

Abstract.—Three species of nephropid lobsters have been recognized in the genus *Homarus*: the American and European lobsters, *H. americanus* and *H. gammarus* of the northwestern and northeastern Atlantic, respectively, and the Cape lobster of South Africa, *H. capensis*, few specimens of which have been studied until recently. Analysis of new specimens allows reconsideration of the systematic status of this species and a subsequent transfer to a monotypic new genus *Homarinus*. Far smaller than its northern relatives, with a maximum observed carapace length of 47 mm, the Cape lobster has first chelae adorned with a thick mat of plumose setae and less abundant setae on the carapace, tail fan, and abdominal pleura, whereas these setae are absent in *Homarus*. Relative length and shape of the carpus on pereopod 1, tooth pattern on cutting edges of first chelae, shape of the linguiform rostrum, large size of oviducal openings, and structure of male pleopods differ from corresponding features in *Homarus*. Comparative analysis of DNA from the mitochondrial 16s rRNA gene demonstrated considerable sequence divergence of the Cape lobster (9.7%) from its putative congeners. The magnitude of this estimate relative to that between the two North Atlantic species (1.3%) further suggests that taxonomic revision is warranted.

Assignment of *Homarus capensis* (Herbst, 1792), the Cape lobster of South Africa, to the new genus *Homarinus* (Decapoda: Nephropidae)

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Until now, three species of nephropid lobsters have been recognized in the genus *Homarus* Weber, 1795 (see Holthuis, 1991): *H. americanus* H. Milne-Edwards, 1837, the northwestern Atlantic American lobster; *H. gammarus* (Linnaeus, 1758), the northeastern Atlantic-Mediterranean European lobster; and *H. capensis* (Herbst, 1792), the South African Cape lobster. All are found in cool or cold temperate waters, and the North Atlantic species range into subarctic waters. The northern *H. americanus* and *H. gammarus* are well-known, abundant, and economically valuable species, but the southern *H. capensis* has long been problematic because only a few specimens (13 males, 1 female) were known to exist in collections (Barnard, 1950; Wolff, 1978; Holthuis, 1991). Gilchrist (1918) had seen only three specimens and remarked (p. 46) that "it is a very rare species, and is not even known to Cape Fishermen." Kensley (1981) recorded its distribution in the Cape Province as Table Bay to East London, and recent new collections ex-

tend the range to Transkei (Kado et al., 1994).

Regardless of its rarity, sufficient specimens of the Cape lobster, living and preserved, are now available for analysis of its distribution, morphological, and genetic attributes, and systematic status. Results of our studies indicate that this species should be removed from *Homarus* and placed in a genus of its own; this paper provides supporting evidence for this action and offers supplementary descriptive information on the species.

Homarinus, new genus Figs. 1–4

Type species—*Homarus capensis* (Herbst, 1792) by present designation and monotypy.

Description—Carapace moderately compressed, narrower than deep, sparsely setose, middorsal carina barely evident on gastric region, obsolescent on thoracic region posterior to deep cervical groove. Rostrum

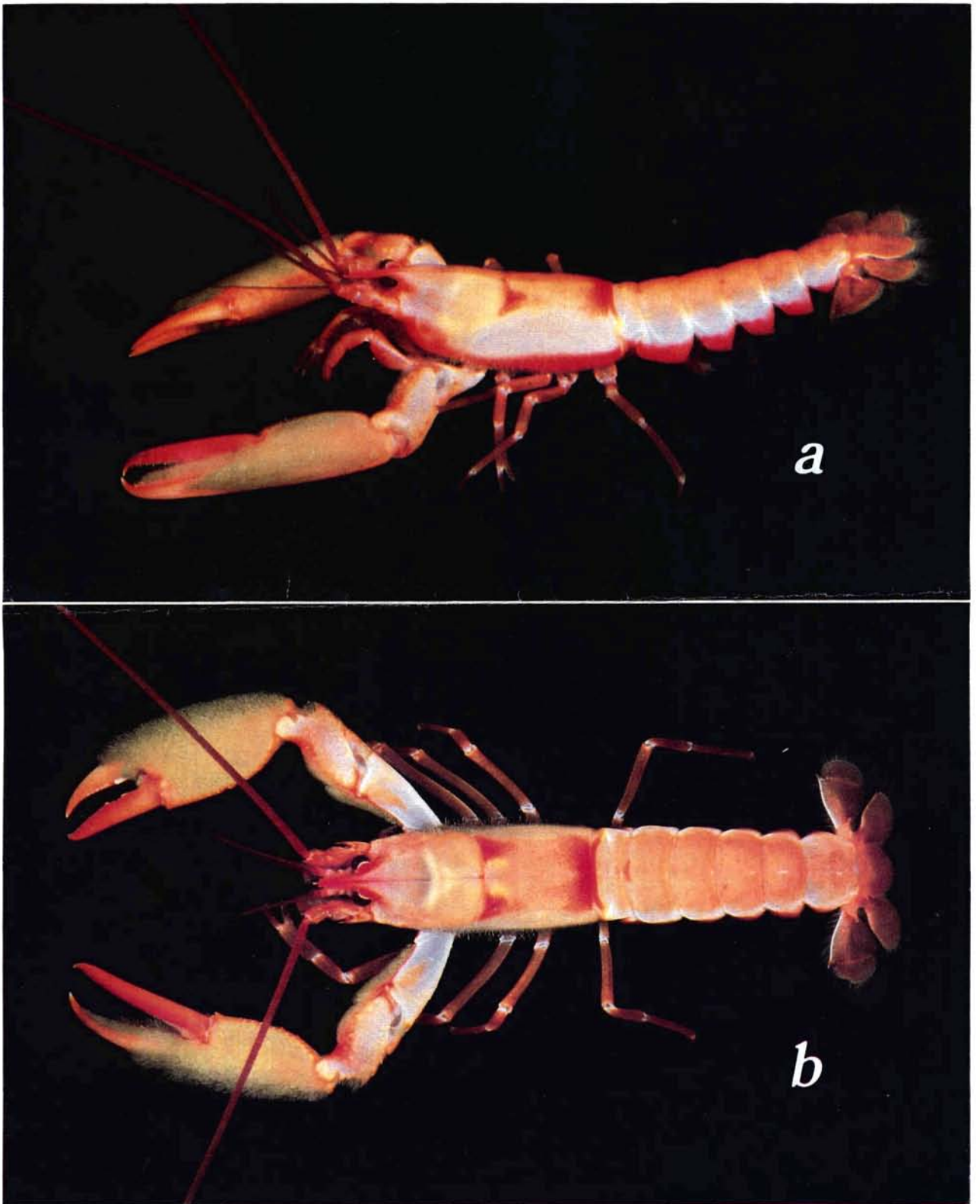


Figure 1

Homarinus capensis (Herbst). Living male, carapace length 3.41 cm, photographed in an aquarium in Sea Fisheries Research Institute, Cape Town, South Africa, by Robert Tarr. (a) Left lateral; (b) dorsal.

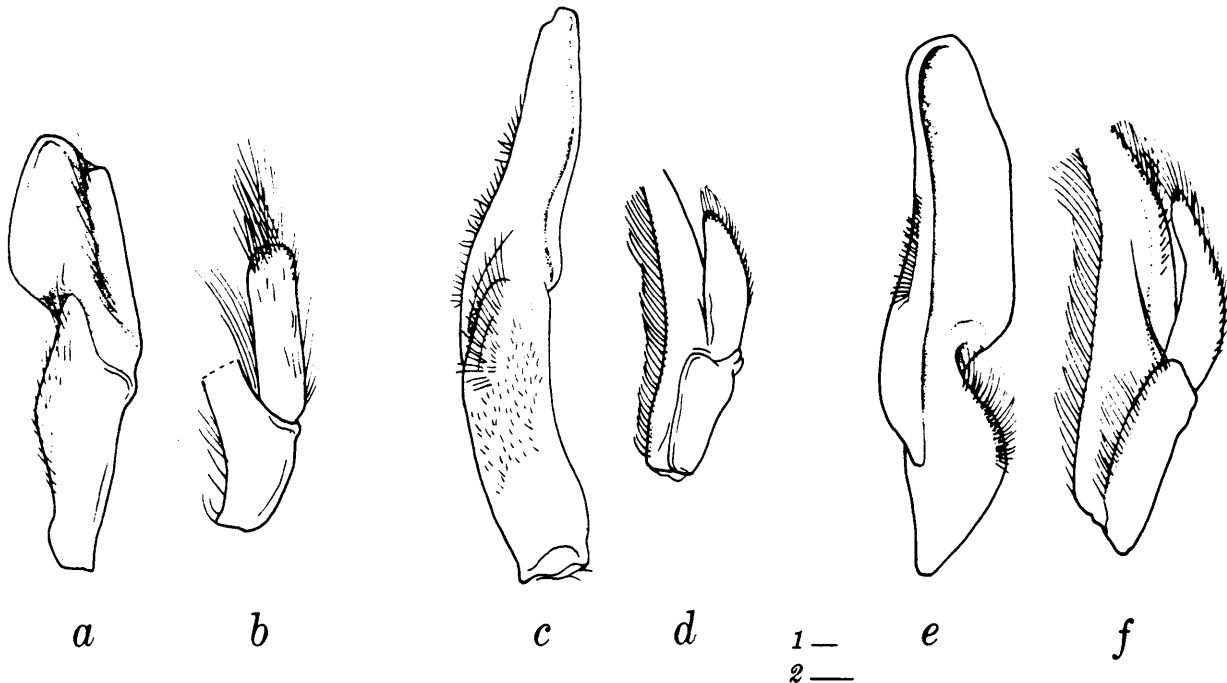


Figure 2

Male pleopods (pl); mesial views of pl 1 (slight lateral folds on tips not shown in these views), and mesial views of appendix masculina on mesial ramus of pl 2: (a and b) *Homarinus capensis*, left (USNM 251452); (c and d) *Homarus americanus*, right (USNM 13952); (e and f) *H. gammarus*, right (USNM 2085). Scale is 1 mm: bar 1 applies to c through f; bar 2 applies to a and b.

linguiform in dorsal view, broad at base where margins coalesce with orbits, margins bearing 4–6 small spines and gradually tapering anteriorly to rather abruptly pointed or narrowly rounded tip, reaching distal 1/3 of penultimate article of antennular peduncle, shallow dorsal concavity running its entire length.

Telson and uropods with thick fringe of plumose setae on distal margin and with scattered non-plumose long setae dorsally on these appendages and sixth abdominal segment. Telson as wide at base as long, with lateral margins slightly sinuous and subparallel bearing obsolescent spines and rugae, each side ending in fixed posterolateral spine; terminal margin beyond spine broadly convex; distal 1/3 of surface bearing obsolescent transverse rugae. Uropods broadly subovate, sparsely setose on dorsal surface; mesial ramus broadest near posterior margin with width about 0.73 length, row of obsolescent lateral marginal spines ending in fixed posterolateral spine; lateral ramus with width about 0.72 length, diaresis well behind midlength bearing row of fixed but irregularly worn spines ending in strongest spine at posterolateral angle.

Chelae of first pereopods with thick coat of long plumose setae on upper surface of palm, overhang-

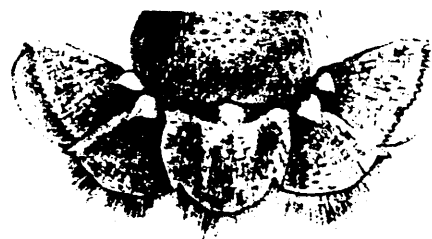


Figure 3

Homarinus capensis (Herbst), tail fan (from figure in H. Milne-Edwards, 1851).

ing extensor margin and distributed a distance along fixed finger; similar setae on mesial surface of carpus and ventral surface of merus. Fingers not gaping; those of major chela with crushing teeth (often worn) opposed from near base to about midlength

Ha	ggctcgcaaactttttgtcgatatgaactctcaaaataaataacgctgtt	50
Hgn.....	
Hcn.....	
Ha	atccctaaagtaacttaaatttttaatacaacaancaanggatcanttaca	100
Hgca.c.a.t.....c.a.	
Hcca.c.a.t.....c.a.	
Ha	cacnnnnnaaatatctctgtatttttaaatataaacagttacnnaatta	150
Hgg.....	
Hc	t.....c.....t.a.....a.t.....	
Ha	tatcatcgctcgcccaacgaaataattntagatatataaataatattaac	200
Hgc.....	
Hc	...t.....ac.c.....g.....t..	
Ha	tttcaactcatctaattatataactaaattattaagctttatagggtctta	250
Hg	...t.....	
Hc	..a...t.....g.a.....	
Ha	tcgtccctttaaataatttaagccttttcaactaaaagtcaaattcaatt	300
Hgc.tg.a.	
Hcc.tg.a.	
Ha	tttgtgtttgagacagtttgcttctgtccaaccattcatacaagcctcc	350
Hg	a...a.....	
Hc	ac.t.t.c.....	
Ha	aattaagagactaatgactatgctaccttc	380
Hg	
Hcg.nn.....	

Figure 4

Partial sequence for the mitochondrial 16s rRNA gene. Sequences for *Homarus americanus* (Ha), *H. gammarus* (Hg), and *Homarinus capensis* (Hc) have been deposited with GenBank Accession Numbers U11238, U11246, and U11247 respectively. Dots indicate nucleotides identical with Ha; letters indicate nucleotide substitutions at the homologous sites. Sites marked 'n' have unresolved nucleotides.

ing form *-inus*, resembling. The gender is masculine.

***Homarinus capensis* (Herbst, 1792), new combination**

Synonymy—Holthuis (1986:243, fig. 1) gave an exhaustive synonymy for *Homarus capensis*, and a later (1991:59) less inclusive account. These treatments are so recent and readily available that reiteration here would be unnecessarily redundant. Succeeding reference to the species follows.

Homarus capensis.—Kado, Kittaka, Hayakawa and Pollock, 1994:72, figs. 2, 3, 4.

Material—Cape Province, South Africa. USNM 251451. 1♂, East London?, R. Melville-Smith, 92-RMS-0, Nov 1992, regurg., dismembered, carapace length (cl) 26.5 mm, short carapace length (scl) 21 mm, abdomen length (abdl) 33.0 mm. USNM 251452. 1♂, southwest Dassen Island [33°26'S, 18°05'E], regurgitated from *Sebastichthys capensis*, badly crushed and partly dismembered, R.S. Steneck, 92-D-2, 1 Dec 1992, cl 32 mm, scl 25.5 mm. USNM 251453. 1♀, Still

Bay [34°23'S, 21°27'E], dismembered, R. Melville-Smith, RMS7, abdl 45 mm. USNM 251454. 1♀, Still Bay, regurg., R. Melville-Smith, RMS8, 5 mm, abdl 47 mm.

Additional specimens reported to us by R. Melville-Smith, Sea Fisheries Institute, Cape Town: 1♂, North Dassen Island, tide pool, RSS, 92-D-1, 3 Feb 1992; 1♀, Port Alfred, RMS 1; 1♂, Houghham Park, Algoa Bay; 1♂, Dassen Island, west side, RMS 3; 1♂, Cape St. Francis, RMS 4; 1♂, Cintsa Reef, East London, RMS 5; 1♂, Sunday's River mouth, RMS 6; 2♂, Cape St. Francis, RMS 9 and 10; 1♀, Haga Haga, Transkei coast, RMS 11.

Description—As for genus with addition of the following details.

Abdominal pleura well developed, with rounded angles; pleuron of segment 1 small; pleuron of segment 2 broad, overlapping first and third pleura; pleura 3–4–5 with anteroventral angle rounded, posterolateral angle subrectangular; pleuron of segment 6 rounded ventrally, posterolateral angle rounded and confluent with anterolateral angle of telson.

followed by row of intermittent noncrushing moderate conical teeth with 4–6 smaller ones in intervals between them; minor chela with latter pattern of noncrushing teeth on cutting edge of each finger; tips of fingers on each chela curved toward each other and crossing.

Carpus of major chela elongate; anterior margin with two prominent spines and smaller ones between, palmar condyle subcircular and flattened, with suggestion of spines or tubercles on its anteromesial margin; dorsomesial margin strongly tuberculate and partly obscured by setae; shorter dorsolateral margin also tuberculate but less prominently so; strong low spines on mesioventral margin. Merus bearing subdistal anterolateral spine, well-separated sharp tubercles on mesiodorsal margin, and mesioventral row of fairly uniform small tubercles.

Minor chela with similar but less developed ornamentation; merus with acute spines and spiniform tubercles.

Etymology—The name *Homarinus* is derived from French *homard*, lobster, and the adjectival combin-

Telson with dorsal setae distributed in 3 longitudinal tracts, central and submarginal on either side; central tuft proximally in midline and another near each anterolateral corner; sparse similar setae on abdominal pleura; lateral ramus of uropod with ventral submarginal row of setae laterally.

Eyes with distal edge of cornea slightly exceeding level of basicerite tip; this tip reaching to midlength of narrowly rounded antennal scale exceeded by its very strong anterolateral spine (rarely doubled) reaching distal edge of penultimate article in antennular peduncle; latter falling short of distal margin of terminal article in antennal peduncle.

Epistome with median anterior spine closely flanked at either side by shorter rounded spine.

Cheliped of pereopod 1 having fixed finger with narrowed extensor margin set off by shallow submarginal groove. Palm with compound row of low forward pointing spines and tubercles on flexor surface, similar development on extensor edge originating at carpal condyle and running along proximal margin of palm, across its basal end, and distally for a distance along palm.

Oviducal opening on coxa of pereopod 3 oval; its axes 1.3×1.8 mm on measured female noted below.

Pleopod 1 with distal article broader than shaft and hollowed mesially, forming flattened tubular opening when appressed to opposite member, tip irregularly rounded. Pleopod 2 with appendix masculina on mesial aspect of endopod bearing tuft of strong setae at apex.

Uropods with protopodite bearing 2 strong spines overhanging proximal end of mesial and lateral ramus respectively.

Variation—There is minor variation in development of spines, tubercles, etc., among the two females and two males examined. According to Stebbing (1900), sides of the rostrum may have 5, 6, or 7 spines on the margin. Density of setae on exoskeletal parts is subject to considerable variation, owing perhaps to recency of molting, age, or abrasion after preservation.

Color—Color of a living animal is shown in Figure 1. Published records summarized by Holthuis (1986) indicate that color may depart considerably from that shown here: coral-red to tawny or reddish yellow, which may have resulted from postmortem changes; or, in the fresh state, "of a rather dark olive colour, not dissimilar to that of the Northern lobster" Gilchrist (1918:45).

Molecular characterization—Comparative analysis of a portion of the 16s ribosomal RNA gene from mitochondrial DNA (mtDNA) was conducted by

using standard protocols (Kocher et al., 1989). Mitochondrial DNA's purified by CsCl ultracentrifugation (Lansman et al., 1981) were amplified by PCR with the conserved primers 16sar and 16sbr of Palumbi et al. (1991). Following asymmetric amplification (*Homarus americanus* and *H. gammarus*) or cycle-sequencing (*Homarinus capensis*), DNA's were manually sequenced by the dideoxy chain-termination method of Sanger et al. (1977). Aligned sequences are presented in Figure 4. Sequence divergence between taxa was estimated by using the two-parameter method of Kimura (1980). Sequence divergence between *Homarus americanus* and *H. gammarus* was 1.3%, whereas average divergence between these two species and *Homarinus capensis* was 9.7%. The 16s rRNA gene is one of the most slowly evolving regions of the mtDNA molecule (Xiong and Kocher, 1994); this conservative property makes it particularly useful for comparative studies among distantly related taxa. Though there is no formal recognition of equivalence between levels of sequence divergence and taxonomic rank (Hillis and Moritz, 1990), it is clear that the relative magnitude of divergence can be a useful taxonomic indicator (Avice, 1994). The magnitude of sequence differentiation that we observed between *H. capensis* and the two North Atlantic taxa strongly suggested the existence of two discrete clades. Molecular divergence reinforced our conclusions from the reexamination of the morphology of these species.

Remarks—Morphological differences between *Homarinus capensis* and the two species of *Homarus* are clear cut. Perhaps the most obvious differences are that *Homarinus capensis* has a dense coat of setae on the outer surface of the palms and on other articles of the chelipeds (P1), and scattered setae distributed over the carapace, tail fan, sixth abdominal segment, and pleurae of the remaining abdominal segments; *Homarus americanus* and *H. gammarus* are smooth and glabrous. The telson of *Homarinus* has subparallel sides and its exposed surface bears many obsolescent transverse rugae (Fig. 3); the telson of *Homarus* species has sides converging toward the tip, giving a subtriangular shape. First pleopods are more elongate and slender in *Homarus* species than in *Homarinus* (Fig. 2).

The two species of *Homarus* attain large size (Wolff, 1978), whereas *Homarinus capensis* appears to be much smaller at maturity. No ovigerous females of *H. capensis* have been found, but openings of the oviducts are at least twice the size of those on comparably sized specimens of the species of *Homarus* (see Kado et al., 1994). This suggests that there are fewer eggs with accelerated larval development in *Homarinus capensis* relative to slower larval devel-

opment from smaller more numerous eggs in *Homarus* species (Kado et al., 1994).

Acknowledgments

Our conclusions converged independently from two viewpoints. A. B. W. and other carcinologists have long understood grounds for generic separation of the Cape lobster from *Homarus* on the basis of morphology. I. K. and R. S. S. concluded this on the basis of genetic divergence and were well into their analysis before forces were joined. A. B. W. drafted the systematic section and assembled the jointly produced text. Keiko Hiratsuka Moore rendered drawings of the pleopods. G. C. Steyskal provided advice on the choice of a new generic name. The manuscript was critically reviewed by W. Glanz, R. B. Manning, and T. A. Munroe. We are indebted especially to colleagues at the Sea Fisheries Institute, Cape Town, South Africa, who helped us in this study; Roy Melville-Smith provided materials and information, and Robert Tarr photographed the living specimen of Cape lobster. George M. Branch, University of Cape Town, provided logistic support and aided in specimen acquisition. Yan Kit Tam and Alex Parker provided sequence data. R. S. S. was supported by grants from the South African Foundation of Research Development, the Visiting Scholar Fund, and the Student Fund for Visiting Scholars of the University of Cape Town. Molecular work was supported by NOAA Sea Grant (NA90AAD-SG499) and NSF (EHR-9108766 and OCE-9203342).

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