total of 553bp of mitochondrial CO-1 was obtained from each of 16 individual stomatopods representing seven of the extant *Neogonodactylus* in the Caribbean and four outgroup taxa. Sequences aligned easily with no gaps or insertions and translated without stop codons. Of these characters, 187 were variable with 22 (11.2%) first, 1 (0.5%) second and 164 third (98.3%) third position changes, resulting three total amino acid changes, only one within the ingroup.

Modeltest 3.0 determined the optimal model to be GTR+I+G with empirical base frequencies, six substitution types (0.4351 14.7593 0.9800 1.6315 13.8116), gamma shape parameter = 1.9843, and the proportion of invariable sites = 0.6305. Results from 1000 random addition replicates recovered two topologies with –lnL = 2666.89636 (Figure 3). These topologies differed only in that one showed *N. bredini* from Bermuda more closely related to *N. wennerae* than to *N. bredini* from the Bahamas, while the other showed these three taxa in an unresolved trichotomy. The *Neogonodactylus* formed a strongly supported monophyletic group (100% bootstrap support). Within this clade, *N. curacaoensis* and *N. spinosissima* were sister taxa (82% bootstrap support), *N. oerstedii* from Belize was more closely related to *N. austrinis* than to *N. oerstedii* from Florida (87% bootstrap support), and *N. wennerae* and *N. bredini* were very closely related (98% bootstrap support) although their precise relationship was equivocal.

Discussion

Stomatopods have some of the most complex color vision systems in the animal kingdom and also may have some of the most plastic. In this report, we show that the light induced, spectral tuning of photostable, colored filters within individual photoreceptors, previously described only in postlarvae, also can occur in adult animals, indicating ecologically mediated, physiological plasticity. While the response varied among species, these visual filters changed both spectrally and in their lengths. The cichlid fish, *Aequidens pulcher,* is the only other well-documented example of an animal that adaptively responds to spectral changes in laboratory light treatments, expressing ontogenetic neural and behavioral changes in varying light conditions (Braun et al. 1997; Kröger et al. 1999; Kröger et al. 2003). Further, whereas cichlids require at least 17-19 months to affect a change, these changes in stomatopods occur within approximately 12 weeks, indicating that facultative responses can occur extremely rapidly.

The ecology of the three *Neogonodactylus* species studied here, specifically the photic properties of typical habitats, as well as evolutionary history seem to be contributing factors in the ability to express the phenotypically plastic color vision trait. The most ecologically restricted species, *N. oerstedii*, occurs primarily in shallow water and expresses spectrally invariant intrarhabdomal filters in different light conditions. Lengths of intrarhabdomal filters in this species also did not vary significantly between the light treatments. Thus, the capacity for a phenotypically plastic change in color vision in this species seems to be limited, at best. Since its adult depth range rarely exceeds a few meters, the largely invariant lighting conditions it experiences do not require active spectral tuning.

In contrast, *N. wennerae* is found over a wide range of depths (commonly 10-20 m but also <5 m) and is likely to experience a wide variety of ambient light environments. As seen in

our previous work, the reduction in intensity as well as the narrow spectrum of deeper water habitats can elicit the physiologically-adaptive changes in stomatopod color vision (Cheroske et al. 2003). While it is known that stomatopod visual systems can vary with organism size and also with intensity (Dore et al. 2005; Dore et al. *in press*), the fact that we sampled similar-sized adults during daylight hours indicates that these factors did not influence our results. Here, both Row 3 filters were spectrally short-wavelength shifted in blue-light treated animals compared to white-light treated individuals. In addition, proximal Row 3 filters in blue-light animals were significantly shorter in length than those in white-light animals. Previous histological work suggests that the density per unit length of stomatopod intrarhabdomal filters is relatively consistent, based on transverse sections of filters of various lengths containing constant-sized pigment vesicles (Marshall et al. 1991). Therefore, shorter filters should reduce the overall filter absorbance, allowing more and broader-spectrum light to be transmitted to underlying photoreceptors. Thus, both the spectral and the length changes in filters modify the spectrum of light reaching the underlying photoreceptors. Changes in the distal Row 3 filter affect spectral tuning not only of the distal photoreceptor but also of the proximal photoreceptor tier.

N. bredini has an intermediate visual response to a varying light environment. Unlike *N. wennerae,* only the distal Row 3 filter class varied spectrally with light treatments in this species. Nevertheless, by retaining phenotypic plasticity in this filter class, *N. bredini* is able to tune both of the underlying photoreceptor tiers. While proximal filters of Row 3 did not change spectrally, their lengths varied adaptively with light environment. *N. bredini* typically occurs in waters as shallow as or shallower than *N. oerstedii*, so the presence of any ability for spectral tuning is surprising. The limited ability to adapt to shifting light conditions in *N. bredini* is likely a result of recent shared evolutionary history with *N. wennerae*, a species that maintains a full

complement of adaptive reactions. The two species are morphologically quite similar, differing

only in the length of the rostral spine and in ventral coloration of the eyestalks (Manning and

Heard 1997), and our phylogenetic analyses confirm that they are very closely related. However,

despite the morphological and genetic similarity of these two species, it seems their ecology has

rapidly shaped the expression of adaptive visual traits.

Stomatopods are common benthic marine predators in shallow tropical and temperate

waters. With their numerous pelagic stages, larval stomatopods often travel passively with major

water currents and can disperse hundreds of miles, potentially expanding population distributions

(Reaka 1986; Reaka-Kudla 2000; Reaka 2001). The ecological and physiological requirements

of individual species can affect the successful establishment of a population and thus the ultimate

distribution of the species. In other gonodactyloid species (e.g. *Haptosquilla glyptocercus*; *H.

pulchella*), accurate predictions of species distributions need to consider not only large scale

water flow patterns but also specific depth and habitat preferences, proving that local ecology

can influence population biology in these animals (Barber et al. 2000; Barber et al. 2002a;

Barber et al. 2002b). As their ranges shift over evolutionary time, species encounter changing

photic environments. By altering intrarhabdomal filter transmission spectra and lengths,

stomatopods can increase the overlap between photoreceptor spectral sensitivity and the

available spectrum of light allowing excellent visual function in a range of photic habitats

(Cronin et al. 2001; Cheroske et al. 2003). The varying visual abilities of closely related mantis

shrimp species are directly linked with their particular habitat preferences, suggesting that the

evolution of sensory flexibility can proceed remarkably swiftly. Such flexibility, when present,

allows individuals that move into new depth environments, such as during juvenile migrations or

when adults hunt for new domiciles, to make efficient use of the available light in a matter of

weeks.

Results of the current work suggest that specific habitat characteristics influence the maintenance of a phenotypically plastic color vision trait in at least some mantis shrimps, and that such a trait can be modified rapidly in recently diverged species. Sensory systems operate at the interface between an animal and its environment, and one might expect these systems to maintain a measure of flexibility that reflects the evolutionary path taken by a species and that is available should its range continue to change. Evolutionary flexibility in sensory function could well be common in species that encounter diverse habitats with divergent assortments of stimuli.

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Table 1. Comparison of absorbance curves from the Row 3 filters in three species of *Neogonodactylus* after 12 weeks in blue or white light treatments. Data are mean 50% absorbance points (nm) with 1 standard deviation in parentheses. Asterisks designate statistically significant differences between treatments at $p < 0.05$.

Species	Light treatment	50% Absorbance points (SD) of Row 3 filters		Sample size (n)
		Distal	Proximal	
N. wennerae	Blue	589.3 (1.5) ⌉ *	643.7 (4.8) ⌉ *	5
	White	603.8 (6.7) ⌋	651.4 (2.6) ⌋	4
N. bredini	Blue	611.7 (4.6) ⌉ *	657.0 (2.7)	3
	White	596.0 (4.2) ⌋	656.5 (2.6)	7
N. oerstedii	Blue	612.6 (3.2)	659.9 (5.1)	8
	White	612.2 (5.1)	661.7 (7.0)	6
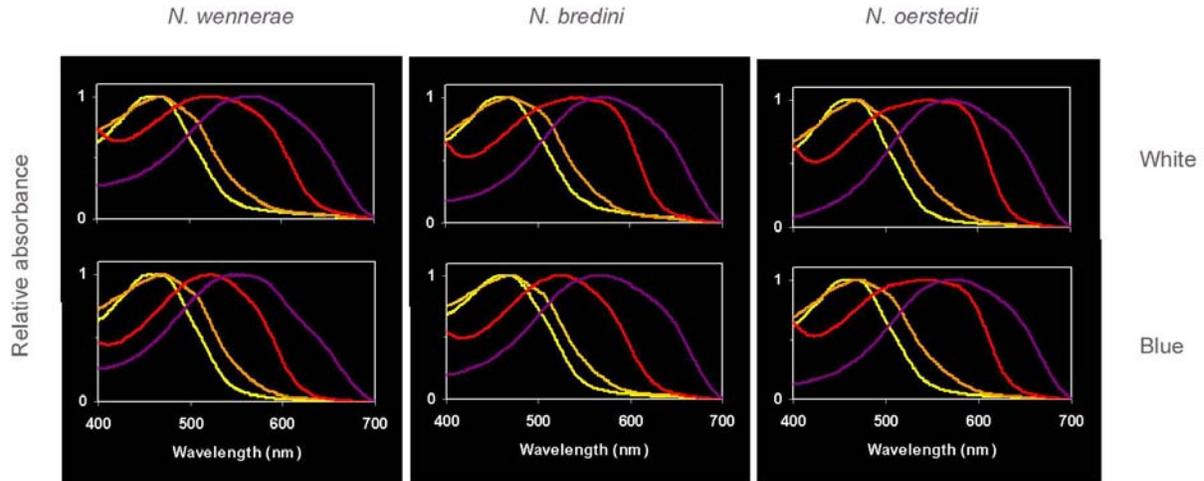
Figure 1. Relative absorbances of four classes of intrarhadomal filters in three species of *Neogonodactylus*. Top panels display data from white light-treated animals; lower panels are from blue light-treated animals. (All curves represent means of all animals within a given treatment group). Shorter-wavelength Row 2 classes are represented in yellow (distal) and orange (proximal). Longer-wavelength Row 3 classes are represented in red (distal) and purple (proximal). Both distal and proximal Row 3 filters are short-wavelength shifted in blue light-treated *N. wennerae* relative to homologous filter classes in white light-treated animals (left panels). Distal Row 3 filters in blue light-treated *N. bredini* (center panels) were short-wavelength shifted significantly compared to white light-treated animals. Row 3 filters in *N. oerstedii* (left panels) did not vary among light treatments. There were no significant spectral changes in either Row 2 filter in any of the *Neogonodactylus* species.
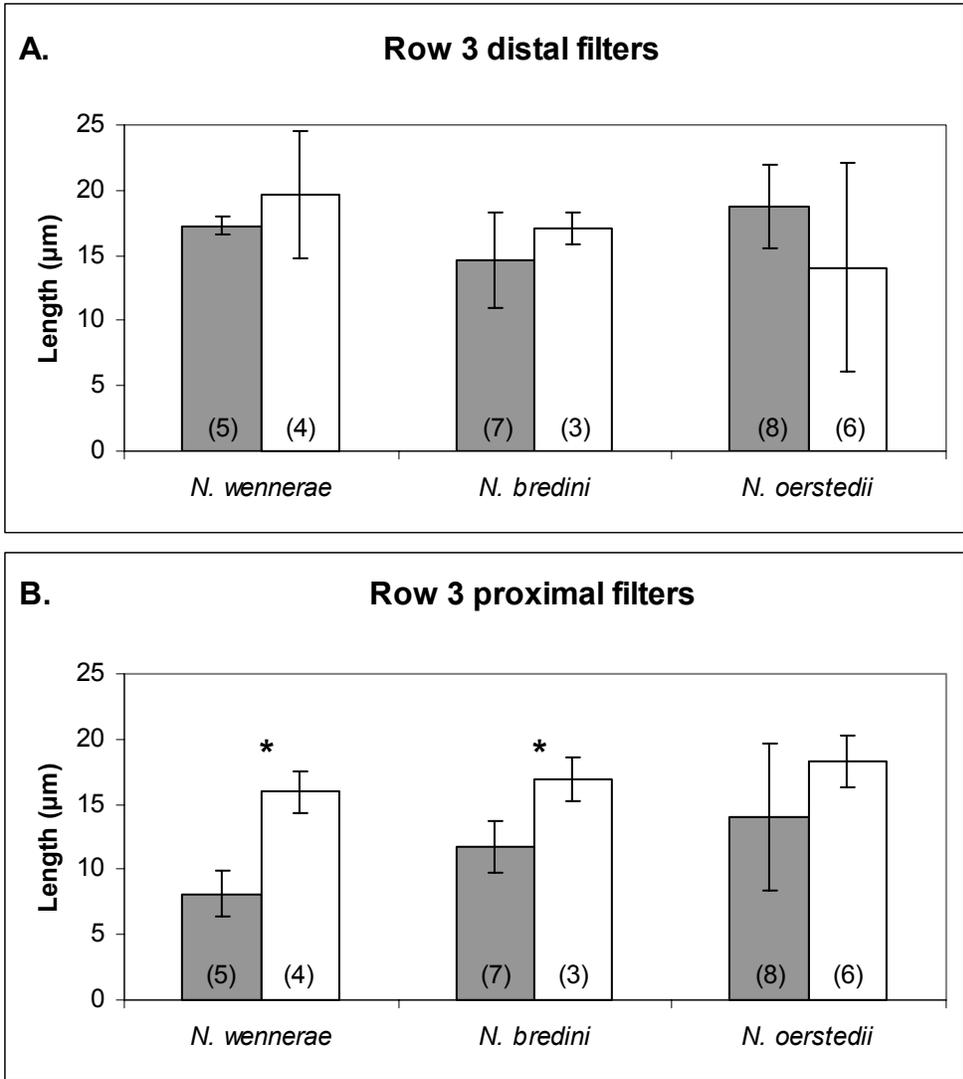
Figure 2. Intrarhabdomal filter lengths in three *Neogonodactylus* species under blue (grey bars) and white (white bars) light treatments. Values are means for all individuals within a treatment of each species and error bars represent ± 1 standard deviation. Asterisks designate statistically significant differences between treatments at $p < 0.05$. Numbers in parentheses represent the sample size for each corresponding bar.
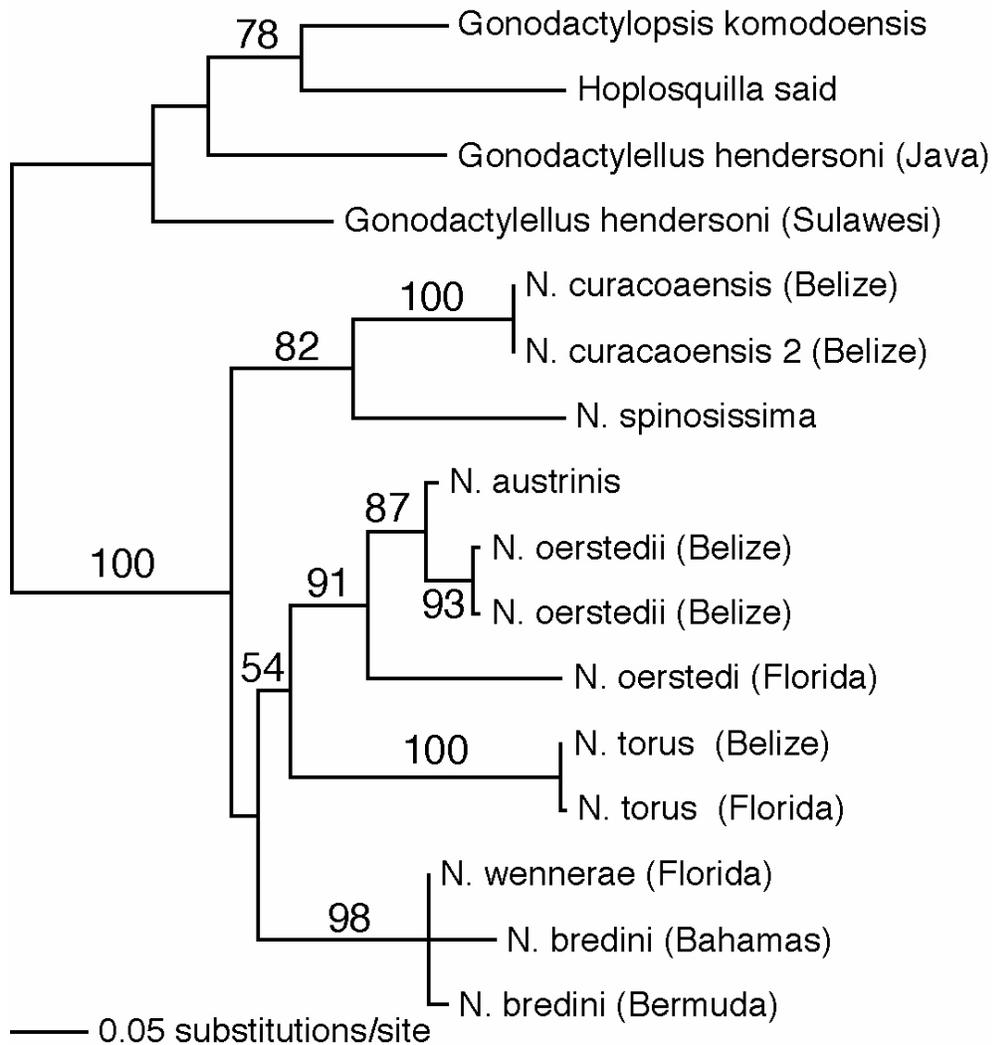
Figure 3. One of two maximum likelihood topologies with length of –lnL = 2666.89636
produced from a GTR+I+G model and a heuristic search with 1000 random addition replicates.
Bootstrap values are from 1000 bootstrap replicates with 10 random addition replicates.