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

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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

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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

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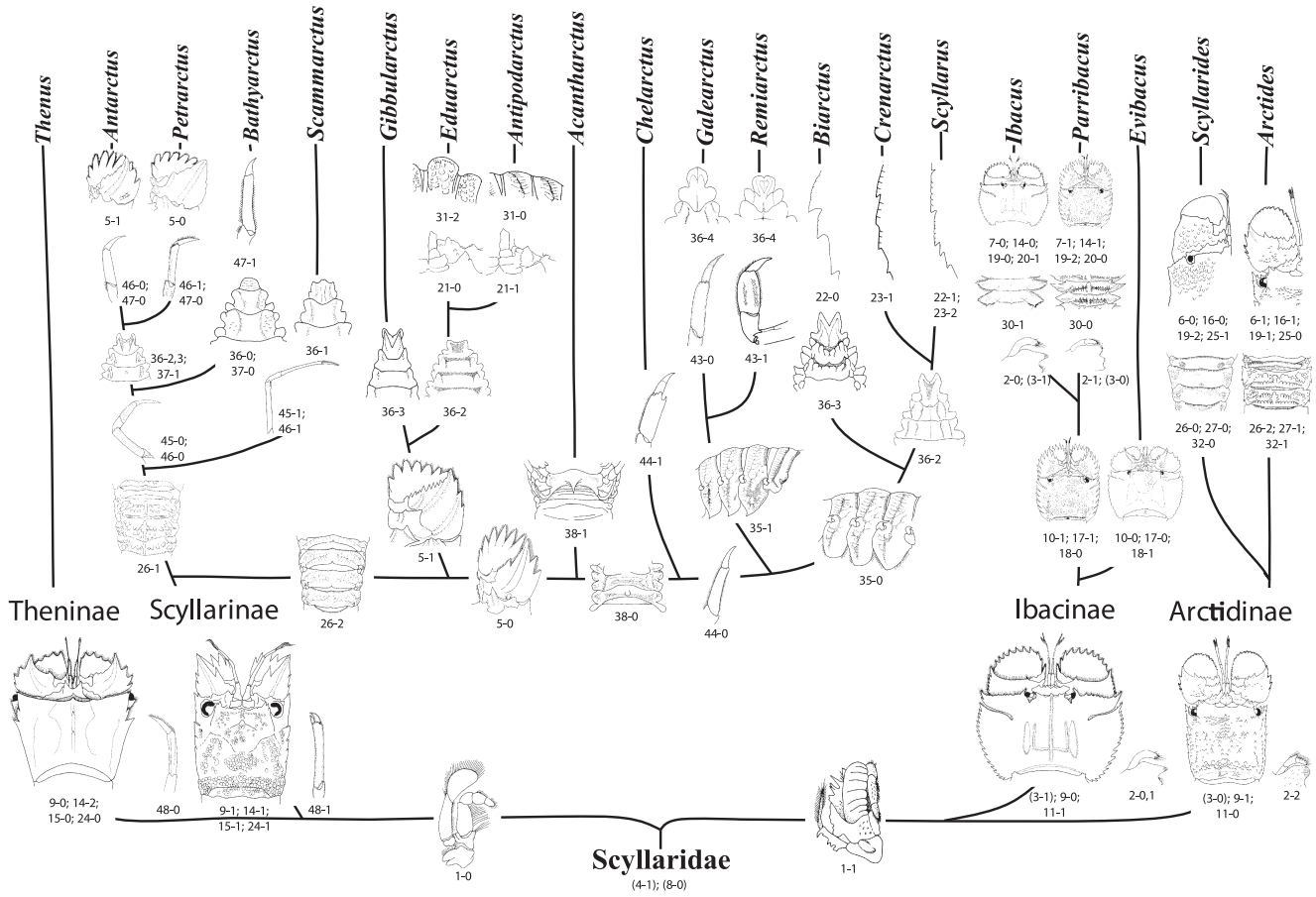

Fig. 1. Schematic relationships of the genera in Scyllaridae based on the key morphological characters used in the current classification scheme based on Holthuis, 1991, 2002. Characters and character states (e.g., 1-1, 4-0) are defined in Table 2, those in parentheses are not illustrated.

using a phylogenetic framework. Here we optimize 49 characters linked to external morphology, coloration, and ecology to examine the phylogenetic significance of these traits. Our findings are related to implications in taxonomy and current classification within the Scyllaridae.

In addition to hypotheses concerning morphological evolution, there has been significant discussion on the evolutionary pathways of both morphological and biogeographic changes leading to and within the slipper lobsters (e.g., Glaessner, 1969; George and Main, 1967; Feldmann and Tshudy, 1989; Davie, 1990; Baisre, 1994; George, 2005, 2006a,b; Chan et al., 2009; Palero et al., 2009; Tsang et al., 2009). Past researchers have suggested a deep-water origin of the Scyllaridae based on larval and adult characteristics (e.g., George and Main, 1967; Baisre, 1994; George, 2005, 2006a,b), while recent molecular analyses suggest the opposite trend (Chan et al., 2009; Palero et al., 2009; Tsang et al., 2009). Here we estimate phylogenetic relationships and use the resulting phylogeny to reconstruct the ancestral states of the slipper lobsters to test these competing hypotheses concerning the ecological transition(s) between the nearshore and offshore habitats during the evolution of the group. We test both the frequency and directionality (nearshore vs. offshore) of habitat shifts in the slipper lobsters and compare our findings with past arguments.

Only a handful of studies have explored the evolutionary relationships among the slipper lobsters (Baisre, 1994; Booth et al., 2005; Patek et al., 2006; Deiana et al., 2007; Schram, 2007; Webber and Booth, 2007; Palero et al., 2009), and the monophyly of the subfamilies and genera within Scyllaridae have not been examined carefully with extensive taxon sampling. Our study includes species from all 20 scyllarid genera (Table 1) for the most comprehensive sampling of slipper lobsters to date. We used partial sequences of five genes (16S rRNA and COI from the mitochondrial genome and 18S rRNA, 28S rRNA, and H3 from the nuclear genome) to elucidate the phylogenetic relationships among subfamilies, genera, and species. We compare our molecular phylogeny against current hypotheses of morphological relationships, identify synapomorphic characters that define taxonomic clades, and test hypotheses concerning habitat transition during the evolution of the slipper lobsters.

2. Materials and methods

2.1. Taxon sampling

A total of 54 species (including one new species) from all 20 genera in Scyllaridae were included in the analysis (Table 3). The specimens, preserved in 75–95% ethanol, are deposited at the National Taiwan Ocean University, Keelung (NTOU), Muséum National d'Histoire Naturelle, Paris (MNHN), University of Florida (UF), Museum Victoria (NMV), Western Australian Museum (WAM) and National Institute of Water and Atmospheric Research, New Zealand (NIWA). Molecular data from *Acantharctus posteli*, *Scyllarus arctus*, *S. caparti*, *S. pygmaeus*, *S. subarctus*, *Scyllarides herklotsii* and *Thenus unimaculatus* were obtained from GenBank. Palero et al. (2009) clearly show that the Palinuridae and the Scyllaridae form reciprocally mononphyletic sister taxa. Therefore, representatives of the Palinuridae were included as outgroup taxa for our study (including *Jasus*, *Justitia*, *Palinurus* and *Panulirus*, see Table 3).

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Table 2
Character list of 49 morphological and ecological characters and states used in the ancestral state reconstruction analysis.

Part	Character	Morphological description
Maxilliped	01	Exopod of maxillipeds with flagella 0: present on maxilliped II 1: present on maxillipeds I to III
	02	Mandibular palp 0: 1 segment 1: 2 segmented 2: 3 segmented
	03	Incisions on merus of maxilliped III 0: absent 1: present
Antennae	04	Flagellum of the antennae II 0: whip like 1: plate-like
	05	Antennal segment IV with distinct additional carina 0: absent 1: present
	06	Teeth on the anterior margin of antennal segment VI 0: absent 1: present
	07	Ratio of length/width of antennal segment IV 0: less than 0.8 1: more than 0.8
Carapace	08	Supraorbital horn 0: absent 1: present
	09	Height of carapace 0: strongly depressed 1: highly vaulted
	10	Cervical incision 0: closed 1: open
	11	Extent of cervical incision 0: shallow 1: deep
	12	Lateral margin between the anterolateral angle and cervical incision 0: absent 1: present
	13	Teeth on lateral margin 0: not equal 1: equal
	14	Distance between eyes/eye to anterolateral angle of carapace 0: less than 1 1: more than 1 2: eyes located at anterolateral angles of carapace
	15	Postcervical incision 0: absent 1: present
	16	Postorbital spine 0: absent 1: present
	17	Margin of orbit 0: entriely closed 1: anteriorly open
	18	Carapace with posteromedian spine 0: absent 1: present
	19	Surface texture of carapace 0: smooth and punctuate 1: spinose 2: squamose-tuberculate
	20	Postrostal and branchial carinae 0: absent 1: present
	21	Rostral tooth 0: absent 1: present
	22	Pregastric tooth 0: absent 1: present
	23	Gastric tooth 0: absent 1: indistinct 2: distinct
	24	Posterolateral margin of carapace 0: unarmed 1: armed with teeth or squamiform tubercles
	25	Anterior margin between the eye and the anterolateral angle of carapace 0: concave 1: convex
Abdomen	26	Pattern on dorsal abdominal surface 0: uniformly granular 1: sculptured pattern 2: arborescent pattern
	27	Tranverse grooves on abdominal tergites II to V 0: absent 1: present
	28	Number of the tranverse groove on each abdominal tergites II to V 0: zero 1: only one 2: over one
	29	Pattern of abdominal transverse groove 0: absent 1: interrupted 2: complete
Abdomen (cont.)	30	The posterior margin of abdominal somite V 0: smooth 1: with posteromedian spine 2: with blunt posteromedian projection
	31	Abdominal somites II to V with median carina 0: none 1: low and indistinct 2: high and distinct
	32	Distinct transverse groove on abdominal somite I 0: absent 1: present
<coloration>	33	Number of spots on surface of abdominal somite I 0: zero 1: one (large) 2: two 3: three or more
<coloration>	34	Abdominal tergite I brightly colored 0: absent 1: present
	35	Shape of abdominal pleura II to IV 0: blunt or rounded 1: sharply pointed
Thoracic sternum	36	Anterior margin of thoracic sternum 0: truncate or convex 1: gutter-like sunken 2: U-shaped 3: V-shaped 4: produced forward
	37	Median incision on anterior of thoracic sternum 0: absent 1: present
	38	Last segment of thoracic sternum 0: with median tubercle 1: with sharp median thorn
Pereiopods	39	Colored bands on pereiopods II to V 0: absent 1: present
<coloration>	40	Spots on all pereiopods 0: absent 1: present
	41	Ventral groove on propodus of pereiopod II 0: absent 1: present
	42	Ventral groove on propodus of pereiopod III 0: absent 1: present
	43	Propodus of pereiopod II /pereiopod III 0: less broadened 1: equally broad
	44	Propodus of pereiopod III 0: simple 1: subchelate
	45	Relatively length of pereiopod IV and V long and slender 0: no 1: yes
	46	Dactylus of pereiopods III to V with the dorsal fringe of setae 0: absent 1: present
	47	Propodus of pereiopods I to IV with ventral setae 0: absent 1: present
	48	Pereiopod V without chela in females 0:no 1: yes
Ecology	49	Depth range distribution 0: < 200 m 1: > 200 m

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2.2. DNA extraction, PCR amplification, and sequencing

Total DNA was extracted from muscle tissue (10–20 mg) using the Genomic DNA Mini kit (Geneaid) or Qiagen DNeasy® Blood and Tissue Kit (Cat. No. 69582). Partial sequence of two mitochondrial genes, COI and 16S rRNA, were amplified by the universal primers respectively: LCO1490/HCO 2198 (~650 bps, Folmer et al., 1994) and 16Sar (Simon et al., 1994)/16S1472 (~550 bps, Crandall and Fitzpatrick, 1996). The nuclear large subunit 28S rRNA and histone H3 genes were amplified by D23/5S or 1.3F/4b (~750 bps, Chen et al., 1995; Whiting, 2002) and H3AF/H3AR (~350 bps, Colgan et al., 1998), respectively. The nuclear small subunit 18S rRNA was amplified by A/L, C/Y, O/B (~1800 bps, Medlin et al., 1988; Apakupakul et al., 1999) or slightly shorter internal primers (~1700 bps, B/D18s1R, D18s2F-D18s2R, D18s3F-D18s3R, D18s4F-D18s4R and D18s5F-A) (Bracken et al., 2009b). PCR reactions were performed in 50 μl reactions with 50–200 ng of the DNA extraction, 5 μl of 10X polymerase buffer (SUPER-THERM), 10–25 mM magnesium chloride ($MgCl_2$) (depending on gene), 2.5 mM of deoxyribonucleotide triphosphate mix (dNTPs) (PROTECH Inc.), 5 μM each primer (MDBio Inc.), 1 units of *Taq* polymerase (5 units/μl, SUPER-THERM) or 25 μl volumes containing 10 μM forward and reverse primer for each gene, 2.5 mM each dNTP, PCR buffer, $MgCl_2$, 1 unit HotMasterTaq polymerase (5 PRIME), and 30–100 ng/μL extracted DNA. We included 0.3 μl of 1% bovine serum albumin (BSA; stock concentration – 0.5 mg/μl) and 1 μl of dimethyl sulfoxide (DMSO) for the COI and 28S rRNA genes, respectively. The PCR cycling profiles were as follows: 5 min at 95 °C for initial denaturation, then 45 cycles of 30 s at 94 °C, 1 min at 45–58 °C (depending on different genes), 1 min at 72 °C, and final extension for 10 min at 72 °C. 1% agarose gel for electrophoresis was used to check the size and quality of PCR products. These products were subsequently purified using the High Pure PCR Product Purification kit (Roche Applied Science) or with PrepEase™ PCR Purification 96-well Plate Kit (USB Corporation) before sequencing. The same PCR primer sets were used for cycle sequencing. Sequencing products were run (forward and reverse) on an ABI 310 Genetic Analyzer (Applied Biosystems) or an ABI 3730 XL automated sequencer. Sequences were assembled, cleaned, and edited using the computer program Sequencher 4.8 (GeneCodes, Ann Arbor, MI, USA).

2.3. Data analysis

All sequences from this study have been deposited in GenBank (Table 3). Multiple sequence alignment was performed using MAFFT, which has been shown to be both more efficient and more accurate than alternative alignment approaches (Katoh et al., 2005). To check for pseudogenes within our dataset, we followed suggestions outlined by Song et al. (2008). Namely, COI and H3 sequences were translated into the corresponding amino acids to check for stop codons and individual gene trees were compared to ensure similar topologies. Additionally, we also downloaded the whole mitochondrial genomic sequences of 29 crustaceans from GenBank and checked our data against these reference sequences. Individual gene trees were checked for inconsistencies in topologies and a combined dataset (5 genes) was used in the final phylogenetic analysis. GBlocks v0.91b was used to identify regions of the alignment with questionable positional homology (Castresana, 2000). Such regions were excluded from subsequent analyses. Individual datasets were concatenated and partitioned for the final analyses.

Phylogenetic trees were constructed by maximum parsimony (MP) using PAUP* (Swofford, 2000), maximum likelihood (ML) using RAxML 7.0.4 (Stamatakis, 2006), and Bayesian inference (BI) using MrBayes (ver. 3.1.2; Huelsenbeck and Ronquist, 2001). Analyses were performed at the Fulton Supercomputing Lab at Brigham Young University on the marylou6 supercomputer. ModelTest v.3.7 (Posada and Crandall, 1998) was used to evaluate a best-fit model of DNA substitution (see Posada and Crandall, 2001; Posada and Buckley, 2004) based on the Akaike's criterion (AIC) and to estimate model parameters used in the ML and BI analyses. For MP analysis, all characters were equally weighted and gaps were treated as missing information. Multiple heuristic searches were performed using 100 starts with random sequence addition for starting trees to explore local tree islands (Maddison, 1991). The maximum likelihood (ML) analysis was conducted using randomized accelerated maximum likelihood (RAxML) (Stamatakis, 2006). The algorithms used in the analysis were the "-f a" and "-f d" (-#200 iterations of random starting trees) options for the best tree search and bootstrap analysis. Likelihoods were compared to determine the best tree and bootstrap support values were mapped on the resulting topology. Likelihood settings followed the General Time Reversible model (GTR) with a gamma distribution following a partitioned dataset, and RAxML estimated all free parameters. Branch support was assessed using 1000 bootstrap replicates for both MP (Pb) and ML (MLb) analyses (Felsenstein, 1985). Three independent BI runs were performed with 20,000,000 generations each sampled every 1000 generations. A mixed model was applied following a partitioned dataset. Convergence of the Bayesian runs was assessed using Tracer v1.4 (Rambaut and Drummond, 2009). Observation of the likelihood (-LnL) scores in Tracer allowed us to determine burn-ins and stationary distributions for the data. Once the split frequency in each analysis was 1% (split frequency of 1% was reached after approximately 700,000 generations (700 tress discarded as burnin), a 50% majority-rule consensus tree was obtained from the remaining saved trees. Posterior probabilities (Pp) for clades were compared for congruence and then combined between individual analyses. Posterior values >0.5 are presented on the BI phylograms (presented as percentages).

2.4. Testing alternative hypotheses

To test whether previous hypotheses of scyllarid evolution (Holthuis 1985, 1991; Baisre, 1994; Booth et al., 2005; Palero et al., 2009) were significantly worse than our best ML tree, we used a partitioned S–H test (Shimodaira and Hasegawa, 1999) as implemented in RAxML 7.0.4 using the same data partitions used in our phylogeny estimation. The GTRGAMMA model was applied to each partition as in the ML analysis. All constrained tree topologies were independently constructed in Mesquite v.2.71 (Maddison and Maddison, 2009). Each constraint was followed by a new search to recover the optimal tree as in the abovementioned ML analysis (f "d" option, -#200 iterations of random starting trees). Topological constraints were enforced as independent hypotheses: (1) Arctidinae + Ibacinae as monophyletic clade (2) *Parribacus* + Arctidinae as a monophyletic clade and (3) Ibacinae as a monophyletic clade. Additionally, to examine the validity of current genera assignments we tested the poly- and paraphyletic genera in our tree against the current classification (see Chan, 2010). Lastly, to test the directionality of an onshore to offshore transition in scyllarid lobsters, we forced the alternative hypothesis (offshore ancestor (i.e., *Bathyarctus*, *Galearctus*)) and used an S–H test to quantify evolutionary change in a statistical framework.

2.5. Character evolution

An effective approach to examining character evolution is through ancestral state reconstruction (ASR) in the context of a phylogeny using statistical approaches (Pagel, 1999). To examine morphological and ecological character evolution given our

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Table 3
Scyllaridae material, locality, voucher number and GenBank numbers used in this study.

Species	Locality	Voucher no.	COI	16S	28S	18S	Histone 3
Subfamily Arctidinae							
Arctides							
A. regalis	Réunion	MNHN-IU-2009-462	JN701651	JN701685	JN701539	N/A	JN701741
A. regalis	Hawaii, USA	KC6003	JN701652	JN701686	JN701540	JN701597	JN701742
A. regalis	Hawaii, USA	KC6004	JN701653	JN701687	JN701541	JN701598	JN701743
A. antipodarum	Australia	KC6076	N/A	JN701688	JN701595	JN701599	JN701744
Scyllarides							
S. brasiliensis	Market in Taiwan, origin unknown	NTOU M00972	JN701654	JN701689	JN701542	N/A	JN701745
S. haanii	Taiwan	NTOU M00973	JN701655	N/A	N/A	N/A	JN701746
S. haanii	Hawaii, USA	KC6018	JN701656	JN701690	JN701543	JN701600	JN701747
S. haanii	Hawaii, USA	KC6019	N/A	JN701691	JN701544	JN701601	JN701748
S. herklotsii	Eastern Atlantic Ocean	ICMD 230/1998	FJ174946	FJ174906	FJ036958	JN701602	FJ174863
S. nodifer	Northern Gulf of Mexico, USA	KC5839/ULLZ7845	JN701657	JN701692	JN701545	JN701603	JN701749
S. squammosus	Australia	KC6093	N/A	N/A	JN701546	JN701604	JN701750
Subfamily Ibacinae							
Evibacus							
E. princeps	Mexico	KC6347	JN701658	JN701693	JN701547	JN701605	JN701751
Ibacus							
I. alticrenatus	Australia	KC6080	JN701659	JN701694	JN701548	JN701606	JN701752
I. alticrenatus	Australia	KC6081	JN701660	JN701695	JN701549	JN701607	JN701753
I. ciliatus	Taiwan	NTOU M00974	JN701661	JN701696	JN701550	N/A	JN701754
I. chacei	Australia	KC6083	JN701662	JN701697	JN701596	JN701608	JN701755
I. chacei	Australia	KC6084	JN701663	JN701698	JN701551	JN701609	JN701756
I. peronii	Australia	KC6085	JN701664	JN701699	JN701552	JN701610	JN701757
I. peronii	Australia	KC6086	JN701665	JN701700	JN701553	JN701611	JN701758
Parribacus							
P. antarcticus	Taiwan	NTOU M00975	JN701666	JN701701	JN701554	N/A	JN701759
P. antarcticus	Hawaii, USA	KC6015	N/A	JN701702	JN701555	JN701612	JN701760
P. antarcticus	Hawaii, USA	KC6016	N/A	JN701703	JN701556	JN701613	JN701761
P. antarcticus	Unknown	KC6087/KC3231	N/A	JN701704	JN701557	JN701614	JN701762
P. japonicus	Taiwan	NTOU M01044	N/A	N/A	JN701558	JN701615	JN701763
P. perlatus	Easter Island	NTOU M01045	N/A	N/A	JN701559	JN701616	JN701764
Subfamily Scyllarinae							
Acantharctus							
A. ornatus	Australia	WAM/KC6719	JN701667	N/A	JN701560	JN701617	JN701765
A. posteli	Eastern Atlantic Ocean	ICMD 218/1998	FJ174967	FJ174910	FJ036956	FJ174929	FJ174864
Antarctus							
A. mawsoni	Australia	J52009/KC6718	EU982702	N/A	N/A	N/A	N/A
Antipodarctus							
A. aoteanus[a]	New Zealand	NIWA 57499	N/A	JN701705	JN701561	N/A	JN701766
Bathyarctus							
B. chani	Taiwan	NTOU M00059/KC6720	EU982703	JN701706	JN701562	JN701618	JN701767
B. formosanus	Taiwan	NTOU M00976/KC6721	JN701668	JN701707	N/A	JN701619	JN701768
B. rubens	Philippines	NTOU M00977/KC6722	JN701669	JN701708	N/A	JN701620	JN701769
Biarctus							
B. vitiensis	Guam	UF2822/KC6723	JN701670	JN701709	JN701563	JN701621	JN701770
B. sordidus	Thailand	NTOU M00978/KC6724	N/A	JN701710	JN701564	JN701622	JN701771
Chelarctus							
C. aureus	Taiwan	NTOU M00979/KC6725	JF411065	JN701711	JN701565	JN701623	JN701772
C. cultrifer	Philippines	NTOU M00980/KC6726	N/A	JN701712	JN701566	JN701624	JN701773
Crenarctus							
C. bicuspidatus	New Caledonia	MNHN-Pa1028/KC6727	N/A	JN701713	JN701567	JN701625	JN701774
Eduarctus							
E. martensii	Taiwan	NTOU M00716/KC6728	JN701671	JN701714	JN701568	JN701626	JN701775
E. modestus	Marquesas Islands	MNHN-Pa1826/KC6730	N/A	JN701715	JN701569	JN701627	JN701776
E. recticulatus	Lansdowne Bank	MNHN-Pa1335/KC6729	N/A	JN701716	JN701570	JN701628	JN701777
Galearctus							
G. aurora	French Polynesia	NTOU M00863/KC6731	JN701672	JN701717	JN701571	JN701629	JN701778
G. kitanoviriosus	Taiwan	NTOU M00981/KC6733	JF331658	JN701718	JN701572	JN701630	JN701779
G. avulsus	New Caledonia	MNHN-IU-2010-1910/ KC6736	JF331656	JN701719	JN701573	JN701631	JN701780
G. rapanus	Austral Island	MNHN-IU-2008-16596/ KC6732	JF331657	JN701720	JN701574	JN701632	JN701781
G. timidus	Philippines	NTOU M00982/KC6734	JN701673	JN701721	JN701575	JN701633	JN701782

Table 3 (*continued*)

Species	Locality	Voucher no.	COI	16S	28S	18S	Histone 3
Gibbularctus							
G. gibberosus	Seychelles	MNHN-Pa1857/KC6737	JN701674	JN701722	JN701576	N/A	JN701783
Petrarctus							
P. brevicornis	Taiwan	NTOU M00741/KC6741	EU982701	JN701723	JN701577	JN701634	JN701784
P. demani	Thailand	NTOU M00734/KC6738	EU982694	JN701724	JN701578	JN701635	JN701785
P. holthuisi	Philippines	NTOU M00735/KC6740	EU982695	JN701725	JN701579	JN701636	JN701786
P. rugosus	Taiwan	NTOU M00737/KC6739	EU982697	JN701726	JN701580	JN701637	JN701787
P. rugosus	Australia	KC6091	N/A	JN701727	JN701581	JN701638	JN701788
P. veliger	Thailand	NTOU M00739/KC6742	EU982699	JN701728	JN701582	JN701639	JN701789
P. sp. nov.	Australia	KC6090	N/A	JN701729	JN701583	JN701640	JN701790
Remiarctus							
R. bertholdii	Philippines	NTOU M00983/KC6743	JN701675	JN701730	JN701584	JN701641	JN701791
Scammarctus							
S. batei	Philippines	NTOU M00984/KC6744	JF411066	JN701731	JN701585	JN701642	JN701792
Scyllarus							
S. americanus	Florida, USA	KC5845/ULLZ8500	JN701676	JN701732	JN701586	JN701643	JN701793
S. arctus	Not specified in GenBank	ICMD 12/1995	FJ174966	FJ174911	FJ036955	FJ174930	FJ174859
S. caparti	Eastern Atlantic Ocean	ICMD 222/1998	N/A	FJ174909	FJ036953	FJ174928	FJ174860
S. chacei	Florida, USA	KC5837/ULLZ6596	JN701677	JN701733	JN701587	JN701644	JN701794
S. chacei	Northern Gulf of Mexico, USA	KC5838/ULLZ7594	JN701678	JN701734	N/A	JN701645	JN701795
S. depressus	Southern Gulf of Mexico, USA	KC5850/ULLZ8168	JN701679	JN701735	JN701588	JN701646	JN701796
S. pygmaeus	Not specified in GenBank	ICMD 5/1995	FJ174965	FJ174908	FJ036954	FJ174931	FJ174861
S. subarctus	Eastern Atlantic Ocean	ICMD 299/1991	N/A	FJ174912	N/A	FJ174932	FJ174865
Subfamily Theninae							
Thenus							
T. indicus	Singapore	NTOU M00985	JN701680	JN701736	JN701589	N/A	JN701797
T. orientalis	Gulf of Thailand	KC5849/ULLZ9338	JN701681	JN701737	JN701590	JN701647	JN701798
T. unimaculatus	Not specified in GenBank	FP 0012	FJ174950	FJ174915	FJ036952	FJ174942	FJ174858
Outgroups							
Family Palinuridae							
Jasus							
J. edwardsii	Not specified in GenBank	KC725/KC3209	FJ174951	DQ079716	DQ079791	AF235972	EU921064
Justitia							
J. longimana	Not specified in GenBank	Jus-0101-01	N/A	AF502953	FJ174841	AF498674	FJ174873
Palinurus							
P. barbarae	Not specified in GenBank	FP0001	FJ174960	FJ174903	FJ036949, FJ174817, FJ174849	FJ174925	FJ174876
Panulirus							
P. interruptus	Hawaii, USA	KC6006	JN701682	JN701738	JN701591	JN701648	JN701799
P. japonicus	Not specified in GenBank	Pjaponic	FJ174968	AB070201	N/A	AF498670	N/A
P. japonicus	Taiwan	NTOU M00986	N/A	N/A	JN701592	N/A	JN701800
P. marginatus	Hawaii, USA	KC6012	JN701683	JN701739	JN701593	JN701649	JN701801
P. penicillatus	Hawaii, USA	KC6009	JN701684	JN701740	JN701594	JN701650	JN701802

N/A = not available for inclusion in this study.

[a] Found to be a synonym of *Crenarctus crenatus* by the present study.

phylogenetic hypothesis, we used maximum parsimony as implemented in Mesquite v.2.71 (Maddison and Maddison, 2009) along with a maximum likelihood approach in BayesTraits v 1.0 (available at www.evolution.reading.ac.uk), which considers branch length and all character state probabilities during reconstruction analysis. Morphological characters used in the monographic works of Holthuis (1991, 2002) for separating the families and genera in Scyllaridae (i.e., those in Fig. 1, Table 2), as well as 11 characters for separating species (i.e., characters 12, 13, 28, 29, 33, 34, 39, 40, 41, 42), were defined as homologies and coded into a morphomatrix (Table 2, A.1). Species depth distributions (nearshore vs. offshore) were accumulated from the literature and added into the matrix as a single ecological character. A nearshore distribution was defined as 0–200 m while an offshore distribution was defined as >200 m. In many cases a species had overlapping distributions and was coded as both character states. A total of 48 morphological characters and 1 ecological character were optimized across our tree (Bayesian consensus topology) using ASR. Since we are focused on character evolution within the Scyllaridae, reconstructions among the outgroups are not shown.

3. Results

We sampled 66 individuals belonging to 54 species across the Scyllaridae and 8 individuals belonging to 7 species across the Palinuridae (outgroups), including data already available on GenBank (Table 3). Our analysis suggests one sample is a new species (i.e., *Petrarctus* n. sp.) and a second recently described species is confirmed and placed in a phylogenetic context (i.e., *Galearctus avulsus* Yang, Chen and Chan, 2011). We were successful in obtaining 16S data (612 total aligned nucleotide positions including gaps) from 68 individuals, 18S data (1903 characters) from 63 individuals, 28S (816 characters) from 64 individuals, COI (657 characters) from 54 individuals and H3 (327 characters) from 72 individuals. Our novel data for this study represent 82% of the total data set

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(59 GenBank sequences out of a total of 323 total sequences) and 86% within the Scyllaridae (43 Genbank of 290 Total). After the GBlock analysis, the resulting concatenated data set consisted of 3962 total characters with relative contributions of 486 characters from 16S, 1788 characters from 18S, 702 characters from 28S, 656 characters from COI, and 326 characters from H3. A few species are missing various genes due to the vagaries of DNA sequencing.

The best-fit model of evolution for these data using the AIC criterion for model selection in ModelTest was the GTR + I + G (28S), TrN + I + G (16S), TrNef + I + G (18S), and TVM + I + G (COI, H3). Our resulting maximum likelihood tree (not shown) and Bayesian tree (Figs. 2 and 3), were almost identical with only a minor difference at a shallow weakly supported node (position of *Galearctus timidus* in relation to other *Galearctus*). The parsimony tree (not shown) supported subfamily, genus and species level relationships, however intrasubfamilial (Arctinidae and Ibacinae) and intrageneric relationships (Scyllarinae) were less resolved. The Bayesian phylogenetic estimate incorporating all samples used in this study is available as Supplemental Fig. A.1. In Fig. 2, we trimmed duplicate species representation once we verified that these individuals fell out in a monophyletic and sister clade. Therefore, for ease of legibility and discussion, our final tree is a Bayesian tree with a single representative from each species sampled for this study (Fig. 2).

3.1. Phylogenetic relationships

The family Scyllaridae was recovered as a monophyletic group (100/71/100 = Pp, MLb, Pb respectively, see methods) along with three of the four subfamilies (i.e., Arctidinae (100/100/100), Scyllarinae (100/100/87) and Theninae (100/100/100)). The subfamily Ibacinae is paraphyletic with the genera *Evibacus* and *Parribacus* forming a sister group to the Theninae + Scyllarinae clade. The subfamily Arctidinae is strongly supported and an early branching lineage within the Scyllaridae followed by Ibacinae, Theninae and Scyllarinae (strong support defined as $\geqslant$95 Pp, $\geqslant$70 MLb, Pb).

The genera within the subfamilies Arctidinae and Ibacinae are monophyletic with strong support ($\geqslant$95 Pp, $\geqslant$70 MLb, Pb). Although Theninae is monogeneric, three of the five species from this subfamily are included and form a strongly supported clade (100/100/100). Many genera within the Scyllarinae recently created by Holthuis (2002) are poly- or paraphyletic. Except for the monotypic genera (i.e., *Antarctus, Antipodarctus, Gibbularctus, Remiarctus,* and *Scammarctus*) and the genus *Crenarctus* with one single species in the present analysis (see Taxonomic Appendix), only *Bathyarctus, Biarctus, Chelarctus* and *Eduarctus* fall out as monophyletic groups (though the support values for *Chelarctus* and *Biarctus* are low). The genera *Acantharctus*, *Petrarctus, Scyllarus* and *Galearctus* are poly- or paraphyletic.

Individual gene trees (not shown) were compared for congruence and all genes showed similar relationships, however with different levels of resolution. Generic and species level relationships were well resolved in 16S, COI, and 28S gene trees while 18S helped resolved deeper (intrageneric, intrasubfamilial) level relationships. The 16S gene tree showed one difference from other gene trees (18S, 28S, COI) in recovering a monophyletic Ibacinae + Theninae albeit with low support (MLb = 54).

3.2. Alternative hypotheses

A Shimodaira–Hasegawa (S–H) test was conducted to test whether alternative hypotheses proposed by previous studies (Holthuis, 1985, 1991; Baisre, 1994; Booth et al., 2005; Palero et al., 2009) were significantly worse than our best ML tree. The S–H test results did not find any of the previous hypotheses to be significantly worse ($P_{all} > 0.05$) than our unconstrained maximum likelihood topology (ML_{best} = -32571.968; ML_{H1} = −32588.278338 D(LH): −16.310074; ML_{H2} = -32583.452472 D(LH): −11.484208 SD, ML_{H3} = −32575.565544 D(LH): −3.597281). Alternatively, when we forced all polyphyletic or paraphyletic genera (*Acantharctus*, *Petrarctus*, *Scyllarus*, *Galearctus*) in our tree to be monophyletic (independent hypotheses), following the current classification, the topology was significantly worse in all cases ($P_{all} < 0.05$; $ML_{Acantharctus}$ = −32747.802092 D(LH): −175.833828; $ML_{Petrarctus}$ = −32858.020004 D(LH): −286.051741; $ML_{Scyllarus}$ = −32650.281421 D(LH): −78.313158) with the exception of *Galearctus* ($P_{Galearctus} > 0.05$; $ML_{Galearctus}$ = −32594.416021 D(LH): −22.447758). The S–H test examining an offshore to onshore transition in slipper lobsters was significantly worse ($P_{offshore} < 0.05$, $ML_{offshore}$ = −32659.241625 D(LH): −87.273362) than the alternative hypothesis (onshore to offshore).

3.3. Character evolution

A total of 48 characters (including coloration) associated with the maxilliped (n = 3), antennae (n = 4), carapace (n = 18), abdomen (n = 10), thoracic sternum (n = 3) and pereiopods (n = 10) were included in the morphological matrix (Table 2, A.1). An additional character based on depth distribution (nearshore vs. offshore) was included (Table 2, A.1). All characters (n = 49) were optimized across the tree (Table 2) using parsimony and/or maximum likelihood ancestral state reconstruction, but only those recovered as synapomorphies are superimposed on the Bayesian cladogram (Fig. 3). In total, we recovered 12 synapomorphic characters associated with the following structures: maxilliped (n = 2), antennae (n = 2), carapace (n = 5), abdomen (n = 1) and pereiopods (n = 2). No synapomorphic characters were associated with the thoracic sternum, coloration, or ecology. Ten characters define clades within the Scyllaridae while 2 define the family. In total, 37 characters represented homoplasies, ten of which were selected as exemplars and presented in Fig. 3 (colored grid). Our parsimony analysis suggests that slipper lobsters invaded deep waters (>200 m) 15 times with 2 invasions resulting in restricted habitats of over 200 m. A second reconstruction method that considers branch lengths and estimates the probabilities of all possible character states (maximum likelihood) was implemented and recovered nine independent invasions with two invasions restricted to deep waters (>200 m).

4. Discussion

4.1. Evolutionary relationships of slipper lobsters

The present molecular phylogenetic study confirms the family Scyllaridae and subfamilies Arctidinae, Scyllarinae and Theninae as monophyletic groups. Previous studies (Holthuis, 1985, 1991) have suggested Scyllarinae is more closely related to Theninae while Ibacinae shares an affinity with Arctidinae based on morphological characters (Fig. 1, Table 2). A recent molecular study (Palero et al., 2009) corroborates these findings although with limited taxon sampling (one genus per family) and low support for some clades (Ibacinae + Arctidinae). Based on larval morphology, Baisre (1994) also suggests a Scyllarinae + Theninae relationship, but places *Parribacus* closer to Arctidinae rather than the other genera in Ibacinae (also see Booth et al., 2005). Our results strongly support previous larval and genetic studies suggesting a sister relationship between the subfamilies Theninae and Scyllarinae (100/100/84). However, contrary to all previously suggested relationships deduced from morphological, larval, and molecular studies, the Ibacinae form a paraphyletic group removed as a sister clade from the Arctidinae. Although we could not reject Ibacinae monophyly using the S–H test ($P > 0.05$), our best estimate shows this subfamily as paraphyletic.

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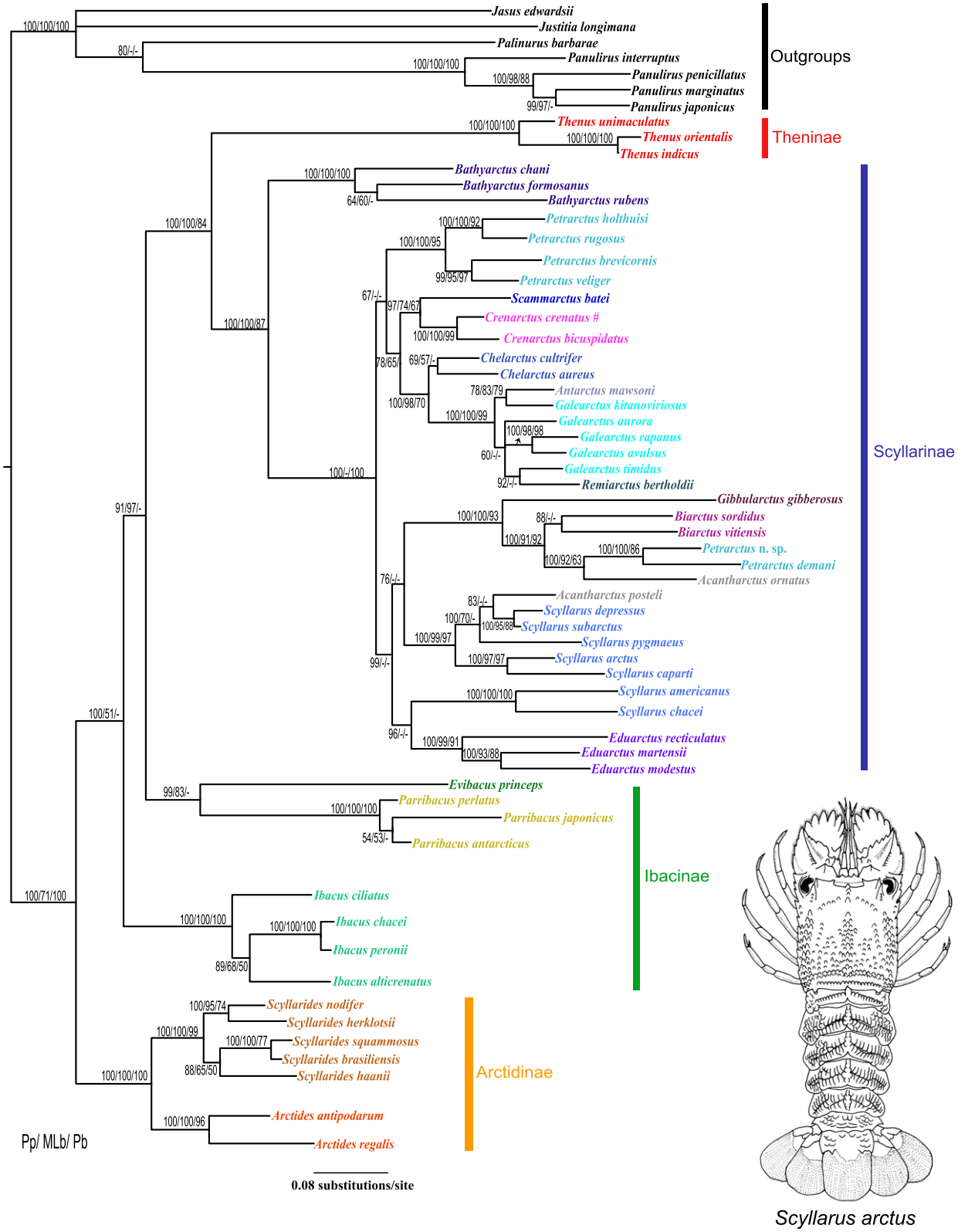

Fig. 2. Bayesian estimated phylogram of the Scyllaridae. Subfamilies are indicated with vertical colored bars and genera are given in different colors. Nodal support values represent Bayesian posterior probabilities (Pp)/maximum likelihood bootstrap values (MLb)/maximum parsimony bootstrap values (Pb). #*Antipodarctus aoteanus* is found to be a synonym of *Crenarctus crenatus* by the present study (new taxonomy followed herein).

The Arctidinae represents an early branching lineage within our phylogeny, which differs from previous evolutionary schemes suggested for slipper lobsters. Compared to Ibacinae and Theninae, carapace morphology within Arctidinae is more conserved in being highly vaulted and not extremely flattened. Our findings are also in accordance with the scyllarid fossil record. *Scyllarides punctatus*

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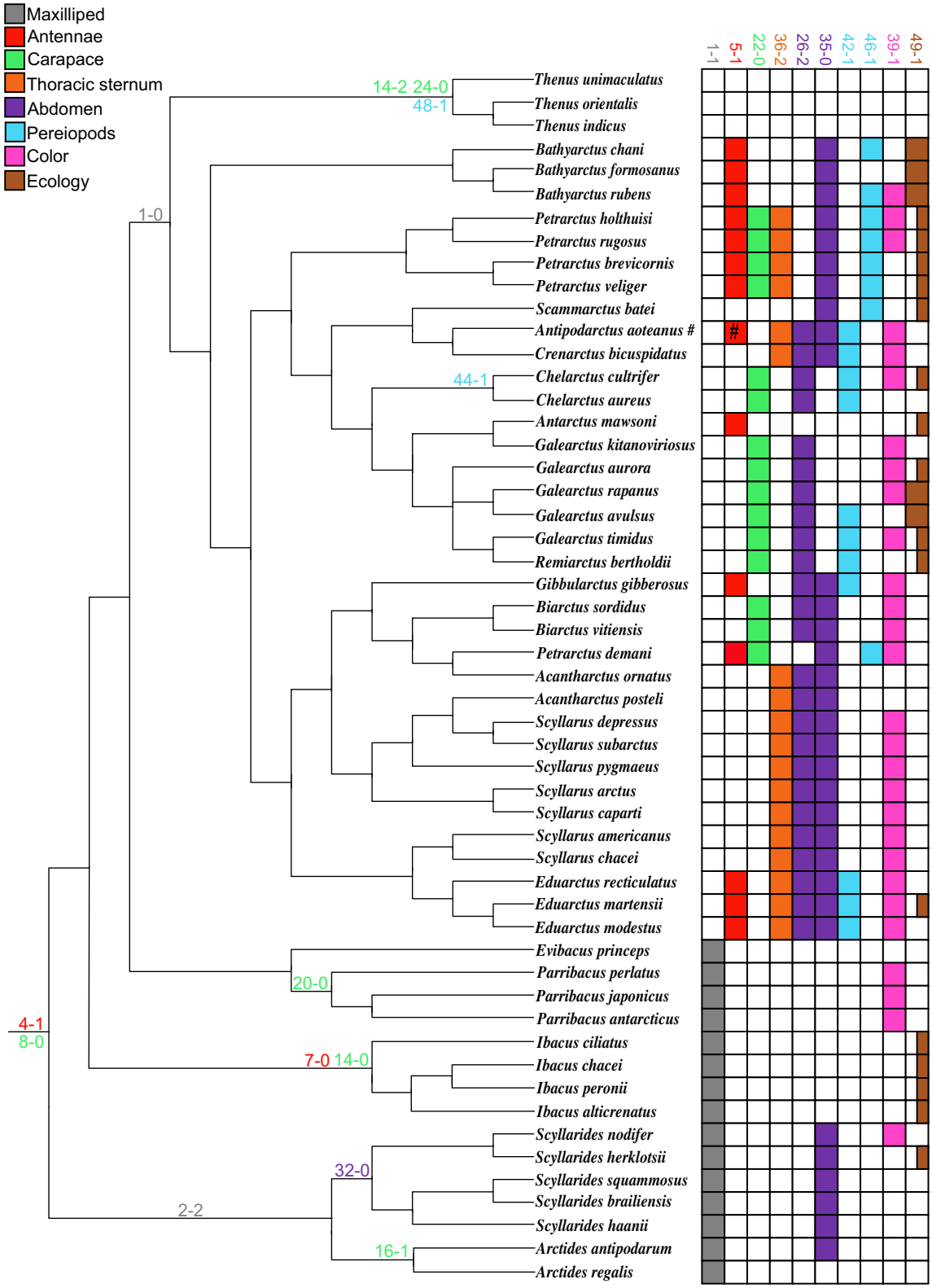

Fig. 3. Bayesian cladogram and character evolution within the Scyllaridae. The numbering along branches represent synapomorphic characters identified using parsimony ancestral state reconstruction methods. The color-coded grid represents character homoplasy for selected traits ($n = 10$). Colors indicate morphological and ecological characters defined in the legend. All numbers (e.g., 1-1) represent character and character state defined in Table 2 and with most of them illustrated in Fig. 1. #*Antipodarctus aoteanus* is found to be a synonym of *Crenarctus crenatus* by the present study, but the character no. 5 of this species is coded here according to the description given by Holthuis (2002) (hence with a character state 5-1) instead of following the actual specimens (should be actually 5-0).

(Arctidinae) and *Scyllarella gardneri* (unplaced subfamily assignment) represent the oldest known fossils from the mid-Cretaceous and both species possess a high-vaulted carapace morphology that resembles present day Arctidinae (Webber and Booth, 2007).

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Moreover, Scyllarinae has the youngest fossil record, which corresponds to their derived phylogenetic position in the tree.

4.2. Character evolution

Ancestral state reconstruction was performed on 48 morphological characters and one ecological character (Table 2, A.2) to explore evolutionary changes in the characters across the Scyllaridae and to identify morphological synapomorphies defining significant clades. The analysis revealed a plate-like flagellum of the second antennae and absence of a supraorbital horn (i.e., characters state 4-1, 8-0, Fig. 3) unites the family Scyllaridae. The subfamily Ibacinae was recovered as a non-natural group and the morphological characters used in previous classifications, such as a strongly depressed carapace, deep cervical incision, and the shape of mandibular palp (i.e., characters 2, 9, 11 in Figs. 1 and 3) are not synapomorphies. On the other hand, the Arctidinae and Theninae are supported by both the molecular data and morphological characters (i.e., characters 2, 24, 48 in Fig. 1, Table 2) that define these clades (Figs. 2 and 3).

Our analysis recovered several synapomorphic characters uniting the subfamilies and genera within the Scyllaridae. Traditionally, the mouthparts have been considered to be very important characters (Fig. 1, Table 2) in predicting subfamily affinity. Our analysis reveals the presence of a flagellum only on the exopod of the second maxilliped (character state 1-0) uniting Scyllarinae and Theninae, whereas the presence of flagella on all maxilliped exopods (character state 1-1) have arisen multiple times within the Arctidinae and Ibacinae. Similarly, the 3-segmented mandibular palp (character state 2-2) represents a synapomorphy for the Arctidinae, and alternative character states (i.e., 2-0, 2-1) of the mandibular palp are homoplasious characters (Fig. 3). Among the Ibacinae, closer eyes (Fig. 3: character state 14-0) and the shape of the fourth antennal segment (Fig. 3: character state 7-0), are found to be defining traits for the genus *Ibacus*.

The presence of additional ridges or row of tubercles on the fourth antennal segment was considered to be a rather important character by Holthuis (2002) in dividing Scyllarinae. The determination of this character is sometimes rather arbitrary (see Taxonomic Appendix) and we found it to be homoplasious for *Gibbularctus, Eduarctus*, and *Petrarctus* (i.e., character state 5-1 in Fig. 3). Among the many characters proposed by Holthuis (2002) for subdividing Scyllarinae, nearly all are rejected to be true synapomorphies (10 characters were chosen as exemplars, Fig. 3). These include some characters that have long been considered (e.g., De Man, 1916; Holthuis, 1960, 2002; Chan and Yu, 1986, 1993; Chan, 1998) to be extremely important in separating the Scyllarinae such as the abdominal sculpture composed of an arborescent pattern or wide transverse grooves (Figs. 1 and 3: character 26), and the shape of the anterior part of the thoracic sternum (Figs. 1 and 3: character 36). Therefore, these characters have likely arisen from parallel evolution instead of plesiomorphic features, as seen in other decapod examples (e.g., carcinization, Tsang et al., 2011). The only character found to be phylogenetically significant among genera within the Scyllarinae was the subchelate third pereiopod in the genus *Chelarctus* (i.e., character state 44-1 in Figs. 1 and 3). Evidently, further exploration of novel characters will be necessary to define the synapomorphies for the many of the new relationships supported among the slipper lobsters by the present study. Although slipper lobsters generally have many external characters that have been extensively used in taxonomy, the exact origins of the various teeth, carinae/grooves on the carapace have not been examined in detail. Increased understanding on the internal anatomy of the cephalothorax in various taxa will be able to verify the exact status of these structures and their evolution. On the other hand, comparisons of the microscopic structures of the setae and gills may also shed light on diagnostic characters within the Scyllaridae.

One of our characters of interest was the ecological character of shallow water vs. deep-water habitat for the slipper lobsters. Earlier studies based on adult similarity and a larval cladistic analysis (e.g., George and Main, 1967; Baisre, 1994; George, 2005, 2006a,b) proposed a hypothesis of deep water to shallow water evolution. Our results, however, show the subfamily Arctidinae to be an early-branching shallow-water lineage within Scyllaridae (Fig. 4). Arctidinae also has the oldest fossil representatives among Scyllaridae (about 120 MYA at mid-Cretaceous, Woods, 1925; Webber and Booth, 2007) and both genera included in this family have a world-wide (*Scyllarides*) or near world-wide (*Arctides*) geographical distribution (see Holthuis, 1991; Webber and Booth, 2007) – all supporting the relative antiquity of this group. Nearly all members of Arctidinae occur in shallow waters (Holthuis, 1991; Webber and Booth, 2007) with only two of the 14 species of *Scyllarides* (i.e., *S. elisabethae* and *S. herklotsii*) having distributions that extend into deeper habitats (200 m, Holthuis, 1991). These results are in concordance with recent molecular studies and support a general onshore (shallow) to offshore (deep) evolutionary hypothesis in lobsters (Fig. 3: character state 49-0) (e.g., Chan et al., 2009; Tsang et al., 2009, Tsoi et al., 2011). Interestingly, the subfamily Scyllarinae has the youngest fossil representatives and most derived phylogenetic position, further supporting the recent invasion into deeper waters. We can force a reconstruction of an ancestral deep-water lineage (i.e., Scyllarinae including *Bathyarctus* and *Galearctus*) as an alternative and we reject this hypothesis (S-H test, $P_{\text{offshore}} < 0.05$). Our results suggest the slipper lobsters evolved from a shallow water ancestor and invaded the deep waters (>200 m) 9–15 times (see results, Character Evolution) during the evolution of the group, with 2 accounts restricted to deep waters (Fig. 4). Our parsimony analysis also suggests that restriction to the deep waters occurred through 2 separate intermediaries, once from a shallow/deep water ancestor (i.e., some *Galearctus* species) and once from a shallow water ancestor (i.e., *Bathyarctus*) (Fig. 4), whereas our likelihood reconstruction suggests deep-water intermediaries in both cases. We acknowledge the discordance in the two methods, however likelihood approaches are often preferred over parsimony reconstructions, because they take into account branch lengths, model evolution, and calculate a probability of all character states across a tree (Cunningham et al., 1998).

4.3. Taxonomic implications

The present study has important taxonomic implications in the current classification of the slipper lobsters. The monophyletic status of the long established genera in the three subfamilies Arctidinae, Ibacinae and Theninae are strongly supported. However, Ibacinae is shown as paraphyletic. With the current data, we cannot reject the monophyly hypothesis of this subfamily, but given our estimated phylogeny, this subfamily deserves further consideration. Although synapomorphies to split Ibacinae were not recovered in this analysis (Fig. 3), the discovery of novel characters may provide strong evidence for subfamily division (namely, Ibacinae and Parribacinae). Many of the genera recently divided in the subfamily Scyllarinae are found to be poly- or paraphyletic and almost all the defining characters used to delimit this subfamily are homplasies. Furthermore, when we constrained poly- or paraphyletic genera to be monophyletic, most resulting topologies were significantly worst (see results), providing strong evidence that taxonomic revisions are needed. Nevertheless, the present molecular analysis does reveal two distinct clades within the Scyllarinae; namely the basal branch consisting of only species of *Bathyarctus* (supported by Pp, MLb, Pb) and the other clade containing the rest

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of the species (supported by Pp, Pb). Several well supported species groupings are also shown within the larger clade but most of them do not correspond to previous taxonomic schemes. Only *Scammarctus* (however a monotypic genus), *Chelarctus*, *Gibbularctus* (however a monotypic genus) and *Biarctus* with their members constitute well defined clades. Yet synapomorphic characters cannot be identified for all these clades except *Chelarctus*, which is nested deep inside the Scyllarinae. Therefore, for the time being the subfamily Scyllarinae at most can only be subdivided into two genera, namely *Bathyarctus* for the basal clade and *Scyllarus* for the rest of the species.

Cryptic diversity is often revealed in molecular analyses, as seen in previous work on spiny and clawed lobsters (e.g., Brasher et al., 1992; Sarver et al., 1998; Chan and Chu, 1996; Gopal et al., 2006; Chan et al., 2009; Tsoi et al., 2011), as well as in other decapods crustaceans (e.g., Buhay et al., 2007; Tsoi et al., 2007; Yang and Chan, 2010; Yang et al., 2010). Moreover, a few studies have demonstrated the usefulness of molecular tools in delimiting species within the slipper lobsters (Burton and Davie, 2007; Yang et al., 2008; Yang and Chan, 2010). During the course of this study, we identified two new cryptic species; one in the genus *Petrarctus* and the other in the genus *Galearctus*. At the time of the present study only five species were described in *Galearctus* (excluding the recently described *G. lipkei*, which is yet another cryptic species discovered in a separated study, see Yang and Chan, 2010) and four of them were included in the analysis. The unknown *Galearctus* sample from New Caledonia (now named as *G. avulsus*) has at least 14.5% COI genetic divergence from the other four species and morphologically it is very different from the unsampled species *G. umbilicatus* (known only from the east coast of Australia between 26°30′S and 37°S (Holthuis, 2002). Re-examination and detailed comparisons of the New Caledonian material with the other known species of *Galearctus* revealed constant morphological differences in the shape of the anterior part of the thoracic sternum, and therefore, it is recently described as new (Yang et al., 2011).

We identified a second cryptic species belonging to the genus *Petrarctus* after including all the described species of *Petrarctus* in the phylogeny. Our results suggest the unknown *Petrarctus* (*P.* n. sp.) from Australia is genetically distinct from all species in the analysis. Although its genetic sequence is closest to *P. demani*, this lineage has a genetic divergence of 16.7% in the 16S gene from this sister taxon, an amount well within the range of divergence between species within our study. Examination of this specimen is underway to validate genetic findings with morphological evidence.

5. Conclusion

The present molecular phylogenetic analysis on the slipper lobsters has the most comprehensive sampling to date and with all the genera of the family included in the study. The inferred topology has strong nodal support for most of the branches. The

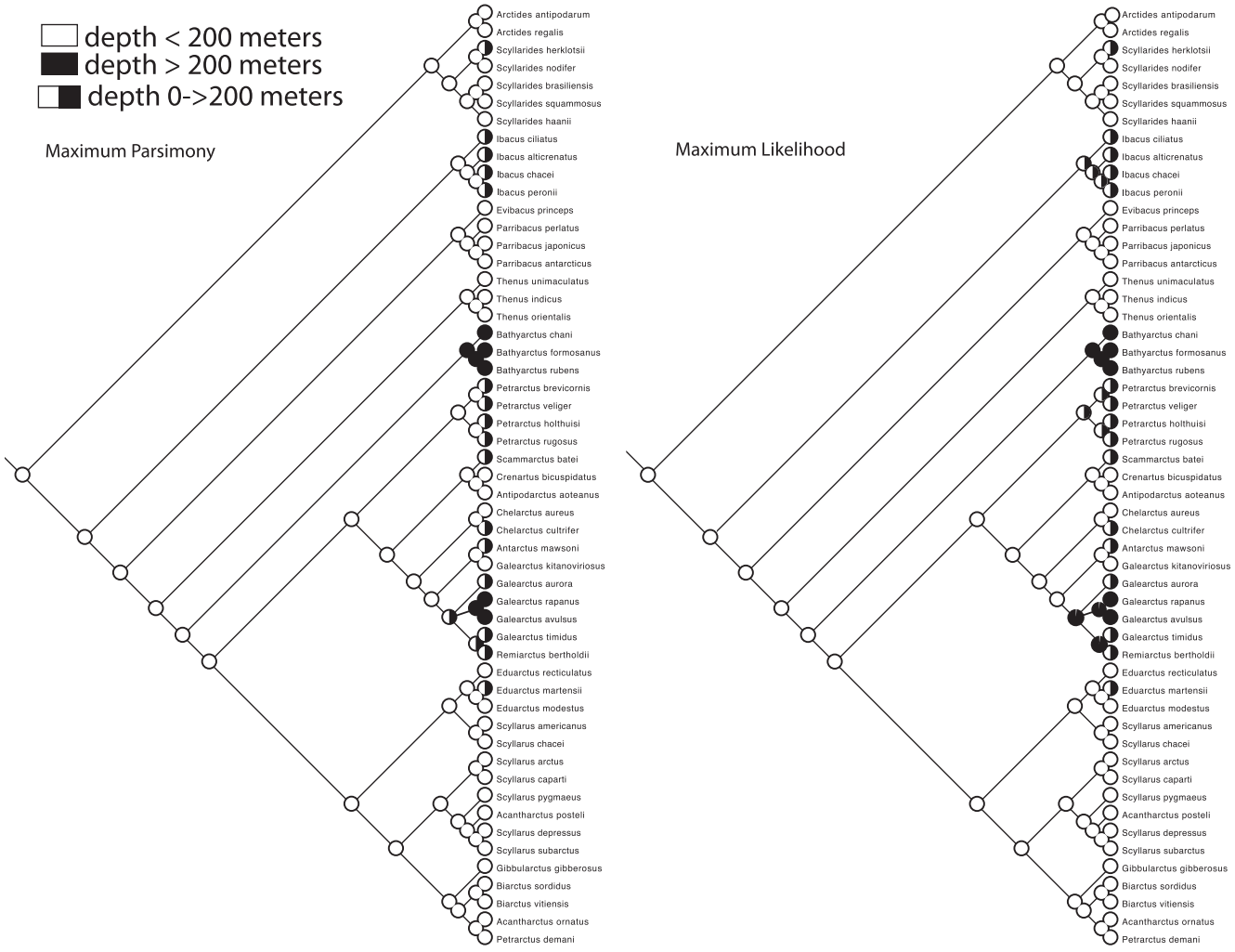

Fig. 4. Ancestral state reconstruction analysis using parsimony (left) and maximum likelihood (right) methods for depth distribution within the Scyllaridae. Onshore (<200 m) or offshore (>200 m) ecological character (number 49, Table 2, A.2) optimized across the Bayesian cladogram.

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monophyletic status of three of the four subfamilies, namely Arctidinae, Theninae and Scyllarinae, is supported and the subfamily Ibacinae is paraphyletic. Arctidinae represents the earliest branching lineage during the evolution of the slipper lobsters, which corresponds to the fossil record and the onshore to offshore hypothesis, suggesting slipper lobsters have evolved from shallow (onshore) to deep (offshore). Indeed, our results reject the alternative hypothesis. Through ancestral state reconstructions, we identified morphological characters defining well-supported clades and rejection of previous hypotheses concerning characters defining unique groups within the Scyllaridae.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ympev.2011.09.019.

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