VNIVERSITAT DE VALÈNCIA

Programa de Doctorat en Biodiversitat i Biologia Evolutiva
Rd. 99/2011

Facultat de Ciències Biològiques

TESI DOCTORAL

Slipper lobsters from Atlantic waters: revision of *Scyllarus* Fabricius, 1775 (Crustacea: Scyllaridae) using a multiple-evidence approach

Rebeca Genís Armero

València, Juny 2020

***Directors*: Ferran Palero Pastor i Romana Capaccioni Azzati**

Programa de Doctorat en Biodiversitat i Biologia Evolutiva
Rd. 99/2011

Facultat de Ciències Biològiques

TESI DOCTORAL

Slipper lobsters from Atlantic waters: revision of *Scyllarus* Fabricius, 1775 (Crustacea: Scyllaridae) using a multiple-evidence approach

Rebeca Genís Armero

València, Juny 2020

***Directors*: Ferran Palero Pastor i Romana Capaccioni Azzati**

Tesi presentada per REBECA GENÍS ARMERO, candidata al grau de Doctor per la Universitat de València, amb el títol

Slipper lobsters from Atlantic waters: revision of *Scyllarus* Fabricius, 1775 (Crustacea: Scyllaridae) using a multiple-evidence approach

València, Juny 2020

En Ferran Palero Pastor, Investigador Doctor de l'Institut Cavanilles de Biodiversitat i Biologia Evolutiva i Na Romana Capaccioni Azzati, Professora Titular del Departament de Zoologia de la Facultat de Ciències Biològiques de la Universitat de València,

CERTIFIQUEN que Na Rebeca Genís Armero, Graduada en Ciències Biològiques per la Universitat de València, ha realitzat, sota la nostra direcció i tutela respectivament, i amb el major dels aprofitaments, el treball d'investigació titulat: *Slipper lobsters from Atlantic waters: revision of Scyllarus Fabricius, 1775 (Crustacea: Scyllaridae) using a multiple-evidence approach* , i que havent estat conclòs, autoritzem la seua presentació amb la finalitat que puga ser jutjat pel tribunal corresponent i optar així al grau de Doctor en Ciències Biològiques per la Universitat de València, dins del Programa de Doctorat en Biodiversitat i Biologia Evolutiva.

I per a que així conste, en compliment de la legislació vigent, signe el present certificat en València, a 7 de juny de 2020.

Signat: Ferran Palero Pastor

Director de la Tesi

Signat: Romana Capaccioni Azzati

Directora i Tutora de la Tesi

A ma tia Rafaela,

i a les meues iaies Maruja i Ramona

‘‘...the adaptation of the larva to its conditions of life is just as perfect and as beautiful as in the adult animal.’’

Charles Darwin, The Origin of Species

AGRAÏMENTS

Sentir-se agraïda és sinònim de felicitat, i jo, per sort, hem sent realment agraïda per l'ajuda i el suport que m'ha donat una extensa llista de persones. Disculpeu per endavant si em deixe a algú.

En primer lloc, m'agradaria donar les gràcies als meus directors de Tesi, Ferran i Romana. Gràcies per tota la confiança que heu depositat en mi durant aquestos 7 anys. Sí, 7 anys, perquè treballe amb vosaltres des del projecte de final de carrera. Romana, gràcies per la teua comprensió, sempre disposta a fer el que siga per a ajudar-me en tot el que ha esta a les teues mans. Em vas obrir les portes del laboratori de Biologia Marina, que malgrat ser un grup menut hem aconseguit fer una xicoteta família Universitària. Estaré agraïda sempre a la meua "mare universitària". I Ferran, moltes gràcies per haver-me donat l'oportunitat de conèixer la ciència fora de les fronteres de Burjassot. Gràcies a tu he conegut el Museu de Història Natural de Londres, el INRA, la Universitat de Càdis, visita clau per a elaborar aquest treball, el Centre d'Estudis Avançats de Blanes, la Universitat de Lodz, i gràcies per fer possible conèixer a l'il·lustrador del Museu Nacional de Història Natural de Paris, Pier Opic, el qual s'ha convertit en un referent per a mi en il·lustració científica. En definitiva, gràcies per donar-me l'oportunitat de realitzar aquesta Tesi Doctoral.

No m'agradaria deixar passar l'ocasió per donar les gràcies a una sèrie d'investigadors, dels quals he pogut aprendre molt. Gràcies Prof. Clark per rebre'ns al Museu de Londres i permetrem conèixer les grans col·leccions de larves fil·losoma, THANK YOU A LOT. Gràcies Nacho, la meua estada al teu laboratori a la UCA va possibilitar l'inici d'aquesta aventura, GRACIAS. Peyre Opic, la vostra dona Thérèse i vostè ens obrireu les portes de la vostra casa i vaig saber reconèixer que la ciència i l'art efectivament poden anar de la mà, MERCI BEAUCOUP! Gràcies Ola, per compartir amb mi els teus coneixements en il·lustració digital, al final em fareu passar-me al "lado oscuro"! DZIĘKUJĘ CI. També he tingut l'oportunitat de creuar l'Atlàntic, al igual que les meues larvetes, i conèixer a grans investigadors i apassionats de les fil·losomes. Gràcies al Dr. Alvaro Behnke per deixar-me realitzar la meua estada doctoral a la seua empresa i cedir-me aquella col·lecció de larves, i gràcies al Dr. Pedro Baez per aquella tarda a Santiago de Chile i explicar-me en persona les seues observacions sobre fil·losomes. GRACIAS a los dos.

No puc deixar passar per alt als meus companys del laboratori de Bio Marina, Júlia, Alicia, Rebeca, Núria i Héctor. Sé que ja cadascú ha anat a parar a un lloc diferent del món, perquè la vostra qualitat com a persones també es reflexa en la vostra qualitat professional. Féreu que el temps al laboratori fora més que treballar. Gràcies en especial a Joan i Borja, sempre heu sigut els "veterans" del lab i això es va veure reflectit en tots els consells encertats que m'heu donat en l'àmbit acadèmic, i per què no dir-ho?! de la vida! Gràcies per confiar en mi com a il·lustradora científica, va significar molt per a mi. I com no, gràcies als meus companys de carrera, Esther, Maria, Isa, Albe, Inma, Maria Asins, Núria, i un llar etc., vàreu fer la biologia més bonica encara. Però tinc que fer especial menció a la "secta", Miquel, Clara, Maria "la hippies" i Noe, sou els màxims responsables dels millors 4 anys de Universitat que haja pogut tindre.

Si més no, una tesi no sols s'escriu al laboratori o la Universitat. Fora d'ells ha hagut molta gent que sempre m'ha donat el seu suport incondicional i m'agradaria donar-los les gràcies des d'ací. Gràcies als qui heu suportat les nits de "lo dejo todo" Teresa, Jose, Gemma, Sandra i Paula, sense eixes xarrades hagués sigut molt difícil continuar en els moments més durs. Gràcies Pep i Marina, per ser dos pilars fonamentals.

Gràcies a Josefa i Francis. Gràcies mama i papa per TOT. Heu sigut el motor i la força de tot el què he fet en aquestos 28 anys. Gràcies per fer-me qui sóc.

Índex

ABREVIACIONS

A1	antènula
A2	antena
Abd	abdomen
ae	peduncle ocular
ArBr	artrobrànquia
Bas	basis
CCDE-IEOCD	Colección de Crustáceos Decápodos y Estomatópodos del Centro Oceanográfico de Cádiz
CCLME	Canary Current Large Marine Ecosystem
Cph	cèfalon
CL	longitud del cèfalon
Crp	carp
Cox	coxa
CSIC	Consejo Superior de Investigaciones Científicas
CVF	Front de Cap Verd
CW	amplada màxima del cèfalon
Dct	dàctil
End	endopodi
Exp	exopodi
Isch	isqui
ICM	Institut de Ciències del Mar (Barcelona)
IEO	Instituto Español de Oceanografía
IFAN	Institut fondamental d'Afrique noire (Dakar)
IPP	Instituto de Investigaciones Pesqueras
Mer	meros
Mdb	mandíbula
Mx1	maxíl·lula (maxil·la I)
Mx2	maxil·la (maxil·la II)
Mxp1-3	maxil·lípede 1-3
MfN	Museum für Naturkunde (Berlin)
NHM	Natural History Museum (Londres)
MNHN	Muséum national d'Histoire naturelle (Paris)

ORSTOM	Office de la recherche scientifique et technique Outre-Mer
P1-5	pereiopodis 1-5
PDL	longitud del plèon
PlBr	pleurobrànquia
PdBr	podobrànquia
Pld	pleopodis
Prd	propodi
RBINS	Royal Belgian Institute of Natural Sciences (Brussel·les)
RMNH	Rijksmuseum van Natuurlijke Historie (Leiden)
ThSp	espina toràcica
Thx	tòrax
TL	longitud total
Tel	tèlson
Urp	uropodi
ULL	Universidad de La Laguna (Tenerife)
UCA	Universidad de Cádiz
USNM	U.S. National Museum, Smithsonian Institution (Washington)
ZIM	Zoologisches Institut und Museum der Universität Hamburg

Introducció

Les llagostes de l'infraordre Achelata són crustacis decàpodes amb un elevat interès comercial i que tenen un paper fonamental en diferents ecosistemes marins (Holthuis 1991). Disposar d'informació completa sobre la biologia de les llagostes, i en particular sobre la seua dinàmica poblacional i reclutament larval, és fonamental per poder gestionar les pesqueries d'una manera eficaç i sostenible. Les diferències morfològiques entre les larves i els adults han dificultat tradicionalment la identificació dels estadis larvals de llagosta. Tanmateix, gràcies a les noves eines moleculars, aquestes dificultats han sigut minimitzades en els últims anys. En concret, l'ús del gen codificant per a la citocrom oxidasa 1 (COX1) o codi de barres d'ADN (conegut com *DNA barcoding* en anglès) permet identificar les mostres de plàncton a nivell d'espècie. El codi de barres d'ADN s'ha aplicat amb èxit en l'estudi de larves de llagosta al Mediterrani (Palero *et al.* 2011; Palero *et al.* 2014b; Palero *et al.* 2016). Tot i això, les larves de la majoria d'espècies presents a l'oceà Atlàntic oriental encara són desconegudes. Aquesta tesi inclou el major nombre de larves de Scyllarinae identificades mitjançant mètodes moleculars fins al moment. Campanyes oceanogràfiques recents, dirigides a la investigació del bentos i del plàncton d'aigües atlàntiques, ens han permès accedir a una gran quantitat de mostres de la costa africana i la Macaronèsia. Afortunadament, el plàncton obtingut fou emmagatzemat en etanol, fet que ens ha possibilitat la realització de probes moleculars per identificar el material a nivell d'espècie. Els resultats obtinguts ens han permès també adreçar diferents qüestions sobre el cicle larval i l'evolució de les llagostes africanes.

Objectius

1. Revisar la sistemàtica dels Scyllarinae centrant-se en les espècies de l'Àfrica occidental amb un enfocament taxonòmic integrador (combinant trets morfològics i moleculars.

2. Recopilar exemplars d'adults i larves de dues campanyes oceanogràfiques recents (ex. CETOBAPH i MAFIA) i múltiples col·leccions de museu.

3. Obtenir seqüències genètiques a partir de larves prèviament seleccionades per identificar-les a nivell d'espècie (Codi de barres d'ADN).

4. Analitzar les distàncies genètiques entre les diferents espècies de *Scyllarus* i inferir les relacions evolutives entre elles.

5. Generar una base de dades amb la localització, profunditat i estat de desenvolupament (fil·losoma, decapodid, juvenil o adult) dels *Scyllarus* analitzats.

6. Actualitzar la biogeografia dels *Scyllarus* africans amb les noves dades obtingudes de campanyes recents i col·leccions de museu.

7. Realitzar les descripcions i il·lustracions de diferents estadis larvals prèviament identificats mitjançant mètodes moleculars, i seguint els estàndards actuals.

8. Elaborar una clau d´identificació actualitzada de les larves fil·losoma de *Scyllarus* conegudes.

9. Finalment, comparar les fil·losomes, decapodids i adults d'espècies de *Scyllarus* amb altres gèneres de la subfamília, per tal d'identificar trets de rellevància taxonòmica.

Material i Mètodes

- **Revisió bibliogràfica i *Databasing***: Els exemplars analitzats en aquesta tesi (N = 241) es varen obtenir a partir de la revisió i classificació del material recollit a diferents campanyes oceanogràfiques recents (e.g. MAFIA i CETOBAPH) i la revisió del material procedent de col·leccions de museu (NHM, MNHN, RMNH, USNM, RBINS, MfN, CCDE-IEOCD i ICM). La revisió de material s'ha complementat amb l´obtenció de bibliografia poc accessible (publicada en revistes de poca difusió internacional, en portuguès o francès) i documents no publicats del Prof. Alan Crosnier (MNHN, Paris) i l'il·lustrador Pierre Opic. Aquests documents han sigut fonamentals per a completar aquest estudi de les fil·losomes de *Scyllarus* africans. Tota la bibliografia va ser registrada amb el software Mendeley (https://www.mendeley.com/).

- **Mètodes morfològics**: Les descripcions de les larves es basen en l'esquema de somites dels malacostracis, descrit d'anterior a posterior, i descrivint els apèndixs de proximal a distal (Clark *et al.* 1998). Els estadis larvals es van determinar en base als treballs de Robertson (1968) i Webber & Booth (2001). Per a cada individu es varen prendre les següents mesures mitjançant el software ImageJ (https://imagej.net): longitud total (TL) des del marge anterior de l'escut cefàlic fins al marge posterior del tèlson; longitud cefàlica (CL) des del marge anterior al posterior de l'escut cefàlic; l'amplada cefàlica (CW) mesurada a la part més ampla de l'escut cefàlic i longitud del plèon (PDL) des del marge anterior del plèon fins al marge posterior del tèlson. Es van diseccionar les antènules, apèndix bucals, maxil·lípedes i pereiopodis de les larves abans de dibuixar-los. Les il·lustracions es van realitzar amb una càmera lúcida unida a un estereoscopi de gran rendiment Leica (M165C; Leica Microsystems, Wetzlar, Alemanya). També s'han realitzat fotografies amb el mateix sistema i el software Leica Application Suite (LAS) (https://www.leica-microsystems.com/es/). Els dibuixos digitals es van obtenir mitjançant una tauleta gràfica (Wacom, Intuos) i el software Adobe Illustrator CC9 (http://www.adobe.com/Illustrator), seguint les recomanacions de Coleman (2003).

- **Mètodes moleculars**: Les extraccions d'ADN a partir de teixit muscular de larves i adults es varen realitzar amb el mètode Chelex-protK (Palero *et al.* 2010). La identificació de les mostres per *DNA barcoding* es va basar en seqüències parcials del gen 16S rDNA (Marco-Herrero *et al.* 2013), ja que aquest marcador mostra una taxa d'amplificació més elevada que el gen COX1 (Palero *et al.* 2009a; Bracken-Grissom *et al.* 2014). Els productes de PCR amplificats es van purificar amb el QIAquick PCR purification Kit (QIAGEN Inc.) i es van seqüenciar mitjançant el kit BigDye v3.1 (Applied Biosystems) en un seqüenciador ABI Prism 3770. La qualitat dels cromatogrames de cada seqüència d'ADN es va inspeccionar mitjançant BioEdit ver. 7.2.5 (Hall 1999). Abans de realitzar els diferents anàlisis moleculars, les seqüències es van alinear amb Muscle ver. 3.6 (Edgar 2004) usant els paràmetres predeterminats. Les estimacions de les distàncies p (proporció de diferències genètiques) i la divergència evolutiva Kimura 2-paràmetres (K2P) es varen obtenir mitjançant MEGA X (Kumar *et al.* 2016; Kumar *et al.* 2018). Els arbres filogenètics es van construir utilitzant el mètode de màxima versemblança (*Maximum likelihood*) amb el mateix software.

Resultats i Discussió

L'anàlisi de seqüències d'ADN de les mostres recollides durant les campanyes CETOBAPH i MAFIA ens ha permès identificar, per primer cop a nivell d´espècie, la presència de larves de *Scyllarus arctus, S. caparti, S. pygmaeus* i *S. subarctus*, en les aigües nord-occidentals de la costa africana (capítols 1 i 3). Les larves de *S. caparti* i *S. subarctus* eren desconegudes fins a l´elaboració d´aquesta tesi doctoral. En el cas d'ambdues espècies, el nostre estudi morfològic inclou la descripció detallada de 3 estadis larvals: un estadi intermedi (VII), l'estadi sub-final (IX) i el final (X). A més, la revisió i anàlisi molecular de les mostres procedents d'expedicions recents també ens ha permès identificar la fase decapodid de *S. subarctus* (capítol 2). Els nostres resultats ens han permès crear una clau d'identificació per a les fil·losomes del gènere *Scyllarus* i ens han proporcionat dades rellevants per tal d´actualitzar la sistemàtica dels Scyllarinae. Entre els resultats, cal assenyalar la troballa, inesperada, d´una estreta relació filogenètica entre l'espècie africana *S. subarctus* i l´espècie americana *S. depressus.* Les distàncies genètiques entre aquestes espècies (1,9 - 2,4%) són 3 vegades inferiors a les observades entre *S. subarctus* i altres espècies africanes (5,8 - 7,9%) i 8 vegades respecte a la resta d'espècies d'Amèrica (14,2 - 17,3%). Aquest resultat està recolzat per la morfologia larval i dels adults i implica un procés d'especiació relativament recent, després que l´ancestre de *S. depressus* i *S. subarctus* colonitzés el continent americà des de les costes d'Àfrica. De fet, la post-larva de *S. subarctus* és la més gran coneguda dintre de la subfamília, el que podria conferir-li una major capacitat de dispersió. Tant la fil·losoma d'estadi final de *S. depressus* com de *S. subarctus* representen les larves més grans conegudes al gènere *Scyllarus* (poden sobrepassar els 3 cm de longitud total) i es distingeixen d'altres espècies per la gran densitat d'espines en la superfície dels pereiopodis i la forma del seu cèfalon. De la mateixa manera, ambdues espècies presenten un mateix patró d'espines, a més d'un marge antenal i de la pleura dels somites abdominals molt semblants, en la fase decapodid.

Els resultats obtinguts tenen fortes implicacions per a la sistemàtica del gènere *Scyllarus* i la relació amb gèneres pròxims. Al darrer dels nostres treballs (capítol 3) es posa en evidència l'origen polifilètic d'*Acantharctus* Holthuis 2002. D´una banda, *A. delfini* estaria estretament relacionat (formant un clade monofilètic ben recolzat) amb espècies de *Crenarctus* Holthuis 2002 de l'Oceà Pacífic, com ara *C. crenatus* i *C. bicuspidatus*; mentre que l´espècie *A. posteli* apareix estretament relacionada amb espècies de *Scyllarus* de l´Atlàntic, com ara *S. paradoxus*.

La morfologia del marge anterior de l'esternita toràcica en la fase adulta dona un patró congruent amb la biogeografia i les filogènies moleculars. Les espècies del Pacífic de *Crenarctus* i *A. delfini* comparteixen un marge anterior toràcic amb una forma característica de corona (en forma de W). Per contra, les espècies Atlàntiques de *Scyllarus* y *A. posteli* presenten una esternita amb un patró en forma de "U" (*S. arctus* i *S. subarctus*) o "V" (*S. paradoxus* i *A. posteli*), o una forma intermèdia (*S. caparti* i *S. pygmaeus*). En aquesta tesi, basant-nos tant en les evidències moleculars com les morfològiques, proposem restablir el basiònim *Scyllarus posteli*.

Conclusions

1. Les espècies de *Scyllarus* s'agrupen en dos clades recíprocament monofilètics (e.g. Atlàntic Occidental i Atlàntic Oriental). L'única excepció és *S. depressus*, que s'agrupa dintre del clade de l'Atlàntic oriental com a espècie germana de *S. subarctus*. Aquest resultat, amb suport d'evidències moleculars i morfològiques, suggereix un procés d'especiació relativament recent després d'una colonització del continent Americà.

2. Els nous resultats moleculars suggereixen un origen polifilètic del gènere *Acantharctus*, amb espècies de l'Oceà Atlàntic (*A. posteli*) i del Pacífic (*A. delfini*) agrupades en clades diferents. La morfologia del marge anterior de l'esternita toràcica és congruent amb la biogeografia i els patrons filogenètics moleculars.

3. Les noves evidències morfològiques i moleculars aconsellen la inclusió de *A. posteli* al gènere *Scyllarus*, com a espècie germana de *S. paradoxus*. Per tant, el basiònim *Scyllarus posteli* deuria restablir-se. L'estreta relació genètica i morfològica entre *A. delfini* i diferents taxa del Oceà Pacífic, com *Crenarctus crenatus* i *C. bicuspidatus,* suggereixen que *A. delfini* deuria anomenar-se *Crenarctus delfini*.

4. El nou material estudiat durant aquesta tesi ens permet expandir la distribució geogràfica de manera significativa per a *S. subarctus* i *S. caparti*. Mentre que *S. subarctus* s'estén des dels 34 N als 18 S (prèviament 21 N – 17 S), *S. caparti* es distribueix dels 27 N fins als 9 S (front al límit 22 N anterior a la tesi).

5. Tant l'estadi fil·losoma final com l'etapa nisto de *S. subarctus* són les més grans entre les larves de Scyllarinae conegudes. Aquest tamany, juntament amb la llarga durada de la fase planctònica, podria estar relacionat amb una gran capacitat de dispersió i explicar la colonització d'illes remotes com Santa Helena.

6. En aquesta tesi es descriuen per primera vegada el decapodid de *S. subarctus* i 3 estadis fil·losoma (VII, IX i X) tant de *S. subarctus* com de *S. caparti*. Tots els exemplars descrits han estat identificats prèviament mitjançant tècniques moleculars.

7. Es necessària una nova definició dels estadis fil·losoma, integrant els canvis morfològics amb canvis en l'alimentació i comportament. Aquesta nova definició seria molt més significativa per a estudis d'ecologia larval que l'actual sistema basat en petits canvis morfològics.

8. Es proposen nous caràcters per identificar les fil·losomes de *Scyllarus* a nivell d'espècie, com ara la forma del cèfalon, presència d'espines toràciques dorsals i la seua talla relativa i la quantitat de sedes i espines als pereopodis.

9. Hem completat una nova clau d'identificació per a les fil·losomes de *Scyllarus*, descrivint en detall diferents estructures larvals, com els pleopodis dels nistos o els dàctils de les fil·losomes. Aquests trets han rebut poca atenció en estudis anteriors, però deurien tenir-se en compte per a futurs estudis taxonòmics dels Scyllarinae.

10. Els nostres resultats tenen implicacions directes per a la sistemàtica dels Scyllarinae. Es poden definir dos grups de gèneres, un d'ells incloent els *Crenarctus* de l'Oceà Pacífic, i els *Scyllarus* africans; i l'altre que inclouria els *Scyllarus* americans i *Eduarctus*. Les fil·losomes d'aquests dos grups poden diferenciar-se en base a la presència/absència d'espines toràciques, la longitud relativa de les antènules i les espines postero-laterals del tèlson. Es recomana la revisió morfològica dels adults en futurs estudis.

INTRODUCCIÓ GENERAL

Llagostes de l´infraordre Achelata

Les llagostes de l'infraordre Achelata Scholtz and Richter, 1995 són un grup important de crustacis decàpodes que podem trobar a diferents ecosistemes marins, des de la zona litoral fins a grans profunditats (> 800 m) (Webber and Booth 2007). A diferència de la resta de llagostes, els Achelata es caracteritzen per no presentar pinces al primer parell de pereiopodis i per la presència d'una forma larval altament especialitzada per a la dispersió a llarga distància. Estudis morfològics i moleculars recents han confirmat que aquest infraordre està format per dues famílies ben diferenciades, els Palinuridae Latreille, 1802 i els Scyllaridae Latreille, 1825 (Palero *et al.* 2009a; Bracken-Grissom *et al.* 2014) (Figura 1).

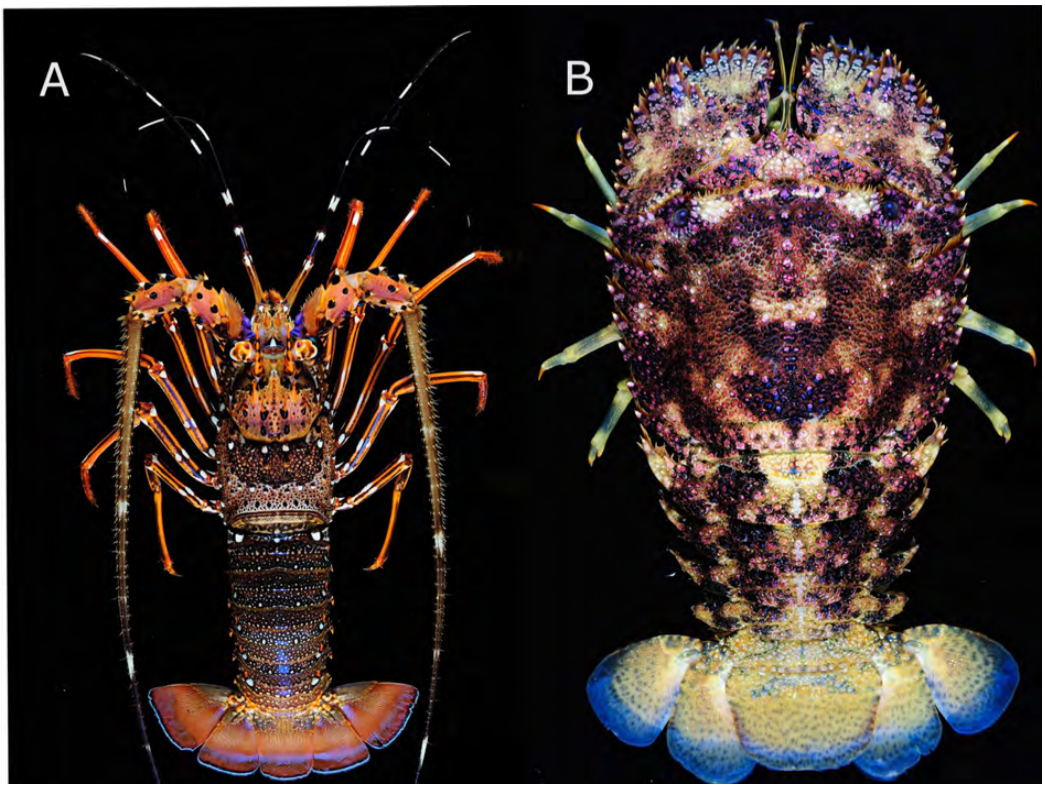


Fig.1: Morfologia externa de les llagostes Achelata. (A) *Panulirus longipes longipes* (A. Milne-Edwards, 1868) (MNHN-IU-2010-5072); (B) *Parribacus antarcticus* (Lund 1793) (MNHN-IU-2010-5069). Fotografies obtingudes de la web https://science.mnhn.fr/institution/mnhn/collection/

Aquests crustacis tenen un paper fonamental a les xarxes tròfiques de diferents ecosistemes, a més d'un alt valor comercial (Booth and Phillips 1994). Malgrat la seua importància, encara sabem molt poc sobre la biologia de les llagostes, en particular sobre la seua dinàmica poblacional i reclutament larval (Palero *et al.* 2014a). Açò és degut al seu

complex i extens cicle vital, que dificulta el seu estudi al laboratori (Figura 2). Les llagostes adultes arriben a la maduresa sexual als 4-5 anys, segons l'espècie, i generalment tenen una o dues temporades reproductives cada any amb un llarg període d'incubació dels ous. Dels ous surten unes larves aplanades dorso-ventralment que anomenem larva *fil·losoma*. La metamorfosi del darrer estadi larval origina un estadi de transició entre la fase planctònica i la fase bentònica adulta (anomenat "nisto" en espècies de Scyllaridae o "puerulus" en espècies de Palinuridae) (Booth *et al.* 2005).

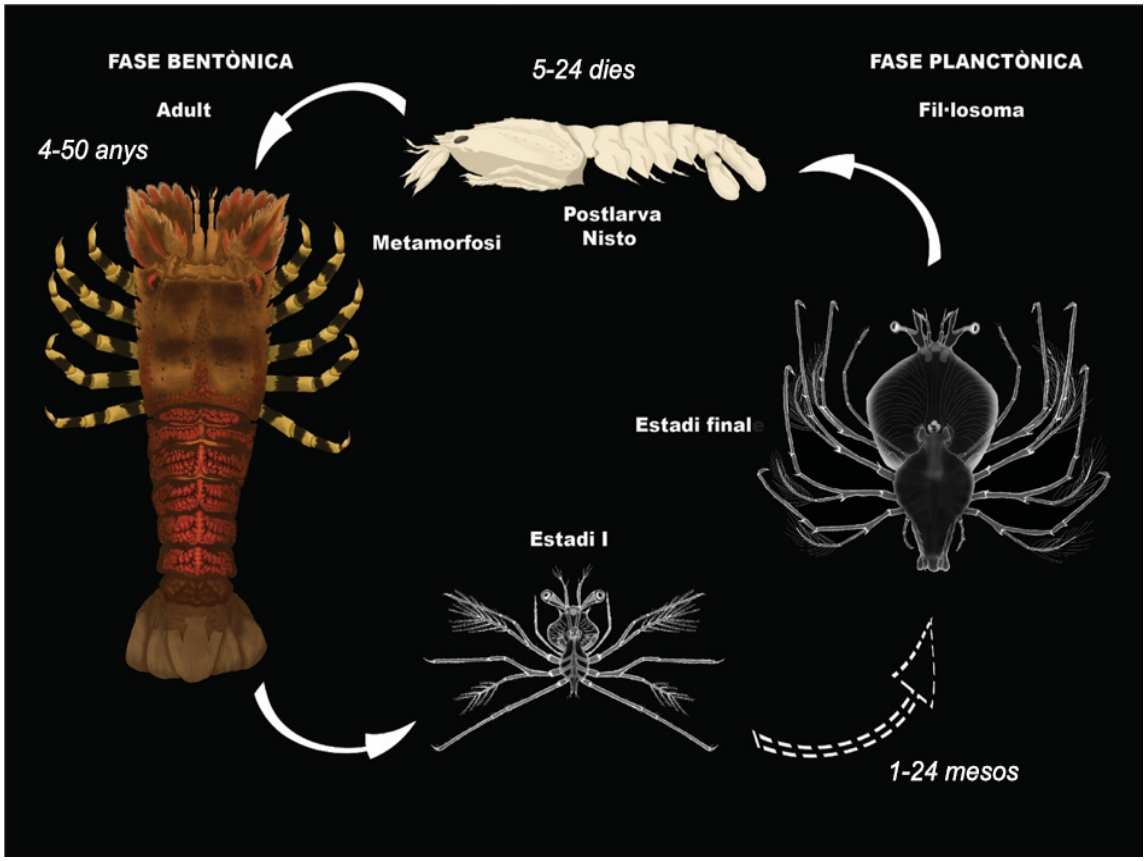


Fig. 2: Cicle vital d'una llagosta Scyllaridae Latreille, 1825.

Els Scyllaridae es caracteritzen per tenir el darrer segment antenal completament aplanat, ja que actua de timó per escapar dels depredadors (Barshaw and Spanier 1994). Coneguts en anglès com a *spanish lobsters, slipper lobsters* o *bulldozer lobsters*, els pescadors del nostre litoral mediterrani les coneixen com a «castanyoles» perquè recorden aquest instrument musical quan colpegen l'abdomen contra el tòrax en la reacció d´escapada. Tot i que la biologia dels Palinuridae ha estat més estudiada pel seu valor comercial, els Scyllaridae contenen una major diversitat d'espècies i es distribueixen arreu del món, ocupant les franges tropicals i subtropicals (Chan 2010; Yang *et al.* 2014). El grup taxonòmic dels Scyllaridae conté

un total de 20 gèneres i més de 90 espècies diferents, dividides en quatre subfamílies: Arctidinae Holthuis, 1985, Ibacinae Holthuis, 1985, Theninae Holthuis, 1985 i Scyllarinae Latreille, 1825. L'objectiu principal d'aquesta tesi és la revisió del gènere tipus dels Scyllarinae, *Scyllarus* Fabricius, 1775. Aquest gènere està format actualment per 9 espècies que es distribueix arreu de les costes atlàntiques orientals i occidentals, 5 espècies a Europa i Àfrica i 4 espècies a les costes d'Amèrica (Taula 1).

Taula 1. Espècies del gènere *Scyllarus* Fabricius, 1775 , 1825. Ecoregions basades en Spalding *et al*. (2007) TNA (Nord Atlàntic Temperat), TrA (Atlàntic Tropical), TSA (Amèrica del Sud Temperada), TSAf (Sud Àfrica temperada).

Espècie	Ecoregió	Batimetria	Referències
S. americanus (Smith, 1869)	TNA, TrA	< 46 m	6, 11, 18
S. arctus (Linnaeus, 1758)	TNA	4 – 143 m	1, 12, 14, 15, 21, 22
S. caparti Holthuis, 1952	TNA, TrA	17 – 105 m	2, 9, 12, 17, 25
S. chacei Holthuis, 1960	TNA, TrA	10-330 m	2, 18, 24
S. depressus (Smith, 1881)	TNA, TrA, TSA	20 – 265 m	8
S. paradoxus (Miers, 1881)	TrA	4 – 46 m	4
S. planorbis Holthuis, 1969	TrA	19 – 99 m	5, 19
S. pygmaeus (Bate, 1888)	TNA, TrA	5 – 162 m	3, 10, 13, 20
S. subarctus Crosnier, 1970	TrA, TASf	41 – 240 m	7, 16, 23, 25

Referències: (1) Gurney 1936; 2) Holthuis 1960; 3) Forest and Holthuis 1960; 4) Forest 1963; 5) Holthuis 1969; 6) Lyons 1970; 7) Crosnier 1970; 8) Robertson 1971; 9) Froglia 1974; 10) Lewinsohn 1974; 11) Coelho 1981; 12) Anadon 1981; 13) García Raso 1982; 14) Garcia Socias and Massuti Jaume 1987; 15) Holthuis 1991; 16) Macpherson 1991; 17) Fransen 1991; 18) Tavares 1997; 19) Navas S. and Campos C. 1998; 20) Palero *et al.* 2008; 21) Quigley *et al.* 2010; 22) Palero *et al.* 2011; 23) Muñoz *et al.* 2012; 24) Silva *et al.* 2012; 25) de Matos-Pita *et al.* 2018).

Scyllarus americanus presenta una àmplia distribució en aigües costaneres (<50 m) des de North Carolina fins a Pernambuco (Coelho 1981; Tavares 1997). La distribució de *S. chacei* és més meridional, arribant a trobar-se a l'estat de Bahia (Brasil), i pot trobar-se a major profunditat que *S. americanus*. *Scyllarus depressus*, descrita per Smith (1881) com a *Arctus depressus*, també es troba des de North Carolina fins Brasil. La darrera de les espècies

típicament americanes, *S. planorbis*, ha estat molt poc estudiada, però es troba a Hondures, Panamà, Colòmbia, Veneçuela, Surinam i Guyana. En l'Atlàntic oriental podem trobar *Scyllarus arctus*, espècie típica del Mediterrani que també es troba al Nord-Est Atlàntic, des de les illes Britàniques fins a les Açores, Madeira i les Illes Canàries. *Scyllarus pygmaeus* també es troba àmpliament distribuïda per tota la costa mediterrània, però té una distribució una mica més meridional i pot arribar fins l'arxipèlag de Cap Verd (Pessani and Mura 2007). Ambdues espècies són considerades espècies d'aigües temperades i comparteixen un rang batimètric similar. *Scyllarus caparti* s'estén per latituds tropicals i subtropicals al llarg de la costa atlàntica africana. La cita de Froglia (1974) al mar Adriàtic es podria considerar una introducció puntual per aigua de llast. Una espècie amb distribució més restringida a la franja tropical és *S. paradoxus*, present típicament en aigües poc profundes. Per últim, tot i que *S. subarctus* tenia originalment una distribució restringida a les costes de Namíbia, investigadors de l'Institut Espanyol d'Oceanografia suggereixen recentment la presència de 5 individus de *S. subarctus* a les costes de Guinea Bissau (Muñoz *et al.,* 2012).

La larva fil·losoma

La forma aplanada dorso-ventralment de la larva *fil·losoma* (literalment "cos de fulla") té unes propietats de flotació molt particulars, i permet a les larves aprofitar les corrents marines per a la dispersió passiva durant llargs períodes de temps (Booth and Phillips 1994; Phillips *et al.* 2006). La *fil·losoma* se correspon amb la fase zoea dels crancs i altres decàpodes, i passa per múltiples estadis de desenvolupament, generalment entre 4 i 13 (Booth *et al.* 2005; Palero and Abello 2007). Durant molts anys, l'estudi de les larves fil·losoma ha estat una tasca complexa, ja que la seua morfologia tan diferent a l'adult dificultava la seua identificació. De fet, fins fa molt poc els estudis sobre fil·losomes es basaven en dades morfològiques molt limitades i alguns experiments de cultiu (Kittaka 1994; Kittaka 1997). Les larves de diferents espècies en un mateix gènere són molt semblants entre si, sobretot als primers estadis, i la correspondència entre fil·losoma i adult encara és una incògnita en la majoria de casos.

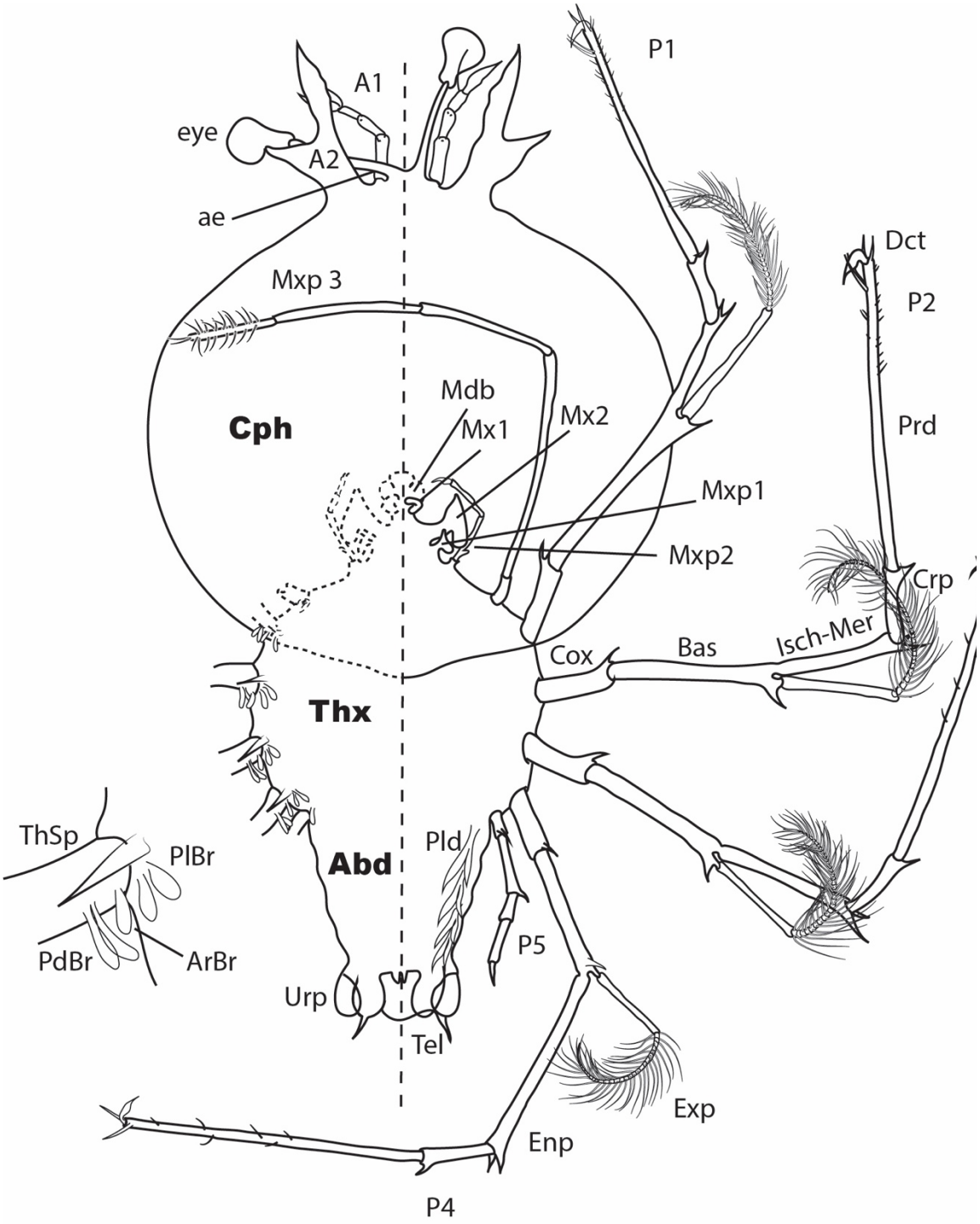


Fig. 3: Morfologia de la larva fil·losoma en estadi final. Dreta vista dorsal. Esquerra vista ventral

Els escil·làrids tenen un període de desenvolupament larval molt variable entre gèneres, i pot comprendre des d'unes setmanes fins a 9 mesos (Robertson 1968b; Lyons 1970; Robertson 1971; Robertson 1979; Booth *et al.* 2005). Açò fa que en molts casos romanguin llargs períodes de temps al plàncton, exposades a la depredació i les corrents. La transparència gairebé total del cos és possiblement una de les característiques més notòries de les fil·losomes, ja que dificulta la detecció per depredadors i evita l'alta mortalitat. Una altra

adaptació d'aquestes larves per maximitzar la seua supervivència, és associar-se amb el zooplàncton gelatinós (Shojima 1963; Thomas 1963; Herrnkind *et al.* 1976; Barnett *et al.* 1986). Les larves aprofitarien el transport "gratuït" cap a la costa, a més de servir-se de les meduses com a font d'alimentació (Shojima 1963; Sims and Brown 1968). Els dàctils modificats en forma de "ganxos" de les fil·losomes probablement facilita un ancoratge eficient a les meduses (Figura 4), que les larves usen com a vehicles de flotació (Wakabayashi and Tanaka 2012).

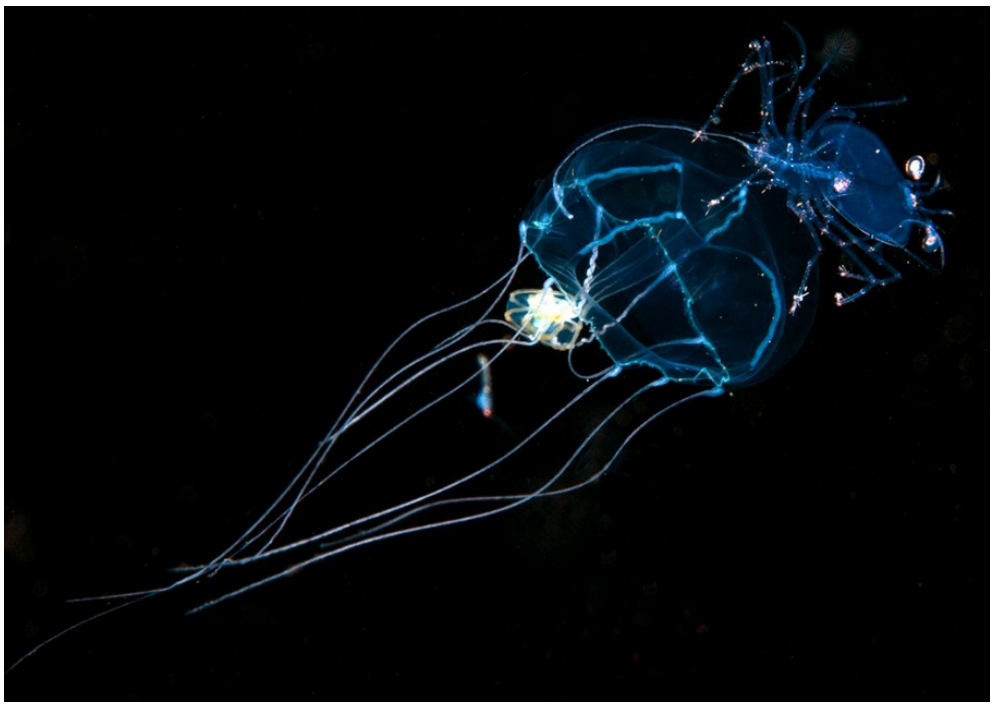


Fig. 4: Larva fil·losoma fent *piggy-riding* sobre una medusa. Fotografia cedida per Yury Ivanov.

Les larves fil·losoma realitzen migracions verticals al llarg del seu desenvolupament. Durant les hores de llum es mantenen a majors profunditats per evitar possibles depredadors, mentre que a la nit les podem trobar a capes superficials (Phillips *et al.* 1981; Palma *et al.* 2011). S'ha proposat que les habilitats de natació augmenten a mesura que avança el creixement larval, així les larves d'estadis tardans podrien realitzar migracions verticals a majors profunditats (Phillips *et al.* 1981). Així, la seua capacitat de desplaçament podria ser utilitzada com a mecanisme de retenció per evitar les corrents superficials i romandre prop de la zona de posta (Yeung and McGowan 1991; Rodríguez *et al.* 2001).

L'Atlàntic està dominat per dos grans girs oceànics, un a l'hemisferi sud i l'altre a l'hemisferi nord (Figura 5). En els seus trajectes paral·lels a la costa occidental africana, els girs alimenten dues corrents importants: la corrent de Benguela i la Corrent de Canàries, respectivament. Ambdues són corrents que afavoreixen la surgència d'aigües profundes, més fredes i riques en nutrients.

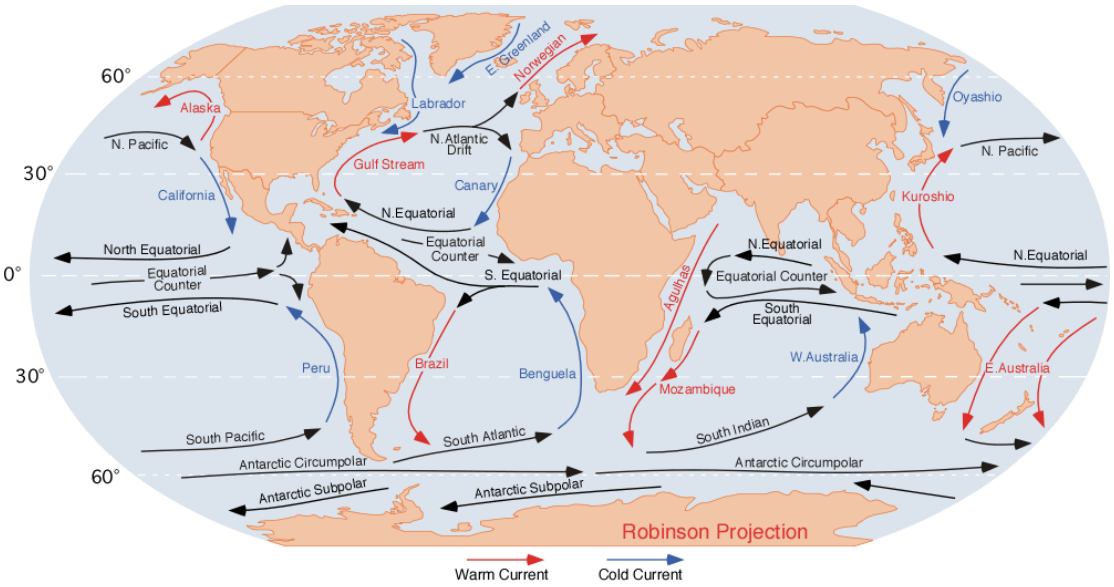


Fig. 5: Principals corrents oceàniques (http://blue.utb.edu/paullgj/geog3333/lectures/physgeog.html)

La Corrent de Canàries origina el *Canary Current Large Marine Ecosystem* (CCLME), que comunica les illes de la Macaronèsia (Figura 6) (García-Isarch and Muñoz 2015). El flux entre illes s'ha observat en diferents grups faunístics, com peixos (Almada *et al.* 2001; Almada *et al.* 2005) o mol·luscs (De Wolf *et al.* 1998). Alguns autors però, apunten que l'arxipèlag de Cap Verd presenta una biodiversitat més propera al continent africà que amb la resta d'illes de la regió, a més d'una elevada taxa d'endemismes (Freitas *et al.* 2019). S'ha suggerit que el Front del Cap Verd (CVF) podria actuar com a barrera biogeogràfica, aïllant l'Arxipèlag de Cap Verd de la resta d'illes (Quinteiro *et al.* 2007; Freitas *et al.* 2019). El CVF s'estén fins les illes de Cap Verd des d'aproximadament 20º - 23º N (Pelegrí and Peña-Izquierdo 2015; Kämpf and Chapman 2016). Tot i l'efecte barrera del CVF, el CCLME sembla estar connectat per una corrent sud-nord entre els 200-300 metres de profunditat (Figura 6), i que pot assolir els 800 m a l'estiu i la tardor boreals (Barton, 1989).

A més de les corrents oceàniques superficials, la CCLME es caracteritza per una intensa surgència d'aigües profundes. Aquests afloraments són de gran importància per a l'ecologia de les comunitats que habiten les illes oceàniques de la Macaronèsia, ja que transporten plàncton i matèria orgànica (Landeira *et al.* 2009; Landeira *et al.* 2010; Landeira *et al.* 2012; Pelegrí and Benazzouz 2015). Les illes poden generar pertorbacions o remolins que actuen com a zones de retenció del plàncton (Rodríguez et al. 2001; Landeira 2010), restringint la dispersió passiva (Chiswell and Booth 1999; Inoue *et al.* 2001; Rudorff *et al.* 2009). Aquests remolins mantenen grans concentracions de nutrients i permeten un creixement òptim de les larves prop de la costa, facilitant l'auto-reclutament d'espècies costaneres (Chiswell and Booth 1999).

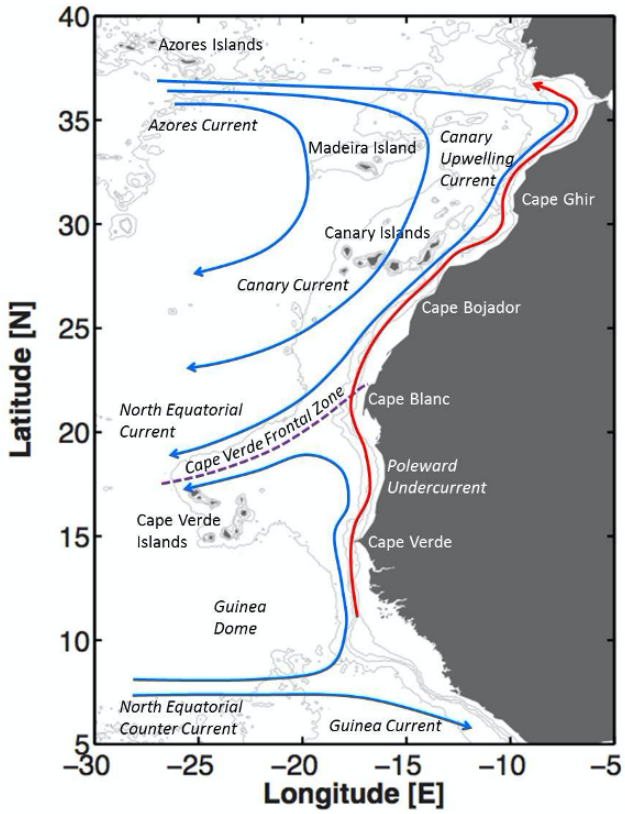


Fig. 6: Principals corrents oceanogràfiques (cursiva) a la termoclina permanent del CCLM. La línia vermella mostra la *Poleward Undercurrent*. Imatge: (Pelegrí and Peña-Izquierdo 2015).

Campanyes d´exploració en l´Àfrica occidental

Després de les grans campanyes de finals del segle XIX i principis del segle XX, la costa atlàntica africana va romandre poc estudiada, però en les últimes dècades s´han produït vàries campanyes importants (Taula 2). El centre d'investigació francès O.R.S.T.O.M, conegut avui en dia com l'Institut de Recherche pour le Développement (IRD), dugué a terme una extensa campanya oceanogràfica a la regió oriental de l'Atlàntic tropical (Crosnier & Forest 1973). El

vaixell OMBANGO (1960-1962) va recórrer la costa des de l'Illa de Sao Tomé fins a Angola i les mostres obtingudes varen ser comparades amb el material recol·lectat a bord del *Talisman* (1883) o el vaixell *Geronimo* (1963), del Servei de Pesca i Vida Silvestre dels EEUU. Gràcies a aquesta campanya es publicaren diversos treballs on s'estudiaven més de 150 espècies de crustacis (Crosnier 1967; Crosnier 1970; Crosnier and Forest 1973). Algunes d'aquestes publicacions tractaren les larves fil·losoma de *Scyllarides* i *Panulirus* (Crosnier 1971; Crosnier 1972). Entre 1970 i 1975, el vaixell d'investigació *Almoravide*, del laboratori de pesqueries de Nouadhibou (IFAN), va dur a terme diverses campanyes de pesca a les costes de Mauritània i Senegal. Tot i que les larves no varen poder identificar-se a nivell d'espècie, amb el material obtingut es publicaren articles molt importants sobre l'ecologia de les fil·losomes (Maigret 1975; Maigret 1978). Altres centres europeus, incloent els holandesos, espanyols i alemanys, també s'han interessat per la biodiversitat marina de l´Atlàntic africà. Per exemple, l'expedició CANCAP (1976-1986), a mans d'investigadors del RMNH, es va centrar en la Macaronèsia, mentre que el projecte BENGUELA (1979-1981) i les campanyes SNEC I-II varen permetre recórrer la costa de Namíbia a diferents membres del "Instituto de Investigaciones Pesqueras" (IPP).

Taula 2: Campanyes realitzades durant la segona meitat del segle XX i principis del XXI. Es detallen les institucions i països involucrats, sector mostrejat, any i referencia bibliogràfica.

Campanya Oceanogràfica	Institució	Sector	Període	Referència
OMBANGO	O.R.S.T.O.M	Golf de Guinea	1960-1969	Crosnier and Forest 1973
ALMORAVIDE	IFAN	Mauritània-Senegal	1970-1975	Maigret 1975, 1978
CANCAP (I-VII)	RMNH	Macaronèsia	1976-1986	Land 1987
BENGUELA (I-IV)	IPP	Namíbia	1979-1981	Macpherson 1983
SUBTROPEX82	ZIM	CCLME	1982	Tan and Rüger 1989
SNEC (I-II)	IPP	Namíbia	1985-1986	Macpherson 1991
Múltiples campanyes	IEO	CCLME	2004-2009	García-Isarch and Muñoz 2015
CETOBAPH	ULL	Illes Canàries	2012	Landeira *et al.* 2014
MAF	UCA	Cap Verd - Brasil	2015	Hernández-León *et al*. 2019

Més recentment, diverses institucions espanyoles han dut a terme una sèrie de campanyes oceanogràfiques des de la costa nord-africana fins Guinea-Bissau, incloent els arxipèlags de Canàries i Cap Verd. El Instituto Español de Oceanografía (IEO) ha estudiat la biodiversitat de decàpodes a la regió del CCLME mitjançant mostrejos de pesca des de l'any 2004. El projecte GUINEA-BISSAU 0810 fou de les últimes campanyes realitzades a bord del *R/V Vizconde de Eza* de les que se disposa informació (Muñoz *et al.* 2012). La campanya CETOBAPH, realitzada a l'abril del 2012, va estar centrada en l'estudi del plàncton a l'arxipèlag Canari i la influència dels afloraments d'aigües profundes des de la costa africana (Landeira *et al.* 2009; Landeira *et al.* 2010; Landeira *et al.* 2012). El projecte "Migrants and Active Flux In the Atlantic ocean" (MAFIA) dirigit per investigadors de la Universidad de Cádiz (UCA), va explorar les aigües que van des de les illes Canàries fins a les costes de Brasil.

Tècniques recents i l'estudi de larves fil·losoma

Tenint en compte que la morfologia larval és molt semblant entre diferents gèneres i espècies i la falta de correlació entre caràcters específics dels adults i la morfologia larval, no podem tenir la certesa que les larves descrites estiguin ben identificades. De fet, la correspondència entre la fil·losoma i la forma adulta de llagosta és una incògnita que encara està per resoldre's en la majoria de casos (Palero *et al.* 2016). En els últims anys, la inclusió de noves tècniques moleculars ha revolucionat els estudis de zoologia i taxonomia. El codi de barres molecular (*DNA barcoding*) permet identificar una mostra a nivell d'espècie basant-nos en l´amplificació d'una regió del gen codificant per a la subunitat I de la citocrom oxidasa (COX1) (Hebert *et al.* 2003). L'amplificació d'aquesta regió (i d´altres) mitjançant PCR ha demostrat ser eficient en estudis d'identificació de larves de crustacis (Palero *et al.* 2011; Marco-Herrero *et al.* 2013; Palero *et al.* 2014b). Les identificacions de larves mitjançant *DNA barcoding*, ens permet la identificació d'exemplars recollits del plàncton i fixats en etanol, i representa un pas fonamental per resoldre les identificacions del material disponible en col·leccions històriques de museu.

Altres avanços tecnològics importants en la descripció de noves espècies o formes larvals inclouen l´ús de programes informàtics per a la il·lustració científica. El dibuix digital presenta diversos avantatges front a l'ús tradicional dels estilogràfics de tinta (Coleman 2003). Programes com *Adobe Illustrator* corregeixen traços que no són fàcils de dibuixar perfectament

a mà alçada, i els vectoritza directament. Açò permet dur a terme un procés de correccions molt més eficient, ja que podem editar cada línia de manera individualitzada. A més, és possible crear estructures complexes amb l'apilament de diverses capes vectorials de forma elegant (Coleman 2009). Per exemple, una zona amb una gran densitat de sedes seria confusa al dibuixar-la a llapis, però amb l'ús de l'ordinador podem augmentar la imatge fins a 64 vegades. Caràcters morfològics amb importància taxonòmica queden així reflectits a les descripcions de manera clara, evitant possibles confusions en futures identificacions.

OBJECTIUS

OBJECTIUS

1. Revisar la sistemàtica dels Scyllarinae centrant-se en les espècies de l'Àfrica occidental amb un enfocament taxonòmic integrador (combinant trets morfològics i moleculars.

2. Recopilar exemplars d'adults i larves de dues campanyes oceanogràfiques recents (ex. CETOBAPH i MAFIA) i múltiples col·leccions de museu.

3. Obtenir seqüències genètiques a partir de larves prèviament seleccionades per identificar-les a nivell d'espècie (Codi de barres d'ADN).

4. Analitzar les distàncies genètiques entre les diferents espècies de *Scyllarus* i inferir les relacions evolutives entre elles.

5. Generar una base de dades amb la localització, profunditat i estat de desenvolupament (fil·losoma, decapodid, juvenil o adult) dels *Scyllarus* analitzats.

6. Actualitzar la biogeografia dels *Scyllarus* africans amb les noves dades obtingudes de campanyes recents i col·leccions de museu.

7. Realitzar les descripcions i il·lustracions de diferents estadis larvals prèviament identificats mitjançant mètodes moleculars, i seguint els estàndards actuals.

8. Elaborar una clau d´identificació actualitzada de les larves fil·losoma de *Scyllarus* conegudes.

9. Finalment, comparar les fil·losomes, decapodids i adults d'espècies de *Scyllarus* amb altres gèneres de la subfamília, per tal d'identificar trets de rellevància taxonòmica.

OBJECTIVES

1. To review Scyllarinae systematics focusing on western Africa species with an integrative taxonomy approach (which combines morphological and molecular traits).

2. To gather adult and larval samples from recent oceanographic campaigns (ex. CETOBAPH and MAFIA) and several museum collections.

3. To obtain genetic sequences from previously selected larvae in order to identify them to species level (DNA barcoding).

4. To analyse genetic distances between different *Scyllarus* spp. and infer evolutionary divergences between them.

5. To build a database including location, depth and developmental stage (phyllosoma, decapodid, juvenile or adult) for the *Scyllarus* specimens analysed.

6. To update our current understanding of African *Scyllarus* biogeography, with new data obtained from recent campaigns and museum collections.

7. To carry out the morphological descriptions and illustrations of different larval stages previously identified through molecular methods and following current standards.

8. To prepare an updated identification key of every known *Scyllarus* phyllosoma larvae.

9. Finally, phyllosomae, decapodids and adults of *Scyllarus* are compared with other genera to identify new characters of taxonomic value.

MATERIAL I MÈTODES

Revisió bibliogràfica i *Databasing*: Els exemplars analitzats en aquesta tesi (N = 241) es varen obtenir a partir de la revisió i classificació del material recollit a diferents campanyes oceanogràfiques recents (e.g. MAFIA i CETOBAPH) i la revisió del material procedent de col·leccions de museu (NHM, MNHN, RMNH, USNM, RBINS, MfN, CCDE-IEOCD i ICM). Tota la informació recopilada s'ha emmagatzemat en una base de dades pròpia i ha servit per actualitzar les identificacions del material de les col·leccions. La revisió de material s'ha complementat amb l´obtenció de bibliografia poc accessible (publicada en revistes de poca difusió internacional, en portuguès o francès) i documents no publicats del Prof. Alan Crosnier (MNHN, Paris) i l'il·lustrador Pierre Opic. Aquests documents han sigut fonamentals per a completar aquest estudi de les fil·losomes de *Scyllarus* africans. Tota la bibliografia va ser registrada amb el software Mendeley (https://www.mendeley.com/).

Mètodes morfològics: Les descripcions de les larves es basen en l'esquema de somites dels malacostracis, descrit d'anterior a posterior, i descrivint els apèndixs de proximal a distal (Clark *et al.* 1998). Els estadis larvals es van determinar en base als treballs de Robertson (1968) i Webber & Booth (2001). Per a cada individu es varen prendre les següents mesures amb l'ús del software ImageJ (https://imagej.net): longitud total (TL) des del marge anterior de l'escut cefàlic fins al marge posterior del tèlson; longitud cefàlica (CL) des del marge anterior al posterior de l'escut cefàlic; l'amplada cefàlica (CW) mesurada a la part més ampla de l'escut cefàlic i longitud del plèon (PDL) des del marge anterior del plèon fins al marge posterior del tèlson (Figura 7). Es van disseccionar les antènules, apèndix bucals, maxil·lípedes i pereiopodis de les larves abans de dibuixar-los. Les il·lustracions es van realitzar amb una càmera lúcida unida a un estereoscopi de gran rendiment Leica (M165C; Leica Microsystems, Wetzlar, Alemanya). També s'han realitzat fotografies amb el mateix sistema i el software Leica Application Suite (LAS) (https://www.leica-microsystems.com/es/). Els dibuixos digitals es van obtenir mitjançant una tauleta gràfica (Wacom, Intuos) i el software Adobe Illustrator CC9 (http://www.adobe.com/Illustrator), seguint les recomanacions de Coleman (2003).

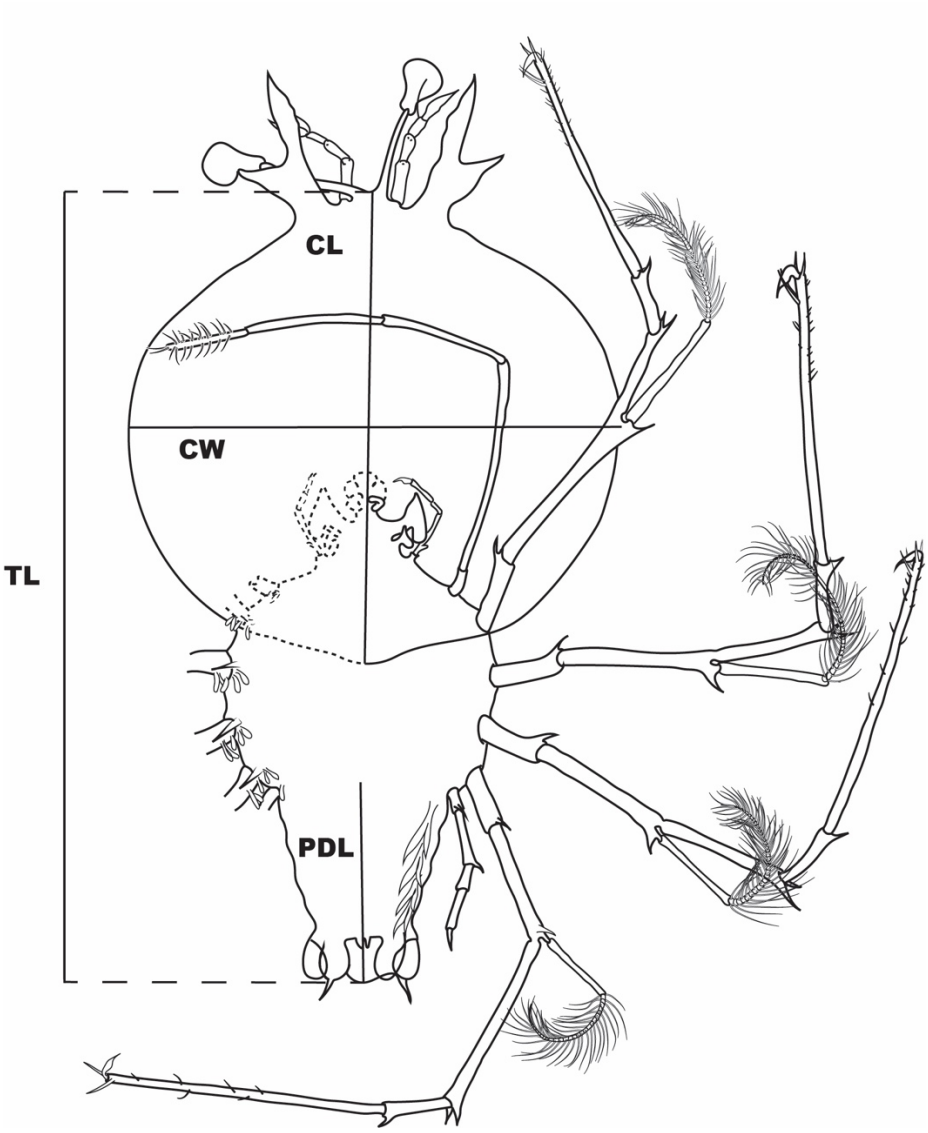


Fig. 7: Mesures preses: longitud total (TL), longitud cefàlica (CL), amplada cefàlica (CW) i longitud del plèon (PDL).

Mètodes moleculars: Les extraccions d'ADN a partir de teixit muscular de larves i adults es varen realitzar amb el mètode Chelex-protK (Palero *et al.* 2010). La identificació de les mostres per *DNA barcoding* es va basar en seqüències parcials del gen 16S rDNA (Marco-Herrero *et al.* 2013), ja que aquest marcador mostra una taxa d'amplificació més elevada que el gen COX1 (Palero *et al.* 2009a; Bracken-Grissom *et al.* 2014). Els productes de PCR amplificats es van purificar amb el QIAquick PCR purification Kit (QIAGEN Inc.) i es van seqüenciar mitjançant el kit BigDye v3.1 (Applied Biosystems) en un seqüenciador ABI Prism 3770. La qualitat dels cromatogrames de cada seqüència d'ADN es va inspeccionar mitjançant BioEdit ver. 7.2.5 (Hall 1999). Abans de realitzar els diferents anàlisis moleculars, les seqüències es van alinear amb Muscle ver. 3.6 (Edgar 2004) usant els paràmetres

predeterminats. Les estimacions de les distàncies p (proporció de diferències genètiques) i la divergència evolutiva Kimura 2-paràmetres (K2P) es varen obtenir mitjançant MEGA X (Kumar *et al.* 2016; Kumar *et al.* 2018). Els arbres filogenètics es van construir utilitzant el mètode de màxima versemblança (*Maximum likelihood*) amb el mateix software.

RESULTATS

Informe dels Directors

Títol de la Tesi: Slipper lobsters from Atlantic waters: revision of *Scyllarus* Fabricius, 1775 (Crustacea: Scyllaridae) using a multiple-evidence approach

Autora: Rebeca Genís Armero

Directors: Dr. Ferran Palero Pastor i Dra. Romana Capaccioni Azzati

a) Factor d'impacte de les publicacions

CERTIFIQUEN:

La memòria de Tesi Doctoral presentada per Rebeca Genís Armero titulada "Slipper lobsters from Atlantic waters: revision of *Scyllarus* Fabricius, 1775 (Crustacea: Scyllaridae) using a multiple-evidence approach", ha estat dirigida conjuntament pel Dr. Ferran Palero Pastor de l'Institut Cavanilles de Biodiversitat i Biologia Evolutiva (ICBIBE) i la Dra. Romana Capaccioni Azzati de la Universitat de València. Aquesta tesi inclou 4 articles publicats en revistes indexades, 1 d'ells com Annex.

Tots els articles han passat per la revisió d'investigadors anònims designats pels editors. A continuació es detalla l'índex d'impacte de les revistes i la posició en l'àrea segons les dades del ISI Web of Science. Cal assenyalar que, tot i que la candidata a Doctor signa en segon lloc l'article incorporat com Annex, hem decidit incorporar aquest article per la seua rellevància i relació en la temàtica de la tesi. Així mateix, cal indicar que la resta de signants són Doctors, per la qual cosa, el treball no ha estat, ni estarà, formant part d'altra Tesi Doctoral.

Publicació 1 Possible amphi-Atlantic dispersal of *Scyllarus* lobsters (Crustacea: Scyllaridae): molecular and larval evidence

Zootaxa

Impact Factor, 2017: **0.931**

Posició en l'àrea: 94/167 (Zoology)

Publicació 2 Updated distribution and first description of *Scyllarus subarctus* (Crustacea: Scyllaridae) decapodid stage

Journal of the marine biological association of the United Kingdom

Impact Factor, 2018 (latest available): **1.578**

Posició en l'àrea: 52/108 (Marine and Freshwater Biology)

Publicació 3 Revision of the West African species of *Scyllarus* Fabricius, 1775 (Decapoda: Achelata: Scyllaridae), with the description of three phyllosoma stages of *S. caparti* Holthuis, 1952 and an updated identification key

Journal of Crustacean Biology

Impact Factor, 2018: **1.069**

Posició en l'àrea: 74/108 (Marine and Freshwater Biology)

92/170 (Zoology)

Publicació 4 DNA barcoding the phyllosoma of *Scyllarides squammosus* (H. Milne Edwards, 1837) (Decapoda: Achelata: Scyllaridae)

Zootaxa

Impact Factor, 2016**: 0.972**

Posició en l'àrea: 87/163 (Zoology)

I per a que així conste, en compliment de la legislació vigent, signem el present certificat a València, a 7 de juny de 2020.

Signat: Ferran Palero Pastor i Romana Capaccioni Azzati, Directors de la Tesi Doctoral

b) Contribució del candidat en publicacions amb més signants

Publicació 1

Genis-Armero, R., Guerao, G., Abelló, P., González-Gordillo, J.I., Cuesta, J.A., Corbari, L., Clark, P.F., Capaccioni-Azzati, R., and Palero, F. (2017). Possible amphi-atlantic dispersal of *Scyllarus* lobsters (Crustacea: Scyllaridae): Molecular and larval evidence. *Zootaxa 4306*, 325–338. http://dx.doi.org/10.11646/zootaxa.4306.3.2

La candidata va recopilar les mostres de la campanya MAFIA i de la col·lecció CCDE-IEOCD durant una estada al laboratori del Dr. J. Ignacio González Gordillo a la Universidad de Càdiz (UCA) que van ser deixades en préstec a la Universitat de València. Ha realitzat l'estudi morfològic de les mostres (dissecció i il·lustració) i ha redactat la major part de l'article.

Publicació 2

Genis-Armero, R., Landeira J., Capaccioni-Azzati R., and Palero F. (2019). Updated distribution and first description of *Scyllarus subarctus* (Crustacea: Scyllaridae) decapodid stage. *Journal of the Marine Biological Association of the United Kingdom 99(5),* 1181-1188. https:// doi.org/10.1017/S0025315419000067

La candidata va realitzar part de l'anàlisi molecular de les mostres durant una estada al Centre d'Estudis Avançats de Blanes (CEAB), ha realitzat l'estudi morfològic de les mostres (dissecció i il·lustració) i ha redactat la major part de l'article.

Publicació 3

Genis-Armero, R., González-Gordillo, J.I., Cuesta, J.A., Capaccioni-Azzati, R., and Palero, F. (2020). Revision of the West African species of *Scyllarus* Fabricius, 1775 (Decapoda: Achelata: Scyllaridae), with the description of three phyllosoma stages of *S. caparti* Holthuis, 1952 and an updated identification key. *Journal of Crustacean Biology*. https://doi.org/10.1093/jcbiol/ruaa025

La candidata va recopilar les mostres de la campanya MAFIA i de la col·lecció CCDE-IEOCD durant una estada a la Universidad de Càdiz (UCA). Ha reunit la informació existent sobre la subfamília Scyllarinae en la bibliografia i les col·leccions de museu, ha realitzat l'estudi morfològic (dissecció i il·lustració) i ha redactat la major part de l'article.

Publicació 4

Palero, F., **Genis-Armero, R**., Hall, M. and Clark, P.F. (2016). DNA barcoding the phyllosoma of *Scyllarides squammosus* (H. Milne Edwards, 1837) (Decapoda: Achelata: Scyllaridae). *Zootaxa. 4139(4)*, 481 - 497. http://dx.doi.org/10.11646/zootaxa.4139.4.2

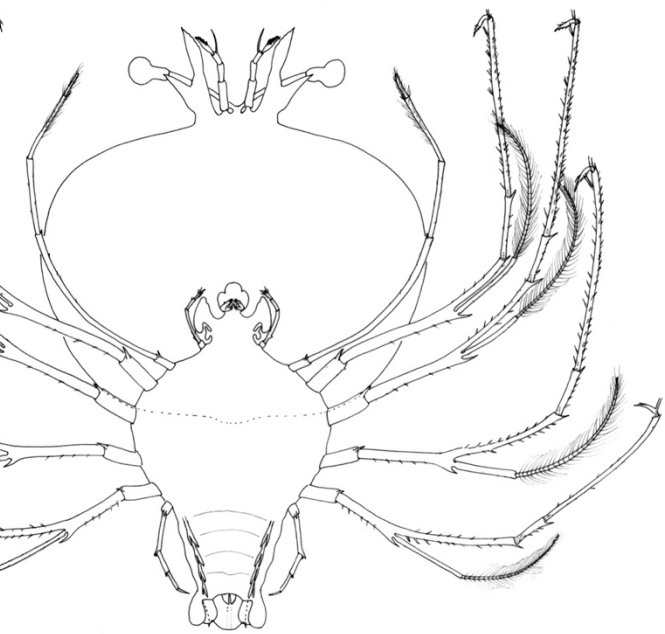
La candidata va realitzar l'estudi morfològic del material descrit (dissecció i il·lustracions)

I per a que així conste, en compliment de la legislació vigent, signem el present certificat a València, a 7 de juny de 2020.

Signat: Ferran Palero Pastor i Romana Capaccioni Azzati, Directors de la Tesi Doctoral

CAPÍTOL 1

Possible amphi-Atlantic dispersal of *Scyllarus* lobsters (Crustacea: Scyllaridae): molecular and larval evidence



Zootaxa 4306 (3): 325–338
http://www.mapress.com/j/zt/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.4306.3.2
http://zoobank.org/urn:lsid:zoobank.org:pub:FB980743-F2EF-43B4-8682-710F6B5684CB

Possible amphi-Atlantic dispersal of *Scyllarus* lobsters (Crustacea: Scyllaridae): molecular and larval evidence

REBECA GENIS-ARMERO[1], GUILLEM GUERAO[2], PERE ABELLÓ[3], J. IGNACIO GONZÁLEZ-GORDILLO[4], JOSÉ A. CUESTA[5], LAURE CORBARI[6], PAUL F. CLARK[7], ROMANA CAPACCIONI-AZZATI[1] & FERRAN PALERO[7,8,9,10]

[1]*Department of Zoology, School of Biological Sciences, University of Valencia, Spain.*
[2]*Independent Researcher, Barcelona, Spain.*
[3]*Institut de Ciències del Mar, CSIC. Passeig Marítim de la Barceloneta 37-49, 08003 Barcelona, Spain.*
[4]*Instituto Universitario de Investigación Marina, Universidad de Cádiz, CEIMAR, Avd República Saharaui, 11510 - Puerto Real, Cadiz, Spain.*
[5]*Instituto de Ciencias Marinas de Andalucía, CSIC. Campus de Excelencia Internacional del Mar. Avda. Republica Saharaui, 2, 11519 Puerto Real, Cádiz, Spain.*
[6]*UMR 7205, Institut de Systematique, Evolution et Biodiversite, Departement Systematique et Evolution, Muséum National d'Histoire Naturelle, 55 Rue Buffon, CP51, 75005 Paris, France.*
[7]*Department of Life Sciences, The Natural History Museum, Cromwell Road, London SW7 5BD, England.*
[8]*Centre d'Estudis Avançats de Blanes (CEAB-CSIC), Carrer D'accés a la Cala Sant Francesc 14, 17300 Blanes, Spain.*
[9]*Institut National de la Recherche Agronomique, UMR ISA INRA/UNSA/CNRS, Equipe BPI. 400, Route Des Chappes, Bp 167, 06903 Sophia-Antipolis, France.*
[10]*Corresponding author. E-mail: fpalero@ceab.csic.es*

Abstract

DNA methods may contribute to better understand larval dispersal of marine lobsters. The molecular analysis of phyllosoma specimens from the East Atlantic facilitated for the first time here the description of *Scyllarus subarctus* Crosnier, 1970 larvae. The identification of *S. subarctus* phyllosomae from Cabo Verde confirmed that this species has a much wider geographic distribution than previously thought. Moreover, the phylogenetic analyses placed *S. depressus* from the Western Atlantic together with the African species *S. subarctus*, instead of other American *Scyllarus*. In fact, *S. depressus* and *S. subarctus* formed a strongly supported clade with comparatively low genetic differentiation, suggesting the possibility that they might be recently-diverged sister taxa with an amphi-Atlantic distribution. Support for this is provided by the examination of S. subarctus larvae and the lack of any qualitative character that would allow for differentiation between the adults of S. subarctus and S. depressus. The results obtained highlight the challenges of current *Scyllarus* systematics and the need for further research on Atlantic slipper lobsters.

Key words: Slipper lobster, phylogenetics, amphi-Atlantic distribution, planktonic larval duration, DNA barcoding

Introduction

Slipper lobsters, Scyllaridae Latreille, 1825, constitute a monophyletic group of crustaceans characterized by possessing a completely flattened last antennal segment (Spanier 1991; Haug *et al.* 2015). Together with palinurid lobsters, scyllarid lobsters have a unique larval form particularly adapted to planktonic life and long-distance dispersal, the *phyllosoma* (Palero & Abello 2007). This planktonic phase contains multiple stages that finally transform into a benthic decapodid, taking up to 2 years to fully develop and metamorphose depending on species (Booth *et al.* 2005; Palero *et al.* 2014a). Scyllaridae includes more than 90 species consigned to 20 genera (Chan 2010) and comprises four subfamilies: Arctidinae Holthuis, 1985 (including *Scyllarides* Gill, 1898 and *Arctides* Holthuis, 1960), Ibacinae Holthuis, 1985 (*Ibacus* Leach, 1815, *Evibacus* Smith, 1869 and *Parribacus* Dana, 1852), Theninae Holthuis, 1985 (*Thenus* Leach, 1816) and Scyllarinae Latreille, 1825 (*Scyllarus* Fabricius, 1775 and 13

Accepted by J. Goy: 30 May 2017; published: 17 Aug. 2017

additional new genera proposed by Holthuis (1960, 1985, 2002). The latest molecular and phyllosoma morphology results support the monophyly of Arctidinae, Theninae and Scyllarinae, but Ibacinae appears to be a paraphyletic group (Yang *et al.* 2012; Bracken-Grissom *et al.* 2014; Palero *et al.* 2014b). The study of phyllosoma larvae is a difficult task though, mainly due to the great difficulty in rearing them in the laboratory and establishing the identification of plankton-caught material.

Subsequent to the revision of *Scyllarus* by Holthuis (2002), only 9 species were retained within the original genus. Four species are distributed in Western Atlantic waters: *S. americanus* (Smith, 1869), *S. chacei* Holthuis, 1960, *S. depressus* (Smith, 1881) and *S. planorbis* Holthuis, 1969; and 5 in European and African waters: *S. arctus* (Linnaeus, 1758), *S. caparti* Holthuis, 1952, *S. paradoxus* Miers, 1881, *S. pygmaeus* Bate, 1888 and *S. subarctus* Crosnier, 1970. *Scyllarus americanus, S. depressus*, and *S. chacei* have been recorded from North Carolina to Brazil (Holthuis 1960; Robertson 1968b; Lyons 1970; Tavares 1997), and *S. planorbis* has a restricted distribution ranging from Honduras to Suriname (Dall'Occo 2010). With regard to the Eastern Atlantic species, *S. arctus* and *S. pygmaeus* are commonly reported from the Mediterranean Sea and North-East Atlantic (Pessani & Mura 2007; Palero *et al.* 2011), while *S. paradoxus* is limited to Senegal, Sierra Leone, Guinea and St. Tomé (Forest 1963), and *S. caparti* extends mostly along the East Atlantic coast in tropical and subtropical latitudes (Holthuis 1952), with an isolated specimen reported by Froglia (1974) from the Adriatic Sea. Although originally described from South-East Atlantic waters (Crosnier 1970; Macpherson 1991), some specimens from Guinea Bissau and Mauritania have been tentatively assigned to *S. subarctus* (Muñoz *et al.* 2012; Garcia-Isarch *et al.* 2015), suggesting that this species may have an intertropical distribution.

Complete larval descriptions for American *Scyllarus* were provided by Robertson (1968a, 1971, 1979) from laboratory breed material, with some series complemented using planktonic specimens. In comparison, for Eastern Atlantic species, only the final phyllosoma and nisto stages of *S. arctus* and *S. pygmaeus* have been confirmed by DNA barcoding (Palero *et al.* 2008, 2009a, 2011). The identification of lobster larvae from Africa has been limited by difficulties in obtaining ethanol-preserved planktonic material, so that species assignments from previous records remain uncertain (Lindley *et al.* 2004). Recently, a large collection of phyllosomae from East Atlantic waters was obtained during the Migrants and Active Flux in the Atlantic Ocean (MAFIA) project expedition. DNA methods allow for the first time the identification and description of *S. subarctus* phyllosoma stages VII, IX, and X. The present study confirms that *S. subarctus* has a much wider geographic distribution than previously thought and suggests the possibility of amphi-Atlantic dispersal of *Scyllarus* larvae.

Materials and methods

The phyllosomae used for molecular analysis and descriptions were obtained during the MAFIA cruise between 3rd and 29th April 2015. A total of 13 stations were sampled on board of the RV *Hesperides*, which crossed the Atlantic from Salvador de Bahia, Brazil, to Las Palmas, Canary Islands. Micronekton samples were collected with a mid-water trawl (Mesopelagos net) with a mean mouth opening of 5 × 7 m and a final cod-end of 4 mm. This system allowed discriminating samples from different levels into the water column to depths around 1000 m. Phyllosoma specimens from the MAFIA cruise were obtained near Cabo Verde, 900–1000 km away from continental Africa. Sampling co-ordinates, date and depth are shown in Table I. Samples were preserved in absolute ethanol and registered in the invertebrate collections of the Universidad de Cádiz.

Phyllosoma specimens showing identical morphological traits to our DNA-identified material from Cabo Verde were found among the Institut de Ciències del Mar collections (Table I). These specimens were sampled during the SNEC-II cruise from North of Lüderitz (18°S 10°30'E), at about 217 km off the Namibian coast. A Rectangular Mid-water Trawl plankton net with 1 m^2 opening and 200 µm mesh was used to sample a single station between 0 and 200 m depth. SNEC-II collected specimens were, however, preserved in formalin and their specific identification was based on morphology only. Finally, reference DNA sequences were obtained from type specimens of *Scyllarus subarctus* deposited in the Muséum National d'Histoire Naturelle, France, and GenBank (see Table I for accession codes).

DNA analyses. Total genomic DNA extraction was performed using the Chelex-protK method (Palero *et al.* 2010). The standard universal primers for the 16S rDNA gene (Marco-Herrero *et al.* 2013) were used for DNA barcoding, since this marker shows a higher amplification rate than COI primers in Achelata (Palero *et al.* 2009b;

Bracken-Grissom *et al.* 2014). Amplifications were carried out with ~30 ng of genomic DNA in a reaction containing 1 U of Taq polymerase (Amersham), 1 × buffer (Amersham), 0.2 mM of each primer and 0.12 mM dNTPs. The polymerase chain reaction (PCR) thermal profile used was 94°C for 4 min for initial denaturation, followed by 30 cycles of 94°C for 30 s, 50°C for 30 s, 72°C for 30 s and a final extension at 72°C for 4 min. Amplified PCR products were purified with QIAquick PCR Purification Kit (QIAGEN Inc.) before direct sequencing of the product. The sequences were obtained using the kit BigDye v3.1 (Applied Biosystems) on an ABI Prism 3770. The chromatograms for each DNA sequence were checked using the software BioEdit ver. 7.2.5 (Hall 1999). Sequence alignment was conducted using the program Muscle ver. 3.6 (Edgar 2004) with default parameters. Selection of the nucleotide substitution model was performed according to the BIC criterion as implemented in MEGA v7 (Kumar *et al.* 2016). The aligned sequences and selected evolutionary model were used to estimate genetic distances and the corresponding Maximum Likelihood phylogenetic tree in MEGA.

Larval description. The larval accounts were based on the malacostracan somite plan, described from anterior to posterior and proximal to distal (Clark *et al.* 1998; Palero *et al.* 2016). Morphological illustrations of the larvae were drawn using a *camera lucida* attached to a Leica high-performance stereo microscope (M165C, Leica Microsystems) and the maxillae and mandibles were dissected before drawing. The stage assignment of *Scyllarus* phyllosoma larvae is based on Robertson (1968a, 1971) and Webber & Booth (2001). The following measures were taken for each individual analysed: total length (TL) from the anterior margin of the cephalic shield between the eyes to the posterior margin of the telson; cephalic length (CL) from the anterior to the posterior margin of the cephalic shield; cephalic width (CW) measured at the widest part of the cephalic shield; pleon length (PDL) from the anterior margin of the pleon to the posterior margin of the telson.

Results

Molecular identification of phyllosoma larvae. DNA sequences obtained from the MAFIA phyllosomae and adult specimens included 428 bp positions after alignment. The DNA substitution model selected according to the BIC method was the Hasegawa-Kishino-Yano model (HKY) with invariant positions. The rate variation model allowed for 61% of the sites to be evolutionarily invariable. The phylogenetic tree obtained by Maximum Likelihood (Ln = -1652.65) strongly supported the species-level assignment of the Cabo Verde larvae, clustering with adult *S. subarctus* and genetic distances below 0.01 (ranging between 0.005 and 0.007). *S. depressus* and *S. subarctus* formed a monophyletic clade with high bootstrap support (97%) (Fig. 1). Genetic distances between *S. subarctus* and *S. depressus* (between 1.9 and 2.4%) were 3 times lower than those observed between *S. subarctus* and other African species (5.8 to 7.9%) and 8 times lower than genetic distances with species from America (between 14.2 and 17.3%).

Morphological description. A total of 18 specimens, 11 from the MAFIA cruise and 7 from SNEC-II, were used for morphological characterization of *S. subarctus* phyllosomae. The larvae could be assigned to 3 different stages based on morphology namely, stage VII, IX (subfinal) and X (final), and which also correspond with separate groups based on total length. Correlation between TL and both CL and CW values was linear, with CL ($CL=0.67\ TL + 1.67$; $R^2=0.981$) increasing much faster than CW ($CW=0.51\ TL + 2.02$; $R^2=0.985$) during these late stages.

Scyllarus subarctus Crosnier, 1970

Phyllosoma, stage VII (PHMF 13, PHMF 51)

Dimensions. N = 7; TL = 9.1–10.9 mm; CL = 6.4–7.7 mm; CW = 7.4–8.7 mm; PDL = 1.1–1.4 mm.

Cephalic shield (Fig. 2A). Sub-rectangular; 1.2 × wider than long.

Antennule (Fig. 5A). Peduncle 3-segmented, last segment shorter and carrying two flagella (primary and accessory); accessory flagellum longer than primary, unsegmented with 2 setae in external side and 1–3 longer setae in the apical region; primary flagellum unsegmented with 8–9 rows of sensory setae (aesthetascs).

Antenna (Fig. 5A). Biramous and unsegmented; longer than antennule.

Mandibles (Fig. 5D, G). Asymmetrical dentition. Left mandible (Fig. 5D) larger and with more teeth on incisor process than right (Fig. 5G). Right mandible teeth are curved towards molar process while teeth of left mandible are elongated. Both mandibles with abundant small teeth distributed over surface and molar process crowned with many denticles.

Maxillule (Fig. 5J). Uniramous. Coxal and basial endites with 7 setae (2 and 3 strong setae, respectively). Palp (endopod) absent.

Maxilla (Fig. 6A**)**. Endites, endopod and exopod (scaphognathite) not differentiated.

First maxilliped (Fig. 6A). Unsegmented and cone-shaped; rudimentary bud.

Second maxilliped (Fig. 6D). Five-segmented, with 0,1,2,10,3 setae respectively.

Third maxilliped (Fig. 4, 6H, G). Five-segmented, with ventral coxal spine; distal part of propodus and dactyl densely setose. Two serrated and curved setae in distal end of propodus.

Pereiopods (Fig. 2A–E; 6L). P1–4 biramous with ventral coxal spine and 5-segmented endopod; basis-ischio-merus (fused) with abundant spines scattered over the surface. Two large distal spines on ischio-merus and carpus; with long and strong spines on distal end of propodus, increasing in length from P1 to P4. Exopods with 22–26, 21–24, 18–22, 14–18 annulations respectively, each annulation carrying two long setae. Dorsal side of P1–3 covered with many spines, fewer on P4. P5 rudimentary and 2-segmented; exopod absent.

Pleon (Fig. 6L). Undeveloped and unsegmented; with 4 pairs of rudimentary pleopods. Biramous uropods undeveloped. Telson with 2 long processes and 4 setae on posterior margin (one pair on dorsal and one pair on ventral sides).

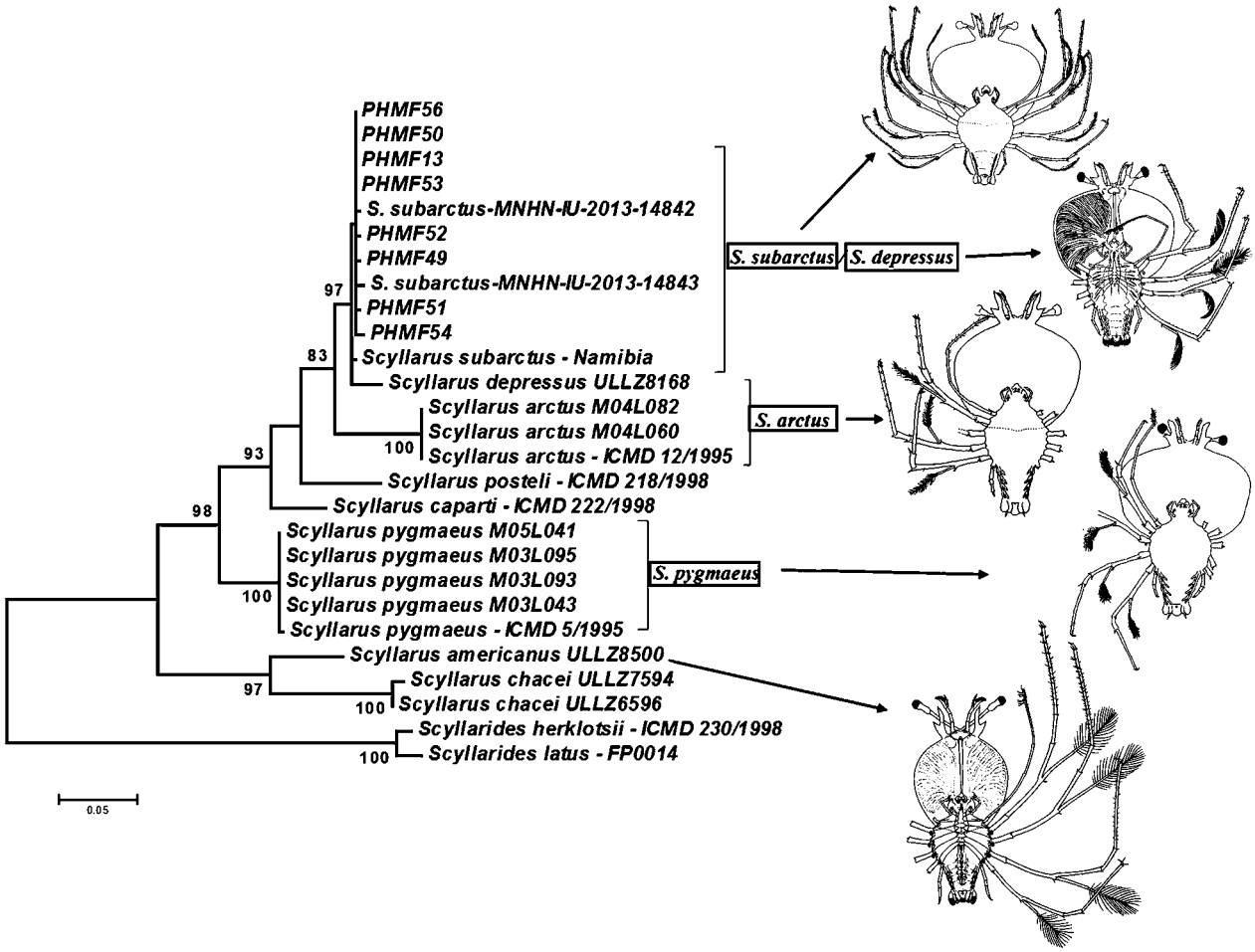


FIGURE 1. Molecular Phylogenetic tree obtained by Maximum Likelihood. Only bootstrap support values above 80 are shown. Larval images adapted from Robertson (1968a, 1968b, 1971) and Palero *et al*. (2008, 2011).

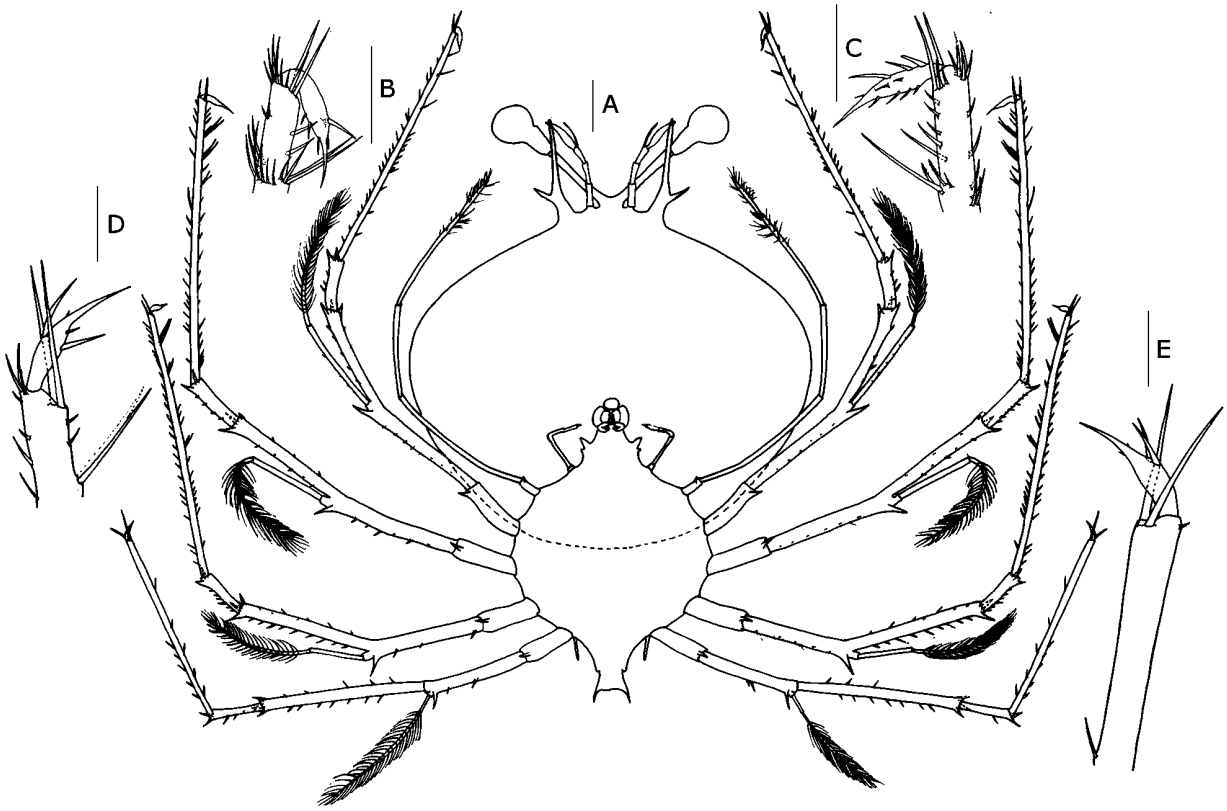


FIGURE 2. *Scyllarus subarctus*, Phyllosoma stage VII (PHMF 13, PHMF 51). (**A**) ventral view, (**B**) dactylus of first pereiopod; (**C**) dactylus of second pereiopod, (**D**) dactylus of third pereiopod, (**E**) dactylus of fourth pereiopod. Scale bars: A = 1 mm; B-E = 500 μm.

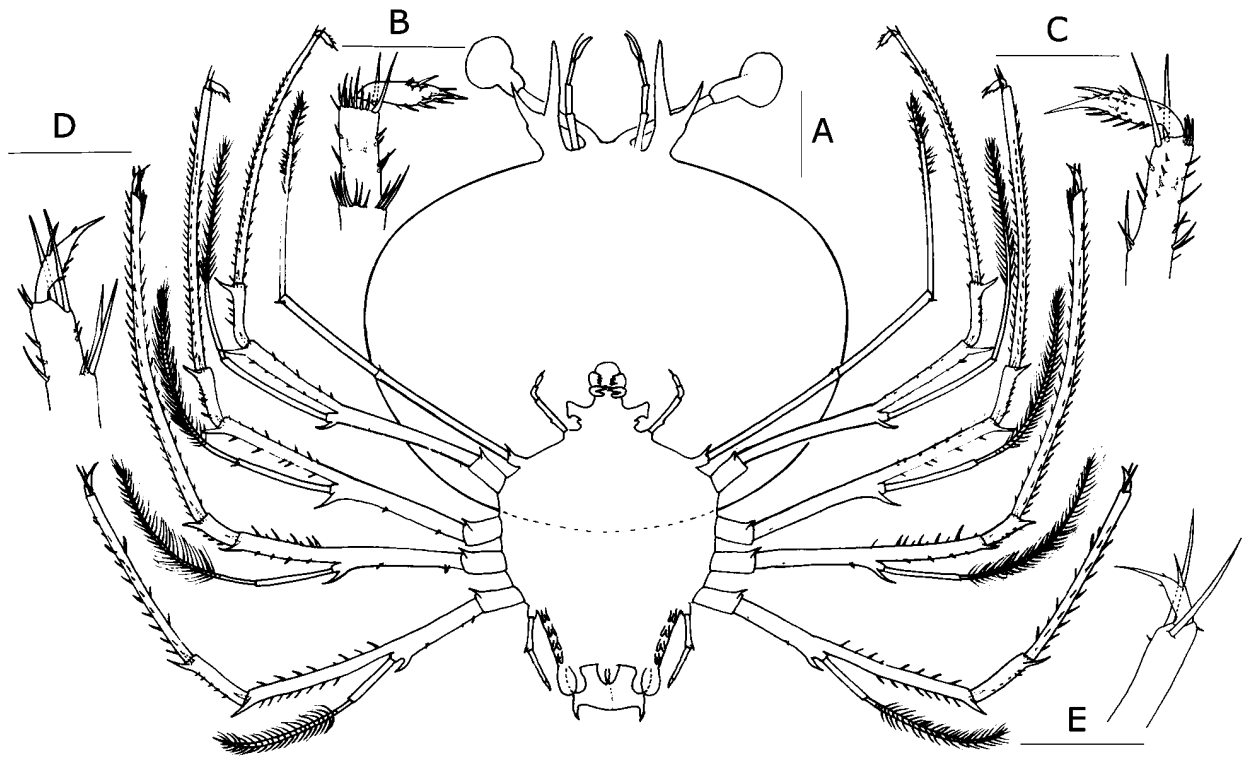


FIGURE 3. *Scyllarus subarctus*, Phyllosoma subfinal stage (PHMF 56, PHMF 48, SNECII-E89_02). (**A**) ventral view, (**B**) dactylus of first pereiopod, (**C**) dactylus of second pereiopod, (**D**) dactylus of third pereiopod, (**E**) dactylus of fourth pereiopod. Scale bars: A = 42 mm; B-E = 500 μm.

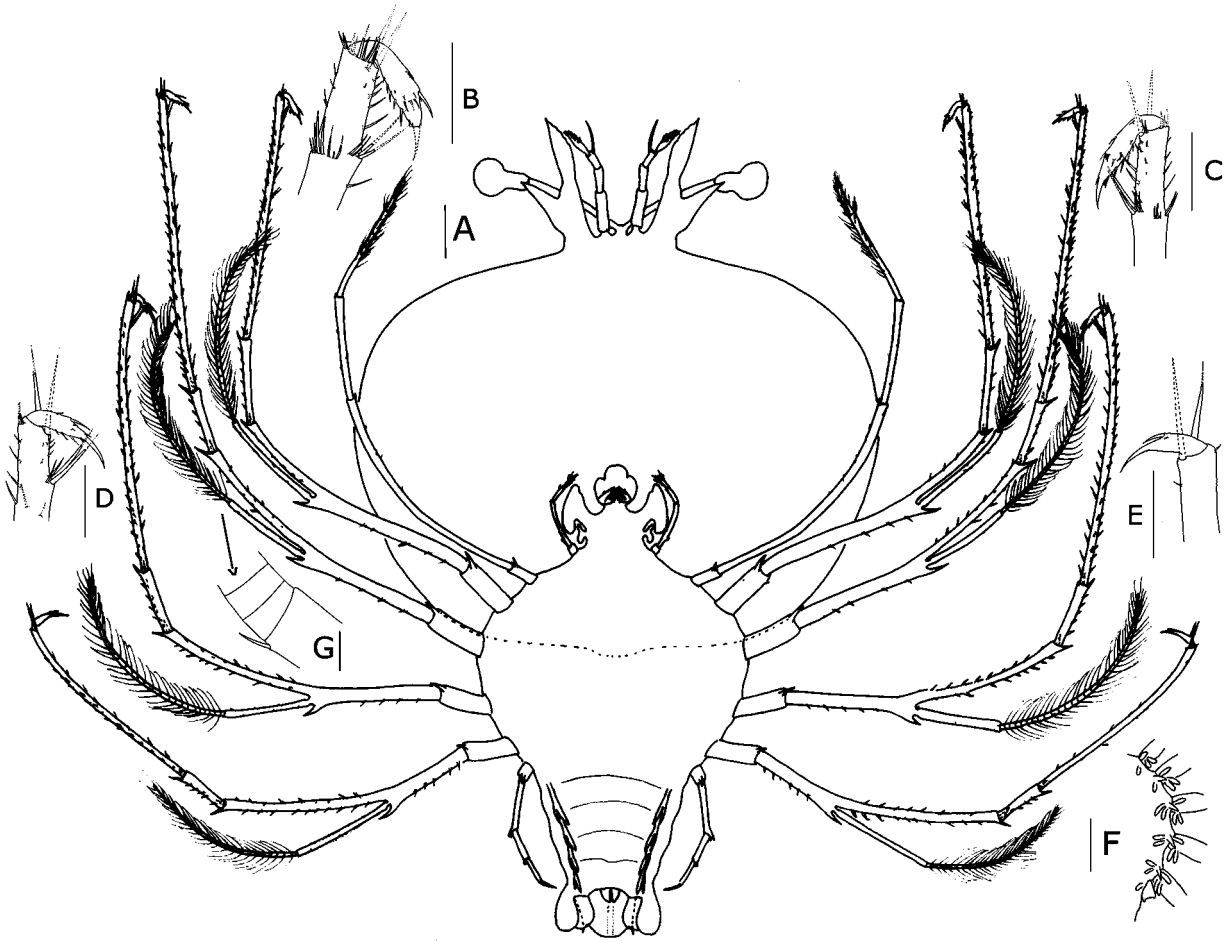


FIGURE 4. *Scyllarus subarctus*, Phyllosoma final stage (PHMF 92). (**A**) ventral view, (**B**) dactylus of first pereiopod, (**C**) dactylus of second pereiopod, (**D**) dactylus of third pereiopod, (E) dactylus of fourth pereiopod, (F) left side of thorax, dorsal view, (G) detailed view of distal part of proximal exopod segment. Scale bars: A = 2 mm; B-F = 1 mm; G = 0.1 mm.

Phyllosoma, subfinal stage (PHMF 56, PHMF 48, SNECII-E89_02)

Dimensions. N = 3; TL = 19.4–20.3 mm; CL = 12.6–13.1 mm; CW = 15.3–16.2 mm; PDL = 4.1–5.4 mm.

Cephalic shield (Fig. 3A). Subrectangular, 1.2 × wider than long.

Antennule (Fig. 5B). Accessory flagellum slightly longer than primary. Primary flagellum with 13–14 rows of aesthetascs.

Antenna (Fig. 5B). Widening inner ramus. Same length as antennule.

Mandibles (Fig. 5E, H). Similar to stage VII but with more teeth on both mandibles.

Maxillule (Fig. 5K). Uniramous. Coxal endite with 12 setae (2 long and strong, and 10 small setae) and basial endite with 13 setae (3 long and strong, and 10 small setae).

Maxilla (Fig. 6B). Endite and endopod poorly differentiated. Scaphognathite (exopod) rectangular shaped and with small anterior and posterior expansions. Lateral process of endite with trapezoidal shaped.

First maxilliped (Fig. 6B). Rudimentary and slightly bilobed.

Second maxilliped (Fig. 6B). 5-segmented with 0,1,3,13,3 setae respectively. Spines of fourth segment form a crown around the base of dactyl.

Third maxilliped (Fig. 6I, J). More spines than previous stage.

Pereiopods (Fig. 3A–E; 6M). P1–4 with more spines than stage VII; exopods with 32–34, 27–34, 30–32, and 23–30 annulations respectively. P5 without exopod, 3–segmented and reaching base of uropods; coxa with ventral spine and 2 spines on ischio-merus.

Pleon (Fig. 6M). Four pairs of bilobed pleopods longer and narrower than stage VII; bilobed uropods; margin

of telson is concave; elongated processes of telson shorter with respect to telson length. Two rows of 14–15 setae on ventral and dorsal side of telson.

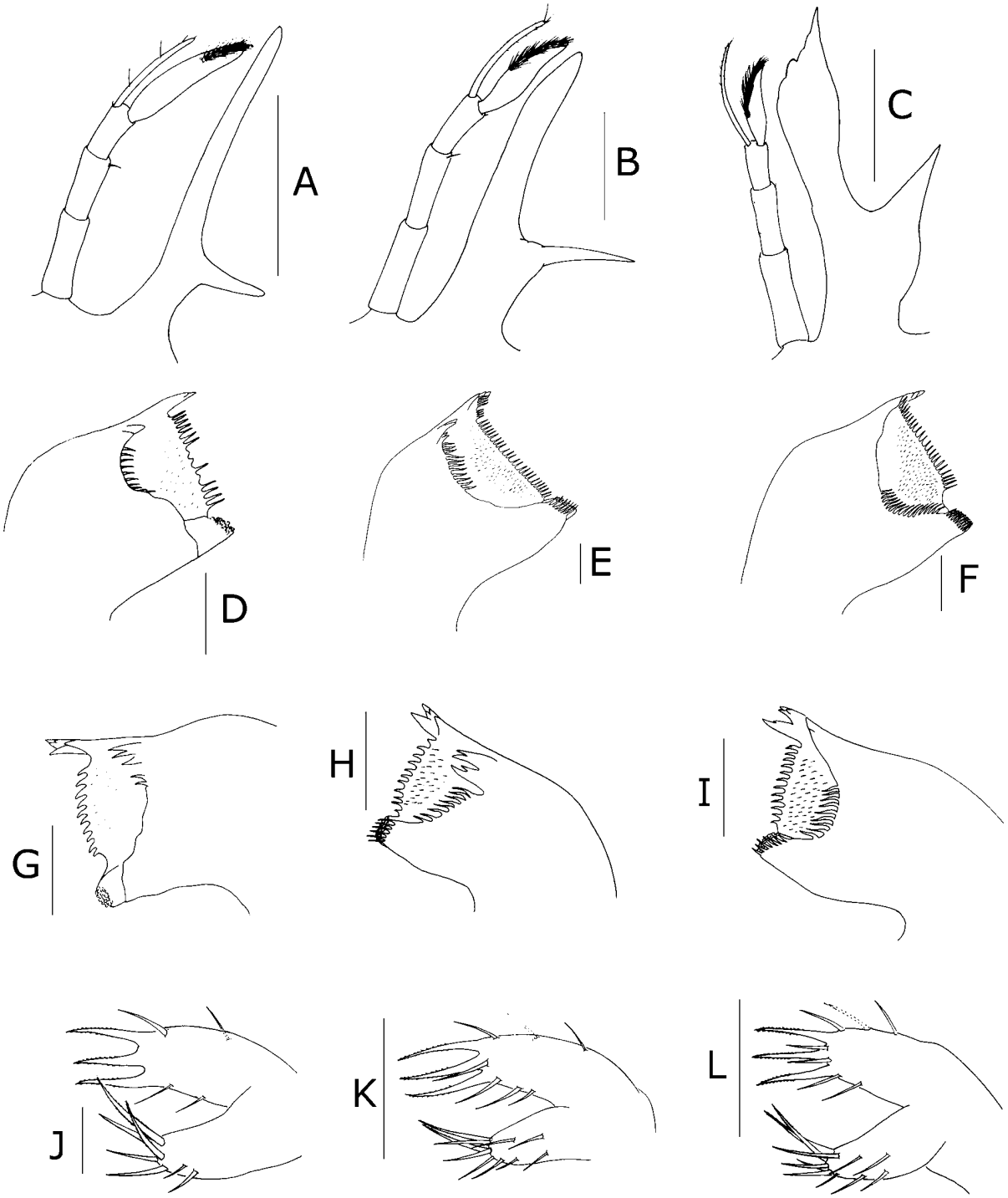


FIGURE 5. *Scyllarus subarctus*, (**A**)–(**C**) antennule and antenna, (**D**)–(**F**) left mandible, (**G**)–(**I**) right mandible, (**J**)–(**L**) maxillule of stage VII, subfinal and final stage respectively. Scale bars: A and B = 1 mm; C = 2 mm; D, E, G and J = 100 µm; F, H and I = 200 µm; K and L = 500 µm.

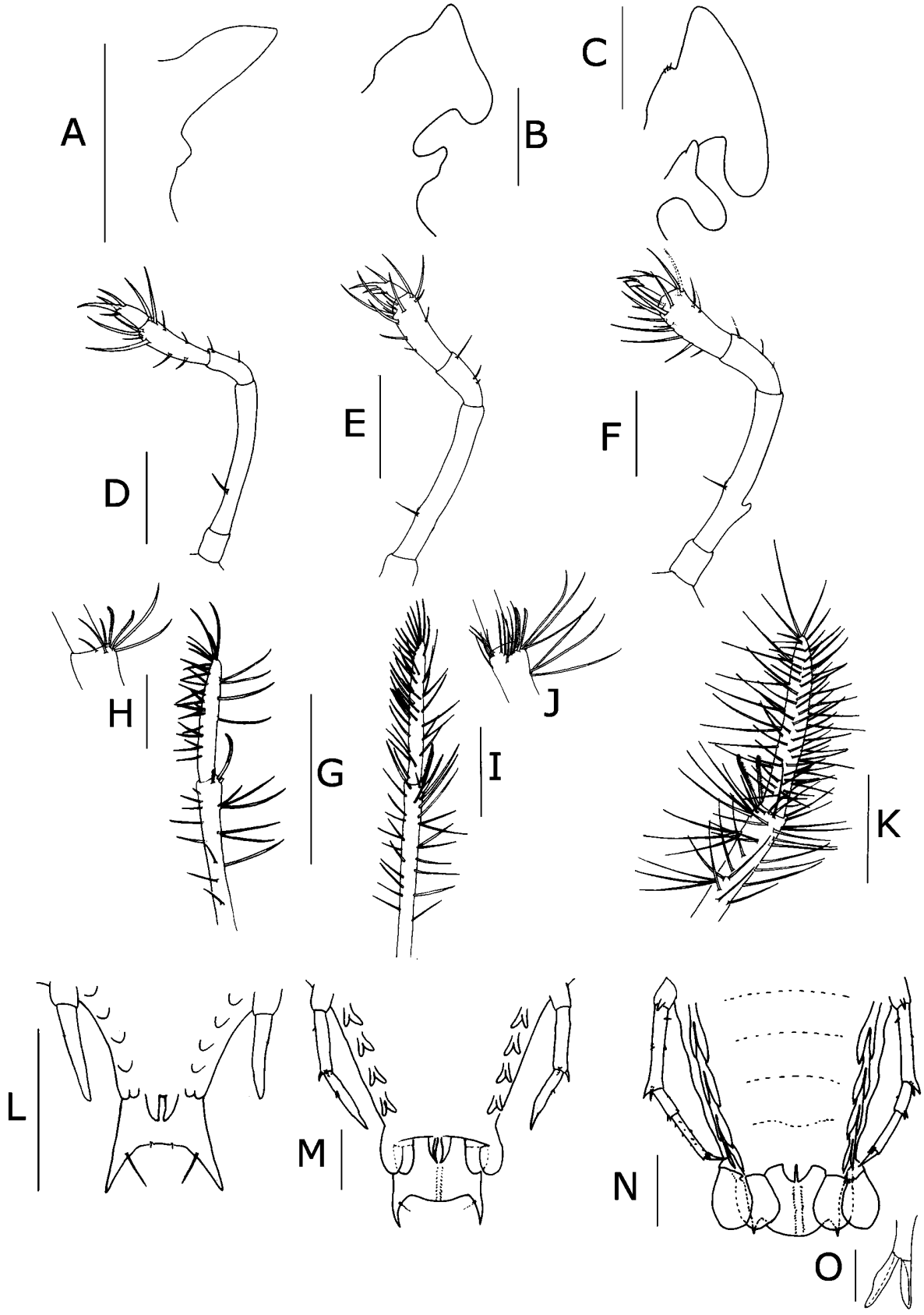


FIGURE 6. *Scyllarus subarctus*, (**A**)–(**C**) maxilla and first maxilliped, (**D**)–(**F**) second maxilliped, (**H**)–(**K**) third maxilliped, (**L**)–(**N**) pleon and fifth pereiopod, ventral view, (**O**) pleopods of stage VII, subfinal and final stage respectively. Scale bars: A, B, D, H and I = 500 µm; C, E, F, G, L, M and O = 1 mm; N = 2 mm.

TABLE 1. List of specimens used in the present study. Sampling information includes date, coordinates and depth. Morphological measurements (in millimetres) of phyllosomae include total length (TL), cephalic length (CL), cephalic width (CW) and pleon length (PDL).

Stage	Specimen ID	Museum code	Cruise	Date	Latitude	Longitude	Depth	TL	CL	CW	PDL	GenBank Acc.
Adult	*Scyllarides herklotsii*	ICMD 230/1998	---	20/01/1985	11.6500	-17.3333	217	---	---	---	---	FJ174906
Adult	*Scyllarides latus*	FP0014	---	---	---	---	---	---	---	---	---	FJ174907
Adult	*Scyllarus americanus*	ULLZ8500	---	07/27/1998	27.4520	-80.2655		---	---	---	---	JN701732
Adult	*S. arctus*	ICMD 12/1995	---	13/01/1993	40.6128	0.5937	25–23	---	---	---	---	DQ079732
Adult	*S. caparti*	ICMD 222/1998	---	30/12/1984	11.3000	-17.0833	33	---	---	---	---	FJ174909
Adult	*S. chacei*	ULLZ7594	---	07/04/2006	28.6210	-84.4730	---	---	---	---	---	JN701734
Adult	*S. chacei*	ULLZ6596	---	06/01/2004	24.5968	-83.4748	---	---	---	---	---	JN701733
Adult	*S. depressus*	ULLZ8168	---	06/06/2005	22.2678	-90.7143	---	---	---	---	---	JN701735
Adult	*S. posteli*	ICMD 218/1998	---	07/02/1985	11.5833	-17.2500	58–55	---	---	---	---	FJ174910
Adult	*S. pygmaeus*	ICMD 5/1995	---	30/10/1991	41.6785	2.8124	40–35	---	---	---	---	FJ174908
Adult	*S. subarctus*	MNHN-IU-2013-14842	---	18/08/1968	16.6166	11.3666	126	---	---	---	---	MF460387
Adult	*S. subarctus*	MNHN-IU-2013-14843	---	18/08/1968	16.6166	11.3666	126	---	---	---	---	MF460388
Adult	*S. subarctus*	ICMD 299/1991	---	25/03/1981	-17.4833	11.3833	300–293	---	---	---	---	FJ174912
VII	PHMF 13	MA017008PN07DPH01	MAFIA	19/04/2015	20.26	-24.25	100–0	9.6	6.6	7.7	1.3	MF460389
Sub-Final	PHMF 48	MA017008PED05PH01	MAFIA	19/04/2015	20.26	-24.25	100–0	19.4	12.8	15.3	4.1	---
Final	PHMF 49	MA017008PED05PH02	MAFIA	19/04/2015	20.26	-24.25	100–0	35.1	20.7	25.9	10.2	MF460391
VII	PHMF 50	MA017008PED05PH03	MAFIA	19/04/2015	20.26	-24.25	100–0	10.9	7.7	8.7	1.1	MF460392
VII	PHMF 51	MA017008PED05PH04	MAFIA	19/04/2015	20.26	-24.25	100–0	10.0	7.0	8.1	1.2	MF460393
VII	PHMF 52	MA017008PED05PH05	MAFIA	19/04/2015	20.26	-24.25	100–0	9.3	6.5	7.5	1.2	MF460394
VII	PHMF 53	MA017008PED05PH06	MAFIA	19/04/2015	20.26	-24.25	100–0	10.8	7.6	9.4	1.7	MF460395
VII	PHMF 54	MA017008PED05PH07	MAFIA	19/04/2015	20.26	-24.25	100–0	9.1	6.4	7.4	1.4	MF460396
Sub-Final	PHMF 56	MA019009PEN05PH01	MAFIA	21/04/2015	16.16	-26.03	100–0	20.3	13.1	16.2	5.4	MF460390

……continued on the next page

TABLE 1. (Continued)

Stage	Specimen ID	Museum code	Cruise	Date	Latitude	Longitude	Depth	TL	CL	CW	PDL	GenBank Acc.
Final	PHMF 91	MA025012PEN00PH19	MAFIA	27/04/2015	9.56	-25.99	250–0	27.5	15.9	20.5	7.9	---
Final	PHMF 92	MA025012PEN00PH20	MAFIA	27/04/2015	9.56	-25.99	250–0	28.6	16.7	21	7	---
VII	E89_01	ICMD001081	SNEC-II	25/04/1986	-18	10.55	200–0	9.7	6.8	8.2	1.1	---
Sub-Final	E89_02	ICMD001082	SNEC-II	25/04/1986	-18	10.55	200–0	19.4	12.6	15.4	4.1	---
Final	E89_03	ICMD001083	SNEC-II	25/04/1986	-18	10.55	200–0	27.0	15.5	19.6	8.2	---
Final	E89_04	ICMD001084	SNEC-II	25/04/1986	-18	10.55	200–0	27.2	15.8	19.5	7.8	---
Final	E89_05	ICMD001085	SNEC-II	25/04/1986	-18	10.55	200–0	28.6	16.9	21.7	8.4	---
Final	E89_06	ICMD001086	SNEC-II	25/04/1986	-18	10.55	200–0	28.7	16.9	21.5	8.4	---
Final	E89_07	ICMD001087	SNEC-II	25/04/1986	-18	10.55	200–0	31.6	16.4	20.0	8.2	---
Final	*S. arctus*	ICMD-69/2007	MEDITS	16/05/2003	41.9058	3.5156	401–450	---	---	---	---	GQ922071
Final	*S. arctus*	ICMD-68/2007	MEDITS	16/05/2003	42.1091	3.5930	401–450	---	---	---	---	GQ922070
Final	*S. pygmaeus*	---	MEDITS	19/05/2005	38.0803	0.0001	601–650	---	---	---	---	GQ922075
Final	*S. pygmaeus*	ICMD-64/2007	MEDITS	19/05/2004	38.9838	0.4998	701–750	---	---	---	---	GQ922074
Sub-Final	*S. pygmaeus*	---	MEDITS	23/05/2004	41.0235	1.3763	101–150	---	---	---	---	GQ922073
Final	*S. pygmaeus*	ICMD-63/2007	MEDITS	05/05/2003	38.1211	-0.0626	251–300	---	---	---	---	GQ922072

Phyllosoma, final stage (PHMF 92)

Dimensions. N = 8; TL= 27.0–35.1 mm; CL = 15.5–20.7 mm; CW = 19.6–25.9 mm; PDL = 7.0–10.2 mm.

Cephalic shield (Fig. 4A). Subrectangular, 1.3 × wider than long.

Antennule (Fig. 5C). Accessory flagellum unsegmented; primary flagellum shorter than accessory, unsegmented, with 16–17 rows of sensory setae.

Antenna (Fig. 5C). Longer than antennule.

Mandibles (Fig. 5F, I). Similar to stage VII, but internal row of teeth approaches the external row so that both rows meet.

Maxillule (Fig. 5L). Coxal and basial endite with 11 and 10 setae respectively. Palp (endopod) absent.

Maxilla (Fig. 6C). Endite and endopod poorly differentiated with 3 setae on superior margin of lateral process of endite. Scaphognathite (exopod) without setae, flattened and anterior and posterior parts considerably expanded.

First maxilliped (Fig. 6C). Unsegmented and bilobed; outer lobe flattened and round; inner lobe conic-shaped and shorter.

Second maxilliped (Fig. 6F). 5-segmented with 0,1,3,15,4 setae respectively; exopod bud present.

Third maxilliped (Fig. 6K). Densely setose.

Pereiopods (Fig. 4A–G; 6N). Exopods of P1–4 with 32–38, 27–38, 32–35 and 29–33 annulations respectively. One spine-like seta present at the distal end of the proximal segment of exopod. P5 reaching uropods, 5-segmented with ventral coxal spine, 2 distal spines on ischio-merus, carpus and propodus.

Gills (Fig. 4F). Gill buds present: mxp3 and P1 with 1 pleurobranch, 1 arthrobranch and 2 podobranchs; P2–4 with 2 pleurobranchs, 1 arthrobranch, 2 podobranchs; P5 with 1 pleurobranch.

Pleon (Fig. 6N, O). Pleopods biramous. Posterior margin of telson rounded with two postero-lateral processes. Two rows of 17–22 setae on dorsal and ventral sides of telson.

Discussion

The ethanol-preserved phyllosoma material collected by MAFIA facilitated the identification of *Scyllarus subarctus* larvae using molecular techniques and the description of its late developmental stages. Phyllosomae of *S. subarctus* are consistently larger than those from closely-related species such as *S. arctus* (Palero *et al.* 2011) or *S. pygmaeus* (Palero *et al.* 2008), reaching over 3 cm in total length in the final stage. The most distinctive morphological characteristic of *S. subarctus* phyllosomae is that pereiopods are covered with abundant spines. All pereiopods show 2 strong spines on the carpus (occasionally 3, one smaller) and one spine-like seta on the distal end of the proximal segment of the exopod, although it can be easily broken and it is not always visible. Such spine-like setae have never been described in a phyllosoma before, so it could either be a species-specific trait of *S. subarctus* or it may be a previously overlooked character. Even though morphological traits are seldom shared between phyllosoma and adult stages, the third finger-like lobe of the antennal flagellum is pointed and protruding in the final phyllosoma stage, a characteristic also present on *S. subarctus* adults. The final stage described here also presents the greatest number of sensory setae on the antennule and annulations on P1 exopod typically found in *Scyllarus* larvae (Robertson 1968a, 1971; Webber & Booth 2001; Palero *et al.* 2008, 2011). *Scyllarus subarctus* late stage phyllosomae share a rectangular cephalic shape with other congeneric species such as *S. arctus* and *S. pygmaeus*, but the TL/CW ratio is lower in *S. subarctus* than in *S. pygmaeus* or *S. arctus*.

Phylogenetic analyses separate Western Atlantic *Scyllarus* (excluding *S. depressus*) from East Atlantic taxa. *Scyllarus depressus* formed a strongly supported clade together with *S. subarctus*, an African species, which suggests that they could be a single species with an amphi-Atlantic distribution (see also Yang *et al.* 2012; Bracken-Grissom *et al.* 2014). Crosnier (1970) did not provide any qualitative character that would allow for differentiation between the adults of these two species, and distinguished them based in the more slender appearance of *S. subarctus*, the anterior part of its median carina directed upwards or a sternum widening much less towards the back. Further support for the sister relationship of *S. subarctus* and *S. depressus* was provided by larval morphology, with previous descriptions of *S. depressus* phyllosomae being remarkably similar to the MAFIA specimens (Robertson 1968b, 1971). *Scyllarus depressus* and *S. subarctus* larvae both possess many spines scattered over the pereiopods, identical first maxilliped and a comparatively long P5. Almost identical larvae and comparatively low genetic differentiation levels imply recent divergence between both *S. depressus* and *S.*

subarctus, suggesting the possibility that they might be a single species with an amphi-Atlantic distribution. The synonymy of species from American and African waters has been proposed in other marine taxa based on larval evidence (i.e. Sebastidae fish; Sabates & Olivar 1990), and amphi-Atlantic patterns have been observed in Grapsidae crabs (Schubart 2011) with long planktonic larval duration (>2 months; see Cuesta *et al.* 2011).

Long planktonic larval duration could explain the amphi-Atlantic pattern observed here, since some *Scyllarus* species have a comparatively long larval phase which would allow for transoceanic dispersal (e.g. 75 days for *S. depressus*; Robertson 1971). Previous simulation studies based on Atlantic Ocean dynamics suggest that phyllosomae could disperse between continents following a stepping-stone path through offshore islands (Rudorff *et al.* 2009). The distribution of *S. subarctus* is still poorly known, but it might be present in islands along the mid-Atlantic ridge, such as Azores or Ascension Island. In a recent study, several adult specimens from Guinea Bissau and Mauritania waters, in the Northern hemisphere, have been tentatively assigned to this species, expanding its range from 17ºS to 20 N (García-Isarch & Muñoz 2015; García-Isarch *et al.* in press). DNA sequences obtained from phyllosoma larvae collected near Cabo Verde and type specimens of *S. subarctus* from Angola are shown here to be identical. Marine currents might contribute to phyllosoma dispersal over long distances and could explain this wide distribution (Lass & Mohrholz 2008). Little is known about phyllosoma dispersal however, and passive movements could be restricted by eddies (Chiswell & Booth 1999) or modified by behavioural interaction with jellyfish (Booth *et al.* 2005; O'Rorke *et al.* 2015).

Larval morphology and molecular phylogeny results obtained in the present study highlight the need for a revision of *Scyllarus* systematics, with *S. depressus* being much closer to African species, in particular to *S. subarctus*, than to another American species. These results highlight unexpected evolutionary relationships within *Scyllarus,* and suggest that more fundamental research is required on African slipper lobsters. Future investigations should focus on revising morphological characters in both adults and larvae and obtaining supplementary molecular data.

Acknowledgements

This paper is dedicated to the memory of Francesc Pagès (1962–2007), a gelatinous zooplankton specialist from the ICM-CSIC (Barcelona, Spain) who kindly provided us the Namibian specimens that initiated this study. We thank all participants on board of the RV *Hesperides* during the MAFIA cruise for collecting larval specimens and C. Sánchez (ICMAN, Cadiz) for sequencing the larval specimens. Thanks are due to E. Macpherson (CEAB, Blanes), A. Crosnier (MNHN, Paris), P. Martin-Lefevre (MNHN, Paris), and M.P. Olivar (ICM-CSIC, Barcelona) for assistance and encouraging the completion of this work.

Funding. This research was funded by projects CHALLENGEN (CTM2013-48163) and MAFIA (CTM2012-39587-C04-02) of the Spanish Government and EU-Synthesys grants (DK-TAF-4873: Morphological study of Achelata lobsters and phyllosoma larvae from Danish collections and FR-TAF-5980: Description of phyllosoma stages of West-African lobster species). FP acknowledges project FP7 Marie Curie IAPP #324475 'Colbics' of the European Union and a post-doctoral contract funded by the Beatriu de Pinos Programme of the Generalitat de Catalunya.

References

Booth, J.D., Webber, W.R., Sekiguchi, H. & Coutures, E. (2005) Diverse larval recruitment strategies within the Scyllaridae. *New Zealand Journal of Marine and Freshwater Research*, 39, 581–592. https://doi.org/10.1080/00288330.2005.9517337

Bracken-Grissom, H.D., Ahyong, S.T., Wilkinson, R.D., Feldmann, R.M., Schweitzer, C.E., Breinholt, J.W., Bendall, M., Palero, F., Chan, T.Y., Felder, D.L., Robles, R., Chu, K.H., Tsang, L.M., Kim, D., Martin, J.W. & Crandall, K. (2014) The emergence of lobsters: Phylogenetic relationships, morphological evolution and divergence time comparisons of an ancient group (Decapoda: Achelata, Astacidea, Glypheidea, Polychelida). *Systematic Biology*, 63, 457–479. https://doi.org/10.1093/sysbio/syu008

Chan, T.Y. (2010) Annotated checklist of the world's marine lobsters (Crustacea: Decapoda: Astacidea, Glypheidea, Achelata, Polychelida). *The Raffles Bulletin of Zoology*, 23, 153–181.

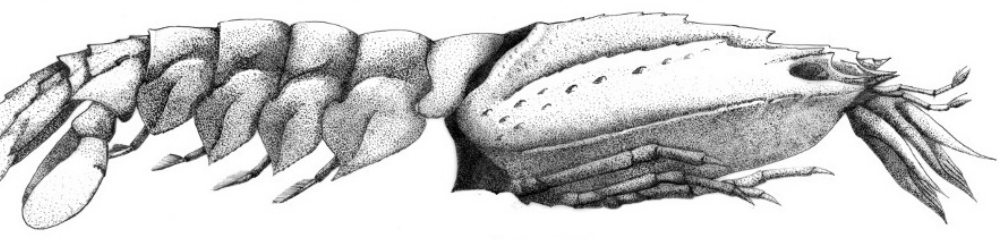
Chiswell, S.M. & Booth, J.D. (1999) Rock lobster *Jasus edwardsii* larval retention by the Wairarapa Eddy off New Zealand. *Marine Ecology Progress Series*, 183, 227–240.

https://doi.org/10.3354/meps183227
Clark, P.F., Calazans, D.K. & Pohle, G.W. (1998) Accuracy and standardization of brachyuran larval descriptions. *Invertebrate Reproduction and Development*, 33, 127–144.
https://doi.org/10.1080/07924259.1998.9652627
Crosnier, A. (1970) Crustacés décapodes Brachyoures et Macroures recueillis par l'Undaunted au sud de l'Angola. Description de *Scyllarus subarctus* sp. nov. *Bulletin du Muséum National d'Histoire Naturelle*, 41, 1214–1227.
Cuesta, J.A., Guerao, G., Schubart, C.D. & Anger, K. (2011) Morphology and growth of the larval stages of *Geograpsus lividus* (Crustacea, Brachyura), with the descriptions of new larval characters for the Grapsidae and an undescribed setation pattern in extended developments. *Acta Zoologica*, 92, 225–240.
https://doi.org/10.1111/j.1463-6395.2010.00482.x
Dall'Occo, P.L. (2010) *Taxonomia e distribuição das lagostas (Crustacea: Decapoda: Achelata e Polychelida) no Oceano Atlântico*. Universidade Estadual Paulista (UNESP), São Paulo, 432 pp.
Edgar, R.C. (2004) MUSCLE: multiple sequence alignment with high accuracy and high throuhput. *Nucleic Acids Research*, 32, 1792–1797.
https://doi.org/10.1093/nar/gkh340
Forest, J. (1963) Sur deux *Scyllarus* de l'Atlantique tropical africain: *S. paradoxus* Miers et *S. posteli* sp. nov. Remarques sur les *Scyllarus* de l'Atlantique oriental. *Bulletin de l'Institut océanographique, Monaco*, 60, 1–20.
Froglia, C. (1974) Preliminary report of the Crustacea Decapoda of Adriatic deep waters. *Thalassia Jugoslavica*, 8, 75–79.
García-Isarch, E., de Matos-Pita, S., Muñoz, I., Mohamed, S. & Ramil, F. (2017) Decapod assemblages in Mauritanian waters. *In*: Ramos, A., Sanz, J. L. & Ramil, F. (Eds.), *Deep-sea ecosystems off Mauritania: Researching marine biodiversity and habitats in West African deepwaters*. Springer, Heidelberg. [in press]
García-Isarch, E. & Muñoz, I. (2015) Biodiversity and biogeography of decapod crustaceans in the Canary Current Large Marine Ecosystem. *In*: Valdés, L. & Déniz?González, I. (Eds.), *Oceanographic and biological features in the Canary Current Large Marine Ecosystem*. *IOC Technical Series. No. 115*. IOC?UNESCO, Paris, pp. 257–272.
Hall, T. (1999) BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series*, 41, 95–98.
Hasegawa, M., Kishino, H. & Yano, T.A. (1985) Dating of the human-ape splitting by a molecular clock of mitochondrial DNA. *Journal of Molecular Evolution*, 22, 160–174.
https://doi.org/10.1007/BF02101694
Haug, J.T., Audo, D., Charbonnier, S., Palero, F., Petit, G., Abi Saad, P. & Haug, C. (2015) The evolution of a key character, or how to evolve a slipper lobster. *Arthropod structure and development*, 45, 97–107.
https://doi.org/10.1016/j.asd.2015.08.003
Holthuis, L.B. (1952) Crustacés Décapodes, Macrures. *Expédition Océanographique Belge dans les Eaux Côtières Africaines de l'Atlantique Sud (1948-1949)*, 3, 1–88.
Holthuis, L.B. (1960) Preliminary descriptions of one new genus, twelve new species and three new subspecies of Scyllarid lobsters (Crustacea Decapoda Macrura). *Proceedings of the Biological Society of Washington*, 73, 147–154.
Holthuis, L.B. (1969) A new species of shovel-nose lobster, *Scyllarus planorbis*, from the Southwestern Caribean and Northern South America. *Bulletin of Marine Science*, 19, 149–158.
Holthuis, L.B. (1985) A Revision of the family Scyllaridae (Crustacea Decapoda Macrura). I. Subfamily Ibacinae. *Zoologische Verhandelingen*, 218, 1–130.
Holthuis, L.B. (2002) The Indo-Pacific scyllarine lobsters (Crustacea, Decapoda, Scyllaridae). *Zoosystema*, 24, 499–683.
Kumar, S., Stecher, G. & Tamura, K. (2016) MEGA7: Molecular Evolutionary Genetics Analysis Version 7.0 for Bigger Datasets. *Molecular Biology and Evolution*, 33, 1870–1874.
https://doi.org/10.1093/molbev/msw054
Lass, H.U. & Mohrholz, V. (2008) On the interaction between the subtropical gyre and the Subtropical Cell on the shelf of the SE Atlantic. *Journal of Marine Systematic*s 74, 1–43
Lindley, J.A., Hernández, F., Tejera, E. & Correia, S.M. (2004) Phyllosoma larvae (Decapoda: Palinuridea) of the Cape Verde Islands. *Journal of Plankton Research*, 26, 235–240.
https://doi.org/10.1093/plankt/fbh019
Lyons, W.G. (1970) Scyllarid Lobsters (Crustacea, Decapoda). *Memoirs of the Hourglass Cruises*, 1, 1–74.
Macpherson, E. (1991) Biogeography and community structure of the decapod crustacean fauna off Namibia (Southeast Atlantic). *Journal of Crustacean Biology*, 11, 401–415.
https://doi.org/10.2307/1548466
Marco-Herrero, E., Torres, A.P., Cuesta, J.A., Guerao, G., Palero, F. & Abelló, P. (2013) The systematic position of *Ergasticus* (Decapoda, Brachyura) and allied genera, a molecular and morphological approach. *Zoologica Scripta*, 42, 427–439.
https://doi.org/10.1111/zsc.12012
Muñoz, I., García-Isarch, E., Sobrino, I., Burgos, C., Funny, R. & González-Porto, M. (2012) Distribution, abundance and assemblages of decapod crustaceans in waters off Guinea-Bissau (north-west Africa). *Journal of the Marine Biological Association of the United Kingdom*, 92, 475–494.
https://doi.org/10.1017/S0025315411001895
O'Rorke, R., Lavery, S.D., Wang, M., Waite, A.M., Beckley, L.E., Thompson, P.A. & Jeffs, A.G. (2015) Hitching Rides and Stealing Bites. *ICES Journal of Marine Science*, 72, 124–127.
https://doi.org/10.1093/icesjms/fsu163
Palero, F. & Abelló, P. (2007) The first phyllosoma stage of *Palinurus mauritanicus* (Crustacea : Decapoda : Palinuridae).

Zootaxa, 1508, 49–59.
Palero, F., Clark, P.F. & Guerao, G. (2014a) Infraorden Achelata. *In*: Martin, J., Olesen, J. & Hoeg, J.T. (Eds.), *Atlas of Crustacean Larvae*. Johns Hopkins University Press, Maryland, pp. 272–278.
Palero, F., Crandall, K.A., Abelló, P., Macpherson, E. & Pascual, M. (2009b) Phylogenetic relationships between spiny, slipper and coral lobsters (Crustacea, Decapoda, Achelata). *Molecular Phylogenetics and Evolution*, 50, 152–162. https://doi.org/10.1016/j.ympev.2008.10.003
Palero, F., Guerao, G. & Abelló, P. (2008) Morphology of the final stage phyllosoma larva of *Scyllarus pygmaeus* (Crustacea: Decapoda: Scyllaridae), identified by DNA analysis. *Journal of Plankton Research*, 30, 483–488. https://doi.org/10.1093/plankt/fbn012
Palero, F., Guerao, G., Clark, P.F. & Abelló, P. (2009a) The true identities of the slipper lobsters *Nisto laevis* and *Nisto asper* (Crustacea: Decapoda: Scyllaridae) verified by DNA analysis. *Invertebrate Systematics*, 23, 77–85. https://doi.org/10.1071/IS08033
Palero, F., Guerao, G., Clark, P.F. & Abelló, P. (2010) Final-stage phyllosoma of *Palinustus* A. Milne Edwards, 1880 (Decapoda : Achelata : Palinuridae)—The first complete description. *Zootaxa*, 2403, 42–58.
Palero, F., Guerao, G., Clark, P.F. & Abelló, P. (2011) *Scyllarus arctus* (Crustacea: Decapoda: Scyllaridae) final stage phyllosoma identified by DNA analysis, with morphological description. *Journal of the Marine Biological Association of the United Kingdom*, 91, 485–492. https://doi.org/10.1017/S0025315410000287
Palero, F., Guerao, G., Hall, M., Chan, T.Y. & Clark, P.F. (2014b) The 'giant phyllosoma' are larval stages of *Parribacus antarcticus* (Decapoda : Scyllaridae). *Invertebrate Systematics*, 28, 258–276. https://doi.org/10.1071/IS13037
Palero, F., Genis-Armero, R., Hall, M. & Clark, P.F. (2016) DNA barcoding the phyllosoma of *Scyllarides squammosus* (H. Milne Edwards, 1837) (Decapoda: Achelata: Scyllaridae). *Zootaxa*, 4139 (4), 481–498. https://doi.org/10.11646/zootaxa.4139.4.2
Pessani, D. & Mura, M. (2007) The Biology of the Mediterranean Scyllarids. *In*: *The Biology and Fisheries of the Slipper Lobster.* CRC Press, Boca Raton, Florida, pp. 263–286. https://doi.org/10.1201/9781420005165.ch13
Robertson, P.B. (1968a) The complete larval development of the sand lobster *Scyllarus americanus* (Smith), (Decapoda, Scyllaridae) in the laboratory with notes on larvae from the plankton. *Bulletin of Marine Science*, 18, 294–432.
Robertson, P.B. (1968b) *The Larval Development of Some Western Atlantic Lobsters of the Family Scyllaridae*. The University of Miami, Coral Gables, Florida, 513 pp.
Robertson, P.B. (1971) The larvae and postlarvae of the Scyllarid lobster *Scyllarus depressus* (Smith). *Bulletin of Marine Science*, 21, 841–865.
Robertson, P.B. (1979) Larval development of the Scyllarid Lobster *Scyllarus planorbis* Holthuis reared in the laboratory. *Bulletin of Marine Science*, 29, 320–328.
Rudorff, C.A.G., Lorenzzetti, J.A., Gherardi, D.F.M. & Lins-Oliveira, J.E. (2009) Modeling spiny lobster larval dispersion in the Tropical Atlantic. *Fisheries Research*, 96, 206–215. https://doi.org/10.1016/j.fishres.2008.11.005
Sabates, A. & Olivar, M.P. (1990) Early development and spawning of *Sebastes capensis* in the Southeast Atlantic. *Marine Biology*, 107, 389–395. https://doi.org/10.1007/BF01313420
Schubart, C.D. (2011) Reconstruction of phylogenetic relationships within Grapsidae (Crustacea: Brachyura) and comparison of trans-isthmian and amphi-atlantic differentiation based on mtDNA. *Zoologischer Anzeiger*, 250, 472–478. https://doi.org/10.1016/j.jcz.2011.06.003
Smith, S.I. (1869) Descriptions of a new genus and two new species of Scyllaridae and a new species of *Aethra* from North America. *American Journal Science and Arts* Série 2, 48, 118–121.
Smith, S.I. (1881) Preliminary notice of the Crustacea dredged, in 64 to 325 fathoms, off the south coast of New England, by the United States Fish Commisssion in 1880. *Proceedings of the United States National Museum*, 3, 413–452. https://doi.org/10.5479/si.00963801.172.413
Spanier, E. (1991) Swimming of the Mediterranean slipper lobster. *Journal of Experimental Marine Biology and Ecology*, 145, 15–31. https://doi.org/10.1016/0022-0981(91)90003-F
Tavares, M. (1997) *Scyllarus ramosae*, new species, from the Brazilian continental slope, with notes on congeners occurring in the area (Decapoda: Scyllaridae). *Journal of Crustacean Biology*, 17, 716–724. https://doi.org/10.2307/1549374
Webber, W.R. & Booth, J.D. (2001) Larval stages, developmental ecology, and distribution of *Scyllarus* sp. Z (probably *Scyllarus aoteanus* Powell, 1949) (Decapoda: Scyllaridae). *New Zealand Journal of Marine and Freshwater Research*, 35, 1025–1056. https://doi.org/10.1080/00288330.2001.9517061
Yang, C.H., Bracken-Grissom, H., Kim, D., Crandall, K. & Chan, T.Y. (2012) Phylogenetic relationships, character evolution, and taxonomic implications within the slipper lobsters (Crustacea: Decapoda: Scyllaridae). *Molecular Phylogenetics and Evolution*, 62, 237–250. https://doi.org/10.1016/j.ympev.2011.09.019

CAPÍTOL 2

Updated distribution and first description of *Scyllarus subarctus* (Crustacea: Scyllaridae) decapodid stage.



Journal of the Marine Biological Association of the United Kingdom

cambridge.org/mbi

Original Article

Cite this article: Genis-Armero R, Landeira J, Capaccioni-Azzati R, Palero F (2019). Updated distribution and first description of *Scyllarus subarctus* (Crustacea: Scyllaridae) decapodid stage. *Journal of the Marine Biological Association of the United Kingdom* 1–8. https://doi.org/10.1017/S0025315419000067

Received: 21 June 2018
Revised: 2 January 2019
Accepted: 17 January 2019

Key words:
DNA barcoding; larval dispersal; nisto description; recruitment; *Scyllarus subarctus*

Author for correspondence:
Ferran Palero, E-mail: fpalero@ceab.csic.es

Updated distribution and first description of *Scyllarus subarctus* (Crustacea: Scyllaridae) decapodid stage

Rebeca Genis-Armero[1], José Landeira[2], Romana Capaccioni-Azzati[1] and Ferran Palero[3,4]

[1]Department of Zoology, School of Biological Sciences, University of Valencia, Spain; [2]Department of Ocean Sciences, Tokyo University of Marine Science and Technology, 4-5-7 Konan, Minato, Tokyo 108-8477, Japan; [3]Centre d'Estudis Avançats de Blanes (CEAB-CSIC), Carrer D'accés a la Cala Sant Francesc 14, 17300 Blanes, Spain and [4]Department of Invertebrate Zoology and Hydrobiology, Faculty of Biology and Environmental Protection, University of Lodz, ul. Banacha 12/16, 90-237 Łódź, Poland

Abstract

The phyllosoma larva of spiny and slipper lobsters (Palinuridae and Scyllaridae respectively) can disperse during several months before metamorphosing into a decapodid stage, which is the key phase for a successful settlement. The largest *Scyllarus* decapodid known to date was recently collected near the Canary Islands and identified by DNA analysis as *Scyllarus subarctus*. This species had never been previously reported from the area, and the decapodid stage is described here for the first time. The examination of further museum specimens has now significantly expanded the current distribution of *S. subarctus*, including much of the NW African coast, St Helena and Canary Islands. These results highlight the importance of combining molecular analysis of recently collected specimens with historical collections.

Introduction

Spiny and slipper lobsters are characterized by the presence of a unique larval form (phyllosoma) especially adapted for long-distance dispersal (Palero & Abello, 2007). The phyllosoma phase may take up to 2 years to complete larval development (Booth *et al.*, 2005) and metamorphose into a decapodid stage (Kaestner, 1980; Felder *et al.*, 1985). The decapodid stage of Achelata lobsters, which has been traditionally called puerulus, nisto or pseudibacus due to the existence of former generic names, is a key transitional stage linking the planktonic zoea and the benthic adult (Jeffs *et al.*, 2005; Ventura *et al.*, 2015). The nisto stage of slipper lobsters remains poorly known because few specimens are generally obtained from plankton samples and the great difficulties in rearing phyllosoma larvae in the laboratory (Palero *et al.*, 2008). The complete laboratory-reared larval sequence has only been obtained for *S. americanus* Smith, 1869 (Robertson, 1968) and *Petrarctus demani* Holthuis, 1946 (Ito & Lucas, 1990), so further advances will most likely rely on molecular methods.

Only 16 Scyllarinae nisto morphotypes have been assigned to species level and previous identifications may be incorrect. Bouvier (1913) originally proposed *Scyllarus arctus* Linnaeus, 1758 to have two nisto stages, but those two stages have been shown to correspond to the decapodid stages of *S. arctus* and *S. pygmaeus* Bate, 1888 respectively (Palero *et al.*, 2008, 2009*a*, 2011). The recent results on the phyllosoma of *Scyllarides squammosus* (H. Milne Edwards, 1837) confirm the importance of using DNA barcoding methods to characterize these larvae (Palero *et al.*, 2016). Nevertheless, some studies on scyllarid larvae still confuse the decapodid of *Scyllarus* with that of *Scyllarides* (Pagliarino *et al.*, 2013) and stress the necessity of further morphological descriptions and taxonomic research.

The largest *Scyllarus* decapodid known to date was recently collected near the Canary Islands and identified by DNA analysis as *Scyllarus subarctus* Crosnier, 1970. This species had never been previously reported from the area and its decapodid stage is described here for the first time. A thorough examination of material from previous expeditions across West Africa also significantly expanded the known species range, identifying further material from NW Africa (e.g. Morocco) and several specimens from St Helena (one nisto and two adults). These results highlight the importance of associating molecular analysis of recently collected specimens with historical collections.

Materials and methods

Sampling

Several specimens corresponding to undetermined *Scyllarus* species were collected in April 2012 during the CETOBAPH experimental fishing cruise on board the RV 'Cornide de Saavedra'. Sample stations were located around the Canary Islands, between the 1000 and 2000 m isobaths, off El Hierro, La Palma and Tenerife. Sampling was performed using a pelagic net (300 m^2 mouth area, 45 m length, mesh size of 80 cm near the opening, decreasing to

1 cm in the cod end) towed during 1 h, at speed of 3 knots between 40 and 800 m depth. Hauls were performed horizontally along narrow depth ranges within the different scattering layers using the information provided by echosounders and Scanmar depth sensors (for more details see Ariza *et al.*, 2016). Further *S. subarctus* material from several museum collections included specimens from Angola, Namibia, St Helena, Guinea, Cape Verde, Senegal, Mauritania, West Sahara, Morocco and Canary Islands (Figure 1; Table 1).

DNA analyses

Total genomic DNA extraction of five small and one large *Scyllarus* decapodid from the CETOBAPH expedition was performed using the Chelex-protK method (Palero *et al.*, 2010). The standard universal primers for the 16S rDNA gene (Hillis *et al.*, 1996) were used for DNA barcoding, since this marker shows a higher amplification rate than COI primers in Achelata (Palero *et al.*, 2009*b*; Bracken-Grissom *et al.*, 2014). Amplifications were carried out with ~30 ng of genomic DNA in a reaction containing 1 U of Taq polymerase (Amersham), 1 × buffer (Amersham), 0.2 mM of each primer and 0.12 mM dNTPs. The polymerase chain reaction (PCR) thermal profile used was 94 °C for 4 min for initial denaturation, followed by 30 cycles of 94 °C for 30 s, 50 °C for 30 s, 72 °C for 30 s and a final extension at 72 °C for 4 min. Amplified PCR products were purified with QIAquick PCR Purification Kit (QIAGEN Inc.) before direct sequencing of the product. The sequences were obtained using the kit BigDye v3.1 (Applied Biosystems) on an ABI Prism 3770. The chromatograms for each DNA sequence were checked using the software BioEdit ver. 7.2.5 (Hall, 1999). Sequence alignment was conducted using the program Muscle v3.6 (Edgar, 2004) with default parameters. The Kimura 2-parameter (K2P) genetic distance was estimated between the Canary Island decapodid and sequences of Atlantic slipper lobsters available in GenBank using MEGA v7 (Kumar *et al.*, 2016) (Table 2).

Larval description

Description of the *S. subarctus* nisto stage was based on the malacostracan somite plan, from anterior to posterior and proximal to distal (Clark *et al.*, 1998; Clark & Cuesta, 2015). Larval illustrations were obtained using a *camera lucida* attached to a Leica high-performance stereo microscope (M165C, Leica Microsystems). Antennule, mandible, maxillule, maxilla, maxillipeds and pereopods were dissected before drawing. The following measurements were taken: total length (TL) from the anterior margin of the antennae to the posterior margin of the telson; cephalic length (CL) from the anterior to the posterior margin of the carapace; carapace width (CW) measured at the widest part of the carapace; pleon length (PDL) from the anterior margin of the pleon to the posterior margin of the telson. Morphological nomenclature follows Holthuis (1985).

Results

Molecular identification and updated distribution of S. subarctus

As expected based on the known distribution of the species, molecular data allowed us to assign the small nisto samples to *S. arctus* and *S. pygmaeus*. K2P genetic distances between the DNA sequence obtained from the large nisto and adults from either *S. depressus* (0.015 ± 0.006) or *S. subarctus* (0.010 ± 0.005) were smaller than of other African *Scyllarus* (*S. arctus*: 0.064 ± 0.012; *S. pygmaeus*: 0.074 ± 0.014). Genetic distances were larger when compared with *S. americanus* (0.142 ± 0.020) and *S. chacei* (0.166 ± 0.023). Therefore, the nisto could be assigned with confidence to *S. subarctus*. The DNA sequence obtained from the *S. subarctus* nisto is now available from GenBank (accession number: MK421157).

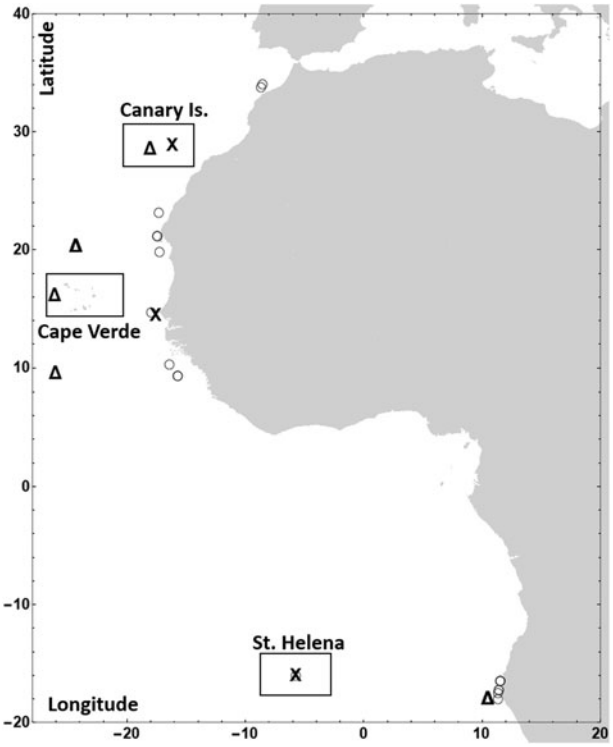


Fig. 1. Localities where *Scyllarus subarctus* has been found in the Eastern Atlantic. × : nisto, o: adult, Δ: phyllosoma.

The results provide further evidence to recent observations of *S. subarctus* phyllosoma stages collected near Cape Verde islands (Genis-Armero *et al.*, 2017) and expand the known latitudinal range. Compared with the few adult specimens originally described from the Angola/Namibia border (Crosnier, 1970; Macpherson, 1983), the morphological revision of further museum specimens allowed us to significantly expand the current spatial distribution including much of the NW African coast, St Helena and Canary Islands (Figure 1).

Morphological description

Order DECAPODA Latreille, 1802
Family SCYLLARIDAE Latreille, 1825
Genus *Scyllarus* Fabricius, 1775
Scyllarus subarctus Crosnier, 1970

Nisto stage (MNHN-IU-2016-10733; ICMD002350; CCDE-IEOCD:1105-1)

Dimensions. TL = 24.8–27.8 mm; CL = 7.1–7.7 mm; CW = 9.2–9.8 mm; PDL = 12.4–13.8 mm.

Carapace (Figure 2A, B). Slightly wider than long, broadest near middle section; surface mostly smooth; short and rounded rostrum; orbits deep, subrectangular, lined with cilia; lateral margin with two incisions (cervical and postcervical, latter less obtuse) and ~29 teeth (9 anterolateral, 7 mediolateral and 13 posterolateral); pregastric tooth small, gastric and cardiac low and bilobed; posterior submedian ridge with small spine; anterior branchial ridge with 7 spines ending in two large blunt teeth; posterior branchial ridge formed by 2 arches, inner carina more pronounced with 14–18 teeth and outer carina with 7 teeth; cervical groove shallow; intestinal ridge with 12–14 triangular-shape

https://doi.org/10.1017/S0025315419000067

Table 1. List of *Scyllarus subarctus* specimens analysed in the present study.

Museum collection	Voucher code	Date	Area	Latitude	Longitude	Depth (m)	Study	Stage
IEOCD	CCDE-IEOCD:987-1	15/12/2011	Morocco	34.04	−8.48	271–271	Present study	Adult
IEOCD	CCDE-IEOCD:987-2	15/12/2011	Morocco	34.04	−8.48	271–271	Present study	Adult
IEOCD	CCDE-IEOCD:987-3	15/12/2011	Morocco	34.04	−8.48	271–271	Present study	Adult
IEOCD	CCDE-IEOCD:987-4	15/12/2011	Morocco	34.04	−8.48	271–271	Present study	Adult
IEOCD	CCDE-IEOCD:995-1	14/12/2011	Morocco	33.75	−8.66	46–46	Present study	Adult
ICM	ICMD002350	19/4/2012	Canary Islands	28.84	−16.14	50–150	Present study	Nisto
ICM	ICMD002513	13/4/2012	Canary Islands	28.54	−18.00	410–620	Present study	Phyllosoma
IEOCD	CCDE-IEOCD:984-1	22/11/2011	Morocco	23.16	−17.31	150–150	Present study	Adult
IEOCD	CCDE-IEOCD:984-2	22/11/2011	Morocco	23.16	−17.31	150–150	Present study	Adult
IEOCD	CCDE-IEOCD:984-3	22/11/2011	Morocco	23.16	−17.31	150–150	Present study	Adult
MfN	ZMB27241-1	1/3/1975	West Sahara	21.15	−17.38	68–70	Present study	Adult
MfN	ZMB27241-2	1/3/1975	West Sahara	21.15	−17.38	68–70	Present study	Adult
UCA	MA017008PN07DPH01	19/4/2015	Cape Verde	20.26	−24.25	0–100	Genis-Armero *et al.* (2017)	Phyllosoma
UCA	MA017008PED05PH01	19/4/2015	Cape Verde	20.26	−24.25	0–100	Genis-Armero *et al.* (2017)	Phyllosoma
UCA	MA017008PED05PH02	19/4/2015	Cape Verde	20.26	−24.25	0–100	Genis-Armero *et al.* (2017)	Phyllosoma
UCA	MA017008PED05PH03	19/4/2015	Cape Verde	20.26	−24.25	0–100	Genis-Armero *et al.* (2017)	Phyllosoma
UCA	MA017008PED05PH04	19/4/2015	Cape Verde	20.26	−24.25	0–100	Genis-Armero *et al.* (2017)	Phyllosoma
UCA	MA017008PED05PH05	19/4/2015	Cape Verde	20.26	−24.25	0–100	Genis-Armero *et al.* (2017)	Phyllosoma
UCA	MA017008PED05PH06	19/4/2015	Cape Verde	20.26	−24.25	0–100	Genis-Armero *et al.* (2017)	Phyllosoma
UCA	MA017008PED05PH07	19/4/2015	Cape Verde	20.26	−24.25	0–100	Genis-Armero *et al.* (2017)	Phyllosoma
IEOCD	CCDE-IEOCD:968-1	9/6/2012	Mauritania	19.82	−17.20	69–69	Present study	Adult
IEOCD	CCDE-IEOCD:968-2	9/6/2012	Mauritania	19.82	−17.20	69–69	Present study	Adult
UCA	MA019009PEN05PH01	21/4/2015	Cape Verde	16.16	−26.03	0–100	Genis-Armero *et al.* (2017)	Phyllosoma
IEOCD	CCDE-IEOCD:999-1	4/11/2011	Senegal	14.70	−17.91	154–154	Present study	Adult
IEOCD	CCDE-IEOCD:999-2	4/11/2011	Senegal	14.70	−17.91	154–154	Present study	Adult
IEOCD	CCDE-IEOCD:999-3	4/11/2011	Senegal	14.70	−17.91	154–154	Present study	Adult
IEOCD	CCDE-IEOCD:999-4	4/11/2011	Senegal	14.70	−17.91	154–154	Present study	Adult
IEOCD	CCDE-IEOCD:1105-1	27/5/2012	Senegal	14.47	−17.51	103–103	Present study	Nisto
IEOCD	CCDE-IEOCD:197-1	4/11/2008	Guinea	10.28	−16.37	65–65	Present study	Adult
IEOCD	CCDE-IEOCD:197-2	4/11/2008	Guinea	10.28	−16.37	65–65	Present study	Adult
UCA	MA025012PEN00PH19	27/4/2015	Cape Verde	9.56	−25.99	0–250	Genis-Armero *et al.* (2017)	Phyllosoma
UCA	MA025012PEN00PH20	27/4/2015	Cape Verde	9.56	−25.99	0–250	Genis-Armero *et al.* (2017)	Phyllosoma
IEOCD	CCDE-IEOCD:989-1	23/10/2011	Guinea	9.34	−15.67	116–116	Present study	Adult
IEOCD	CCDE-IEOCD:989-2	23/10/2011	Guinea	9.34	−15.67	116–116	Present study	Adult
MNHN	Pa-257		Mauritania				Present study	Adult (Monod coll.)
MNHN	MNHN-IU-2016-10733		St Helena	−16.01	−5.70		Present study	Nisto
NHM			St Helena	−16.01	−5.70		Present study	Adult

(*Continued*)

https://doi.org/10.1017/S0025315419000067

Table 1. (*Continued.*)

Museum collection	Voucher code	Date	Area	Latitude	Longitude	Depth (m)	Study	Stage
NHM			St Helena	−16.01	−5.70		Present study	Adult
MNHN	MNHN-IU-2013-14842	18/3/1968	Angola	−16.45	11.58	90–126	Crosnier (1970)	Adult
MNHN	MNHN-IU-2013-14843	18/3/1968	Angola	−16.45	11.58	90–126	Crosnier (1970)	Adult
USNM	USNM 127765	18/3/1968	Angola	−16.62	11.37	126–126	Crosnier (1970)	Adult
RMNH	RMNH D 30937	24/3/1968	Angola	−17.22	11.45	155–155	Crosnier (1970)	Adult
USNM	USNM 127766	24/3/1968	Angola	−17.22	11.45	155–155	Crosnier (1970)	Adult
ICM	ICMD002512	28/9/1983	Namibia	−17.25	11.45		Present study	Adult
ICM	ICMD 299/1991	25/3/1981	Namibia	−17.48	11.38	293–300	Macpherson (1983)	Adult
ICM	ICMD 300/1991	28/8/1980	Namibia	−18.00	11.42	270–274	Macpherson (1983)	Adult
ICM	ICMD001081	25/4/1986	Namibia	−18.00	10.55	0–200	Genis-Armero *et al.* (2017)	Phyllosoma
ICM	ICMD001082	25/4/1986	Namibia	−18.00	10.55	0–200	Genis-Armero *et al.* (2017)	Phyllosoma
ICM	ICMD001083	25/4/1986	Namibia	−18.00	10.55	0–200	Genis-Armero *et al.* (2017)	Phyllosoma
ICM	ICMD001084	25/4/1986	Namibia	−18.00	10.55	0–200	Genis-Armero *et al.* (2017)	Phyllosoma
ICM	ICMD001085	25/4/1986	Namibia	−18.00	10.55	0–200	Genis-Armero *et al.* (2017)	Phyllosoma
ICM	ICMD001086	25/4/1986	Namibia	−18.00	10.55	0–200	Genis-Armero *et al.* (2017)	Phyllosoma
ICM	ICMD001087	25/4/1986	Namibia	−18.00	10.55	0–200	Genis-Armero *et al.* (2017)	Phyllosoma

IEOCD, Centro Oceanográfico de Cádiz; ICM, Instituto de Ciencias del Mar; MfN, Museum für Naturkunde; MNHN, Muséum national d'Histoire naturelle; NHM, Natural History Museum; RMNH, Rijksmuseum van Natuurlijke Historie; USNM, Smithsonian National Museum of Natural History; UCA, Universidad de Cádiz.

tubercles and posterior carina with 12–14 tubercles; ∼8 tubercles in posterior lateral margin.

Antennule (Figure 3A). Longer than antennae; peduncle with 3 articles, proximal article stout, compressed at middle with long stiff setae, dorsal extension on the left distal margin; primary flagellum (12 annuli) with dense plumose setae on distal half and widening in the middle, shorter than accessory flagellum (13 annuli), which is more slender and with scattered setae along entire length; antennular somite with a blunt central spine and one or two smaller spines on inner margin.

Antenna (Figure 2A). Uniramous with exopod absent, 4-segmented endopod, broad and flat; first segment trapezoidal with 2 spines; second segment (proximal squame) triangular with pronounced median ridge, outer lateral margin serrated with two deep notches; third segment with irregular margin and 2 spines; fourth segment with 7 serrated lobes with setae in margin, first three lobes pointier.

Mandible (Figure 3B). Not fully developed. Endopod present as unsegmented palp and exopod absent.

Maxillule (Figure 3C). Not fully developed, with short spines on coxal (6 spines) and basial (8 spines) endites. Endopod and exopod absent.

Maxilla (Figure 3D). Coxal and basial endites inconspicuous. Endopod unsegmented; scaphognathite (exopod) well developed and setose.

First maxilliped (Figure 3E). Coxal and basial endites inconspicuous. Epipod elongated and without setae. Biramous with unsegmented ramii. Endopod with 5 setae. Poorly developed. Exopod with ∼16 and 9 plumose setae on outer and inner margin respectively.

Second maxilliped (Figure 3F). Biramous, endopod 4-segmented; carpus, and propodus with 3 and 6 setae respectively, dactylus with ∼11 spines; exopod superficially 2-segmented, outer margin of distal segment with ∼20 short setae.

Third maxilliped (Figure 3G). Biramous; endopod 5-segmented; merus, carpus and propodus with 5, ∼150 and ∼28 setae respectively; dactylus with 13 spines; exopod 2-segmented, as long as ischium.

Sternum (Figure 2C). Anterior margin with U-shaped incision in the middle and longitudinal depression; surface smooth, last sternite with acute lateral spines; posterior margin convex.

Pereopods (Figure 4A, E). P1 (pereopod 1) to P4 (pereopod 4) biramous with a 5-segmented endopod and a residual exopod, P5 (pereopod 5) uniramous with exopod absent; P1 endopod short and robust, merus, carpus and propodus with 5, 2 and 13 setae respectively, dactylus with 12 spines (2 missing); P2 with 7, 13, 5 and 13 setae on coxa, merus, carpus and propodus respectively, 7 spines and 4 setae on dactylus; P3–P5 more setose.

Pleon (Figure 2A, B). Smooth median carina in the midline of pleomeres 2–5, with shallow transverse grooves; pleomeres 1–4 with a deep subtriangular notch at midline of posterior margin; posterior margin of fifth somite rounded and ending with acute corners; posterior margin of sixth pleomere with 2 long spines on posterior corners, and 3 less acute spines between previous ones; 11 pairs of smaller bulges on the surface; seventh somite with 2 pairs of long spines in the margin and 3 pairs on the surface; pleura of pleomere 1 with a minute spine in margin; pleura of pleomeres 2–5 with serrated margin and sharp ending, pleura of fifth somite less acute; rami of uropods faintly serrated on outer margins.

Pleopods (Figure 3H). Present on pleomeres 2–5; biramous; protopod with ∼8 setae; exopod and endopod with ∼35 and ∼45 long plumose natatory setae respectively; appendix interna without setae, not reaching distal tip of endopod; cincinnuli present.

https://doi.org/10.1017/S0025315419000067

Table 2. Estimates of 16S gene evolutionary divergence (below diagonal) and the corresponding standard deviation (above diagonal) between the large Canary Island decapodid and Atlantic slipper lobsters (sequences available in GenBank).

Nisto-ICMD002350		0.021	0.021	0.023	0.023	0.019	0.012	0.013	0.022	0.022	0.005	0.012	0.014	0.004
Parribacus antarcticus-JN701702	0.179		0.000	0.024	0.026	0.024	0.021	0.022	0.025	0.025	0.021	0.024	0.022	0.021
Parribacus antarcticus-JN701703	0.179	0.000		0.024	0.026	0.024	0.021	0.022	0.025	0.025	0.021	0.024	0.022	0.021
Scyllarides herklotsii-FJ174906	0.204	0.216	0.216		0.006	0.023	0.023	0.023	0.025	0.025	0.022	0.025	0.022	0.023
Scyllarides latus-FJ174907	0.194	0.229	0.229	0.017		0.024	0.023	0.023	0.025	0.025	0.022	0.025	0.022	0.023
Scyllarus americanus-ULLZ8500	0.141	0.207	0.207	0.190	0.190		0.021	0.019	0.015	0.015	0.019	0.021	0.017	0.019
Scyllarus arctus-JN701732	0.063	0.179	0.179	0.201	0.191	0.147		0.014	0.024	0.024	0.012	0.015	0.017	0.011
Scyllarus caparti-FJ174909	0.071	0.185	0.185	0.212	0.202	0.138	0.084		0.019	0.020	0.013	0.013	0.014	0.013
Scyllarus chacei-JN701733	0.166	0.223	0.223	0.227	0.227	0.098	0.178	0.138		0.004	0.022	0.022	0.020	0.022
Scyllarus chacei-JN701734	0.169	0.223	0.223	0.224	0.224	0.101	0.181	0.141	0.007		0.022	0.022	0.020	0.022
Scyllarus depressus-JN701735	0.014	0.176	0.176	0.201	0.191	0.135	0.063	0.071	0.169	0.172		0.013	0.014	0.006
Scyllarus posteli-FJ174910	0.071	0.214	0.214	0.239	0.228	0.159	0.096	0.073	0.159	0.162	0.082		0.016	0.012
Scyllarus pygmaeus-FJ174908	0.074	0.178	0.178	0.185	0.181	0.117	0.110	0.082	0.141	0.144	0.076	0.104		0.014
Scyllarus subarctus-FJ174912	0.009	0.182	0.182	0.214	0.204	0.141	0.058	0.071	0.166	0.169	0.019	0.068	0.079	

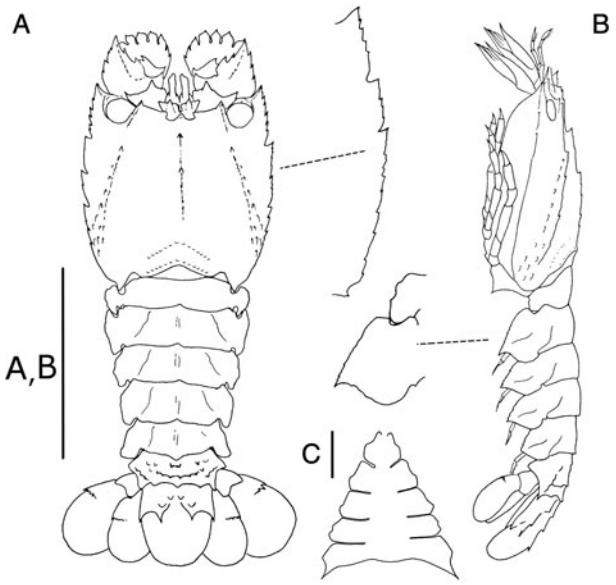


Fig. 2. *Scyllarus subarctus* Crosnier, 1970, nisto stage: (A) dorsal view and detail of carapace profile; (B) lateral view and pleura of second abdominal somite (detail); (C) sternum. Scale bars: A–B, 10 mm; C, 2 mm.

Discussion

Considered as data deficient in the IUCN Red List of Threatened Species, the distribution of *Scyllarus subarctus* was previously known from only a few localities including Angola (type locality), northern Namibia and NW Africa (Crosnier, 1970; Macpherson, 1983; Muñoz *et al.*, 2012). The results presented here enlarge significantly the distribution area of the species through new records obtained from several oceanographic expeditions and museum collections. The nisto stage of *S. subarctus* is also described based on material collected around the oceanic islands of St Helena and the Canaries as well as the continental coast of Senegal. The most characteristic features of *S. subarctus* nisto are the number of setae on the pereopods, the relative position and morphology of the rostral, pre-gastric and gastric teeth and a pronounced 'U-shaped' anterior margin of the fourth thoracic sternite. The nisto of both *S. subarctus* and *S. depressus* present a larger number of setae on the pereopods compared with *S. pygmaeus* or *S. arctus* (Palero *et al.*, 2009*b*) and this difference is also observed during the phyllosoma stages (Genis-Armero *et al.*, 2017). Although the nisto stages of *S. subarctus* and *S. depressus* are similar, the specimens described here are up to 50% larger (Robertson, 1971) and they have 8–7 setae on the protopod of the pleopods instead of 6 setae as in *S. depressus* (Lyons, 1970). The identification of nisto stages based on morphology remains difficult, and the lack of detail in previous descriptions prevents us from further comparison.

The new distribution data presented here shows that the type locality, placed in the temperate area of Angola/Namibia (around 17°S), actually represents the southern limit of *S. subarctus* (Crosnier, 1970). The Benguela upwelling system, which appeared in the Miocene and intensified during the later Pliocene (Siesser, 1980), acts as a natural barrier between the Atlantic and Indian biota, delimiting the biogeography of many marine species (Lessios *et al.*, 2003). *Scyllarus subarctus* is now shown to be mostly distributed along the Tropical Eastern Atlantic, including North-west and South-west Africa, St Helena, Canary Islands, and Cape Verde. Previous records had established the northern limit of *S. subarctus* as near Cape Verde, around 20°N (Genis-Armero *et al.*, 2017), but the new data presented here expand

https://doi.org/10.1017/S0025315419000067

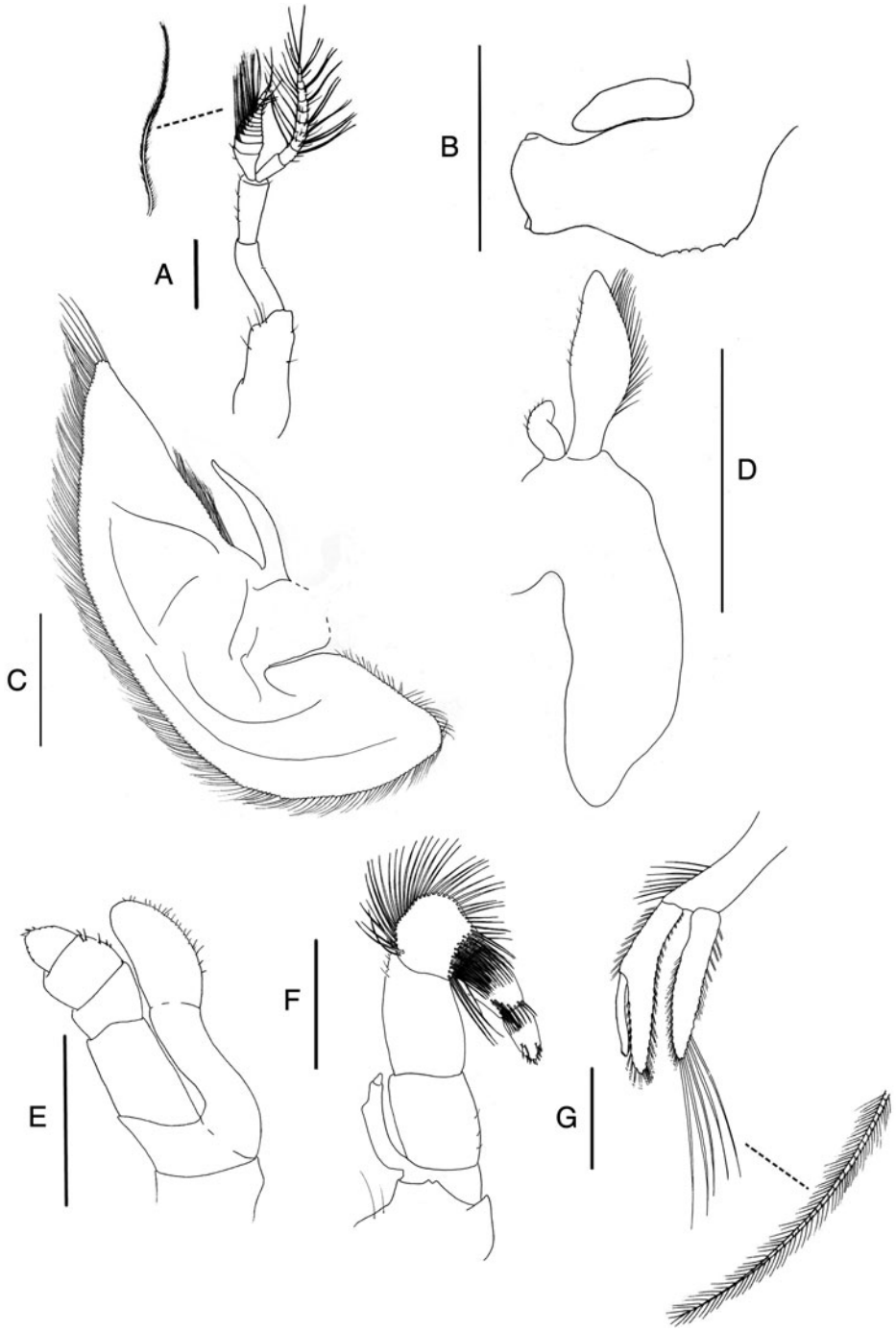


Fig. 3. *Scyllarus subarctus* Crosnier, 1970, nisto stage: (A) antennule (detail of aesthetasc); (B) mandible; (C) maxillule; (D) maxilla; (E) maxilliped 1; (F) maxilliped 2; (G) maxilliped 3; (H) pleopod (detail of seta). Scale bars: A, 1 mm; B, 0.5 mm; C, 0.2 mm; D–H, 1 mm.

the known latitudinal range to 34°N, near Rabat, Morocco. A possible expansion due to warming trends remains speculative, and the new northernmost citations for *S. subarctus* can simply be the result of improved sampling.

Long planktonic life duration facilitates dispersal, and the large size of the *S. subarctus* nisto stage suggests increased swimming abilities (Booth *et al.*, 2005), which is in agreement with the wide distribution of the species. It might be hypothesized that prevalent east-to-west oceanic currents in the Tropical Atlantic (Rodríguez *et al.*, 2000; de Lestang & Caputi, 2015; Pelegrí & Benazzouz, 2015) facilitated *S. subarctus* colonization of St Helena from Africa (Gillespie, 2007). Oceanic islands such as St Helena could have functioned in that case as stepping-stones (Muss *et al.*, 2001), and this type of long-distance dispersal between Africa and America has already been reported in fish or sea urchins (Joyeux *et al.*, 2001; Lessios *et al.*, 2003). This hypothetical scenario would be consistent with the fact that *S. depressus* is phylogenetically and morphologically much closer to *S. subarctus* than to other American species such as *S. americanus* or *S. chacei* (Genis-Armero *et al.*, 2017) and merits further attention.

Adult specimens of both *S. subarctus* and *S. depressus* can be distinguished from *S. arctus* by the presence of 5–6 antennal lobes, the antennular plate showing just one or two pairs of small teeth, the 8th thoracic sternite presenting a strong and larger tubercle and the dorsal sculpturing of abdominal segments being narrower and less branched. According to Crosnier (1970), *S. subarctus* and *S. depressus* can be distinguished by the gastric tooth in the caparace pointing upwards (lateral view) in *S. subarctus*, the posterior part of the dorsal carina being wider in *S. depressus* (volcano-like from

https://doi.org/10.1017/S0025315419000067

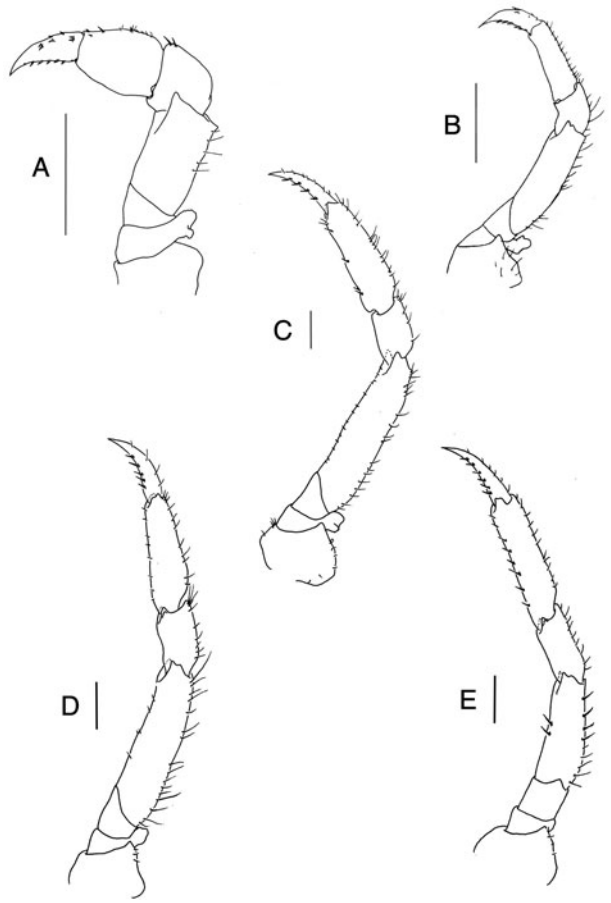


Fig. 4. *Scyllarus subarctus* Crosnier, 1970, nisto stage: (A) pereopod 1; (B) pereopod 2; (C) pereopod 3; (D) pereopod 4; (E) pereopod 5. Scale bars: A–B, 2 mm; C–E, 1 mm.

dorsal view), and the pregastric tooth being closer to rostral than to gastric tooth in *S. subarctus*. A thorough morphological analysis of our *S. subarctus* samples revealed that some character states assigned to *S. depressus* are also present in the African specimens studied here. The low morphological and genetic differentiation observed between *S. subarctus* and *S. depressus* could be explained by *S. depressus* resulting from a relatively recent colonization of America, but this hypothesis would need further testing. Future studies should include more samples from western Atlantic waters and new molecular markers in order to obtain an accurate delimitation of the geographic distribution of *Scyllarus* species and test the relationship between *S. subarctus* and *S. depressus*.

Author ORCIDs. José Landeira, 0000-0001-6419-2046
Ferran Palero, 0000-0002-0343-8329

Acknowledgements. Thanks are due to Eva García (IEOCD), Eli Muñoz (IEOCD), Oliver Coleman (MfN), Paul Clark (NHM), Alain Crosnier (MNHN), Pierre Opic, Laure Corbari (MNHN) and Paula Martin-Lefevre (MNHN). They were key to the completion of this study through both museum loans and their joyful encouragement.

Financial support. This research was funded by projects CETOBAPH (CGL2009-1311218) and POPCOMICS (CTM2017-88080) of the Spanish Government and EU-Synthesys grants (DK-TAF-4873: Morphological study of Achelata lobsters and phyllosoma larvae from Danish collections; DE-TAF-7058: Achelata lobsters from the Museum für Naturkunde and FR-TAF-5980: Description of phyllosoma stages of West-African lobster species). FP acknowledges project FP7 Marie Curie IAPP #324475 'Colbics' of the European Union and a post-doctoral contract funded by the Beatriu de Pinos Programme of the Generalitat de Catalunya.

References

Ariza A, Landeira JM, Escánez A, Wienerroither R, Aguilar de Soto N, Rostad A, Kaartvedt S and Hernández-León S (2016) Vertical distribution, composition and migratory patterns of acoustic scattering layers in the Canary Islands. *Journal of Marine Systems* **157**, 82–91.

Booth JD, Webber WR, Sekiguchi H and Coutures E (2005) Diverse larval recruitment strategies within the Scyllaridae. *New Zealand Journal of Marine and Freshwater Research* **39**, 581–592.

Bouvier EL (1913) Sur les genres Pseudibacus et Nisto et les stade natant des Crustacés Décapodes macroures de la famille des Scyllaridés. *Comptes Rendus Hebdomadaires des Seances de l'Academie des Sciences* **156**, 1643–1648.

Bracken-Grissom HD, Ahyong ST, Wilkinson RD, Feldmann RM, Schweitzer CE, Breinholt JW, Bendall M, Palero F, Chan TY, Felder DL, Robles R, Chu KH, Tsang LM, Kim D, Martin JW and Crandall K (2014) The emergence of lobsters: phylogenetic relationships, morphological evolution and divergence time comparisons of an ancient group (Decapoda: Achelata, Astacidea, Glypheidea, Polychelida). *Systematic Biology* **63**, 457–479.

Clark PF and Cuesta JA (2015) Larval systematics of Brachyura. In Castro P, Davie PJF, Guinot D, Schram FR and Von Vaupel Klein JC (eds), *Decapoda: Brachyura, Treatise on Zoology – Anatomy, Taxonomy, Biology. The Crustacea, Complementary to the Volumes Translated From the French of the Traité de Zoologie [Founded by P.-P. Grassé (†)] 9C-II*. Leiden: Brill. pp. 639–1221.

Clark PF, Calazans DK and Pohle GW (1998) Accuracy and standardization of brachyuran larval descriptions. *Invertebrate Reproduction and Development* **33**, 127–144.

Crosnier A (1970) Crustacés décapodes Brachyoures et Macroures recueillis par l'Undaunted au sud de l'Angola. Description de Scyllarus subarctus sp. nov. *Bulletin Du Muséum National d'Histoire Naturelle* **41**, 1214–1227.

de Lestang S and Caputi N (2015) Climate variability affecting the contranatant migration of *Panulirus cygnus*, the western rock lobster. *Marine Biology* **162**, 1889–1900.

Edgar RC (2004) MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* **32**, 1792–1797.

Felder DL, Martin JW and Goy J (1985) Patterns in early postlarval development of decapods. *Crustacean Issues* **2**, 163–225.

Genis-Armero R, Guerao G, Abelló P, Ignacio González-Gordillo J, Cuesta JA, Corbari L, Clark PF, Capaccioni-Azzati R and Palero F (2017) Possible amphi-atlantic dispersal of *Scyllarus* lobsters (Crustacea: Scyllaridae): molecular and larval evidence. *Zootaxa* **4306**, 325–338.

Gillespie RG (2007) Oceanic islands: models of diversity. In Levin SA (ed.), *Encyclopedia of Biodiversity*. Oxford: Elsevier, pp. 1–13.

Hall T (1999) BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series*.

Hillis DM, Moritz C and Mable BK (1996) *Molecular Systematics*, 2nd Edn. Sunderland, MA: Sinauer Associates.

Holthuis LB (1985) A revision of the family Scyllaridae (Crustacea: Decapoda: Macrura). I. Subfamily Ibacinae. *Zoologische Verhandelingen* **218**, 1–130.

Ito M and Lucas JS (1990) The complete larval development of the scyllarid lobster, *Scyllarus demani* Holthuis, 1946 (Decapoda; Scyllaridae), in the laboratory. *Crustaceana* **58**, 144–167.

Jeffs AG, Montgomery JC and Tindle CT (2005) How do spiny lobster postlarvae find the coast? *New Zealand Journal of Marine and Freshwater Research* **39**, 605–617.

Joyeux JC, Floeter SR, Ferreira CEL and Gasparini JL (2001) Biogeography of tropical reef fishes: the south Atlantic puzzle. *Journal of Biogeography* **28**, 831–841.

Kaestner A (1980) *Invertebrate Zoology*. New York, NY: Krieger Publishing Company.

Kumar S, Stecher G and Tamura K (2016) MEGA7: Molecular Evolutionary Genetics Analysis Version 7.0 for bigger datasets. *Molecular Biology and Evolution* **33**, 1870–1874.

Lessios HA, Kane J and Robertson DR (2003) Phylogeography of the pantropical sea urchin *Tripneustes*: contrasting patterns of population structure between oceans. *Evolution* **57**, 2026–2036.

Lyons WG (1970) Scyllarid lobsters (Crustacea, Decapoda). *Memoirs of the Hourglass Cruises* **1**, 1–74.

Macpherson E (1983) Crustáceos Decápodos capturados en las costas de Namibia. *Resultados Expediciones Científicas* **11**, 3–80.

https://doi.org/10.1017/S0025315419000067

Muñoz I, García-Isarch E, Sobrino I, Burgos C, Funny R and González-Porto M (2012) Distribution, abundance and assemblages of decapod crustaceans in waters off Guinea-Bissau (north-West Africa). *Journal of the Marine Biological Association of the United Kingdom* **92**, 475–494.

Muss A, Robertson DR, Stepien C, Wirtz P and Bowen B (2001) Phylogeography of *Ophioblennius*: the role of ocean currents and geography in reef fish evolution. *Evolution* **55**, 561–572.

Pagliarino E, Massi D, Canali E, Costa C, Pessani D and Bianchini ML (2013) Findings of phyllosoma larvae and nistos of the family Scyllaridae (Crustacea, Decapoda) in the Southern Mediterranean Sea. *Open Marine Biology Journal* **7**, 8–13.

Palero F and Abello P (2007) The first phyllosoma stage of *Palinurus mauritanicus* (Crustacea: Decapoda: Palinuridae). *Zootaxa* **1508**, 49–59.

Palero F, Guerao G and Abelló P (2008) Morphology of the final stage phyllosoma larva of *Scyllarus pygmaeus* (Crustacea: Decapoda: Scyllaridae), identified by DNA analysis. *Journal of Plankton Research* **30**, 483–488.

Palero F, Crandall KA, Abelló P, Macpherson E and Pascual M (2009*a*) Phylogenetic relationships between spiny, slipper and coral lobsters (Crustacea, Decapoda, Achelata). *Molecular Phylogenetics and Evolution* **50**, 152–162.

Palero F, Guerao G, Clark PF and Abello P (2009*b*) The true identities of the slipper lobsters *Nisto laevis* and *Nisto asper* (Crustacea: Decapoda: Scyllaridae) verified by DNA analysis. *Invertebrate Systematics* **23**, 77–85.

Palero F, Guerao G, Clark PF and Abelló P (2010) Final-stage phyllosoma of *Palinustus* a. Milne Edwards, 1880 (Decapoda : Achelata : Palinuridae)—The first complete description. *Zootaxa* **2403**, 42–58.

Palero F, Guerao G, Clark PF and Abelló P (2011) *Scyllarus* arctus (Crustacea: Decapoda: Scyllaridae) final stage phyllosoma identified by DNA analysis, with morphological description. *Journal of the Marine Biological Association of the United Kingdom* **91**, 485–492.

Palero F, Genis-Armero R, Hall M and Clark PF (2016) DNA barcoding the phyllosoma of *Scyllarides squammosus* (H. Milne Edwards, 1837) (Decapoda: Achelata: Scyllaridae). *Zootaxa* **4139**, 481–498.

Pelegrí JL and Benazzouz A (2015) Coastal upwelling off North-West Africa. In Valdés L and Déniz-González I (eds), *Oceanographic and Biological Features in the Canary Current Large Marine Ecosystem*. Paris: IOC Technical Series, pp. 93–103.

Robertson PB (1968) The complete larval development of the sand lobster *Scyllarus americanus* (Smith), (Decapoda, Scyllaridae) in the laboratory with notes on larvae from the plankton. *Bulletin of Marine Science* **18**, 294–432.

Robertson PB (1971) The larvae and postlarvae of the Scyllarid lobster *Scyllarus depressus* (Smith). *Bulletin of Marine Science* **21**, 841–865.

Rodríguez JM, Braun JG and García A (2000) Spatial variability of the mesozooplankton biomass and ichthyoplankton in the Canary region, in autumn 1991. *Journal of Plankton Research* **22**, 1377–1391.

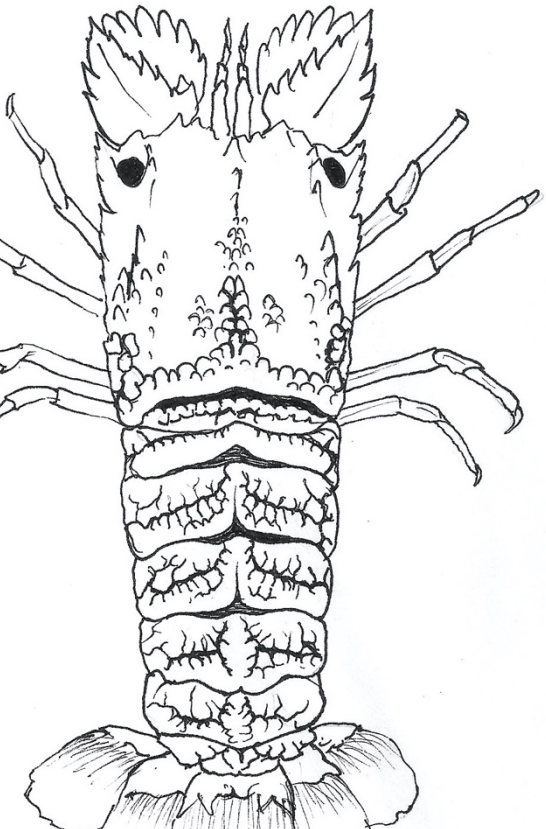
Siesser WG (1980) Late Miocene origin of the Benguela upwelling system off northern Namibia. *Science* **208**, 283–285.

Smith SI (1869) Descriptions of a new genus and two new species of Scyllaridae and a new species of *Aethra* from North America. *American Journal of Science and Arts* **48**, 118–121.

Ventura T, Fitzgibbon QP, Battaglene SC and Elizur A (2015) Redefining metamorphosis in spiny lobsters: molecular analysis of the phyllosoma to puerulus transition in *Sagmariasus verreauxi*. *Scientific Reports* **5**, 13537.

CAPÍTOL 3

Revision of the West African species of *Scyllarus* Fabricius, 1775 (Decapoda: Achelata: Scyllaridae), with the description of three phyllosoma stages of *S. caparti* Holthuis, 1952 and an updated identification key



Journal of Crustacean Biology Advance Access published 29 May 2020

The Crustacean Society

Journal of Crustacean Biology

Journal of Crustacean Biology (00) 1–13. doi:10.1093/jcbiol/ruaa025

Revision of the West African species of *Scyllarus* Fabricius, 1775 (Decapoda: Achelata: Scyllaridae), with the description of three phyllosoma stages of *S. caparti* Holthuis, 1952 and an updated identification key

Rebeca Genis-Armero[1,2], J. Ignacio González-Gordillo[3], Jose A. Cuesta[4], Romana Capaccioni-Azzati[1] and Ferran Palero[2,5,6]

[1]*Department de Zoologia, Facultat de Ciències Biològiques, Universitat de València, 46100 Burjassot, Spain;*
[2]*Institut Cavanilles de Biodiversitat i Biologia Evolutiva, Universitat de València, 46980 Paterna, Spain;*
[3]*Instituto Universitario de Investigación Marina (INMAR), Campus de Excelencia Internacional del Mar, Universidad de Cádiz, Avenida República Saharaui s/n, 11510 Puerto Real, Cádiz, Spain;*
[4]*Instituto de Ciencias Marinas de Andalucía (ICMAN-CSIC), Campus de Excelencia Internacional del Mar, Avenida República Saharaui, 2, 11519 Puerto Real, Cádiz, Spain;*
[5]*Department of Life Sciences, The Natural History Museum, Cromwell Road, London SW7 5BD, England, UK; and*
[6]*Department of Invertebrate Zoology and Hydrobiology, Faculty of Biology and Environmental Protection, Uniwersytet Łódzki, ul. Banacha 12/16, 90–237 Łódź, Poland*

Correspondence: F. Palero; email: Ferran.Palero@uv.es

(Received 24 March 2020; accepted 30 April 2020)

ABSTRACT

West African species of *Scyllarus* Fabricius, 1775 (Achelata, Scyllaridae) are poorly known, mostly due to the difficulties of sampling Eastern Atlantic tropical waters. Recent expeditions carried out by the Universidad de Cádiz and the Instituto Español de Oceanografía collected phyllosoma larvae from Cape Verde Islands (CVI) and fresh *Scyllarus* adults from continental West Africa. Larval stages VII, IX, and X (final stage) of *S. caparti* Holthuis, 1952 are analyzed using DNA barcoding methods and described for the first time. A comprehensive identification key is provided, summarizing our current knowledge on the phyllosomas of *Scyllarus*. Together with a revision of museum collections, the new molecular and morphological data obtained here supports the polyphyletic origin of *Acantharctus* Holthuis, 2002. The West African *A. posteli* (Forest, 1963) is found to belong to *Scyllarus* and it is closest to another species from Atlantic shallow waters (i.e. *S. paradoxus* Miers 1881), whereas the Pacific Ocean *A. delfini* (Bouvier, 1909) would belong to *Crenarctus* Holthuis, 2002.

Key Words: DNA barcoding, Eastern Tropical Atlantic region, larvae, phylogenetics, plankton, slipper lobsters

INTRODUCTION

Slipper lobster species of *Scyllarus* Fabricius, 1775 (Crustacea: Scyllaridae) from West Africa have a complicated taxonomic history, mostly resulting from the lack of sampling and difficulties in establishing significant morphological traits to define generic taxa. Adults of the small-sized *S. pygmaeus* (Bate, 1888), a species originally described from Cape Verde islands (CVI), were misidentified as juvenile stages of *S. arctus* (Linnaeus, 1758) until Forest & Holthuis (1960) confirmed the presence of *S. pygmaeus* in the Mediterranean. The larval stages for these two species were confused for two centuries (Bouvier, 1913, 1925; Palero *et al.*, 2008, 2009b, 2011) and morphological differences among early stages have yet to be confirmed. Similarly, two *Scyllarus* species from West African tropical waters were included in *S. paradoxus* Miers, 1881 for almost a century until Forest (1963) revised the type material of Miers (1881) and described *S. posteli* Forest, 1963 as a new species. In his comprehensive revision of the Indo-West Pacific Scyllarinae Latreille, 1825; Holthuis (2002) assigned the eastern Atlantic species *S. posteli* to *Acantharctus* Holthuis, 2002 and grouped it with two Pacific Ocean taxa: *A. delfini* (Bouvier, 1909) and *A. ornatus* (Holthuis, 1960). Holthuis (2002) definition of *Acantharctus* is considered valid in current checklists (Chan, 2019; WoRMS (http://www.marinespecies.org/aphia.php?p=taxdetails&id=382777), accessed on 14 April 2020), but phylogenetic relationships among Pacific and Atlantic scyllarids have yet to be confirmed using modern DNA techniques.

The complex life cycle of slipper lobsters includes a long-lived, dorsoventrally flattened phyllosoma larva (Palero & Abelló, 2007; Palero *et al.*, 2014). Little is known about the ecology and biology of the phyllosomas. They prove difficult to rear and have extremely low survival rates when hatched directly in the laboratory, mostly due to their longevity and the problems to provide them a suitable food source. Alternatively, the lack of diagnostic morphological characters hampers species-level identification of plankton-caught phyllosomas. Early accounts from Eastern Atlantic waters (Stephensen, 1923; Gurney, 1936) erroneously assigned several *Scyllarus* phyllosomas to *Scyllarides* Gill, 1898 until Robertson (1969) established morphological generic differences. The first West African phyllosomas that can be assigned with confidence (nowadays) to *Scyllarus* date back to the HMS *Challenger* Expedition (1872–1876) collected from CVI (Bate, 1888). Some later larval assignments should also be taken with caution (Crosnier, 1972; Ribeiro, 1973; Maigret, 1975, 1978). Ribeiro (1973) assigned four larval stages from CVI to *S. pygmaeus* based the on the argument that it was the only *Scyllarus* known from the archipelago, but another three species (*S. subarctus* Crosnier, 1970, *S. posteli*, and *S. caparti* Holthuis, 1952) are known to occur at similar latitudes from continental West Africa (Muñoz *et al.*, 2012). Similarly, the four *Scyllarus* phyllosoma types (A–D) described by Maigret (1975, 1978) from Banc d'Arguin, Mauritania, remain unassigned to species level. The use of molecular analysis on plankton samples has proven to be successful for specific assignment of *Scyllarus* phyllosomas (*S. pygmaeus*: Palero *et al.*, 2008; *S. arctus*: Palero *et al.*, 2011; *S. subarctus*: Genis-Armero *et al.*, 2017). Nevertheless, DNA barcoding techniques present some limitations and rely on obtaining reference sequences from correctly identified adult specimens of every candidate taxa (Genis-Armero *et al.*, 2017; Palero *et al.*, 2008, 2011).

The West African species of *Scyllarus* are distributed throughout poorly sampled tropical areas, where collecting fresh material is particularly difficult (Table 1). Difficulties obtaining fresh material of Eastern Atlantic species have prevented a molecular comparison between *S. paradoxus* and *A. posteli*, and previous attempts to amplify *S. paradoxus* DNA from museum material were unsuccessful (Palero *et al.*, 2009a; unpublished data). The Instituto Español de Oceanografía (IEO-CD, Cádiz, Spain) has carried out during recent years several expeditions along northwestern Africa, reporting the presence of *A. posteli* and four *Scyllarus* species including *S. arctus*, *S. caparti*, *S. subarctus*, and an unidentified species of slipper lobster (Muñoz *et al.*, 2012). This new material provided a unique opportunity to revise adult morphology and obtain reference sequences for every known West African *Scyllarus*. The new morphological and molecular evidence gathered was used to test phylogenetic relationships between the species of *Scyllarus* and *Acantharctus* from Atlantic and Pacific waters. Furthermore, DNA barcoding methods were applied on a collection of East Atlantic phyllosomas obtained during the Migrants and Active Flux in the Atlantic Ocean (MAF) Expedition. Three *S. caparti* larval stages (VII, IX, and X) are described in detail for the first time and compared with the phyllosoma of other West African *Scyllarus*. Previous research and new morphological evidence are furthermore summarized through a new identification key for *Scyllarus* phyllosomas.

MATERIALS AND METHODS

Adult and larval material studied

Specimens of the West African species of *Scyllarus* kept at the Muséum national d'Histoire naturelle, Paris (MNHN), including adults of *S. paradoxus* and *A. posteli* studied by Forest (1963), were used as a reference to review the material collected by RV *Vizconde de Eza* during 2002–2010 and briefly reported by Muñoz *et al.* (2012). Several museum collections were revised in search of further *Scyllarus* from West Africa, including Institut de Ciències del Mar, Barcelona (ICM); Instituto Español de Oceanografía, Cadiz (IEO-CD); Natural History Museum, London (NHM); Muséum des Sciences naturelles de Belgique/Museum voor Natuurwetenschappen van België, Bruxelles (RBINS); Rijksmuseum van Natuurlijke Historie, Leiden (RMNH); Senckenberg Naturmuseum Frankfurt (SMF), and United States National Museum of Natural History (Smithsonian), Washington (USNM). Phyllosoma larvae were also obtained during a cruise through tropical and subtropical Atlantic waters (MAF campaign) 3–29 April 2015. A total of

Table 1. Species of Scyllarinae Latreille, 1825 from African waters. Ecoregions based on Spalding *et al.* (2007): Ben (Benguela [Namibia]), GoG (Gulf of Guinea), Lus (Lusitania [Portugal]), MedSea (Mediterranean Sea), St. H (St. Helena I.), TNA (Temperate Northern Atlantic), TrA (Tropical Atlantic), TSAf (Temperate South Africa), WAfT (West African Transition). *One record from Baia di Portonovo, Adriatic Sea (Froglia, 1979).

Species	Area	Subarea	Depth range	References
S. arctus (Linnaeus, 1758)	TNA	Lus MedSea	4 –143 m	Gurney, 1936; Anadón, 1981; Gracia Socias & Massuti Jaume, 1979; Holthuis, 1991; Relini, 1999; Quigley *et al.*, 2010; Palero *et al.*, 2011
S. caparti Holthuis 1952	TNA	Lus MedSea*	17–105 m	Holthuis, 1960; Froglia, 1979; Anadón, 1981; Fransen, 1991; de Matos-Pita *et al.*, 2018
	TrA	WAfT GoG		
S. paradoxus Miers, 1881	TrA	WAfT GoG	5–46 m	Forest, 1963; Muñoz *et al.*, 2012
Acantharctus posteli Forest, 1963	TNA	MedSea Lus	5–70 m	Forest, 1963; Anadón, 1981; García-Raso, 1982; González-Gordillo & Rodríguez, 2000
	TrA	GoG		
S. pygmaeus Bate, 1888	TNA	Lus MedSea	5–162 m	Gurney, 1936; Forest & Holthuis, 1960; Lewinsohn, 1974; García-Raso, 1982; Palero *et al.*, 2008
	TrA	WAfT		
S. subarctus Crosnier, 1970	TNA TrA	Lus St. H WAfT	41–240 m	Crosnier, 1970; Macpherson, 1991; Muñoz *et al.*, 2012; Genis-Armero *et al.*, 2017; de Matos-Pita *et al.*, 2018; Genis-Armero *et al.*, 2019
	TASf	Ben		

13 stations were sampled on board of RV *Hespérides*, which crossed the Atlantic from Salvador de Bahia, Brazil to Las Palmas de Gran Canaria, Canary Islands. Micronekton samples were collected with a mid-water trawl (mesopelagic net) with a mean mouth opening of 5 × 7 m and a cod-end mesh size of 4 mm. Samples were preserved in absolute ethanol and deposited in the invertebrate collections of the Universidad de Cádiz (UCA). Phyllosoma larvae were used for molecular analyses and sent to the Marine Invertebrate Laboratory of the Universitat de València (UV) for morphological study (Supplementary material Table S1).

DNA analyses

Total genomic DNA extraction was performed using the ChelexprotK method (Palero *et al.*, 2010). The standard universal primers for the 16S rDNA gene (Marco-Herrero *et al.*, 2013) were used for DNA barcoding, since this marker shows a higher amplification rate than COI primers in Achelata (Palero *et al.*, 2009a; Bracken-Grissom *et al.*, 2014). Amplifications were carried out with ~30 ng of genomic DNA in a reaction containing 1 U of Taq polymerase (Amersham Biosciences, Little Chalfont, UK), 1× buffer (Amersham), 0.2 mM of each primer, and 0.12 mM dNTPs.

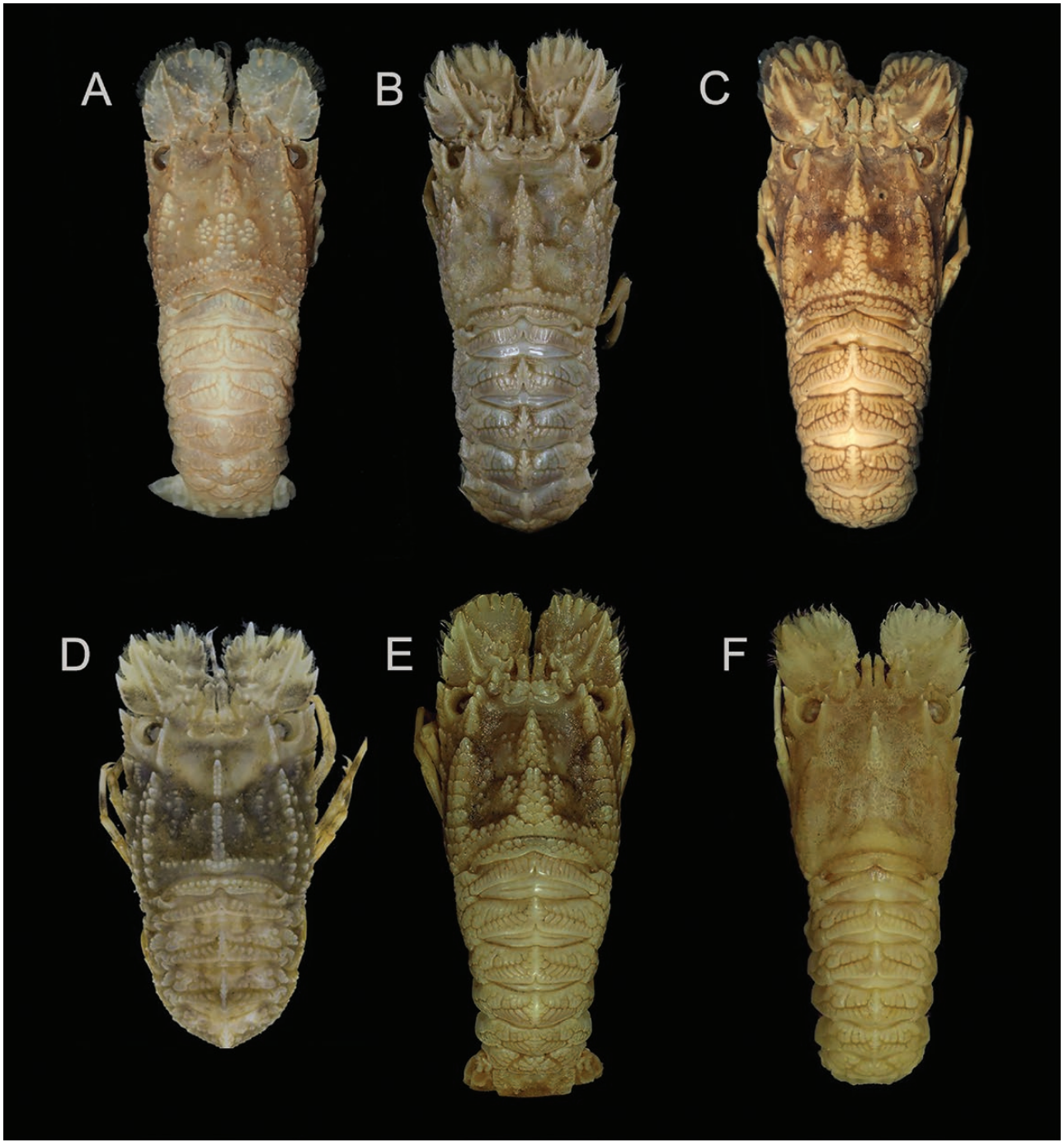


Figure 1. Species of *Scyllarus* from the Eastern Atlantic Ocean. *Scyllarus pygmaeus* (MNHN-IU-2014–20740) female (**A**), *Acantharctus posteli* (MNHN-IU-2013–14853) female (**B**), *Scyllarus arctus* (CCDE-IEOCD:963) female (**C**), *Scyllarus caparti* (CCDE-IEOCD:200) female (**D**), *Scyllarus paradoxus* (MNHN-IU-2013–14844) male (**E**), *Scyllarus subarctus* (MNHN-IU-2013–14842) female (**F**) This figure is available in color at *Journal of Crustacean Biology* online.

The polymerase chain reaction (PCR) thermal profile used was 94 °C for 4 min for initial denaturation, followed by 30 cycles of 94 °C for 30 s, 50 °C for 30 s, 72 °C for 30 s and a final extension at 72 °C for 4 min. Amplified PCR products were purified with QIAquick PCR Purification Kit (Qiagen, Hilden, Germany) before direct sequencing of the product. The sequences were obtained using the kit BigDye v3.1 (Applied Biosystems, Foster City, CA, USA) on an ABI Prism 3770. The chromatograms for each DNA sequence were checked using BioEdit ver. 7.2.5 (Hall, 1999). Sequence alignment was conducted using MUSCLE ver. 3.6 (Edgar, 2004) with default parameters. Estimates of p-distances (proportion of genetic differences) and the Kimura 2-Parameter (K2P) evolutionary divergence between groups were obtained from the aligned dataset using MEGA X (Kumar *et al.*, 2018). Before running molecular phylogenetic analyses, the most suitable nucleotide substitution model was selected according to the AICc criterion as implemented in MEGA X (Kumar *et al.*, 2018). The aligned sequences and selected evolutionary model were then used

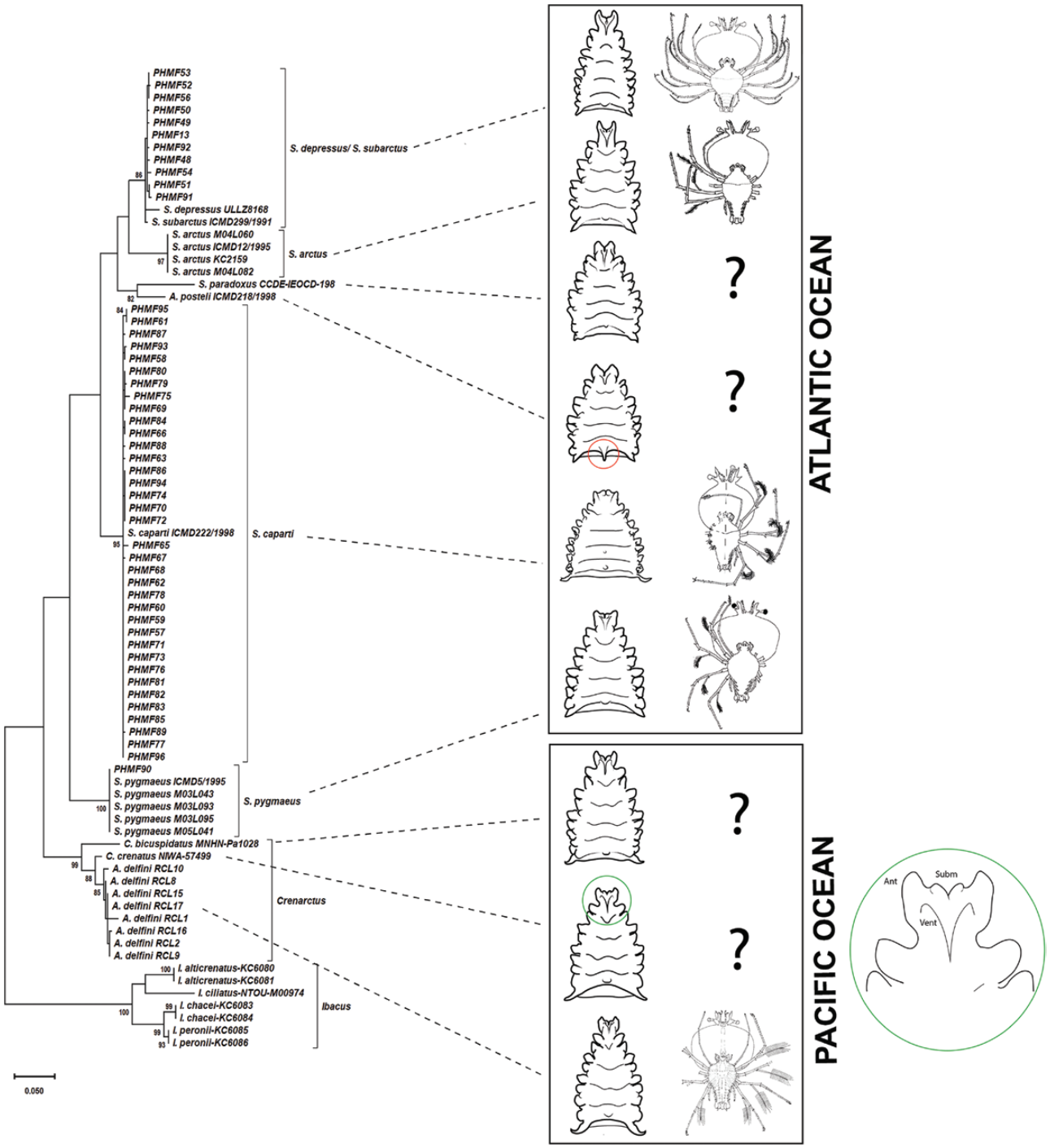


Figure 2. Maximum likelihood tree of African *Scyllarus* obtained from 16S rDNA data, including species of *Crenarctus* species and *Ibacus* taxa to root the tree. Only bootstrap support values above 70 are shown. Sternum morphology drawn from the same individuals presented in Figure 1 plus *Crenarctus bicuspidatus* (MNHN-IU-2010–5104), *Crenarctus crenatus* (AM P.15601), and *Acantharctus delfini* (USNM 1004677). Larval images adapted from Baez (1973), Genis-Armero *et al.* (2017) and Palero *et al.* (2008, 2011).

to estimate the maximum likelihood phylogenetic tree in MEGA X (Kumar *et al.*, 2018). Node support was evaluated with 1,000 bootstrap replicates.

Larval descriptions

Larval accounts are based on the malacostracan somite plan, described from anterior to posterior and proximal to distal (Clark *et al.*, 1998; Clark & Cuesta, 2015; Palero *et al.*, 2016). Larval stage definition followed Robertson (1968b) and Webber & Booth (2001). Morphological illustrations of the larvae were drawn using a *camera lucida* attached to a Leica high-performance stereo microscope (M165C; Leica Microsystems, Wetzlar, Germany) and the maxillae and mandibles were dissected before drawing. Digital drawings were obtained using a graphic tablet and Adobe Illustrator CC9 (http://www.adobe.com/Illustrator). The following measures were taken for each individual: total length (TL) from anterior margin of cephalic shield to posterior margin of telson; cephalic length (CL) from anterior to posterior margin of cephalic shield; cephalic width (CW) measured at the widest part of cephalic shield; pleon length (PDL) from anterior margin of pleon to posterior margin of telson. An identification key for West African *Scyllarus* phyllosoma larvae was completed using previous studies (Robertson, 1968b, 1969, 1971, 1979; Palero *et al.*, 2008, 2011) and our own observations including the cephalic shape in final stages, number of exopod annulations, exopod of third maxilliped, length of pereiopod 5 (P5) relative to abdomen length, spines on the ischium-merus, carpus, and propodus, and the degree of development of the dorsal thoracic spines.

RESULTS

Revision of the *Scyllarus paradoxus* and *Acantharctus posteli* type specimens originally studied by Forest (1963) allowed us to identify one *S. paradoxus* adult (Fig. 1) among the recent material reported as *Scyllarus* sp. by Muñoz *et al.* (2012). The revision of museum collections also allowed us to expand the latitudinal ranges for *S. paradoxus* and *S. caparti* and define their northernmost limits above 10° N and 27° N, respectively (Table S1). Morphological analyses revealed that the sharp

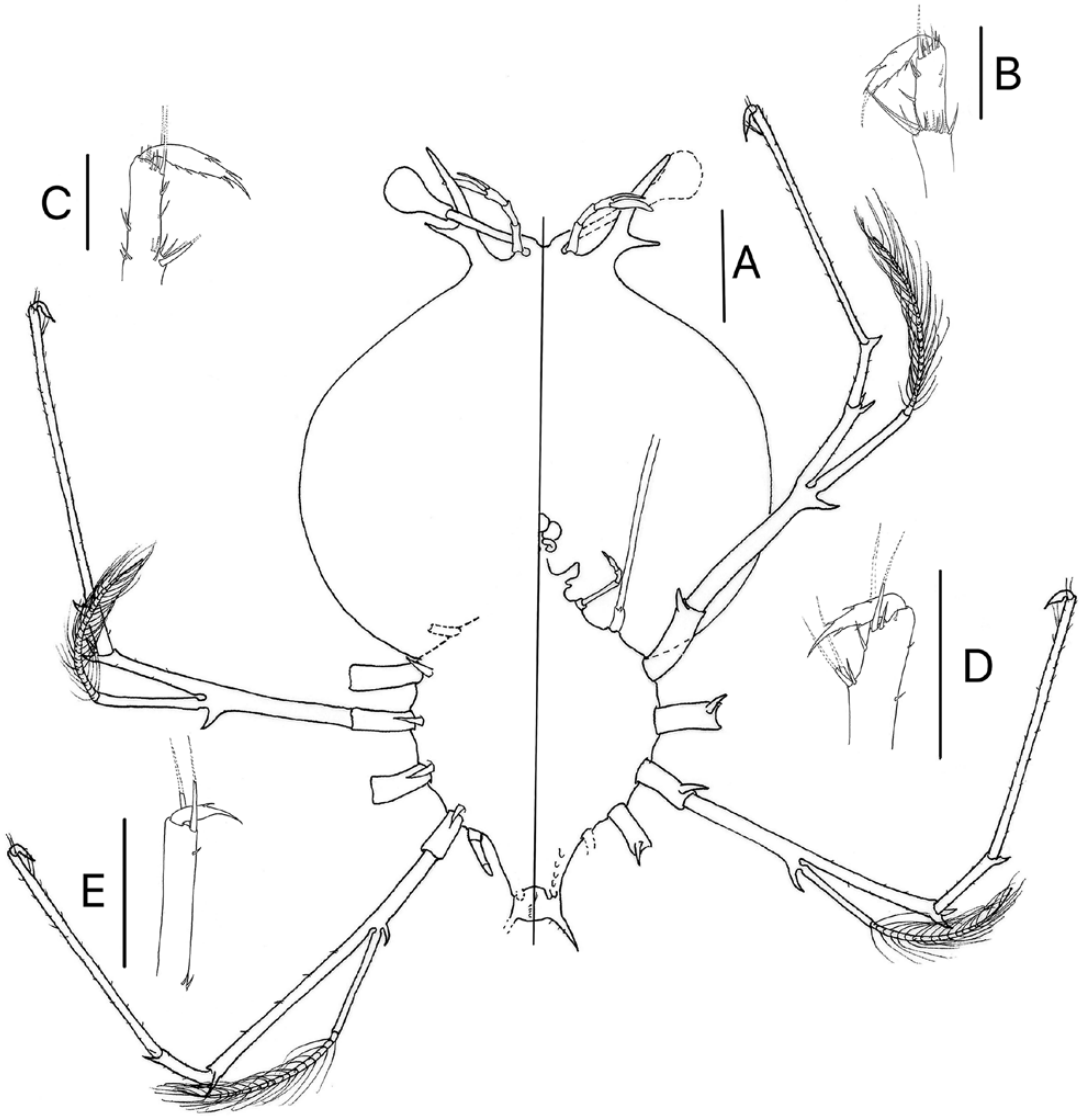


Figure 3. Phyllosoma stage VII of *Scyllarus caparti*. Ventral view (right) and dorsal view (left) (**A**). First pereiopod dactylus (**B**), second pereiopod dactylus (**C**), third pereiopod dactylus (**D**), fourth pereiopod dactylus (**E**). Scale bars: A = 2 mm; B–C = 500 μm; D–E = 1 mm.

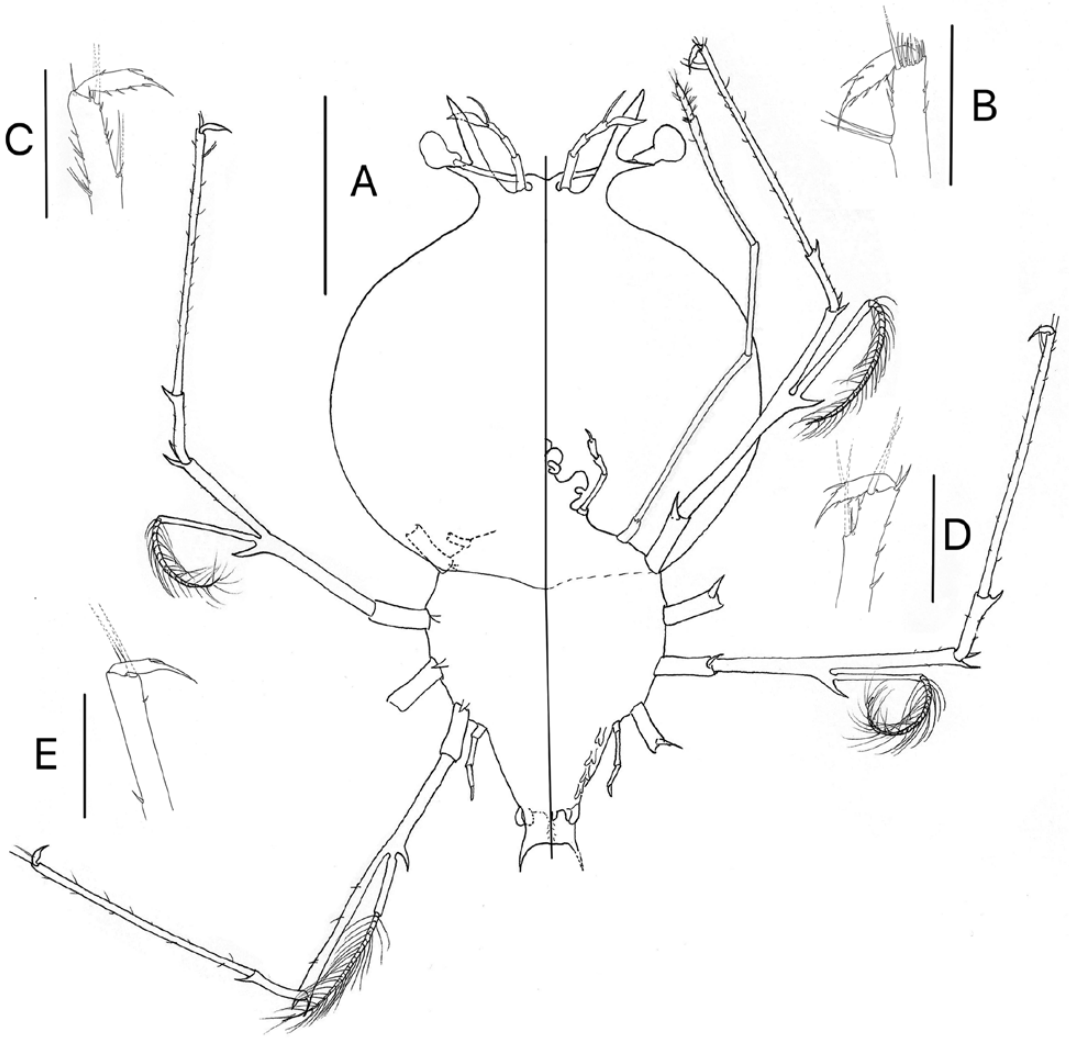


Figure 4. Phyllosoma stage IX of *Scyllarus caparti*. Ventral view (right) and dorsal view (left) (**A**). First pereiopod dactylus (**B**), second pereiopod dactylus (**C**), third pereiopod dactylus (**D**), fourth pereiopod dactylus (**E**). Scale bars: A = 5 mm; B–E = 1 mm.

median spine on the last thoracic sternite is not as well developed in the Pacific Ocean species of *Acantharctus* (i.e., *A. delfini*) as in the West African species (*A. posteli*). This trait varies depending on age and gender for Atlantic species (Forest, 1963; unpublished data). In contrast, the morphology of the anterior margin of the thoracic sternum was found to correlate with biogeography and phylogenetic relationships (Fig. 2). Pacific taxa such as *A. delfini*, *Crenarctus crenatus* (Whitelegge, 1900), and *C. bicuspidatus* (De Man, 1905) were closely related and forming a well-supported monophyletic clade. All these taxa share a characteristic crown-like (W-shaped) anterior margin, with two anterolateral teeth, two submedian tubercles, and two ventral teeth in the surface of the sternum. The anterior margin is U-shaped in *S. arctus* and *S. subarctus* and V-shaped in *S. paradoxus* and *A. posteli*, whereas *S. caparti* and *S. pygmaeus* have an intermediate form (Fig. 2).

New molecular data were obtained for the adult specimen of *S. paradoxus* from IEO-CD collections (CCDE-IEOCD:198) and 48 larvae from the MAF Campaign (Genbank accession numbers: MT378173–MT378211). Complete DNA barcoding reference sequences are now available for every known *Scyllarus* from West Africa. The global sequence alignment included a total of 526 bp and the DNA substitution model selected using the BIC method was the Hasegawa-Kishino-Yano (HKY) model with gamma parameter (G = 0.24). The phylogenetic tree inferred using maximum likelihood strongly supported a polyphyletic origin of *Acantharctus*, with samples of the Indo-West Pacific species (*A. delfini* and *Crenarctus spp.*) clustering with high bootstrap support (99%) and the Atlantic species *A. posteli* forming a well-supported clade (82%) with *S. paradoxus*. MAF phyllosomas from CVI were assigned to species-level by comparing them with adult reference sequences, so that 36 phyllosomas were identified as *S. caparti* (all sequences clustering with the adult reference and showing very low genetic distances, between 0.001 and 0.006), 11 as *S. subarctus*, and one as *S. pygmaeus* (Supplementary material Table S1, Fig. 2).

The morphology of three *S. caparti* phyllosoma stages, which were unknown to date, is described in full detail and compared with previously described *Scyllarus* larvae. The larvae could be assigned to stages VII, IX (subfinal), and X (final). Only morphological changes are included in descriptions of later stages, otherwise appendages remain unchanged. A summary of each studied specimen, with information on species identification, data, coordinates, depth, and development stage is shown in Supplementary material Table S1.

Scyllarus caparti Holthuis, 1952

Phyllosoma stage VII (PHMF 82)

Size: N = 1; TL = 12.7 mm, CL = 8.3 mm, CW = 9.0 mm; PDL = 2.3 mm.

Cephalic shield (Fig. 3A): Subcircular, slightly wider than long (CL/CW = 0.92).

Antennule (Figs. 3A, 6A): Peduncle 3-articled, last article carrying 2 flagella (primary, accessory): Primary flagellum with 10 rows of sensory setae (aesthetascs), but no annuli; accessory flagellum shorter than primary, with minute simple setae, without annuli.

Antenna (Figs. 3A, 6A): Biramous, not articulated, longer than antennule.

Mandibles (Fig. 6D): Coxa with abundant small teeth distributed over surface, molar process crowned with many denticles. Right mandible teeth curved towards molar process; left mandible teeth elongated, incisor process with 2 teeth. Possibly asymmetrical dentition, but left mandible damaged during dissection. Palp absent.

Maxillule (Fig. 6I): Coxal endite with 5 setae, 2 plumodenticulate, long, strong; basial endite with 8 setae, 3 terminal, strong, serrate. Endopod, exopod absent.

Maxilla (Fig. 7A): Uniramous. Coxa and basis undifferentiated. Basis with 3 small setae. Exopod (scaphognathite) rudimentary. Endopod absent.

First maxilliped (Fig. 7A): Undifferentiated lobe.

Second maxilliped (Figs. 3A, 7D): Uniramous (exopod absent) and 5-segmented. Coxa differentiated; basis and ischium-merus undifferentiated, with distal limit of basis marked by ventral seta; 3 distal segments endopodal with 1, 6, 5 setae, respectively.

Third maxilliped (Fig. 3A): Damaged, incomplete. Uniramous. Coxa with small distal ventral spine; basis and ischium-merus undifferentiated. Exopod absent.

Pereiopods (Figs. 3A–E, 7I): P1–4 biramous. Coxa with distal ventral spine; basis and ischium-merus undifferentiated, with limit of basis marked by spine, separation from carpus marked by 2 distal spines; carpus with distal spine, propodus with several small setae scattered over the surface, dactylus with 8, 7, 5, 1 setae in P1–P4, respectively. Exopod present, with 22–24, 20–22, (> 11)–20, 16–18 annulations respectively, each annulation carrying 2 long plumose setae. P5 uniramous. Coxa with large ventral distal spine; basis and ischium undifferentiated; endopod as one distal segment. Exopod absent.

Thorax (Fig. 3A): Sternites 4–7 with prominent distal spine. Sternite 8 without spine.

Pleon (Figs. 3A, 7I): Not articulated, with 4 pairs of minute dorsal setae; 4 pairs of rudimentary pleopods. Biramous uropods. Telson with 2 long processes, each with 2 setae on inner margin; 2 rows of 5–6 dorsal setae.

Phyllosoma stage IX (subfinal) (PHMF 60)

Size: N = 6, TL = 14.7–17.2 mm, CL = 9.1–10.7 mm, CW = 10.0–11.4 mm, PDL = 3.6–3.9 mm.

Cephalic shield (Fig. 4A): Subcircular (CL/CW = 0.91–0.94).

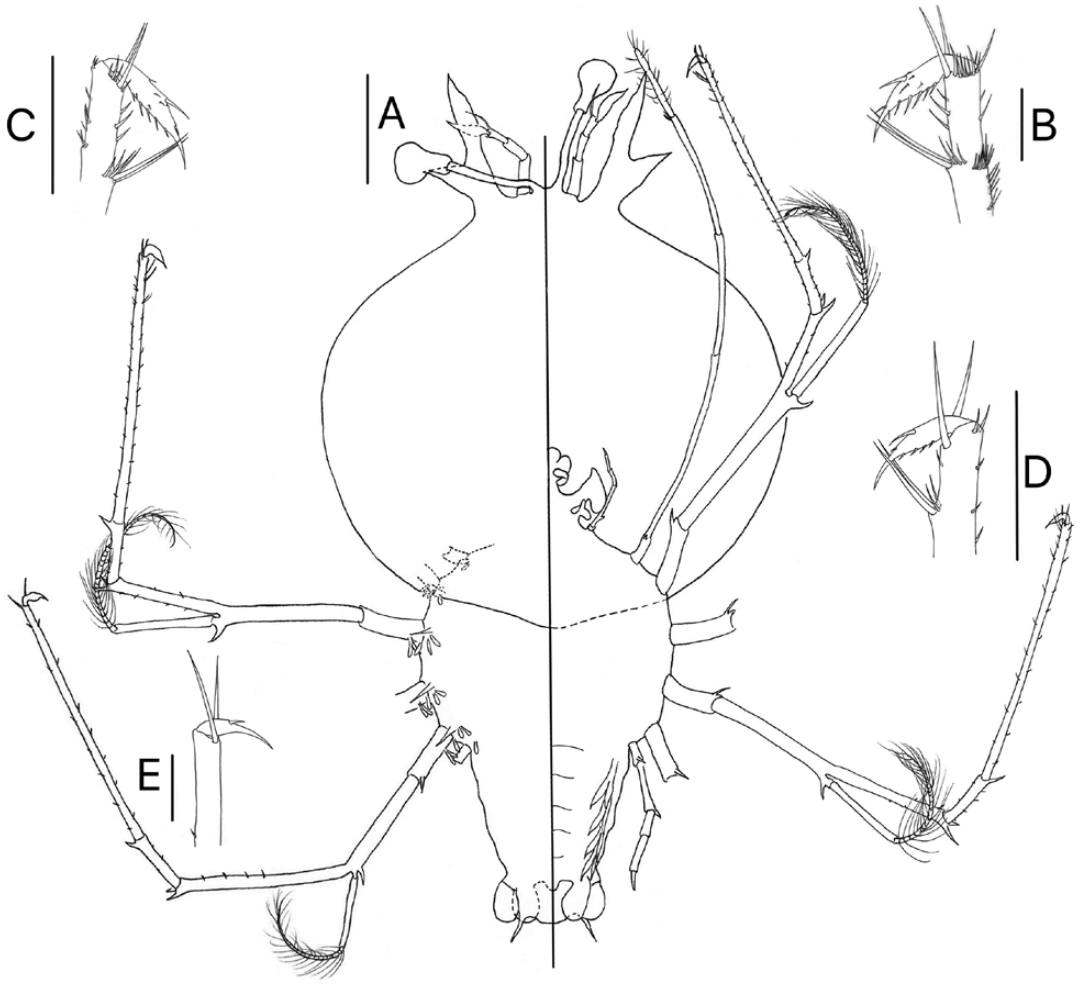


Figure 5. Phyllosoma stage X (final) of *Scyllarus caparti*. Ventral view (right) and dorsal view (left) (**A**). First pereiopod dactylus (**B**), second pereiopod dactylus (**C**), third pereiopod dactylus (**D**), fourth pereiopod dactylus (**E**). Scale bars: A = 3 mm; B = 500 μm; C–E = 1 mm.

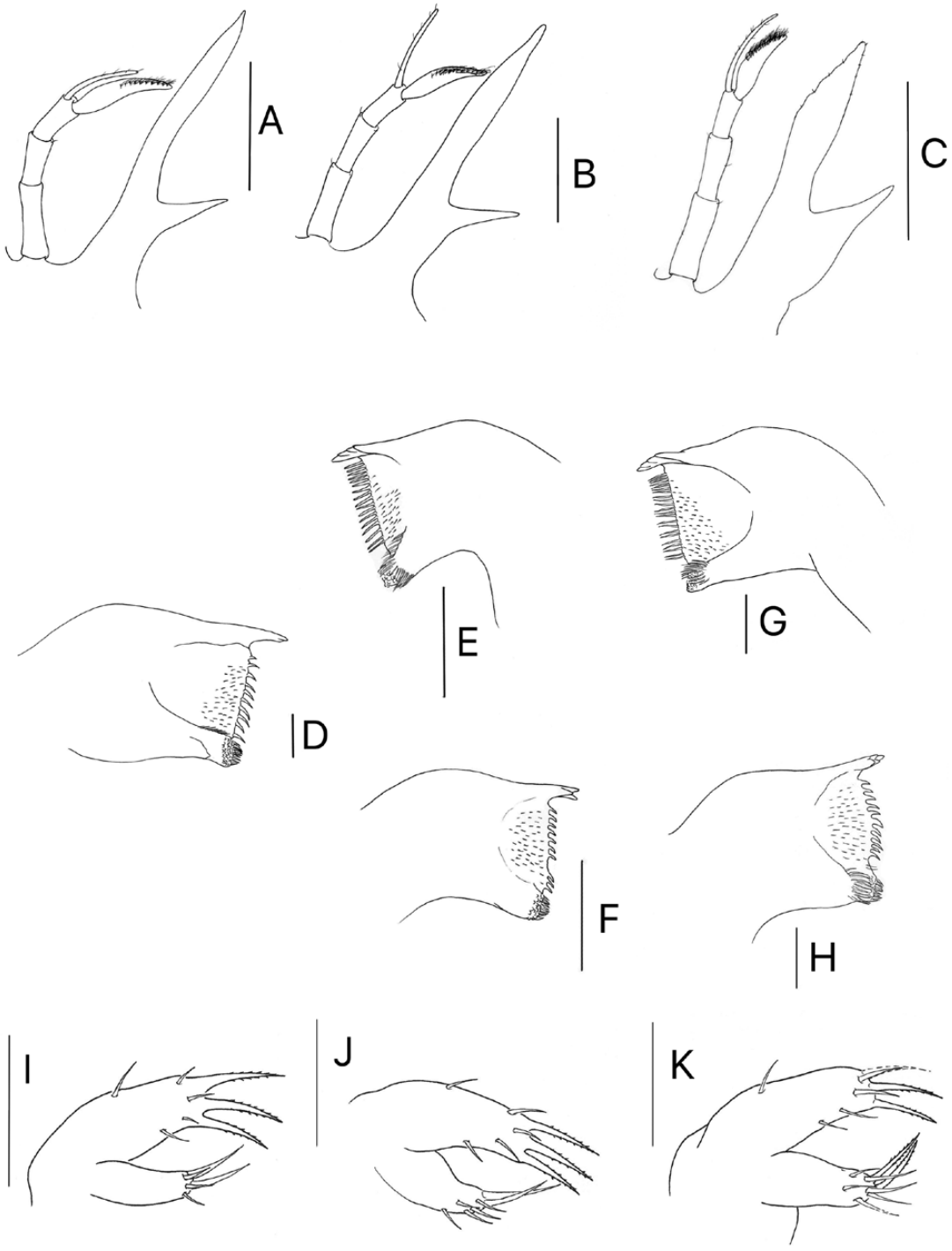


Figure 6. Features of *Scyllarus caparti* phyllosoma stages VII, IX, and X (from left to right). Antennule and antenna (**A**–**C**), right mandible (**E**, **G**, stages IX and X respectively), left mandible (**D, F**, **H**), maxillule (**I**–**K**). Scale bars: A and B = 1 mm; C = 2 mm; E and F = 500 µm; D, G and H = 200 µm; I–K = 500 µm.

Antennule (Figs. 4A, 6B): Primary flagellum with 12–14 rows of aesthetascs; accessory flagellum slightly longer than primary.

Antenna (Figs. 4A, 6B): Endopod medially broader than in Stage VII.

Mandibles (Fig. 6E, F): Coxa with asymmetrical dentition. Incisor process with 4 (right mandible) and 3 teeth (left mandible).

Maxillule (Fig. 6J): Coxal endite with 7 setae, 2 plumodenticulate, long, strong; basial endite with 8 setae, 3 serrate, long, strong.

Maxilla (Fig. 7B): Scaphognathite slightly more developed than in Stage VII, rectangular with small anterior, posterior expansions.

First maxilliped (Fig. 7B): Biramous. Endopod and exopod lobes minute.

Second maxilliped (Figs. 4A, 7E): Carpus, propodus, dactylus with 1, 8, 5 setae, respectively.

Third maxilliped (Figs. 4A, 7G): Carpus with < 5 distal setae; propodus with > 5 setae (2 distal serrated); dactyl with ~ 30 setae.

Pereiopods (Figs. 4A–E, 7J): P1–4 exopods with 18–19, 21–22, 23–24, 21–24 annulations, respectively. P5 basial, ischial segments undifferentiated, with distal spine.

Pleon (Figs. 4A, 7J): Pleopods biramous. Uropods further developed. Telson margin concave; 2 dorsal rows of 6–9 setae; 2 long processes each with seta.

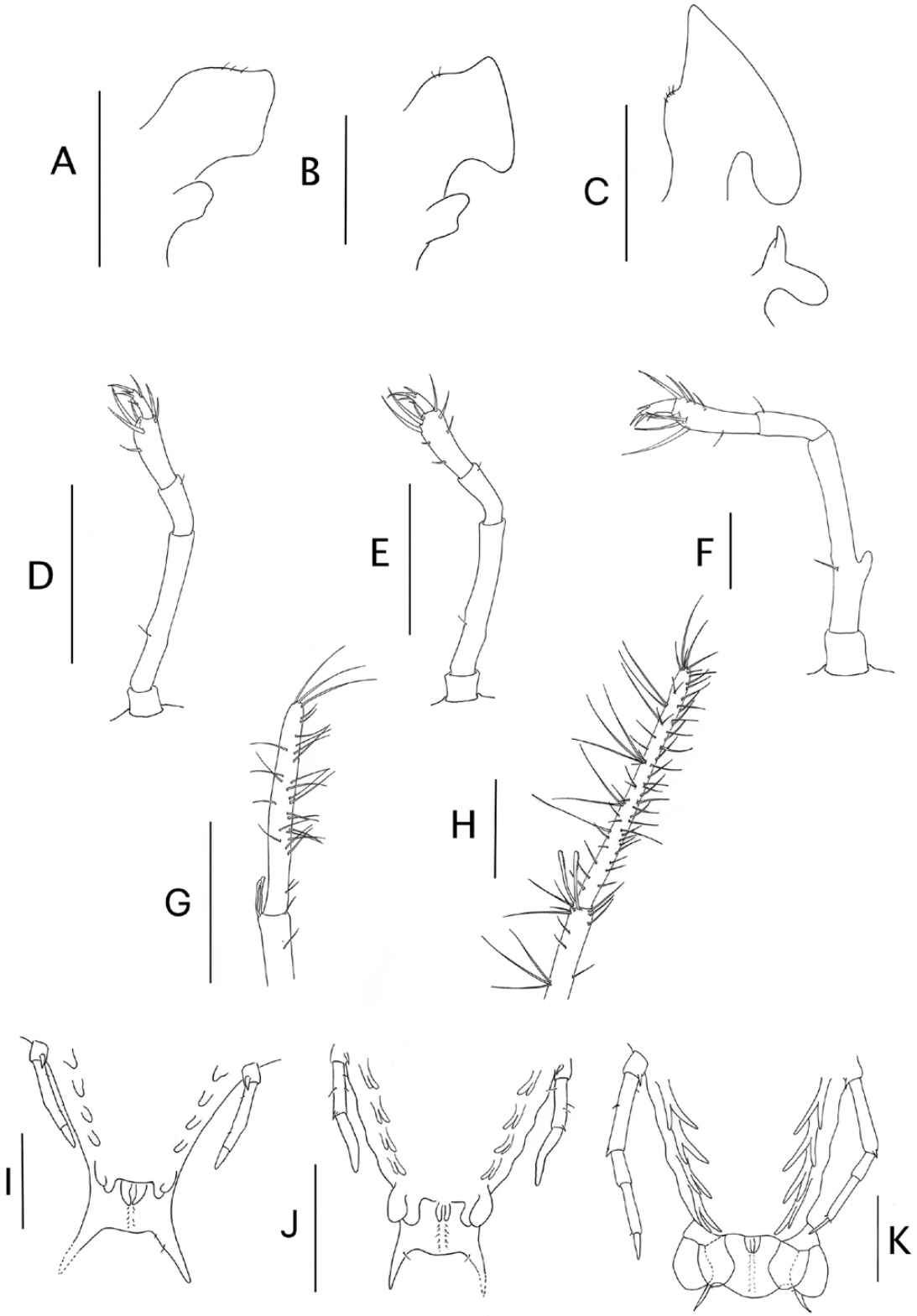


Figure 7. Features of *Scyllarus caparti* phyllosoma stages VII, IX, and X (from left to right). Maxilla and first maxilliped (drawn separately in final stage) (**A**–**C**), second maxilliped (**D**–**F**), third maxilliped dactylus (**G**, **H**, stages IX and X respectively). Pleon and fifth pereiopod (setae of pleon in dorsal view) (**I**–**K**). Scale bars: A–E, G, I = 1 mm; F and H = 500 μm; J and K = 2 mm.

Phyllosoma stage X (final) (PHMF 57, PHMF 65, PHMF 77, PHMF 87)

Size: N = 29, TL = 19.7–22.8 mm, CL = 11.3–13.2 mm, CW = 12.7–14.5 mm, PDL = 5.6–7.1 mm.

Cephalic shield (Fig. 5A): Subcircular (CL/CW = 0.89–0.93).

Antennule (Figs. 5A, 6C): Primary flagellum with 14–16 rows of aesthetascs.

Antenna (Figs. 5A, 6C): Endopod broader than in Stage IX; 5 distal lobes on inner margin; small setae on both margins.

Mandibles (Fig. 6G, H): Coxa with 4 (right mandible) and 5 teeth (left mandible).

Maxillule (Fig. 6K): Coxal, basial endites with 8 setae each.

Maxilla (Fig. 7C): Coxa, basis undifferentiated, with 3–6 distal setae. Scaphognathite (exopod) more developed, considerably more expanded than in Stage IX.

First maxilliped (Fig. 7C): Segments undifferentiated, Biramous, endopod (inner lobe) cone-shaped, exopod (outer lobe) flattened, round.

Second maxilliped (Figs. 5A, 7F): Biramous. Carpus, propodus, dactylus with 1, 7–10, 4 setae, respectively. Exopod bud present.

Third maxilliped (Figs. 5A, 7H): Carpus with < 5 distal setae; propodus with ~15 setae (2 distally serrated); dactylus with ~63 setae.

Pereiopods (Figs. 5A-E, 7K): P1–4 exopods with 24–25, 24–23, 24–23, 21–20 annulations, respectively. P5 endopod with 3 distal segments.

Gills (Fig. 5A): Gill buds present. Third maxilliped with 2 pleurobranchs; P1 with 1 pleurobranch, 1 arthrobranch, 2 podobranchs; P2–4 with 2 pleurobranchs, 1 arthrobranch, 2 podobranchs; P5 with 1 pleurobranch.

Pleon (Figs. 5A, 7K): Incomplete segmentation. Pleopods, uropods more developed than in Stage IX. Telson margin rounded; 2 dorsal rows of 10–11 setae; 2 long processes with single seta each.

DISCUSSION

The molecular analysis of the recent material analyzed provides reference DNA sequences for all known West African species of *Scyllarus*. The new molecular and morphological evidence confirms the close affinity of *S. paradoxus* and *A. posteli* and the polyphyletic origin of *Acantharctus* with Atlantic (*A. posteli*) and Pacific (*A. delfini*) species belonging to different clades. The molecular results agree with biogeography and data on adult morphology, particularly the structure of the anterior part of the thoracic sternum. *Acantharctus delfini* is closer to other Pacific Ocean taxa (*Crenatus crenatus* and *C. bicuspidatus*) than to *A. posteli* and should be assigned to *Crenarctus* Holthuis, 2002. Similarly, the morphological affinity of *A. posteli* and *S. paradoxus*, their similar ecology, and their overlapping distribution explains why both species were confused for almost a century; and provides further support for grouping these two taxa together. The presence of a strong spine on the last sternite, originally used to define *Acantharctus*, is known to be variable throughout ontogeny and gender (Forest, 1963; unpublished data). The current definition of *Acantharctus* cannot be considered valid and the basionym *Syllarus posteli* Forest, 1963 should be re-established. A complete and thorough revision of adult specimens of *A. ornatus* and different species of *Crenarctus* is needed before an updated diagnosis of *Acantharctus* can be established.

Shallow-water Scyllarinae have a comparatively short larval development among slipper lobsters, and their phyllosomas are usually found near the coast (Sekiguchi & Inoue, 2002; Booth *et al.*, 2005; Inoue & Sekiguchi, 2005; Phillips *et al.*, 2006). No Scyllarinae phyllosomas were found along oceanic waters during the MAF cruise, but they appeared in stations near CVI. Most of these phyllosomas can now be attributed to *S. caparti*, a species that was absent from previous accounts (Ribeiro, 1973). In fact, morphological comparisons suggest that larvae A–D of Ribeiro (1973) correspond to the subfinal and final phyllosoma stages of *S. pygmaeus* (phyllosomas A and B) and *S. subarctus* (phyllosomas C and D). Both taxa were also present in the MAF material studied here, and their morphology has been reported elsewhere (Palero *et al.*, 2008; Genis-Armero *et al.*, 2017). The geographical origin of our *S. caparti* larvae remains unclear because no adults have been cited in the CVI. They could have been dragged by upwelling filaments coming from the African coast, where *S. caparti* is known to occur (Landeira *et al.*, 2010, 2012). Alternatively, self-sustained

KEY TO THE *SCYLLARUS* PHYLLOSOMAS KNOWN TO DATE FROM EASTERN (EA) AND WESTERN ATLANTIC (WA)

S. americanus Smith, 1869 (Robertson 1968a, b) – WA
S. arctus Linnaeus, 1758 (Palero *et al.*, 2011) – EA
S. caparti Holthuis 1952 (present study) – EA
S. chacei Holthuis, 1960 (Robertson 1968a) – WA
S. depressus Smith, 1881 (Robertson, 1971) – WA
S. planorbis Holthuis, 1969 (Robertson, 1979) – WA
S. pygmaeus Bate, 1888 (Palero *et al.*, 2008) – EA
S. subarctus Crosnier, 1970 (Genis-Armero *et al.*, 2017) – EA

1. Stage I: P4 bud present. Stage II: P5 bud present. Stage IV: P5 reaching uropod end. Final stage: exopod annulation formula (P1:P2:P3:P4) equal or lower than 17:18:17:13; dorsal thoracic coxal spines absent; posterolateral margin of cephalic shield not exceeding P1 coxa. Western Atlantic (except *S. depressus*) 2
- Stage I: P4 bud absent. Stage II: P5 bud absent. Stage IV: P5 not reaching uropod end. Final stage: exopod annulation formula (P1:P2:P3:P4) equal or higher to 20:19:19:16; dorsal thoracic coxal spines present; posterolateral margin of cephalic shield exceeding P1 coxa. Eastern Atlantic 4
2. Stage I: exopod annulation formula (P1:P2) 7:8. Maxilla 2 with 3 apical setae in early stages. Final stage: oval cephalon (*CL/CW* > 1) ..... *S. americanus*
- Stage I: exopod annulation formula (P1:P2) equal or lower to 7:7. Maxilla 2 often with 4 apical setae in early stages. Final stage: trapezoidal or pentagonal cephalon (*CL/CW* ≤ 1) 3
3. Stage I: exopod annulation formula (P1:P2) equal or higher to 6:6. Final stage: eyestalk 1,1–1,4 times length of antennule.... *S. chacei*
- Stage I: exopod annulation formula (P1:P2) equal or higher 5:6. Final stage: eyestalk 1,4–1,6 times length of antennule... *S. planorbis*
4. Final stage: *TL/CW* = 1,50; circular/pentagonal cephalon. TL ≤ 22,8 mm 5
- Final stage: *TL/CW* ≤ 1,40; rectangular cephalon. TL ≥ 24 mm 6
5. Final stage: dorsal thoracic coxal spines poorly developed, equal in size. Pentagonal cephalic shield. Mxp3 exopod bud present. P5 not reaching fourth pleopod, ischium-merus with 2 distal spines ..... *S. arctus*
- Final stage: dorsal thoracic coxal spines unequal, more developed in P3-P4. Circular cephalic shield. Mxp3 exopod absent. P5 reaching fourth pleopod, ischium-merus with distal spine ..... *S. caparti*
6. Final stage: *CL/CW* = 0,80; P5 with 2 distal spines on ischium-merus and carpus, propodus with 2 subdistal setae ..... *S. subarctus/S. depressus*
- Final stage: *CL/CW* = 0,85-0,92; P5 ischium-merus and carpus with 1-0 distal spines, propodus without setae ..... S. *pygmaeus*

adult populations from CVI could have been generated larvae locally that were retained by eddies (Chiswell & Booth, 1999; Rodríguez *et al.*, 2001; Sangrà *et al.*, 2009). The lack of adult reports in the area may be caused by the low economic interest of these small lobsters.

The new evidence presented here allows for the re-evaluation of the four *Scyllarus* phyllosoma types (A–D) described by Maigret (1975, 1978) from Banc d'Arguin, Mauritania. Assuming that it is the most frequent *Scyllarus* species in Mauritanian waters, Maigret (1978) suggested the most abundant phyllosoma in his collection (type C) to correspond to *S. subarctus* (referred by him as *Scyllarus* sp. aff. *arctus*). Recent descriptions of *S. subarctus* phyllosomas by Genis-Armero *et al.* (2017) and our results suggest that the type C phyllosoma of Maigret (1978) belongs in fact to *S. caparti*. The degree of development of the dorsal coxal spines, together with a uniquely round cephalic shield, distinguish *S. caparti* phyllosomas. The relevance of the degree of development of the dorsal coxal spines was already highlighted by Robertson (1979) and A. Crosnier (unpublished field notebooks). The type D larva of Maigret (1978) and those described by Ribeiro (1973) correspond to *S. pygmaeus* and *S. subarctus*. Only three *Scyllarus* species (*S. posteli*, *S. paradoxus* and *S. caparti*) are found in shallow-waters from the Gulf of Guinea region and can be considered as truly intertropical (Forest, 1963; Anadón, 1981; Muñoz *et al.*, 2012), whereas other eastern Atlantic *Scyllarus* are commonly found below a depth of 100 m (Muñoz *et al.*, 2012; de Matos-Pita *et al.*, 2018). The phyllosoma types A, B (Maigret, 1978), which seem to represent a pair of sister taxa from shallow waters, could therefore belong to *S. posteli* or *S. paradoxus*, although specific assignment for these larvae remains to be confirmed.

We show that resolving phyllosomas identities using DNA barcoding methods can open access to historical collections including thousands of larvae. Key studies on the geographic and bathymetric distribution of both larval and adult stages of *Scyllarus* lobsters are necessary to better understand their larval ecology, biogeography, and evolution. Holthuis (2002) classification of Scyllarinae genera has already been questioned using moleculars tools (Yang *et al.*, 2012; Chan *et al.*, 2013), and new morphological evidence suggest that an extensive update of the subfamily is required. Clarification of previous identifications of phyllosomas will certainly provide new and valuable morphological evidence to resolve slipper lobster systematics.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Crustacean Biology* online.

Table S1. Specimens examined in the study.

ACKNOWLEDGMENTS

This article is dedicated to Dr. Pere Abelló (ICM) and Prof. Jacques Maigret (MNHN) who kindly provided the first specimens and bibliography that initiated our study of Scyllarinae phyllosomas. We thank all participants on board of the RV *Hespérides* during the MAF cruise for collecting larval specimens, Carlos Sánchez (ICMAN) for sequencing the larval specimens, and Eva García and Isabel Muñoz (IEO) for providing us adult specimens from IEO Collections. Thanks are due to Laure Corbari (MNHN), Paula Martin-Lefevre (MNHN), Jørgen Olesen (Zoologisk Museum, Københavns Universitet, Copenhagen), and Dr. Yves Samyn (RBINS, Brussels) for sharing details of museum material, and Dr. Enrique Macpherson (Centre d'Estudis Avançats de Blanes, Spain), and Dr. Alain Crosnier (MNHN) for encouraging the completion of this work. This research was funded by project MAF (CTM2012-39587-C04-02) of the Spanish Government and EU-Synthesys grants (DK-TAF-4873, "Morphological study of Achelata lobsters and phyllosoma larvae from Danish collections" and FR-TAF-5980 "Description of phyllosoma stages of West-African lobster species). FP acknowledges project "CIDEGENT/2019/028 - BIOdiversity PAtterns of Crustacea from Karstic Systems (BIOPACKS): molecular, morphological, and functional adaptations" funded by the Conselleria d'Innovació, Universitats, Ciència i Societat Digital. Thanks are also due to the anonymous reviewers for their helpful comments that certainly improved the original version of the manuscript.

REFERENCES

Anadón, R. 1981. Crustáceos Decápodos (excl. Paguridea) recogidos durante la campaña "Atlor VII" en las costas noroccidentales de África (Noviembre 1975). *Resultados Expediciones Científicas B/O Cornide de Saavedra*, **9**: 151–159.

Baez, P. 1973. Larvas phyllosoma del Pacífico Oriental (Crustacea, Macrura, Scyllaridae). *Revista de Biologia Marina y Oceanografia*, **15**: 115–130.

Bate, C.S. 1888. Report on the Crustacea Macrura collected by H. M. S. Challenger during the years 1873–76. *Report of the scientific results of the Voyage of H. M. S. Challenger during the years 1873–76, Zoology*, **24**(52): i–xc, 1–942, pls. 1–150.

Booth, J.D., Webber, W.R., Sekiguchi, H. & Coutures, E. 2005. Diverse larval recruitment strategies within the Scyllaridae. *New Zealand Journal of Marine and Freshwater Research*, **39**: 581–592.

Bouvier, E.L. 1909. *Arctus delfini* sp. nov. *Revista Chilena de Historia Natural*, **13**: 213–215.

Bouvier, E.L. 1913. Sur les genres *Pseudibacus* et Nisto, et le stade natant des Crustacés décapodes macroures de la famille des Scyllarides. *Comptes rendus hebdomadaires des Seances de l'Académie des Sciences*, **156**: 1643–1648.

Bouvier, E.L. 1925. Les Macroures Marcheurs. *Memoirs of the Museum of Comparative Zoology at Harvard College*, **47**: 401–472, pls. 1–11.

Bracken-Grissom, H.D., Ahyong, S.T., Wilkinson, R.D., Feldmann, R.M., Schweitzer, C.E., Breinholt, J.W., Bendall, M., Palero, F., Chan, T.Y., Felder, D.L., Robles, R., Chu, K.H., Tsang, L.M., Kim, D., Martin, J.W. & Crandall, K. 2014. The emergence of lobsters: phylogenetic relationships, morphological evolution and divergence time comparisons of an ancient group (Decapoda: Achelata, Astacidea, Glypheidea, Polychelida). *Systematic Biology*, **63**: 457–479.

Chan, T.Y. 2019. Updated checklist of the World's marine lobsters. In: *Lobsters: Biology, fisheries and aquaculture* (E.V. Radhakrishnan, B.F. Phillips & G. Achamveetil, eds.), pp. 35–64. Springer, Singapore.

Chan, T.Y., Ahyong, S.T. & Yang, C.H. 2013. Priority of the slipper lobster genus *Crenarctus* Holthuis, 2002, over *Antipodarctus* Holthuis, 2002 (Crustacea, Decapoda, Scyllaridae). *Zootaxa*, **3701**: 471–472.

Chiswell, S.M. & Booth, J.D. 1999. Rock lobster *Jasus edwardsii* larval retention by the Wairarapa Eddy off New Zealand. *Marine Ecology Progress Series*, **183**: 227–240.

Clark, P.F., Calazans, D.K. & Pohle, G.W. 1998. Accuracy and standardization of brachyuran larval descriptions. *Invertebrate Reproduction and Development*, **33**: 127–144.

Clark, P.F. & Cuesta, J.A. 2015. Larval systematics of Brachyura. In: *The Crustacea. Treatise on Zoology – Anatomy, Taxonomy, Biology.. Decapoda: Brachyura. Part II* (P. Castro, P.J.F. Davie, D. Guinot, F.R. Schram & J.C.von Vaupel Klein, eds.), **Vol. 9C–II** pp. 981–1048. Brill, Leyden, The Netherlands.

Crosnier, A. 1970. Crustacés décapodes Brachyoures et Macroures recueillis par l'Undaunted au sud de l'Angola. Description de *Scyllarus subarc*tus sp. nov. *Bulletin du Muséum national d'Histoire naturelle*, **41**: 1214–1227.

Crosnier, A. 1972. Naupliosoma, Phyllosomes et Pseudibacus de *Scyllarides herklotsii* (Herklots) (Crustacea, Decapoda, Scylllaridae) récoltés par l'Ombango dans le sud du Golfe de Guinneé. *Cahiers ORSTOM, série Océanographie*, **10**: 139–149.

De Man, J.G. 1905. Diagnoses of new species of macrurous decapod Crustacea from the "Siboga-Expedition". *Nederlandsch Tijdschrift voor de Dierkunde*, **9**: 587–614.

de Matos-Pita, S.S., Ramil, F. & Ramos, A. 2018. Marine lobsters and lithodids (Crustacea: Decapoda) from Mauritanian deep-waters (NW Africa). *Regional Studies in Marine Science*, **23**: 32–38.

Edgar, R.C. 2004. MUSCLE: multiple sequence alignment with high accuracy and high throuhput. *Nucleic Acids Research*, **32**: 1792–1797.

Fabricius, J.C. 1775. *Systema Entomologiae, sistens Insectorum Classes, Ordines, Genera, Species, adjectis Synonymis, Locis, Descriptionibus, Observationibus.* Officina Libraria Kortii, Flensburgi & Lipsiae.

Forest, J. 1963. Sur deux *Scyllarus* de l'Atlantique tropical africain: *S. paradoxus* Miers et *S. posteli* sp. nov. Remarques sur les *Scyllarus* de l'Atlantique oriental. *Bulletin de l'Institut océanographique de Monaco*, **60**: 1–20.

Forest, J. & Holthuis, L.B. 1960. The occurrence of *Scyllarus pygmaeus* (Bate) in the Mediterranean. *Crustaceana*, **1**: 156–163.

Fransen, C.H.J.M. 1991. *Preliminary report on Crustacea collected in the eastern part of the North Atlantic during the CANCAP and MAURITANIA expeditions of the former Rijksmuseum Van Natuurlijke Historie, Leiden.* Nationaal Natuurhistorisch Museum, Leiden, The Netherlands. Froglia, C. 1974. Preliminary report of the Crustacea Decapoda of Adriatic deep waters. *Thalassia Jugoslavica*, **8**: 75–79.

Froglia, C.J. 1979. Segnalazione di alcuni corstacei decapodi nuovi per la fauna adriatica. *Quaderni del Loboratorio di Tecnologia della Pesca*, **2**: 191–196.

García-Raso, J.E. 1982. Familia Scyllaridae Latreille 1825 (Crustácea, Decapada) en la región sur-mediterránea española. *Boletin de la Associación Española de Entomología*, **6**: 73–78.

Gracia Socias, L.I. & Massuti Jaume, C.1987. Inventari bibliogràfic dels crustacis decàpodes de les balears (Crustacea Decapoda). *Bolletí de la Societat d'Història Natural de les Illes Balears*, **31**: 67–92.

Genis-Armero, R., Guerao, G., Abelló, P., Ignacio González-Gordillo, J., Cuesta, J.A., Corbari, L., Clark, P.F., Capaccioni-Azzati, R. & Palero, F. 2017. Possible amphi-atlantic dispersal of *Scyllarus* lobsters (Crustacea: Scyllaridae): Molecular and larval evidence. *Zootaxa*, **4306**: 325–338.

Genis-Armero, R., Landeira, J., Capaccioni-Azzati, R. & Palero, F. 2019. Updated distribution and first description of *Scyllarus subarctus* (Crustacea: Scyllaridae) decapodid stage. *Journal of the Marine Biological Association of the United Kingdom*, **99**: 1181–1188.

Gill, T. 1898. The crustacean genus *Scyllarides*. *Science*, **7**(160): 98–99.

González-Gordillo, J.I. & Rodríguez, A. 2000. First larval stage of *Scyllarus posteli* Forest, 1963 and *Processa macrodactyla* Holthuis, 1952 hatched in the laboratory (Crustacea, Decapoda). *Ophelia*, **53**: 91–99.

Gurney, R. 1936. Larvae of decapod Crustacea: part I- Stenopidea. Part II- Amphionidae. Part III-Phyllosoma. *Discovery Reports*, **12**: 377–440.

Hall, T. 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series*, **41**: 95–98.

Holthuis, L.B. 1952. Crustacés Décapodes Macrures. *Expédition Océanographique Belge dans les Eaux Côtières Africaines de l'Atlantique Sud (1948–1949). Résultats Scientifiques*, **3**: 1–88.

Holthuis, L.B. 1960. Preliminary descriptions of one new genus, twelve new species and three new subspecies of scyllarid lobsters (Crustacea Decapoda Macrura). *Proceedings of the Biological Society of Washington*, **73**: 147–154.

Holthuis, L.B. 1969. A new species of shovel-nose lobster, *Scyllarus planorbis*, from the Southwestern Caribean and Northern South America. *Bulletin of Marine Science*, **19**: 149–158.

Holthuis, L.B. 1991. FAO species catalogue. Vol. 13. Marine lobsters of the world. An annotated and illustrated catalogue of species of interest to fisheries known to date. *FAO Fisheries Synopsis No. 125*. FAO, Rome.

Holthuis, L.B. 2002. The Indo-Pacific scyllarine lobsters (Crustacea, Decapoda, Scyllaridae). *Zoosystema*, **24**: 499–683.

Inoue, N. & Sekiguchi, H. 2005. Distribution of scyllarid phyllosoma larvae (Crustacea: Decapoda: Scyllaridae) in the Kuroshio Subgyre. *Journal of Oceanography*, **61**: 389–398.

Kumar, S., Stecher, G., Li, M., Knyaz, C. & Tamura, K. 2018. MEGA X: molecular Evolutionary Genetics Analysis across computing platforms. *Molecular Biology and Evolution*, **35**: 1547–1549.

Landeira, J.M., Lozano-Soldevilla, F. & Barton, E.D. 2012. Mesoscale advection of *Upogebia pusilla* larvae through an upwelling filament in the Canaries Coastal Transition Zone (CTZ). *Helgoland Marine Research*, **66**: 537–544.

Landeira, J.M., Lozano-Soldevilla, F., Hernández-León, S. & Barton, E.D. 2010. Spatial variability of planktonic invertebrate larvae in the Canary Islands area. *Journal of the Marine Biological Association of the United Kingdom*, **90**: 1217–1225.

Latreille, P.A. 1825. *Familles naturelles du règne animal: exposées succinctement et dans un ordre analytique, avec l'indication de leurs genres*. J.B. Baillière, France.

Lewinsohn, C. 1974. The occurrence of *Scyllarus pygmaeus* (Bate) in the Eastern Mediterranean (Decapoda, Scyllaridae). *Crustaceana*, **27**: 43–46.

Linnaeus, C. 1758. *Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis.* **Vol. 1**, Edn. 10. Reformata. Laurentii Salvii, Holmiae [= Stockholm].

Macpherson, E. 1991. Biogeography & community structure of the decapod crustacean fauna off Namibia (Southeast Atlantic). *Journal of Crustacean Biology*, **11**: 401–415.

Maigret, J. 1975. Larves phyllosomes capturées au large du Banc d'Arguin. *Bulletin de l'Institut fondamental de l'Afrique*, **37**: 784–794.

Maigret, J. 1978. Contribution à l'étude des langoustes de la côte occidentale d'Afrique (Crustacés, Décapodes, Palinuridae). *Bulletin de l'Institut fondamental de l'Afrique*, **40**: 36–80.

Marco-Herrero, E., Torres, A.P., Cuesta, J.A., Guerao, G., Palero, F. & Abelló, P. 2013. The systematic position of *Ergasticus* (Decapoda, Brachyura) and allied genera, a molecular and morphological approach. *Zoologica Scripta*, **42**: 427–439.

Miers, E.J. 1881. On a collection of Crustacea made by Baron Hermann Maltzan at Goree Island, Senegambia. *Journal of Natural History*, **8**: 364–377.

Muñoz, I., García-Isarch, E., Sobrino, I., Burgos, C., Funny, R. & González-Porto, M. 2012. Distribution, abundance and assemblages of decapod crustaceans in waters off Guinea-Bissau (north-west Africa). *Journal of the Marine Biological Association of the United Kingdom*, **92**: 475–494.

Palero, F. & Abelló, P. 2007. The first phyllosoma stage of *Palinurus mauritanicus* (Crustacea: Decapoda: Palinuridae). *Zootaxa*, **1508**: 49–59.

Palero, F., Clark, P.F. & Guerao, G. 2014. Infraorden Achelata. In: *Atlas of crustacean larvae* (J. Martin, J. Olesen & J.T. Hoeg, eds.), pp. 272–278. Johns Hopkins University Press, Baltimore, MD, USA.

Palero, F., Crandall, K.A., Abelló, P., Macpherson, E. & Pascual, M. 2009a. Phylogenetic relationships between spiny, slipper and coral lobsters (Crustacea, Decapoda, Achelata). *Molecular Phylogenetics and Evolution*, **50**: 152–162.

Palero, F., Genis-Armero, R., Hall, M. & Clark, P.F. 2016. DNA barcoding the phyllosoma of *Scyllarides squammosus* (H. Milne Edwards, 1837) (Decapoda: Achelata: Scyllaridae). *Zootaxa*, **4139**: 481–498.

Palero, F., Guerao, G. & Abelló, P. 2008. Morphology of the final stage phyllosoma larva of *Scyllarus pygmaeus* (Crustacea: Decapoda: Scyllaridae), identified by DNA analysis. *Journal of Plankton Research*, **30**: 483–488.

Palero, F., Guerao, G., Clark, P.F. & Abelló, P. 2009b. The true identities of the slipper lobsters *Nisto laevis* and *Nisto asper* (Crustacea: Decapoda: Scyllaridae) verified by DNA analysis. *Invertebrate Systematics*, **23**: 77–85.

Palero, F., Guerao, G., Clark, P.F. & Abelló, P. 2010. Final-stage phyllosoma of *Palinustus* A. Mile Edwards, 1880 (Decapoda: Achelata: Palinuridae) — The first complete description. *Zootaxa*, **2403**: 42–58.

Palero, F., Guerao, G., Clark, P.F. & Abelló, P. 2011. *Scyllarus arctus* (Crustacea: Decapoda: Scyllaridae) final stage phyllosoma identified by DNA analysis, with morphological description. *Journal of the Marine Biological Association of the United Kingdom*, **91**: 485–492.

Phillips, B.F., Booth, J.D., Cobb, J.S., Jeffs, A.G. & McWilliam, P. 2006. Larval and postlarval ecology. In: *Lobsters: Biology, management, aquaculture and fisheries* (B.F. Phillips, ed.), pp. 231–262. Blackwell Publishing, Oxford.

Quigley, D.T.G., Flannery, K., Herdson, D., Lord, R. & Holmes, J.M.C. 2010. Slipper lobster (*Scyllarus arctus* (L.)) (Crustacea: Decapoda) from Irish, U.K. and Channel Island waters. *The Irish Naturalists' Journal*, **31**: 33–39.

Relini, G. 1999. Synthesis of the knowledge on bottom fishery resources in Central Mediterranean (Italy and Corsica). *Biologia Marina Mediterranea*, **6**: 276–291.

Ribeiro, J. 1973. Decapod crustaceans from the waters of Cabo Verde Islands collected by the research ship "Walther Herwig" in 1970. *Notas do Centro de Biologia Aquática Tropical*, **36**: 1–21.

Robertson, P.B. 1968a. *The larval development of some Western Atlantic lobsters of the Family Scyllaridae.* Ph.D. thesis, University of Miami, Coral Gables, FL, USA.

Robertson, P.B. 1968b. The complete larval development of the sand lobster *Scyllarus americanus* (Smith), (Decapoda, Scyllaridae) in the laboratory with notes on larvae from the plankton. *Bulletin of Marine Science*, **18**: 294–432.

Robertson, P.B. 1969. The early larval development of the scyllarid lobster *Scyllarides aequinioctalis* (Lund) in the laboratory, with a revision of the larval characters of the genus. *Deep Sea Research*, **16**: 557–586.

Robertson, P.B. 1971. The larvae and postlarvae of the Scyllarid lobster *Scyllarus depressus* (Smith). *Bulletin of Marine Science*, **21**: 841–865.

Robertson, P.B. 1979. Larval development of the scyllarid lobster *Scyllarus planorbis* Holthuis reared in the laboratory. *Bulletin of Marine Science*, **29**: 320–328.

Rodríguez, J.M., Barton, E.D., Eve, L. & Hernández-León, S. 2001. Mesozooplankton and ichthyoplankton distribution around Gran Canaria, an oceanic island in the NE Atlantic. *Deep-Sea Research I: Oceanographic Research Papers*, **48**: 2161–2183.

Sangrà, P., Pascual, A., Rodríguez-Santana, Á., Machín, F., Mason, E., McWilliams, J.C., Pelegrí, J.L., Dong, C., Rubio, A., Arístegui, J., Marrero-Díaz, Á., Hernández-Guerra, A., Martínez-Marrero, A. & Auladell, M. 2009. The Canary Eddy Corridor: a major pathway for long-lived eddies in the subtropical North Atlantic. *Deep-Sea Research I: Oceanographic Research Papers*, **56**: 2100–2114.

Sekiguchi, H. & Inoue, N. 2002. Recent advances in larval recruitment processes of scyllarid and palinurid lobsters in Japanese waters. *Journal of Oceanography*, **58**: 747–757.

Smith, S.I. 1869. Description of a new genus and two new species of Scyllaridae and a new species of *Aethra* from North America. *American Journal Science and Arts*, Series 2, **48**: 118–121.

Smith, S.I. 1881. Preliminary notice of the Crustacea dredged, in 64 to 325 fathoms, off the south coast of New England, by the United States Fish Commission in 1880. *Proceedings of the United States National Museum*, **3**: 413–452.

Spalding, M.D., Fox, H.E., Allen, G.R., Davidson, N., Ferdaña, Z., Finlayson, M., Halpern, B.S., Jorge, M., Lombana, A., Lourie, S. a., Martin, K.D., Mcmanus, E., Molnar, J., Recchia, C. & Robertson, J. 2007. Marine ecoregions of the World: a bioregionalization of coastal and shelf areas. *BioScience*, **57**: 573.

Stephensen, K. 1923. Decapoda-Macrura excl. Sergestidae. (Penaeidae, Pasiphaeidae, Hoplophoridae, Nematocarcinidae, Scyllaridae, Eryonidae, Nephropsidae, Appendix). *Report on the Danish Oceanographical Expeditions 1908–10 to the Mediterranean and Adjacent Seas*, **2**: 1–85.

Webber, W.R. & Booth, J.D. 2001. Larval stages, developmental ecology, and distribution of *Scyllarus* sp. Z (probably *Scyllarus aoteanus* Powell, 1949) (Decapoda: Scyllaridae). *New Zealand Journal of Marine and Freshwater Research*, **35**: 1025–1056.

Whitelegge, T. 1900. Crustacea. Part I. Scientific results of the trawling expedition of H.M.C.S. "Thetis", off the coast of New South Wales, in February and March, 1898. *Australian Museum Memoir*, **4**: 135–199, pls. 33–35.

Yang, C.H., Bracken-Grissom, H., Kim, D., Crandall, K. & Chan, T.Y. 2012. Phylogenetic relationships, character evolution, and taxonomic implications within the slipper lobsters (Crustacea: Decapoda: Scyllaridae). *Molecular Phylogenetics and Evolution*, **62**: 237–250.

DISCUSSIÓ GENERAL

Rellevància i abast dels resultats obtinguts

Els resultats presentats evidencien la necessitat de revisar la sistemàtica actual de la subfamília Scyllarinae. Els nostres resultats confirmen l'origen polifilètic d'*Acantharctus* tal i com es defineix actualment, però seria necessari revisar material de l´espècie *A. ornatus* abans de descartar completament la validesa del gènere. Amb la incorporació de *Scyllarus posteli*, abans considerat com *Acantharctus posteli*, el gènere *Scyllarus* inclou 6 espècies a la costa oriental Atlàntica (*S. arctus*, *S. caparti*, *S. paradoxus*, *S. pygmaeus*, *S. posteli* i *S. subarctus*). Amb l´excepció de *Scyllarus depressus*, els *Scyllarus* de l'atlàntic occidental presenten una clara diferenciació genètica i morfològica respecte a les espècies de l'atlàntic oriental. D'altra banda, l'estreta relació genètica i morfològica entre *A. delfini* i altres espècies del Pacífic com *Crenarctus crenatus* i *C. bicuspidatus* (Johnson 1971b; Phillips *et al.* 1981; Webber and Booth 2001), suggereix que aquesta espècie pertany al gènere *Crenarctus*. Expandir el mostreig a altres àrees, incloent exemplars d'altres gèneres presents en l'Oceà Índic i el Pacífic, és fonamental per a poder resoldre definitivament les relacions filogenètiques dins de la subfamília Scyllarinae. Igualment, la manca de dades procedents de regions com el Golf de Guinea no ens ha permès obtenir una visió completa de la biogeografia dels *Scyllarus* de l'Atlàntic oriental.

La nova clau de identificació larval dels *Scyllarus* atlàntics, generada en aquesta tesi, permetrà fer estudis retrospectius i identificar fil·losomes de col·leccions històriques que no es poden estudiar mitjançant proves moleculars. Tant les mostres recollides per la campanya MAFIA com CETOBAPH es realitzaren durant un breu període de temps, inferior al necessari per completar el desenvolupament larval. Aquest motiu explica que solament poguérem identificar estadis de l'última etapa del desenvolupament, la gran majoria pertanyents a les fases final i sub-finals (Genis-Armero *et al.* 2017; Genis-Armero *et al.* 2019). Les mostres larvals disponibles depenen quasi exclusivament de mostrejos puntuals en campanyes que no tenen com objectiu principal l'estudi de la fase fil·losoma, així que és prou habitual tindre sèries incompletes (Phillips *et al.* 1981; Phillips and McWilliam 1989; Webber and Booth 2001; Palero *et al.* 2011). De fet, el cicle larval complet dels *Scyllarus* africans encara és desconegut i caldria realitzar mostrejos de plàncton en una mateixa regió i durant una sèrie temporal molt més llarga (mínim 3 mesos) per resoldre l'ontogènia larval completa.

La utilització de caràcters arbitraris per definir estadis (Johnson and Knight 1966) i la gran variabilitat en el nombre de mudes (Phillips *et al.* 2006) fan difícil la delimitació del nombre exacte d´estadis de desenvolupament. El creixement de les larves s'acompanya del desenvolupament progressiu (i canvis funcionals) de diferents apèndixs, així que les característiques específiques apareixen de manera gradual fins arribar a la fase fil·losoma final (Booth *et al.* 2005; Phillips *et al.* 2006). Durant els primers estadis, la morfologia larval canvia de manera qualitativa, amb modificacions importants en les antenes i antènules, i l'aparició de pereiopodis, exopodis, uropodis i pleopodis. Per contra, la definició dels estadis finals es basa generalment en el grau de desenvolupament de pereiopodis i uropodis (Webber and Booth 2001), el que resulta en classificacions confuses. La capacitat de les fil·losomes per manipular preses augmenta amb el desenvolupament i la mida de la larva (Cox and Johnston 2003a; Cox and Johnston 2003b), així que el sistema de classificació dels estadis larvals deuria incorporar factors com l´estructura dels apèndix bucals. La transformació és molt notable en la segona maxil·la, que inicialment presenta unes sedes plomoses apicals allargades que desapareixen en estadis intermedis (Robertson 1971; Webber and Booth 2001). Aquest patró sembla ser general dintre dels Achelata, i altres autors, com Chakraborty *et al.* (2011) i Matsuda *et al.* (2006), també assenyalen aquests canvis en l'estructura de l'aparell bucal en Palinuridae. De la mateixa manera, es poden definir diferents fases en base als canvis en la taxa de creixement del plèon (Hamasaki *et al.* 2012). Una nova classificació dels estadis fil·losoma directament relacionada amb canvis en l'alimentació i el comportament probablement seria més acurada i molt més significativa per a estudis d'ecologia larval.

Múltiples factors ambientals, com les reserves nutricionals o la presència o no de certs oligoelements, poden afectar el procés de muda, així que no és estrany trobar variacions en el desenvolupament larval (Costlow 1965; Sims 1966; Conlan *et al.* 2014). Una fil·losoma ben alimentada avançarà a estadis successius més ràpidament (Robertson 1968b; Conlan *et al.* 2014), i aquest efecte és patent si comparem fil·losomes de cultiu o de plàncton (Robertson 1968a; Robertson 1969b; Robertson 1971). Generalment, cadascun dels primers estadi larvals es correspon amb una muda, mentre que en estadis finals poden haver diverses mudes sense un canvi d'estadi (Booth *et al.* 2005; Hamasaki *et al.* 2012). Johnson & Knight (1966) abordaren la definició d'estadis i mudes en *Panulirus inflatus* i conclogueren que ambdós es poden

identificar a partir de l'augment del nombre de parells de sedes natatòries dels exopodis, sobretot al primer i segon pereiopodi. Aquest resultat és coherent amb el desenvolupament dels *Scyllarus* americans, on un parell de sedes es van afegint a cada estadi (Robertson 1968a; Robertson 1969b; Robertson 1971; Robertson 1979). D'acord amb aquestes observacions, els *Scyllarus* africans (i *S. depressus*) tindrien un major nombre de mudes que els americans ja que presenten un major nombre de sedes, el que equivaldria a un període de creixement larval més llarg. *Scyllarus americanus* presenta un desenvolupament larval que pot variar entre 32 i 40 dies (Robertson 1968a) i aproximadament 56 dies en *S. planorbis* (Robertson 1979). Per altra banda, el període de desenvolupament és més llarg encara (2,5 mesos) en *S. depressus*, espècie germana de *S. subarctus* (Genis-Armero *et al.* 2017). Totes dues espècies tenen larves amb un major nombre d'anul·lacions als exopodis que la resta d'espècies americanes, així que podem deduir que el desenvolupament larval deu tindre una durada superior als 2 mesos en l'espècie africana.

Concepte de decapodid

La fase decapodid, també mal anomenada etapa post-larval, és una etapa de transició entre la vida larval planctònica i l'adult bentònic. Gurney (1942) afirma que aquesta metamorfosi és la transformació més profunda en una sola muda coneguda en els Decapoda. El decapodid presenta una mida corporal més menuda que les formes adultes i pot diferir d'aquestes en les taxes de creixement, exigències metabòliques, hàbitat, comportament, morfologia, susceptibilitat a la predació o requeriments nutricionals (Felder *et al.* 1985). La forma de decapodid més coneguda és la fase megalopa dels braquiürs, i s'han utilitzat diverses designacions dintre de l'infraordre Achelata, com puerulus, pseudibacus o nisto als gèneres *Panulirus*, *Scyllarides* i *Scyllarus,* respectivament (Crosnier 1972; Phillips 1972; Lyons 1980; Genis-Armero *et al.* 2019). Lyons (1970) discuteix aquesta problemàtica en la nomenclatura, remarcant la necessitat d'estandarditzar els termes que s'utilitzen per a definir aquest estadi. El decapodid pot mostrar característiques observables en la fil·losoma, com l'abundància de sedes als pereiopodis de *S. subarctus* (Genis-Armero *et al.* 2019), però també presenta trets morfològics que el separen dels juvenils i adults, com són la manca de coloració just després de la metamorfosi, un exosquelet generalment llis en lloc d'espinós o granular, un cefalotòrax deprimit dorso-ventralment, uns pleopodis proporcionalment grans i equipats amb llargues sedes natatòries o amb un apèndix intern ben desenvolupat (Lyons 1970; Booth *et al.* 2005; Phillips *et al.* 2006).

La capacitat natatòria del decapodid ha sigut motiu de debat i ha quedat reflectit en els diferents termes utilitzats per a referir-se'n, "etapa nadadora" i "etapa reptant" (Lyons 1970; Barnett *et al.* 1986; Phillips and McWilliam 1986). Les sedes terminals de l'apèndix intern dels pleopodis funcionen al decapodid com a "ganxos d'acoblament terminal" per connectar-los i permetre la natació sincrònica (Anger 2001; Lavalli and Spanier 2010). S'ha proposat que els puerulus tinguen major activitat natatòria que els nistos (Barnett *et al.* 1986), però aquets últims també disposen de pleopodis desenvolupats. Autors com Holthuis i Loesch (1967) o Michel (1968) reporten exemplars de decapodid de *Scyllarides* a l'estòmac de una tonyina, per el que podem pensar que es trobava nadant quan va ser depredada. Als nostres mostrejos de plàncton realitzats a les proximitats de les Illes Canàries s'han pogut capturar decapodids de *Scyllarus* (Genis-Armero *et al.* 2019). El fet de trobar-los a la columna d'aigua i la presència de sedes d'acoblament entre els parells de pleopodis defensen clarament la capacitat natatòria del decapodid.

Importància dels caràcters larvals en estudis de sistemàtica

D'acord amb Felder *et al.* (1985), els anàlisis comparats d'estadis larvals (i en particular dels decapodids) poden ser útils per a resoldre la sistemàtica dels decàpodes. Fins a la data, les relacions evolutives entre els diferent gèneres de llagosta s'han basat principalment en comparacions morfològiques d'adults o dades moleculars (Palero *et al*., 2009; Yang *et al*., 2011; Bracken-Grissom *et al.*, 2014). L´únic treball de cladística basat en les fil·losoma es va realitzar molt abans que la revisió dels Scyllarinae (Baisre 1994; Holthuis 2002), per la qual cosa aquesta aproximació no s'ha utilitzat encara per resoldre les relacions evolutives entre diferents gèneres de la subfamília. Les larves de Scyllarinae es poden discriminar d'altres Scyllaridae pel seu tòrax amb una forma arrodonida i presentar generalment una ratio CL/CW baixa (CL/CW < 1). A més, presenten un abdomen relativament gran i no invaginat, i el P5 es troba subdesenvolupat als darrers estadis (longitud relativa menuda i sense exopodi). Per comparació, els Arctidinae (*Scyllarides* i *Arctides*) són fàcilment distingibles per presentar un cèfalon en forma oval amb una ratio CL/CW més alta (CL/CW > 1) i un abdomen invaginat (Robertson 1969b; Robertson 1969a; Johnson 1971c; Palero *et al.* 2016). La subfamília Theninae, representada per un sol gènere (*Thenus*), és la més propera als Scyllarinae segons les filogènies moleculars més recents (Bracken-Grissom *et al*., 2014). La morfologia larval suporta una estreta relació entre aquests dos grups, ja que les seues fil·losomes comparteixen un plèon gran no invaginat i un P5 sense exopodi (Barnett *et al.* 1984; Mikami and Greenwood 1997;

Kizhakudan and Krishnamoorthi 2014; Wakabayashi and Phillips 2016). Tanmateix, les larves de *Thenus* poden ser diferenciades dels Scyllarinae, ja que presenten un P5 més desenvolupat i el marge del cèfalon dibuixa una depressió marcada a la base de les antenes. La manca d´exopodi al P5 sembla recurrent al llarg de l´evolució de la família, i és compartida amb alguns *Scyllarides* (*S. herklotsii*, *S. latus, S. nodifer* i *S. squammosus*) (Robertson 1969b; Palero *et al.* 2016). Aquest fet podria suposar una disminució en la capacitat natatòria de la larva i per tant en la seua capacitat dispersiva.

Eduarctus i *Crenarctus* semblen ser els gèneres de Scyllarinae filogenèticament més propers amb *Scyllarus* (Bracken-Grissom *et al.* 2014). Les dades obtingudes en aquesta tesi no permeten establir sinapomorfies que agrupen aquests tres gèneres, i suggereixen que en realitat els *Scyllarus* deurien dividir-se en dos grups d´espècies. Així, els *Scyllarus* americans serien més propers al gènere *Eduarctus* que als *Scyllarus* de l'atlàntic oriental (excepte *S. depressus*). L'estadi final de les fil·losomes d'aquests dos grups no presenten espines dorsals toràciques (Johnson 1971c; Prasad *et al.* 1975; Robertson 1979), mentre que les espècies de *Crenarctus* i els *Scyllarus* de l'atlàntic oriental (+ *S. depressus*) sí les presenten (Johnson 1971b; Baez 1973; Palero *et al.* 2008; Palero *et al.* 2011). El prof. Alain Crosnier i el Dr. Robertson ja varen remarcar la importància d'aquestes espines per diferenciar tipus larvals dins dels *Scyllarus* (Robertson, 1968b; Crosnier, pers. comm.). A més a més, les espines postero-laterals del tèlson d'*Eduarctus* i *Scyllarus* americans (exc. *S. depressus*) són curtes i no sobrepassen els uropodis, al contrari que en *Crenarctus* i *Scyllarus* africans, que també presenten unes antènules més llargues que les antenes (Webber and Booth 2001). *Eduarctus* es pot distingir dels *Scyllarus* americans pels uropodis lanceolats i un P5 que no els sobrepassa (Johnson 1971a; Phillips and McWilliam 1986). De la mateixa manera, les espècies de *Crenarctus* disposen d'un nombre menor de sedes sensorials a les antènules que les espècies de *Scyllarus*, tot i que cal fer una revisió més exhaustiva de les espècies del Pacífic.

En aquest treball hem observat una sèrie d'estructures de les fil·losomes i els decapodids que tenen una funcionalitat evident però no han rebut gaire atenció en estudis previs. Per exemple, el tercer pereiopodi es troba directament involucrat en la subjecció de les fil·losomes a les meduses (William 1976, observacions pròpies), i és raonable pensar que la talla o el nombre d'espines afecten a la subjecció de la larva. Efectivament, les fil·losomes dels Scyllarinae presenten un parell d'espines ventrals distals al propodi dels P1-4 de gran longitud en relació als dàctils (Robertson 1969b), mentre que els tercers pereiopodis de *Scyllarides* o

Parribacus tenen uns dàctils més allargats i amb unes espines curtes (Robertson 1968a; Higa and Shokita 2004; Genis-Armero *et al.* 2017; Genis-Armero *et al.* 2020). De la mateixa manera, els pleopodis o l'apèndix intern dels nistos es troben implicats directament en la mobilitat i presenten diferències entre gèneres de Scyllaridae. Els decapodids de *Scyllarides* presenten pleopodis més desenvolupats que els Scyllarinae, i un apèndix intern que no supera la meitat de l'endopodi (Lyons 1970; Johnson 1975). Els pleopodis en *Eduarctus* i els *Scyllarus* americans disposen al voltant de 45 sedes plomoses (Robertson 1968a; Phillips and McWilliam 1986; Wakabayashi *et al.* 2017) mentre que els pleopodis dels decapodids de *Scyllarus* africans i *Crenarctus* presenten gairebé el doble de sedes (Webber and Booth 2001; Palero *et al.* 2009b; Genis-Armero *et al.* 2019). Malauradament, aquestes estructures no han sigut detallades en la majoria de les descripcions i no podem realitzar una comparativa més extensa entre gèneres de Scyllarinae. Els futurs treballs de sistemàtica de llagostes deurien assegurar-se d'incloure aquests caràcters de les larves.

Perspectives futures

En conclusió, podem assenyalar que els futurs esforços en revisar la sistemàtica de la subfamília Scyllarinae necessitaran centrar-se en obtenir nous exemplars, tant de larves com d'adults, per poder testar la validesa dels gèneres actuals (e.g. *Acantharctus ornatus*). És particularment interessant mostrejar regions poc estudiades com el Golf de Guinea, on són especialment abundants les espècies de *Scyllarus* per a les quals les larves d'estadi final resten desconegudes (*S. paradoxus* i *S. posteli*). Caldrà realitzar descripcions detallades i completes de les fil·losomes per tal de descobrir sinapomorfies i confirmar la separació de les espècies americanes de les espècies africanes. La importància de les dades larvals en la resolució de la filogènia dels Scyllaridae queda reflectida als resultats presentats en aquesta tesi. Caràcters com la longitud relativa de les antènules, el nombre d'estetascs, les espines dorsals toràciques, el desenvolupament del P5, forma dels uropodis i les espines postero-laterals del tèlson són taxonòmicament útils. Finalment, les variacions en la morfologia larval no són simplement el resultat de la història evolutiva del grup. Tant l'habitat com l'ecologia d'aquestes larves també actuen modelant la morfologia de les fil·losomes, per la qual cosa el seu estudi probablement encara ens deparará nous descobriments.

CONCLUSIONS

CONCLUSIONS

1. Les espècies de *Scyllarus* s'agrupen en dos clades recíprocament monofilètics (e.g. Atlàntic Occidental i Atlàntic Oriental). L'única excepció és *S. depressus*, que s'agrupa com a espècie germana de *S. subarctus*. Aquest resultat, recolzat per evidències morfològiques i moleculars, suggereix un procés d'especiació recent i una colonització secundària d'Americà.

2. Els nous resultats moleculars suggereixen que el gènere *Acantharctus* és polifilètic, amb espècies de l'Oceà Atlàntic (*A. posteli*) i del Pacífic (*A. delfini*) separades en diferents clades. La morfologia del marge anterior de l'esternita toràcica és congruent amb la biogeografia i els patrons filogenètics moleculars.

3. Les noves evidències morfològiques i moleculars mostren que *A. posteli* s'agrupa dins de *Scyllarus*, com a espècie germana de *S. paradoxus*. Per tant, s'hauria de restablir el basiònim *Scyllarus posteli*. L'estreta relació genètica i morfològica entre *A. delfini* i altres taxons de l'Oceà Pacífic com *Crenarctus crenatus* i *C. bicuspidatus,* suggereix que *A. delfini* haria de nombrar-se *Crenarctus delfini*.

4. El nou material estudiat durant aquesta tesi ens permet ampliar significativament la distribució geogràfica coneguda de *S. subarctus* i *S. caparti*. Mentre que *S. subarctus* s'estén des dels 34 N als 18 S (prèviament 21 N – 17 S), *S. caparti* es distribueix dels 27 N fins als 9 S (en lloc del límit més septentrional 22 N anterior a la tesi).

5. Tant l'estadi fil·losoma final com l'etapa nisto de *S. subarctus* són les més grans entre les larves de Scyllarinae. Aquest tamany, juntament amb la llarga durada de la fase planctònica, podria estar relacionat amb una major capacitat de dispersió i explicar la colonització d'illes oceàniques remotes com Santa Helena.

6. El decapodid de *S. subarctus* i 3 estadis fil·losoma (VII, IX i X), tant de *S. subarctus* com de *S. caparti,* es descriuen en aquesta tesi per primera vegada. S'han identificat mitjançant l'ús de tècniques moleculars.

7. S'hauria d'establir una nova definició dels estadis fil·losoma, relacionant els canvis morfològics amb l'alimentació i els canvis de comportament. Aquesta nova definició seria més significativa per als estudis d'ecologia larvària.

8. Es proposen nous caràcters morfològics per identificar les larves de *Scyllarus* a nivell d'espècies, com ara la forma del cèfalon, la presència d'espines dorsals toràciques i la seva mida relativa, i la configuració i presència d'espines als pereiopodis.

9. S'ha elaborat una nova clau d'identificació actualitzada per a les fil·losomes de *Scyllarus*. Descrivim detalladament les estructures larvals clau, com ara els pleòpodes dels nistos o els dàctils de les fil·losomes. Aquests trets han rebut poca atenció anteriorment, però seran significatius en futurs estudis taxonòmics dins de Scyllarinae.

10. Els nostres resultats tenen implicacions directes sobre la sistemàtica dels Scyllarinae. Es poden definir dos grups de gèneres, un d'ells incloent *Crenarctus* de les aigües del Pacífic i els *Scyllarus* africans, i l'altre incloent els *Scyllarus* americans i *Eduarctus*. Aquests grups es poden distingir a l'estadi fil·losoma en funció de la presència / absència d'espines toràciques, la longitud relativa de les antenes i les espines postero-laterals del tèlson. Es recomana revisar la morfologia dels adults.

CONCLUSIONS

1. *Scyllarus* species group into two reciprocal monophyletic clades (i.e. West Atlantic and East Atlantic). The only exception being *S. depressus*, which clusters as sister species of *S. subarctus*. This result, supported by molecular and morphological evidence, suggest a recent speciation process and secondary colonization of America.

2. New molecular results suggest the genus *Acantharctus* to be polyphyletic, with species from the Atlantic Ocean (*A. posteli*) and Pacific Ocean (*A. delfini*) split in different clades. The morphology of the thoracic sternum's anterior margin is congruent with biogeography and molecular phylogenetic patterns.

3. New molecular and morphological evidence show *A. posteli* to group within *Scyllarus*, as sister species of *S. paradoxus*. Therefore, the basionym *Scyllarus posteli* should be re-established. The close genetic and morphological relationship between *A. delfini* and other Pacific Ocean taxa like *Crenarctus crenatus* and *C. bicuspidatus* suggests that *A. delfini* should be renamed as *Crenarctus delfini*.

4. The new material studied during this PhD thesis allow us to significantly expand the known distribution of *S. subarctus* and *S. caparti*. While *S. subarctus* extends from 34 N to 18 S (previously 21 N – 17 S), *S. caparti* is distributed from 27 N to 9 S (instead of the previous northernmost limit at 22 N).

5. Both the final phyllosoma and nisto stage of *S. subarctus* are the largest among Scyllarinae larvae. Together with its long planktonic larval duration, this could be related to a greater dispersal capacity and explain its ability to colonize remote oceanic islands such as St. Helena.

6. The decapodid of *S. subarctus*, and three phyllosoma stages (VII, IX and X) for both *S. subarctus* and *S. caparti* are described in this thesis for the first time. They have been identified by using molecular techniques.

7. A new definition of phyllosoma stages should be established, relating morphological changes with feeding and behavioural changes. This new definition would be more meaningful for larval ecology studies.

8. New morphological characters are proposed to identify *Scyllarus* larvae to species level, such as cephalon shape, presence of thoracic dorsal spines and their relative size, and setation and presence of spines on pereiopods.

9. A new update identification key for *Scyllarus* phyllosoma was done. We describe in detail key larval structures, such as pleopods of nistos or dactyls of phyllosomae. These traits have received little attention previously, but they will prove significant in future taxonomic studies within Scyllarinae.

10. Our results have direct implications on the systematics of Scyllarinae. Two groups of genera can be defined, one of them including *Crenarctus* from Pacific waters and the African *Scyllarus*, and the other including the American *Scyllarus* and *Eduarctus*. These groups can be distinguished at the phyllosoma stage based on the presence/absence of thoracic spines, relative length of antennules and postero-lateral spines on telson. Revision of adult morphology is recommended.

REFERÈNCIES

Almada, F., Almada, V. C., Domingues, V., Brito, A., and Santos, R. S. (2005). Molecular validation of the specific status of *Parablennius sanguinolentus* and *Parablennius parvicornis* (Pisces: Blenniidae). *Scientia Marina* **69**, 519–523. doi:10.3989/scimar.2005.69n4519

Almada, V. C., Oliveira, R. F., Gonçalves, E. J., Almeida, A. J., Santos, R. S., and Wirtz, P. (2001). Patterns of diversity of the north-eastern Atlantic blenniid fish fauna (Pisces: Blennniidae). *Global Ecology and Biogeography* **10**, 411–422. doi:10.1046/j.1466-822X.2001.00244.x

Anadon, R. (1981). Crustáceos Decápodos (excl. Paguridea) recogidos durante la campaña <<Atlor VII>> en las costas noroccidentales de África (Noviembre 1975). *Resultados Expediciones Cientificas, Supl.* **9**, 151–159.

Anger, K. (2001). 'The Biology of Decapod Crustacean Larvae' Crustacea Issues, Vol. 14. (A.A. Balkema: Lisse, The Netherlands.) doi:10.1016/s0044-8486(02)00262-4

Baez, P. (1973). Larvas phyllosoma del Pacífico Sur Oriental (Crustacea, Macrura, Scyllaridea). *Revista de Biologia Marina* **15**, 115–130.

Baisre, J. A. (1994). Phyllosoma larvae and the phylogeny of Palinuroidea (Crustacea: Decapoda): A Review. *Marine and Freshwater Research* **45**, 925–944. doi:10.1071/MF9940925

Barnett, B. M., Hartwick, R. F., and Milward, N. E. (1986). Descriptions of the Nisto Stage of *Scyllarus demani* Holthuis, Two Unidentified *Scyllarus* Species, and the Juvenil of *Scyllarus martensii* Pfeffer (Crustacea: Decapoda: Scyllaridae), reared in the Laboratory; and Behavioural Observations of the nistos of *S. demani*, *S. martensii* and *Thenus orientalis* (Lund). *Marine and Freshwater Research* **37**, 595–608.

Barnett, B. M., Hartwick, R. F., and Milward, N. E. (1984). Phyllosoma and nisto stage of the morton bay bug, *Thenus orientalis* (Lund) (crustacea: Decapoda: Scyllaridae), from shelf waters of the great barrier reef. *Marine and Freshwater Research* **35**, 143–152. doi:10.1071/MF9840143

Barshaw, D. E., and Spanier, E. (1994). Anti-predator behaviors of the Mediterranean slipper lobster, *Scyllarides latus*. *Bulletin of Marine Science* **55**, 375–382.

Bate, C. S. (1888). Report on the Crustacea Macrura collected by the Challenger during the years 1873-76. Report on the Scientific Results of the Voyage of H.M.S. "Challenger" during the years 1873-76. In 'Report on the scientific results of the voyage of H.M.S. Challenger during the yerars 1873-76'. pp. i–xc, 1–942, Plates 1-157

Booth, J. D., and Phillips, B. F. (1994). Early life history of spiny lobster. *Crustaceana* **66**, 271–294. doi:10.1163/156854094X00035

Booth, J. D., Webber, W. R., Sekiguchi, H., and Coutures, E. (2005). Diverse larval recruitment strategies within the Scyllaridae. *New Zealand Journal of Marine and Freshwater Research* **39**, 581–592. doi:10.1080/00288330.2005.9517337

Bracken-Grissom, H. D., Ahyong, S. T., Wilkinson, R. D., Feldmann, R. M., Schweitzer, C. E., Breinholt, J. W., Bendall, M., Palero, F., Chan, T. Y., Felder, D. L., Robles, R., Chu, K. H., Tsang, L. M., Kim, D., Martin, J. W., and Crandall, K. A. (2014). The emergence of lobsters: Phylogenetic relationships, morphological evolution and divergence time comparisons of an ancient group (Decapoda: Achelata, Astacidea, Glypheidea, Polychelida). *Systematic Biology* **63**, 457–479. doi:10.1093/sysbio/syu008

Chakraborty, R. D., Radhakrishnan, E. V., Sanil, N. K., Thangaraja, R., and Unnikrishnan, C. (2011). Mouthpart morphology of phyllosoma of the tropical spiny lobster *Panulirus homarus* (Linnaeus, 1758). *Indian Journal of Fisheries* **58**, 1–7.

Chan, T.-Y. (2010). Annotated Checklist of the World's Marine Lobsters (Crustacea:

Decapoda: Astacidea, Glypheidea, Achelata, Polychelida). *The Raffles Bulletin of Zoology* **23**, 153–181.
Chiswell, S. M., and Booth, J. D. (1999). Rock lobster *Jasus edwardsii* larval retention by the Wairarapa Eddy off New Zealand. *Marine Ecology Progress Series* **183**, 227–240. doi:10.3354/meps183227
Clark, P. F., Calazans, D. K., and Pohle, G. W. (1998). Accuracy and standardization of brachyuran larval descriptions. *Invertebrate Reproduction and Development* **33**, 127–144. doi:10.1080/07924259.1998.9652627
Coelho, P. A. (1981). Ocorrência no litoral do Brasil de *Scyllarus americanus* (Smith) e de *S. chacei* Holthuis (Crustacea, Decapoda, Scyllaridae). *Trabalhos oceanográficos da Universidade Federal de Pernambuco.* **16**, 13–22.
Coleman, C. O. (2003). 'Digital inking': How to make perfect line drawings on computers. *Organisms Diversity and Evolution* **3**, 303–304. doi:10.1078/1439-6092-00081
Coleman, C. O. (2009). Drawing setae the digital way. *Zoosystematics and Evolution* **85**, 305–310. doi:10.1002/zoos.200900008
Conlan, J. A., Jones, P. L., Turchini, G. M., Hall, M. R., and Francis, D. S. (2014). Changes in the nutritional composition of captive early-mid stage *Panulirus ornatus* phyllosoma over ecdysis and larval development. *Aquaculture* **434**, 159–170. doi:10.1016/j.aquaculture.2014.07.030
Costlow, J. D. (1965). Variability in larval stages of the blue crab, *Callinectes sapidus*. *The Biological Bulletin* **128**, 58–66. doi:10.2307/1539389
Cox, S. L., and Johnston, D. J. (2003a). Developmental changes in the structure and function of mouthparts of phyllosoma larvae of the packhorse lobster, *Jasus verreauxi* (Decapoda: Palinuridae). *Journal of Experimental Marine Biology and Ecology* **296**, 35–47. doi:10.1016/S0022-0981(03)00303-4
Cox, S. L., and Johnston, D. J. (2003b). Feeding biology of spiny lobster larvae and implications for culture. *Reviews in Fisheries Science* **11**, 89–106. doi:10.1080/713610924
Crosnier, A. (1970). Crustacés décapodes Brachyoures et Macroures recueillis par l'<<Undaunted>> au sud de l'angola. Description de *Scyllarus subarctus* sp. nov. *Bulletin du Muséum National d'Histoire Naturelle* **41**, 1214–1227.
Crosnier, A. (1972). Naupliosoma, phyllosomes et pseudibacus de *Scyllarides herklotsi* (Herklots) (Crustacea, Decapoda, Scyllaridae) rêcoltês par l'ombango dans le sud du golfe de Guinée. *Cahiers ORSTOM Séries Océanographique* **10**, 139–149.
Crosnier, A. (1971). Ponte et développement de la langouste verte *Panulirus regius* de Brito Capello dans le sud du golfe de Guinée. *Cahiers O.R.S.T.O.M., série océanographie* **9**, 339–361.
Crosnier, A. (1967). Remarques sur quelques crustacés décapodes benthiques ouest-africains. Description de *Heteropanope acanthocarpus* et *Medaeus rectifrons* spp. nov. *Bulletin du Muséum national d'Histoire naturelle, Paris, 2e série* **39**, 320–344.
Crosnier, A., and Forest, J. (1973). Les crevettes profondes de l'Atlantique Oriental Tropical. In 'Faune Tropicale'. pp. 1–409
Edgar, R. C. (2004). MUSCLE: Multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* **32**, 1792–1797. doi:10.1093/nar/gkh340
Felder, D. L., Martin, J. W., and Goy, J. W. (1985). Patterns in early postlarval development of decapods. In 'Crustacean growth: Larval growth'. (Ed A. M. Wenner.) pp. 248. (University of California: Santa Barbara.)
Forest, J. (1963). Sur deux *Scyllarus* de l'Atlantique tropical africain: *S. paradoxus* Miers et *S. posteli* sp. nov. Remarques sur les *Scyllarus* de l'Atlantique oriental. *Bulletin de l'Institut Océanographique de Monaco* **60**, 1–20.
Forest, J., and Holthuis, L. B. (1960). The occurrence of *Scyllarus pygmaeus* (Bate) in the

Mediterranean. *Crustaceana* **1**, 156–163. doi:10.1163/156854060X00177
Fransen, C. H. J. M. (1991). Preliminary report on Crustacea collected in the eastern part of the North Atlantic during the CANCAP and Mauritania expeditions of the former Rijksmuseum van Natuurlijke Historie, Leiden.
Freitas, R., Romeiras, M., Silva, L., Cordeiro, R., Madeira, P., González, J. A., Wirtz, P., Falcón, J. M., Brito, A., Floeter, S. R., Afonso, P., Porteiro, F., Viera-Rodríguez, M. A., Neto, A. I., Haroun, R., Farminhão, J. N. M., Rebelo, A. C., Baptista, L., Melo, C. S., Martínez, A., Núñez, J., Berning, B., Johnson, M. E., and Ávila, S. P. (2019). Restructuring of the 'Macaronesia' biogeographic unit: a marine multi-taxon biogeographical approach. *Scientific Reports* **9**, 1–18. doi:10.1038/s41598-019-51786-6
Froglia, C. (1974). Preliminary report of the Crustacea Decapoda of Adriatic deep waters. *Thalassia Jugoslavica* **8**, 75–79.
García-Isarch, E., and Muñoz, I. (2015). Biodiversitiy and biogeography of decapods crustaceans in the Canary Current Large Marine Ecosystem. In 'Oceanographic and biological features in the Canary Current Large Marine Ecosystem.' (Eds L. Valdés and I. Déniz-González.) pp. 257–271
García Raso, J. E. (1982). Familia Scyllaridae Latreille 1825 (Crustacea, Decapada) en la Región Sur-mediterránea española. *Boletín de la Asociación Española de Entomología* **6**, 73–78.
Garcia Socias, L., and Massuti Jaume, C. (1987). Inventari bibliogràfic dels crustacis decàpodes de les balears (Crustacea Decapoda). *Bolletí de la Societat d'Història Natural de les Illes Balears* **31**, 67–92.
Genis-Armero, R., González-Gordillo, J. I., Cuesta, J. A., Capaccioni-Azzati, R., and Palero, F. (2020). Revision of the West African species of *Scyllarus* Fabricius, 1775 (Decapoda: Achelata: Scyllaridae), with the description of three phyllosoma stages of *S. caparti* Holthuis, 1952 and an updated identification key. *Journal of Crustacean Biology* **0**, 1–13. doi:10.1093/jcbiol/ruaa025
Genis-Armero, R., Guerao, G., Abelló, P., Ignacio González-Gordillo, J., Cuesta, J. A., Corbari, L., Clark, P. F., Capaccioni-Azzati, R., and Palero, F. (2017). Possible amphi-atlantic dispersal of *Scyllarus* lobsters (crustacea: Scyllaridae): Molecular and larval evidence. *Zootaxa* **4306**, 325–338. doi:10.11646/zootaxa.4306.3.2
Genis-Armero, R., Landeira, J., Capaccioni-Azzati, R., and Palero, F. (2019). Updated distribution and first description of *Sc yllarus subarctus* (Crustacea: Scyllaridae) decapodid stage. *Journal of the Marine Biological Association of the United Kingdom* **99**, 1181–1188. doi:10.1017/S0025315419000067
Gurney, R. (1936). Larvae of Decapod Crustacea: Part I- Stenopidea. Part II- Amphionidae. Part III- Phyllosoma. *Discovery Reports* **12**, 377–440.
Gurney, R. (1942). 'Larvae of decapod crustacea'. (The Ray Society: London.) doi:10.1038/140692a0
Hall, T. (1999). Symposium on RNA Biology. III. RNA, Tool and Target. Research Triangle Park, North Carolina, USA. October 15-17, 1999. Proceedings. *Nucleic acids symposium series* **41**, 1–218. Available at: http://jwbrown.mbio.ncsu.edu/JWB/papers/1999Hall1.pdf
Hamasaki, K., Mizumoto, Y., Jinbo, T., and Murakami, K. (2012). Ontogenetic change of body density and shape of the phyllosoma larvae of the japanese spiny lobster *Panulirus japonicus*. *Journal of Crustacean Biology* **32**, 395–404. doi:10.1163/193724012X626548
Hebert, P. D. N., Cywinska, A., Ball, S. L., and DeWaard, J. R. (2003). Biological identifications through DNA barcodes. *Proceedings of the Royal Society: Biological Sciences* **270**, 313–321. doi:10.1098/rspb.2002.2218
Hernández-León, S., Olivar, M. P., Fernández de Puelles, M. L., Bode, A., Castellón, A., López-Pérez, C., Tuset, V. M., and González-Gordillo, J. I. (2019). Zooplankton and

Micronekton Active Flux Across the Tropical and Subtropical Atlantic Ocean. *Frontiers in Marine Science* **6**, 1–20. doi:10.3389/fmars.2019.00535

Herrnkind, W., Halusky, J., and Kanciruk, P. (1976). A further note on phyllosoma larvae associated with medusae. *Bulletin of Marine Science* **26**, 110–112. doi:10.1017/CBO9781107415324.004

Higa, T., and Shokita, S. (2004). Late-stage phyllosoma larvae and metamorphosis of a scyllarid lobster, *Chelarctus cultrifer* (Crustacea: Decapoda: Scyllaridae), from the Northwestern Pacific. *Species Diversity* **9**, 221–249.

Holthuis, L. B. (1969). A new species of shovel-nose lobster, *Scyllarus planorbis*, from the Southwestern Caribbean and Northern South America. *Bulletin of Marine Science* **19**, 149–158.

Holthuis, L. B. (1952). Crustacés Décapodes, Macrures. *Expédition Océanographique Belge dans les Eaux Côtières Africaines de l'Atlantique Sud (1948-1949)* **3**, 1–88.

Holthuis, L. B. (1991). FAO species catalogue Vol. 13. Marine lobsters of the world An annotated and illustrated catalogue of species of interest to fisheries known to date. *FAO Fisheries Synopsis No. 125* **13**, 1–4.

Holthuis, L. B. (1960). Preliminary descriptions of one new genus, twelve new species and three new subspecies of scyllarid lobsters (Crustacea Decapoda Macrura). *Proceedings of the Biological Society of Washington* **73**, 147–154.

Holthuis, L. B. (2002). The Indo-Pacific scyllarine lobsters (Crustacea, Decapoda, Scyllaridae). *Zoosystema* **24**, 499–683.

Holthuis, L. B., and Loesch, H. (1967). The lobsters of the Galápagos Islands (Decapoda, Palinuridea). *Crustaceana* **12**, 214–222.

Inoue, N., Sekiguchi, H., and Yeh, S.-P. (2001). Spatial Distributions of Phyllosoma Larvae (Crustacea: Decapoda: Palinuridae and Scyllaridae) in Taiwanese Waters. *Journal of Oceanography* **57**, 535–548.

Johnson, M. W. (1971a). On Palinurid and Scyllarid Lobster Larvae and Their Distribution in the South China Sea (Decapoda, Palinuridea). *Crustaceana* **21**, 247–282. doi:10.2307/20101842

Johnson, M. W. (1971b). The Phyllosoma Larva of *Scyllarus delfini* (Bouvier) (Decapoda, Palinuridea). *Crustaceana* **21**, 161–164. doi:10.2307/20101826

Johnson, M. W. (1971c). The phyllosoma larvae of slipper lobsters from the Hawaiian Islands and adjacent areas. *Crustaceana* **20**, 77–103.

Johnson, M. W. (1975). The postlarvae of *Scyllarides astori* and *Evibacus princeps* of the eastern tropical Pacific (Decapoda, Scyllaridae). *Crustaceana* **28**, 139–144.

Johnson, M. W., and Knight, M. (1966). The phyllosoma larvae of the spiny lobster *Panulirus inflatus* (Bouvier). *Crustaceana* **10**, 31–47.

Kämpf, J., and Chapman, P. (2016). The Canary/Iberia Current Upwelling System. In 'Upwelling Systems of the World. A Scientific Journey to the Most Productive Marine Ecosystems'. (Eds J. Kämpf and P. Chapman.) pp. 203–250. (Springer Nature.) doi:10.1007/978-3-319-42524-5

Kittaka, J. (1997). Application of ecosystem culture method for complete development of phyllosomas of spiny lobster. *Aquaculture* **155**, 319–331. doi:10.1016/S0044-8486(97)00100-2

Kittaka, J. (1994). Culture of phyllosomas of spiny lobster and its application to studies of larval recruitment and aquaculture. *Crustaceana* **66**, 258–270.

Kizhakudan, J. K., and Krishnamoorthi, S. (2014). Complete larval development of *Thenus unimaculatus* Burton & Davie, 2007 (Decapoda, Scyllaridae). *Crustaceana* **87**, 570–584. doi:10.1163/15685403-00003306

Kumar, S., Stecher, G., Li, M., Knyaz, C., and Tamura, K. (2018). MEGA X: Molecular

Evolutionary Genetics Analysis across Computing Platforms Ed F. U. Battistuzzi. *Molecular Biology and Evolution* **35**, 1547–1549. doi:10.1093/molbev/msy096

Kumar, S., Stecher, G., and Tamura, K. (2016). MEGA7: Molecular Evolutionary Genetics Analysis Version 7.0 for Bigger Datasets. *Molecular biology and evolution* **33**, 1870–1874. doi:10.1093/molbev/msw054

Land, J. Van Der (1987). Report on the CANCAP-Project for marine biological research in the Canarian - Cape Verdean Region of the North Atlantic Ocean (1976-1986). Part I. List of stations. *Zoologische Verhandelingen* **243**, 1–94.

Landeira, J. M., Chan, T.-Y., Aguilar-Soto, N., Jiang, G.-C., and Yang, C.-H. (2014). Description of the decapodid stage of Plesionika narval (Fabricius, 1787) (Decapoda: Caridea: Pandalidae) identified by DNA barcoding. *Journal of Crustacean Biology* **34**, 377–387. doi:10.1163/1937240X-00002234

Landeira, J. M., Lozano-Soldevilla, F., and Barton, E. D. (2012). Mesoscale advection of *Upogebia pusilla* larvae through an upwelling filament in the Canaries Coastal Transition Zone (CTZ). *Helgoland Marine Research* **66**, 537–544. doi:10.1007/s10152-011-0289-5

Landeira, J. M., Lozano-Soldevilla, F., Hernández-León, S., and Barton, E. D. (2009). Horizontal distribution of invertebrate larvae around the oceanic island of Gran Canaria: the effect of mesoscale variability. *Scientia Marina* **73**, 761–771. doi:10.3989/scimar.2009.73n4757

Landeira, J. M., Lozano-Soldevilla, F., Hernández-León, S., and Barton, E. D. (2010). Spatial variability of planktonic invertebrate larvae in the Canary Islands area. *Journal of the Marine Biological Association of the United Kingdom* **90**, 1217–1225. doi:10.1017/S0025315409990750

Lavalli, K. L., and Spanier, E. (2010). Infraorder Palinura Latreille, 1802. In 'Treatise on Zoology-Anatomy, Taxonomy, Biology. The Crustacea, Volume 9 Part A'. (Eds F. R. Schram and J. C. von Vanpel Klein.) pp. 425–532. (Brill.) doi:10.1163/ej.9789004164413.i-562.80

Lewinsohn, C. H. (1974). The occurrence os *Scyllarus pygmaeus* (Bate) in the eastern Mediterranean (Decapoda, Scyllaridae). *Crustaceana* **27**, 43–46. doi:10.1163/156854074X00217

Linnaeus, C. (1758). 'Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis.' 10th ed. (Laurentii Salvii: Holmiae (Stockholm).)

Lyons, W. G. (1970). Scyllarid Lobsters (Crustacea, Decapoda). *Memoirs of the Hourglass Cruises* **1**, 1–74.

Lyons, W. G. (1980). The postlarval stage of Scyllaridean lobsters. *Fisheries* **5**, 47–49. doi:10.1577/1548-8446-17-4

Macpherson, E. (1991). Biogeography and community structure of the decapod crustacean fauna off Namibia (Southeast Atlantic). *Journal of Crustacean Biology* **11**, 401–415. doi:10.2307/1548466

Macpherson, E. (1983). Crustáceos decápodos capturados en las costas de Namibia. *Resultados Expediciones Científicas* **11**, 3–79.

Maigret, J. (1978). Contribution à l'étude des langoustes de la côte occidentale d'Afrique (Crustacés, Décapodes, Palinuridae). *Bulletin de l'Institut Fondamental de l'Afrique Noire* **40**, 36–80.

Maigret, J. (1975). Larves phyllosomes capturées au large du banc d'Arguin. *Bulletin de l'Institut Fondamental de l'Afrique Noire* **37**, 784–794.

Marco-Herrero, E., Torres, A. P., Cuesta, J. A., Guerao, G., Palero, F., and Abelló, P. (2013). The systematic position of *Ergasticus* (Decapoda, Brachyura) and allied genera, a molecular and morphological approach. *Zoologica Scripta* **42**, 427–439.

doi:10.1111/zsc.12012
de Matos-Pita, S. S., Ramil, F., and Ramos, A. (2018). Marine lobsters and lithodids (Crustacea: Decapoda) from Mauritanian deep-waters (NW Africa). *Regional Studies in Marine Science* **23**, 32–38. doi:10.1016/j.rsma.2018.01.001
Matsuda, H., Takenouchi, T., Goldstein, J. S., and Hampshire, N. (2006). The complete larval development of the pronghorn spiny lobster *Panulirus penicillatus* (Decapoda: Palinuridae) in culture. *Journal of Crustacean Biology* **26**, 579–600.
Michel, A. (1968). Les larves phyllosomes et la post-larve de *Scyllarides squammosus* (H. Milne-Edwards)-Scyllaridae (Crustacés Décapodes). *Cahiers O.R.S.T.O.M. (Office de la Recherche Scientifique et Technique Outre-Mer). Sér. Océanogr.,* **VI**, 47–53.
Miers, E. J. (1881). XXXVII.— On a collection of Crustacea made by Baron Hermann Maltzan at Goree Island, Senegambia . *Annals and Magazine of Natural History* **8**, 364–377. doi:10.1080/00222938109487471
Mikami, S., and Greenwood, J. G. (1997). Complete development and comparative morphology of larval *Thenus orientalis* and *Thenus* sp. (Decapoda: Scyllaridae) reared in the laboratory. *Journal of Crustacean Biology* **17**, 289–308.
Muñoz, I., García-Isarch, E., Sobrino, I., Burgos, C., Funny, R., and González-Porto, M. (2012). Distribution, abundance and assemblages of decapod crustaceans in waters off Guinea-Bissau (north-west Africa). *Journal of the Marine Biological Association of the United Kingdom* **92**, 475–494. doi:10.1017/S0025315411001895
Navas S., G. R., and Campos C., N. H. (1998). Las langostas chinas (Crustacea: Decapoda: Scyllaridae) del caribe colombiano. *Boletin de investigaciones marino costeras* **27**, 51–66.
Palero, F., and Abello, P. (2007). The first phyllosoma stage of *Palinurus mauritanicus* (Crustacea : Decapoda : Palinuridae). *Zootaxa* **1508**, 49–59.
Palero, F., Clark, P. F., and Guerao, G. (2014a). Infraorden Achelata. In 'Atlas of Crustacean Larvae'. (Eds J. Martin, J. Olesen, and J. T. Hoeg.) pp. 272–278. (Johns Hopkins University Press: Maryland, USA.)
Palero, F., Crandall, K. A., Abelló, P., Macpherson, E., and Pascual, M. (2009a). Phylogenetic relationships between spiny, slipper and coral lobsters (Crustacea, Decapoda, Achelata). *Molecular Phylogenetics and Evolution* **50**, 152–162.
Palero, F., Genis-Armero, R., Hall, M., and Clark, P. (2016). DNA barcoding the phyllosoma of *Scyllarides squammosus* (H. Milne Edwards, 1837) (Decapoda: Achelata: Scyllaridae). *Zootaxa* **4139**, 481. Available at: http://biotaxa.org/Zootaxa/article/view/zootaxa.4139.4.2 [accessed 7 September 2016]
Palero, F., Guerao, G., and Abelló, P. (2008). Morphology of the final stage phyllosoma larva of *Scyllarus pygmaeus* (Crustacea: Decapoda: Scyllaridae), identified by DNA analysis. *Journal of Plankton Research* **30**, 483–488.
Palero, F., Guerao, G., Clark, P. F., and Abelló, P. (2011). *Scyllarus arctus* (Crustacea: Decapoda: Scyllaridae) final stage phyllosoma identified by DNA analysis, with morphological description. *Journal of the Marine Biological Association of the United Kingdom* **91**, 485–492.
Palero, F., Guerao, G., Clark, P. F., and Abelló, P. (2009b). The true identities of the slipper lobsters Nisto laevis and Nisto asper (Crustacea: Decapoda: Scyllaridae) verified by DNA analysis. *Invertebrate Systematics* **23**, 77–85. doi:10.1071/IS08033
Palero, F., Guerao, G., Hall, M., Chan, T. Y., and Clark, P. F. (2014b). The 'giant phyllosoma' are larval stages of *Parribacus antarcticus* (Decapoda : Scyllaridae). *Invertebrate Systematics* **28**, 258–276.
Palero, F., Hall, S., Clark, P. F., Johnston, D., Mackenzie-Dodds, J., Thatje, S., and Johnston, J. (2010). DNA extraction from formalin-fixed tissue: new light from the Deep-Sea. *Scientia Marina* **74**, 465–470.

Palma, Á. T., Cáceres-Montenegro, I., Bennett, R. S., Magnolfi, S., Henríquez, L. A., Guerra, J. F., Manríquez, K., and Palma, R. E. (2011). Near-shore distribution of phyllosomas of the two only lobster species (Decapoda: Achelata) present in Robinson Crusoe Island and endemic to the Juan Fernández archipelago. *Revista Chilena de Historia Natural* **84**, 379–390. doi:10.4067/S0716-078X2011000300006

Pelegrí, J. L., and Benazzouz, A. (2015). Coastal upwelling off North-West Africa. In 'Oceanographic and biological features in the Canary Current Large Marine Ecosystem'. (Eds L. Valdés and I. Déniz-González.) pp. 93–103

Pelegrí, J. L., and Peña-Izquierdo, J. (2015). Eastern boundary currents off north-west Africa. In 'Oceanographic and biological features in the Canary Current Large Marine Ecosystem.' (Eds L. Valdés and I. Déniz-González.) pp. 83–92

Pessani, D., and Mura, M. (2007). The Biology of the Mediterranean Scyllarids. In 'The Biology and Fisheries of the Slipper Lobster'. (Eds K. L. Lavalli and E. Spanier.) pp. 263–286 doi:10.1201/9781420005165.ch13

Phillips, B. F. (1972). A semi-quantitative collector of the puerulus larvae of the western rock lobster *Panulirus longipes cygnus* George (Decapoda, Palinuridae). *Crustaceana* **22**, 147–154.

Phillips, B. F., Booth, J. D., Cobb, J. S., Jeffs, A. G., and McWilliam, P. (2006). Larval and Postlarval Ecology. In 'Lobsters: Biology, Management, Aquaculture and Fisheries'. pp. 231–262 doi:10.1002/9780470995969.ch7

Phillips, B. F., Brown, P. A., Rimmer, D. W., and Braine, S. J. (1981). Description, distribution and abundance of late larval stages of the scyllaridae (slipper lobsters) in the South-eastern Indian Ocean. *Marine and Freshwater Research* **32**, 417–437. doi:10.1071/MF9810417

Phillips, B. F., and McWilliam, P. S. (1989). Phyllosoma larvae and the ocean currents off the hawaiian islands. *Pacific Science* **43**, 352–361.

Phillips, B. F., and McWilliam, P. S. (1986). The pelagic phase of spiny lobster development. *Canadian Journal of Fisheries and Aquatic Sciences* **43**, 2153–2163.

Prasad, R. R., George, M. J., and Tampi, P. R. S. (1975). Phyllosoma larvae from the indian ocean collected by the DANA expedition 1928-1930. *Journal of the Marine Biological Association of India.* **17**, 56–107.

Quigley, D. T. G., Flannery, K., Herdson, D., Lord, R., and Holmes, J. M. C. (2010). Slipper lobster (*Scyllarus arctus* (L.)) (Crustacea: Decapoda) from Irish, U. K. and Channel Island waters. *The Irish Naturalists' Journal* **31**, 33–39.

Quinteiro, J., Rodríguez-Castro, J., and Rey-Méndez, M. (2007). Population genetic structure of the stalked barnacle *Pollicipes pollicipes* (Gmelin, 1789) in the northeastern Atlantic: Influence of coastal currents and mesoscale hydrographic structures. *Marine Biology* **153**, 47–60. doi:10.1007/s00227-007-0783-0

Robertson, P. (1969a). Biological investigations of the deep sea. No. 48. Phyllosoma larvae of a scyllarid lobster, *Arctides guineensis*, from the western Atlantic. *Marine Biology* **4**, 143–151. doi:10.1007/BF00347040

Robertson, P. B. (1979). Larval development of the scyllarid lobster *Scyllarus planorbis* Holthuis reared in the laboratory. *Bulletin of Marine Science* **29**, 320–328.

Robertson, P. B. (1968a). The complete larval development of the sand lobster *Scyllarus americanus* (Smith), (Decapoda, Scyllaridae) in the laboratory with notes on larvae from the plankton. *Bulletin of Marine Science* **18**, 294–432.

Robertson, P. B. (1969b). The early larval development of the scyllarid lobster *Scyllarides aequinoctialis* (Lund) in the laboratory, with a revision of the larval characters of the genus. *Deep-Sea Research and Oceanographic Abstracts* **16**, 557–586. doi:10.1016/0011-7471(69)90059-X

Robertson, P. B. (1971). The larvae and postlarvae of the scyllarid lobster *Scyllarus depressus*

(Smith). *Bulletin of Marine Science* **21**, 841–865.
Robertson, P. B. (1968b). The larval development of some western Atlantic lobsters of the family Scyllaridae. The University of Miami.
Rodríguez, J. M., Barton, E. D., Eve, L., and Hernández-León, S. (2001). Mesozooplankton and ichthyoplankton distribution around Gran Canaria, an oceanic island in the NE Atlantic. *Deep-Sea Research Part I* **48**, 2161–2183. doi:10.1016/S0967-0637(01)00013-9
Rudorff, C. A. G., Lorenzzetti, J. A., Gherardi, D. F. M., and Lins-Oliveira, J. E. (2009). Modeling spiny lobster larval dispersion in the Tropical Atlantic. *Fisheries Research* **96**, 206–215. doi:10.1016/j.fishres.2008.11.005
Scholtz, G., and Richter, S. (1995). Phylogenetic systematics of the reptantian Decapoda (Crustacea, Malacostraca). *Zoological Journal of the Linnean Society* **113**, 289–328. doi:10.1111/j.1096-3642.1995.tb00936.x
Shojima, Y. (1963). Scyllarid phyllosomas' habit of accompanying the jelly-fish. *Bulletin of the Japanese Society for the Science of Fish* **29**, 349–353.
Silva, K. C. A., Fransen, C. H. J. M., Ramos-Porto, M., Paiva, K. S., Cintra, I. H. A., and Cruz, R. (2012). Report of *Scyllarus chacei* Holthuis, 1960 (Decapoda, Scyllaridae) in Amapá State continental shelf of Brazil. *Crustaceana* **85**, 1171–1177. doi:10.1163/156854012X651493
Sims, H. W. (1966). Notes on Spiny Lobster Larvae in the North Atlantic. *Quarterly Journal of the Florida Academy of Sciences* **29**, 257–264. doi:10.2307/24315262
Sims, H. W., and Brown, C. L. (1968). A giant scyllarid phyllosoma larva taken north of Bermuda (Palinuridea). *Crustaceana Supplement 2: Studies of Decapod Larval Development*, 80–82. Available at: SERTC larval reprints/Decapoda
Smith, S. I. (1869). Descriptions of a new genus and two new species of Scyllaridae and a new species of Aethra from North America. *American Journal of Science and Arts* **48**, 118–121.
Smith, S. I. (1881). Preliminary notice of the Crustacea dredged, in 64 to 325 fathoms, off the south coast of New England, by the United States Fish Commisssion in 1880. *Proceedings of the United States National Museum* **3**, 413–452.
Spalding, M. D., Fox, H. E., Allen, G. R., Davidson, N., Ferdaña, Z. A., Finlayson, M., Halpern, B. S., Jorge, M. A., Lombana, A., Lourie, S. A., Martin, K. D., Mcmanus, E., Molnar, J., Recchia, C. A., and Robertson, J. (2007). Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. *BioScience* **57**, 573. doi:10.1641/B570707
Tan, T., and Rüger, H.-J. (1989). Benthic studies of the Northwest African upwelling region: bacteria standing stock and ETS-activity, ATP-biomass and Adenylate Energy Charge. *Marine Ecology Progress Series* **51**, 167–176. doi:10.3354/meps051167
Tavares, M. (1997). Scyllarus ramosae, new species, from the brazilian continental slope, with notes on congeners occurring in the area (Decapoda: Scyllaridae). *Journal of Crustacean Biology* **17**, 716–724.
Thomas, L. R. (1963). Phyllosoma larvae associated with Medusae. *Nature* **198**, 208.
Wakabayashi, K., and Phillips, B. F. (2016). Morphological descriptions of laboratory reared larvae and post-larvae of the Australian shovel-nosed lobster *Thenus australiensis* Burton & Davie, 2007 (Decapoda, Scyllaridae). *Crustaceana* **89**, 97–117. doi:10.1163/15685403-00003511
Wakabayashi, K., and Tanaka, Y. (2012). The jellyfish-rider: phyllosoma larvae of spiny and slipper lobsters associated with jellyfish. *TAXA: Proceedings of the Japanese Society of Systematic Zoology* **33**, 5–12.
Wakabayashi, K., Yang, C.-H., Shy, J.-Y., He, C.-H., and Chan, T.-Y. (2017). Correct identification and redescription of the larval stages and early juveniles of the slipper lobster *Eduarctus martensii* (Pfeffer, 1881) (Decapoda: Scyllaridae). *Journal of Crustacean*

Biology **37**, 204–219. doi:10.1093/jcbiol/rux009
Webber, W. R., and Booth, J. D. (2001). Larval stages, developmental ecology, and distribution of *Scyllarus* sp. Z (probably *Scyllarus aoteanus* Powell, 1949) (Decapoda: Scyllaridae. *New Zeland Journal of Marine and Freshwater Research* **35**, 1025–1056. doi:10.1080/00288330.2001.9517061 To
Webber, W. R., and Booth, J. D. (2007). Taxonomy and Evolution. In 'The Biology and Fisheries of the Slipper Lobster'. (Eds K. L. Lavalli and E. Spanier.) pp. 39–66. (CRC Press.) doi:10.1201/9781420005165.pt2
De Wolf, H., Backeljau, T., Van Dongen, S., and Verhagen, R. (1998). Large-scale patterns of shell variation in *Littorina striata*, a planktonic developing periwinkle from Macaronesia (Mollusca: Prosobranchia). *Marine Biology* **131**, 309–317. doi:10.1007/s002270050324
Yang, C., Lin, C., and Chan, T. (2014). Additional slipper lobsters of the subfamily Scyllarinae Latreille, 1825 (Crustacea, Achelata, Scyllaridae) from Taiwan. *Zootaxa* **3852**, 336–346.
Yeung, C., and McGowan, M. F. (1991). Diferences in inshore-offshore and vertical distribution of phyllosoma larvae of *Panulirus*, *Scyllarus* and *Scyllarides* in the Florida Keys in May-June, 1989. *Bulletin of Marine Science* **49**, 699–714. doi:10.1017/CBO9781107415324.004

ANNEXES

ANNEX 1

Species	*Country*	*Voucher code*	*Date*	*Latitude*	*Longitude*	*Depth (m)*	*Reference*	*Stage*
S. arctus	Spain	ICMD12|1995	13/01/1993	40.61	0.59	23–25	Genis-Armero et al. 2017	Adult
S. arctus	Spain	ICMD69|2007	16/05/2003	41.91	3.52	401–450	Genis-Armero et al. 2017	Phyllosoma
S. arctus	Spain	ICMD68|2007	16/05/2003	42.11	3.59	401–450	Genis-Armero et al. 2017	Phyllosoma
S. caparti	Angola	RBINS/INV.13276 (Holotype)	12/04/1949	-9.78	13.18	35	Holthuis 1952	Adult
S. caparti	Angola	RBINS/INV.13276 (Paratype)	12/04/1949	-9.78	13.18	35	Holthuis 1952	Adult
S. caparti	Angola	RMNH/CRUS.D.8617 (Paratype)	13/04/1949	-9.37	13.02	50	Holthuis 1952	Adult
S. caparti	Angola	RBINS/INV.13273	03/08/1949	-6.07	12.16	50	Holthuis 1952	Juvenile
S. caparti	Angola	RBINS/INV-13275 (Paratype)	24/03/1949	-5.17	11.85	53	Holthuis 1952	Adult
S. caparti	Gabon	-	28/11/1963	-2.63	9.5	50	Crosnier 1967	Adult

S. caparti	Gabon	RBINS/INV.13274 (Paratype)	08/03/1949	-0.88	8.67	-	Holthuis 1952	Adult
S. caparti	Nigeria	RMNH/CRUS.D.26021	13/05/1965	4.05	5.68	-	Unpublished	Adult
S. caparti	Nigeria	USNM/122846	13/05/1965	4.05	5.68	33	Unpublished	Adult
S. caparti	Nigeria	RMNH/CRUS.D.24950	14/05/1965	4.07	6.3	-	Unpublished	Adult
S. caparti	Nigeria	RMNH/CRUS.D.24949	13/05/1965	4.22	5.5	-	Unpublished	Adult
S. caparti	Liberia	RMNH/CRUS.D.21062	02/06/1964	4.25	-7.53	-	Unpublished	Adult
S. caparti	Ghana	USNM/126149	28/05/1964	4.66	-2.02	49–53	Unpublished	Adult
S. caparti	Ghana	RMNH/CRUS.D.21063	28/05/1964	4.67	-2	-	Unpublished	Adult
S. caparti	Nigeria	USNM/122845	13/05/1965	4.73	5.28	37	Unpublished	Adult
S. caparti	Ghana	USNM/126152	01/06/1964	4.75	-6.23	46	Unpublished	Adult
S. caparti	Ghana	USNM/126148	28/05/1964	4.8	-1.7	33	Unpublished	Adult
S. caparti	Ghana	RMNH/CRUS.D.21058	28/05/1964	4.93	-0.78	-	Unpublished	Adult
S. caparti	Ghana	USNM/126147	28/05/1964	4.93	-0.78	35–37	Unpublished	Adult
S. caparti	Ghana	RMNH/CRUS.D.21065	28/05/1964	4.96	-1.27	-	Unpublished	Adult
S. caparti	Côte d'Ivoire	RMNH/CRUS.D.21064	31/05/1964	5.07	-4.86	-	Unpublished	Adult
S. caparti	Côte d'Ivoire	RMNH/CRUS.D.21061	31/05/1964	5.08	-4.99	-	Unpublished	Adult
S. caparti	Côte d'Ivoire	USNM/126145	31/05/1964	5.08	-4.99	22	Unpublished	Adult
S. caparti	Côte d'Ivoire	USNM/126151	31/05/1964	5.08	-4.86	37	Unpublished	Adult
S. caparti	Ghana	RMNH/CRUS.D.21060	30/05/1964	5.12	-4.53	-	Unpublished	Adult
S. caparti	Côte d'Ivoire	USNM/1004700	21/10/1963	5.12	-3.37	20	Unpublished	Adult
S. caparti	Ghana	USNM/126150	30/05/1964	5.12	-4.53	38–42	Unpublished	Adult
S. caparti	Ghana	RMNH/CRUS.D.21066	27/05/1964	5.42	-0.02	-	Unpublished	Adult

S. caparti	Ghana	RMNH/CRUS.D.9993	26/04/1951	5.55	-0.18	26–32	Unpublished	-
S. caparti	Ghana	RMNH/CRUS.D.9994	04/04/1951	5.55	-0.18	40–43	Unpublished	-
S. caparti	Ghana	RMNH/CRUS.D.9995	02/05/1951	5.55	-0.18	37–51	Unpublished	-
S. caparti	Ghana	RMNH/CRUS.D.26022	05/04/1951	5.55	-0.18	64	Unpublished	Adult
S. caparti	Ghana	USNM/97164	04/04/1951	5.55	-0.18	40–43	Unpublished	Adult
S. caparti	Ghana	USNM/97165	26/02/1951	5.55	-0.18	21	Unpublished	Adult
S. caparti	Ghana	USNM/97166	02/05/1951	5.55	-0.18	37–51	Unpublished	Adult
S. caparti	Ghana	RMNH/CRUS.D.21059	25/05/1964	5.67	0.5	-	Unpublished	Adult
S. caparti	Ghana	USNM/126146	26/05/1964	5.67	0.5	46	Unpublished	Adult
S. caparti	Togo	-	18/10/1963	5.97	1.28	42–50	Crosnier 1967	Adult
S. caparti	Togo	-	18/10/1963	6	1.33	45–50	Crosnier 1967	Adult
S. caparti	Benin	-	-/10/63	6.18	2.2	40–45	Crosnier 1967	Adult
S. caparti	Benin	RMNH/CRUS.D.21558	23/02/1964	6.22	1.75	-	Unpublished	Adult
S. caparti	CVI	UCA/MA023011PED02PH01	27/04/2015	9.56	-25.99	0–250	Genis-Armero et al. 2020	Phyllosoma
S. caparti	CVI	UCA/MA023011PEN04PH01	27/04/2015	9.56	-25.99	0–250	Genis-Armero et al. 2020	Phyllosoma
S. caparti	CVI	UCA/MA023011PEN05PH01	27/04/2015	9.56	-25.99	0–250	Genis-Armero et al. 2020	Phyllosoma
S. caparti	CVI	UCA/MA023011PEN05PH02-02	27/04/2015	9.56	-25.99	0–250	Genis-Armero et al. 2020	Phyllosoma

S. caparti	CVI	UCA/MA023011PEN05PH04	27/04/2015	9.56	-25.99	0–250	Genis-Armero et al. 2020	Phyllosoma
S. caparti	CVI	UCA/MA023011PEN05PH07	27/04/2015	9.56	-25.99	0–250	Genis-Armero et al. 2020	Phyllosoma
S. caparti	CVI	UCA/MA023011PEN05PH08	27/04/2015	9.56	-25.99	0–250	Genis-Armero et al. 2020	Phyllosoma
S. caparti	CVI	UCA/MA023011PEN05PH09	27/04/2015	9.56	-25.99	0–250	Genis-Armero et al. 2020	Phyllosoma
S. caparti	CVI	UCA/MA023011PEN05PH10	27/04/2015	9.56	-25.99	0–250	Genis-Armero et al. 2020	Phyllosoma
S. caparti	CVI	UCA/MA025012PEN00PH02	27/04/2015	9.56	-25.99	0–250	Genis-Armero et al. 2020	Phyllosoma
S. caparti	CVI	UCA/MA025012PEN00PH03	27/04/2015	9.56	-25.99	0–250	Genis-Armero et al. 2020	Phyllosoma
S. caparti	CVI	UCA/MA025012PEN00PH04	27/04/2015	9.56	-25.99	0–250	Genis-Armero et al. 2020	Phyllosoma
S. caparti	CVI	UCA/MA025012PEN00PH05	27/04/2015	9.56	-25.99	0–250	Genis-Armero et al. 2020	Phyllosoma
S. caparti	CVI	UCA/MA025012PEN00PH06	27/04/2015	9.56	-25.99	0–250	Genis-Armero et al. 2020	Phyllosoma

S. caparti	CVI	UCA/MA025012PEN00PH09	27/04/2015	9.56	-25.99	0–250	Genis-Armero et al. 2020	Phyllosoma
S. caparti	CVI	UCA/MA025012PEN00PH13	27/04/2015	9.56	-25.99	0–250	Genis-Armero et al. 2020	Phyllosoma
S. caparti	CVI	UCA/MA025012PEN00PH16	27/04/2015	9.56	-25.99	0–250	Genis-Armero et al. 2020	Phyllosoma
S. caparti	CVI	UCA/MA025012PEN00PH21	27/04/2015	9.56	-25.99	0–250	Genis-Armero et al. 2020	Phyllosoma
S. caparti	CVI	UCA/MA025012PEN00PH22	27/04/2015	9.56	-25.99	0–250	Genis-Armero et al. 2020	Phyllosoma
S. caparti	CVI	UCA/MA025012PEN00PH23	27/04/2015	9.56	-25.99	0–250	Genis-Armero et al. 2020	Phyllosoma
S. caparti	CVI	UCA/MA025012PEN00PH24	27/04/2015	9.56	-25.99	0–250	Genis-Armero et al. 2020	Phyllosoma
S. caparti	Guinea-Bissau	RBINS/INV-13277 (Paratype)	08/06/1949	10.07	-16.5	60	Holthuis 1952	Adult
S. caparti	Guinea-Bissau	CCDE-IEOCD:1525	11/05/2012	10.49	-14.9	50	Unpublished	Adult
S. caparti	Guinea-Bissau	CCDE-IEOCD:201	08/11/2008	10.53	-16.43	37	Muñoz et al. 2012	Adult
S. caparti	Guinea-Bissau	CCDE-IEOCD:199	26/10/2008	11.14	-17.09	52	Muñoz et al. 2012	Adult
S. caparti	Guinea-Bissau	CCDE-IEOCD:200	09/11/2008	11.27	-17.11	45	Muñoz et al. 2012	Adult

S. caparti	Guinea-Bissau	ICMD222|1998	30/12/1984	11.3	-17.08	33	Genis-Armero et al. 2017	Adult
S. caparti	Guinea-Bissau	ICMD223|1998	31/12/1984	11.5	-16.83	33	Genis-Armero et al. 2020	Adult
S. caparti	CVI	UCA/MA023011PED05PH01	25/04/2015	12.5	-25.99	0–100	Genis-Armero et al. 2020	Phyllosoma
S. caparti	CVI	UCA/MA023011PEN04PH02	25/04/2015	12.5	-25.99	0–50	Genis-Armero et al. 2020	Phyllosoma
S. caparti	CVI	UCA/MA023011PEN05PH02-01	25/04/2015	12.5	-25.99	400–700	Genis-Armero et al. 2020	Phyllosoma
S. caparti	CVI	UCA/MA023011PEN05PH03	25/04/2015	12.5	-25.99	0–50	Genis-Armero et al. 2020	Phyllosoma
S. caparti	CVI	UCA/MA023011PEN05PH05	25/04/2015	12.5	-25.99	0–100	Genis-Armero et al. 2020	Phyllosoma
S. caparti	CVI	UCA/MA023011PEN05PH06	25/04/2015	12.5	-25.99	0–50	Genis-Armero et al. 2020	Phyllosoma
S. caparti	CVI	UCA/MA025012PEN00PH01	25/04/2015	12.5	-25.99	0–50	Genis-Armero et al. 2020	Phyllosoma
S. caparti	CVI	UCA/MA025012PEN00PH07	25/04/2015	12.5	-25.99	0–50	Genis-Armero et al. 2020	Phyllosoma

S. caparti	CVI	UCA/MA025012PEN00PH08	25/04/2015	12.5	-25.99	0–50	Genis-Armero et al. 2020	Phyllosoma
S. caparti	CVI	UCA/MA025012PEN00PH10	25/04/2015	12.5	-25.99	0–50	Genis-Armero et al. 2020	Phyllosoma
S. caparti	CVI	UCA/MA025012PEN00PH11	25/04/2015	12.5	-25.99	0–50	Genis-Armero et al. 2020	Phyllosoma
S. caparti	CVI	UCA/MA025012PEN00PH12	25/04/2015	12.5	-25.99	50–100	Genis-Armero et al. 2020	Phyllosoma
S. caparti	CVI	UCA/MA025012PEN00PH14	25/04/2015	12.5	-25.99	0–50	Genis-Armero et al. 2020	Phyllosoma
S. caparti	CVI	UCA/MA025012PEN00PH15	25/04/2015	12.5	-25.99	50–100	Genis-Armero et al. 2020	Phyllosoma
S. caparti	CVI	UCA/MA025012PEN00PH17	25/04/2015	12.5	-25.99	0–50	Genis-Armero et al. 2020	Phyllosoma
S. caparti	Senegal	CCDE-IEOCD:970	22/05/2012	12.86	-17.55	57	Unpublished	Adult
S. caparti	Mauritania	RMNH/CRUS.D.50904	18/03/2004	17.72	-16.47	-	Unpublished	Adult
S. caparti	Mauritania	RMNH/CRUS.D.50900	16/03/2004	18.2	-16.445	-	Unpublished	Adult
S. caparti	Mauritania	CCDE-IEOCD:981	11/11/2011	18.54	-16.47	32	Unpublished	Adult
S. caparti	Mauritania	RMNH/CRUS.D.39249	10/06/1988	18.8	-16.72	260–280	Fransen 1991	Juvenile
S. caparti	Mauritania	RMNH/CRUS.D.39248	09/06/1988	18.82	-16.37	23	Fransen 1991	Adult
S. caparti	Mauritania	RMNH/CRUS.D.39242	08/06/1988	18.83	-16.35	21	Fransen 1991	Adult

S. caparti	Mauritania	RMNH/CRUS.D.39243	08/06/1988	18.83	-16.32	18	Fransen 1991	Adult
S. caparti	Mauritania	RMNH/CRUS.D.39244	08/06/1988	18.83	-16.37	26	Fransen 1991	Adult
S. caparti	Mauritania	RMNH/CRUS.D.39245	08/06/1988	18.83	-16.38	30	Fransen 1991	Adult
S. caparti	Mauritania	RMNH/CRUS.D.39246	08/06/1988	18.83	-16.47	60–66	Fransen 1991	Adult
S. caparti	Mauritania	RMNH/CRUS.D.39247	09/06/1988	18.83	-16.34	20	Fransen 1991	Adult
S. caparti	Mauritania	RMNH/CRUS.D.39264	08/06/1988	18.83	-16.4	37	Fransen 1991	Adult
S. caparti	Mauritania	RMNH/CRUS.D.39269	08/06/1988	18.83	-16.42	37	Fransen 1991	Adult
S. caparti	Mauritania	RMNH/CRUS.D.39280	29/10/1978	18.93	-16.45	32	Fransen 1991	Adult
S. caparti	Mauritania	RMNH/CRUS.D.39279	29/10/1978	18.97	-16.53	51	Fransen 1991	Adult
S. caparti	Mauritania	RMNH/CRUS.D.39278	29/10/1978	19	-16.4	21	Fransen 1991	Adult
S. caparti	Mauritania	RMNH/CRUS.D.39250	11/06/1988	19.07	-16.45	25	Fransen 1991	Adult
S. caparti	Mauritania	RMNH/CRUS.D.39251	11/06/1988	19.08	-16.47	30	Fransen 1991	Adult
S. caparti	Mauritania	RMNH/CRUS.D.39252	11/06/1988	19.08	-16.48	30	Fransen 1991	Adult
S. caparti	Mauritania	CCDE-IEOCD:969	08/06/2012	19.31	-16.75	30	Unpublished	Adult
S. caparti	Mauritania	RMNH/CRUS.D.39257	16/06/1988	19.43	-16.83	45	Fransen 1991	Adult
S. caparti	Mauritania	CCDE-IEOCD:1088	08/06/2012	19.52	-17	105	Unpublished	Juvenile
S. caparti	Mauritania	RMNH/CRUS.D.39255	15/06/1988	19.58	-16.85	38	Fransen 1991	Adult

S. caparti	Mauritania	RMNH/CRUS.D.49596	-	19.58	-16.83	19	Unpublished	Adult
S. caparti	Mauritania	RMNH/CRUS.D.39256	15/06/1988	19.58	-16.95	85–90	Fransen 1991	Juvenile
S. caparti	Mauritania	RMNH/CRUS.D.39266	16/06/1988	19.72	-16.98	61–78	Fransen 1991	Adult
S. caparti	Mauritania	RMNH/CRUS.D.57150	16/06/1988	19.75	-17.08	-	Unpublished	Adult
S. caparti	Mauritania	CCDE-IEOCD:1104	09/06/2012	19.82	-17.2	69	Unpublished	Adult
S. caparti	Mauritania	RMNH/CRUS.D.39254	14/06/1988	19.98	-17.5	100	Fransen 1991	Adult
S. caparti	Mauritania	RMNH/CRUS.D.39253	14/06/1988	20	-17.28	35	Fransen 1991	Adult
S. caparti	Mauritania	RMNH/CRUS.D.39258	13/06/1988	20	-17.18	25	Fransen 1991	Adult
S. caparti	Mauritania	RMNH/CRUS.D.39265	13/06/1988	20	-17.28	32	Fransen 1991	Adult
S. caparti	Mauritania	RMNH/CRUS.D.39270	13/06/1988	20	-17.3	38–41	Fransen 1991	Adult
S. caparti	Mauritania	RMNH/CRUS.D.39274	13/06/1988	20	-17.2	28	Fransen 1991	Adult
S. caparti	Mauritania	RMNH/CRUS.D.39275	13/06/1988	20	-17.35	43	Fransen 1991	Adult
S. caparti	Mauritania	RMNH/CRUS.D.39259	13/06/1988	20.02	-17.25	30	Fransen 1991	Adult
S. caparti	Mauritania	RMNH/CRUS.D.57151	14/06/1988	20.03	-17.43	-	Unpublished	Adult
S. caparti	Mauritania	RMNH/CRUS.D.25482	01/04/1968	20.07	-17.33	33–40	Unpublished	Adult
S. caparti	Mauritania	RMNH/CRUS.D.39195	22/01/1969	20.17	-17.2	18	Unpublished	Adult
S. caparti	Mauritania	RMNH/CRUS.D.39281	02/11/1978	20.33	-17.45	42	Fransen 1991	Adult
S. caparti	Mauritania	RMNH/CRUS.D.39260	18/06/1988	20.4	-17.32	35–40	Fransen 1991	Adult

S. caparti	Mauritania	RMNH/CRUS.D.39262	19/06/1988	20.4	-17.5	55–60	Fransen 1991	Adult
S. caparti	Mauritania	RMNH/CRUS.D.39263	19/06/1988	20.4	-17.57	62–75	Fransen 1991	Adult
S. caparti	Mauritania	CCDE-IEOCD:973	10/06/2012	20.42	-17.59	80	Unpublished	Adult
S. caparti	Mauritania	CCDE-IEOCD:975	10/06/2012	20.42	-17.59	80	Unpublished	Adult
S. caparti	Mauritania	RMNH/CRUS.D.39267	19/06/1988	20.42	-17.1	17	Fransen 1991	Adult
S. caparti	Mauritania	RMNH/CRUS.D.39268	19/06/1988	20.42	-17.43	47	Fransen 1991	Adult
S. caparti	Mauritania	RMNH/CRUS.D.39277	19/06/1988	20.42	-17.67	95–100	Fransen 1991	Adult
S. caparti	Mauritania	RMNH/CRUS.D.39261	19/06/1988	20.43	-17.35	37	Fransen 1991	Adult
S. caparti	Mauritania	RMNH/CRUS.D.39271	19/06/1988	20.45	-17.25	32	Fransen 1991	Adult
S. caparti	Mauritania	RMNH/CRUS.D.57149	09/09/2004	20.57	-17.56	-	Unpublished	Adult
S. caparti	Mauritania	RMNH/CRUS.D.39273	21/06/1988	20.7	-17.5	63–71	Fransen 1991	Adult
S. caparti	Mauritania	RMNH/CRUS.D.39276	21/06/1988	20.72	-17.38	50	Fransen 1991	Adult
S. caparti	Mauritania	RMNH/CRUS.D.39272	21/06/1988	20.73	-17.42	54–62	Fransen 1991	Adult
S. caparti	Mauritania	CCDE-IEOCD:972	10/06/2012	20.74	-17.2	81	Unpublished	Adult
S. caparti	Mauritania	CCDE-IEOCD:974	10/06/2012	20.74	-17.56	81	Unpublished	Adult
S. caparti	Morocco	CCDE-IEOCD:977	18/11/2011	21.1	-17.68	77	Unpublished	Adult
S. caparti	Western Sahara	SMF 24025	01/03/1975	21.15	-17.38	68–70	Unpublished	Adult
S. caparti	Mauritania	CCDE-IEOCD:978	17/11/2011	21.25	-17.92	79	Unpublished	Adult
S. caparti	Western Sahara	SMF 24018	28/02/1975	21.3	-17.37	85	Unpublished	Juvenile

S. caparti	Western Sahara	SMF 24010	25/02/1975	21.35	-17.35	80–100	Unpublished	Adult
S. caparti	Morocco	CCDE-IEOCD:979	22/11/2011	23.49	-17.26	57	Unpublished	Adult
S. caparti	Morocco	CCDE-IEOCD:980	25/11/2011	24.98	-16.23	69	Unpublished	Adult
S. caparti	Morocco	CCDE-IEOCD:976	03/12/2011	27.13	-13.93	70	Unpublished	Adult
S. caparti	Gabon	-	27/05/1960	-	-	65–70	Crosnier 1967	Adult
S. caparti	Gabon	-	-/6/60	-	-	40	Crosnier 1967	Adult
S. paradoxus	São Tomé Island	MNHN-IU-2013-14844	12/06/1956	0.38	6.72	4–5	Genis-Armero et al. 2020	Adult
S. paradoxus	Cameroun	NHMUK 1957.5.26.305-306	-	3.88	9.03	-	Unpublished	Adult
S. paradoxus	Ghana	NHMUK 1954.12.7.101	-	5.53	-0.19	-	Unpublished	Adult
S. paradoxus	Ghana	NHMUK 1954.12.7.90-96	-	5.53	-0.19	-	Unpublished	Adult
S. paradoxus	Ghana	NHMUK 1954.12.7.97-100	-	5.53	-0.19	-	Unpublished	Adult
S. paradoxus	Nigeria	NHMUK 1957.5.26.303	-	6.25	3.98	-	Unpublished	Adult
S. paradoxus	Nigeria	NHMUK 1957.5.26.304	-	6.27	2.83	-	Unpublished	Adult
S. paradoxus	Nigeria	NHMUK 1914.11.30.12-16	-	6.36	3.4	-	Unpublished	Adult

S. paradoxus	Guinea	MNHN-IU-2013-14845	14/03/1953	9.37	-13.7	20	Genis-Armero et al. 2020	Adult
S. paradoxus	Guinea	MNHN-IU-2016-10587	18/05/1988	9.5	-14.9	40	Genis-Armero et al. 2020	Adult
S. paradoxus	Guinea	CCDE-IEOCD:198	03/11/2008	10.32	-16.17	24	Genis-Armero et al. 2020	Adult
S. posteli	Angola	SMF 19728	21/05/1989	-8.53	12.27	41	Unpublished	Adult
S. posteli	Congo	RMNH/CRUS.D.8556	29/03/1949	-4.88	11.72	70	Genis-Armero et al. 2020	Adult
S. posteli	Guinea-Bissau	CCDE-IEOCD:202	09/11/2008	11.27	-17.11	45	Genis-Armero et al. 2020	Adult
S. posteli	Guinea-Bissau	MNHN-IU-2013-14853	09/04/2014	11.42	-15.57	15–25	Genis-Armero et al. 2020	Adult
S. posteli	Guinea-Bissau	ICMD218|1998	07/02/1985	11.58	-17.25	55–58	Genis-Armero et al. 2017	Adult
S. posteli	Spain	CCDE-IEOCD:858	24/02/2013	36.59	-6.44	26	Genis-Armero et al. 2020	Adult
S. pygmaeus	CVI	UCA/MA025012PEN00PH18	27/04/2015	9.56	-25.99	0–250	Genis-Armero et al. 2020	Phyllosoma
S. pygmaeus	Spain	-	19/05/2005	38.08	0	601–650	Genis-Armero et al. 2017	Phyllosoma

S. pygmaeus	Spain	ICMD63|2007	05/05/2003	38.12	-0.0626	251–300	Genis-Armero et al. 2017	Phyllosoma
S. pygmaeus	Spain	ICMD64|2007	19/05/2004	38.98	0.5	701–750	Genis-Armero et al. 2017	Phyllosoma
S. pygmaeus	Spain	-	23/05/2004	41.02	1.38	101–150	Genis-Armero et al. 2017	Phyllosoma
S. pygmaeus	Spain	ICMD5|1995	30/10/1991	41.68	2.81	35–40	Genis-Armero et al. 2017	Adult
S. subarctus	Namibia	ICMD 300/1991	28/08/1980	-18	11.42	270–274	Macpherson, 1983	Adult
S. subarctus	Namibia	ICMD001081	25/04/1986	-18	10.55	0–200	Genis-Armero et al. 2017	Phyllosoma
S. subarctus	Namibia	ICMD001082	25/04/1986	-18	10.55	0–200	Genis-Armero et al. 2017	Phyllosoma
S. subarctus	Namibia	ICMD001083	25/04/1986	-18	10.55	0–200	Genis-Armero et al. 2017	Phyllosoma
S. subarctus	Namibia	ICMD001084	25/04/1986	-18	10.55	0–200	Genis-Armero et al. 2017	Phyllosoma
S. subarctus	Namibia	ICMD001085	25/04/1986	-18	10.55	0–200	Genis-Armero et al. 2017	Phyllosoma
S. subarctus	Namibia	ICMD001086	25/04/1986	-18	10.55	0–200	Genis-Armero et al. 2017	Phyllosoma

S. subarctus	Namibia	ICMD001087	25/04/1986	-18	10.55	0–200	Genis-Armero et al. 2017	Phyllosoma
S. subarctus	Namibia	ICMD 299/1991	25/03/1981	-17.48	11.38	293–300	Macpherson, 1983	Adult
S. subarctus	Namibia	ICMD002512	28/09/1983	-17.25	11.45	-	Genis-Armero et al. 2019	Adult
S. subarctus	Angola	RMNH D 30937	24/03/1968	-17.22	11.45	155	Crosnier 1970	Adult
S. subarctus	Angola	USNM 127766	24/03/1968	-17.22	11.45	155	Crosnier 1970	Adult
S. subarctus	Angola	USNM 127765	18/03/1968	-16.62	11.37	126	Crosnier 1970	Adult
S. subarctus	Angola	MNHN-IU-2013-14842	18/03/1968	-16.45	11.58	126	Crosnier 1970	Adult
S. subarctus	Angola	MNHN-IU-2013-14843	18/03/1968	-16.45	11.58	126	Crosnier 1970	Adult
S. subarctus	St. Helena	-	-	-16.01	-5.7	-	Genis-Armero et al. 2019	Adult
S. subarctus	St. Helena	-	-	-16.01	-5.7	-	Genis-Armero et al. 2019	Adult
S. subarctus	St. Helena	MNHN-IU-2016-10733	-	-16.01	-5.7	-	Genis-Armero et al. 2019	Nisto
S. subarctus	Guinea	CCDE-IEOCD:989-1	23/10/2011	9.34	-15.67	116	Genis-Armero et al. 2019	Adult

S. subarctus	Guinea	CCDE-IEOCD:989-2	23/10/2011	9.34	-15.67	116	Genis-Armero et al. 2019	Adult
S. subarctus	CVI	UCA/MA025012PEN00PH19	27/04/2015	9.56	-25.99	0–250	Genis-Armero et al. 2017	Phyllosoma
S. subarctus	CVI	UCA/MA025012PEN00PH20	27/04/2015	9.56	-25.99	0–250	Genis-Armero et al. 2017	Phyllosoma
S. subarctus	Guinea	CCDE-IEOCD:197-1	04/11/2008	10.28	-16.37	65	Genis-Armero et al. 2019	Adult
S. subarctus	Guinea	CCDE-IEOCD:197-2	04/11/2008	10.28	-16.37	65	Genis-Armero et al. 2019	Adult
S. subarctus	Senegal	CCDE-IEOCD:1105-1	27/05/2012	14.47	-17.51	103	Genis-Armero et al. 2019	Nisto
S. subarctus	Senegal	CCDE-IEOCD:999-1	04/11/2011	14.7	-17.91	154	Genis-Armero et al. 2019	Adult
S. subarctus	Senegal	CCDE-IEOCD:999-2	04/11/2011	14.7	-17.91	154	Genis-Armero et al. 2019	Adult
S. subarctus	Senegal	CCDE-IEOCD:999-3	04/11/2011	14.7	-17.91	154	Genis-Armero et al. 2019	Adult
S. subarctus	Senegal	CCDE-IEOCD:999-4	04/11/2011	14.7	-17.91	154	Genis-Armero et al. 2019	Adult

S. subarctus	CVI	UCA/MA019009PEN05PH01	21/04/2015	16.16	-26.03	0–100	Genis-Armero et al. 2017	Phyllosoma
S. subarctus	Mauritania	SMF 24011	16/02/1975	17.09	-16.73	131	Unpublished	Adult
S. subarctus	Mauritania	SMF 24012	17/02/1975	17.09	-16.73	127	Unpublished	Juvenile
S. subarctus	Mauritania	SMF 24013	19/02/1977	17.1	-16.75	198–200	Unpublished	Adult
S. subarctus	Mauritania	SMF 24027	13/02/1982	17.29	-16.46	95	Unpublished	Adult
S. subarctus	Mauritania	CCDE-IEOCD:968-1	09/06/2012	19.82	-17.2	69	Genis-Armero et al. 2019	Adult
S. subarctus	Mauritania	CCDE-IEOCD:968-2	09/06/2012	19.82	-17.2	69	Genis-Armero et al. 2019	Adult
S. subarctus	CVI	UCA/MA017008PED05PH01	19/04/2015	20.26	-24.25	0–100	Genis-Armero et al. 2017	Phyllosoma
S. subarctus	CVI	UCA/MA017008PED05PH02	19/04/2015	20.26	-24.25	0–100	Genis-Armero et al. 2017	Phyllosoma
S. subarctus	CVI	UCA/MA017008PED05PH03	19/04/2015	20.26	-24.25	0–100	Genis-Armero et al. 2017	Phyllosoma
S. subarctus	CVI	UCA/MA017008PED05PH04	19/04/2015	20.26	-24.25	0–100	Genis-Armero et al. 2017	Phyllosoma
S. subarctus	CVI	UCA/MA017008PED05PH05	19/04/2015	20.26	-24.25	0–100	Genis-Armero et al. 2017	Phyllosoma
S. subarctus	CVI	UCA/MA017008PED05PH06	19/04/2015	20.26	-24.25	0-100	Genis-Armero et al. 2017	Phyllosoma

S. subarctus	CVI	UCA/MA017008PED05PH07	19/04/2015	20.26	-24.25	0-100	Genis-Armero et al. 2017	Phyllosoma
S. subarctus	CVI	UCA/MA017008PN07DPH01	19/04/2015	20.26	-24.25	0-100	Genis-Armero et al. 2017	Phyllosoma
S. subarctus	Mauritania	MNHN-IU-2013-7181	-	20.41	-16.84	-	Genis-Armero et al. 2020	Adult
S. subarctus	Western Sahara	SMF 24026	01/03/1975	21.15	-17.38	68–70	Unpublished	Adult
S. subarctus	West Sahara	ZMB27241-1	01/03/1975	21.15	-17.38	68–70	Genis-Armero et al. 2019	Adult
S. subarctus	West Sahara	ZMB27241-2	01/03/1975	21.15	-17.38	68–70	Genis-Armero et al. 2019	Adult
S. subarctus	Western Sahara	SMF 24017	28/02/1975	21.3	-17.37	85	Unpublished	Adult
S. subarctus	Western Sahara	SMF 24028	27/02/1975	21.35	-17.47	168–177	Unpublished	Adult
S. subarctus	Western Sahara	SMF 24016	27/02/1975	21.35	-17.47	168–177	Unpublished	Juvenile
S. subarctus	Western Sahara	SMF 24019	20/02/1982	21.77	-17.43	125	Unpublished	Adult
S. subarctus	Western Sahara	SMF 24020	20/02/1982	21.85	-17.3	65	Unpublished	Juvenile
S. subarctus	Western Sahara	CCDE-IEOCD:984-1	22/11/2011	23.16	-17.31	150	Genis-Armero et al. 2019	Adult

S. subarctus	Western Sahara	CCDE-IEOCD:984-2	22/11/2011	23.16	-17.31	150	Genis-Armero et al. 2019	Adult
S. subarctus	Western Sahara	CCDE-IEOCD:984-3	22/11/2011	23.16	-17.31	150	Genis-Armero et al. 2019	Adult
S. subarctus	Canary Islands	ICMD002513	13/04/2012	28.54	-18	410-620	Genis-Armero et al. 2019	Phyllosoma
S. subarctus	Canary Islands	ICMD002350	19/04/2012	28.84	-16.14	50-150	Genis-Armero et al. 2019	Nisto
S. subarctus	Morroco	CCDE-IEOCD:995-1	14/12/2011	33.75	-8.66	46	Genis-Armero et al. 2019	Adult
S. subarctus	Morroco	CCDE-IEOCD:987-1	15/12/2011	34.04	-8.48	271	Genis-Armero et al. 2019	Adult
S. subarctus	Morroco	CCDE-IEOCD:987-2	15/12/2011	34.04	-8.48	271	Genis-Armero et al. 2019	Adult
S. subarctus	Morroco	CCDE-IEOCD:987-3	15/12/2011	34.04	-8.48	271	Genis-Armero et al. 2019	Adult
S. subarctus	Morroco	CCDE-IEOCD:987-4	15/12/2011	34.04	-8.48	271	Genis-Armero et al. 2019	Adult
S. subarctus	Mauritania	Pa-257	-	-	-	-	Genis-Armero et al. 2019	Adult

Zootaxa 4139 (4): 481–498
http://www.mapress.com/j/zt/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

http://doi.org/10.11646/zootaxa.4139.4.2
http://zoobank.org/urn:lsid:zoobank.org:pub:247A52DC-530C-46FB-A985-ED8E0444CF09

DNA barcoding the phyllosoma of *Scyllarides squammosus* (H. Milne Edwards, 1837) (Decapoda: Achelata: Scyllaridae)

FERRAN PALERO[1,2,6], REBECA GENIS-ARMERO[3], MICHAEL R. HALL[4] & PAUL F. CLARK[5]

[1]*Centre d'Estudis Avançats de Blanes (CEAB-CSIC), Carrer d'Accés a la Cala Sant Francesc 14, 17300 Blanes, Spain. E-mail: fpalero@ceab.csic.es*
[2]*INRA, Univ. Nice Sophia Antipolis, CNRS, UMR 1355-7254 Institut Sophia Agrobiotech, 06900 Sophia Antipolis, France.*
[3]*Department of Zoology, School of Biological Sciences, University of Valencia, Spain. E-mail: regear@alumni.uv.es*
[4]*Australian Institute of Marine Science, PMB No. 3, Townsville MC, Townsville QLD 4810, Australia. E-mail: M.Hall@aims.gov.au*
[5]*Department of Life Sciences, The Natural History Museum, Cromwell Road, London SW7 5BD, England. E-mail: p.clark@nhm.ac.uk*
[6]*Corresponding author. E-mail: fpalero@ceab.csic.es*

Abstract

Scyllarides has the largest number of species with commercial importance within the Scyllaridae family. As for other achelate lobsters, however, little is known of the unique long-lived planktonic phyllosoma stages of any of these tropical and temperate species. Recently, a large and diverse collection of Scyllaridae phyllosoma, compiled from cruises along the Coral Sea and spanning several years, has been analysed. Molecular evidence from DNA-barcoding and phylogenetic analyses is provided here on the identity of *S. squammosus* phyllosoma larvae, including stages that were previously undescribed or poorly known. As a consequence, the growth and morphological changes that occur during the mid- to late-stages of *S. squammosus* larval development is now well-documented. Furthermore, an additional collection of *S. squammosus* larvae, described by Alain Michel and thought to be no longer extant, were discovered in the crustacean collection of the Muséum national d'Histoire naturelle, Paris. This new molecular and morphological information is complemented by a review of the literature. As a result, descriptions of key larval characters by a number of authors were evaluated and appear to suggest the existence of distinct groups of larvae within *Scyllarides*. From a combination of adult and larval morphology, and molecular data, the results presented here revealed inconsistencies with regard to the affinities of species assigned to *Scyllarides*. This new evidence will contribute to future studies addressing the phylogenetic relationships within the genus.

Key words: Slipper lobster, larval phase, COI, plankton, Coral Sea

Introduction

Achelata is a group of decapod crustaceans characterized by the absence of chela and the presence of a specialized larval form known as phyllosoma (Scholtz & Richter 1995; Palero *et al.* 2014a). Epibenthic achelate lobsters are adapted for crawling and inhabitation of cracks and holes in reefs and rocky habitats (Booth & Phillips 1994). Recent morphological and molecular studies (Bracken-Grissom *et al.* 2014; Palero *et al.* 2014a) have confirmed that the Achelata comprises two distinct families, the Palinuridae (spiny and 'furry' lobsters) and the Scyllaridae (slipper lobsters). Palinuridae biology has been thoroughly studied due to the fact that this family is one of the most commercially important crustacean groups (Holthuis 1991). In comparison, slipper lobsters have been relatively poorly studied even though they contain a greater diversity of species (Chan 2010). The Scyllaridae contains 20 genera, 89 species (Chan 2010; Yang *et al.* 2014) and it is divided into four subfamilies: Arctidinae (including *Scyllarides* and *Arctides*), Ibacinae (*Ibacus*, *Evibacus* and *Parribacus*), Theninae (*Thenus*) and Scyllarinae (*Scyllarus* and 13 new genera proposed by Holthuis, 2002; see Holthuis 1985, 2002). Slipper lobsters constitute a monophyletic group that can be distinguished from other decapods by having the last antennal segment completely reduced to a flat plate that can act as a steer to escape predators (Spanier 1991; Haug *et al.* 2015).

Scyllarides Gill, 1898 species are present in tropical and subtropical areas around the world, from the intertidal

Accepted by J. Goy: 14 Jun. 2016; published: 22 Jul. 2016

zone to 800 m depth (Holthuis 1991). Most *Scyllarides* species are omnivores and scavengers that live on rocky substrates, but some prefer sandy or muddy bottoms where they dig their own burrows (Santana *et al.* 2007). According to Lavalli & Spanier (2007), this genus comprises a total of 14 species distributed mainly in the Atlantic Ocean namely *S. aequinoctialis* (Lund, 1793); *S. brasiliensis* Rathbun, 1906; *S. deceptor* Holthuis, 1963; *S. delfosi* Holthuis, 1960; *S. herklotsii* (Herklots, 1851); *S. latus* (Latreille, 1803); *S. nodifer* (Stimpson, 1866); and *S. obtusus* Holthuis, 1993; and the Indo-Pacific including *S. elisabethae* (Ortmann, 1894); *S. tridacnophaga* Holthuis, 1967; *S. squammosus* (H. Milne Edwards, 1837); *S. astori* Holthuis, 1960; *S. haanii* (De Haan, 1841) and *S. roggeveeni* Holthuis, 1967. Some of these species such as *S. nodifer* and *S. astori* have relevance in the marine aquarium trade, while other *Scyllarides* support local fisheries of economic importance, such as *S. herklotsii* on the island of St. Helena (Robertson 1969), or *S. squammosus* and *S. haanii* in Australia and Hawaii (Sumpton *et al.* 2004). In recent years, overexploitation on spiny lobster populations has forced part of the artisanal fishery in Northeastern Brazil to focus on trapping scyllarid lobsters (Santana *et al.* 2007).

Little is known about *Scyllarides* larval development. This is primarily due to the scarcity of plankton caught material and the longevity of phyllosoma stages, which thwarts laboratory rearing through all developmental stages (Booth *et al.* 2005). The wide oceanic dispersal capacity of phyllosoma implies that they can be found far from their place of origin, and most studies on *Scyllarides* life history have one important drawback in that their identifications are based on the assumption that larvae collected from the plankton belong to local species (Gurney 1936). However, this may be in error as the larval morphology of species assigned to the same genus is remarkably similar. Consequently, identification of phyllosoma to species level based on morphological traits is virtually impossible, especially in early larval stages (Phillips & McWilliam 1989). The first assignments of phyllosoma larvae to *Scyllarides* were apparently made by Stephensen (1923) and Gurney (1936) based on larvae from Mediterranean waters (which in fact correspond to *Scyllarus* species; see Palero *et al.* 2008, 2010a). This identification was criticized by several authors and again due to the paucity of samples covering all developmental stages (Robertson 1969; Johnson 1970). However, in a study of New Caledonia phyllosoma, Michel (1968) found final stage larvae undergoing metamorphosis, which allowed him to correctly assign for the first time a late phyllosoma stage to *Scyllarides*. As only one *Scyllarides* species was known in the area, Michel (1968) assigned his larvae to *S. squammosus*. Robertson (1969) reached similar conclusions by studying phyllosoma from Atlantic waters and comparing them with *Scyllarides aequinoctialis* early stage larvae reared in the laboratory, while Crosnier (1972) completed the description of several Eastern Atlantic phyllosoma and considered them to be the larvae of *S. herklotsii*. Following these two studies, Johnson (1971, 1977) assigned some larvae from the Pacific Ocean to *S. squammosus*. But since two *Scyllarides* species co-exist in this region (i.e., *S. haanii* and *S. squammosus*), some doubts arise on the specific level of identification based solely on morphological analysis of plankton caught phyllosoma from the Indo-Pacific.

Recently, a large collection of *Scyllarides* phyllosoma from the Coral Sea, Australia, was made available for study. In 2011 and 2012, two cruises were made in the region of Osprey Reef (13°4' to 14°0'S, 146.6°E) to collect phyllosoma larvae. Collection samples for Cruise 5160, spanning 24 May to 10 June 2011, were expected to include earlier phyllosoma stages, whereas Cruise 5441, spanning 16 to 26 July 2012, should consist of later larval stages. The purpose of the present study is to identify these larvae as either *S. haanii* or *S. squammosus* using molecular evidence, describe the larval development of the *Scyllarides* species concerned and, on the basis of adult morphology, larval descriptions and molecular results, discuss the current affinities of *Scyllarides* species.

Material and methods

Plankton samples were collected between 1 and 4 m deep with respect to the surface using a modified Isaac Kidd trawl during periods of new moon. The larvae were collected in the vicinity of Osprey Reef, a submerged atoll in the Coral Sea which rises from a depth of about 2,000 m. The reef is some 200 km of the eastern coast of northeast Queensland with the nearest reefs approximately 60 km away. The co-ordinates, date, and time of launch of the plankton net are detailed for each sample in Table 1. The specimens were stored directly in absolute ethanol at low temperature (-20 °C). Subsequently, the samples were deposited in the Natural History Museum (NHM) London. Coral Sea larvae used for morphological descriptions of each stage were given specific NHMUK registration numbers (NHMUK 2015.3279-85). The old phyllosoma collections were reviewed and compared with the material

from the Coral Sea. In addition, the larvae described by Michel (1968), which were once thought to be lost, were re-discovered in the Muséum national d'Histoire naturelle (MNHN) Paris and given individual registration numbers (Table 1).

Molecular analysis. Total genomic DNA extraction was performed on the Coral Sea larvae using the Chelex-resin method (Palero *et al.* 2010b) on muscle tissue from broken appendages after morphological examination and the drawing of the specimens. The standard universal primers for the COI gene (Folmer *et al.* 1994) were used for DNA barcoding the phyllosoma larvae, since this marker has previously been tested in all Achelata genera (Palero *et al.* 2009; Bracken-Grissom *et al.* 2014). Amplifications were carried out with ~30 ng of genomic DNA in a reaction containing 1 U of Taq polymerase (Amersham), 1 × buffer (Amersham), 0.2 mM of each primer and 0.12 mM dNTPs. The polymerase chain reaction (PCR) thermal profile used was 94°C for 4 min for initial denaturation, followed by 30 cycles of 94°C for 30 s, 50°C for 30 s, 72°C for 30 s and a final extension at 72°C for 4 min. Amplified PCR products were purified with Qiagen QIAquick PCR Purification Kit (Qiagen Inc.) before direct sequencing of the product. The sequences were obtained using the Big-Dye Ready-Reaction kit ver. 3.1 (Applied Biosystems) on an ABI Prism 3770 automated sequencer from the Scientific and Technical Services of the Center for Public Health Research, Valencia, Spain.

The chromatograms for each DNA sequence were checked using the software BioEdit ver. 7.2.5 (Hall 1999). Alignment of the genetic dataset was conducted using the program Muscle ver. 3.6 (Edgar 2004) with default parameters. Model selection of nucleotide substitution was performed according to the BIC criterion as implemented in MEGA ver. 6 (Tamura *et al.* 2013). The aligned dataset was then used to estimate the phylogenetic tree following the Bayesian approach implemented in BEAST ver. 1.8.0 (Drummond *et al.* 2012) with the corresponding model of sequence evolution previously inferred and a Yule process for the tree prior. Convergence of the analysis was checked by examining the generation plot visualised with Tracer ver. 1.6 (Rambaut & Drummond 2013) and a consensus tree was calculated after omitting the first 25% of the iterations as burn-in. The COI gene has been claimed to be an informative molecular marker at several taxonomic scales, but particularly at the species level. Matzen da Silva *et al.* (2011) obtained the frequency distribution of intra-species, intra-genus and intra-family K2P genetic distances from COI sequences of 302 species, 154 genera and 58 families of decapod crustaceans (Matzen da Silva *et al.* 2011). In order to allow for comparison with these previous estimates, K2P genetic distances were also estimated for the Scyllaridae COI gene dataset using MEGA ver. 6 (Tamura *et al.* 2013).

Morphological description. Morphological illustrations of larval appendages were made using a *camera lucida* and by photographing phyllosoma under a digital camera attached to a microscope (VHX-2000 series). The following measurements were recorded: total length (TL) from the anterior margin of the cephalic shield between the eyes to the posterior margin of the telson; cephalic length (CL) from the anterior to the posterior margin of the cephalic shield and cephalic width (CW) measured at the widest part of the cephalic shield. The missing leg segments were not drawn. The sequence of larval descriptions was based on the malacostraca somite plan and described from anterior to posterior and proximal to distal (Clark *et al.* 1998). Boxshall (2004) has challenged the traditional description of the malacostracan antennule developing from a uniramous appendage to a biramous structure with endopod and exopod. The terminology biramous is considered inappropriate for the antennule, and instead of exopod and endopod, the terms primary and accessary flagella should be used (see Boxshall *et al*. 2010 for review). The earliest phyllosoma is described in full (except mandibles), so that for the subsequent stages only the main differences from the previous stage are described in detail. Division of the development into defined stages was made on the basis of morphological development and changes in total length, following Johnson (1971). Measurements for phyllosoma larvae assigned to *S. squammosus* in the literature were obtained directly from the text and/or from drawings published together with a scale bar (e.g., typo found in the Mariana waters phyllosoma description of Sekiguchi 1990).

Given their dorso-ventrally flattened body, phyllosoma larvae are particularly suitable for morphometric studies. Changes on the ratio of cephalic width over the total length during the phyllosoma development were described using a quadratic model ($y = ax^2 + bx + c$). Nonlinear regression of these measurements was performed using the NonlinearModelFit function as implemented in the software package Mathematica ver. 10.1 (Wolfram Inc., USA). In order to extract further statistics about individual parameter estimates, carry out tests of significance, and obtain confidence intervals, we used the options 'ParameterConfidenceIntervalTable' and 'ParameterTable' within the NonlinearModelFit function.

TABLE 1. Stations of the Australian Institute of Marine Science (AIMS) campaigns where *Scyllarides* phyllosoma were collected.

Specimen	Stage	Registration number	Date	Time	Latitude	Longitude	Area	Study
Stade 5,7 mm	II	MNHN-IU-2014-15134					New Caledonia	Michel, 1968
Stade 7,8 mm	III	MNHN-IU-2014-15133					New Caledonia	Michel, 1968
Cruise 5160.65-02	VI	NHMUK 2015.3279	29/05/2011	0:45	14°07'S	146°42'E	Coral Sea	Present study
Cruise 5160.65-03	VII	NHMUK 2015.3280	29/05/2011	0:45	14°07'S	146°42'E	Coral Sea	Present study
Phyllosoma (Fig.72)	VII						Hawaii	Johnson, 1971
Cruise 5160.20-01	VIII	NHMUK 2015.3281	27/05/2011	0:40	13°43'S	146°24'E	Coral Sea	Present study
Cruise 5160.25-01	VIII		27/05/2011	1:35	13°44'S	146°25'E	Coral Sea	Present study
Cruise 5160.90-01	VIII		29/05/2011	3:25	14°02'S	146°34'E	Coral Sea	Present study
Phyllosoma (Fig.75)	VIII						Hawaii	Johnson, 1971
Stade 21,4 mm	VIII	MNHN-IU-2014-15131					New Caledonia	Michel, 1968
Cruise 5160.25-02	IX		27/05/2011	1:35	13°44'S	146°25'E	Coral Sea	Present study
Cruise 5160.65-01	IX	NHMUK 2015.3282	29/05/2011	0:45	14°07'S	146°42'E	Coral Sea	Present study
Cruise 5160.90-02	IX		29/05/2011	3:25	14°02'S	146°34'E	Coral Sea	Present study
Cruise 5160.90-05	IX		29/05/2011	3:25	14°02'S	146°34'E	Coral Sea	Present study
Cruise 5160.90-06	IX		29/05/2011	3:25	14°02'S	146°34'E	Coral Sea	Present study
Phyllosoma (Fig.79)	IX	S 7885 (Bishop Mus.)					Hawaii	Johnson, 1971
Cruise 5441.118-03	X		21/07/2012	21:55	13º46'S	146º34'E	Coral Sea	Present study
Cruise 5441.118-04	X		21/07/2012	21:55	13º46'S	146º34'E	Coral Sea	Present study
Cruise 5441.118-05	X		21/07/2012	21:55	13º46'S	146º34'E	Coral Sea	Present study
Cruise 5441.118-07	X		21/07/2012	21:55	13º46'S	146º34'E	Coral Sea	Present study
Cruise 5441.118-08	X		21/07/2012	21:55	13º46'S	146º34'E	Coral Sea	Present study
Cruise 5441.125-10	X		21/07/2012	22:50	13°47'S	146°35'E	Coral Sea	Present study
Cruise 5441.130-01	X	NHMUK 2015.3283	21/07/2012	23:42	13°48'S	146°36'E	Coral Sea	Present study

……continued on the next page

TABLE 1. (Continued)

Specimen	Stage	Registration number	Date	Time	Latitude	Longitude	Area	Study
Phyllosoma (Fig.83)	X						Hawaii	Johnson, 1971
Cruise 5441.125-01	XI		21/07/2012	22:50	13°47'S	146°35'E	Coral Sea	Present study
Cruise 5441.125-03	XI		21/07/2012	22:50	13°47'S	146°35'E	Coral Sea	Present study
Cruise 5441.125-05	XI		21/07/2012	22:50	13°47'S	146°35'E	Coral Sea	Present study
Cruise 5441.125-07	XI		21/07/2012	22:50	13°47'S	146°35'E	Coral Sea	Present study
Cruise 5441.125-08	XI		21/07/2012	22:50	13°47'S	146°35'E	Coral Sea	Present study
Cruise 5441.125-09	XI	NHMUK 2015.3284	21/07/2012	22:50	13°47'S	146°35'E	Coral Sea	Present study
Cruise 5441.130-02	XI		21/07/2012	23:42	13°48'S	146°36'E	Coral Sea	Present study
Cruise 5441.130-04	XI		21/07/2012	23:42	13°48'S	146°36'E	Coral Sea	Present study
Phyllosoma (Fig.1)	XII-Final						Hawaii	Johnson, 1975
Scyllarides squammosus	XII-Final						Mariana Waters	Sekiguchi, 1990
Stade 48 mm	XII-Final	MNHN-IU-2014-15127					New Caledonia	Michel, 1968
Cruise 5441.118-01	XII-Final		21/07/2012	21:55	13°46'S	146°34'E	Coral Sea	Present study
Cruise 5441.118-02	XII-Final	NHMUK 2015.3285	21/07/2012	21:55	13°46'S	146°34'E	Coral Sea	Present study
Cruise 5441.118-06	XII-Final		21/07/2012	21:55	13°46'S	146°34'E	Coral Sea	Present study
Cruise 5441.118-09	XII-Final		21/07/2012	21:55	13°46'S	146°34'E	Coral Sea	Present study
Cruise 5441.118-10	XII-Final		21/07/2012	21:55	13°46'S	146°34'E	Coral Sea	Present study
Cruise 5441.125-02	XII-Final		21/07/2012	22:50	13°47'S	146°35'E	Coral Sea	Present study
Cruise 5441.125-04	XII-Final		21/07/2012	22:50	13°47'S	146°35'E	Coral Sea	Present study
Cruise 5441.125-06	XII-Final		21/07/2012	22:50	13°47'S	146°35'E	Coral Sea	Present study
Cruise 5441.130-03	XII-Final		21/07/2012	23:42	13°48'S	146°36'E	Coral Sea	Present study

Results

Molecular analyses

The new sequences obtained from the Australian phyllosoma larvae have been deposited in GenBank with accession numbers KX373661-KX373667. The length of the aligned dataset for the COI gene was 658 bp, and the corresponding model selected for the alignment was the GTR+G+I model (lnL = -11623.03). The phylogenetic tree obtained strongly supported the species-level assignment of the Coral Sea larvae, with the clade formed by the phyllosoma specimens studied and the sequences available for *S. squammosus* adults showing a high posterior probability (Fig. 1). The K2P genetic distance found for the COI gene between the larval samples and the adult *S. squammosus* (0.003 ± 0.002) was much smaller than the distance with the adult *S. brasiliensis* (0.068 ± 0.011), *S. haanii* (0.160 ± 0.018), *S. herklotsii* (0.178 ± 0.019), *S. latus* (0.191 ± 0.020) or *S. nodifer* (0.185 ± 0.025). Genetic distances were also much smaller than those between the Coral Sea larvae and other Scyllaridae genera, with *Arctides regalis* showing the next smaller distances (0.234 ± 0.022).

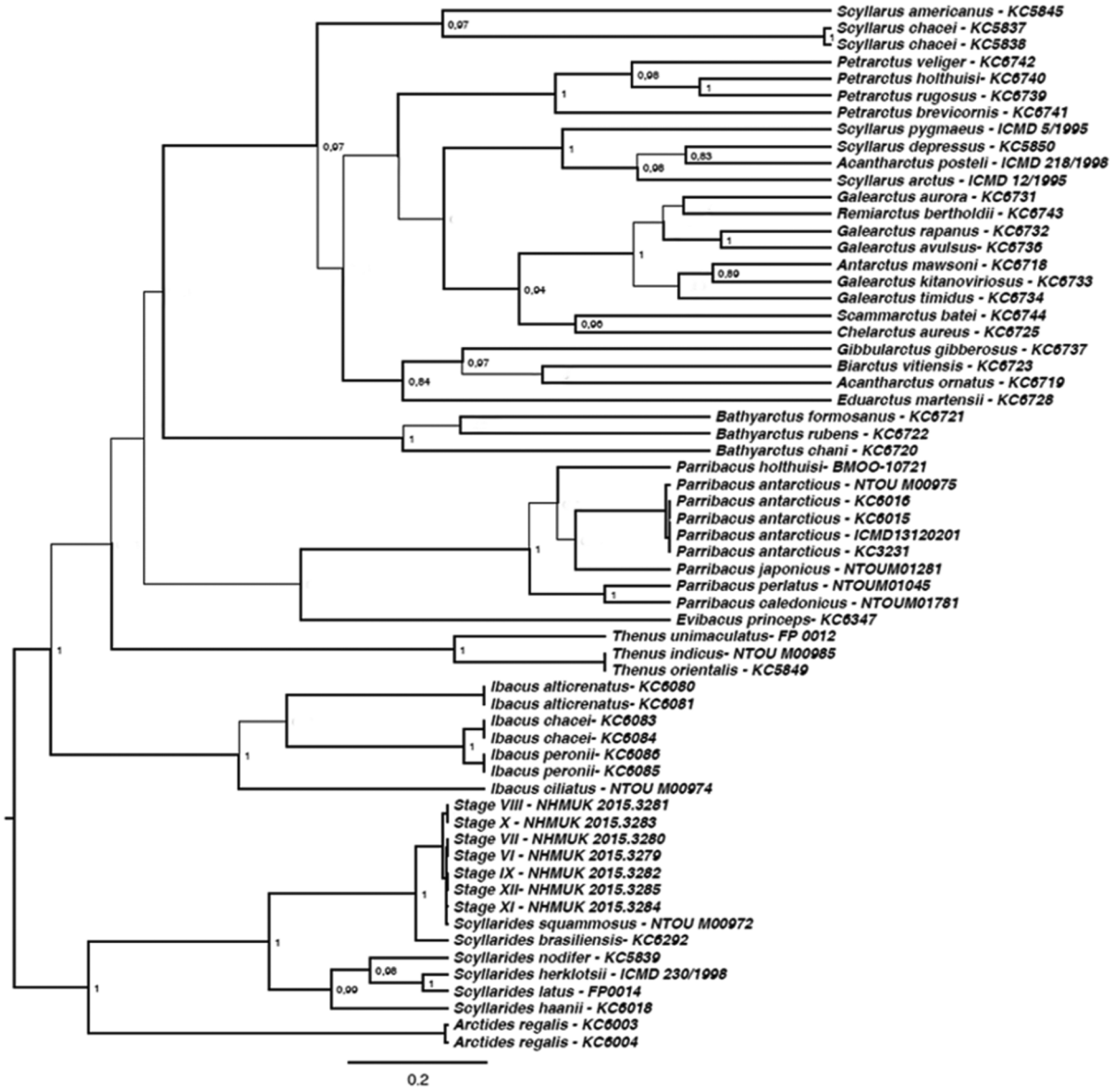


FIGURE 1. Bayesian phylogenetic tree. Only posterior probability values above 80 are shown, and branch width is proportional to posterior values.

Morphological descriptions and morphometric analyses

***Scyllarides squammosus* (H. Milne Edwards, 1837)**

Stage VI (NHMUK 2015.3279)

Measurements (Fig. 2A). TL = 11.7 mm; CW = 6.3 mm; CL = 9.0 mm.

Cephalic shield (Fig. 2A). Spindle-shaped, longer than wide (CL/CW = 1.42), maximum width located to mid length.

Antennule (Fig. 2B). Peduncle 3-segmented, each segment with similar length. Distal segment biflagellated, accesory flagellum half the length of primary flagellum. Primary flagellum with 7 rows of aesthetascs on inner margin.

Antenna (Fig. 2B). Biramous, endopod 2-segmented. The inner ramus reaching the anterior end of first antennular segment.

Maxillule (Fig. 2C). Uniramous, palp (endopod) absent. Coxal endite with 4 setae (three strong terminal cuspidate setae). Basal endite with 4 setae (three long strong terminal cuspidate setae).

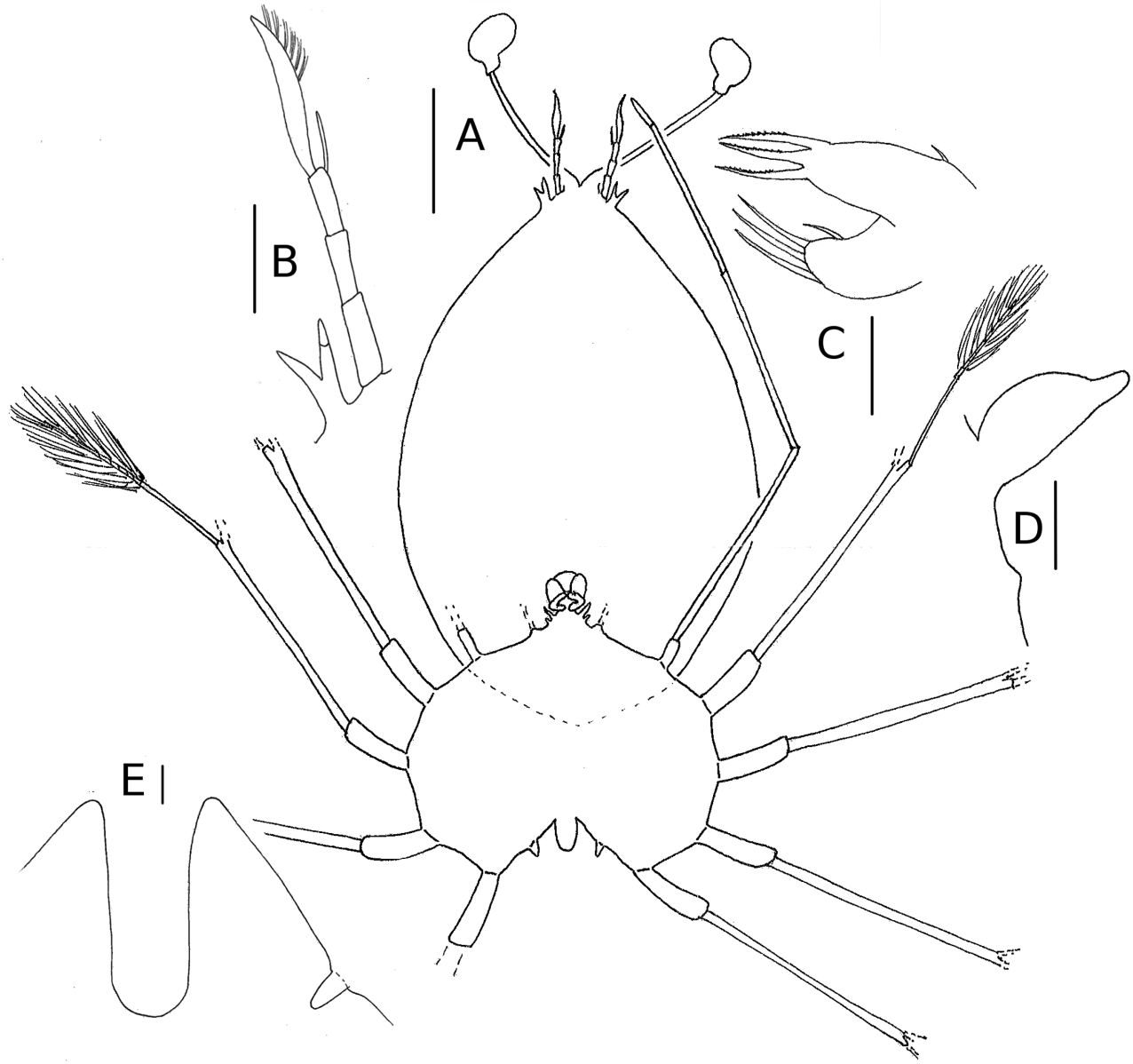


FIGURE 2. *Scyllarides squammosus*, State VI. A, ventral view; B, details of antennule and antenna; C, detail of maxillule; D, maxilla and first maxilliped; E, detail of abdomen and 5th pereiopod. A scale bar = 1 mm; B = 0.5 mm; C–E = 0.1 mm.

Maxilla (Fig. 2D). Rudimentary bud with small elongation at distal end. Triangular shape. Endites, endopod and scaphognathite not differentiated.

First maxilliped (Fig. 2D). Undeveloped, present as small conical protuberance.

Third maxilliped (Fig. 2A). Uniramous. Five segmented (ischio-merus fused to basis). Without ventral coxal spine.

Pereiopods (Fig. 2A). Biramous, without coxal or subexopodal spines. Exopods of pereiopods 1–4 flagellated distally with ~12–14 annulations, each annulation bears a pair of plumose natatory setae. Pereiopod 5 underdeveloped, small single segment with conical shape. Distal end nearly reaching the telson.

Pleon (Fig. 2E). Unsegmented. Pleopods or uropods absent.

Stage VII (NHMUK 2015.3280)

Measurements (Fig. 3A). TL = 14.9 mm; CW = 8.2 mm; CL = 12.0 mm.

Cephalic shield (Fig. 3A). Pear-shaped, longer than wide (CL/CW = 1.46), maximum width located to mid length.

Antennule (Fig. 3B). Primary flagellum with 8 rows of aesthetascs on inner margin.

Antenna (Fig. 3B). Longer than first antennular segment. Endopod 2-segmented, reaching the middle of the second antennular segment. Exopod retracts and widens, becoming triangular-shaped.

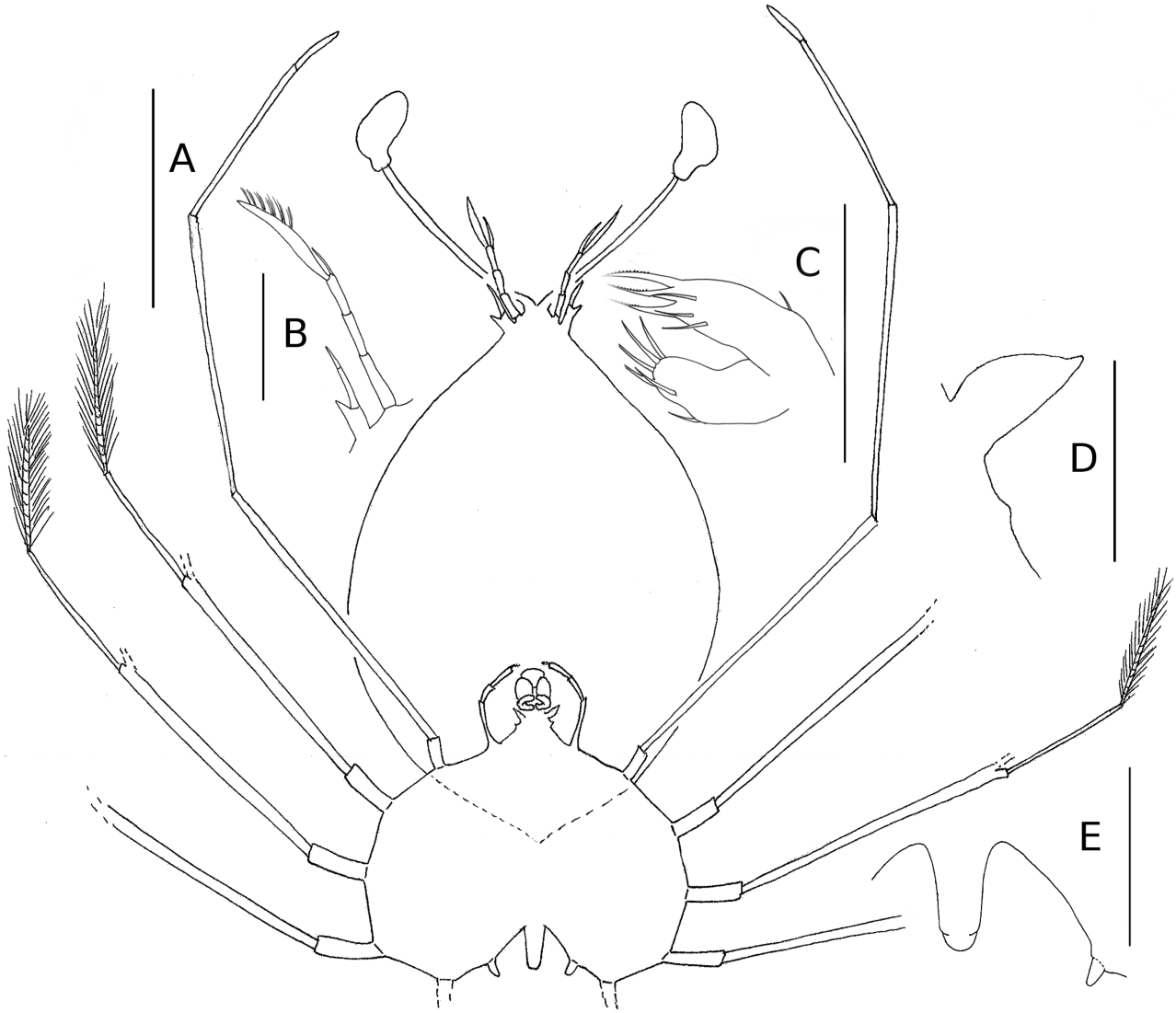


FIGURE 3. *Scyllarides squammosus*, Stage VII. A, ventral view; B, details of antennule and antenna; C, detail of maxillule; D, maxilla and first maxilliped; E, detail of abdomen and 5th pereiopod. Scale bar: A = 5 mm; B, E = 1 mm; C, D = 0.5 mm.

Maxillula (Fig. 3C). Coxal endite with 6 setae, 4 located in apical position and 2 in basal position. Basal endite with 6 setae (3 terminal, elongated, with strong structure and serrated laterally).

Maxilla (Fig. 3D). Small tapered elongation becomes less evident, reduced in length. Triangular shape.

First maxilliped (Fig. 3D). Unchanged.

Third maxilliped (Fig. 3A). Unchanged.

Pereiopods (Fig. 3E). Exopods of pereiopods 1–4 distally flagellated with 15–17 annulations. Pereiopod 5 underdeveloped, with conical base at thorax. Distal end reaches beyond telson.

Pleon (Fig. 3E). Pleon non-segmented, uropods present as small uniramous buds. Telson more developed, longer than previous stage.

Stage VIII (NHMUK 2015.3281)

Measurements (Fig. 4A). TL = 19.5 mm; CW = 10.6 mm; CL = 15.5 mm.

Cephalic shield (Fig. 4A). Pear-shaped, longer than wide (CL/CW = 1.46), maximum width located to mid length.

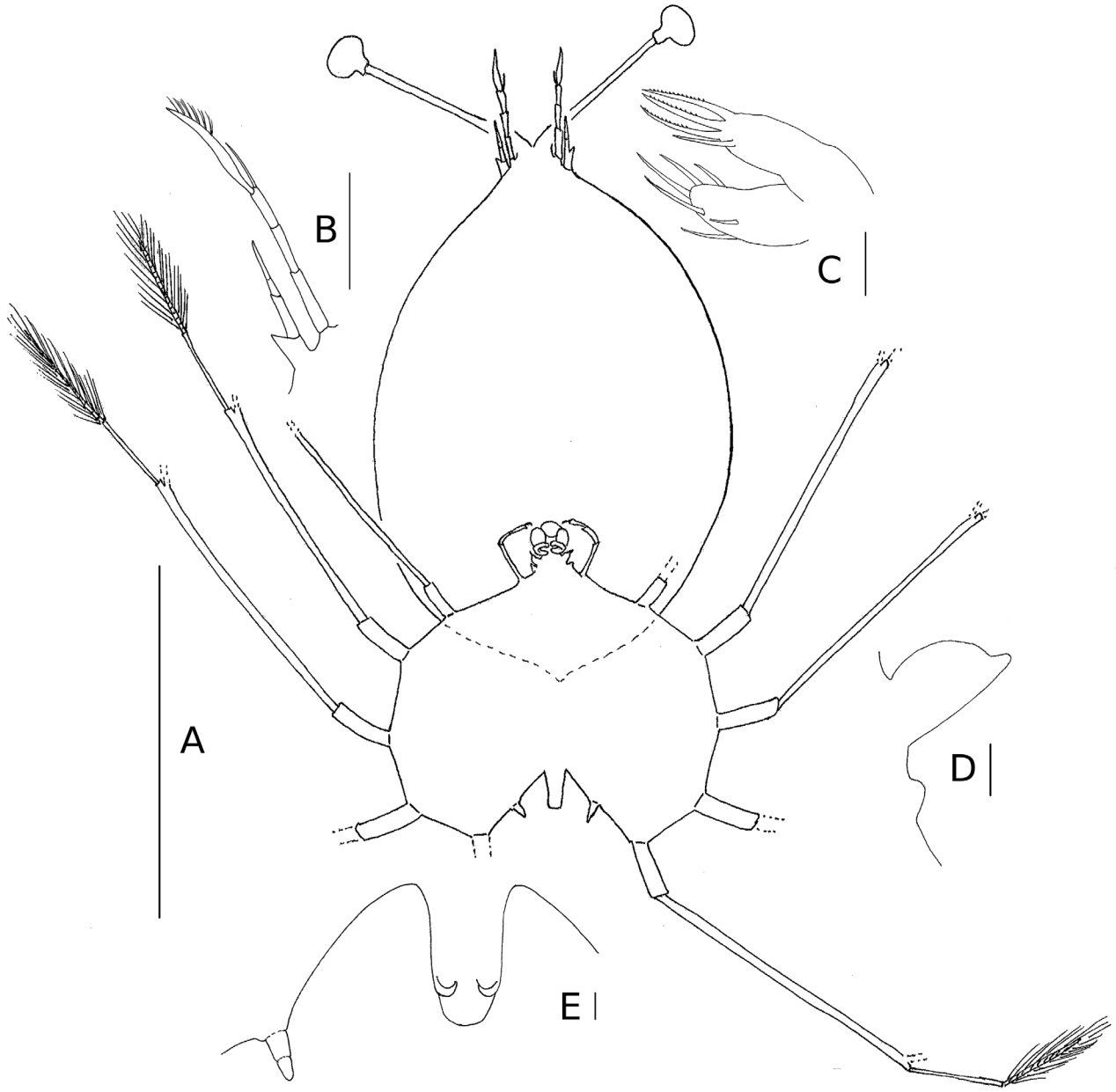


FIGURE 4. *Scyllarides squammosus*, Stage VIII. A, ventral view; B, details of antennule and antenna; C, detail of maxillule; D, maxilla and first maxilliped; E, detail of abdomen and 5th pereiopod. Scale bar: A = 10 mm; B = 1 mm; C–E = 0.1 mm.

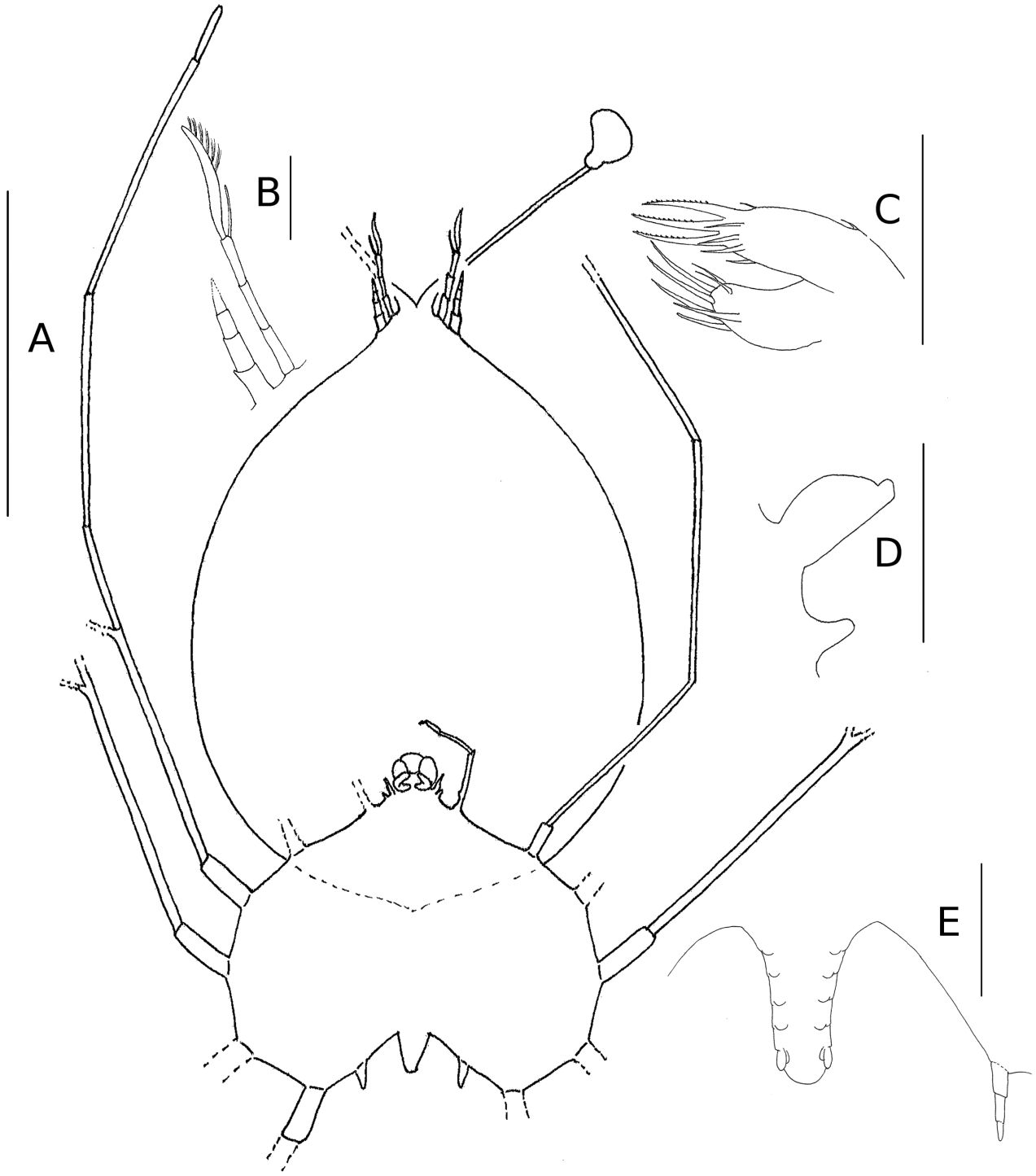


FIGURE 5. *Scyllarides squammosus*, Stage IX. A, ventral view; B, details of antennule and antenna; C, detail of maxillule; D, maxilla and first maxilliped; E, detail of abdomen and 5th pereiopod. Scale bar: A = 10 mm; B, E = 1 mm; C, D = 0.5 mm.

Antennule (Fig. 4B). Accessary flagellum reaches middle length of primary flagellum. Primary flagellum with 8–9 rows of aesthetascs on inner margin.

Antenna (Fig. 4B). Reaches proximal end of third antennular segment. Endopod now 3-segmented. Significant increase in length of second segment. Triangular outer ramus becomes shorter and stouter.

Maxillule (Fig. 4C). Coxal endite with 6 setae, 4 located at distal portion and 2 located in basal position. Basal endite with 7 setae (3 terminal, elongated).

Maxilla (Fig. 4D). Still underdeveloped, but wider than in previous stages.

First maxilliped (Fig. 4D). Present as a minute protuberance. Diameter of conical base significantly larger than previous stages.

Pereiopods (Fig. 4E). Exopods of pereiopods 1–4 distally flagellated with 16–18 annulations. Pereiopod 5 now 2-segmented, and reaching beyond telson.

Pleon (Fig. 4E). Somite divisions incomplete. Uropods are biramous.

Stage IX (NHMUK 2015.3282)

Measurements (Fig. 5A). TL = 23.6 mm; CW = 13.8 mm; CL = 19.0 mm.

Cephalic shield (Fig. 5A). Pear-shaped, longer than wide (CL/CW = 1.37). Slightly narrower than thorax.

Antennule (Fig. 5B). Primary flagellum with 9–10 rows of aesthetascs on inner margin.

Antenna (Fig. 5B). Exceeds second antennular segment. Four segments remain but the exopod now reduced to small tip.

Maxillule (Fig. 5C). Coxal endite with 7 setae (3 longer setae in distal portion). Basal endite with 9 setae (3 terminal, long and serrated).

Maxilla (Fig. 5D). Similar to previous stages, but scaphognathite acquires rudimentary rectangular shape.

First maxilliped (Fig. 5D). Adopting more tubular form with length significantly larger than previous stages.

Pereiopods (Fig. 5A, E). Exopods of pereiopods 1–4 distally flagellated. Pereiopod 5 now 3-segmented and reaching beyond telson.

Pleon (Fig. 5E). Divisions of somites becomes evident. Pleopods present, underdeveloped and biramous. Uropods biramous, length of internal lobe half than outer lobe. Telson unchanged.

Stage X (NHMUK 2015.3283)

Measurements (Fig. 6A). TL = 31.0 mm; CW = 18.5 mm; CL = 24.0 mm.

Cephalic shield (Fig. 6A). Pear-shaped, longer than wide (CL/CW = 1.29), but relatively wider than previous stages.

Antennule (Fig. 6B). Accessory flagellum longer than half length of primary flagellum. Primary flagellum with 10–12 rows of aesthetascs on inner margin.

Antenna (Fig. 6B). Five-segmented and reaching beyond third antennular segment. Second antennal segment develops a lateral extension (lateral process) while first segment becomes cylindrical.

Maxillule (Fig. 6C). Coxal endite with 13 setae. Basal endite with 9 setae (3 long, strong and serrated).

Maxilla. (Fig. 6D). Scaphognathite slightly differentiated, without setae, flattened and reduced in size.

First maxilliped (Fig. 6D). Like previous stage.

Second maxilliped (Fig. 6A). Five-segmented, with rudimentary and unarmed minute exopod bud present.

Third maxilliped (Fig. 6A, F). Uniramous. Five segmented (ischio-merus fused to basis). Without ventral coxal spine. Distal part of propodus and dactylus densely setose.

Pereiopods (Fig. 6E, G). Pereiopods 1–4 biramous, without coxal or subexopodal spines. Exopods of pereiopods 1–4 flagellated distally with 17–19 annulations, each annulation bears a pair of plumose natatory setae. Pereiopod 5 with four-segmented endopod, without setae. Distal end reaches beyond telson.

Pleon (Fig. 6E). Five-segmented (five somites plus telson, somite 1 not differentiated). Pleonites 2–5 with a pair of biramous pleopods, unsegmented and unarmed. Uropods biramous and incipiently segmented, but not outreaching posterior margin of telson. Telson rounded posteriorly, without processes or teeth.

Stage XI (NHMUK 2015.3284)

Measurements (Fig. 7A). TL = 39.0 mm; CW = 23.1 mm; CL = 29.0 mm.

Cephalic shield (Fig. 7A). Pear-shaped, longer than wide (CL/CW = 1.26), maximum width located to mid length.

Antennule (Fig. 7B). Primary flagellum with 12–14 rows of aesthetascs on inner margin.

Antenna (Fig. 7B). Almost equal in length to antennule. Lateral expansion on the second segment widens while segment 4 gets narrower.

Maxillule (Fig. 7C). Coxal endite with 14 setae (2 terminal setae considerably longer and stronger). Basal endite with 9 setae (3 long, strong and serrated).

Maxilla (Fig. 7D). Similar to previous stage, but scaphognathite more differentiated, without setae, flattened and slightly expanded anteriorly and posteriorly.

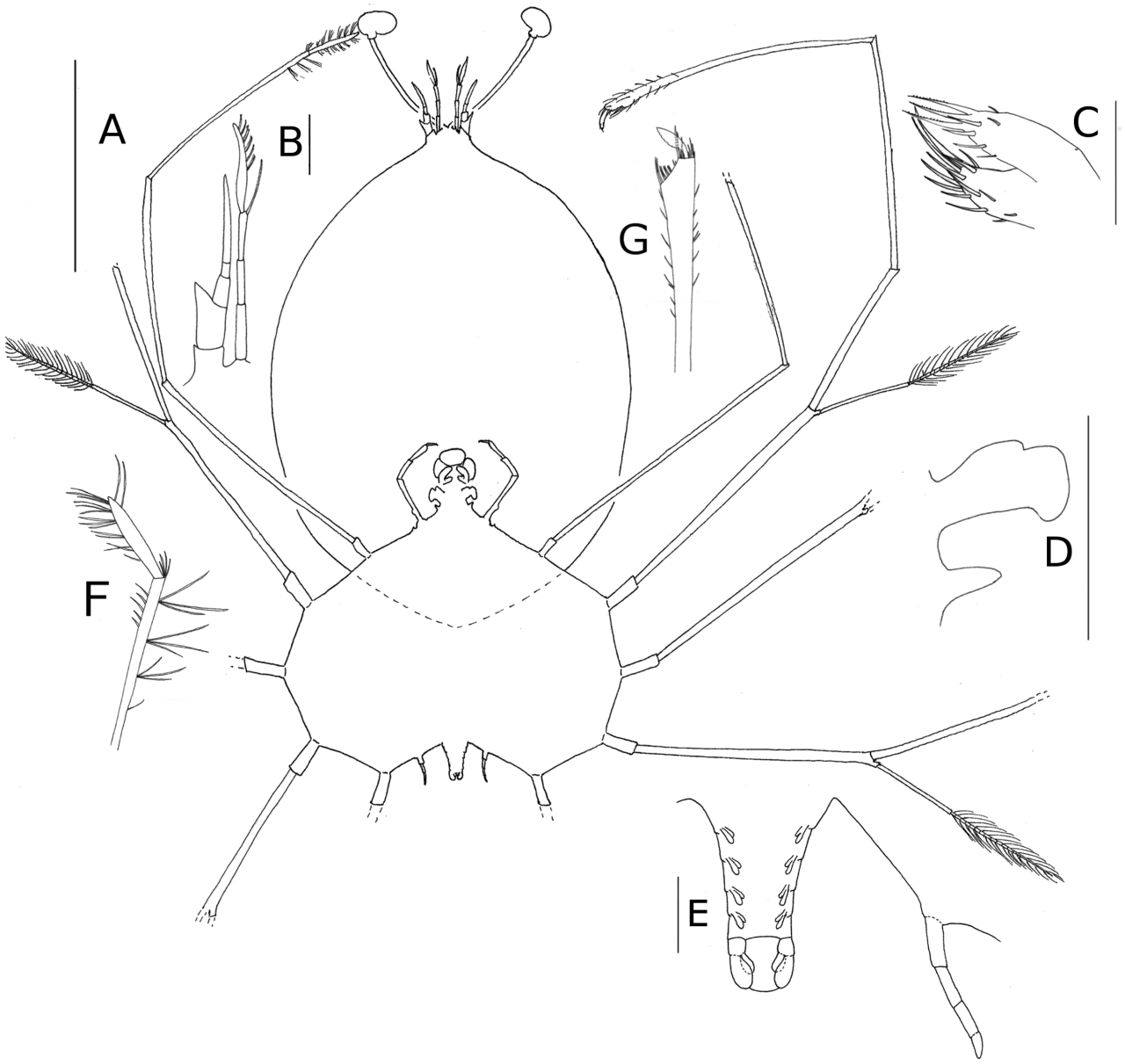


FIGURE 6. *Scyllarides squammosus,* Stage X. A, ventral view; B, details of antennule and antenna; C, detail of maxillule; D, maxilla and first maxilliped; E, detail of abdomen and 5th pereiopod; F, 3rd maxilliped; G, 5th segment and dactyl of 1 st pereiopod. Scale bar: A = 10 mm; B, E = 1 mm; C, D = 0.5 mm.

First maxilliped (Fig. 7D). Further developed.

Pereiopods (Fig. 7E). Biramous, without coxal or subexopodal spines. Exopods of pereiopods 1–4 flagellated distally with >18 annulations, each annulation bears a pair of plumose natatory setae. Pereiopod 5 with 5 segments present, segment 2 with rudimentary exopod.

Pleon (Fig. 7E, F). Segmented, with six pleonites plus telson. Pleonites 2–5 with a pair of biramous and unsegmented pleopods each, without appendix interna. Presence of two dorsal spines on pleonites 3–4. Biramous uropods outreaching posterior margin of telson.

Stage XII (NHMUK 2015.3285)

Measurements (Fig. 8A). TL = 51.0 mm; CW = 26.5 mm; CL = 36.0 mm

Cephalic shield (Fig. 8A). Pear-shaped, longer than wide (CL/CW = 1.35), but proportionally longer than previous stage.

Antennule (Fig. 8B). Accessory flagellum extended, equal in length to primary flagellum. Primary flagellum with 13–15 rows of aesthetascs on inner margin.

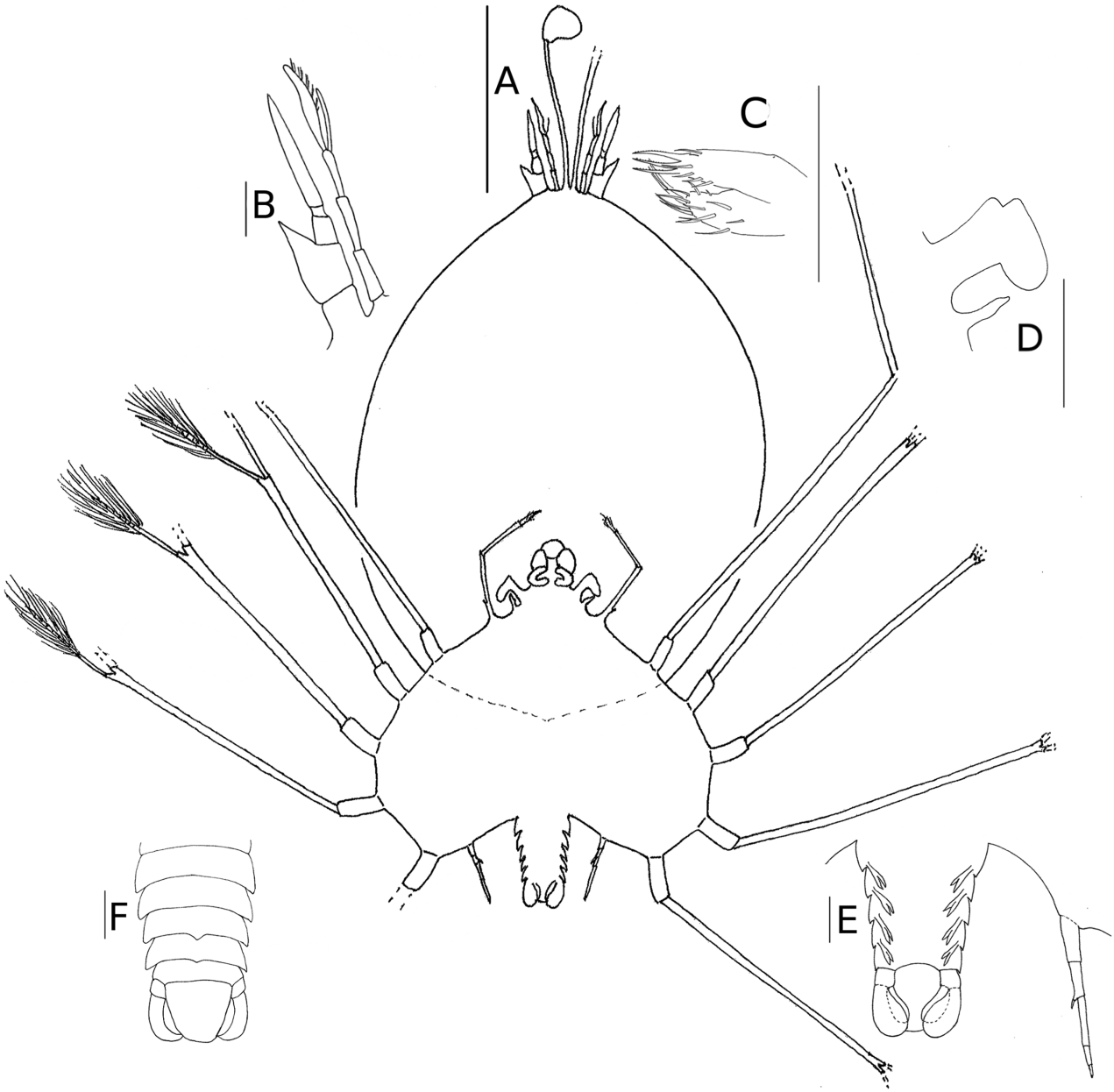


FIGURE 7. *Scyllarides squammosus*, Stage X. A, ventral view; B, details of antennule and antenna; C, detail of maxillule; D, maxilla and first maxilliped; E, detail of abdomen and detail of 5th pereiopod; F, dorsal view of abdomen. Scale bar: A = 10 mm; B–F = 1mm.

Antenna (Fig. 8B). Longer than antennule. Segments fully developed. Lateral expansion on second segment directed anteriorly (more developed than previous stage). Last antennal segment leaf-shaped.

Maxillule (Fig. 8C). Coxal endite with 14 setae (2 terminal setae considerably longer and stronger). Basal endite with 11 setae (3 long, strong and serrated).

Maxilla (Fig. 8D). Fully developed, scaphognathite considerably expanded anteriorly and posteriorly. Endopod becomes triangular.

First maxilliped (Fig. 8D). Fully developed and markedly biramous.

Second maxilliped (Fig. 8A). Exopod bud elongated.

Third maxilliped (Fig. 8A). Gill buds present, with one pleurobranch, one arthrobranch and epipod with podobranch.

Pereiopods (Fig. 8E). Pereiopod 1 with one pleurobranch, one arthrobranch and epipod with podobranch. Pereiopods 2–4 with two pleurobranchs, one arthrobranch and epipod with podobranch. Pereiopod 5 with one pleurobranch. Pereiopod 5 now 6-segmented. Basis with exopod bud and ischium and merus are fused.

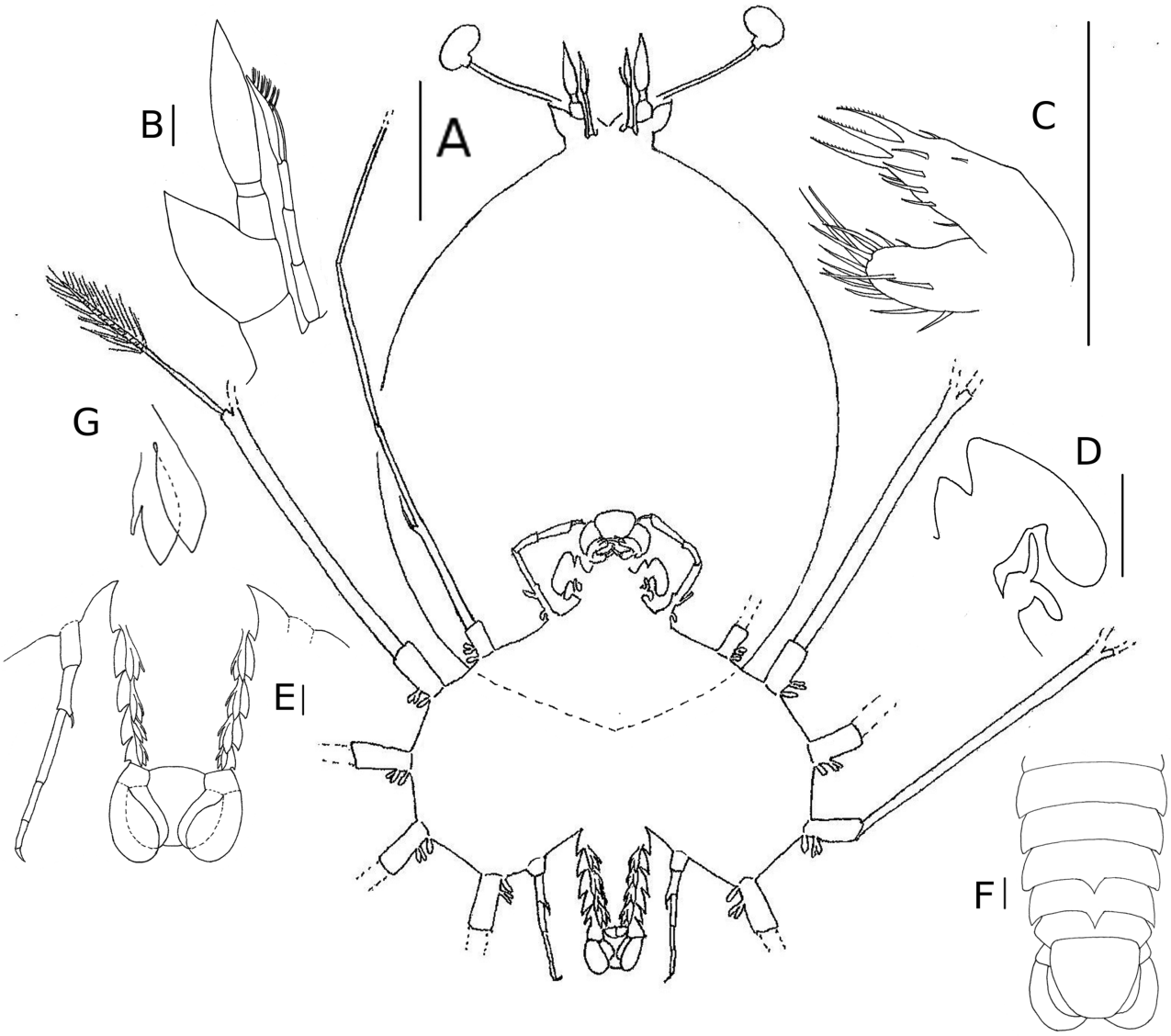


FIGURE 8. *Scyllarides squammosus*, Stage XII-Final. A, ventral view; B, details of antennule and antenna; C, detail of maxillule; D, maxilla and first maxilliped; E, detail of abdomen and detail of 5th pereiopod; F, dorsal view of abdomen; G, detail of pleopods. Scale bar: A = 10 mm; B–F = 1mm.

Pleon (Fig. 8E, F). Fully segmented with 4 pairs of segmented pleopods. Posterolateral margin of the pleura of somites 2, 3, 4 and 6 ended with acute spine. Dorsally, somites 4 and 5 bear a strong median spine. Pleopods biramous, segmented and without setae, endopod with appendix interna. Biramous uropods outreaching posterior margin of telson.

Morphometric analyses showed that total length of the larvae follows an exponential growth in late stages of development (see Table 2). The ratio of cephalic width over the total length increased during phyllosoma development up to a maximum value of CW/TL = 0.61 at around 30 mm TL (see Fig. 9) and then decreased again in the sub-final and final stages (CW/ TL = 0.43 + 0.011 TL–0.00018 TL^2; $r^2 = 0.999$). The relative growth of CL and CW during larval development in phyllosoma larvae assigned to *Scyllarides squammosus* was found to follow a power law equation ($CW = 0.84\ CL^{0.96}$), with a high correlation coefficient ($r^2 = 0.996$). However, the confidence interval for the exponent parameter comprised the value b = 1 (0.91–1.01), which indicates that the growth of CW does not show a significantly allometric pattern.

TABLE 2. Larval development of *Scyllarides squammosus* phyllosoma.

Stage	N	TL Range (mm)	TL Mean (mm)
VI	1	11.7	11.7
VII	1	14.9	14.9
VIII	3	19.5–22.0	19.8
IX	5	22.3–26.8	24.6
X	7	29.0–35.6	31.4
XI	8	37.0–40.0	38.7
XII-Final	9	47.0–51.0	49.3

Stage = Stage of development; N = Sample size; Range = range of lengths per stage; Mean = Average total length per stage. Total length (TL) measured from the anterior margin of the cephalic shield between the eyes to the posterior margin of the telson.

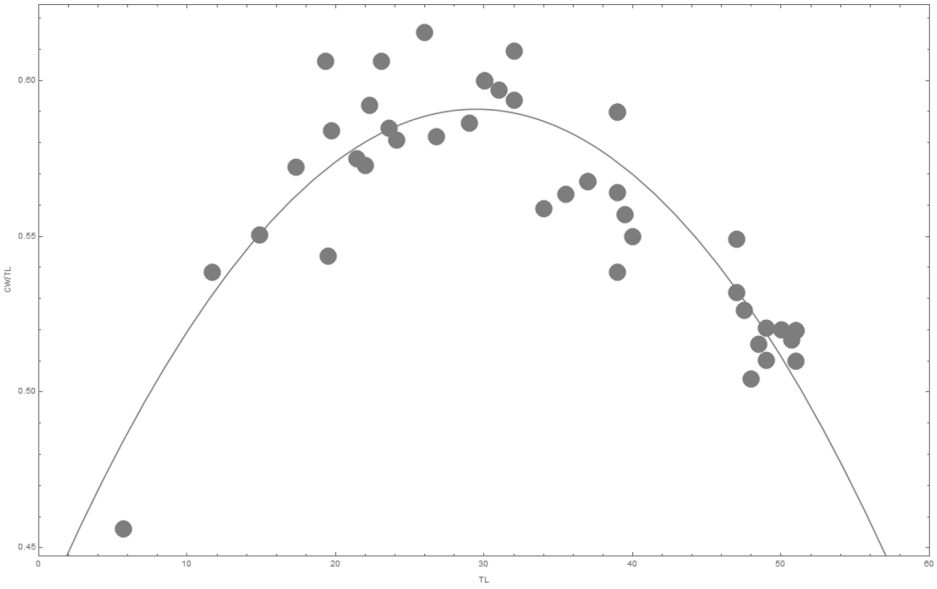


FIGURE 9. Relationship between CW / TL ratio and TL using all *Scyllarides squammosus* larvae sampled in this study (n = 34, including stages VI and VII) and those present in the previous literature.

Discussion

The majority of studies describing phyllosomas collected in the wild lack confirmation of identification as they have relied solely on morphometric parameters with limited reference material. Few species of Achelata have complete documentation of the entire larval developmental stages and hence most samples cannot be unambiguously resolved. However, with the advent of DNA barcoding as a taxonomic tool the accurate identification of a particular species from a tissue sample is now possible (Radulovici *et al.* 2010). In this study, DNA barcoding was used to confidently assign species identification of several larvae collected from the Coral Sea to *Scyllarides squammosus*. The assignment of the phyllosoma was further supported through phylogenetic analyses, since both larvae and adult *S. squammosus* cluster with 100% posterior probability. It should be noted here that, despite the Genbank sequence with accession number JN701654 is identified in the public database as *S. brasiliensis*, the actual identity of the adult specimen kept in the Crustacea collections of the National Taiwan Ocean University (registration number: NTOU M00972) is *S. squammosus* (Dr. TY Chan; personal communication). The range of intra-species divergence levels (from 0.28% to 1.37%) observed in other decapods (Matzen da Silva *et al.* 2011) when using the COI gene region are in agreement with the observed K2P distances

between adult *S. squammosus* and Coral Sea larvae (0.3%). Genetic distances were significantly larger when the larvae are compared with other *Scyllarides* species (6.8–19.1%), which also agrees with ranges found within decapod genera (6.37–20.92%) by Matzen da Silva *et al.* (2011). Identification of the Coral Sea larvae to species level allowed this study to confirm the main characters distinguishing the phyllosoma of *Scyllarides* from the larvae of other slipper lobster genera (Robertson 1969; Johnson 1971). *Scyllarides* phyllosoma can be differentiated by the morphology of their antennae, maxillules without endopod, maxillae without setae and expanding during later stages of development, and by the first maxilliped being well developed in the final stage. Early larval stages of *Scyllarides* and *Parribacus* have an extremely similar larval form and morphometrics and can be easily confused (Coutures 2001). In later stages though, *Scyllarides* phyllosoma differ from *Parribacus* 'giant phyllosoma' larvae (Palero *et al.* 2014b) by their smaller size and the outline of the cephalic shield, with its posterior margin just overlapping the coxa of the third maxilliped.

The large number of specimens obtained during the Australian Institute of Marine Science (AIMS) cruises at different times of the year was unexpected, with more *Scyllarides* phyllosoma obtained here than previously reported in the literature. The origin and developmental changes of the key character which distinguish adult Scyllaridae from all other decapods, e.g., the flat antennae (Haug *et al.* 2015), can now be completely understood. The *Scyllarides* antennae are initially biramous in early stages, with a single segment on the inner ramus and a strong outer ramus, which resembles the lateral process found near the base of the antennae in palinurid larvae (Palero & Abello 2007). The inner ramus then increases in length by adding a new segment every stage until it reaches stage X, at which point it has acquired the final number of segments. In contrast to what could be expected, the outer ramus is not at the origin of the characteristic lateral expansion present in the adult antennae. Instead, it decreases during development until stage IX, when the antenna becomes almost cylindrical in shape and, with the moult to stage X, the triangular lateral extension begins to grow at the second segment. The evolution of this lateral expansion continues until stage XII, when the antenna acquires its final shape.

Robertson (1969) pointed out the presence of two types of *Scyllarides* phyllosoma depending on the degree of development of pereiopod 5. In larvae tentatively assigned to *S. aequinoctalis* and *S. astori*, the fifth pereiopod appears to be well developed at an early stage, whereas larvae assigned to *S. nodifer*, *S. latus* and *S. herklotsii* show the fifth pair of legs underdeveloped until late stages (Robertson 1969). From the literature and recently collected larvae, *S. elisabethae* phyllosoma described by Berry (1974) can be assigned to one group and *S. squammosus* into a second. Furthermore, morphometric ratios of the cephalic shield also appear to support the existence of two *Scyllarides* groups. In later stage larvae of *S. herklotsii*, *S. nodifer* and *S. squammosus* the cephalic shield is oval shaped with its maximum width midway along a longitudinal axis (Robertson 1969; Crosnier 1972), whereas both *Scyllarides astori* and *S. aequinoctialis* phyllosoma present the maximum width at the anterior portion of the cephalon (Johnson 1970; Johnson & Knight 1975). Interestingly, the affinities between *Scyllarides* species based on adult morphology do not agree with this larval classification into two main groups (Holthuis 1991). Molecular data, however, also seem to challenge adult affinities, since *S. haani* appears to be more distant from *S. latus* than it is suggested by adult morphology (Bracken-Grissom *et al.* 2014). The molecular results are also consistent with the geographic distribution of the taxa, because *S. nodifer* and *S. latus* are Atlantic species and *S. haani* is found in the Indo-Pacific (Holthuis 1991). The incongruences observed when comparing genetics, adult and larval morphology of *Scyllarides* species could be due to misidentification of phyllosoma larvae collected from the plankton in previous studies. The DNA barcoding results presented here confirm the identity of the Coral Sea phyllosoma as *S. squammosus*, but the larvae of *S. haanii* still remain unknown. Further studies for key species including new genetic data and larval descriptions are needed in order to resolve the existence of distinct groups within *Scyllarides*.

Acknowledgements

Thanks are due to the crew of the Research Vessel *Cape Ferguson* and staff and volunteers on the collection trips and the Australian Institute of Marine Science for ship time. We also thank Alain Crosnier, Laure Corbari and Paula Martin-Lefevre (Muséum national d'Histoire naturelle, Paris) and Romana Capaccioni and her team (Marine Biology Lab, University of Valencia) for encouraging the completion of this work. This research was funded by project CHALLENGEN (CTM2013-48163) of the Spanish Government and EU-Synthesys grants (GB-TAF-2737:

DNA barcoding identification of phyllosoma larvae from Coral Sea waters; DK-TAF-4873: Morphological study of Achelata lobsters and phyllosoma larvae from Danish collections and FR-TAF-5980: Description of phyllosoma stages of West-African lobster species). FP acknowledges project FP7 Marie Curie IAPP #324475 'Colbics' of the European Union and a post-doctoral contract funded by the Beatriu de Pinos Programme of the Generalitat de Catalunya.

References

Berry, P.F. (1974) Palinurid and Scyllarid lobster larvae of the Natal coast, South Africa. *Investigational Report Oceanographic Research Institute*, 34, 1–44.

Booth, J.D. & Phillips, B.F. (1994) Early life history of spiny lobster. *Crustaceana*, 66, 271–294. http://dx.doi.org/10.1163/156854094X00035

Booth, J.D., Webber, W.R., Sekiguchi, H. & Coutures, E. (2005) Diverse larval recruitment strategies within the Scyllaridae. *New Zealand Journal of Marine and Freshwater Research*, 39, 581–592. http://dx.doi.org/10.1080/00288330.2005.9517337

Boxshall, G., Danielopol, D., Horne, D., Smith, R. & Tabacaru, I. (2010) A critique of biramous interpretations of the crustacean antennule. *Crustaceana,* 83, 153–167. http://dx.doi.org/10.1163/001121609X12530988607434

Boxshall, G.A. (2004) The evolution of arthropod limbs. *Biological Reviews,* 79, 253–300. http://dx.doi.org/10.1017/S1464793103006274

Bracken-Grissom, H.D., Ahyong, S.T., Wilkinson, R.D., Feldmann, R.M., Schweitzer, C.E., Breinholt, J.W., Bendall, M., Palero, F., Chan, T.Y., Felder, D.L., Robles, R., Chu, K.H., Tsang, L.M., Kim, D., Martin, J.W. & Crandall, K. (2014) The emergence of lobsters: Phylogenetic relationships, morphological evolution and divergence time comparisons of an ancient group (Decapoda: Achelata, Astacidea, Glypheidea, Polychelida). *Systematic Biology,* 63, 457–479. http://dx.doi.org/10.1093/sysbio/syu008

Chan, T.Y. (2010) Annotated checklist of the world's marine lobsters (Crustacea: Decapoda: Astacidea, Glypheidea, Achelata, Polychelida). *The Raffles Bulletin of Zoology,* 23, 153–181.

Clark, P.F., Calazans, D.K. & Pohle, G.W. (1998) Accuracy and standardization of brachyuran larval descriptions. *Invertebrate Reproduction and Development,* 33, 127–144. http://dx.doi.org/10.1080/07924259.1998.9652627

Coutures, E. (2001) On the First Phyllosoma Stage of *Parribacus caledonicus* Holthuis, 1960, *Scyllarides squammosus* (H. Milne-Edwards, 1837) and *Arctides regalis* Holthuis, 1963 (Crustacea, Decapoda, Scyllaridae) from New Caledonia. *Journal of Plankton Research,* 23, 745–751. http://dx.doi.org/10.1093/plankt/23.7.745

Crosnier, A. (1972) Naupliosoma, Phyllosomes et Pseudibacus de *Scyllarides herklotsii* (Herklots) (Crustacea, Decapoda, Scylllaridae) récoltés par l'ombango dans le sud du Golfe de Guinneé. Cahiers O.R.S.T.O.M. (Office de la Recherche Scientifique et Technique Outre-Mer). *Sér. Océanogr.,* 10, 139–149.

Drummond, A.J., Suchard, M.A., Xie, D. & Rambaut, A. (2012) Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Molecular biology and evolution,* 29, 1969–73. http://dx.doi.org/10.1093/molbev/mss075

Edgar, R.C. (2004) MUSCLE: multiple sequence alignment with high accuracy and high throuhput. *Nucleic Acids Research,* 32, 1792–1797. http://dx.doi.org/10.1093/nar/gkh340

Folmer, O., Black, M., Hoeh, W., Lutz, R. & Vrijenhoek, R. (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular marine biology and biotechnology,* 3, 294–299.

Gurney, R. (1936) Larvae of Decapod Crustacea: Part I- Stenopidea. Part II- Amphionidae. Part III- Phyllosoma. *Discovery Reports,* 12, 377–440.

Hall, T. (1999) BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series,* 41, 95–98.

Haug, J.T., Audo, D., Charbonnier, S., Palero, F., Petit, G., Abi Saad, P. & Haug, C. (2015) The evolution of a key character, or how to evolve a slipper lobster. *Arthropod structure & development,* 45, 97–107. http://dx.doi.org/10.1016/j.asd.2015.08.003

Holthuis, L.B. (1985) A Revision of the family Scyllaridae (Crustacea Decapoda Macrura). I. Subfamily Ibacinae. *Zoologische Verhandelingen,* 218, 1–130.

Holthuis, L.B. (1991) FAO Fisheries Synopsis *FAO species catalogue. Vol. 13 Marine lobsters of the world*.

Holthuis, L.B. (2002) The Indo-Pacific scyllarine lobsters (Crustacea, Decapoda, Scyllaridae). *Zoosystema,* 24, 499–683.

Johnson, M.W. (1970) On the phyllosoma larvae of the genus Scyllarides Gill (Decapoda, Scyllaridae). *Crustaceana,* 18, 13–20. http://dx.doi.org/10.1163/156854070X00022

Johnson, M.W. (1971) The Phyllosoma Larvae of Slipper Lobsters from the Hawaiian Islands and Adjacent Areas. *Crustaceana,* 20, 77–103. http://dx.doi.org/10.1163/156854071X00544

Johnson, M.W. (1977) The final phyllosoma larval stage of the slipper lobster *Scyllarides squamosus* (H. Milne Edwards) from the Hawaiian Islands (Decapoda, Scyllaridae). *Bulletin of Marine Science,* 27, 338–340.
Johnson, M.W. & Knight, M. (1975) A Supplementary Note on the Larvae of *Scyllarides astori* Holthuis (Decapoda , Scyllaridae). *Crustaceana,* 28, 109–112.
http://dx.doi.org/10.1163/156854075X00955
Lavalli, K. & Spanier, E. (2007) *The biology and fisheries of the slipper lobster*. *In:* Lavalli, K. & Spanier, E., (Eds), Taylor & Francis Group, Boca Raton, London, New York.
http://dx.doi.org/10.1201/9781420005165
Matzen da Silva, J., Creer, S., dos Santos, A., Costa, A.C., Cunha, M.R., Costa, F.O. & Carvalho, G.R. (2011) Systematic and evolutionary insights derived from mtDNA COI barcode diversity in the Decapoda (Crustacea: Malacostraca). *PLOS ONE,* 6, e19449.
http://dx.doi.org/10.1371/journal.pone.0019449
Michel, A. (1968) Les larves phyllosomes et la post-larve de *Scyllarides squammosus* (H. Milne-Edwards)-Scyllaridae (Crustacés Décapodes). Cahiers O.R.S.T.O.M. (Office de la Recherche Scientifique et Technique Outre-Mer). *Sér. Océanogr.,* VI, 47–53.
Palero, F. & Abello, P. (2007) The first phyllosoma stage of *Palinurus mauritanicus* (Crustacea : Decapoda : Palinuridae). *Zootaxa,* 1508, 49–59.
Palero, F., Clark, P.F. & Guerao, G. (2014a) Infraorden Achelata. *In*: Martin, J., Olesen, J. & Hoeg, J.T. (Eds), *Atlas of Crustacean Larvae*. Johns Hopkins University Press, Maryland, USA, pp. 272–278.
Palero, F., Crandall, K.A., Abelló, P., Macpherson, E. & Pascual, M. (2009) Phylogenetic relationships between spiny, slipper and coral lobsters (Crustacea, Decapoda, Achelata). *Molecular Phylogenetics and Evolution,* 50, 152–162.
http://dx.doi.org/10.1016/j.ympev.2008.10.003
Palero, F., Guerao, G. & Abelló, P. (2008) Morphology of the final stage phyllosoma larva of *Scyllarus pygmaeus* (Crustacea: Decapoda: Scyllaridae), identified by DNA analysis. *Journal of Plankton Research,* 30, 483–488.
http://dx.doi.org/10.1093/plankt/fbn012
Palero, F., Guerao, G., Clark, P.F. & Abelló, P. (2010a) *Scyllarus arctus* (Crustacea: Decapoda: Scyllaridae) final stage phyllosoma identified by DNA analysis, with morphological description. *Journal of the Marine Biological Association of the United Kingdom*, 91, 485–492.
http://dx.doi.org/10.1017/S0025315410000287
Palero, F., Guerao, G., Hall, M., Chan, T.Y. & Clark, P.F. (2014b) The ‘ giant phyllosoma ’ are larval stages of *Parribacus antarcticus* (Decapoda : Scyllaridae). *Invertebrate Systematics,* 28, 258–276.
http://dx.doi.org/10.1071/IS13037
Palero, F., Hall, S., Clark, P.F., Johnston, D., Mackenzie-Dodds, J., Thatje, S. & Johnston, J. (2010b) DNA extraction from formalin-fixed tissue: new light from the Deep-Sea. *Scientia Marina,* 74, 465–470.
http://dx.doi.org/10.3989/scimar.2010.74n3465
Phillips, B.F. & McWilliam, P.S. (1989) Phyllosoma larvae and the ocean currents off the hawaiian islands. *Pacific Science,* 43, 352–361.
Radulovici, A.E., Archambault, P. & Dufresne, F. (2010) DNA Barcodes for Marine Biodiversity: Moving Fast Forward? *Diversity,* 2, 450–472.
http://dx.doi.org/10.3390/d2040450
Rambaut, A. & Drummond, A.J. (2013) Tracer V1.6. Available from: http://beast.bio.ed.ac.uk/Tracer (Accessed 21 Jul. 2016)
Robertson, P.B. (1969) The early larval development of the scyllarid lobster *Scyllarides aequinioctalis* (Lund) in the laboratory, with a revision of the larval characters of the genus. *Deep Sea Research,* 16, 557–586.
Santana, W., Pinheiro, A.P. & Oliveira, J.E.L. (2007) Additional records of three *Scyllarides* species (Palinura: Scyllaridae) from Brazil, with the description of the fourth larval stage of *Scyllarides aequinoctialis*. *Nauplius,* 15, 1–6.
Scholtz, G. & Richter, S. (1995) Phylogenetic systematics of the reptantian Decapoda (Crustacea, Malacostraca). *Zoological Journal of the Linnean Society,* 113, 289–328.
http://dx.doi.org/10.1111/j.1096-3642.1995.tb00936.x
Sekiguchi, H. (1990) Four species of phyllosoma larvae from the Mariana waters. *Bulletin of the Japanese Society of Fisheries Oceanography,* 54, 242–248.
Spanier, E. (1991) Swimming of the Mediterranean slipper lobster. *Journal of Experimental Marine Biology and Ecology,* 145, 15–31.
http://dx.doi.org/10.1016/0022-0981(91)90003-F
Stephensen, K. (1923) Decapoda-Macrura excl. Sergestidae. (Penaeidae, Pasiphaeidae, Hoplophoridae, Nematocarcinidae, Scyllaridae, Eryonidae, Nephropsidae, Appendix). *Report on the Danish Oceanographical Expeditions 1908—10 to the Mediterranean and Adjacent Seas,* 2, 1–85.
Sumpton, W., Campbell, M., McLennan, M., Gaddes, S., Ryan, S. & Hagedoorn, W. (2004) Communities *Ecological Assessment of the Developmental Slipper Lobster Fishery in South-East Queensland Waters*.
Tamura, K., Stecher, G., Peterson, D., Filipski, A. & Kumar, S. (2013) MEGA6 : Molecular Evolutionary Genetics Analysis Version 6. 0. *Molecular Biology and Evolution,* 30, 2725–2729.
http://dx.doi.org/10.1093/molbev/mst197
Yang, C., Lin, C. & Chan, T. (2014) Additional slipper lobsters of the subfamily Scyllarinae Latreille, 1825 (Crustacea, Achelata, Scyllaridae) from Taiwan. *Zootaxa,* 3852 (3), 336–346.
http://dx.doi.org/10.11646/zootaxa.3852.3.3