Phylogenetics of *Cancer* Crabs (Crustacea: Decapoda: Brachyura)

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We used morphological, mitochondrial DNA sequence, paleontological, and biogeographical information to examine the evolutionary history of crabs of the genus *Cancer*. Phylogenies inferred from adult morphology and DNA sequence of the cytochrome oxidase I (COI) gene were each well resolved and well supported, but differed substantially in topology. Four lines of evidence suggested that the COI data set accurately reflected *Cancer* phylogeny: (1) in the phylogeny inferred from morphological data, each Atlantic species was sister taxon to an ecologically similar Pacific species, suggesting convergence in morphology; (2) a single trans-Arctic dispersal event, as indicated by the phylogeny inferred from COI, is more parsimonious than two such dispersal events, as inferred from morphology; (3) test and application of a maximum likelihood molecular clock to the COI data yielded estimates of origin and speciation times that fit well with the fossil record; and (4) the tree inferred from the combined COI and morphology data was closely similar to the trees inferred from COI, although notably less well supported by the bootstrap. The phylogeny inferred from maximum likelihood analysis of COI suggested that *Cancer* originated in the North Pacific in the early Miocene, that the Atlantic species arose from a North Pacific ancestor, and that *Cancer* crabs invaded the Atlantic from the North Pacific 6–12 mya. This inferred invasion time is notably prior to most estimates of the date of submergence of the Bering Strait and the trans-Arctic interchange, but it agrees with fossil evidence placing at least one *Cancer* species in the Atlantic about 8 mya. © 1999 Academic Press

INTRODUCTION

Crabs of the genus *Cancer* (Crustacea: Decapoda: Brachyura) comprise 23 phenotypically diverse species distributed in a variety of intertidal and subtidal habitats worldwide (Table 1; Nations, 1975; Lawton and Elner, 1985; Creswell and Marsden, 1990; Jensen, 1995). *Cancer* species have long been the subject of intense interest from evolutionary biologists, paleontologists, and systematists (Bell, 1835; Weymouth, 1910; Way, 1917; Imaizumi, 1962; Nations, 1975, 1979; Car-

vacho, 1989), behavioral ecologists (Mackay, 1943; Garth and Abbott, 1980; Orensanz and Galluci, 1988; Creswell and McLay, 1990; Orensanz *et al.*, 1995), and fisheries researchers (e.g., Anderson and Ford, 1976; Haeffner, 1976; Reilly and Saila, 1978; Ingle, 1981; Carroll, 1982; Lawton and Elner, 1985; Hines, 1991), and as a result, there exists a plethora of ecological, behavioral, and biogeographic information on the genus. Despite the ecological, evolutionary, and economic importance of *Cancer* crabs, phylogenetic hypotheses for the analysis of their evolution and adaptations have yet to be developed and their diversity has yet to be examined in a temporal or comparative context.

In this paper, we infer a phylogeny for selected species of the genus *Cancer* using both DNA sequence and morphological data, and we use this phylogeny to examine the origin, diversification, and biogeographic history of these *Cancer* species. The paper has two main goals. First, we assess the usefulness of data from DNA sequence of the mitochondrial cytochrome oxidase I gene and from external adult morphological traits for phylogenetic inference in the genus; we analyze the degree of congruence of the data and trees derived from these two sources and then decide upon our best-supported hypothesis of ancestry. Second, we examine the relationship between our phylogeny and the extensive fossil record of *Cancer* crabs (Nations, 1975) to investigate their date of origin, temporal pattern of diversification, and biogeographic history, particularly with regard to the timing of one of the most critical dispersal events in the history of marine biodiversity, the trans-Arctic interchange (Gladenkov, 1979; Herman and Hopkins, 1980; Vermeij, 1989a,b, 1991).

MATERIALS AND METHODS

Taxonomy and Biogeography of the Genus Cancer

Nations (1975) divided the genus *Cancer* into four subgenera: *Romaleon, Metacarcinus, Glebocarcinus,* and *Cancer* sensu stricto. Based on paleontological and morphological evidence, he proposed that (1) the relatively small, highly ornate crabs of the subgenus *Romaleon* are ancestral to the other *Cancer* species because *Romaleon* species appear earliest in the fossil record,

TABLE 1

Selected Life History Characteristics for the Species Used in the Molecular Analysis

Species (common name)	*Cancer* subgenus†	Distribution*†	Reported depth range*¥¶	Primary habitat type*¥	Collection site/date	GenBank Accession No.
Petrolithes cinctipes (Flat porcelain crab)	●	Porcher Island, British Columbia to Santa Barbara, California	Upper and middle intertidal	Under rocks on or near the outer coast; abundant in mussel beds	Diana Island, B.C. May-95	AF060776
Hemigrapsus nudus (Purple shore crab)	●	Yakobi Island, Alaska to Bahia de Tortuga, Mexico	Upper and middle intertidal	Under rocks on exposed beaches; estuaries	Diana Island, B.C. May-95	AF060775
Cancer oregonensis (Pygmy rock crab)	*Glebocarcinus*	Pribilof Islands to Palos Verdes, California	Low intertidal to 436 m	Under rocks in low intertidal; subtidally in broken shell	First Beach, B.C. Jun-95	AF060772
Cancer branneri (Furrowed rock crab)	*Romaleon*	Granite Cove, Alaska to Isla de Cedros, Baja California	Subtidal to 179 m	Coarse gravel and sand; most abundant on broken shell	Helby Island, B.C. Jun-96	AF060774
Cancer gracilis (Graceful crab)	*Metacarcinus*	Prince William Sound, Alaska to Bahia Playa Maria, Mexico	Low intertidal to 143 m	Mud and muddy sand	Grappler Inlet, B.C. May-95	AF060769
Cancer novaezealandiae (New Zealand rock crab)	*Metacarcinus*	New Zealand; North, South, Auckland and Chatham Islands; introduced to Tasmania and Victoria, Australia	Intertidal to 60 m	Fine sediment, under rocks, stones, and among seaweed	New Zealand Oct-96	AF060768
Cancer antennarius (Pacific rock crab)	*Romaleon*	Queen Charlotte Sound, British Columbia to Cabo San Lucas, Mexico	Low intertidal to 91 m	Mud, sand, gravel, and rock	Diana Island, B.C. May-95	AF060773
Cancer borealis (Jonah crab)	*Metacarcinus*	Grand Banks to south of Tortugas, Florida	Intertidal to 870 m; most abundant at intermediate depths	Mud, sand, and near shore rocky areas	Nova Scotia Oct-96	AF060767
Cancer productus (Red rock crab)	*Cancer* sensu stricto	Kodiak, Alaska to Isla San Martin, Baja California	Mid intertidal to 79 m	Mud, sand, gravel, and boulder beaches	Grappler Inlet, B.C. May-95	AF060770
Cancer magister (Dungeness crab)	*Metacarcinus*	Pribilof Islands to Santa Barbara, California	From low intertidal to 230 m	Common subtidally on sand and mud	Pachena Bay, B.C. May-95	AF060766
Cancer pagurus (Edible crab)	*Cancer* sensu stricto	From northwest coast of Norway, south to Portugal: Mediterranean Sea	Intertidal to 100 m	Primarily mud and sand, some rock	Great Britain Jun-95	AF060771

Note. Sources of information: † = Nations, 1975; ¥ = Lawton and Elner, 1985; ¶ = Creswell and Marsden, 1990; * = Jensen, 1995.

(2) crabs of the subgenus *Cancer* sensu stricto, which are characterized by large size, smooth carapace margins, pronounced lateral carapace expansions, and unornamented chelipeds, were the most recently derived group, and (3) *Metacarcinus* species appear to represent an intermediate stage between *Romaleon* and *Cancer.* Nations (1975) also noted that the evolutionary position of crabs of the subgenus *Glebocarcinus* remains unclear, as *Glebocarcinus* species have relatively large, wide carapaces, yet retain a high degree of cheliped and carapace ornamentation.

Previous paleontological research has suggested that the genus *Cancer* originated in the Miocene in the North Pacific and dispersed south along the coast of North and South America, west toward Japan, and north across the Arctic into the Atlantic Ocean, with

speciation events subsequent to or concomitant with dispersal into each new area (Fig. 12 of Nations, 1975; Nations 1979). According to Nation's (1975) biogeographic hypotheses, the basal species of *Cancer* should be North Pacific species and the Atlantic species should be more closely related to one another than to any of the Pacific species. Furthermore, if *Cancer* species participated in the trans-Arctic interchange and speciated once they reached the Atlantic Ocean, Atlantic taxa should have diverged from the North Pacific species sometime after the seaway between Alaska and Siberia opened, 5.2–3.4 million years ago (Gladenkov, 1979; Herman and Hopkins, 1980; Vermeij, 1989a,b, 1991).

Choice of Taxa

Our analyses included 9 of the 23 extant *Cancer* species, including at least 1 species representative from each of the four subgenera proposed by Nations (1975). These taxa include all *Cancer* species from the northeast Pacific, 2 Atlantic species, and the single species from the southwest Pacific (New Zealand). Two other crabs, *Hemigrapsus nudus* (Decapoda: Brachyura: Grapsidae) and *Petrolithes cinctipes* (Decapoda: Anomura: Porcellanidae), representing a different brachyuran family and decapod order, respectively, were used as the outgroups. These outgroup taxa were chosen because multiple outgroup taxa can increase resolution and support for basal ingroup nodes (Maddison *et al.,* 1984) and these two species were readily available.

COI Data Collection

DNA was isolated from frozen or preserved (in 99% ethanol or guanidine isothiocyanate) specimens by crushing cheliped muscle tissue in Lifton buffer (0.2 M sucrose, 0.05 M EDTA, 0.1 M Tris, 0.5% SDS). Total DNA was extracted from this homogenate using phenol–chloroform–isoamyl alcohol, precipitated in 70% ethanol with 0.7 M sodium acetate, and suspended in sterile distilled water. The primers designated S1718a or S1718b were used with A2238, A2316, A3500, or A3662 (Table 2) to amplify sequence from the mitochondrial cytochrome oxidase I (COI) gene using the polymerase chain reaction (PCR). After processing with exonuclease I and shrimp alkaline phosphatase, double-stranded PCR products were sequenced using 35^S and Sequenase kits (U.S. Biochemical) or 33^P Thermo Sequenase radiolabeled terminator cycle sequencing kits (Amersham Life Sciences) (30 cycles; 30 s at 95°C, 30 s at 60°C, and 60 s at 72°C). Sequences were aligned by eye using SEQAPP (Appendix 1). All COI products were sequenced in one direction (annealing with various 'S' primers; Table 2), and the opposite strand was also partially sequenced (annealing with various 'A' primers; Table 2) for all taxa to confirm that there were no inconsistencies in the sequence.

TABLE 2

Primer Sequences Used in the Amplification and Sequencing of the COI Region

Primer name	Primer sequence								
	5′								3′
S1718a	GGA	GGA	TTT	GGA	AAT	TGA	TTA	GTT	C
S1718b	GGA	GGA	TTT	GGA	AAT	TGA	TT		
S1834	AAG	AGG	WWT	AGT	AGA	AAG	WGG		
S1841	ATA	GTA	GAA	AGA	GGW	GTT	GG		
S1976	GTA	AAY	TTT	ATA	ACA	AC			
S1991	ACM	GTW	ATT	AAT	ATA	CG			
S2045	GTT	TGA	GCT	GTA	TTT	AT			
S2118	TWY	TAA	CTG	ACC	GAA	A			
S2219	ATT	CTT	ATT	TTA	CCY	GCT	T		
S2249	ATG	ATT	TCT	CAY	ATT	GTT	AG		
S2329	ACT	GTA	AAT	ATA	TGA	TGA	GCT	CA	
S2417	ACW	ATA	ATT	ATT	GCY	RTH	CC		
A1887	ARR	GGD	GGR	TAR	ACR	GTY	CA		
A2051	CTR	GTT	TAT	GGW	GAR	AAR	CA		
A2064	GTA	ATA	AAW	ACA	GCT	CAA			
A2238	GGY	AAA	ATW	ARA	ATA	TAD	AC		
A2316	TAA	ATT	ATY	CCW	ARG	GTC	CC		
A3389	TCA	TAA	GTT	CAR	TAT	CAT	TG		
A3500	TAA	GAR	TCA	AAT	TTC	TAC	TTG		
A3662	CCA	CAA	ATT	TCT	GAA	CAT	TGI	CC	

Note. Primer numbers correspond to 3′ positions in the *D. yakuba* genome (Clary and Wolstenholme, 1985). Nonstandard and mixed bases as follows: I = deoxyinosine, R = A + G, Y = C + T, M = A + C, W = A + T, D = A + T + G, H = A + T + C.

Morphological Data Collection

An extensive morphological character matrix was constructed from the literature, using characters developed in previous systematic studies of fossil and extant *Cancer* crabs (Bell, 1835; Weymouth, 1910; Way, 1917; Imaizumi, 1962; Nations, 1975; Carvacho, 1989) (Appendix 2). Data were restricted to adult features because of the high degree of intraspecific variability in larval morphology (Orensanz and Galluci, 1988).

Phylogenetic Analyses

Phylogenetic analyses and the test of the validity of a molecular clock model for the COI data were conducted using PAUP (beta test version *d63, written by D. L. Swofford). In both the morphology and the COI data sets, all characters were weighted equally. Multistate morphological characters were ordered because we assumed that character transitions in *Cancer* crabs have occurred in a stepwise manner. Both the COI and the morphological data sets were analyzed in PAUP*d63 using maximum parsimony with the branch and bound algorithm. The robustness of trees inferred from these analyses was evaluated using bootstrap analyses with heuristic searching (1000 replicates; Felsenstein, 1985), decay indices (Bremer support; Bremer, 1994), and skewness analysis of tree length frequency distributions (Hillis, 1991; Huelsenbeck, 1991; Hillis and

Huelsenbeck, 1992). The COI data set was also analyzed using neighbor-joining with the default settings under the Kimura two-parameter model and maximum likelihood using the empirical nucleotide frequencies with a transition–transversion ratio of 2.0 under the Hasegawa–Kishino–Yano model. For the COI data, we tested an hypothesis of a molecular clock by comparing the log-likelihood of the maximum likelihood tree constrained to clockwise behavior with the log-likelihood of a tree with the same topology inferred using the unconstrained model, using the Kishino–Hasegawa test.

Considerable debate in the systematic literature has centered on the analysis and ability of different types of data to accurately reflect phylogenetic history (Eernisse and Kluge, 1993; Larson, 1994; reviewed in Swofford 1991; Bull *et al.,* 1993; deQueiroz *et al.,* 1995; Miyamoto and Fitch, 1995; Huelsenbeck *et al.,* 1996; Huelsenbeck and Bull, 1996). Much of this controversy focuses on the relative merits of morphological versus molecular characters (e.g., Lewin, 1985; Hillis, 1987) and the methods of combining such diverse information. The two main approaches are taxonomic congruence and total evidence: taxonomic congruence involves inferring a consensus tree from separately analyzed data sets, while total evidence involves using character congruence to find the best-fitting topology for all of the available data (Eernisse and Kluge, 1993). The strategy followed in this paper was to analyze the degree of congruence between the data sets using a variety of approaches and to assess the influence of data set combining on tree topology, resolution, and support. A finding of well-supported incongruence between data sets would motivate investigation of its causes, using evidence ancillary to the data sets themselves.

Four methods were used to assess the degree of congruence between the COI and the morphology data sets. First, we evaluated the magnitude of the bootstrap values and decay indices on the trees inferred from each data set separately. Second, Templeton's Wilcoxon test (1983) was used to compare the topologies of the trees produced by maximum parsimony analyses of each data set. Templeton's test compares two topologies by summing the number of characters that undergo a different number of changes on the two trees. The sign and magnitude of these character by character differences are then analyzed using a Wilcoxon rank sum test. Third, to determine if the tree inferred from the combined data was only slightly suboptimal with respect to the trees inferred from each data set separately, the number of steps each data set required on the combined tree was compared to the number of steps required on the shortest trees inferred from the separate data sets (Swofford, 1991). Fourth, the Mickevich–Farris incongruence index (I_{MF}) (Swofford, 1991) and its associated statistical test (the partition homogeneity or incongruence length difference test; Farris *et al.,* 1994; see also Cunningham, 1997)

were used to assess the extent of character incongruence between the data sets. I_{MF} values partition total character incongruence (homoplasy) into between and within data set components; smaller I_{MF} values indicate that the disagreement between two data sets is low relative to the amount of incongruence among characters within the separate data sets. Statistical significance of I_{MF} need not engender substantial erosion of resolution and support of a tree inferred from the combined data relative to trees inferred from the separate data sets (e.g., Crespi *et al.,* 1998; Remsen and DeSalle, 1998), which suggests that it represents a necessary, though not sufficient, condition for convincing deviation from congruence.

RESULTS

Data Sets

The COI data set consisted of 1072 characters, 307 of which were cladistically informative and 240 of which were informative within the ingroup (Appendix 1). Using all three nucleotide positions yielded pairwise distances ranging from 7.2 to 17.2% within the ingroup, 19.9 to 23.6% between ingroup taxa and outgroup species, and 23.0% between the two outgroups (Table 3).

The morphology data set included 44 characters, which comprised 13 carapace traits and 31 claw characters. Thirty-eight of these characters were cladistically informative in the entire data set, and 37 were informative in the ingroup (Appendix 3).

Phylogenetic Analyses

Ten thousand random trees were generated from each data set to analyze the skewness of tree length frequency distributions. G_1 values indicated a strongly significant phylogenetic signal in both data sets (morphology: $g_1 = -0.913, P < 0.05$; COI: $g_1 = -0.834, P < 0.05$).

Analysis of COI data. Maximum parsimony analysis of the COI data yielded one tree of length 1043 (consistency index CI = 0.587, retention index RI = 0.383) (Fig. 1A). Both bootstrap values and decay indices for this tree gave strong support (99% and 21 steps, respectively) for the branch differentiating the *Cancer* genus from the outgroups and for four of the ingroup nodes (≥70% and ≥3 steps, respectively). In particular, the monophyly of the two Atlantic species, *C. borealis* and *C. pagurus,* was supported by a high bootstrap value (81%) and a high decay index (5 steps).

The topologies of the phylogenetic trees inferred from neighbor-joining (Fig. 1B) and maximum likelihood (Fig. 1C) analyses did not differ substantially from the topology of the tree inferred from maximum parsimony analysis. All three trees agreed with respect to the node connecting the two Atlantic species, the branch supporting *C. novaezealandiae, C. antennarius,* and *C. magister,* and the clade containing *C. gracilis, C. branneri,* and *C. oregonensis.* In addition, 1000 bootstrap repli-

TABLE 3

Pairwise Distance Matrix for the COI Data Set

	Pairwise differences between taxa										
	P. cinctipes	*H. nudus*	*C. branneri*	*C. antennarius*	*C. oregonensis*	*C. pagurus*	*C. productus*	*C. gracilis*	*C. novaezealandiae*	*C. borealis*	*C. magister*
P. cinctipes	●										
H. nudus	0.230	●									
C. branneri	0.226	0.220	●								
C. antennarius	0.227	0.232	0.137	●							
C. oregonensis	0.218	0.230	0.118	0.162	●						
C. pagurus	0.208	0.215	0.165	0.151	0.160	●					
C. productus	0.211	0.214	0.150	0.148	0.172	0.134	●				
C. gracilis	0.217	0.199	0.107	0.148	0.138	0.172	0.157	●			
C. novaezealandiae	0.213	0.236	0.163	0.072	0.165	0.146	0.146	0.169	●		
C. borealis	0.213	0.228	0.149	0.162	0.165	0.109	0.141	0.161	0.154	●	
C. magister	0.232	0.224	0.159	0.147	0.166	0.148	0.149	0.172	0.138	0.165	●

cates of the neighbor-joining tree (Fig. 1B) provided strong support (>70%) for all nodes except the branches supporting *C. branneri* and *C. gracilis* (67%), and the clade encompassing *C. productus* and the two Atlantic species (65%). The only difference among the three trees was the position of *C. productus;* on the tree derived from maximum parsimony analysis, *C. productus* was the most basal *Cancer* species, whereas on the trees resulting from neighbor-joining and maximum likelihood analyses, *C. productus* formed a monophyletic group with the two Atlantic species and *C. oregonensis, C. branneri,* and *C. gracilis* comprised the most basal *Cancer* clade.

Analysis of morphology data. Maximum parsimony analysis of the morphology data set yielded four trees with 167 steps (CI = 0.557, RI = 0.529). One thousand bootstrap replicates and the decay index again gave strong support for the branch differentiating the genus *Cancer* from the outgroups (98% and 8 steps, respectively) on the strict consensus tree (Fig. 2). Three internal nodes were also supported by strong bootstrap values (>75%) and decay indices (2 or 3 steps), and the node separating *C. magister* from the other *Cancer* species received some support (67%, 1 step).

Analysis of combined data. Maximum parsimony analysis of the combined COI and morphology data yielded one shortest tree of length 1250 (CI = 0.56, RI = 0.36) (Fig. 3A) that was identical to the maximum parsimony, neighbor-joining, and maximum likelihood trees inferred from COI with regard to the presence of the monophyletic group ((*C. antennarius, C. novaezealandiae*), *C. magister*) and shared the clade (*C. productus,* (*C. borealis, C. pagurus*)) with the tree inferred from neighbor-joining. The combined tree was also similar to the tree inferred from morphology in that *C. gracilis* and *C. branneri* were basal taxa in both trees, although *C. magister* formed the sister taxon to the other *Cancer* species in the tree inferred from morphology. Bootstrap support for the combined tree

was generally quite low (Fig. 3B), with strong support restricted to the clade ((*C. antennarius, C. novaezealandiae*), *C. magister*), a group also well supported by the bootstrap analysis of the COI data.

Congruence analysis. None of the nodes on the trees inferred from the COI and morphology data sets defined identical monophyletic groups. We note in particular that in the tree inferred from the morphology data, each of the two Atlantic species forms the sister group to a Pacific species, whereas in the COI data, the Atlantic species form a well-supported monophyletic group (Fig. 2). The bootstrap and decay index values for conflicting nodes were generally high (Figs. 1A, 1B, and 2), such that the differences between topologies cannot be attributed to weakness of support for relationships and concomitant topological uncertainty. Templeton's (1983) test also provided strong evidence for substantive difference between the topologies (Wilcoxon rank sum test; *P* < 0.001).

To determine if a single tree existed that was only slightly suboptimal with respect to the trees inferred from both data sets, the number of steps each data set required on the combined tree (Fig. 3) was compared to the number of steps required on the shortest trees inferred from the separate data sets (Swofford, 1991). The COI and morphology data sets required 16 and 20 more steps, respectively, on the tree inferred from the combined data set than they did on the tree inferred from each data set separately; thus, for the COI data the combined tree was 1.5% (16/1059) longer than the shortest COI tree of 1043 steps, and for the morphology data the combined tree was 11% (20/187) longer than the shortest tree from morphology alone. The morphology data required 43 additional steps on the tree based on COI data, and the COI data set required 111 additional steps on the tree produced by the morphology data. These results suggest that the COI data set fit a tree from the combined data reasonably well but the morphology data set did not and that the topologies

constructed from the separate data sets were substantially different.

The trees inferred from the separate morphology, COI, and combined data sets each contained 74, 431, and 545 homoplasies, or extra steps, respectively. These extra steps represent the difference between the amount of character change required (the tree length) on the tree being evaluated and the minimum amount of change that the characters could show on any tree. Analysis of character congruence yielded a congruence
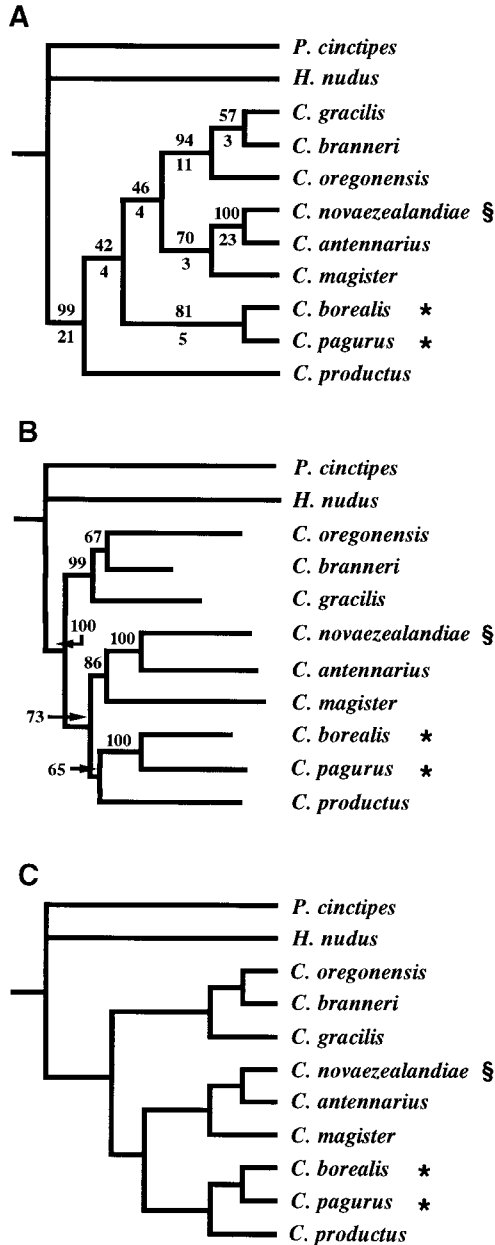

FIG. 1. Results of analyses of COI data using (A) maximum parsimony (one tree; length = 1043, CI = 0.587, RI = 0.383), (B) neighbor-joining, and (C) maximum likelihood (ln likelihood = −6083.04). Bootstrap values (1000 replicates) are indicated above branches and decay indices are shown below branches. * and § denote Atlantic and South Pacific species, respectively.
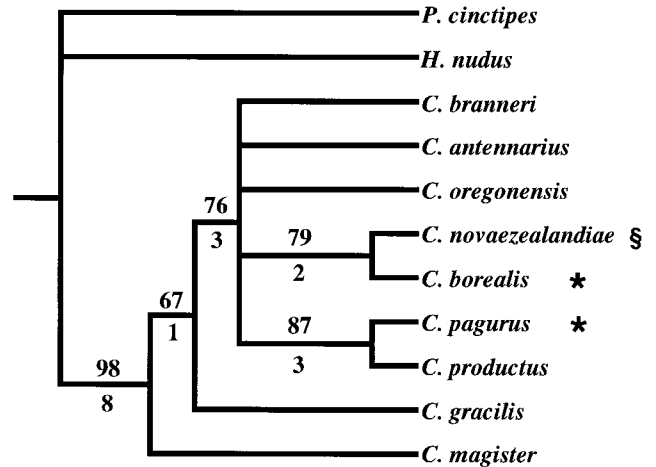

FIG. 2. Results of maximum parsimony analysis of the morphology data set, showing the strict consensus tree (four trees; length = 167, CI = 0.557, RI = 0.529); bootstrap values (1000 replicates) are indicated above branches and decay indices are shown below branches. * and § denote Atlantic and South Pacific species, respectively.

index (I_{MF}) of 0.073, indicating that 7.3% of the total character incongruence was due to disparity between the data sets. Thus, the relative degree of between-data set incongruence was low relative to the extent of character incongruence within the two separate data sets. However, the incongruence length difference test indicated that this degree of incongruence between data sets was statistically highly significant ($P = 0.001$).

All four of our approaches to analyzing congruence suggested that the morphology and COI characters provided strongly conflicting information. To determine whether certain characters in each data set were obscuring the true phylogeny of *Cancer* crabs, we reanalyzed both data sets by excluding specific character types. First, we partitioned the COI data set into hydrophobic and hydrophilic regions. Second, we excluded third position nucleotides, which have a relatively high substitution rate (Simon *et al.*, 1994). Neither method yielded substantially different results. Third, we excluded the claw characters from a reanalysis of the morphological data, using the justification that claws may be under stronger selective pressures because of their role in a variety of functions, such as feeding, defense, and mate acquisition (Orensanz and Galluci, 1988) and therefore may tend to be convergent. However, the tree produced by this analysis was also weakly supported, and the two Atlantic species remained nonmonophyletic.

To what degree do the trees inferred from each of the two separate data sets conflict with the combined tree? Consideration of the degree of support for the relationships in the combined tree indicates that this tree is more similar to the COI tree than the single most-parsimonious combined tree would indicate. Thus, the bootstrap majority-rule tree inferred from the com-

bined data (Fig. 3B) has nearly the same topology as the trees inferred from COI (Fig. 1), differing only with regard to nodes exhibiting extremely weak bootstrap support in one or both analyses. Indeed, a combined tree with the same topology as the maximum parsimony COI tree has only three more steps than the shortest combined tree, a 0.2% difference in length. The main difference between the trees inferred from the COI and the combined data is therefore the reduced degree of bootstrap support for relationships in the tree from combined data. The tree inferred from morphology remains highly incompatible with the combined tree, especially with regard to the placements of *C. novaezealandiae, C. borealis,* and *C. magister.*

Analysis of Evolutionary History and Biogeography

To draw inferences concerning the origin and tempo of diversification in the genus *Cancer* and to compare the results of our phylogenetic analyses with the information in the fossil record, we presumed that the COI
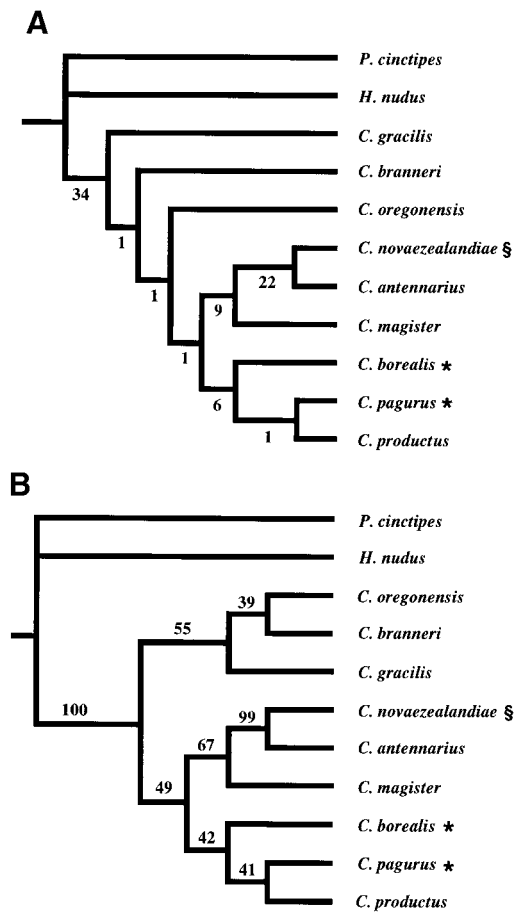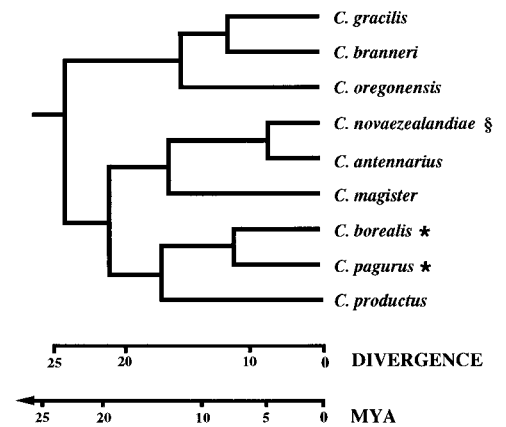

COI: Maximum likelihood analysis with molecular clock
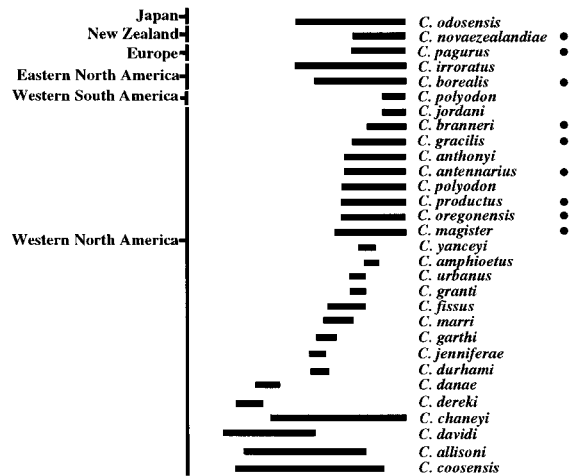
Fossil record:

FIG. 4. Comparison of results of maximum likelihood analysis of the COI data constrained to a molecular clock and the stratigraphic distribution of *Cancer* crabs (after Nations, 1975). * and § denote Atlantic and South Pacific species, respectively, and ● indicates those species for which COI data was collected.

FIG. 3. (A) Shortest tree resulting from maximum parsimony analysis of the combined data sets (one tree; length = 1250, CI = 0.564, RI = 0.363; decay indices are shown below branches). (B) Bootstrap majority-rule consensus tree (plus compatible groups) of combined data set; bootstrap values (1000 replicates) are indicated above branches. * and § denote Atlantic and South Pacific species, respectively.

data yielded an accurate phylogeny and we explored the ramifications of this presumption. Analysis of the COI data using maximum likelihood analysis did not lead to statistical rejection of the validity of the molecular clock (Kishino and Hasegawa test; Ln L with clock = −6090.9, Ln L without clock = −6087.4; difference in Ln L = 3.5, SD = 2.5; $P = 0.18$). We therefore used the tree constrained to the molecular clock generated from the COI data and COI clock calibrations from Juan *et al.* (1995, 1996; see also Brower, 1994) to attach an approximate time scale to the evolutionary history of *Cancer* (Fig. 4). This tree and the clock calibration suggested that *Cancer* crabs arose during the Miocene, 20–25 million years ago, and that the majority of the diversification within this clade occurred by the end of the Miocene, about 5 million years ago. On this tree, north Pacific species were the most basal taxa, and the clade containing *C. novaezealandiae,* the South Pacific

species, and *C. antennarius,* a North Pacific crab, was the most recently derived group, diverging approximately 6 million years ago. The two Atlantic species (*C. pagurus* and *C. borealis*) were paired as sister species, branching off from their Pacific ancestors 6 to 12 million years before present.

The fossil record also exhibits good correspondence with the results of the maximum likelihood molecular clock model with regard to the ages of the different species. Thus, none of the extant species is recorded in the fossil record as clearly being older than the age of its lineage as inferred from the COI tree, though ancestors along internal branches of the tree may well closely resemble one of the descendant species. Similarly, the three lineages inferred as relatively old from the COI tree, *C. oregonensis, C. magister,* and *C. productus,* also arose relatively early, among extant species, in the fossil record, and two of the relatively young lineages as inferred from the COI tree, those leading to *C. novaezealandiae* and *C. pagurus,* are also relatively recent in the paleontological record. Inclusion in our phylogenetic analysis of species that are most recent in the fossil record, *C. polyodon* and *C. jordani,* will allow more extensive tests of the correspondence between phylogenetic and paleontological information, but given the uncertainties inherent in both sources of data, the general agreement between them in the data analyzed here lends credence to both.

DISCUSSION

Systematics and Phylogenetics of the Genus Cancer

The phylogenetic trees inferred from the morphological and COI characters supported notably different, though each strongly supported, hypotheses of relationship among crabs of the genus *Cancer.* In particular, analysis of the COI data indicated sister taxon status of the two Atlantic species, whereas analysis of the morphology data resulted in pairing of each Atlantic species with a Pacific species. The incongruence of the two topologies was strongly supported by the high bootstrap values on both of the trees derived from the separate data sets, the lack of a slightly suboptimal tree consistent with both data sets, and the highly significant results of the incongruence length difference and Templeton tests. Although the COI and morphology data sets provided notably incongruent trees, the combined data set yielded a tree that was closely similar to the trees inferred from COI using maximum parsimony, neighbor-joining, and maximum likelihood, although this combined tree was substantially less well supported by bootstrap analysis. Faced with such evidence of incongruence, we attempted to determine which, if either, phylogenetic hypothesis accurately represented the genealogical relationships of *Cancer* crabs. To this end, we first sought to diagnose the source of the incongruence and then evaluated the

ancillary evidence for and against the alternative phylogenetic hypotheses.

Consideration of the distributions, habitats, and feeding ecology of the species exhibiting divergent positions on the trees inferred from COI and morphology, *C. pagurus, C. productus, C. borealis,* and *C. novaezealandiae,* suggests that the source of incongruence between the data sets is extensive convergence in adult crab morphology. All four species live in intertidal and subtidal habitats and consume a wide variety of prey (Lawton and Elner, 1985; Creswell and Marsden, 1990; Jensen, 1995), and the pairs of species joined in the analysis of morphology, with each pair comprising species in different oceans, exhibit notable ecological similarities. Thus, *C. borealis* and *C. novaezealandiae* are most common in more structurally complex microhabitats and consume primarily hard-shelled molluscan and crustacean prey (Creswell and Marsden, 1990; Creswell and McLay, 1990), whereas adult *C. pagurus* and *C. productus* are more omnivorous and most frequently occupy open-bottom substrates or habitats with large hiding places (Lawton and Elner, 1985; Orensanz and Galluci, 1988). Consequently, *C. borealis* and *C. novaezealandiae* appear to have converged with respect to their relatively stout, robust claws and oval-shaped carapace; correspondingly, *C. pagurus* and *C. productus* have smaller, weaker claws and wide carapaces with concave sides, which minimize lateral resistance to water flow in open benthic habitats (Blake, 1985). Our analyses suggest that the similarities in habitat across each pair of species have selected for convergence not just in overall size and shape, but in a sufficient number of external morphological traits to bias the results of the morphological analysis and make the separation of homoplasious from nonhomoplasious characters problematic.

Our hypothesis of convergence between *C. borealis* and *C. novaezealandiae* and between *C. pagurus* and *C. productus* is consistent with the taxonomic treatment of *Cancer* by Nations (1975), in that he places the former two species in the subgenus *Metacarcinus* and the latter two species in the subgenus *Cancer* sensu stricto. Other systematic studies of brachyuran crabs have encountered evidence of substantial homoplasy in external adult morphology (Rice, 1980; Spears *et al.,* 1992). For example, the division Podotremata, which comprised the families Ranindae and Dromiidae, was proposed by Guinot (1977) on the basis of similar gonopore location; however, analysis of spermatozoan ultrastructure (Jamieson, 1990), zoel morphology (Rice, 1980), and sequence from 18S rRNA (Spears *et al.,* 1992) all suggest that the Dromiidae should be removed from the Brachyura. Similarly, 18S rRNA sequence data failed to support the monophyly of the Dromiidae; the morphological similarity (particularly the carapace) of the dromiid genera *Dromidia* and *Hypoconcha* appears to reflect convergence in response to the shared behavior of carrying objects (e.g., sponges)

over their dorsal surface (Spears *et al.,* 1992). Several researchers have concluded that the accuracy of trees inferred from morphological data may be improved by the inclusion of characters that are presumably less subject to the selective pressures that may lead to convergence, such as setae number, antennae form, and gonopod structure (Jamieson, 1990; Abele, 1991).

Given the apparent high degree of morphological convergence among the allopatric species of *Cancer* crabs in this study, we believe that the COI and combined data sets provide a more accurate guide to the genealogical relationships of the genus *Cancer* than the tree inferred from morphological characters. Ancillary evidence for this hypothesis is provided by two sources. First, the biogeographic implications of the tree inferred from COI data agree with the most plausible dispersal pattern of *Cancer* crabs. Based on paleontological evidence, the genus is thought to have originated in the North Pacific, dispersing south along the coast of North and South America, west toward Japan, and north across the Bering Strait to the Atlantic Ocean (Nations, 1975, 1979). Thus, presuming a single trans-Arctic invasion, Atlantic species should be more closely related to one another than to any of the Pacific species, and indeed, in the tree inferred from the COI data, the two Atlantic taxa form a well-supported monophyletic group. Second, the phylogeny inferred via maximum likelihood analysis of the COI data, under the molecular clock model, is consistent with the fossil record of *Cancer* crabs with respect to the timing and location of the origin, diversification, and speciation patterns of the genus (Fig. 4). The stratigraphic distribution of *Cancer* crabs suggests that the genus arose in the Pacific in the early Miocene and diversified relatively rapidly. According to our COI-based time scale (Fig. 4), the genus *Cancer* arose in the early Miocene, the basal taxa are Pacific species, and the majority of the diversification within the genus occurred by the early Miocene, about five million years ago. The inclusion of DNA sequence from the Japanese and South American *Cancer* species in future studies will enable better resolution of the patterns of diversification of *Cancer* crabs and may allow further tests of our hypothesis that morphological phylogenetics in this genus can be prone to ecologically driven convergence.

Evolutionary History of Cancer Crabs and the Trans-Arctic Interchange

Due to the absence of *Cancer* fossils in the Asian-Arctic and the eastern Atlantic, previous studies have assumed that the probable migration route of *Cancer* crabs between the northern Pacific and the northern Atlantic was via the Bering Strait (Nations, 1975, 1979). Migration between North and South America before the closure of the Isthmus of Panama approximately 3.1 million years ago (Saito, 1976; Keigwin, 1978) is an alternative, but less plausible route, given that no *Cancer* fossils have been found in Central

America and that *Cancer* crabs are restricted to water temperatures below 24°C (Nations, 1975).

The Bering Strait, currently a shallow seaway, was a land bridge connecting Alaska and Siberia until it flooded in the late Miocene or early Pliocene, opening a migration route between the northern Pacific and Atlantic for many marine species, such as gastropods, echinoderms, barnacles, and marine vertebrates (Vermeij, 1989a,b, 1991). The date of submergence of the Bering land bridge is based primarily upon the stratigraphic distribution of fossil deposits in both the Pacific and Atlantic oceans. The occurrence of similar species of walruses in Miocene fossil beds from California and Virginia, and common molluscan species on both sides of the Atlantic Ocean, suggested to early researchers that the Bering Sea first opened briefly around 10–12 million years ago (MacNeil, 1965; Durham and MacNeil, 1967; Hopkins, 1967, 1972). However, these early deposits probably represent remnants of animals that dispersed into the Atlantic Ocean by way of the former Panama seaway before its closure around 3.1 million years ago (Repenning, 1976; Gladenkov, 1979; Herman and Hopkins, 1980). Currently, most researchers agree that the initial opening of the Bering Strait occurred approximately 5.2–3.4 million years ago (Hopkins, 1967; Gladenkov, 1979; Herman and Hopkins, 1980; Vermeij, 1989a,b, 1991).

The COI data places the invasion of the Atlantic Ocean from the North Pacific by the genus *Cancer* at approximately 6–12 million years ago, prior to most estimates of the date of submergence of the Bering Strait. Our results agree with previous paleontological research that dates *Cancer* fossils found in Atlantic deposits from the late Miocene (approximately 8 million years ago; Nations, 1975). Collins *et al.* (1996) point out that inferences from fossil data are subject to errors in fossil identification and estimates of divergence time, as well as gaps in the fossil record; however, several other DNA-based studies have also suggested an early date for trans-Arctic dispersal. For example, Collins *et al.* (1996) proposed that *Nucella* invaded the Atlantic from the North Pacific 7–8 million years ago, and studies of over 30 allozyme loci of ray-finned fish have yielded estimated divergence times of 1.7–4.5, 3.6–6.6, and 4.8–8.9 million years ago between closely related Atlantic and North Pacific species (Grant *et al.,* 1984; Grant, 1986; Grant and Stahl, 1988). These studies of molluscs and fish, taken in conjunction with our analysis and the fossil record of *Cancer* crabs, should motivate further investigation into the timing and geography of dispersal between the Atlantic and Pacific oceans.

ACKNOWLEDGMENTS

APPENDIX 1

Mitochondrial Cytochrome Oxidase I (COI) Sequence Used in the Molecular Analyses

Taxon	Position

```
       1                                                                                          100
PC,    -ggaggatttggaaattgat   tagttcccttaatattagga   gcccccgatatggctttccc   tcgtataaacaacataagat   tttgattacttcccccatct
HN,    -ggaggatttggaaattgat   tagttccactaatactaggg   gcgccagacatagcattccc   tcgtataaacaatataagat   tttggcttttaccgccctct
CB,    --------------------   --------------------   --------------------   --------------------   --------------------
CA,    -ggaggatttggaaattgat   tagttcctcttatattagga   gctcctgatatagctttccc   tcgtataaacaatatgagtt   tttgactcttacctccttct
CO,    -ggaggatttggaaattgat   tagttcccttaatactaggg   gcacctgatatggctttccc   ccgaataaataatataagat   tttgacttttaccccccttca
CPa,   aggaggatttggaaattgat   tagttcctcttatgctggga   gcgcctgacatagcctttcc   tcgaataaataacataagtt   tctgattattaccccccttca
CP,    -ggaggatttggaaattgat   tagttcctcttatattagga   gcccctgatatagctttccc   gcgtataaacaacataaggt   tttgattattaccccccttct
CG,    -ggaggatttggaaattgat   tagttcccttaatattagga   gcccctgatatagctttccc   tcgaataaataatataagat   tttgacttcttcctccctcc
CN,    --------------------   -agttcctcttatattagga   gctcctgatatagctttccc   tcgtataaacaatatgagtt   tttgactcttacctccttct
CBo,   --------------------   -agtccccttaatattagga   gcacctgatatagcctttcc   tcgaataaataatataagtt   tctggttactacccccttca
CM,    -ggaggatttggaaattgat   tagttcccctaatgctagga   gcacccgatatagctttccc   tcgtataaataatataagtt   tctgactattacctccttct
       101                                                                                        200
PC,    ctaacactccttctaataag   aggaatagttgaaagaggtg   ttggaacaggatgaactgtt   tatccacctctttctgccag   gattgcacacgcaggagctt
HN,    ttatcccttcttttaacaag   aagaatagtagagagtggag   ttggcacaggtgaactgtt    tacccctcccctctccgctgc   tattgcccacgctggcgcct
CB,    --------------------   --------------------   --------------------   ---cctcctttagcaggagc   tattgctcat--cggggcct
CA,    ctaacattactccttataag   aggtatagtagaaagaggag   ttggaacaggctgaactgtt   taccctcctttagcaggagc   tattgctcatcgtggcgcct
CO,    ttaacactgcttcttataag   aggtatggtagaaagagggg   ttgggacaggatgaaccgtc   taccctcctttagcgggggc   tattgctcacgcagggcct
CPa,   ctaacactacttcttataag   aggaatagtagaaagaggag   ttggaacaggtggactgtt    tatccccctttagcaggtgc   tattgcccacgctggagcct
CP,    ctaaccctcttcttataag    aggattagtagaaagaggtg   ttggaactggctgaactgtc   taccctcctttagcaggtgc   tattgcccatgcaggtgcct
CG,    ttaacattgctccttataag   aggtatagtagaaagtggag   ttgggacaggatgaactgtt   tncccctcctttggcaggtgc   tattgctcacgctggagcct
CN,    ctaactttacttcttataag   aggaatagtagagagagggg   ttggaacaggttggactatc   taccctcccctagcgggcgc   tattgctcatgctggagcct
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CM,    ttaaccttacttcttataag   aggaatagtagaaagaggag   taggaacaggatgggaccgtc   taccctcccttagcgggggc   tatcgctcatgccggagcct
       201                                                                                        300
PC,    ctgttgacatggggattttc   tctctccatcttgcaggtat   ttcttcgattctaggtgcag   taaattttataacaacagta   attaatatacgaccgaaagg
HN,    ctgtcgatctcgggatttc    tcactacatcttgcaggggt   ctcttcaattttaggagcag   taaattttataactaccgtt   attaatatacgatcttacgg
CB,    cagttgacataggaatttttc   tccttacatttagcaggggt   ttcttctatcttaggagctg   taaattttataacaactgta   attaatatgcgatcctttgg
CA,    cagttgatataggaattttc   tccttacacttagcaggggt   ttcttctatcttaggagctg   taaactttataacaaccgta   attaatatacgatcttttgg
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CPa,   cagtagatataggaatttt    tctctccatttagcaggagt   ttcttctattttaggagctg   taaattttataacaactgta   atcaacatacgatcatttgg
CP,    cagtagatataggaatcttt   tcgcttcacttggcaggagt   ttcctcaatcttaggagctg   taaattttataacaaccgta   attaatatacgatcatttgg
CG,    cagttgatataggaattttc   tccttacacttagcaggagt   ttcttctatcttagggggctg   taaactttataacaactgtg   attaatatacggtcctttgg
CN,    cagtagatatgggaatcttt   tctctcatttagcaggggt    ttcttctatcttaggagctg   taaattttataacaactgta   attaatatgcgctcatttgg
CBo,   cagtggacatggggatttttt   tctcttcattagctggggt   ttcttcaatcctaggagctg   tgaattttataacaactgta   atcaacatacggtcatttgg
CM,    cagtcgatataggaatcttt   tcccttcatttacgtggggt   ttcctctattttaggagcag   taaattttataacaaccgta   attaacatacgttcttttgg
       301                                                                                        400
PC,    agttacaatagaccgtatgc   cacttttcgtttgagctgtt   tttattactgctattctttt   acttctttctttacctgtct   tagccggagcaattaccatg
HN,    gaggacaatggaccaaatac   ctctttttgtgtgagctgta   ttcattactgctattctctt   acttttatctcttccagttc   tagcaggtgctatcactatg
CB,    gataacccttagatcaaatac   ctctcttcgtttgagctgta   ttttattgctattcctatt   actcctctctccctgttc     tagcaggtgcaattactata
CA,    aataaccttagatcaaatac   ctctctcttgtttgagctgta   tttattactgccatcctatt   acttttatctctccctgtct   tagcaggtgcaattactata
CO,    tataaccctagatcaaatac   ctctttttcgtttgggctgta   tttattacagctatcttact   actactctctctgcctgttt   tagcaggggcaattactata
CPa,   aataactctagaccaaatgc   cacttttcgtctgagctgtc   tttattactgctatcctttt   acttctatcactccctgtct   tagctggagccatcactatt
CP,    aataaccttagaccaaatac   cacttttcgtttgagccgta   tttattactgccatccttt    acttttatctctcccagtat   tagcaggagctattactata
CG,    aataaccttagaccaaatac   ctctctttgtttgagctgta   tttattaccgctatcctgtt   acttttatctctctccctgttt   tagcaggtgcaattactatg
CN,    gataactttagaccaaatac   cactttttgtttgagctgta   tttattactgctattctttt   acttttatctctccctgttt   tagcaggagcaattactata
CBo,   gataagcttagaccaaatac   cacttttcgtttgggctgtg   tttattactgccatccttt    gctgctatccctccctgttt   tagccggagctattaccata
CM,    gataactttagatcaaatac   cactcttcgtttgagctgta   tttatcaccgctattctttt   actactatcccttcctgtac   tagcaggtgccatcactata
       401                                                                                        500
PC,    cttctaacagaccgaaatct   taataacctcgtttttttgacc   ccgcggagg-tggagatcca   gtactttaccaacatttatt   ttgattcttcggtcaccctg
HN,    ttgcttactgatcgaaattt   aaatacatctttctttgacc   ctgctggcg-gggggggacca   gttttataccaacatttatt   ttggttcttttggtcatcctg
CB,    ttattaactgatcgaaatct   taatacttcttctttgacc   ccgcaggag-gggtgaccct   gttctttatcaacacctttt   ttgatttttttgggcaccag
CA,    ttattgactgaccgaaatct   taataacctcattctttgacc   ccgcagagg-aggagaccct   gttctttaccaacacctttt   ctgatttttttgg-cacccag
CO,    ttattaactgaccgaaacct   taatacttctttttttcgacc   cagcggagg-gggtgatcct   gttctctatcaacacctttt   ttgattcttcgggcaccctg
CPa,   cttttaacagaccgaaacct   caatacttccttctttgacc   ccgctgagg-aggtgaccct   gttctttatcaacacctctt   ctgatttttcgggcacctcg
CP,    cttctcactgaccgaaatct   taatacttctttcttcgatc   cagcaggag-gggagatcct   gttctctatcaacatctctt   ctgatttttttgggcaccctg
CG,    ttactaactgatcgaaatct   taatacttctttctttgatc   ctgcgggcg-ggggggacct   gttctctatacaacacctttt   ttgattttttggacacccag
CN,    cttctaaccgaccgaaacct   taatacttctttcttcgacc   ccgcaggag-gggagatcct   gtactctaccaacacctttt   ttgattctttggacaccctg
CBo,   ctcttaacggaccgaaacct   aaacacttccttctttgatc   ctgcagagg-aggtgaccct   gttctttaccaacatctttt   ttggtttttttgggcaccccg
CM,    cttctaactgaccgaaatct   taacacatctttctttgatc   cggcaaggg-aggagaccct   gttctttaccaacacctttt   ttgact---tgggcaccctg
```

APPENDIX 1—*Continued*

Taxon	Position

```
         501                                                                                                    600
PC,   aagtctacattttaatttta  ccggcttttgggatgatttc  tcacattgttagtcaggagt  cagggaaaaaagantctttt  ggaaccgtggggataattta
HN,   aagtttatattttgatctta  cctgccttcggaatgatttc  tcatattgttagtcaagaat  ctggtaaaaaagaatctttt  ggtactttgggtatgatttta
CB,   aagtatatattcttattttg  cctgctttttggaataatttc  ccatattgtaagacaagaat  ctgggaaaaaagagtcctttt  gggacccttgggataattta
CA,   aggttatatatcttatttta  cctgctttttggaataatttc  tcatattgtgagacaagaat  ctggtaaaaaagagtcctttt  gggaccctaggaataattta
CO,   aagtttatattctcattctt  cctgcttttgggataatctc  tcatattgatagacaagaat  ctggtaaaaaagagtctttt  gggacccttgg–atgattta
CPa,  aagtttatattcttatttta  cccgcttttggtataatctc  tcatattgtaagtcaagaat  ctggaaaaaaagaatctttt  ggtaccttaggaataaattta
CP,   aagtatatattcttatttta  ccggcttttggaataatttc  tcatattgtaagccaagaat  ctgggaaaaaagaatctttt  gggaccctaggggataatcta
CG,   aagtctatattcttatctta  cctgctttcggaataatctc  ccatattgtaagacaagaat  ctggtaaaaaagaatcctttt  gggacccttggaataattta
CN,   aggtctatattctaatttta  cctgcttttggtataatctc  tcatattgtaagtcaagagt  cggggaaaaaagaatcctttt  gggacccaggaataattta
CBo,  aagtctatattcttatttta  ccggcttttggaataatttc  tcatattgtaagccaagaat  ctgggaaaaaagaatctttt  gggacccgaggaataattta
CM,   aagtgtacattcttattcta  cctgctttcggcataatctc  tcatattgtaagccaagagt  ctggaaaaaaagaatctttt  ggaactttaggaataatcta

         601                                                                                                    700
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HN,   tgctatactagccattggaa  tttttaggatttgtagtatga  gctcaccatatatttacatt  gggaatagacgtagacactc  gagcatactttacatctgca
CB,   cgctatattggccattggta  tttttaggctttgtggtctga  gctcatcacatgtttacagt  tggaatggacgttgatactc  gagcttactttacctcagct
CA,   cgccatattagctattggaa  tcctaggggtttgttgtttga  gcacaccatatatttacagt  gggtatagacgtagacaccc  gagcctattttacctcagcc
CO,   tgctatattagctattggta  tcttaggttttgttgtttga  gcccaccacatatttacagt  tggaatggatgttgatactc  gcgcttattttacttccgcc
CPa,  tgctatactagccattggta  ttctagatttgttggtctga  gctcatcatatatttacagt  tggaatgatgtagatactc  gcgcttactttacctccgcc
CP,   tgctatattagccatggta   tttttaggctttgttgtctga  gcccacatatatttacagt   tggaatagatgttgataccc  gagcttacttcacctcagcc
CG,   tgctatactagccattggta  tcttaggttttgtagtctga  gcccaccatatattcacagt  cggaatagacgttgatactc  gagcttactttacctcagct
CN,   cgccatattagctattggaa  tcctaggggtttgttgtttga  gcacaccatatatttacagt  gggtatagacgtacacaccc  gagcctattttacctcagcc
CBo,  tgctatactagccattggta  ttctagatttgttgtctga   gctcaccatatatttacagt  cggaatagatgtagatactc  gggcttactttacctcagcc
CM,   tgctatgttagccattggta  tttttaggatttgttgtttga  gctcatcatatatttacagt  tggtatagacgtcgataccc  gagcttattttacttccgcc

         701                                                                                                    800
PC,   acaataattattgctattcc  cacaggaattaaaattttta  gttgactaggaactcttcag  ggtaatcaaatagtctacag  accctctataatttgagctc
HN,   acaataattattgctattcc  cactggaattaaaattttca  gatgattaaggactctacat  ggtacgcagatgaattactc  cccgtccctattatgagccc
CB,   actataattattgccgttcc  cactgggattaaaatcttta  gttgactaaggactctccac  ggaactcaaattaatttttag  accttcaatgctttgagctc
CA,   actataattattgctgttcc  caccggcatcaaaattttta  gttgattgagcacactccat  ggaactcaaattaacttcag  tccatctatactttgggccc
CO,   actataattattgctggtcc  aactggaattaaaatcttta  gttgactaagaactctccac  ggaactcaaatcaattttag  cccttcaatactttgagccc
CPa,  actataattattgctgtacc  taccggtattaaaattttta  gttggttaagaactctacat  ggaacacaaattaacttttag  gccttctatactttgagccc
CP,   actataattattgctatccc  cactggtattaaaattttca  gttgactaagaactcttcat  ggaacacaaattaacttttag  gccttcgatactttgagccc
CG,   actataattattgccgtccc  tactggaattaagatcttca  gttgactaagaacccttcac  ggaactcaaattaactttag  accctcaatactttgggcct
CN,   actataattattgctgttcc  caccggcatcaaaattttta  gttgattgagcacactccat  ggaactcaaattaacttcag  tccatctatactttgggccc
CBo,  actataattattgctgtccc  taccggaattaaaattttta  gttgattaaggacacttcat  ggaactcaaattaatttttag  gccttctatgctctgagccc
CM,   actataattattgctgttcc  tactggaatcaaaattttta  gttggctaagcactcttcac  ggcacacaaatcaacttcag  tccttctatactttgggctt

         801                                                                                                    900
PC,   taggttttattttttcttttt  actgttggaggtcttacagg  agtaattttagcaaactctt  caattgacaccgtccttcat  gacacatactatgtggtagc
HN,   tagggtttatcttcttatttt  actatcggaggattaactgg  ggtagtactagctaattcat  cgattgatattattctccat  gatacatactatgtagttgc
CB,   taggttttattttttcttttc  actgtaggaggattaactgg  agtagttctagctaactctt  ctcttgatattattcttcat  gatacttactacgttgttgc
CA,   taggtttattttttctattc   acagtgggggcctaactgg   tgtagttttagccaattctt  ctattgatatcatcctccat  gatacttattatgttgttgc
CO,   taggtttcattttttcttttt  actgtaggtgggttaacagg  agtagttctagctaattctt  ctattgatattatccttcat  gacacttattatgttggtgc
CPa,  taggttttatcttcttatttt  acagtaggtgggattaactgg  tgtagttttagctaattctt  ccattgatattatcctccac  gatacatattatgttgtagc
CP,   taggtttcatcttcctatttt  acagtaggaggactaactgg  tgttgtattggccaactcct  ctcttgacattattctccac  gatacttattatgttgtagc
CG,   tagggtttattttcctttttt  actgtaggaggattaactgg  agtagttctagctaactctt  ctatcgacattattcttcat  gatacttactatgttgtagc
CN,   taggttttattttttctattc  acagtggggggcctaactgg  tgtagttttagccaattctt  ctattgatatcatcctccat  gatacttattatgttgttgc
CBo,  taggttttttttttttttattt  acagtaggaggattaacggg  agttgttttagctaactctt  caattgatattatcct----  --------------------
CM,   taggttttatcttcctatttt  acagtaggaggactaactgg  agtagtttagccaattctt   ctcttgatattattctccac  gatacttattatgttgttgc

         901                                                                                                   1000
PC,   tcattttcactatgtattat  caatgggcgcagtattcgga  attttcgccggtattaccca  ctgattcccctattcacag   gtctttccgttaatcccaaa
HN,   tcactttcattatgttcttt  caataggagctgtattcgga  attttcgctggggtagcaca  ctgattctccttaataaccg  gcctatccatgaaccctaaa
CB,   ccattttcactatgttctat  ccataggagctgtgttcggt  attttcgccggtatcgctca  ttgattcctttattcaccg   gagtatctttaaaccctaag
CA,   tcatttccattacgttattat  ctataggagctgttttttggt  attttcgccggaatcgccca  ttgatttcctcttttttactg  gagtgtctttaaaccccaaa
CO,   tcatttccattatgttctat  ctataggggctgtctttgga  atcttcgccggtattgctca  ctgattcccccttattcaccg  gggtctctttaaacccaaa
CPa,  tcatttccattatgtattat  cgataggagctgtatttggt  attttgctgggatctccca   ttgattcccccttatttactg  gggtttccttaaatcctaaa
CP,   ccactttcattatgttttat  ctataggagctgttttttggt  attttgccggaatctctca   ttgatttcccctgttcaccg  gtgtatccttaaacccaaaa
CG,   acactttcactatgtcctat  ccataggtgctgtcttcggg  attttcgccggaattgctca  ttgattccctttatttactg  gagtt---------------
CN,   tcatttccattacgttattat  ctataggagctgttttttggt  attttgccggaatccgccca  ttgatttcctcttttttactg  gagtgtctttaaaccccaaa
CBo,  -------------gttttat  ctataggtgctgtatttggt  attttcgccggtatctccca  ctgattcccccttattcaccg  gggtttccttaaacccaaa
CM,   ccatttccattacgttctat  ctataggagctgtcttcgga  attttgctggaatcgccca   ttgattccctctttttacag  gtatatccttaaaccccaaa

         1001                                                               1072
PC,   tgattaaaaaattcactttc  aactatattcctaggagtaa  atttaactttttttcctcaa  cactttttagg
HN,   tgattgaaagttcatttctt  agttactttcatcggagtaa  atctcacattcttcccccaa  catttcctagg
CB,   tgacttaaaattcactttct  tgtta---------------  --------------------  -----------
CA,   tgacttaaaatccactttct  tgtaatgtttatcggagtta  atactacttttttcccgcaa  catttttagg
CO,   tgacttaaaatccactttct  tgttatgttattggggtaa   atactactttcttttcctcaa  cattcttagg
CPa,  tgacttaaaatccactttct  tgttatatttattggagtaa  acataactttttttcctcaa  catttcttagg
CP,   tgacttaaaatccatttttt  tgttatatttacaggagtta  acctcacttttttccctcaa  cattttttagg
CG,   --------------------  --------------------  --------------------  -----------
CN,   tgacttaaaatccactttct  tgtaatgtttatcggagtta  atactactttt--------  -----------
```

Note. PC, *Petrolithes cinctipes;* HN, *Hemigrapsus nudus;* CB, *Cancer branneri;* CA, *C. antennarius;* CO, *C. oregonenesis;* CPa, *C. pagurus;* CP, *C. productus;* CG, *C. gracilis;* CN, *C. novaezealandiae;* CBo, *C. borealis;* CM, *C. magister.* Missing nucleotides denoted by "-".

APPENDIX 2

Characters and States Used in the Morphological Analyses

1. Number of anterolateral teeth
   0: twelve
   1: ten
   2: nine
   3: three
   4: none
2. Number of posterolateral teeth
   0: none
   1: rudimentary
   2: one
   3: two
   4: three
3. Separation of anterolateral teeth
   0: no
   1: at base
   2: with fissures at base
   3: only by fissures
   4: not applicable
4. Curvature of anterolateral teeth
   0: absent
   1: present
   2: not applicable
5. Anterolateral teeth tip shape
   0: round
   1: single spine
   2: jagged
   3: not applicable
6. First anterolateral tooth shape
   0: acute
   1: triangular
   2: round
   3: not applicable
7. Carpace granule
   0: absent
   1: present
8. Number of dactyl teeth
   0: four
   1: five
   2: six
   3: seven
   4: eleven
   5: twelve
   6: many small
9. Outer dactyl carinae
   0: absent
   1: present
10. Outer dactyl ridges
    0: absent
    1: present
11. Outer dactyl setiferous pits
    0: absent
    1: present
12. Outer dactyl setiferous grooves
    0: absent
    1: present
13. Inner dactyl setiferous pits
    0: absent
    1: present
14. Number of dactyl spines
    0: none
    1: many small
    2: many large

15. Number of finger teeth
    0: four
    1: five
    2: six
    3: seven
    4: ten
    5: eleven
    6: many small
16. Outer finger carinae
    0: absent
    1: present
17. Outer finger ridges
    0: absent
    1: present
18. Inner finger setiferous pits
    0: absent
    1: present
19. Number of outer manus carinae
    0: none
    1: four
    2: five
    3: six
    4: seven
20. Number of outer manus setiferous pits
    0: absent
    1: present
21. Inner manus carinae
    0: absent
    1: present
22. Inner manus ridges
    0: absent
    1: present
23. Inner manus setiferous pits
    0: absent
    1: present
24. Manus spines
    0: absent
    1: present
25. Outer carpus carinae
    0: absent
    1: present
26. Outer carpus ridges
    0: absent
    1: present
27. Carpus spines
    0: absent
    1: present
28. Merus spines
    0: absent
    1: present
29. Frontal teeth shape
    0: rounded
    1: blunt
    2: triangular
    3: acute
    4: none
30. Degree of production of front of carapace
    0: none
    1: little
    2: moderate
    3: high

31. Degree of carapace aerolation
    0: none
    1: little
    2: moderate
    3: high
32. Carapace shape
    0: oval
    1: wide, sides concave
    2: round
33. Carapace hair
    0: absent
    1: present
34. Cheliped hair
    0: none
    1: little
    2: moderate
    3: high
35. Leg hair
    0: none
    1: little
    2: high
36. Dense finger material
    0: none
    1: <25% of finger
    2: <50% of finger
    3: >50% of finger
    4: to proximal tooth
    5: to base of finger
37. Dense dactyl material
    0: none
    1: <25% of dactyl
    2: <50% of dactyl
    3: >50% of dactyl
    4: to proximal tooth
    5: to base of finger
38. Finger tip color
    0: absent
    1: present
39. Male carapace size
    0: small (<75 mm width)
    1: medium ($\geq$75 $\times$ $\leq$180 mm width)
    2: large (>180 mm width)
40. Relative leg length
    0: small (<1.10)
    1: medium ($\geq$1.10 $\times$ $\leq$1.20)
    2: large (>1.20)
41. Relative claw size
    0: small (<0.230)
    1: medium ($\geq$0.230 $\times$ $\leq$0.280)
    2: large (>0.280)
42. Mechanical advantage
    0: small (<0.340)
    1: medium ($\geq$0.340 $\times$ $\leq$0.365)
    2: large (>0.365)
43. Relative dactyl length
    0: small (<0.500)
    1: medium ($\geq$0.500 $\times$ $\leq$0.550)
    2: large (>0.550)
44. Relative propodus height
    0: small (<0.460)
    1: medium ($\geq$0.460 $\times$ $\leq$0.500)
    2: large (>0.500)

Note. All multistate characters (except 39) are ordered. Sources of information: Nations, 1975; Lawton and Elner, 1985 (characters 40–44); Jensen, 1995, and references therein.

APPENDIX 3

Morphological Data Matrix

P. cinctipes†	40423316010000600000000001012312011000?????
H. nudus†	30111014001100500000000001040120100000?????
C. antennarius	21111011001110001141100000111221022441102212
C. branneri	21111013011112211130110110112221132441021010
C. borealis	23102111101111101400001001?2130000441202212
C. gracilis	23100111101110201030000100100110000000120000
C. magister	10102113001102301130001110113110000??0210000
C. novaezealandiae	11202112101111101400001001121100004411?????
C. oregonensis	00112011001010001140000000101130101551022122
C. pagurus	11300210001100101020000000110311001441201111
C. productus	11201210001010001130101010100311001331201211

Note. Refer to Appendix 2 for character and state names.
† Denotes outgroup taxa.

Note added in proof: Marincovich and Gladenkov (Nature **397**: 149–151, 1999) provide stratigraphic evidence from molluscs and diatoms that the Bering Strait first opened 4.8 to 7.4 million years ago, which is consistent with our COI-based estimate.

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