Molecular Phylogenetics and Evolution 62 (2012) 237–250

Contents lists available at SciVerse ScienceDirect

Molecular Phylogenetics and Evolution

journal homepage: www.elsevier.com/locate/ympev

Phylogenetic relationships, character evolution, and taxonomic implications within the slipper lobsters (Crustacea: Decapoda: Scyllaridae)

Chien-Hui Yang [a,1], Heather Bracken-Grissom [b,*,1], Dohyup Kim [b], Keith A. Crandall [b,c], Tin-Yam Chan [a,d]

[a] Institute of Marine Biology, National Taiwan Ocean University, Keelung 20224, Taiwan, ROC
[b] Department of Biology, 401 Widtsoe Building, Brigham Young University, Provo, UT 84602, USA
[c] Monte L. Bean Life Science Museum, Brigham Young University, Provo, UT 84602, USA
[d] Center of Excellence for Marine Bioenvironment and Biotechnology, National Taiwan Ocean University, Keelung 20224, Taiwan, ROC

ARTICLE INFO

Article history:
Received 27 June 2011
Revised 23 September 2011
Accepted 26 September 2011
Available online 7 October 2011

Keywords:
Lobster
Decapoda
Phylogeny
Systematics
Morphology
Taxonomy
DNA barcode

ABSTRACT

The slipper lobsters belong to the family Scyllaridae which contains a total of 20 genera and 89 species distributed across four subfamilies (Arctidinae, Ibacinae, Scyllarinae, and Theninae). We have collected nucleotide sequence data from regions of five different genes (16S, 18S, COI, 28S, H3) to estimate phylogenetic relationships among 54 species from the Scyllaridae with a focus on the species rich subfamily Scyllarinae. We have included in our analyses at least one representative from all 20 genera in the Scyllaridae and 35 of the 52 species within the Scyllarinae. Our resulting phylogenetic estimate shows the subfamilies are monophyletic, except for Ibacinae, which has paraphyletic relationships among genera. Many of the genera within the Scyllarinae form non-monophyletic groups, while the genera from all other subfamilies form well supported clades. We discuss the implications of this history on the evolution of morphological characters and ecological transitions (nearshore vs. offshore) within the slipper lobsters. Finally, we identify, through ancestral state character reconstructions, key morphological features diagnostic of the major clades of diversity within the Scyllaridae and relate this character evolution to current taxonomy and classification.

1. Introduction

The slipper lobsters of the family Scyllaridae are a unique group of decapod crustaceans characterized by the strong modification of the antennal flagellum flattened to a plate and used for steering during the escape response (Spanier and Weihs, 1990). Some members have a ventrally-flattened body adapted for hiding within crevices or burrowing within the sand (Lavalli et al., 2007; Jones, 2007). Slipper lobsters are distributed world-wide throughout warm waters with a vertical range from very shallow to more than 800 m deep (Webber and Booth, 2007). Many large species are fished commercially (Duarte et al., 2010) although the highest taxonomic diversity is among the smaller species (Holthuis, 1991; Chan, 2010). Despite this high morphological diversity, slipper lobsters have long been considered to be a natural group (see also Webber and Booth, 2007) and this has been supported by recent morphological, molecular, and larval studies (Baisre, 1994; Scholtz and Richter, 1995; Dixon et al., 2003; Patek and Oakley, 2003; Tsang et al., 2008, 2009; Bracken et al., 2009a; Haug et al., 2009; Palero et al., 2009).

Since 1985 formal subdivisions have been proposed within Scyllaridae, which have not been rigorously tested for monophyly. Based on the different carapace shapes as well as the morphology of the maxilliped exopods and mandibular palp, four subfamilies were proposed by Holthuis (1985), namely Arctidinae, Ibacinae, Scyllarinae, and Theninae. At that time, Arctidinae was composed of two genera (*Arctides* and *Scyllarides*), Ibacinae consisted of three genera (*Evibacus*, *Ibacus* and *Parribacus*), while Scyllarinae and Theninae each contained only one single genus (*Scyllarus* and *Thenus*, respectively). In a revision of the subfamily Scyllarinae, which has the highest number of species among the four subfamilies, Holthuis (2002) greatly increased the number of genera from one to as many as 14 (Table 1) based on several external morphological characters such as the pattern of abdominal sculpture (i.e., wide transverse grooves vs. arborescent), the general shape of the anterior part of the thoracic sternum (e.g., anterior margin truncate, convex, V- or U-shaped), and the presence or absence of an additional carina at the fourth antennal segment. Furthermore, there have been a number of new species described since 1985, including one species each in Arctidinae and Ibacinae, 14 species of Scyllarinae, and three species of Theninae (see Chan, 2010; Yang and Chan, 2010; Yang et al., 2011). Altogether there are four subfamilies, 20 extant genera and 89 extant species known to date in the family Scyllaridae (Arctidinae = 17 species, Ibacinae = 15

* Corresponding author.
E-mail address: heather.bracken@gmail.com (H. Bracken-Grissom).
[1] Authors contributed equally to the manuscript.

1055-7903/$ - see front matter © 2011 Elsevier Inc. All rights reserved.
doi:10.1016/j.ympev.2011.09.019

Table 1
Checklist of the family Scyllaridae Latreille, 1825.

Arctidinae Holthuis, 1985[a]		
Arctides Holthuis, 1960[a]		
A. antipodarum Holthuis, 1960[a]	*A. guineensis* (Spengler, 1799)	*A. regalis* Holthuis, 1963[a]
Scyllarides Gill, 1898[a]		
S. aequinoctialis (Lund, 1793)	*S. astori* Holthuis, 1960	*S. brasiliensis* Rathbun, 1906[a]
S. deceptor Holthuis, 1963	*S. delfosi* Holthuis, 1960	*S. elisabethae* (Ortmann, 1894)
S. haanii (De Haan, 1841)[a]	*S. herklotsii* (Herklots, 1851)[a]	*S. latus* (Latreille, 1802)
S. nodifer (Stimpson, 1866)[a]	*S. obtusus* Holthuis, 1993	*S. roggeveeni* Holthuis, 1967
S. squammosus (H. Milne Edwards, 1837)[a]	*S. tridacnophaga* Holthuis, 1967	
Ibacinae Holthuis, 1985[a]		
Evibacus Smith, 1869[a]		
E. princeps Smith, 1869[a]		
Ibacus Leach, 1815[a]		
I. alticrenatus Bate, 1888[a]	*I. brevipes* Bate, 1888	*I. brucei* Holthuis, 1977
I. chacei Brown & Holthuis, 1998[a]	*I. ciliatus* (von Siebold, 1824)[a]	*I. novemdentatus* Gibbes, 1850
I. peronii Leach, 1815[a]	*I. pubescens* Holthuis, 1960	
Parribacus Dana, 1852[a]		
P. antarcticus (Lund, 1793)[a]	*P. caledonicus* Holthuis, 1960	*P. holthuisi* Forest, 1954
P. japonicus Holthuis, 1960[a]	*P. perlatus* Holthuis, 1967[a]	*P. scarlatinus* Holthuis, 1960
Scyllarinae Latreille, 1825[a]		
Acantharctus Holthuis, 2002[a]		
A. delfini (Bouvier, 1909)	*A. ornatus* (Holthuis, 1960)[a]	*A. posteli* (Forest, 1963)[a]
Antarctus Holthuis, 2002[a]		
A. mawsoni (Bage, 1938)[a]		
Antipodarctus Holthuis, 2002[a]		
A. aoteanus (Powell, 1949)[a,b]		
Bathyarctus Holthuis, 2002[a]		
B. chani Holthuis, 2002[a]	*B. faxoni* (Bouvier, 1917)	*B. formosanus* (Chan & Yu, 1992)[a]
B. ramosae (Tavares, 1997)	*B. rubens* (Alcock & Anderson, 1894)[a]	*B. steatopygus* Holthuis, 2002
Biarctus Holthuis, 2002[a]		
B. dubius (Holthuis, 1963)	*B. pumilus* (Nobili, 1906)	*B. sordidus* (Stimpson, 1860)[a]
B. vitiensis (Dana, 1852)[a]		
Chelarctus Holthuis, 2002[a]		
C. aureus (Holthuis, 1963)[a]	*C. crosnieri* Holthuis, 2002	*C. cultrifer* (Ortmann, 1897)[a]
Crenarctus Holthuis, 2002[a]		
C. bicuspidatus (De Man, 1905)[a]	*C. crenatus* (Whitelegge, 1900)	
Eduarctus Holthuis, 2002[a]		
E. aesopius (Holthuis, 1960)	*E. lewinsohni* (Holthuis, 1967)	*E. marginatus* Holthuis, 2002
E. martensii (Pfeffer, 1881)[a]	*E. modestus* (Holthuis, 1960)[a]	*E. perspicillatus* Holthuis, 2002
E. pyrrhonotus Holthuis, 2002	*E. reticulatus* Holthuis, 2002[a]	
Galearctus Holthuis, 2002[a]		
G. aurora (Holthuis, 1982)[a]	*G. avulsus* Yang, Chen & Chan, 2011[a]	*G. lipkei* Yang & Chan, 2010
G. kitanoviriosus (Harada, 1962)[a]	*G. rapanus* (Holthuis, 1993)[a]	*G. timidus* (Holthuis, 1960)[a]
G. umbilicatus (Holthuis, 1977)		
Gibbularctus Holthuis, 2002[a]		
G. gibberosus (De Man, 1905)[a]		
Petrarctus Holthuis, 2002[a]		
P. brevicornis (Holthuis, 1946)[a]	*P. demani* (Holthuis, 1946)[a]	*P. holthuisi* Yang, Chen & Chan, 2008[a]
P. rugosus (H. Milne Edwards, 1837)[a]	*P. veliger* Holthuis, 2002[a]	*P.* sp. nov.[a]
Remiarctus Holthuis, 2002[a]		
R. bertholdii (Paulson, 1875)[a]		
Scammarctus Holthuis, 2002[a]		
S. batei (Holthuis, 1946)[a]		
Scyllarus Fabricius, 1775[a]		
S. americanus (Smith, 1869)[a]	*S. arctus* (Linnaeus, 1758)[a]	*S. caparti* Holthuis, 1952[a]
S. chacei Holthuis, 1960[a]	*S. depressus* (Smith, 1881)[a]	*S. paradoxus* Miers, 1881
S. planorbis Holthuis, 1969	*S. pygmaeus* (Bate, 1888)[a]	*S. subarctus* Crosnier, 1970[a]
Theninae Holthuis, 1985[a]		
***Thenus* Leach**, 1815[a]		
T. australiensis Burton & Davie, 2007	*T. indicus* Leach, 1815[a]	*T. orientalis* (Lund, 1793)[a]
T. parindicus Burton & Davie, 2007	*T. unimaculatus* Burton & Davie, 2007[a]	

[a] Those taxa included in this study.
[b] *Antipodarctus aoteanus* is found to be a synonym of *Crenarctus crenatus* by the present study.

species, Theninae = 5 species, Scyllarinae = 52 species). At present, the 20 genera are divided on the basis of the external morphological characters (see Fig. 1, Table 2, also see Holthuis, 1985, 1991, 2002; Webber and Booth, 2007). Although these morphological characters have traditionally been used to diagnose the various groups within the scyllarids, they have not been formally tested