FRONTISPIECE. A member of the genus *Cancer*. Photograph by T. Hobson.

THE GENUS *CANCER* (CRUSTACEA: BRACHYURA): SYSTEMATICS, BIOGEOGRAPHY AND FOSSIL RECORD

By J. DALE NATIONS

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TABLE OF CONTENTS

THE GENUS *CANCER* (CRUSTACEA: BRACHYURA):
SYSTEMATICS, BIOGEOGRAPHY AND FOSSIL RECORD[1]

By J. DALE NATIONS[2]

ABSTRACT: The Genus *Cancer* (Crustacea: Brachyura) is represented by 23 living species and at least 32 species known only as fossils. All reports of fossil occurrences of *Cancer* are reviewed. The 23 named living species of *Cancer* are described and illustrated and their geographic and stratigraphic ranges are given. Their geographic distributions are correlated with water temperatures and migrational barriers.

Cancer is most diversified on the west coast of North America where nine of the 23 living species occur. Detailed descriptions and illustrations of claw parts of living and fossil species found in this area are given. Interspecific variation in shape and ornamentation of isolated claw parts is adequate for species identification. A biometrical analysis of intraspecific variation provides quantitative data to aid in identification of species and in definition of new taxa.

The time and area of origin of the genus *Cancer*, phylogenetic relationships of its species, and their patterns of dispersal are discussed. Four subgenera, *Cancer (Cancer)* Linnaeus 1758; *Cancer, (Glebocarcinus)* new subgenus; *Cancer (Romaleon)* Gistl 1848; and *Cancer (Metacarcinus)* A. Milne-Edwards 1862, are recognized based on characters of the carapace.

The stratigraphic distribution of all North and South American west coast species is given in modern stratigraphic terminology. The oldest accepted record of *Cancer* is in the Miocene, when the genus had a worldwide distribution. On the west coast of North America six species are known from the Miocene, 18 from the Pliocene, and 13 from the Pleistocene. All Recent west coast species are known as fossils, seven of which range into the Pliocene. Three living species are reported as fossil for the first time and the stratigraphic ranges of five others are extended. One recent South American species is reported from the Pliocene of California, its first known occurrence in the Northern Hemisphere. Additional material of two extinct species is described, extending their geographic and stratigraphic ranges.

Ten new species of *Cancer* are named, described, and illustrated: 2 Miocene, 1 Miocene-Pliocene, 4 Pliocene, 2 Miocene-Pleistocene, and 1 Pleistocene. These are *C. allisoni, marri, danai, dereki, yanceyi, garthi, durhami, coosensis, jenniferae,* and *chaneyi.* Four of the new species, *C. allisoni, dereki, coosensis, chaneyi,* are interpreted as ancestral to the four subgenera proposed here. Two Lower Tertiary west coast species, *C. gabbi* Rathbun 1926 and *C. bainbridgensis* Rathbun 1926 are assigned to other genera.

INTRODUCTION

Purpose

The purpose of this study is basically two-fold. First, to up-date the fossil record of the decapod crustacean genus *Cancer*, and to interpret the biogeography and stratigraphic significance of the group. Second, to describe and evaluate the taxonomic significance and ranges of variation of certain isolated parts (e.g., hands, fingers) of the decapod exoskeleton.

Scope and Method of Study

The fossils assigned to the genus *Cancer* were prepared for study by standard preparation techniques, i.e., hammer and chisel, vibratools, air-abrasive equipment, and needles. Regular sewing needles were found to be best for cleaning matrix from delicate specimens. Each specimen was then compared with the corresponding parts of Recent and fossil species to determine its specific identity. Biometrical techniques were used where direct comparison did not show unquestionable similarity with existing species and the proposal of new species seemed necessary.

The literature on both Recent and fossil crabs usually is inadequate for identification of fossil material because emphasis is placed on the characters of the carapace, which is rarely preserved, and the illustrations of the chelipeds are generally inadequate for detailed comparison. For this reason, identification of fossil material must be preceded by detailed studies on the morphology and variation of various parts (particularly the chelipeds) of Recent species. Much of the research was devoted to the recognition of species using only cheliped characters.

Biometrical analysis has been employed in the comparison of all the species on the west coast of North America to establish reasonable limits of variation and to assist in the identification of poorly preserved material. A standard series of measurements has been established and tested for validity. This provides several parameters for the comparison of the parts of the crab skeleton that most commonly occur as fossils. These measurements and parameters are discussed in the section on Statistical Data and Analysis.

The standard series of measurements was established by carefully measuring between well-defined points on each portion of the skeleton commonly found as fossil, e.g., movable finger, fixed finger, manus, and carpus. These measurements were made on Recent specimens of varying size and sex, and the ratios of pairs of measurements were plotted graphically to test their consistency, thereby evaluating their taxonomic significance. Those ratios which varied widely were discarded as taxonomically insignificant and those which varied within limited ranges and tended to differentiate the previously established species were retained as taxonomically significant. Some species overlap in one or more of the ranges of parameters but can be differentiated on others (see Table 1).

These parameters are not considered as definitive proof of specific identity by themselves, but are to be used more as guides to the degree of similarity between specimens, as a means of quantitatively expressing the normal variation within a species, and, in the case of fragmentary fossil specimens, as a means of comparing isolated parts with those of more complete or better preserved specimens. The final analysis of the identity of fossil material must be based upon the comparison with other specimens in details of shape and ornamentation, but these may be strongly supplemented by the parameters mentioned above.

The following characters are used in the identification of west coast of North America species of *Cancer*.

1. Number, size and shape of anterolateral teeth on carapace. A convenient quantitative expression of these characters can be made by plotting the width of each tooth against its position on the carapace, and is useful in differentiating fossil carapaces.

2. Size, shape and distribution of granules on the carapace and chelipeds.

3. Number, size, shape and distribution of cutting teeth on movable and fixed fingers. Occasionally these will vary markedly from the normal and cannot be used alone. It is my opinion that these variations are, at least in some instances, found on regenerated limbs. In all observed cases, these variants have more and smaller cutting teeth than normal.

4. Number and shape of spines on upper margin of movable finger, manus and carpus. This character is quite constant and useful in identifying spiny species such as *C. magister, polyodon, branneri* and *plebejus*.

5. Ratio of length of upper margin to height of manus (Lu/H).

6. Ratio of thickness to height of manus (T/H).

7. Ornamentation and sculpturing of movable and fixed fingers, particularly the presence and arrangement of ridges, grooves, spines, granules and pits. These characters can be definitive, even in the case of anomalous cutting-tooth form and arrangement noted above.

8. Frontal region:
   a. Ratio fronto-orbital width to carapace width.
   b. Shape, relative length and distance between the five frontal teeth.
   c. Shape of supra- and suborbital lobes or teeth.
   d. Shape and size of orbits.
   e. Degree of production of front.

9. Areolation of carapace, i.e., the division of the carapace into distinct regions, separated by grooves.

Intraspecific variability is greater in characters of the carapace than in those of the chelipeds especially between molt stages, therefore, caution must be used to make direct comparisons only between specimens of similar size. Ontogenetic and sexual variation in the characters of the carapace may lead to misidentification of Recent as well as fossil material. The above noted features of the cheliped appear to remain relatively constant in the ontogeny of *Cancer*. The only significant variation observed due to growth in the cheliped is the increased smoothness (reduction of prominence of carinae) on the manus of large specimens of certain large species (e.g., *C. productus*). No significant sexual dimorphism in cheliped characters has been observed. The chelipeds of *Cancer* are equal and symmetrical.

TABLE 1.
STRATIGRAPHIC DISTRIBUTION OF SPECIES OF *CANCER*
IN WESTERN NORTH AND SOUTH AMERICA

Species columns (left to right): C. amphioetus, C. antennarius, C. anthonyi, C. branneri, C. gracilis, C. jordani, C. magister, C. oregonensis, C. productus, C. polyodon, C. davidi, C. fissus, C. granti, C. urbanus, C. allisoni, C. marri, C. danae, C. dereki, C. yanceyi, C. garthi, C. durhami, C. coosensis, C. jenniferae, C. chaneyi

AGE	Reference	FORMATION	amphioetus	antennarius	anthonyi	branneri	gracilis	jordani	magister	oregonensis	productus	polyodon	davidi	fissus	granti	urbanus	allisoni	marri	danae	dereki	yanceyi	garthi	durhami	coosensis	jenniferae	chaneyi
PLEISTOCENE UPPER	1	Terrace deposits, Baja, Calif.	X	X	⊠		X				X	⊘														X
PLEISTOCENE UPPER	1	Bay Point Formation	X																							
PLEISTOCENE UPPER	1	Palos Verdes Sand	X	X	X	X	X	X	⊠		X															X
PLEISTOCENE UPPER	1	Millerton Formation	X	X							X															
PLEISTOCENE UPPER	9	unnamed, Bandon Quad., Ore.									X															
PLEISTOCENE M	2	Elk River Beds								X	X	X												X		X
PLEISTOCENE LOWER	1	San Pedro Sand	⊠			X		X	X	⊠	⊠	X													X	X
PLEISTOCENE LOWER	1	Timms Point Silt	⊠					X	X																	
PLEISTOCENE LOWER	1	Lomita Marl	⊠					X	X																	
PLEISTOCENE LOWER	1	Saugus Formation				X																				
PLEISTOCENE LOWER	2	Santa Barbara Formation				X																				
PLEISTOCENE LOWER	7	San Joaquin Formation	X	X				X														X				
PLIOCENE UPPER		unnamed (Pico ?), Rustic Canyon																								X
PLIOCENE UPPER	1	Pico Formation		X	X						X	⊠			X	X	X									
PLIOCENE UPPER	2	Cascajo Conglomerate												X												
PLIOCENE UPPER	2	Merced Formation					X		X	X							X									
PLIOCENE UPPER	3	San Diego Formation	X			X			⊠	X	⊠					X										
PLIOCENE UPPER	4	Purisima Formation at Capitola												X												
PLIOCENE UPPER	2	Scotia Bluffs Sandstone																			X					
PLIOCENE M	1	Etchegoin Formation	X	X			X	X			X	X			X					X		X				
PLIOCENE M	10	unnamed, Moonstone Beach, Calif.						X	X																	
PLIOCENE L	2	Coos Conglomerate																								
MIOCENE MIDDLE U	1	Neroly Formation																						X		
MIOCENE MIDDLE U	1	Briones Sandstone																		X						
MIOCENE MIDDLE	6	Monterey Formation																			X					
MIOCENE MIDDLE	1	Round Mountain Silt								X								X								
MIOCENE MIDDLE	1	Olcese Sand								X								X						X		X
MIOCENE MIDDLE	5	unnamed, dredged, Coos Bay, Ore.								X														X		
MIOCENE MIDDLE	8	Sobrante Formation																						X		

Note: This table is composite and some formations shown superposed may be laterally equivalent.

⊠ = Southern extension of geographic range

⊠ = Northern extension of geographic range

Age references:
1. Weaver, *et al*, 1944
2. Keroher, 1966
3. Zullo, 1969a
4. California Division of Mines, 1958
5. Moore, 1963
6. Cummings, *et al*, 1954
7. Durham, *et al*, 1954
8. Lutz, 1951
9. Zullo, 1969b
10. Hertlein and Grant, 1943
11. Zullo, Wolfe and Durham (oral communication, July 9, 1969)

⊘ = Upper Pleistocene, San Juan Bay, Peru

THE GENUS *CANCER* LINNAEUS 1758

Recent species

The genus *Cancer* is widely distributed in temperate oceans, being represented by the following 23 Recent species:

Atlantic Ocean

Cancer bellianus Johnson 1861	Iceland to N.W. Africa
Cancer pagurus Linnaeus 1758	Western and southern Europe
Cancer borealis Stimpson 1859	Eastern North America
Cancer irroratus Say 1817	Eastern North America

Pacific Ocean

Cancer amphioetus Rathbun 1898	Western North America and E. Asia
Cancer antennarius Stimpson 1856	Western North America
Cancer anthonyi Rathbun 1897	Western North America
Cancer branneri Rathbun 1926	Western North America
Cancer gracilis Dana 1852	Western North America
Cancer jordani Rathbun 1900	Western North America
Cancer magister Dana 1852	Western North America
Cancer oregonensis Rathbun 1898	Western North America
Cancer productus Randall 1839	Western North America
Cancer edwardsii Bell 1835	Western South America
Cancer plebejus Poeppig 1836	Western South America
Cancer polyodon Poeppig 1836	Western South America
Cancer porteri Rathbun 1930	Western South America
	Gulf of California
Cancer sakaii Takeda and Miyake 1972	Eastern Asia
Cancer gibbosulus (De Haan 1835)	Eastern Asia
Cancer japonicus Ortmann 1893	Eastern Asia
Cancer nadaensis Sakai 1969	Eastern Asia
Cancer tumifrons Yokoya 1933	Eastern Asia
Cancer novaezealandiae (Jacquinot)	New Zealand, Tasmania
[In: Jacquinot and Lucas 1853]	and Australia

Fossils--a general evaluation

At least 58 fossil species have been assigned to *Cancer*, ranging in age from Upper Cretaceous to Pleistocene (Glaessner 1929; Zoological Record 1926 to 1969). However, Glaessner (1969) recognizes none older than Miocene because "most of the pre-Miocene species listed as *Cancer* in the Fossilium Catalogus (Glaessner 1929) are unrecognizable or undocumented" (personal communication, April 28, 1969). Sixteen of the 58 reported species are thereby eliminated. I have been able to verify 22 and eliminate four of the remaining 42 species, leaving 16 unverified Miocene or younger species of *Cancer*. Specimens or illustrations of these 16 species must be examined to determine their validity.

The following list includes all reports of fossil species of *Cancer* in the Fossilium Catalogus and in the Zoological Record through 1969. The numbers in parentheses on the left margin indicate my evaluation of the reliability of the generic assignment, and the reason for it. The significance of the numbers is given below:

(1) eliminated by Glaessner (see above).
(2) eliminated by examination of specimen, illustration, or description.
(4) unverified by me.
(5) acceptable.

Species listed in Fossilium Catalogus (Glaessner 1929)

	Species		Age	Location
(1)	*C. aldenardensis* Delvaux	1887 nom.nud.	Ypresian	Belgium
(5)	*C. anthonyi* Rathbun	1926	Pleist.-Rec.	N. America
(1)	*C. archiaci* H.M. Edwards	1850 nom.nud.	Lutetian	Austria
(2)	*C. bainbridgensis* Rathbun	1926	Oligocene	N. America
(4)	*C. bittneri* Toula	1904	Tortonian	Austria
(5)	*C. branneri* Rathbun	1926	Pleist.-Rec.	N. America
(1)	*C. burtini* Galeotti	1837	M.&U. Eocene	Belgium
(4)	*C. carniolicus* Bittner	1883	Miocene	Yugoslavia
(4)	*C.* cf. *carniolicus* Bittner	1898	Tortonian	Hungary
(5)	*C. fissus* Rathbun	1908	Pliocene	California
(1)	*C. flandricus* Delvaux	1884 nom.nud	Ypresian	Belgium
(1)	*C. fraasi* Lorenthey	1909	U. Eocene	Egypt
(2)	*C. gabbi* Rathbun	1926	Eocene	N. America
(5)	*C. gracilis* Dana	1852	Pleist.-Rec.	N. America
(4)	*C. illyricus* Bittner	1883	Miocene	Yugoslavia
(5)	*C. jordani* Rathbun	1900	Pleistocene	N. America
(5)	*C. magister* Dana	1852	Pleist.-Rec.	N. America
(1)	*C. meticurensis* Thurmann	1853	Oligocene	E. France
(1)	*C. modestus* Fritsch	1887	Cenomanian	Bohemia
(1)	*C. monodactylus* Michelotti	1861 nom.nud.	Oligocene	N. Italy
(4)	*C. nodosulus* (Reuss	1867)	Helvetian	Galizien
(2)	*C. paguroides* Desmarest	1822	Subfossil	E. Asia?
(5)	*C. pagurus* Linne'	1758	Pliocene	England
			Recent	Atlantic, Mediterranean Sea, Black Sea
(1)	*C. pratti* H.M. Edwards	1850 nom.nud.	Lutetian	S. France
(5)	*C. proavitus* Packard	1900	Miocene	N. America
(5)	*C. productus* Randall	1839	Plio.-Rec	N. America
(1)	*C.?reversus* Fritsch	1887	Cenomanian	Bohemia
(4)	*C. rietmanni* Mayer	1872 nom.nud.	Helvetian	Switzerland
(1)	*C. rotnacensis* Delvaux	1887 nom.nud.	Ypresian	Belgium
(5)	*C. sismondai* v. Meyer	1843	Pliocene	England, Italy, Algeria
			U. Miocene	Sardinia
			Tortonian	Austria
			Helvetian	Spain
			Burdigalian	Sardinia
(4)	*C.* cf.*sismondai* v. Meyer	1843	Tortonian	Austria
(1)	*C.?solitarius* Fritsch	1887	Cenomanian	Bohemia
(4)	*C. spinosus* (Ristori	1886)	Pliocene	Italy
(4)	*C. styriacus* Bittner	1883	Tortonian	Steiermark, Austria
(4)	*C. szontaghi* Lorenthey	1898	Tortonian	Hungary
(2)	*C. tyro* Philippi	1887	Miocene?	S. America
(5)	*C. urbanus* Rathbun	1917	Pliocene	California
(1)	*C. villabersiani* Gary	1907	Eocene	S. France
(1)	*C.?whitfieldi* Pilsbry	1901	U. Cretaceous	N. America
(2)	*C.* species		Miocene	Burma
(4)	*C.* species		Burdigalian	S. France
(4)	*C.?*species		Miocene	S. France
(4)	*Cancerites molassicus* Quenstedt	1867	M. Miocene	Bavaria

Fossil species listed in Zoological Record   1926-1969

(5) *C. deshayesi* A. Milne-Edwards 1861	Miocene Pliocene L. Pleist.	Spain, Netherlands, France England, Algeria Netherlands
(4) *C.* sp. indet. Lorenthey and Beurlen 1929	(?)	Hungary
(5) *C. granti* Rathbun 1932	Pliocene	California
(5) *C. javanicus* Van Straelen 1938	Pliocene	Java
(5) *C. minutiserratus* Nagao 1940	Pliocene	Japan
(4) *C.* species Bernhauser 1955	?	?
(5) *C. novaezealandiae* (Jacquinot) [In: Jacquinot and Lucas 1853]	Plio.-Pleist.	New Zealand
(5) *C. sanbonsugii* Imaizumi 1962	Miocene	Japan
(5) *C. odosensis* Imaizumi 1962	Miocene	Japan
(2) *C.?imamurae* Imaizumi 1962	Miocene	Japan

Additional species not listed in either source

(5) *C. beaumonti* Milne-Edwards 1850	Cenozoic	Europe
(5) *C. polyodon* Poeppig 1836	U. Pliocene U. Pleistocene	California Peru
(5) *C. davidi* Nations 1968	M. Pliocene	California
(5) *C.* species (Van Straelen 1938:98)	U. Miocene	Java
(5) *C. irroratus* Say 1817	Plio.-Pleist.	N. America
(4) *C. borealis* Stimpson 1859	U. Miocene	N. America

The two pre-Miocene species of *Cancer* in western North America which were recognized by Rathbun (1926:56-60) have been examined and are not referable to *Cancer*. *Cancer gabbi* Rathbun 1926 was based on two incomplete right chelipeds from the Eocene of California. Additional preparation of the holotype (Phil. Acad. Nat. Sci., No 4099) revealed that it had a short, broad carpus; a smooth outer surface of the manus with no longitudinal carinae; and a long, laterally and proximally inclined tooth on the dactylus. These characters are unlike those of *Cancer* and are very similar to *Lophopanopeus* Rathbun 1898 (Xanthidae Dana 1851). *Cancer bainbridgensis* Rathbun 1926 was based on two incomplete dactyli from the Upper Oligocene of Washington. Examination of the holotype (Stanford Univ, No 5061) shows a nearly circular cross-section at the proximal cutting tooth (T/H dactylus = .97) and a basal portion which is 2.0 times the height of the finger at the proximal tooth (27.1 mm vs 13.5 mm). This is in strong contrast to the corresponding features of *Cancer productus*, with which it was originally compared (T/H dactylus = .683 and height at base only 1.30 times the height at proximal tooth). The size and shape of *C. bainbridgensis* are very similar to those of *Loxorhynchus grandis* Stimpson 1857 (T/H dactylus = .783 and height at base is 1.83 times the height at proximal tooth). It probably is referable to *Loxorhynchus* Stimpson 1857 (Majidae Samouelle 1819).

The elimination of these two species from *Cancer* confirms Glaessner's belief that Rathbun's material

did not justify its generic assignment (personal communication, April 28, 1969), and verifies his exclusion of the species from the genus in the Treatise of Invertebrate Paleontology. The rejection of *C. gabbi* and *bainbridgensis* invalidates all reports of pre-Miocene occurrence of *Cancer* on the west coast of North America.

Currently there are nine recognized Recent species of *Cancer* on the west coast of North America, only one of which ranges into another province *(C. amphioetus).* One South American species, *Cancer porteri,* previously known as far north as the Bay of Panama, has been reported by Garth (1960:120) in the Gulf of California. All of these species (except *C. porteri*) are now known in the fossil record, with five of them recognizable in the Middle Pliocene. One other Recent species *(C. polyodon)* is known in the Upper Pliocene of North America but is now living only in the southern Hemisphere (Ecuador to Chile). Four extinct species are re-described here. Ten new species of *Cancer* are proposed and described here, five of Pliocene age, three Miocene, one Miocene-Pliocene, and one Miocene(?)-PlioPleistocene. The oldest occurrence of a *Cancer* is that of *C. coosensis* in the Middle Miocene Sobrante Formation.

STATISTICAL DATA AND ANALYSIS

Purpose

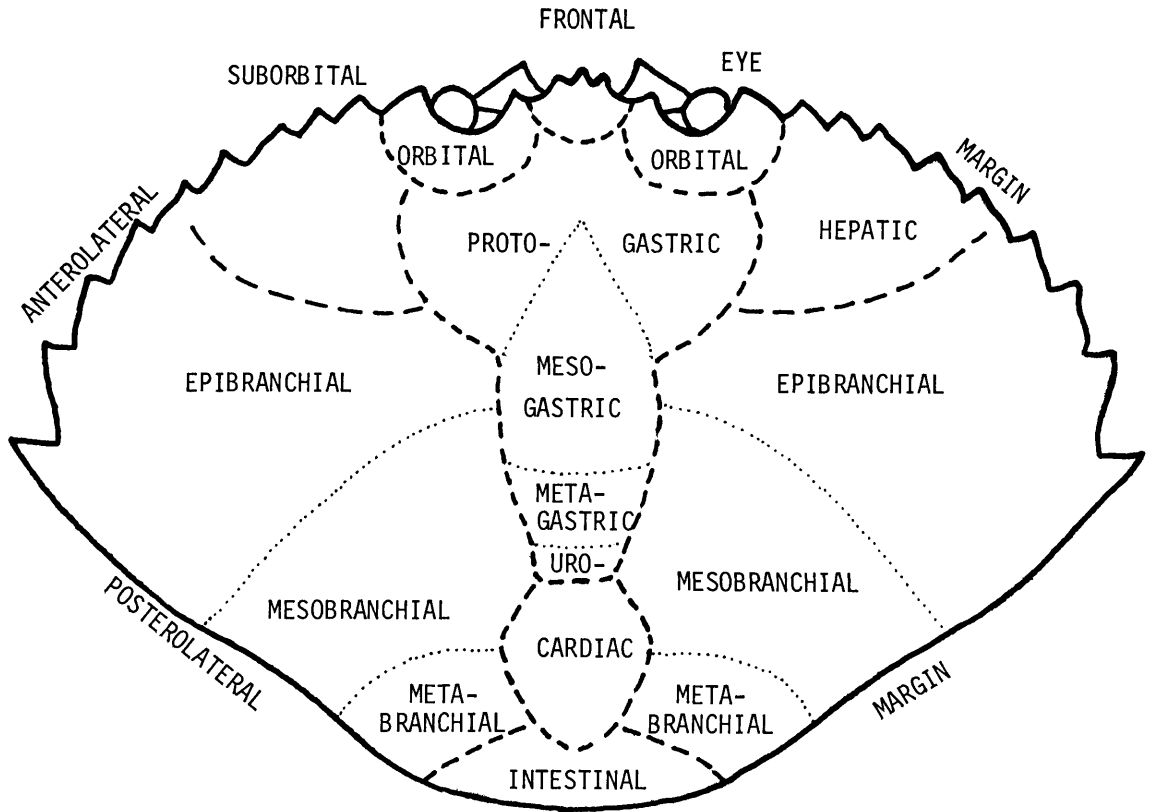An examination of all west coast species of *Cancer* has shown that there are many characters observable

FIGURE 1. Morphological terms for regions of the carapace.

and measurable on crab skeletons that have not been used in the description and comparison of specimens. Recent specimens have been classified into species on a combination of characters including: shape and areolation of carapace, number and shape of anterolateral and posterolateral teeth, general shape of chelipeds and walking legs, shape of antennae, coloration, and setation. These characters, which are adequate to differentiate living species, are inadequate for identification of most fossil material because fossil crabs generally are incomplete (most commonly represented only by fingers), and altered to some degree from their original coloration.

The usefulness and reliability of the identifications of fossil crabs from fragmentary remains depends upon the accurate description of homologous parts of known species. This not only aids the identification of fossil representatives of those species but yields data on the amount of variability which may be expected for extinct species.

To provide a sound basis for the identification of fragmentary fossil crabs, the writer has described the chelipeds of all Recent and fossil species of *Cancer* of the west coast (see section on Systematics). A standard series of measurements has been utilized to provide some quantitative data from which ranges of variation could be calculated (see Fig. 3).

Measurements and statistical data

The number of specimens measured for each species varied from 1 to 15, and was determined by the size and number of specimens available. Specimens of some species, e.g., *C. amphioetus*, were so small that accurate measurements using standard calipers were impossible on all but the largest. Measurements were made to the nearest tenth of a millimeter and ratios calculated to three decimal places. These measurements were made only on western North American species. The measurements, calculated ratios, observed ranges of variation, 95% confidence interval for range of variation (Simpson, Roe and Lewontin 1960:152), coefficient of variation (v) (Simpson et al. 1960:90), and standard deviation (s) are recorded in tables (see systematics of each species). Information on size, sex, and locality of specimens is also given.

The numerical parameters chosen for comparison and analysis were: 1) ratios of pairs of measurements of commonly fossilized parts of the chelipeds, 2) number and position of cutting teeth on dactylus and fixed finger, 3) widths of anterolateral teeth on carapace. Ratios of cheliped measurements were plotted on graphs and statistically analyzed to predict ranges of variation to the 95% confidence interval following the method of Simpson et al. (1960:87-152) (See Table 1). Anterolateral tooth widths vs tooth position have been plotted on graphs without statistical analysis (see Figs. 23 and 26). The number of cutting teeth on the fingers is highly consistent within each species, does not require statistical analysis, and has been used only descriptively.

Graphical presentation of data

Two types of graphs have been used in this study for the presentation and comparison of data:

Variation of cheliped characters (Table 1)—A bar graph showing: 1) ratios of selected pairs of cheliped measurements, plotted individually by short vertical lines on the graph, and 2) the 95% confidence interval of range of variation of those parameters, plotted by a solid line above the observed ratios. Visual inspection of the graph shows the probable range of variation in several parameters for each species. Unidentified material can be compared with the species in the graph by using ratios of the standard measurements (see Fig. 3). The range of variation of some species overlaps for some parameters, but usually can be differentiated on others.

This method is particularly useful in the identification of fossil mani, carpi, and fixed fingers because they are not as distinct morphologically as are the movable fingers. Fortunately, the parameters of these less distinctive parts show better separation on the graph than those of the movable fingers.

This technique is valuable because several parameters are made available for the determination of degrees of similarity between specimens. For example, *Cancer durhami*, represented by a complete cheliped, closely resembles *Cancer magister*. However, in comparing its standard parameters with those of *C. magister* it is found that the two species differ significantly (beyond 95% confidence interval) in 1) Lu/H manus, 2) T/H manus, 3) T/H fixed finger and 4) H/L carpus. On closer inspection, differences in details of ornamentation further support the separation of this specimen from *C. magister*. See following pages for definitions of abbreviations.

Anterolateral tooth-width graph (Fig. 23).—A graph of relative width of anterolateral teeth on the carapace. This graph is not as well established statistically as the "variation of cheliped characters (Table 1)," but is useful in comparison of fossil carapaces, which often are only partially preserved. The con-

stancy of relative widths of anterolateral teeth through growth stages has been tested on *C. magister* by measuring four different-sized specimens and plotting the data on a single graph (see Fig. 23). There is general uniformity in the curves, but they differ in the relative width of the 8th tooth, which becomes wider relative to the 7th and 9th teeth, with increasing carapace width. However the uniformity of the curves is adequate for empirical use and is very helpful in differentiating carapaces which may appear quite similar (see *C. magister* vs *C. danai*, Fig. 23; and *C. davidi* vs *C. jenniferae* vs *C. fissus*,

Abbreviations used in tabulation of statistical data

Measurements and ratios (see Fig. 3)

H	— height
Lu	— length of upper margin of manus
Lm	— length of manus from proximal end of lower margin to extremity of sinus between fingers
Ll	— length of lower margin of manus and fixed finger
T	— thickness
L	— length
L/H m	— ratio length to height of manus.
T/H m	— ratio thickness to height of manus.
Hf/Hm	— ratio height of fixed finger to height of manus.
H/L mf	— ratio height to length of movable finger
H/L f	— ratio height to length of fixed finger
T/H f	— ratio thickness to height of fixed finger
H/L c	— ratio height to length of carpus
S	— standard deviation
V	— coefficient of variance

STRATIGRAPHIC DISTRIBUTION

The stratigraphic distribution of Recent and extinct species of *Cancer* of the west coast of North and South America is presented in Table 2. Fossil occurrences of the genus in western North America extend from Coos Bay, Oregon (43°30′ N) to Bahia del Rosario, Baja California, Mexico (30°N). Age assignments for formations follow Weaver et al. (1944) except for subsequent changes called for by the establishment of the Pliocene-Pleistocene boundary at the base of the Calabrian in Italy by the International Geological Congress decision of 1948 (see Durham, Hahns and Savage 1954:69). Authorities for the ages of units not included in Weaver et al. (1944) are indicated in Table 2.

Each of the nine Recent species of *Cancer* on the west coast of North America, and one of the four South American species, also are known as fossils.
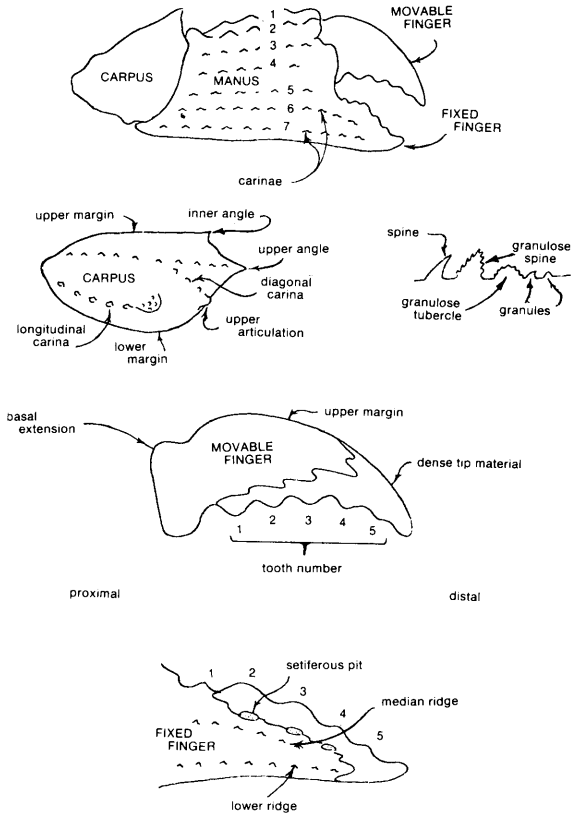
FIGURE 2. Morphological terms used in supplementary descriptions.

FIGURE 3. Statistical parameters.

Two living species, *Cancer amphioetus* and *Cancer polyodon* (living only in South America), are reported as fossils for the first time.

Cancer amphioetus is represented by parts of two individuals (1 finger, 1 carpus and manus) from the Timms Point Silt and Lomita Marl of San Pedro, California. These occurrences extend its stratigraphic range to the Lower Pleistocene and its Pleistocene geographic range in North America further north than its present northern limit (La Jolla, California).

Cancer antennarius is known from 123 fossil fingers in several Upper and Lower Pleistocene formations ranging geographically from Baja California to the San Joaquin Basin. Pliocene occurrences are known in the San Diego Formation (72 fingers, 1 carapace), Etchegoin Formation (3 fingers), and at San Ysidro, Baja California (1 finger). The geographic range of the species in the Pliocene and Pleistocene was no greater than at present.

Cancer polyodon lives today only along the west coast of South America. Fossil specimens have been found in the Upper Pliocene Pico (?) Formation (24 fingers) at Los Angeles, the San Diego Formation (15 fingers, 1 manus) of San Diego, and in the Upper Pleistocene of San Juan Bay, Peru (1 complete cheliped). The California occurrences extend the stra-
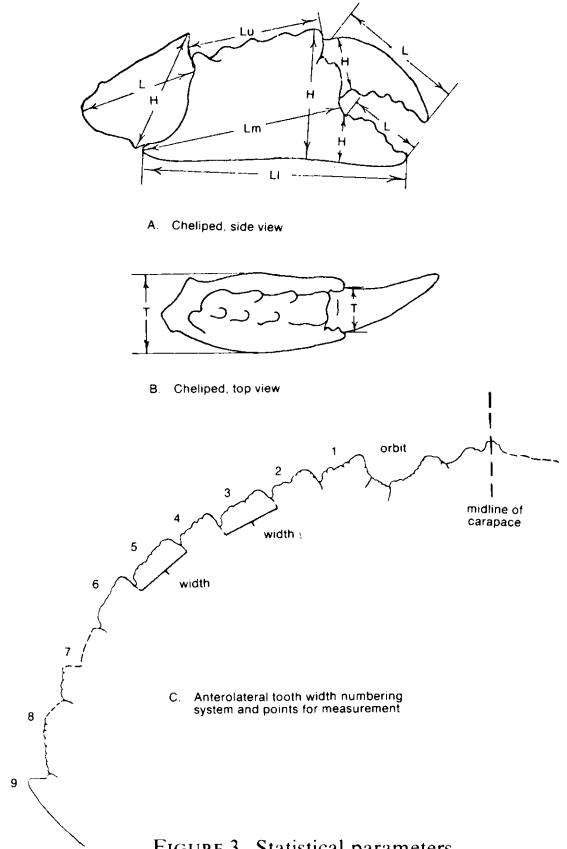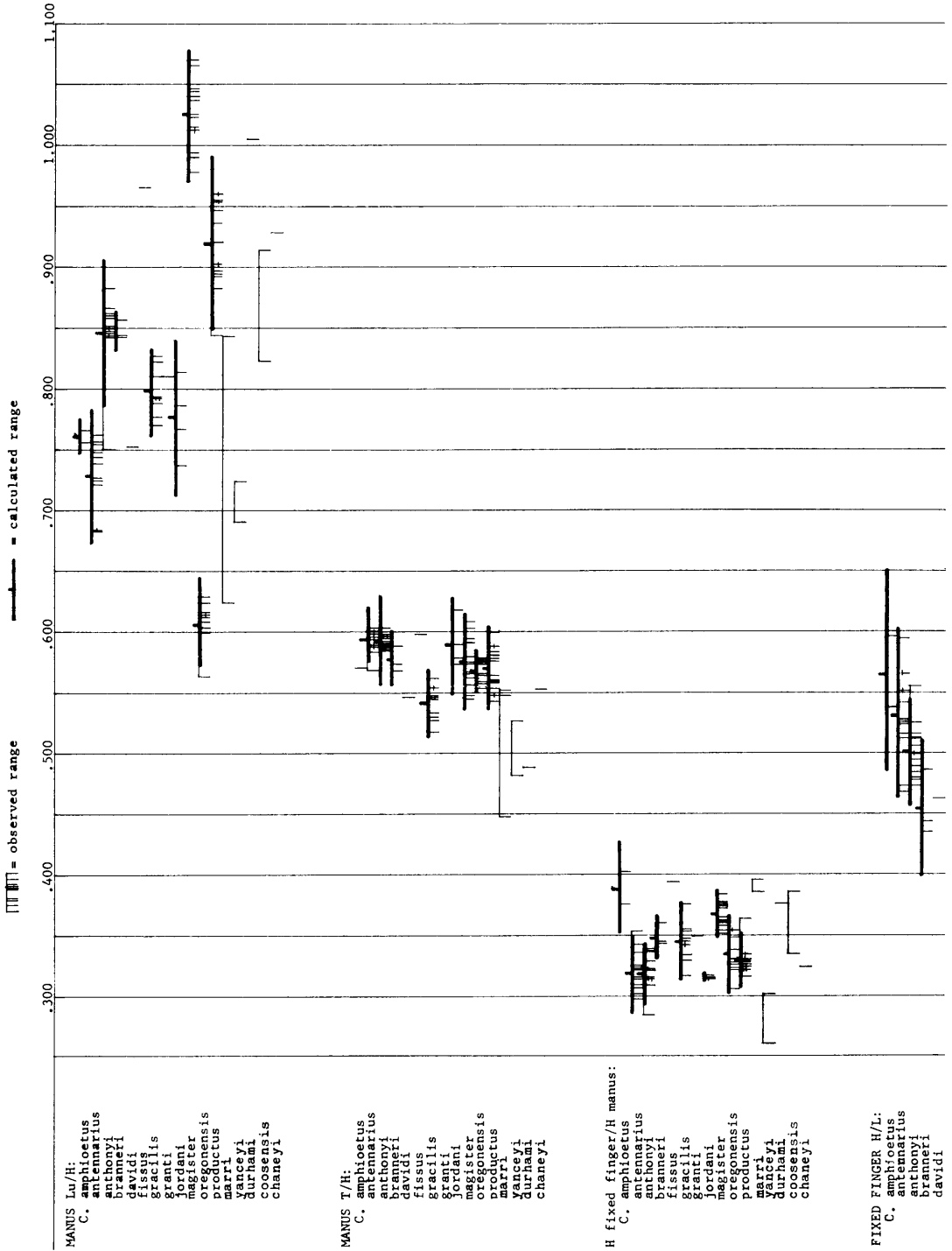
tigraphic range back into the Upper Pliocene and indicate that the species lived in the Northern Hemisphere during that time.

The stratigraphic ranges of five other Recent west coast species, *Cancer branneri*, *Cancer gracilis*, *Cancer anthonyi*, *Cancer magister*, and *Cancer oregonensis* have been extended from Pleistocene (Rathbun 1926; Menzies 1951; Zullo 1969) to Pliocene in this paper. *Cancer branneri* is known from fossil specimens (63 fingers, 1 carpus, 1 carapace) in Pleistocene beds in central and southern California, and Baja California. Six movable fingers have been found in the Upper Pliocene Pico Formation at Santa Barbara. The Pleistocene occurrence in Baja California represents a southward extension beyond the present southern limit of the species.

Cancer gracilis is represented in the Pleistocene of southern California by 246 fingers. Occurrences in the Merced Formation (3 fingers), Pico (?) Formation (1 finger), and San Diego Formation (12 fingers) extend the known stratigraphic range of this species back into the Upper Pliocene. None of the fossil occurrences are outside the present geographic limits.

Cancer magister has been found in the Pleistocene Palos Verdes Sand (13 fingers), San Pedro Sand (5

TABLE 2.
VARIATION OF CHELIPED CHARACTERS
Measurement expressed as ratios

▥▊▌ = observed range   ——— = calculated range

MANUS Lu/H:
C. amphioetus
   antennarius
   anthonyi
   branneri
   davidi
   fissus
   gracilis
   granti
   jordani
   magister
   oregonensis
   productus
   marri
   yanceyi
   durhami
   coosensis
   chaneyi

MANUS T/H:
C. amphioetus
   antennarius
   anthonyi
   branneri
   davidi
   fissus
   gracilis
   granti
   jordani
   magister
   oregonensis
   productus
   marri
   yanceyi
   durhami
   chaneyi

H fixed finger/H manus:
C. amphioetus
   antennarius
   anthonyi
   branneri
   fissus
   gracilis
   granti
   jordani
   magister
   oregonensis
   productus
   marri
   yanceyi
   durhami
   coosensis
   chaneyi

FIXED FINGER H/L:
C. amphioetus
   antennarius
   anthonyi
   branneri
   davidi

fissus
gracilis
granti
jordani
magister
oregonensis
productus
allisoni
marri
durhami
chaneyi

FIXED FINGER T/H:
 C. amphioetus
   antennarius
   anthonyi
   branneri
   davidi
   fissus
   gracilis
   granti
   jordani
   magister
   oregonensis
   productus
   allisoni
   marri
   yanceyi
   durhami
   coosensis
   chaneyi

MOVABLE FINGER H/L:
 C. amphioetus
   antennarius
   anthonyi
   branneri
   davidi
   fissus
   gracilis
   granti
   jordani
   magister
   oregonensis
   productus
   allisoni
   marri
   garthi
   durhami
   coosensis
   chaneyi

CARPUS H/L:
 C. amphioetus
   antennarius
   anthonyi
   branneri
   davidi
   fissus
   gracilis
   granti
   jordani
   magister
   oregonensis
   productus
   marri
   durhami
   chaneyi
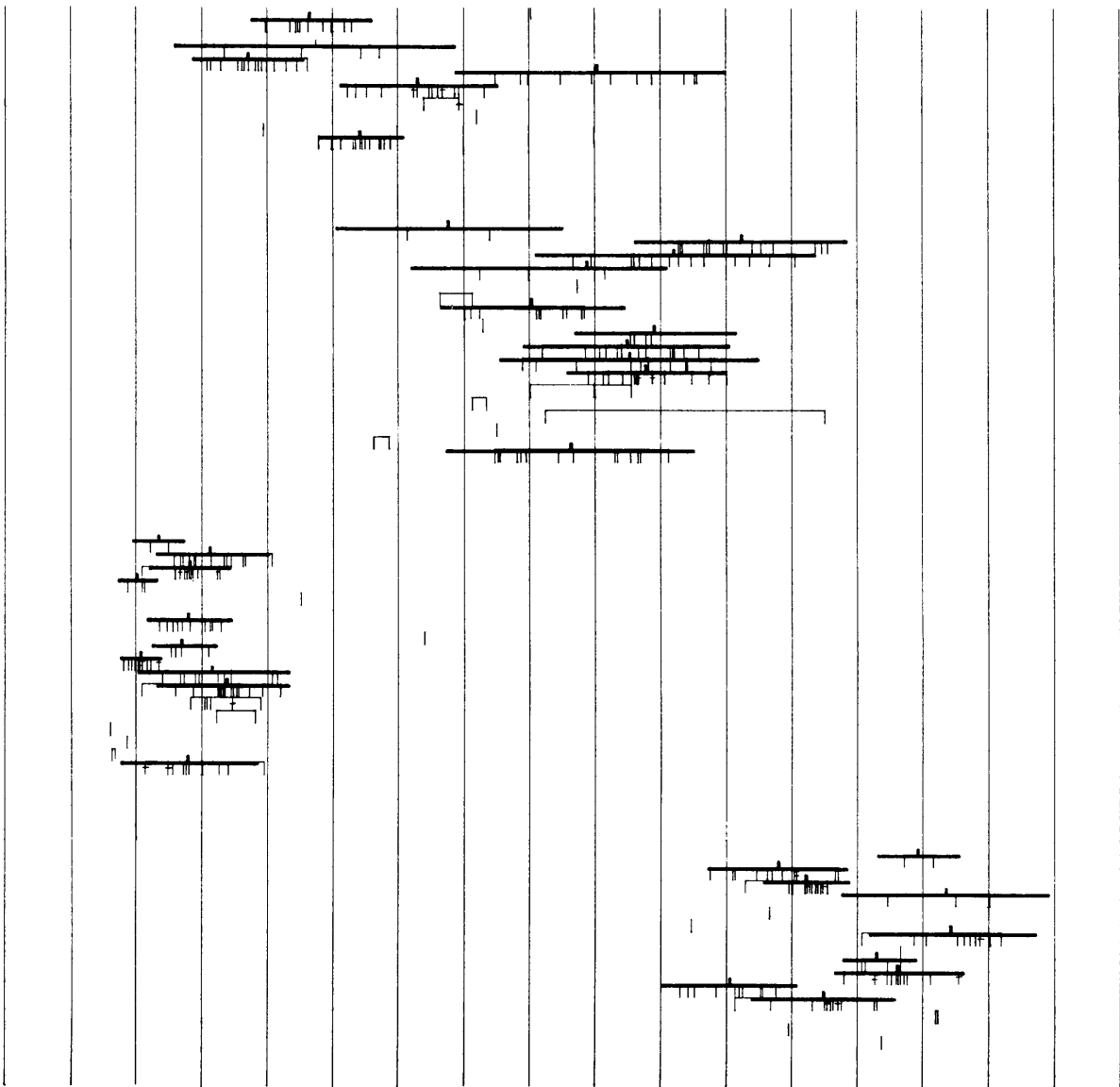
fingers), San Joaquin Formation (1 finger, 2 mani), and the Elk River Formation (19 fingers). Excepting the latter, all these occurrences are south of the present southern limits (Monterey Bay) of this species. Pliocene occurrences are now known in the Etchegoin Formation (1 finger, 1 carapace), Merced Formation (17 fingers, 1 manus), Coos Conglomerate (2 fingers, 1 cheliped), Wildcat Group (1 finger) and in unnamed beds at Moonstone Beach, Humboldt County, California (5 fingers). The Etchegoin localities indicate a more southerly range of *C. magister* during the Pliocene.

Cancer anthonyi is represented in the Pleistocene Palos Verdes Sand (13 fingers), San Joaquin Formation (25 fingers, 1 manus), Saugus Formation (1 finger) and in Pleistocene beds at San Quintin Bay, Baja California (1 finger, 1 carpus, 2 mani). Its occurrence in the Etchegoin Formation is an extension of its stratigraphic range into the Middle Pliocene. None of the fossil occurrences have extended the geographic range of the species.

Cancer oregonensis is known from the Lower Pleistocene San Pedro Formation (3 fingers) and Pleistocene beds at Rincon del Potrero (2 fingers), both in the Los Angeles area. It is also found in unnamed Pleistocene beds near Bandon, Oregon. Pliocene occurrences are known in the Merced Formation (1 finger), San Diego Formation (2 fingers), and unnamed beds at Moonstone Beach, California (129 fingers). The Pleistocene occurrences at Los Angeles and the Pliocene at San Diego indicate a more southerly geographic extent in the past than the southern limit (Santa Barbara) of the species today.

Many new occurrences of *Cancer jordani* and *Cancer productus* are reported but they do not alter significantly the previously known stratigraphic or geographic ranges of these species (see Table 2).

New occurrences of two previously named extinct species are reported, altering their stratigraphic and geographic distribution. *Cancer davidi,* previously known only from its type locality (Middle Pliocene, Etchegoin Formation, near Coalinga, California) has been found in the Etchegoin Formation (1 carapace) near San Benito, in the Middle Miocene Round Mountain Silt (7 fingers, 1 manus) and Olcese Sand (69 fingers) near Bakersfield. These new occurrences extend the stratigraphic range of *C. davidi* from Middle Pliocene to Middle Miocene. Its geographic range now extends from near the southern end of the San Joaquin Basin into the San Benito Trough (Wilson 1943: 222–246), which connected the San Joaquin embayment with the Pacific Ocean during the Miocene and Pliocene.

Cancer fissus was previously known only from its type locality, the Middle Pliocene Etchegoin Forma-

tion near Coalinga, California. New occurrences in the Etchegoin Formation near the type locality (7 carapaces, 1 cheliped) and near San Benito (3 carapaces), extends its Middle Pliocene geographic range. Upper Pliocene occurrences in the Purisima Formation near Santa Cruz (1 carapace) and in the Cascajo Conglomerate (1 nearly complete specimen) near the type locality, further extend its geographic range and increase its stratigraphic range from Middle to Upper Pliocene.

Ten new species of *Cancer* are proposed herein. Two of them, *Cancer danai* (1 carapace) and *Cancer dereki* (2 carapaces) are known only from Miocene rocks, the Briones Sandstone and Monterey Shale respectively. Three new species, *Cancer marri* (7 fingers, 1 carpus, 2 mani, 1 cheliped), *Cancer garthi* (1 finger) and *Cancer durhami* (1 cheliped), are known only from Pliocene rocks. Two previously named extinct species, *Cancer granti* (1 carapace) and *Cancer urbanus* (1 carapace), are still known only from their Pliocene type localities. *Cancer yanceyi* (2 mani) is known only from its type locality, in the Lower Pleistocene part of the San Joaquin Formation. *Cancer allisoni* (8 fingers, 1 manus) occurs in rocks ranging from Middle Miocene to Upper Pliocene. Two species, *Cancer coosensis* (5 fingers, 1 carpus, 2 mani) and *Cancer chaneyi* (187 fingers, 1 carpus, 2 mani) range from Middle Miocene to Pleistocene. The geographic distribution of the former extends from Coos Bay, Oregon to San Francisco Bay and of the latter from the San Joaquin Basin (Middle Miocene) to Baja California (Upper Pleistocene).

BIOGEOGRAPHY

The genus *Cancer* is entirely marine and is represented by 23 living species in the Atlantic and Pacific Oceans. MacKay (1943: 113–115) discussed the distribution of Recent species of *Cancer* and the limiting factor of temperature. He concluded that the genus was restricted to the "temperate zone" with mean annual surface water temperatures between 40° and 75° F. (4.4° to 23.9°C.). This temperature range corresponds roughly to mid-latitudes in the northern and southern hemispheres, except for western South America where temperatures less than 75° (23.9°C.) prevail as far north as the equator, due to the cooling effect of the Humboldt Current. Two species, *C. porteri* and *borealis,* have been found in tropical regions at depths of more than 200 fathoms and 100 fathoms respectively (Garth 1957: 122; MacKay 1943: 113). The temperature at those depths is below 20°C. (Sverdrup 1942: Chart IV), therefore within the tolerances of *Cancer.*

The distribution reported by MacKay is generally correct except that there is no acknowledgment of
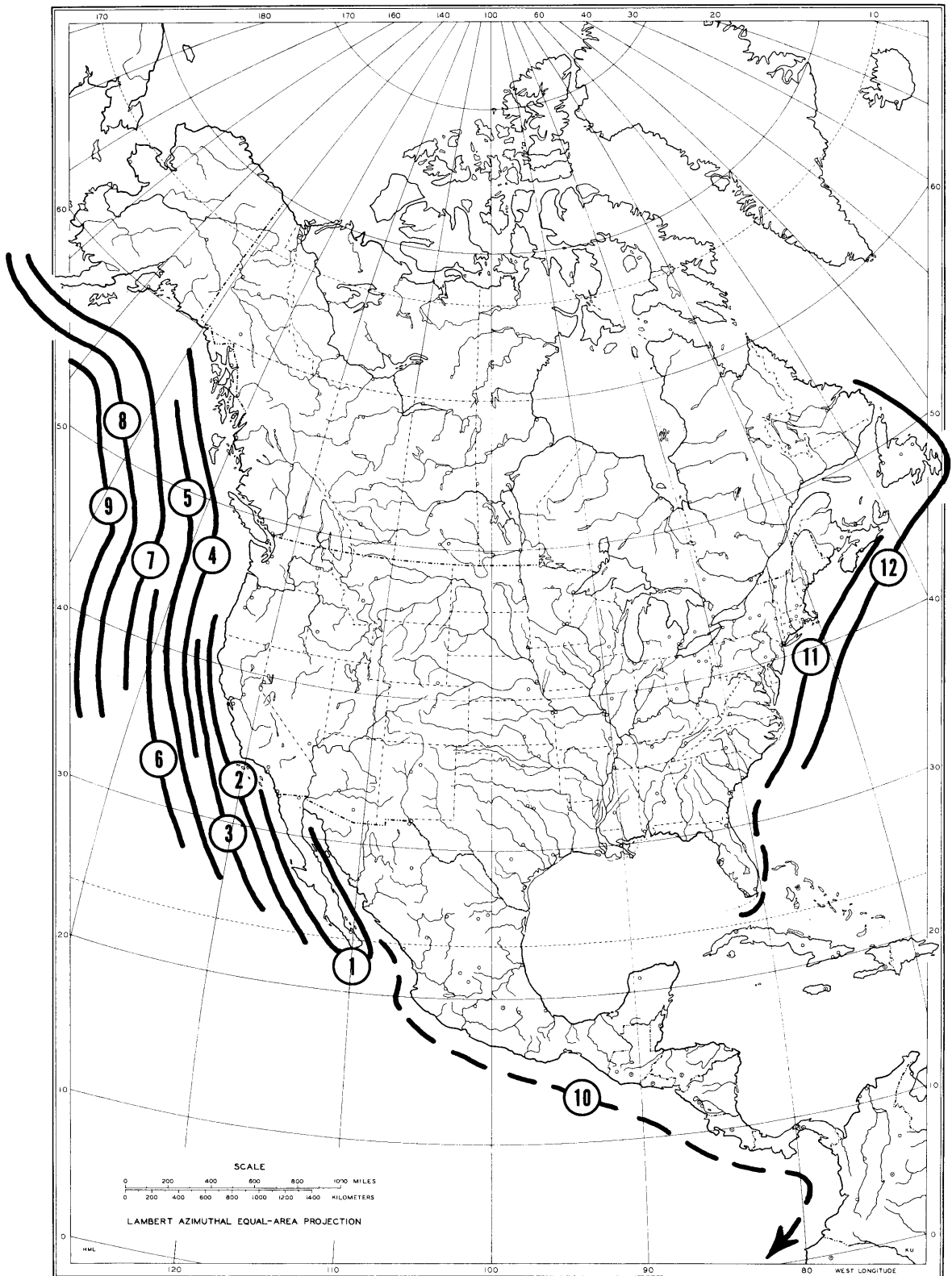
FIGURE 4. Geographic ranges of living species of *Cancer* in North America: **1,** *C. amphioetus;* **2,** *C. antennarius;* **3,** *C. anthonyi;* **4,** *C. branneri;* **5,** *C. gracilis;* **6,** *C. jordani;* **7,** *C. magister;* **8,** *C. oregonensis;* **9,** *C. productus;* **10,** *C. porteri;* **11,** *C. borealis;* **12,** *C. irroratus.* Found only below thermocline————.
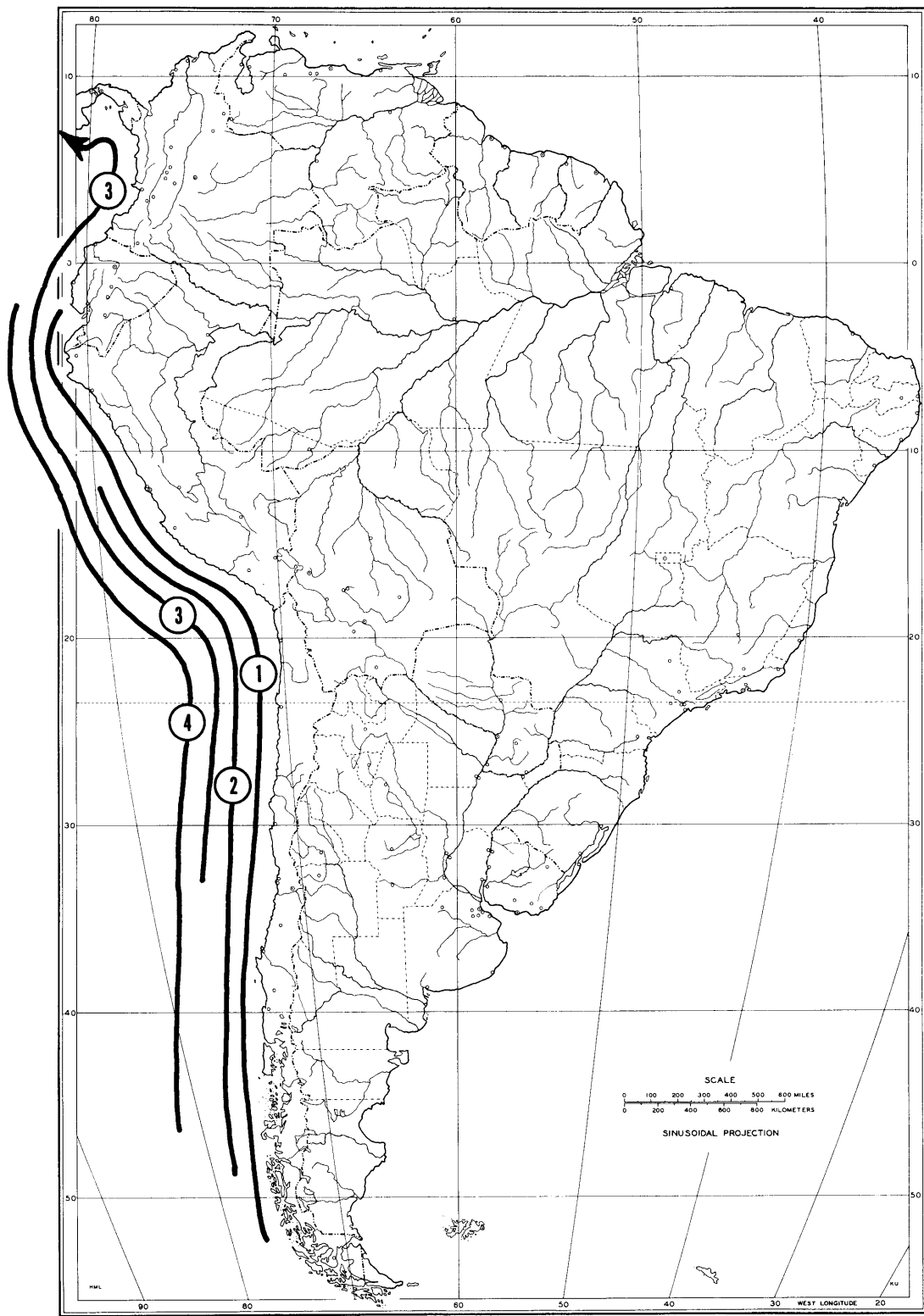
FIGURE 5. Geographic ranges of living species of *Cancer* in South America: **1,** *C. edwardsii;* **2,** *C. plebejus;* **3,** *C. porteri;* **4,** *C. polyodon.*
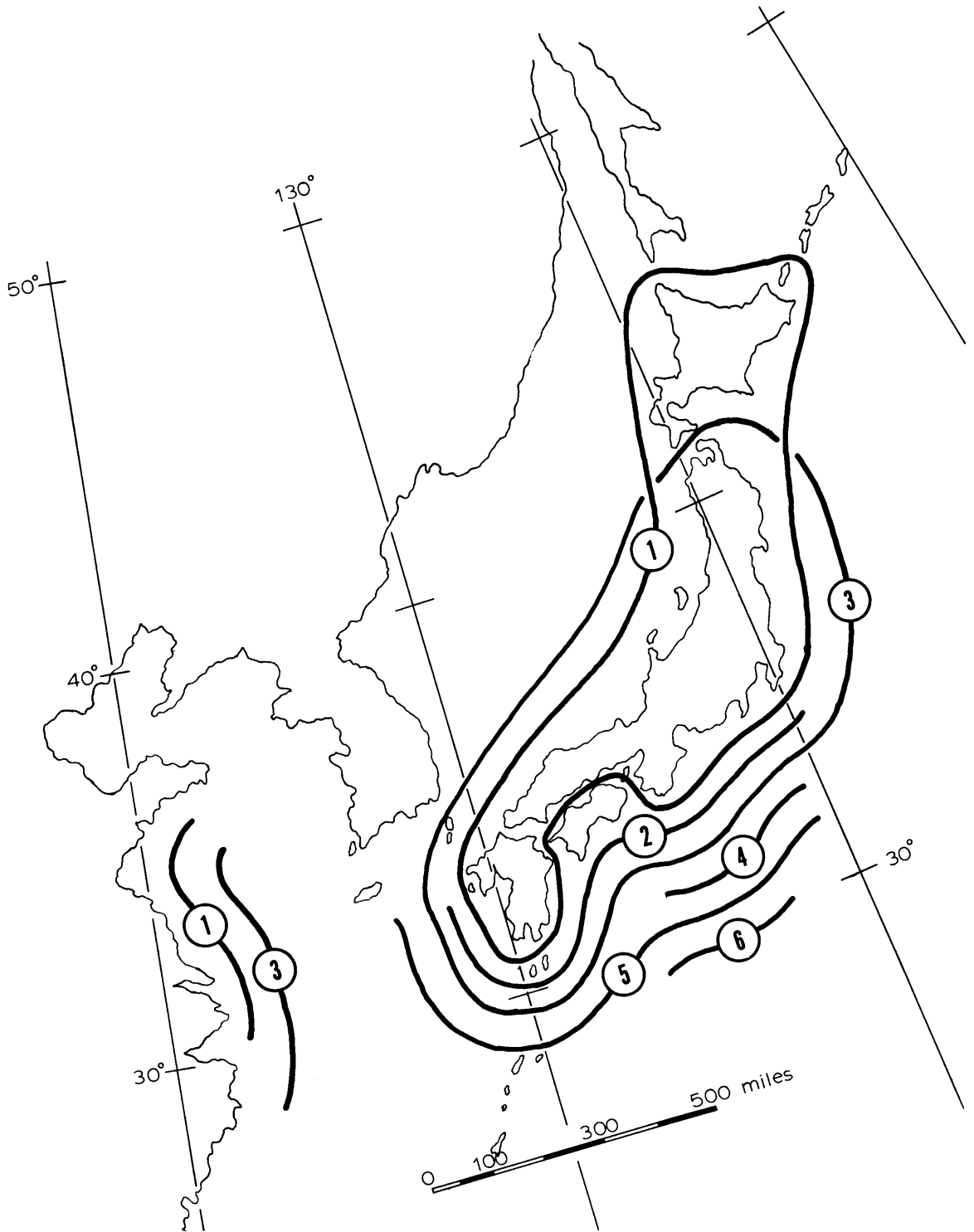
FIGURE 6. Geographic ranges of living species of *Cancer* in Eastern Asia: **1,** *C. amphioetus;* **2,** *C. sakaii;* **3,** *C. gibbosulus;* **4,** *C. japonicus;* **5,** *C. tumifrons;* **6,** *C. nadaensis.*
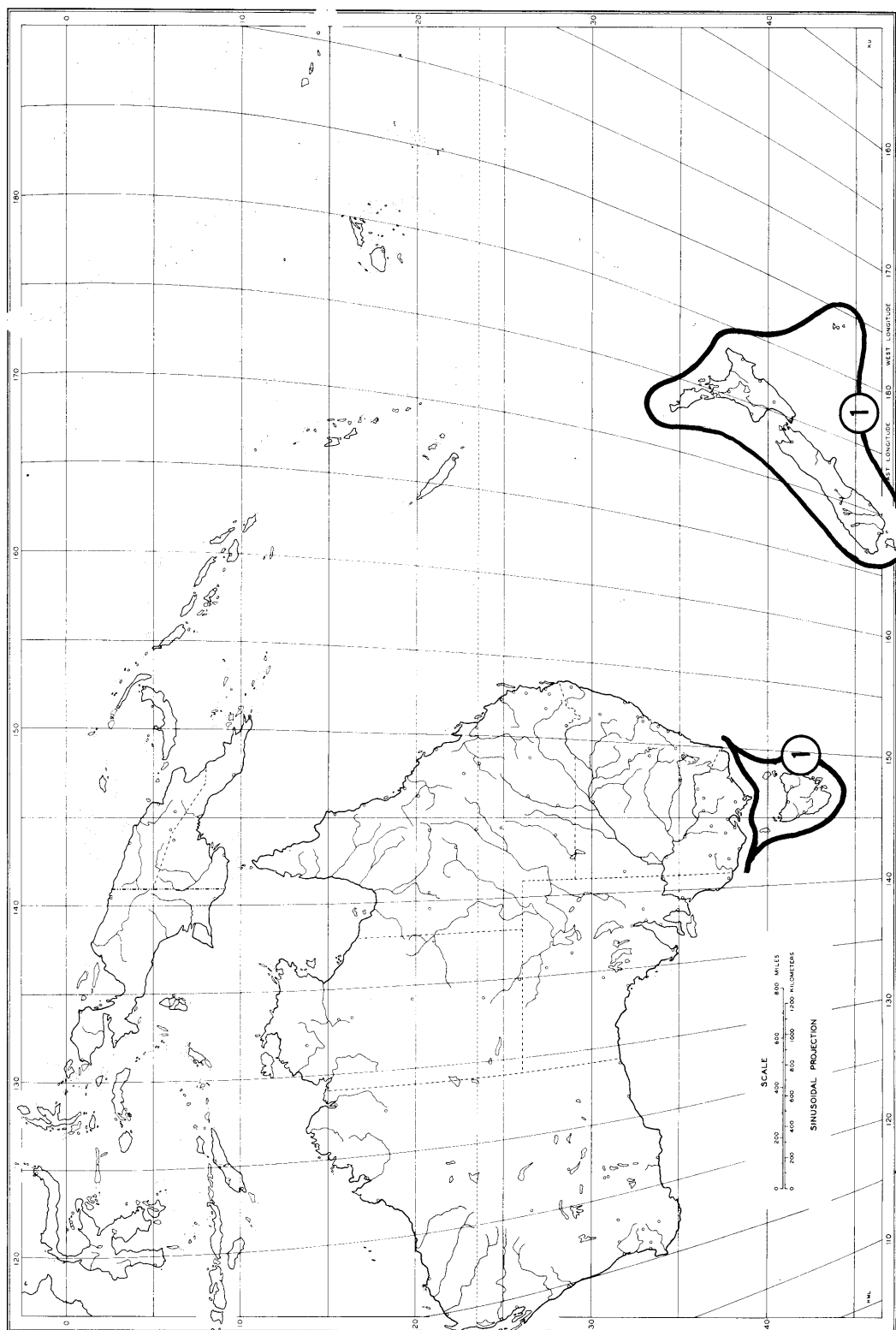
FIGURE 7. Geographic ranges of living species of *Cancer* in Australia–New Zealand: **1,** *C. novaezealandiae.*
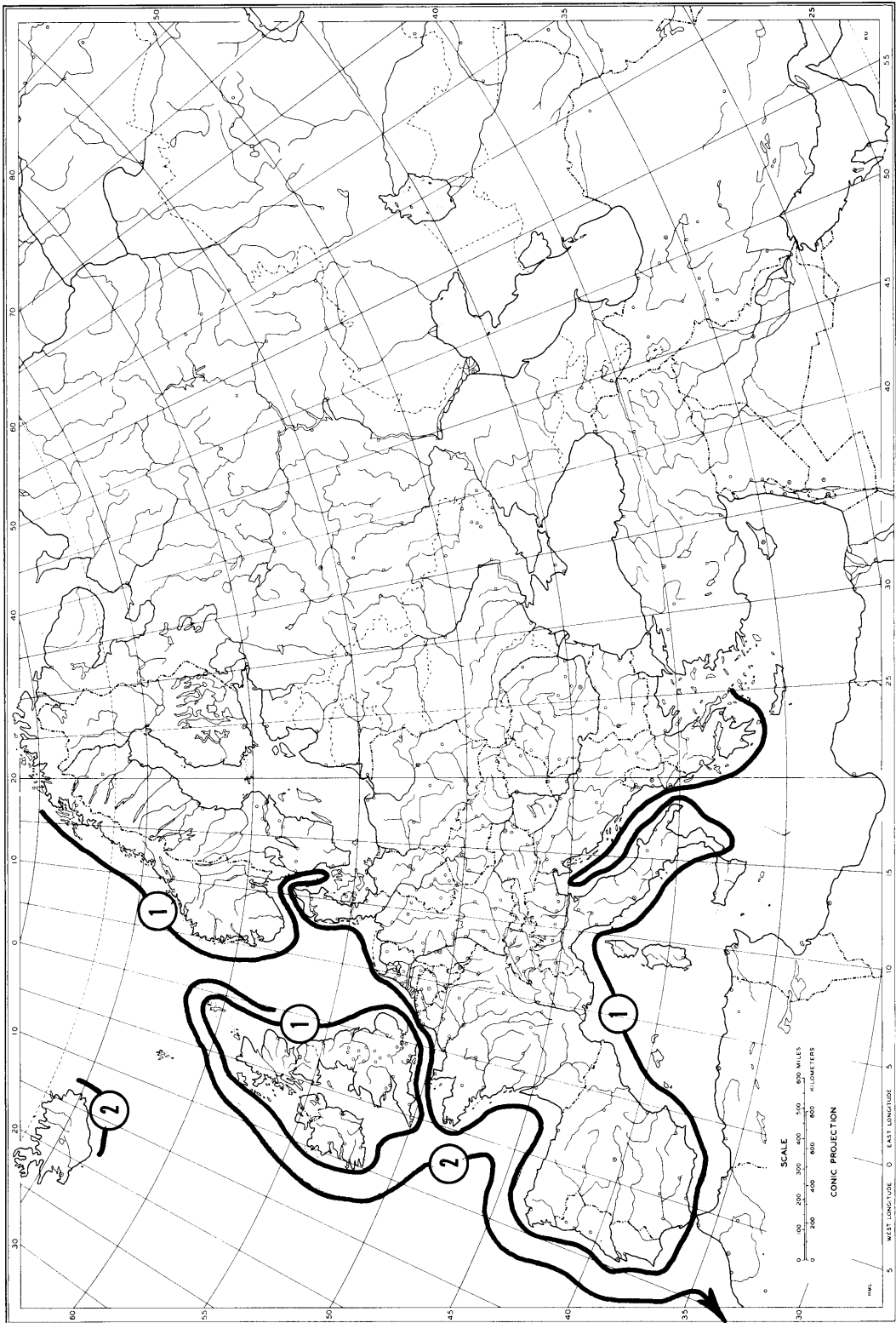
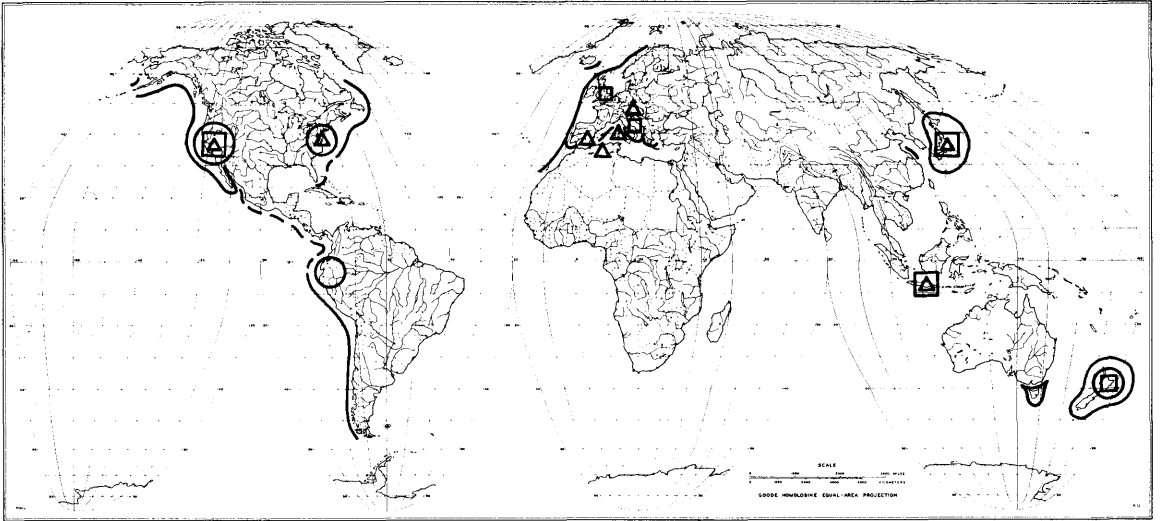FIGURE 8. Geographic ranges of living species of *Cancer* in Europe: **1,** *C. pagurus;* **2,** *C. bellianus.*

FIGURE 9. Recent fossil occurrences of *Cancer:* ⌒ Range of living species, ⌒⌒ Below thermocline only, ● Pleistocene occurrence, ■ Pliocene occurrence, ▲ Miocene occurrence.

several reports (Desmarest 1825: 102; Glaessner 1929: 105; Pesta 1918: 389; Heller 1863: 63) of *Cancer pagurus* in the Mediterranean, Adriatic, and Black Seas. He also did not mention two Recent species, *C. tumifrons* Yokoya 1933 and *C. bellianus* Johnson 1861.

Ekman (1953: 160, fig. 56) discussed the distribution of species of *Cancer,* recognizing its presence in the Mediterranean as well as the areas previously shown by MacKay. However, he apparently overlooked *C. bellianus* because he indicated only one European species and did not include the Madeira Islands in the range of the genus. A current list of Recent species of *Cancer* and their ranges is given in figures 4-8.

PALEOBIOGEOGRAPHY

The following list of species known as fossils and their occurrence have been used in developing the following discussion of paleobiogeography (also Fig. 9).

Western North America

C. allisoni	M. Miocene–U. Pliocene
C. amphioetus	L. Pleist.–Recent
C. antennarius	M. Pliocene–Recent
C. anthonyi	M. Pliocene–Recent
C. branneri	U. Pliocene–Recent
C. chaneyi	M. Miocene–U. Pleistocene
C. coosensis	M. Miocene–U. Pliocene
C. danai	M. Miocene
C. davidi	M. Miocene–M. Pliocene
C. dereki	M. Miocene
C. duryami	M. Pliocene
C. fissus	U. Pliocene
C. garthi	U. Pliocene
C. gracilis	M. Pliocene–Recent
C. granti	U. Pliocene
C. jenniferae	M. Pliocene
C. jordani	L. Pleistocene–Recent
C. magister	L. Pliocene–Recent
C. marri	M. Pliocene–U. Pliocene
C. oregonensis	M. Pliocene–Recent
C. polyodon	U. Pliocene–Recent
C. productus	M. Pliocene–Recent
C. urbanus	U. Pliocene
C. yanceyi	L. Pleistocene

Western South America

C. polyodon	U. Pleistocene, Peru

Japan

C. minutoserratus	Pliocene
C. odosensis	Miocene
C. sanbonsugii	Miocene

Java

C. javanicus	Pliocene
C. species	U. Miocene

New Zealand

C. novaezealandiae	L. Pliocene–M. Pleistocene

Eastern North America

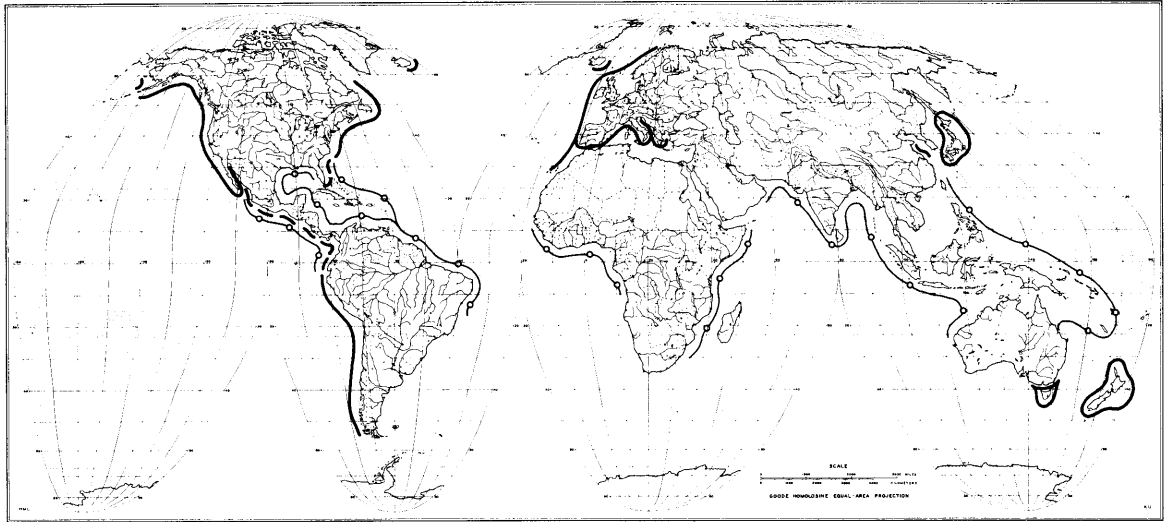|	
C. borealis	U. Miocene(?)–Recent
C. irroratus	M. Miocene–Recent
C. proavitus	U. Miocene

FIGURE 10. Distribution of *Cancer* and surface water temperatures: ⟋ Living species, ⟋ Below thermocline only, ⟋ Temperature greater than 24°C.

	Europe
C. deshayesi	Miocene, Spain, Netherlands, France
	Pliocene, England, Algeria
C. pagurus	Pliocene, England
	L. Pleistocene, Netherlands
C. sismondai	Pliocene, England and Mediterranean

Note: Several other Miocene and Pliocene species listed in Glaessner (1929) have not been verified, therefore, they are not included here. They would not alter the Miocene–Pliocene geographic ranges in any case.

The oldest accepted occurrence of *Cancer* is in the Miocene (Glaessner 1969: R509; and this paper). Species of *Cancer* of this age are known from southern Europe (2 species at least), eastern North America (2 species at least) and western North America (6 species), Japan (2 species), and Java (1 species). The diversity and wide distribution in the Miocene indicate that the genus had an earlier origin, probably in one of those areas. The fossil record of *Cancer* at this writing neither confirms nor contradicts the suggestion by Ekman (1953: 159) that the genus had its origin in the North Pacific, because no pre-Miocene record of the genus has been found. However, the number of fossil species known indicates that the diversity has been greater in the eastern North Pacific than in any other region throughout the known record of the genus.

The relative amount of study in the areas included in Table 3 has not been evaluated; therefore, it may influence the number of species recognized in different areas. The principle of biogeography that "in

the absence of evidence to the contrary, the area in which the genus has undergone the greatest amount of evolution is its probable area of origin" (Cain 1944) would suggest the eastern North Pacific as the area of origin of *Cancer* (See Fig. 12).

The genus is represented in Pliocene rocks of those regions with Miocene occurrences with the exception of eastern North America, where marine Pliocene rocks are poorly represented. However, it is almost certain that species of *Cancer* were present in eastern North America during the Pliocene because three species are known in Miocene rocks of the region, two of which were identified as living species (Rathbun 1935:109). First occurrences are noted in two areas during the Pliocene–England (Glaessner 1929:105) and New Zealand (Glaessner 1960:20, 21); and the last occurrence (Pliocene) in the East Indies (Van Straelen 1938:97-98). There is no valid record of pre-Pleistocene *Cancer* in South America but it is almost certain that the genus was there because of the diversity of Recent species (4), and the probability that it is the ancestral home (Miocene?) of Lower Pliocene New Zealand species. None of the Pliocene species of Japan are recognized as extant (see Imaizumi 1962) while seven of the nine western North American living species are recognized in Pliocene rocks. One South American species. *Cancer polyodon,* is here reported in the Pliocene of southern California.

Pleistocene occurrences (Fig. 9) of *Cancer* are reported from eastern and western North America, western South America, and New Zealand. All are extant species except for two reported herein from western North America.