Phylogenetics links monster larva to deep-sea shrimp

Heather D. Bracken-Grissom  
*Brigham Young University, Department of Biology, Florida International University*, brackengrissom@fiu.edu

Darryl L. Felder  
*University of Louisiana at Lafayette*

Nicole L. Vollmer  
*University of Louisiana at Lafayette; NOAA*

Joel W. Martin  
*Natural History Museum of Los Angeles County*

Keith A. Crandall  
*Brigham Young University; George Washington University*

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Phylogenetics links monster larva to deep-sea shrimp

Heather D. Bracken-Grissom1,2, Darryl L. Felder3, Nicole L. Vollmer3,4, Joel W. Martin5 & Keith A. Crandall1,6

1Department of Biology, Brigham Young University, Provo, Utah, 84602
2Department of Biology, Florida International University-Biscayne Bay Campus, North Miami, Florida, 33181
3Department of Biology, University of Louisiana at Lafayette, Louisiana, 70504
4Southeast Fisheries Science Center, National Marine Fisheries Service, NOAA, Lafayette, Louisiana, 70506
5Natural History Museum of Los Angeles County, Los Angeles, California, 90007
6Computational Biology Institute, George Washington University, Ashburn, Virginia, 20147

Keywords
Cerataspis monstrosa, Decapoda, DNA barcoding, larval–adult linkage, phylogenetics.

Correspondence
Heather D. Bracken-Grissom, Department of Biology, Florida International University, Biscayne Bay Campus, North Miami, FL, 33181. Tel: +305 919-4190; Fax: +305 919-4030; E-mail: heather.brackengrissom@fiu.edu

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Abstract
Mid-water plankton collections commonly include bizarre and mysterious developmental stages that differ conspicuously from their adult counterparts in morphology and habitat. Unaware of the existence of planktonic larval stages, early zoologists often misidentified these unique morphologies as independent adult lineages. Many such mistakes have since been corrected by collecting larvae, raising them in the lab, and identifying the adult forms. However, challenges arise when the larva is remarkably rare in nature and relatively inaccessible due to its changing habitats over the course of ontogeny. The mid-water marine species Cerataspis monstrosa (Gray 1828) is an armored crustacean larva whose adult identity has remained a mystery for over 180 years. Our phylogenetic analyses, based in part on recent collections from the Gulf of Mexico, provide definitive evidence that the rare, yet broadly distributed larva, C. monstrosa, is an early developmental stage of the globally distributed deep-water aristeid shrimp, Plesiopenaeus armatus. Divergence estimates and phylogenetic relationships across five genes confirm the larva and adult are the same species. Our work demonstrates the diagnostic power of molecular systematics in instances where larval rearing seldom succeeds and morphology and habitat are not indicative of identity. Larval–adult linkages not only aid in our understanding of biodiversity, they provide insights into the life history, distribution, and ecology of an organism.

Introduction
Exploration of our largely unknown oceans continues to yield fascinating biodiversity discoveries. In addition to novel forms of life (Osborn et al. 2009), chance collecting coupled with modern molecular genetic tools allow us to better understand longstanding enigmas. For over 180 years, the “monster” larva, C. monstrosa, has been such a puzzle to zoologists. This species, first discovered in the gut contents of a dolphin in 1828 (Gray 1828), is unique in its heavy armor, thick body, and exceptional horn ornamentation (Fig. 1). Nineteenth century collections of marine plankton commonly included developmental stages of crabs, shrimps, and lobsters that differed strikingly from their adult counterparts in morphology and habitat (Williamson 1915; Gurney 1939, 1942; Anger 2001). Not originally identified as a larval decapod, the single specimen of C. monstrosa was described as a “monstrous and misshapen animal” and placed within a new genus and species of primitive crustacean (Leptostraca) (Gray 1828). Although many such larvae have been subsequently linked to adult forms, C. monstrosa has eluded definitive placement despite nearly two centuries of effort due to its scarcity and extreme morphological uniqueness.

Cerataspis monstrosa is encountered only rarely in the wild with most information on this species coming from
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studies of gut contents of its predators, including skipjack (Katsuwonus pelamis), yellowfin (Thunnus albacares) and blackfin (T. atlanticus) tuna, and dolphin (Coryphaena hippurus) (Morgan et al. 1985). Interpretations of its unusual morphology have to date suggested it might represent the larval counterpart of some abyssal adult, the proposed candidates being a yet-to-be discovered shrimp from the family Aristeidae (Penaeoidea), or perhaps even a more distant relative of penaeoids (Heegaard 1966; Osborn et al. 2009; Hubert et al. 2010). Wild-caught planktonic larvae are often collected and reared to early postlarval stages in order to determine their adult identities (Gurney 1942; Rice and Williamson 1970). However, in the case of deep oceanic species, with highly metamorphic development involving striking vertical migrations between near-surface and deep-ocean waters, rearing protocols seldom succeed. In these instances, DNA data provide a common currency for comparison (Webb et al. 2006; Ahrens et al. 2007; Burns et al. 2008; Hubert et al. 2010).

Recently, mid-water oceanic collections in the northern Gulf of Mexico unexpectedly included a single specimen of Cerataspis monstrosa suitable for genetic analyses. We collected DNA sequence data from this specimen to compare to data in our extensive database of decapod crustacean DNA sequences (http://decapoda.nhm.org/, Table 1). Taxon selection was based on previous studies that suggested a relationship between Cerataspis and shrimp-like decapods. By the late nineteenth century, an affinity between Cerataspis to penaeoid shrimp had been proposed (Dohrn 1871; Giard and Bonnier 1892; Heegaard 1966), and by the early twentieth century, new observations suggested this peculiar form represented a protracted pelagic larval stage of the family Aristeidae (Bouvier 1908). As previous studies suggested an affinity between Cerataspis and penaeoid shrimp, and more specifically the family Aristeidae, we sampled heavily within these groups (Boas 1880; Giard and Bonnier 1892; Bouvier 1908; Burkenroad 1934).

Phylogenetic analysis (Fig. 2) places C. monstrosa as identical to the deep-sea penaeoid shrimp P. armatus (Figs. 1, 3). Moreover, our sequencing efforts of 4136 base-pairs over five genes (12S, 16S, 18S, 28S, H3) resulted in a near perfect (99.96%) genetic match between these two “species.” Individual gene trees were not in conflict, with 12S and 16S resolving shallow branches and 28S, 18S, and H3 resolving middle to deep branches. All genetic markers in our analysis were carefully selected to include enough variation to detect species-level differences and resolve systematic placement. Historically, these nuclear and mitochondrial markers have demonstrated their utility in decapod taxonomic, systematic, and barcoding studies (Bracken et al. 2010; Grave et al. 2010; Puillandre et al. 2011). For each gene, the level of divergence between P. armatus and C. monstrosa is considerably less (~0.049–0.18%) when compared with estimates among other congeneric decapod (~2.2–10%, Toon et al. 2009) and aristeid (~3%, pers. observation based on 16S GenBank data, JF899802, GU972651) species. We therefore conclude that P. armatus and C. monstrosa, respectively, represent adult and larval forms of the same species, and recommend both henceforth be referred to as P. armatus (see Taxonomy Note).

Larval–adult linkages allow for the advancement of understanding in ecology, systematics, and taxonomy, and in the case of C. monstrosa, both deep-sea and plankton biology. Linkages shed light on the distribution, ecology, and life history of a species. Known occurrences of C. monstrosa and adults of P. armatus overlap in geographic distribution, which further solidifies the larval–adult identification. Although the first report of C. monstrosa in the Gulf of Mexico was relatively recent (Franks and Russell 2008), the larval form appears to be circumbally distributed in oceanic mid-water pelagic communities, near-surface plankton communities, or in association with surface rafts of Sargassum (Heegaard 1966; Morgan et al. 1985). The reduced abdomen and armored thorax suggests that C. monstrosa has an extended pelagic life, as proposed in previous reports (Bouvier 1908). The adult counterpart, P. armatus, is of similar cosmopolitan distribution, albeit as a true abyssal species ranging widely in deep-ocean basins to depths of at least 5060 m (Gore 1985; Pérez Farfante and Kensley 1997). Specifically throughout the Gulf of Mexico, adults of P. armatus have been reported from depths of 1,764–3,600 m (Roberts and Pequegnat 1970; Crosnier and Forest 1973; Pérez Farfante and Kensley 1997; Felder and
Thus, linking of the adult to larval form provides novel insight into the life history of this species from a mid-water pelagic larva to an abyssal adult. This furthermore establishes the adult source population for larvae that are a common food of pelagic fishes. Findings from this study suggest a second known "species" of Cerataspis, *C. petiti*, is likely a larval stage of the only other known species of *Plesiopenaeus* (*P. coruscans*). Affinities of the closely related and equally bizarre "larval" species *Cerataspides longiremus*, first described as *Cerataspis* by Dohrn

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Table 1. Taxonomy, voucher catalog numbers, and GenBank (GB) accession numbers for gene sequences used in the study. An “N/A” (not available) indicates missing sequence data. New sequences are indicated in bold.

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Gordon Gunter. As past studies have suggested an affinity
trawl collection by cruise participants aboard NOAA Ship
420 m at 27˚ 2009 in the northeastern Gulf of Mexico from a depth of
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as applied here, can be used to confirm these larval
shrimp (Dohrn 1871; Bonnier 1899). Similar approaches,
member of the genus
(1899), may well be a larval stage of an unidentified
taxa (Figure 2. Bayesian (BAY) phylogram for selected dendrobranchiate
taxa (n = 21) and outgroups (n = 6) based on a 12S (mtDNA), 16S
(mtDNA), 18S (nDNA), 28S nDNA and H3 nDNA concatenated
dataset. BAY posterior probabilities and ML bootstrap values are
represented as percentages and noted above or below the branches
(BAY/ML). Values <50% are not shown and represented by “-.”

Vertical colored bars indicate families within Decapoda. Outgroups
not shown.

(1871) and placed in the genus Cerataspides by Bonnier
(1899), may well be a larval stage of an unidentified
member of the genus Plesiopenaeus or of another aristeid
shrimp (Dohrn 1871; Bonnier 1899). Similar approaches,
as applied here, can be used to confirm these larval–adult
linkages once material of these rare individuals becomes
available for molecular systematic studies.

Genetic techniques cross-validated with larval rearing
protocols are the preferred method of identifying adult–
larval linkages. However, molecular phylogenetic tools, as
applied here, provide a powerful alternative to traditional
approaches dependent on rearing of otherwise unidentifi-
able larvae. In this case, the combined application of
modern DNA techniques with robust phylogenetic
methodology allowed us to solve this 184-year-old mystery of the “monster larva” of the deep.

Methods

Taxon sampling
One specimen of C. monstrosa was collected on July 2
2009 in the northeastern Gulf of Mexico from a depth of
420 m at 27˚05.996N, 86˚25.916W during mid-water
trawl collection by cruise participants aboard NOAA Ship
Gordon Gunter. As past studies have suggested an affinity
between C. monstrosa and penaeoids, but specifically the
family Aristeidae, taxon sampling was focused within
these lineages. Additional taxa from the Aristeidae
(including species and/or specimens of Plesiopenaeus)
were not included due to the difficulty in collecting deep-
sea organisms, rarity in nature, and/or unavailability of
molecular grade tissues. In total, 21 ingroup taxa across
the dendrobranchiate superfamilies Penaeoidea and Serge-
stoidea were included in the phylogenetic analysis
(Table 1). Representatives of other shrimp-like groups
including carideans, euphausiaceans, and stenopodideans
were included as outgroups (not shown).

Sequencing and phylogenetic analyses
Total genomic DNA was extracted from either the
abdominal muscle or gill using the Qiagen DNeasy®
Blood and Tissue Kit (Cat. No. 69,582; Qiagen, Califor-
nia), QI Amp DNA Mini Kit (Qiagen) (Cat. No. 51,304)
or QIAamp DNA Micro Kit (Qiagen) (Cat. No. 56,304).
Two mitochondrial (12S, 16S) and three nuclear genes
(18S, 28S, H3) were selected due to their range of phylo-
genetic utility and different inheritance patterns. Initially,
we tried to amplify the barcoding region of COI (Folmer
region), however, multiple attempts failed in our targeted
species. Additionally, 16S, 12S, and partial 28S are often
used in systematic and decapod barcoding studies and
contain enough variation to detect species-level differ-
ences (Bracken et al. 2010; Grave et al. 2010; Puillandre
et al. 2011). Genes were amplified using one or more sets
of primers. These included the mitochondrial genes 16S
large ribosomal subunit (~550 bp, Crandall and Fitzpa-
trick 1996) and 12S small ribosomal subunit (~400 bp,
Buhay et al. 2007), in addition to the nuclear genes 28S
large ribosomal subunit (~2500 bp, Whiting et al. 1997;
Whiting 2002; Palero et al. 2008) 18S small ribosomal subunit (~1800 bps, Medlin et al. 1988; Whiting et al. 1997; Apakupakul et al. 1999; Whiting 2002; Bracken et al. 2009), and protein-coding histone 3 (H3) (~350 bp, Colgan et al. 1998). Polymerase chain reaction (PCR) amplifications were performed in 25–50 μL volumes followed by cycle sequencing reactions using an Applied Biosystems 9800 Fast Thermal Cycler (Applied Biosystems, Foster City, CA, USA). Forward and reverse sequencing products were run on an ABI 3730xl DNA Analyzer 96-capillary automated sequencer in the Brigham Young University (BYU) sequencing center.

After sequence cleaning and editing using Sequencher 4.8 (GeneCodes, Ann Arbor, MI, USA), all sequences were checked for contamination and/or pseudogenes by following suggestions by Song et al. 2008 and BLAST searches. Individual alignments were created using MAFFT (E-INS-I option), and GBLOCKS was used to omit highly divergent and poorly aligned positions. Individual gene trees were generated using Maximum Likelihood (ML, Felsenstein 1981) analyses to ensure similar topologies and gene histories. Alignments were concatenated into a single dataset consisting of 4136 basepairs.

A phylogenetic approach was selected over alternative species delimitation methods (Yang and Rannala 2010; Ence and Carstens 2011; Masters et al. 2011) due to the limited availability of material for inclusion in the analysis. However, in studies where multiple individuals per species are obtainable, we suggest using a combination of phylogenetic and species delimitation approaches. A ML analysis (Felsenstein 1981) was conducted using RAxML (Randomized A(x)ccelerated Maximum Likelihood) (Stamatakis et al. 2005) with computations performed on the computer cluster of the Cyberinfrastructure for Phylogenetic Research Project (CIPRES 2.0) at the San Diego Supercomputer Center. The model of evolution that best fit the individual datasets was determined using MODELTEST 3.7 (Posada and Crandall 1998). The Bayesian (BAY) analysis was conducted in MrBayes v3.1.2b4 (Huelsenbeck and Ronquist 2001) on the Marylou5 Computational Cluster at Brigham Young University. Three independent runs were performed (each consisting of 20 chains and 10 swaps). Each analysis ran for 20,000,000 iterations, which we thinned to every 1000th iteration. Bootstrap support values (1000 pseudoreplicates) (Felsenstein 1985) and posterior probabilities (documented as percentages) are presented on the BAY phylogram (Fig. 2).

**Taxonomy Note**

The International Code of Zoological Nomenclature (http://iczn.org/) requires via its Principle of Priority (Article 23) that an older available name (in this case *C. monstrosa* Gray 1828) has precedence over a younger name (*P. armatus* (Bate 1881)) in a case where “two or more generations, forms, stages, or sexes of a species are named as different nominal taxa” (ICZN 23.3.2.2). If strictly applied in the current case, the two species known as *P. armatus* (Bate 1881) and *Plesiopenaeus coruscans* (Wood-Mason in Wood-Mason & Alcock, 1891) should henceforth be known as *Cerataspis armatus* (Bate 1881) and *Cerataspis coruscans* (Wood-Mason in Wood-Mason & Alcock 1891), respectively. However, the ICZN also has the plenary power to modify an application of the Code “if such application would in its judgment disturb stability or universality or cause confusion” (Article 81.1). As the genus name *Plesiopenaeus* Bate, 1881, is widely recognized and used to refer to the adults (e.g., in Perez-Farfante and Kenseley 1997; Tavares and Martin 2010; Grave and Fransen 2011) as compared to the relatively infrequent use of *Cerataspis* (Gray 1828) (use of which has been restricted to larval forms, which are rare), we are applying to the ICZN to use its plenary action to suppress *Cerataspis* in favor of *Plesiopenaeus* for stability and to avoid confusion. If our application is accepted, the term “cerataspis” could continue to be used as an informal name for these distinctive larval forms, just as the names *zoea*, *megalopa*, *glaucothoe*, *eryoneicus*, and other names once thought to represent decapod adults are still employed.

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**Conflict of interest**

None declared.

**References**


