The Systematics, Postmarsupial Development, and Ecology of the Deep-Sea Family Neotanaidae (Crustacea: Tanaidacea)

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Introduction

The major historical developments in the systematics of the order Tanaidacea were reviewed in 1909 by Calman (1909:190). Relatively few authors had dealt with the biology of the group. Blanc's morphological study of the paratanaid *Tanais* (=*Heterotanais*) *oerstedi* (Blanc, 1884) and the study by Claus (1888) on the morphology of *Apseudes latreillii* (=*A. acutifrons*) were notable exceptions.

Since Calman, most published works have been comprised of the descriptions of species or genera and have appeared, for the most part, in the reports of expeditions or in local faunistic works. Collections often have been erratic, material limited, and various instars have been unknown from developmental series. It frequently has been impossible to pair dimorphic males with their females.

Advancement has been slow in developing an overall systematic framework for the order and in understanding tanaidacean biology. An inadequate understanding of complex and apparently varied patterns of postmarsupial development has greatly hindered progress. In 1937 Dennell published a detailed study of feeding in *Apseudes*. Almost all other relatively recent studies of tanaidacean biol-

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ogy have dealt with postmarsupial development, and they are reviewed in detail in the developmental section of this work.

The most notable recent advance in the study of the Tanaidacea has come through the work of Karl Lang, who, beginning in 1949, has published a long and distinguished series of papers dealing with the order. Lang has greatly increased our understanding of the Tanaidacea, primarily their systematics, and he is responsible for the erection of six of the eight currently recognized families and the modification of the scope of the others.

The present investigation began as a study of the ecology of the deep-sea benthic fauna. I intended to use the Tanaidacea, one of the more important constituents, to represent the fauna, but it soon became apparent that systematic and developmental problems within the order posed insurmountable obstacles to the accomplishment of the proposed study. (These difficulties are discussed in the systematics and development sections, and the historical development of each of these areas of research is reviewed.) Therefore, this investigation has been limited to the clarification of the systematic relationships within a single family, the Neotanaidae, and to the elucidation of its life history and ecology. The Neotanaidae were chosen for study because only a comparatively small number of species had been described, thus limiting the confusion in the taxonomic literature, and because

they are relatively large animals and more easily studied than many other taxa.

The need for a complete revision of the family Neotanaidae became obvious soon after the work was begun. Many species descriptions were incomplete and some were highly inaccurate. Relying on these descriptions, some authors have described new species without examining type specimens and have unwittingly created synonyms.

The collections which formed the basis of this study were obtained from the Gay Head–Bermuda Transect (Sanders, Hessler, and Hampson, 1965). The Transect is a series of stations extending from Gay Head on Martha's Vineyard, Massachusetts, to Bermuda. It crosses the New England Continental Shelf, Slope, and Rise, the Abyssal Plain of the North American Basin, and the Bermuda Rise and Slope. A wide series of environments is transected. Samples were taken from depths as shallow as 70 m on the New England Shelf to over 5050 m on the Abyssal Plain and to 1000 m on the Bermuda Slope.

All neotanaid material known to exist in museums was requested on loan, and all investigators known to be collecting the deep-sea fauna were contacted for additional specimens. These sources of material are listed below in the acknowledgments. The locations at which the animals were collected are listed in Table 1.

The rate of sampling the deep-sea environment has increased substantially during the last decade. The resulting vastly greater accumulation of material has been helpful in eliminating much systematic confusion within the Neotanaidae and has been essential to the understanding of postmarsupial development. Moreover, it has permitted the first realistic analysis of the geographic and vertical distribution of the family together with an examination of its reproductive periodicity.

Much of the literature on the Tanaidacea is in German and in French, and some of it is in Russian. A large part of the information on the postmarsupial development and ecology of the order is scattered throughout this literature. An objective here has been to collect and summarize much of this literature, especially of that dealing with development.

An effort has been made to collect all isolated systematic references to the Neotanaidae. Where descriptions or illustrations have been inadequate, species have been redescribed or reillustrated. Tax-

onomic descriptions have been written and illustrations executed with nonspecialists in mind. Those characters most easily used have been described to facilitate easy identification whenever possible.

Equipped with good descriptions, other biologists should be able to identify species of neotanaids effectively and without unreasonable effort. All species can be identified without resorting to an examination of the mouthparts, and most species with reference to relatively obvious external features, usually without dissection.

Many problems still remain within the Neotanaidae, and the family should serve as a fertile subject for future morphological, physiological, and ecological research.

METHODS

COLLECTING.—Collections from the Gay Head–Bermuda Transect were obtained with the anchor dredge (Sanders, Hessler, and Hampson, 1965) and the epibenthic sled (Hessler and Sanders, 1967). These collections were made between 1960 and 1968 on ships of the Woods Hole Oceanographic Institution (WHOI), primarily on the *Atlantis*, *Atlantis II*, and *Chain*.

Upon arrival at the surface, samples were removed from the collecting device and placed in a large steel can. The animals were separated from the sediment by elutriation, using a large stream of water running at low velocity. The water running off the surface of the sample passed through a 0.42-mm mesh sieve upon which the animals were retained. Following washing, the animals were fixed in 10 percent commercial formalin for about 24 hours. The formalin was then replaced by a seawater rinse for about 12 hours before the sample was placed in 70 percent ethyl alcohol for permanent storage. Sorting to major taxonomic group was done in the laboratory. These techniques, which often yield material of high quality for both taxonomic work and histological examination, are described in detail in the work cited above.

EXAMINATION.—Drawings were made with the aid of camerae lucidae provided with Wild microscopes. Photographic work for the figures was done by personnel of the Graphic Arts Group at the Woods Hole Oceanographic Institution.

Each animal at WHOI Benthic Stations 64 and 76 (and certain other individuals) was assigned an

alphabetic symbol in order to maintain its individuality throughout the studies of intraspecific variation and postmarsupial development. Basic data for each of these animals are presented in Tables 16 (Sta. 64), 17 (Sta. 76), and 18 (other animals). Blank spaces in the tables indicate that measurements were impossible to obtain because of broken or missing parts.

MEASUREMENT.—Consistent with the practice of others (e.g., Lang, 1968; Wolff, 1956a), body length was measured from the anterior tip of the carapace to the posterior medial margin of the pleotelson. Body width was measured across the widest part of the carapace, at the chelipedal coxae (Figure 1B). The methods of measuring other dimensions are illustrated in Figure 1.

Measurement of the oostegites was particularly difficult. It was essential that the broad, flat surface of the oostegite be perpendicular to the line of observation in order to obtain suitably accurate measurements. This was accomplished by placing the specimen under examination in a depression formed in the soft surface of black artist's wax, a material useful throughout the study when it was necessary to examine a specimen from an unusual angle with reflected light. Pieces of wax were placed in a small dish which was then warmed in an oven. The wax melted, forming a smooth surface which could be molded with a needle or probe. If transmitted light was necessary, the animals were supported on piles of translucent, crushed-glass boiling stones rather than artist's wax. The specimens were under 70 percent alcohol at all times.

Oostegites at all stages of development often were very difficult to observe closely because of their thin and consequently translucent nature. In order to visualize these structures clearly, the animals were dipped in a solution of methylene blue and Castile soap [1 g of methylene blue and 0.5 g of Castile soap in 300 ml distilled water (Guyer, 1953)]. The stain and soap were obtained from the Fisher Scientific Company in Medford, Massachusetts. Methylene blue stains the cuticle of the animals. For the purposes of these measurements, the animals were dipped in two or three drops of the solution for several seconds to outline the oostegites or pleopods.

With the aid of the camera lucida, a fine pencil line was traced around each oostegite sheath. The length and width of the outline were then measured at its widest points (Figure 1E). The proximal limit was arbitrarily set at the narrowest point of the peduncle near its juncture with the blade.

The oostegite sheaths on an animal vary slightly in length. To minimize possible error arising from consistent differences in length, the sheath on the left fifth pereopod was measured in all cases. In order to get a quantitative estimate of pleopodal length, the length of the left first pleopodal endopod was measured (Figure 1F).

STAINING FOR OOSTEGITE SCARS AND MALE GONOPORE ANLAGEN.—The male gonopore anlagen and the scars remaining after the oostegites have been shed and the female gonopores have closed are sometimes very difficult to see clearly. Rose bengal, routinely used in sorting benthic samples at Woods Hole, was helpful in visualizing these structures (stock solution of 15 g technical grade Eastman rose bengal in 500 ml distilled water). As with methylene blue (see above), the specimen was dipped in a depression slide containing a few drops of the dye for a minute or less, the length of time depending on the size and stage of the animal. After a quick dip rinse in tap water to wash off the excess stain (not necessary in the case of methylene blue), the oostegite scars were clearly visible, and if the male gonopore anlagen were decalcified they, too, were clearly stained. However, the latter require more time for the stain to penetrate than is necessary for oostegite scars. Rose bengal is effective because it stains the interior of the animal rather than the cuticle and, in areas which are not calcified, the red color of the interior is visible. Both rose bengal and methylene blue completely leach out of the specimens after several days in 70 percent ethyl alcohol, or several weeks in the case of individuals heavily stained with rose bengal.

HISTOLOGICAL METHODS.—Materials used for analysis of the gonads were refixed for 24 hours in a solution of one part of glacial acetic acid to 19 parts of saturated mercuric chloride (Hessler, personal communication). The mercury was then removed by placing the specimens in 70 percent ethyl alcohol to which several drops of iodine solution had been added. The specimens were cleared in benzene and perfused and embedded in "Tissuemat" (Fisher Scientific Company). The animals were sectioned at 8 to 10 μm. Delafield's hematoxylin was used for cellular detail, and Solution II of Mallory's triple connective tissue stain (Guyer,
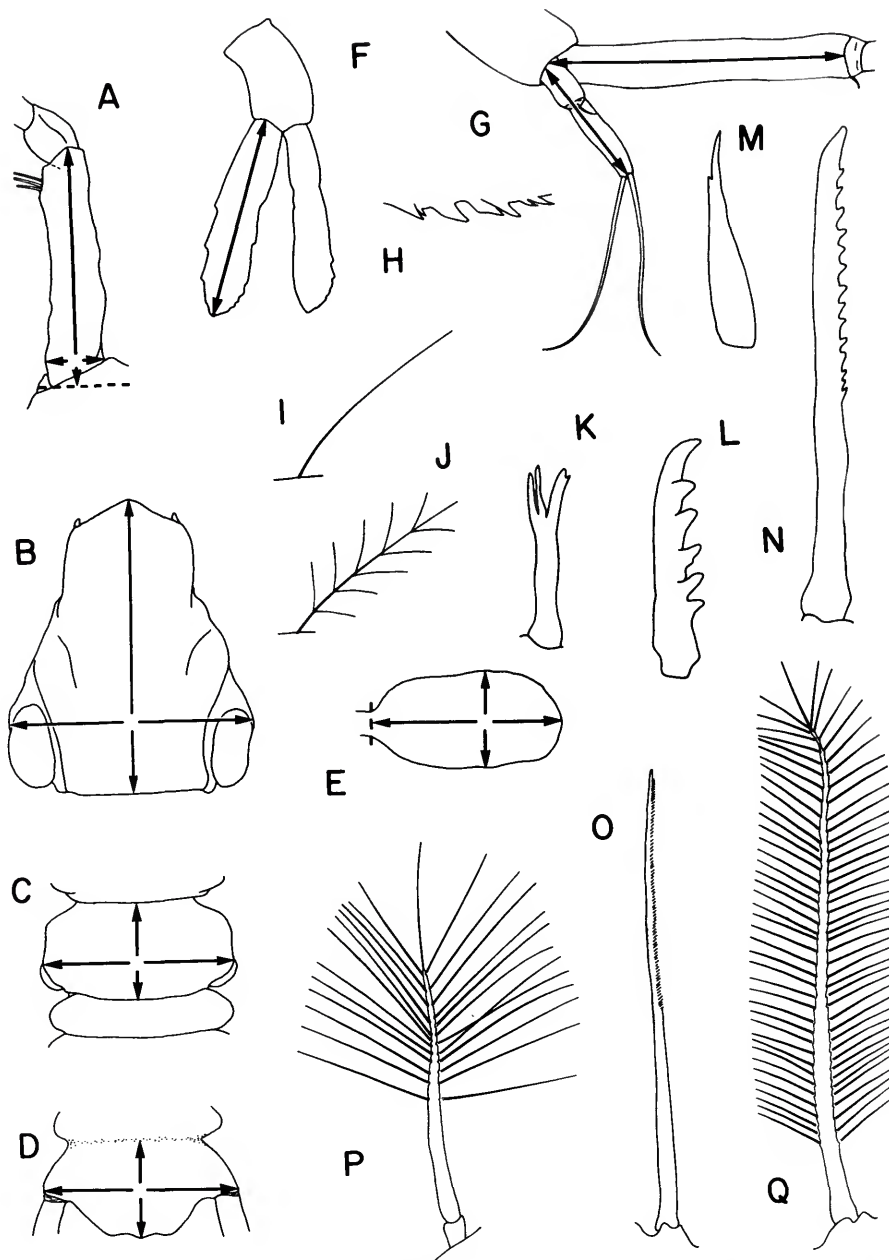
FIGURE 1.—A–G, Methods of measuring bodily dimensions: A, first antenna (=antennule); B, carapace; C, seventh pereonite; D, pleotelson; E, oostegite or oostegite sheath; F, pleopodal endopod; G, uropodal exopod and first endopodal article. H–Q, Types of armament found in the Neotanaidae: H, spinelets such as found on pereopodal propodi; I, cuticular hair typical of pleonal dorsal surface; J, feathered hair; K, cleft spine found on the second maxilla; L, short, terminal propodal spine found on pereopods II–IV; M, short, subterminal carpal spine found on pereopod II; N, long, terminal propodal spine frequently found on pereopods II–IV; O, typical seta such as found on pereopods II–VII; P, broom seta; Q, feathered seta such as borne on pleopods.

1953) was used as a counterstain. Permanent mounts were made with "Permount" (Fisher Scientific Company).

Taxonomic Descriptions

For differences among the genera, refer to the diagnostic key to genera and to the individual generic diagnoses.

The deep-sea fauna is still very poorly sampled, and the number of known species of neotanaids almost certainly will increase substantially. When identifying specimens, there is a tendency to minimize observed differences and to assign specimens to species already listed in a key, especially with morphologically conservative groups such as the Neotanaidae; therefore, a diagnostic key to species is not provided and the diagnoses of the species should be consulted for identifying them.

The figures associated with each species description are indicated below the species name, with the figure numbers of distributional maps italicized. Species diagnoses follow a complete synonymy and include those characters that are particularly useful in distinguishing species. Because neotanaids are sexually dimorphic, diagnoses are presented for copulatory males in addition to the other stages; however, only those characters in which the males differ uniquely from other species are listed (males usually differ from males of other species in some of the same ways as the other stages differ). Because of morphological conservatism, it often is impossible to select one or two characters unique to a species. Therefore, such diagnostic characters are indicated by an asterisk and when used together will provide certain identification for a species.

Detailed descriptions of the holotype and allotype are presented for each species whenever possible. An animal of any stage other than copulatory male, properly described, and preferably older than the manca 2 stage, can represent all stages except the copulatory male. All copulatory male instars are identical to each other except for the chelipeds and, of course, body length and certain meristic characters.

The components of the descriptions are arranged in the following sequence: (1) somites, anteroposteriorly, and (2) appendages, anteroposteriorly. Descriptions of copulatory males usually include only

those characters by which these animals differ significantly from other stages.

Figures are provided with the descriptions of all new species, where species are redescribed, or where needed to supplement the original descriptions. When possible, both textual and illustrative information on intraspecific variation are included.

When more than one sex is figured on a page, the sex is distinguished by the symbols ♂ and ♀. If females were not available to represent stages other than copulatory males, preparatory males—generally identical with the females—or juveniles were used instead. These also are designated by the symbol ♀, and the stage to which they belong is indicated in the legend.

Large, black arrows designate those characters found to be most useful in identifying each species. The abbreviations appearing in the figures are identified below in this section. All scale lines are in millimeters.

With the exception of the maxillipedal epipods, mouthparts are drawn in the inverted position commonly used when describing Crustacea.

The basic features of external neotanaid morphology are indicated in Figures 3–11; secondary sexual structures are illustrated in Figure 94. The nomenclature and means of identifying developmental stages are discussed in a section under "Development." Figure 86 presents a flow diagram of neotanaid life history.

At the end of the section on each species is a list of all material of the species known to exist. All of this material has been examined, except where noted, and the location of all known museum holdings follows. The abbreviations of museum names are included in the list (below) of abbreviations used. If the material of a species is extensive, a brief statement summarizes the species' known geographic and vertical distribution. Table 1 presents additional information on the date, location, and method of collection.

Terminology

Following is a brief summary of some of the terms used. Nonspecialists wishing additional information are referred to the references cited, to Calman (1909), or to Moore and McCormick (1969). For explanations of oceanographic terms, refer to Sverdrup, Johnson, and Fleming (1942).

TABLE 1.—*Collection data on neotanaid material examined*

Program or ship	Station no.	Date	Depth* (meters)	General area	Latitude	Longitude	Gear	Species collected†
WHOI Benthic	E 3	25 May 1961	824	Gay Head–Bermuda	39°50.5′N	70°35′W	AD	4
	F 1	24 May 1961	1500	Transect	39°47′N	70°45′W	AD	4
	G 1	24 May 1961	2000		39°42′N	70°39′W	AD	4, 11
	G 3	23 May 1962	2086		39°41.4′N	70°38.3′W	AD	4
	G 7	06 Sept. 1962	2158		39°41.2′N	70°40′W	AD	11
	G 9	09 Sept. 1962	2021		39°44.7′N	70°38.3′W	AD	4, 11
	G 13	04 Mar. 1963	2036		39°43′N	70°42.6′W	AD	4, 11
	GH 3	03 Oct. 1961	2478		39°27.5′N	70°33.5′W	AD	4, 15
	HH 1	21 May 1961	2873		39°N	70°W	AD	1
	HH 3	21 May 1961	2900		38°47′N	70°08′W	AD	1.3
	KK 3	25 May 1962	4758		36°22.7′N	68°02.2′W	AD	3
	NN 1	26 May 1962	4950		33°56.5′N	65°50.7′W	AD	28
	Ber. 1	13 Apr. 1960	1000	Gay Head–Bermuda Transect, Bermuda Slope	32°16.5′N	64°42.5′W	AD	2
	Ber. 2	18 Apr. 1960	1700		32°16.6′N	64°36.3′W	AD	2
	Ber. 4	02 May 1960	1700		32°17.0′N	64°35′W	AD	2
	Ber. 5	28 Aug. 1960	2000		32°11.4′N	64°41.6′W	AD	29
	Ber. 6	01 Sept. 1961	1500		32°14.3′N	64°42′W	AD	2
	Ber. 7	04 Sept. 1961	2500		32°15′N	64°32.6′W	AD	18
	Ber. 8	05 Sept. 1961	1000		32°21.3′N	64°33′W	AD	2
	61	20 Aug. 1964	2000	Gay Head–Bermuda Transect	39°43.2′N	70°37.8′W	AD	4
	62	21 Aug. 1964	2496		39°26′N	70°33′W	ES	4, 15
	63	21 Aug. 1964	2891		38°46.8′N	70°05.7′W	AD	1, 3
	64	21 Aug. 1964	2886		38°46′N	70°06′W	ES	1, 3, 11, 15
	65	21 Aug. 1964	2891		38°46.8′N	70°06.8′W	AD	1, 3
	66	21 Aug. 1964	2802		38°46.7′N	70°08.8′W	ES	1, 3
	69	23 Aug. 1964	4663		36°15′N	67°51′W	AD	3
	70	23 Aug. 1964	4680		36°23′N	67°58′W	ES	3, 11, 28
	72	24 Aug. 1964	2864		38°16′N	71°47′W	ES	1, 4, 15
	73	25 Aug. 1964	1330–1470		39°46.5′N	70°43.3′W	ES	4
	76	29 June 1965	2862		39°38.3′N	67°57.8′W	ES	1, 3, 11
	78	30 June 1965	3828		38°00.8′N	69°18.7′W	ES	1, 3, 15
	80	02 July 1965	4970		34°49.8′N	66°34′W	ES	3
	83	03 July 1965	5000		34°46.5′N	66°30′W	ES	3
	84	04 July 1965	4749		36°24.4′N	67°56′W	ES	3
	85	05 July 1965	3834		37°59.2′N	69°26.2′W	ES	1, 18
	92	13 Dec. 1965	4694		36°20′N	67°56′W	ES	3
	95	17 Dec. 1965	3753		38°33′N	68°32′W	ES	1, 3, 18
	103	04 May 1966	2022		39°43.6′N	70°37.4′W	ES	4, 11
	109	08 Aug. 1966	4750		36°25′N	68°06.0′W	ES	3
	112	09 Aug. 1966	2900		38°50.4′N	69°54.7′W	ES	1
	118	18 Aug. 1966	1135–1153		32°19.4′N–32°19.0′N	64°34.9′W–64°34.8′W	ES	2

* WHOI Benthic Stations uncorrected; other stations variously corrected and uncorrected.

† Numerical code for species collected: 1, *Neotanais micromopher;* 2, *N. dinotomer;* 3, *N. americanus;* 4, *N. sandersi;* 5, *N. laevispinosus;* 6, *N. mesostenoceps;* 7, *N. hadalis;* 8, *N. robustus;* 9, *N. antarcticus;* 10, *N. bulbodens;* 11, *N. affinis;* 12, *N. vemae;* 13, *N. peculiaris;* 14, *N. pfaffi;* 15, *N. giganteus;* 16, *N. pfaffioides;* 17, *N. armiger;* 18, *N. hastiger;* 19, *N. tricarinatus;* 20, *N. calcarulus;* 21, *N. barfoedi;* 22, *N. bacescui;* 23, *N. hessleri;* 24, *N. insolitus;* 25, *N. wolffi;* 26, *Neotanais* sp. of Kudinova-Pasternak; 27, *Herpotanais kirkegaardi;* 28, *Venusticrus glandurus;* 29, *Carololangia mirabunda.*

TABLE 1.— (Continued)

Program or ship	Station no.	Date	Depth* (meters)	General area	Latitude	Longitude	Gear	Species collected†
					Location			
					Coordinates			
	120	20 Aug. 1966	5018–5023		34°43.0′N–34°40.5′N	66°32.8′W–66°35.0′W	ES	3
	121	21 Aug. 1966	4800		35°50.0′N	65°11.0′W	ES	3
	122	21 Aug. 1966	4833		35°50.0′N–35°52.0′N	64°57.5′W–64°58.0′W	ES	3
	126	24 Aug. 1966	3806		39°37.0′N–39°37.5′N	66°47.0′W–66°44.9′W	ES	1, 3, 11
	128	16 Dec. 1966	1254		39°46.5′N	70°45.2′W	ES	4
	131	18 Dec. 1966	2178		39°38.5′N–39°39.0′N	70°36.5′W–70°37.1′W	ES	4, 11
	146	06 Feb. 1967	2842–2891	Off Guinea, West Africa	10°39.5′N	17°44.5′W	ES	18
	147	06 Feb. 1967	2934		10°38.0′N	17°52.0′W	ES	6
	151	08 Feb. 1967	3861		10°20.0′N	18°22.0′W	AD	15
	155	13 Feb. 1967	3730–3783	Equator near Sts. Peter's and Paul's Rocks	00°03.0′S	27°48.0′W	ES	11
	156	14 Feb. 1967	3459		00°46.0′S–00°46.5′S	29°28.0′W–29°24.0′W	ES	11
	169	21 Feb. 1967	587	Off Recife, Brazil	08°03.0′S–08°02′S	34°23.0′W–34°25.0′W	ES	19
Alaminos	66–A–5, Sta. 5	— — 1966	1550–1740	Gulf of Mexico, S of Alabama	29°00′N	87°29.0′W	—	17
Albatross	2221	06 Sept. 1884	2789	S of Martha's Vineyard, Massachusetts	39°05.5′N	70°44.5′W	—	1
	2570	01 Sept. 1885	3316	SE of Georges Bank	39°54.0′N	67°05.0′W	BT	1, 3
Anton Bruun Cruise 11	95	15 Oct. 1965	4332–4423	Off Peru	08°31′S	81°40′W	SBT	10, 20
	111	18 Oct. 1965	3086–3202		08°23′S	80°40′W	SBT	14, 17
	113	19 Oct. 1965	5986–6134		08°44′S	80°45′W	SBT	17
	149	27 Oct. 1965	3117–3177		11°58′S	78°35′W	BT	14
	157	28 Oct. 1965	3994–4367		12°03′S	78°45′W	SBT	17
	179	04 Nov. 1965	4823–4925		08°54′S	80°41′W	SBT	17
Chain Cruise 35 ("Equalant")	Dredge 12	06 Apr. 1963	770–805	Off Recife, Brazil	07°09′S–07°08′S	34°25.5′W–34°25.0′W	AD	21
Challenger	45	03 May 1873	2268	E of Delaware Bay, New Jersey	38°34′N	72°10′W	—	1
	323	28 Feb. 1876	3475	Off Río de la Plata, Uruguay	35°39′S	50°47′W	—	3
CMS	1597	02 June 1964	598	E of Florida Keys	25°08.0′N	79°52.0′W	CG	17
	2072	07 Aug. 1964	2725	Off North Carolina	36°01.2′N	74°01.0′W	CG	1
	2073	07 Aug. 1964	2610		36°14.6′N	74°00.0′W	CG	1
	2118	14 Aug. 1964	2975	Off Delaware	38°14.4′N	72°16.0′W	CG	1

TABLE 1.— (Continued)

Program or ship	Station no.	Date	Depth* (meters)	General area	Latitude	Longitude	Gear	Species collected†
	2125	15 Aug. 1964	2682	E of Cape May, New Jersey	38°45.9′N	71°44.5′W	CG	1
	2144	17 Aug. 1964	2850	SW of Cape Cod, Massachusetts	38°59.2′N	70°29.3′W	CG	1
	2145	18 Aug. 1964	2925	S of Cape Cod	38°53.0′N	69°59.0′W	CG	1
	2146	18 Aug. 1964	2645		39°15.1′N	69°59.4′W	CG	4
	2151	19 Aug. 1964	1865	SE of Cape Cod	39°46.6′N	69°30.3′W	CG	11
	2154	19 Aug. 1964	2840		39°08.3′N	69°27.8′W	CG	1
	2157	19 Aug. 1964	2460	SW of Georges Bank	39°37.0′N	68°54.0′W	CG	15
	2162	20 Aug. 1964	2295	SE of Cape Cod	39°51.1′N	68°40.3′W	CG	4
	2163	20 Aug. 1964	2695	SW of Georges Bank	39°40.6′N	68°30.8′W	CG	15
	2164	20 Aug. 1964	3015		39°24.3′N	68°20.0′W	CG	1
	2169	21 Aug. 1964	2870	S of Georges Bank	39°50.2′N	67°40.7′W	CG	15
	2188	27 Aug. 1964	2715		40°09.4′N	66°45.0′W	CG	1
	2201	18 Sept. 1964	2451	SE of Georges Bank	41°16.4′N	65°44.4′W	CG	11
Discovery	6710	19 Mar. 1968	2670	S of Gran Canaria	27°23.6′N	15°39.6′W	ES	3
	6711	19 Mar. 1968	2988	Is.	27°14.9′N	15°36.3′W	ES	3
Eastward								
Cruise 47–65	2756	15 Sept. 1965	3017	E of Cape Hatteras, North Carolina	36°02.5′N	73°51.0′W	ES	1, 3, 4, 11, 15
Cruise 32–66	5474	16 Aug. 1966	5340		32°49.0′N	71°16.1′W	SBT	3
	5481	17 Aug. 1966	5080		33°18.0′N	72°45′W	SBT	3
	5491	19 Aug. 1966	3825	S of Cape Hatteras	33°30.0′N	75°51.0′W	SBT	1
	5494	20 Aug. 1966	3620		33°33.0′N	75°04.5′W	SBT	11
Cruise 45–66	6228	07 Nov. 1966	3057	SE of Cape Hatteras	34°05.2′N	75°18.7′W	SBT	1, 3
Cruise 27–67	7530	10 June 1967	4460		33°04.5′N	74°29.0′W	SBT	24
	7542	13 June 1967	4690		33°06.0′N	73°52.5′W	SBT	29
	7547	14 June 1967	3780		33°37.0′N	74°49.0′W	SBT	3
Eltanin								
Cruise 2	25	02 June 1962	2489	Off Colombia (Pacific)	04°53′N– 04°51′N	80°28′W– 80°27′W	SBT	17
	40	11 June 1962	3404– 3495	Off Peru	13°10′S– 13°07′S	77°57′W– 77°57′W	SBT	17
	50	15 June 1962	2599– 2858		16°12′S– 16°10′S	74°41′W– 74°41′W	SBT	14
	75	24 June 1962	1932– 3142	Off Chile	31°10′S– 31°14′S	71°56′W– 71°58′W	PC	17
Cruise 25	366	15 Nov. 1966	5340	South Pacific, SE of Bounty Is.	49°21′S– 49°25′S	172°16′W– 172°20′W	BT	23
Galathea	65	04 Dec. 1950	2770	Off Gabon, West-Central Africa	02°17′S	08°10′E	—	15
	193	06 Feb. 1951	3680	SE of Durban, South Africa	32°34′S	31°52′E	SOT	11
	282	11 Apr. 1951	4040	SW of Ceylon	05°32′N	78°41′E	HOT	22
	471	09 Sept. 1951	2780	Sunda Trench	10°26′S	114°15′E	PG	16
	575	19 Dec. 1951	3710	Tasman Sea	40°11′S	163°35′E	SOT	15
	649	14 Feb. 1952	8210– 8300	Kermedec Trench	35°16′S	178°40′W	ST	7
	651	16 Feb. 1952	6960– 8300		32°10′S	177°14′W	HOT	7, 27
	663	24 Feb. 1952	4410		36°31′S	178°38′W	HOT	8
	664	24 Feb. 1952	4570		36°34′S	178°57′W	HOT	8

TABLE 1.— (Continued)

Program or ship	Station no.	Date	Depth* (meters)	General area	Latitude	Longitude	Gear	Species collected†
				Location				
					Coordinates			
Sarsia	33	13 July 1967	1784	Bay of Biscay off Spain	43°40.8′N	03°36′W	AD	18
	44	16 July 1967	1739		43°40.8′N	03°35.2′W	ES	4, 18
	50	18 July 1967	2379		43°46.7′N	03°38′W	ES	5, 11
	65	25 July 1967	1922		46°15′N	04°50′W	ES	13
Travailleur	Dredge 10	26 July 1880	1960		43°39.05′N	05°48.00′W	—	5, 18
Valorous	9	August 1875	3200	Labrador Sea W of Greenland	59°10′N	50°25′W	—	18
	15	22 Aug. 1875	2715	SE of Greenland	55°58′N	28°42′W	—	3
Vema	15–21	10 Nov. 1958	938	Caribbean Slope of Panama	09°46.3′N	79°37.5′W	SBT	17
	15–39	15 Nov. 1958	3859	Off Pacific coast of Colombia	04°25′N	78°25′W	SBT	17
	15–40	16 Nov. 1958	3700–3757		04°25′N	78°25′W	SBT	17
	15–41	18 Nov. 1958	2270	Off Pacific coast of Panama	07°02′N	83°10′W	SBT	17
	15–46	20 Nov. 1958	3517–3528	W of Costa Rica	09°22′N	89°33′W	SBT	17
	15–55	24 Nov. 1958	3777–3950	Off Pacific coast of El Salvador and Honduras	12°45′N	88°38′W	SBT	14
	15–67	08 Dec. 1958	2816–2846	Off Peru	09°43′S	80°04′W	SBT	17
	15–84	30 Dec. 1958	5657	Off Chile	27°35′S	71°51′W	SBT	12
	16–55	30 Aug. 1960	2452	Labrador Sea SW of Greenland	55°48′N	56°00′W	SBT	11
	17–2	13 Mar. 1961	4030–4036	Off Chile	34°29′S	74°21′W	SBT	17, 20
	17–4	15 Mar. 1961	4116		37°10′S	77°42.5′W	SBT	10
	17–5	16 Mar. 1961	3739–3824		38°15′S	76°00′W	SBT	4
	17–6	21 Mar. 1961	4303–4323		37°57′S	75°08′W	SBT	20
	17–7	22 Mar. 1961	3089–3279		40°32′S	75°08′W	SBT	17
	17–81	27 May 1961	5329–5332	Argentine Basin	44°33′S	49°19′W	SBT	3, 7, 11
	17–82	28 May 1961	5139–5148		45°22′S	46°58′W	SBT	7
Vitjaz	3214	(no date)	6156–6207	E of Honshu, Japan	38°11′N	143°56′E	—	25
	3232	(no date)	6126		33°11′N	149°46′E	—	25
	3655	(no date)	6920–7657	Bougainville Trench	05°49.4′S	152°53.4′E	—	7
	3849	30 Jan. 1958	6680–6830	New Hebrides Trench	20°32′S	168°30′E	—	26

BODY SEGMENTS AND APPENDAGES.—There has been much confusion concerning the nomenclature applied to these parts of the body. Hansen (1913:8), Lang (1953a:342), and Wolff (1956a:188; 1962:15) have discussed the situation. Lang provides a table summarizing the terminology used by a number of earlier authors for the first two pairs of "legs." The terminology of Wolff, used by most modern workers within the Tanaidacea, is applied here.

The first two thoracic somites (=thoracomeres) are fused to the head in the Tanaidacea and respectively bear the maxillipeds and chelipeds. The third through eighth (free) somites are known as pereonites (=pereomeres), collectively as the pereon. They bear pereopods II–VII (=thoracopods III–VIII). The chelipeds are also known as the first pereopods. For a discussion of the rationale behind this terminology refer to Wolff (1956a:188).

There are five free abdominal somites or pleonites (=pleomeres); the sixth is fused to the telson to form the pleotelson. Pleonites and pleotelson collectively are called the pleon. Each pleonite bears a pair of pleopods, and the pleotelson bears the uropods. Body somites are numbered with Arabic numerals, appendages with Roman numerals.

Several of the authors cited above have treated the various ways of spelling pereon (peraeon, pereion, etc.). I accept the reasoning of Wolff (1962: 15); accordingly, pereon, pereonite, and pereopod are used in this study.

The naming of the articles in the cheliped has caused considerable confusion. The situation is reviewed briefly by Lang (1953a:342). According to various authors, the articles are not exactly homologous among tanaidacean taxa. Ignoring problems of homology, Lang used coxa, basis, merus, carpus, propus, and dactylus; and that procedure is followed here. The more common "propodus" is used for the sixth article.

The distal extension of the chelipedal propodus is referred to as the "fixed finger," a term used frequently in the literature. This has been done to avoid confusion with the dactylus, often referred to as the "movable finger."

The terminology used in describing the orientation of appendages follows.

Mouthparts: As if all were directed ventrally, the anterior surface facing forward, the posterior surface facing caudad (equivalent to rostral and caudal as used by Lang (1968:24).

Cheliped: Dorsal, ventral, lateral, and medial, referring to the natural orientation of this limb when extended forward (equivalent to tergal, sternal, caudal, and rostral as used by Lang, 1968:24).

Pereopods II–VII: Medial, lateral, anterior, posterior, dorsal, and ventral (used for various articles, when appropriate) refer to the limbs as directed ventrally and laterally from body in their natural position (Figure 2).

Pleopods: The same as the mouthparts.

Hairs, Setae, and Spines: A "hair" (Figure 1i,j), as used here, is an exceedingly slender and usually very flexible skeletal process. Hairs are found on the sides of the pereonites or on the dorsal surface of the pleonites and pleotelson.

The term "seta" refers to a diverse class of cuticular armaments which usually are long in relation to their diameter. Ordinarily, setae are more or less pointed and almost always have setules along two "sides" distally (Figure 2o). ("Setules" are parallel extensions of various lengths and thicknesses arising from the body of a seta—the distinction between setules and teeth becomes obscure at times. Setules have not been observed by many authors because of their frequently very short length or small diameter.) Most setae occurring in the Neotanaidae are variants of this basic structure and are appendicular in occurrence, being found, with few exceptions, on the antennae, mouthparts, all pereopods, and uropods.

"Naked" setae, or setae without setules, are much less common, usually appearing singly or doubly (but up to 15 in *Carololangia mirabunda*) on the fixed endites of the second maxilla (blunt tips; Figure 8D) or on the first and second antennae or uropods (sharp tips).

Setae are said to be "feathered" if their setules are of appreciable length and lie in a markedly parallel arrangement in one plane (Figure 1Q). Such setae are found only on the pleopods in *Herpotanais*; sometimes also on the pleonal epimeres (actually feathered hairs) in *Neotanais*; on the pereopods and uropods in *Venusticrus*; and on all of these plus the maxillipeds, chelipeds, and pleotelson (modified shape) in *Carololangia*. When located on the pleopods, these setae move the animal in the water; their functions in other locations are more obscure.

"Broom setae" (Figure 1P) are slender and are borne on short bases of a single article. Their set-

ules, borne distally, are very long, exceedingly fine, and usually spread in one plane. These setae are very fragile and often are broken or missing. Occasionally they are referred to as "auditory setae" in the literature (Calman, 1909:19), but evidence in support of such a function apparently is lacking. To avoid this connotation, Lang (1968:24) introduced the term "particular setae" for these structures, also an unfortunate choice because of its ambiguous English meaning. The term "broom setae" (Hessler, 1970:9) refers to the usual appearance of these structures and is neutral in connotation. Among neotanaids, broom setae are found in a very limited number of locations: the antennae, dorsal propodal and medial and lateral basal surfaces of pereopods II–VII, and occasionally on the uropodal endopods—locations similar to those in various other tanaidaceans. Among other functions, these structures may serve to monitor water flow among the pereopods or to apprise the animal of acceleration of the legs or body through the water.

A "spine," as used here, is a stout projection usually bearing heavy setules or teeth and sometimes divided terminally ("cleft" or "forked" spines). Some spines are articulated basally and probably are modified setae (Figure 1K–N). These are found on mouthparts and on pereopods II–VII. Spines not articulated basally apparently are found only on the pars incisiva of the mandibles (Figure 7A,C). All spines appear to function in handling or cutting food, or in locomotion.

"Spinelets" are tiny, sharply pointed, unarticulated processes occurring, for example, ventrally on the propodi of pereopods II–VII (Figure 1H).

"Esthetascs" (=aesthetascs, esthetes, aesthetes) are long, slender structures of two types: "annulated" and "smooth." Annulated esthetascs (Figure 6c) are one to three in number, depending upon taxon and developmental stage; are borne distally on the penultimate two or three articles of the first antennae; and have several narrow and shallow constrictions dividing their length into four or five segments, the segments apparently varying in number and shape among the different taxa. Smooth esthetascs (Figure 6E) are found only in large, ventral clusters on the fourth article of the first antenna in copulatory males; and they are considerably longer, more slender, and without the annuli of the foregoing type. Both types of esthetascs appear to be constricted distally with a fine pore

located at the tip. They probably function in chemosensation and sometimes are referred to as "olfactory filaments" (Calman, 1909:20). The smooth esthetascs probably aid the copulatory males in locating the females.

Setal Formulae: In order to simplify reference to numbers of setae, three setal formulae are used in the present work. Setal numbers which are unique or unusual are italicized. Maxillipedal palp: The number of setae on each article (in order, from the first through the fifth article) is separated by commas; when setae are present on two sides of an article, the number on the medial side is followed by a plus sign and the number of lateral setae. Pereopods II–VII: The number of setae in the anterior and posterior rows of the propodus are followed by the numbers in the same rows on the carpus, all separated by commas. Pleopod: The numbers of medial and lateral setae of the protopod and medial, terminal, and lateral setae of the endopod and the first (terminals lacking) and second exopodal articles occur in this order (for example): (0,0) (0,0,0) (0,0;0,0,0).

Abbreviations and Symbols

Following is an explanation of abbreviations and symbols used in text, tables, and illustrations:

A_1:	first antenna (=antennule)
A_2:	second antenna (=antenna)
AD:	anchor dredge
AlK:	anterolateral keel
AlS:	anterolateral seta
AMNH:	American Museum of Natural History, New York
Ant.:	anterior
AP:	anal plate
approx.:	approximate
B:	basis
B.:	benthic
Bas:	basis
Ber.:	Bermuda
BMNH:	British Museum (Natural History), London
BT:	beam trawl
C:	centigrade
CG:	Campbell grab
CGM:	circular gut muscle
CM:	cellular membrane
CMS:	Continental Margin Survey
Cop ♀:	copulatory female
Cop ♂:	copulatory male
Cox:	coxa
Cp:	cheliped

Crp:	carapace	Mp:	maxilliped
CTL:	connective tissue ligament	Mu:	muscle
Cu:	cuticle	Mx_1:	first maxilla (=maxillule)
CY:	cortical yolk	Mx_2:	second maxilla (=maxilla)
Cyt:	cytoplasm	MY:	medullary yolk
DE:	developing egg	MZM:	Moscow Zoological Museum
DG:	digestive gland	NMNH:	National Museum of Natural History (formerly under United States National Museum), Smithsonian Institution, Washington, D.C.
DLM:	dorsal longitudinal muscle		
DO:	dorsal organ		
EE:	external endite		
ELM:	extrinsic limb muscle	No., no (s).:	number (s)
Epd:	epidermis (=hypodermis)	NSF:	National Science Foundation
Epg:	epignath	Nu:	nucleus
ES:	epibenthic sled	Oc:	ocular lobe
Eso:	esophagus	Od:	oviduct
FE:	fixed endite	Oos, oosteg.:	oostegite (=brood pouch plate)
Fem.:	female	OS:	oostegite scar
fgmt (s).:	fragment (s)	OSU:	Oregon State University
FNMNH:	French National Museum of Natural History, Paris	Ov:	ovary
		OvW:	wall of ovary
FV:	fat vacuole	P ♀ 1:	preparatory female 1
G:	gut	P ♀ 2:	preparatory female 2
g:	gram	P ♂ :	preparatory male
Ga:	ganglion	PC:	Phleger corer
GCe:	germinative cell	PcC:	pericardial cavity
GCn:	male genital cone	PcS:	pericardial septum
GCo:	gut contents	PG:	Petersen grab
GHBT	Gay Head–Bermuda Transect	PI:	pars incisiva
GOM:	gonopore opening muscle	PlS:	posterolateral seta
Gp:	gonopore	PM:	pars molaris
GpAn:	gonopore anlage (n)	Pn:	pereonite
H:	heart	pn:	pleonite
Hc:	hemocoel	Post.:	posterior
HOT:	herring otter trawl	Pp:	pereopod
I:	ischium	pp:	pleopod
IE:	internal endite	Prep.:	preparatory
Int.:	intermediate	pt:	pleotelson
IS:	incisive spine	R:	right
IWSOE:	International Weddell Sea Expedition	RMd:	right mandible
Juv:	juvenile	RMp:	right maxilliped
JNM:	Japanese National Museum	RMx_1:	right first maxilla
L:	length, left	RMx_2:	right second maxilla
Lab:	labium	SBT:	small biology (=Menzies) trawl
Lbr:	labrum	SeG:	supraesophageal ganglion (=brain)
LGM:	longitudinal gut muscle	Spc:	spermatocyte
LM:	lacinia mobilis	SOT:	shrimp otter trawl
LMd:	left mandible	Spt:	spermatid
LMp:	left maxilliped	Spz:	spermatozoan
LTPS:	long, terminal propodal spine	SSCS:	short, subterminal carpal spine
Lu:	lumen	ST:	sledge trawl
m:	meter	Sta (s).:	station (s)
M:	merus	STPS:	short, terminal propodal spine
M1:	manca 1	SV:	seminal vesicle
M2:	manca 2	T:	temperature
Man.:	manca	Te:	testis
ME:	movable endite	TeW:	wall of testis
ml:	milliliter	UCZM:	University of Copenhagen Zoological Museum, Copenhagen
mm:	millimeter		
MOI:	Institution of Oceanology, Moscow	UG, UG?:	unidentified gland

unid.:	unidentified
Up:	uropod
USNM:	designation of specimens in NMNH
VD:	vas deferens
VLM:	ventral longitudinal muscle
VNC:	ventral nerve cord
W:	width
w/:	with
WHOI:	Woods Hole Oceanographic Institution
w/o:	without
YG:	yolk granules
ZIASL:	Zoological Institution of the Academy of Sciences of the U.S.S.R., Leningrad
1°:	primary
2°:	secondary

STATISTICAL SYMBOLS.—Following is a list of the statistical symbols used. For a more detailed discussion of these concepts, see Snedecor (1956).

X: Value of an individual item in a sample or value of a variable plotted on the abscissa

Y: Value of a variable plotted on the ordinate

f: Frequency of occurrence

N: Number of items in a sample

$\bar{x}$: Arithmetic mean (usually stated as an interval estimate at the 95 percent level of confidence)

s: Sample standard deviation from the mean

C: Coefficient of variation; s expressed as a percentage of the arithmetic mean

b: Sample regression coefficient. An estimate of the population regression coefficient; the rate of change of variable Y for each unit of change in variable X.

r: Sample correlation coefficient. An estimate of the population correlation coefficient. An estimate of the degree of association between two variables or the tendency of high or low values of one variable to be associated with high or low values of the other variable respectively.

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Systematics

From the time of its erection (by Beddard, 1886a,b), the genus *Neotanais* was included in the family Tanaidae until Lang placed it in his new family, Paratanaidae (Lang, 1949:10), and later in its own family, the Neotanaidae (Lang, 1956b:474).

At the time of its erection (Lang, 1956b), the Neotanaidae included only six described species in the single genus *Neotanais*. Since then, the only systematic considerations of the family as a whole have been brief statements by Wolff (1956a:207) and Lang (1968:133). Each of these authors had at his disposal a number of additional species of *Neotanais*, each represented by relatively few specimens. Wolff also described the new monotypic genus *Herpotanais*, which is very similar to *Neo-*

tanais. Later Kudinova–Pasternak (1966) described *N. wolffi* from three specimens, and Kussakin (1967) described *N. antarcticus*, also on the basis of three specimens.

With the publication of the present work, 25 species of *Neotanais* are recognized, and these are represented by hundreds of specimens. For many species, the copulatory males also are known. The aberrant new monotypic genera, *Venusticrus* and *Carololangia*, each known from two specimens, permit a much greater understanding of morphological diversity within the Neotanaidae.

Much of the taxonomic literature dealing with the Neotanaidae is inaccurate and of limited value. This is because the limited quantity and poor quality of the material available to investigators have prevented them from understanding patterns of variation and from appreciating the comparatively slight morphological differences between similar species in this conservative family. Developmental complexities (discussed under "Development"), together with problems of sexual dimorphism, have further discouraged interest in the Tanaidacea generally.

Taxonomic Procedure

Even the better works dealing with the neotanaids all too often have suffered from an inadequate conception of intrafamilial variation, and species descriptions often include primarily irrelevant generic characters. I know of no instance in the literature where the morphological conservatism of the Neotanaidae has been discussed, although Lang (1953b) describes the difficulty encountered when attempting to distinguish generic boundaries among certain paratanaid groups. Descriptions often have been too brief—conservative taxa require substantially more description than other groups because of the relatively greater difficulty in distinguishing among species.

Descriptions must be accompanied by illustrations of good quality. Many illustrations in the literature fall short of an acceptable standard because of lack of detail, inadequate size, or for having been printed on paper of inferior quality. Lang's elegant figures (e.g., Lang, 1968) are notable exceptions worthy of emulation.

In 1956 Wolff (1956c) briefly described six species of *Neotanais*, intending "later to publish a full

description . . . together with a study of their varia-
tion, affinities, etc." Subsequently unable to do this
himself, Wolff kindly consented to the redescription
of these species here.

Eight of the 15 previously described species of
neotanaids recognized here are completely rede-
scribed in this work, and additional comments are
offered on other species where appropriate.

A discussion and list of taxonomic characters
useful for the Neotanaidae are presented below.

Taxonomically Useful Characters

Some of the taxonomic characters most useful
when dealing with the tanaidaceans have long been
recognized. Norman and Stebbing (1886:79) state
that various aspects of pereopodal structure "afford
very reliable specific characters." Hansen (1913:10)
recognized the usefulness of the relative shapes of
the proximal articles of the first antennae.

Much has been made of the usefulness of mouth-
parts as taxonomic characters. Hansen (1913) men-
tions the mandibles, especially the pars molaris,
and Lang (1956b) states that the mouthparts are
of "very great systematic significance"; however, I
do not think that the mouthparts are especially
useful for distinguishing among species of neota-
naids. The labrum, labium, first maxilla, and maxil-
lipeds, including the epignath, are practically
identical throughout *Neotanais*. The second max-
illa is similarly identical with the exception of the
number of setae in the medial row, the number of
spines next to this row, and the shapes of the stout,
cleft spines on the fixed endite. Of these characters,
all but the number of medial setae are of uncertain
usefulness because of intraspecific variation. On
occasion, the medial row varies considerably in
number among species and can be used taxonom-
ically.

The mandibles also are uniform throughout the
family. Although the number of molar teeth varies
from species to species, it also varies with age and
between the members of a pair. The pars incisiva
and (occasionally) the lacinia mobilis bear the only
truly useful characters in the incisive spines. But
it is my impression that although these characters
may vary interspecifically, further knowledge of the
family will demonstrate that members of species
groups have very similar mandibular structure,
therefore reducing the usefulness of mandibular

variation as a diagnostic character. Nevertheless, as
new species are discovered, the incisive mandibular
spines, lacinia mobilis, and second maxilla should
be described with care. Their significance may be
revealed as additional species become known.

The mouthparts of copulatory males are greatly
reduced, extremely variable, and of no taxonomic
value below the familial level. However, at that
level their degree of reduction or absence is very
significant, as Lang (1949:6) has demonstrated.

The fusion of the pleotelson with the fifth pleo-
nite, a situation found in three species, is consistent
in all stages of development and is useful taxonom-
ically.

Certain characters vary with age and sex and
therefore must be used with great care. Notable
examples are the numbers of setae found in rows
on the first antenna, pereopods, pleopods, and uro-
pods and the number of articles in the uropodal
endopod. Therefore, it is essential to identify the
developmental stage with which one is dealing and
to use caution when identifying specimens from
published descriptions (see sections on "Intraspe-
cific Variation" and "Development"). To recognize
developmental instars, see page 220.

The copulatory males seem to display greater
interspecific variation than do the other stages. The
males manifest considerable differences even in
those species in which other stages are very similar,
such as the "sibling" species *Neotanais americanus*
and *N. sandersi*. Although the variation apparently
is not as radical as in *Leptochelia*, the males may
be helpful in distinguishing among very difficult
species. In *Leptochelia*, the males not only are
greatly different from each other but the other
stages frequently are very similar, and in some
cases the males provide the only sure means of
differentiating among species.

Listed below are characters useful for distinguish-
ing among species of *Neotanais*. Especially impor-
tant characters are further specified by an asterisk,
and characters frequently shared between copu-
latory males and other instars of their species are
identified by a dagger symbol.

STAGES OTHER THAN COPULATORY MALE.—*Body*:
Length, with caution (considerable developmental
variation and some geographic variation; e.g., dif-
ference between *Neotanais americanus* and *N. ha-
dalis* or *N. hastiger* and *N. tricarinatus*). Length-
width ratio.

Carapace (Figures 3B–D, 4A–C): *†Number and shape of anterolateral and posterolateral setae; *degree to which rostrum is pointed; relative prominence of anterolateral keels and oblique furrows; *degree to which respiratory chambers are expanded and *prominence and shape of chelipedal coxae in dorsal view.

Pereonites (=*Pereomeres, Thoracomers 3–8*) (Figures 2B, 3B–D): *Shape in dorsal view, interspecific differences usually best demonstrated by pereonites 4–6; presence or absence of surface relief.

Pleonites (=*Pleomeres*) (Figures 3, 5): *†Shape of midventral silhouette; *degree of lateral expansion, flaring (turning upwards) and angularity of epimeres in dorsal view; *presence, number, size, and shape of dorsolateral epimeral setae; width relative to pereonite 7.

Pleotelson (Figures 3, 5): *†Dimensions (width-length ratio), *shape of margin, point of uropodal attachment (anteroposteriorly and dorsoventrally), *fusion with pleonite 5.

First Antenna (=*Antennule*) (Figure 5J): *Length-width ratio of first article; relative length of articles 4 and 5–7; number of long distolateral setae on article 1.

Second Antenna (=*Antenna of Some Authors*) (Figure 6D): Not usually taxonomically useful, although relative lengths of articles vary and, in *Neotanais armiger,* this appendage is very slender.

Left Mandible (Figure 4A–C): Dentition of lacinia mobilis occasionally useful, as are spines (see right mandible).

Right Mandible (Figure 4B,D, 7A): *Pattern of serration on incisive spines may be characteristic of infrageneric species groups (q.v.).

Second Maxilla (=*Maxilla of Some Authors*) (Figures 4A,C, 8D): Shape of cleft spines on fixed endite sometimes helpful; number of setae in medial row sometimes useful in certain species.

Maxilliped (Figures 4A,B, 9A): †Number of palpal setae sometimes useful taxonomically and represented by setal formula.

Cheliped (=*Pereopod I, Thoracopod II*) (Figures 9J,K): *Overall shape of chela, length of dactylus relative to fixed finger, *shapes of teeth on both fingers, lengths of medial setae on chela, and number and *length of dorsal carpal setae.

Pereopods II–VII (Figure 12): Divided into two groups, pereopods II–IV and V–VII; the legs in each group resemble each other closely except for certain specializations on II and VII.

Pereopods II–IV: *†Number and *shape of anterior and posterior setae of propodi and carpi only, number represented here by a setal formula; *shape and dentition of short, terminal propodal spine and *short, subterminal carpal spine (latter on pereopod II only); *number and dentition of long, terminal propodal spines (with caution); *†shape and *†relative length of dactylar spine (dactylar setules or serrations, if present, may be useful).

Pereopods V–VII: Terminal dactylar teeth used by some authors but of uncertain value (see intraspecific variation under *Neotanais hastiger*); *number of short, subterminal propodal spines on pereopod VII (with caution).

Pleopods (Figure 64R): *Numbers of setae borne on different articles as reflected by setal formula; *†lengths of setae on protopod; †presence of other than 3 medial endopodal setae; *†whether a distinct terminal endopodal setal row is present or row merges with lateral setae (reflects shape of article).

Uropods: *†Proportions (e.g., relatively slender or stout) and *†number of endopodal articles (with caution, but predictable increase with age); *†relative length of endopod (compared to pleonal length); *†relative length of exopod (compared to first endopodal article); presence or absence of unusual setation (e.g., *Neotanais hadalis*).

COPULATORY MALES.—The copulatory males of different species differ from each other in those nondimorphic characters useful for separating other stages of the same species. These nondimorphic characters are discussed above; only those taxonomically useful characters unique to the male are presented below.

Carapace (Figures 3A, 4D–F): As in other stages.
Pereonites (Figures 2A, 3A): As in other stages.
Pleonites (Figure 3A,B): As in other stages.
Pleotelson (Figures 5H,I, 6A,B): As in other stages.
Cheliped (Figures 2A, 10A–E): *Shape of carpus; *number, length, and location of dorsal and ventral carpal setae; *shape of propodus; *shape, *amount of twisting, and *dentition of fingers.

Pereopods II–VII (Figures 2A, 13): *†Number and *shape of propodal and carpal setae and *shapes of specialized spines as indicated for other stages (†sometimes, cf. Figure 55A,D).

Pleopods (Figure 10M): As in other stages.
Uropods: As in other stages.

INFRAGENERIC SPECIES GROUPS

Neotanais is the largest genus in the family, with 25 species recognized in this work; the other genera are monotypic. With that many species having been described, one can begin to recognize patterns of similarities and differences among species. In fact, it is possible to link the majority of species with others on the basis of one or another set of shared characters. Systematic relationships within the genus will be further clarified as additional species and unknown developmental stages of already described species are collected.

Groups of similar species presumably represent monophyletic stocks which arose sometime after generic separation. The characters used in linking these species are not equally well developed within a group. Indeed, an important character may be missing in one or more species. In such cases, other characters form the basis of group unity. The *micromopher* and *hastiger* groups are much more distinctive than, for example, the *robustus* group. Some groups overlap in unusual characters. At times the copulatory males provide more easily utilizable characters indicating genetic similarity; for instance, the dentition of the chelae in *Neotanais robustus* and *N. antarcticus*.

Certain characters are relatively stable within species groups and therefore provide potential clues to relationships; these are pleotelsonal length, shape and dentition of the chelae, and the relative degree of lateral expansion and flaring of the pleonites. In stages other than those of the copulatory male, the dimension of the first article of the first antenna or the general shape of the entire appendage is sometimes useful in determining relationships. The shapes of the three incisive spines of the right mandible are relatively stable within a group.

Nondimorphic characters shared with other stages also are useful in the case of the copulatory males, as are the shape and ventral setation of the chelipedal carpus.

What is the place of these species groups in the systematic hierarchy? Apparently they are composed of clearly reproductively isolated species. The concept of superspecies, or "Artenkreis," usually implies appreciable allopatry among the constituent species (Mayr, 1969). Several members of the groups recognized here (*Neotanais americanus* and *N. sandersi*, *N. americanus* and *N. hadalis*, and *N. pfaffi*

and *N. armiger*) probably are sympatric, having been collected at the same stations; therefore, the superspecies concept seems inappropriate.

The groups may, in fact, represent subgenera, but because not all species can be satisfactorily assigned to a group and because we may still have a relatively poor understanding of diversity in *Neotanais* and the boundaries of these groups, it seems wise to avoid the use of subgenera. The "species group" is without taxonomic rank and simply indicates propinquity of relationship in a tentative sense (Mayr, 1969). If the same degree of distinction found within the *micromopher* and *hastiger* groups existed elsewhere in the genus, subgenera would be appropriate.

A description of each group precedes the descriptions of its species. The following groups are recognized, and they appear in the following order: the *micromopher* group, two species; the *americanus* group, five species; the *robustus* group, two species; the *affinis* group, three species; the *pfaffi* group, four species; and the *hastiger* group, two species. Six species are not included in any group: *Neotanais bulbodens*, *N. bacescui*, *N. barfoedi*, *N. wolffi*, *N. calcarulus*, *N. insolitus*, and *N. hessleri*.

USE OF THE SUBSPECIES CATEGORY FOR THE DEEP-SEA FAUNA

Wolff (1956a:210) united a population of *Neotanais* from the Kermedec Trench (South Pacific) with *N. serratispinosus*, which at that time was known only from the North Atlantic. He distinguished the two populations by the erection of two subspecies, *N. s. serratispinosus* for the North Atlantic animals and *N. s. hadalis* for the Keremedec Trench population.

The subspecies category currently is used for those populations of a species that are taxonomically distinct from each other (Mayr, 1942, 1963; Mayr, Linsley, and Usinger, 1953). That is, specimens belonging to a subspecies can be recognized as such by taxonomists by diagnostic characters distinguishing them from the members of other subspecies, without knowledge of their geographic origin. Subspecies do not co-occur in breeding condition, and usually they are geographically distinct.

Often the presence of subspecies can be determined with certainty only when appreciable numbers of specimens are available from various

geographic areas. Patterns of distributional changes in morphology or other characters of taxonomic value cannot be recognized when only a few localities have been sampled. For this reason, subspecies are little used in paleontology (Simpson, 1961).

Methods of sampling the deep-sea fauna have yielded singularly limited results for practically the entire period during which it has been under investigation. For many different animal groups it has been virtually impossible to form a realistic impression of intraspecific variation at a single station. Geographic and vertical ranges of distribution are unknown for most species. It is for these reasons that the Atlantic samples of "*Neotanais serratispinosus*" available at the time of Wolff's work actually include four species.

The situation is particularly difficult within the Neotanaidae because of the morphological conservatism of this family. Sibling species demonstrate relatively minor differences from each other (*Neo-*

tanais americanus and *N. sandersi*). One would anticipate difficulty in demonstrating distinct subspecies under the best of conditions by other than the biometric techniques possible only with sizable samples. Under these conditions, widely distributed specimens showing consistent observable differences more likely would be regarded as distinct species rather than subspecific variants.

In view of these considerations, the erection of subspecific taxa for the deep-sea fauna is, for the time being, a practice of questionable merit which probably complicates the taxonomic literature unnecessarily and unprofitably.

Family NEOTANAIDAE Lang, 1956

TANAIDAE.—Beddard, 1886a:116 [in part, *Neotanais* only].
PARATANAIDAE Lang, 1949:10 [in part, *Neotanais* only].
NEOTANAIDAE Lang, 1956b:474.

DIAGNOSES.—*Stages Other Than Copulatory Male*: Antenna 1 composed of 6 or more articles; antenna

Key to the Genera of Neotanaidae

1. Pereopods V–VII with setae slender and relatively finely setulated or thicker and spinelike but never feathered (Figures 12, 13) and bases about 4.0 to 4.5 times longer than wide; uropods bearing setae of modest length with setules or hairs of ordinary length and lacking feathered setae (Figure 6A,B); uropods articulating at sides of pleotelson (except *Neotanais isolitus*) 2
   Pereopods V–VII bearing numerous long, slender, and flexible setae, either feathered (Figure 77A) or with scattered short setules (Figure 72A) and bases only about 2.5 to 3.0 times longer than wide; uropods either with exceedingly long setae, up to one-third as long as uropods, and bearing very long hairs (Figure 72D) or with numerous long, feathered setae including a row of such setae on exopod (Figure 74C); uropods articulating below pleotelson 3

2. Pleopods with 1 ramus; antenna 1 composed of 6 to 8 articles, depending on stage (mancas, 6; juveniles, all females, and preparatory males, 7; copulatory males, 8) ....
   ....*Herpotanais* Wolff
   Pleopods with 2 rami; antenna 1 composed of 6 or 7 articles depending on stage (mancas, 6; all other stages, 7) ....*Neotanais* Beddard

3. Pleotelson about as long as wide, pointed posteriorly with convex sides, acorn-shaped in dorsal view, and with only occasional fine hairs; pereon with only occasional fine hairs; chela with large, thin, brown-bordered dorsal crest; uropodal exopod very small, about one-half to two-thirds the length of first endopodal article, and bearing 1 or 2 smooth, slender terminal setae; meri and carpi of pereopods V–VII with more or less vertical rows of naked or slightly setulated spines on their anterior surfaces; propodi and carpi with rows of long, slender feathered setae ventrally ....*Venusticrus*, new genus
   Pleotelson about one-half as long as wide; posterior edge expanded into a pair of dorsally directed crests, each bearing about 20 thick, feathered setae; pereonites with dorsal and lateral rows of numerous feathered setae; dorsal side of chela (propodus) thick and rounded; uropodal exopod about as long as first 2 endopodal articles and article 2 with a row of long, usually heavily feathered setae; meri of pereopods V–VII bearing only feathered setae, carpi with only feathered setae or heavily setulated spines in the usual anterior and posterior rows; propodi and carpi without long, slender, feathered setae ....
   ....*Carololangia*, new genus

2 composed of more than 6 articles; pleon with 6 segments (pleotelson fused to pleonite 5 in some species); 5 pairs of pleopods present; labium bearing a slender terminal lobe on each side; epignath (=maxillipedal epipod) strongly bent, apparently divided into 2 parts centrally and bearing a tuft of slender hairs on each tapered end; female marsupium composed of 4 pairs of oostegites.

Copulatory Males: Similar to other stages except for mouthparts: maxilla 1 missing; mandibles, labium, maxilla 2, and maxilliped all reduced in various degree; epignath similar to that in other stages.

GENERA.—*Herpotanais* Wolff, 1956a; *Carololangia*, new genus; *Neotanais* Beddard, 1886a, 1886b; and *Venusticrus*, new genus.

REMARKS ON KEY TO THE GENERA.—The purpose of the following key is to simplify the unequivocal separation of the four presently known genera of neotanaids. Because there are probably other, still unknown, genera, the key should be used with caution. The characters used in the key are those which most clearly differ among the taxa. Other diagnostic differences are listed in the respective generic diagnoses. *Herpotanais*, *Carololangia*, and *Venusticrus* are monotypic, and copulatory males are not known for the latter two genera; additional knowledge of introgeneric variability acquired in the future may alter the inferences drawn in the key. Some characters cited in the generic diagnoses actually may be unique at the specific level only.

Genus *Neotanais* Beddard, 1886

Neotanais Beddard, 1886a (February):117; 1886b:124.—Stebbing, 1893:324.—Lang, 1956b:469; 1968:133.—Wolff, 1956a:208.
Alaotanais Norman and Stebbing, 1886 (October):111.

TYPE-SPECIES.—*Neotanais americanus* Beddard, 1886a:118; 1886b:124 [by monotypy].

DIAGNOSIS.—*Stages Other Than Copulatory Male*: Pereonites without setae (occasional fine hairs may be present) in contrast to *Carololangia* and *Venusticrus*; width usually equal to or greater than length (except *Neotanais insolitus*). Pleon of moderate length, making up about 22 percent to 27 percent of total body length. Chela with moderate dorsal crest. Feathered setae occurring only on pleopods (feathered hairs occasionally found on pleonal epi-

meres) in contrast to *Carololangia* and *Venusticrus*. Pleotelson bearing uropods laterally on posteriorly directed processes which form widest point of pleotelson. Bases of pereopods V–VII 4 or 5 or more times longer than wide. Uropods with up to 14 articles in endopod.

Copulatory Males: Chelipeds extremely well developed compared to other stages and to copulatory males of *Herpotanais*: carpus much elongated and often strongly curved; chela massive, often bizarre. Male gonopores usually borne on prominent cones.

REMARKS.—Prior to this work, 17 species of the genus *Neotanais* had been recognized, and *N. serratispinosus* was considered by Wolff (1956a:210) to be represented by two subspecies, *N. s. serratispinosus* and *N. s. hadalis*. Four of these species— *N. deflexirostris* Lang, 1968:135; *N. edwardsi* Dollfus, 1898:77; *N. longimanus* Wolff, 1956c:49; and *N. serratispinosus* (Norman and Stebbing, 1886; 111)—are here considered to be junior synonyms of other names. *Neotanais laevispinosus* is recognized as a species in its own right, and *N. hadalis* is elevated from subspecific to specific rank. Ten new species are described here, bringing the current total number of species of *Neotanais* to 25, an increase of 66.7 percent over the previously described species which are recognized here. The copulatory males of three previously known species (*N. americanus*, *N. hastiger*, and *N. peculiaris*) are described here for the first time, and representatives of stages other than the copulatory males are described for *N. laevispinosus*. The copulatory males of eight species remain unknown. *Neotanais giganteus* and *N. mesostenoceps* are known only from copulatory males.

The pereopods in *Neotanais* appear to be adapted primarily for locomotion by walking. (They may, of course, serve other functions such as egg and brood care in the copulatory female.)

LIST OF SPECIES.—The following species of *Neotanais* are recognized and described in this work. Indication of known stages follows each reference: ♀ represents any or all instars other than copulatory males and ♂ represents one or more copulatory male instars. Stages described for the first time in this work are in parentheses.

N. affinis Wolff, 1956c:51; ♀
N. americanus Beddard, 1886a:118; ♀, (♂)
N. antarcticus Kussakin, 1967:320; ♀, ♂
N. armiger Wolff, 1956c:47; ♀, ♂
N. bacescui Lang, 1968:141; ♀

N. barfoedi Wolff, 1956c:44; ♀, ♂
N. bulbodens, new species; (♀), (♂)
N. calcarulus, new species; (♀)
N. dinotomer, new species; (♀), (♂)
N. giganteus Hansen, 1913:20; ♀, ♂
N. hadalis Wolff, 1956a:210; ♀, ♂
N. hastiger (Norman and Stebbing, 1886:133); ♀, (♂)
N. hessleri, new species; (♀) (manca 1 only)
N. insolitus, new species; (♀)
N. laevispinosus (Norman and Stebbing, 1886:114); (♀), ♂
N. mesostenoceps, new species; (♂)
N. micromopher, new species; (♀), (♂)
N. peculiaris Lang, 1968:147; ♀, (♂)
N. pfaffi Wolff, 1956c:45; ♀, ♂
N. pfaffioides Lang, 1968:152; ♀
N. robustus Wolff, 1956c:41; ♀, ♂
N. sandersi, new species; (♀), (♂)
N. tricarinatus, new species; (♀), (♂)
N. tuberculatus Kudinova-Pasternak, 1970:345; ♀, ♂ (see remarks under *N. bulbodens*, new species)
N. vemae, new species; (♀)
N. wolffi Kudinova-Pasternak, 1966:522; ♀
"*Neotanais* sp.," a specimen described by Kudinova-Pasternak (1966:521) on the basis of a fragment of a copulatory male.

The *micromopher* Group of Species

This group comprises two new species, *Neotanais micromopher* and *N. dinotomer*.

STAGES OTHER THAN COPULATORY MALE.—Pereonites 4–6 rectangular in dorsal view, appearing distinctly wider than long, or with corners markedly rounded; pleotelson vary short and fused to pleonite 5.

Following are the chief distinguishing features between *Neotanais micromopher* and *N. dinotomer* in stages other than copulatory male.

Neotanais micromopher: Large distal teeth on fixed finger of chela with extremely irregular and relatively flattened tops; dactylar spines of pereopods II–IV subterminally inserted; pleonites smooth midventrally, without spurs; anterolateral seta on carapace single; pleonal epimeral hairs of short or moderate length and unfeathered; pereonites naked.

Neotanais dinotomer: Large distal teeth on fixed finger of chela with generally smooth and rounded tops; dactylar spines of pereopods II–IV inserted terminally; pleonites extended into short spurs midventrally; anterolateral setae on carapace 3 to 5 in number; pleonal epimeral hairs long and feathered; pereonites bearing scattered hairs of appreciable length.

COPULATORY MALES.—These are known for both

Neotanais micromopher and *N. dinotomer*, but only one type of male is known for the latter species.

Possibly useful as group characters separating these males from the males of other species are their slender and not sharply bent chelipedal carpi and their long, slender, ventral chelipedal carpal setae. In addition, they differ in those nondimorphic characters by which the other instars differ from the same developmental stages of other species groups.

These males differ from each other in the nondimorphic characters listed for other stages above. *Neotanais micromopher* also is unique in having prominent anterolateral spurs ("shoulders") on pereonite 2, and *N. dinotomer* bears a distomedial spur on its chelipedal carpi.

Neotanais micromopher, new species

FIGURES 2–13, *96*

Neotanais americanus Beddard, 1886a:118 [in part, specimen from North Atlantic only]; 1886b:124 [in part, specimen from North Atlantic only].

DIAGNOSES.—*Stages Other Than Copulatory Males*: *Pereonites all noticeably wider than long and rectangular in shape from above. *Pleonites rounded or almost flat midventrally in lateral view. *Pleotelson fused to pleonite 5; *short, about twice as wide as long; *posterior margin slightly concave on either side. Carapace smooth dorsally, almost lacking in surface relief; a single anterolateral and a single posterolateral seta present. Cuticular surface largely covered by minute hairs, animals appearing pubescent under proper illumination. *Chela bearing very blunt or even flat-topped, irregular teeth distally on fixed finger; dactylus strongly curved compared to many species; dorsal propodal keel very low and short. Pereopods II–IV with a single, long, terminal propodal spine bearing relatively large and irregularly spaced teeth; pereopod VII totally lacking short, subterminal propodal spines. Dactylar spines of pereopods II–IV less than one-fourth length of dactylus and inserted subterminally.

Copulatory Males: *Pereonite 2 bearing very prominent lateral spurs anteriorly unlike any other known species of *Neotanais*; pereonites 3–7 wider than long and gradually rounded anterolaterally. Pleonites wider than pereonite 7; epimeres expanded and angular laterally, sternites rounded midventrally or slightly flattened anteriorly in lateral view.
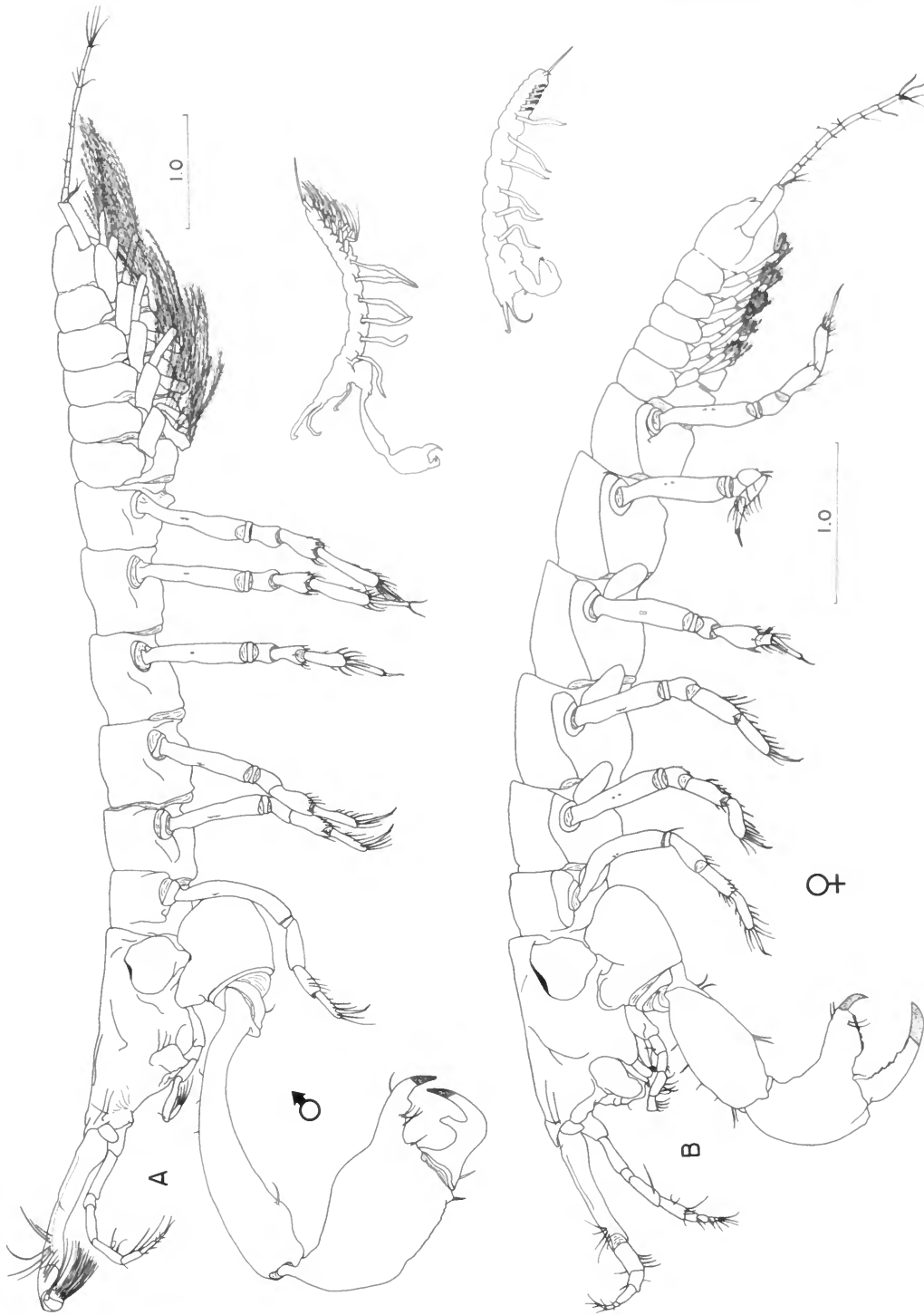
FIGURE 2.—*Neotanais micromopher*, new species: A, lateral view of the secondary copulatory male allotype; B, a preparatory female 2. The inserts illustrate typical postures of these animals when preserved. This species has been found primarily on the Continental Slope off eastern North America at depths of about 2270 to 3830 m.

Pleotelson: As in other stages but not posteriorly concave. *Chelipedal carpus: Slender, strongly curved, and bearing at least 3 or 4 very short dorsal setae and 1 or 2 slender ventral setae far forward on article. Both types of chelae (A and B) with fine dorsal crenations or scales and a slight depression on propodal keel. *Chela of primary male (chela type A) dentition as in Figure 10A,B,D; *chela of secondary male (chela type B) dentition as in Figure 10C,E.

DESCRIPTION OF INTERMEDIATE (?) FEMALE HOLOTYPE (WHOI B. Sta. 64).—*Body* (Figures 2B, 3B): 7.6 mm long and 5.8 times longer than wide. Covered with very short, fine hairs (Figure 12A) of varying density giving animal a pubescent appearance under magnification.

Carapace (Figure 4A–C): 1.2 times longer than wide. Without significant dorsal surface sculpturing; anterolateral keels very slightly raised, oblique furrows shallow; respiratory chambers and chelipedal coxae not well developed laterally in dorsal view. Only 1 anterolateral and 1 posterolateral seta present. Rostrum very low, hardly developed at all, sides sloping toward ocular lobes only very slightly convex.

Pereonites: Appear considerably wider than long and generally rectangular in dorsal view. Pereonite 5, 1.4 times wider than long. Pereonite 2 not tapering evenly anteromedially but slightly angular anteriorly with very low anterolateral "shoulders" (Figure 5C).

Pleonites (Figures 3B, 4A,H, 5A, 6A): Pleonite 1 slightly narrower than pereonite 7 (see copulatory male) but slightly wider than pleonite 5, giving pleon a slightly tapered appearance. Epimeres almost evenly rounded laterally in dorsal view. Sternites slightly flattened but almost evenly rounded midventrally in lateral view.

Pleotelson (Figures 3A, 5A,H, 6A): Short, considerably wider than long, width-length ratio, 2.0; posterior edges noticeably concave on either side in dorsal view; *fused to pleonite 5, with fusion most distinct ventrally.

First Antenna (Figure 5J; see also Figure 6C): Article 1, 3.8 times longer than wide.

Second Antenna: As in Figure 6D.

Labrum: As in Figure 6G.

Right Mandible (Figure 7A): Incisive spines 1 and 2 both serrate along each side, the second spine

along the outer one-third only; third spine serrate at tip.

Left Mandible (Figure 7B): Incisive spines as on right side. Lacinia mobilis with 3 sharply acute teeth; posterior lobe partially cleft.

Labium: As in Figure 7E.

First Maxilla: As in Figure 7G.

Second Maxilla (Figure 8D): Medial setal row with 11 slender, heavily setulated setae with stout bases. The single spine next to this row with or without terminal setules.

Maxilliped (Figure 9A,B): Setal formula of palp, (0,0,5+1,7,14).

Epignath: As in Figure 9H.

Cheliped (Figure 9J,K): Carpus bearing about 9 dorsal setae of moderate length. Propodus with low dorsal keel; fixed finger bearing about 15 small, rounded, brown denticles proximally and about 5 large, brown, very irregular, and relatively flat-topped teeth distally. Dactylus with about 7 low, variable, brown teeth with sharp points along cutting edge, the most proximal tooth being much shorter and more perpendicular to the dactylus than the others; dactylus strongly curved.

Pereopods II–IV (Figure 12A–C,G): Short, terminal propodal spine only slightly curved and bearing 4 to 7 stout teeth. Short, straight, stout, subterminal carpal spine bearing numerous fine teeth. Long, terminal propodal spine single, with relatively large, irregular teeth, and present on pereopod II only. Setal formula (5,4,5,4), (6,7,3,6), and (7,7,3,6), respectively. Dactylar spine very short, only about 0.2 times the length of dactylus, inserted subterminally on dactylus, and tip tapering relatively abruptly.

Pereopods V–VII (Figure 12D–F): Short, subterminal propodal spines of pereopod VII absent. Setal formulae (6,6,5,6), (6,6,5,6), and (5,6,3,4), respectively. Dactyli of all bearing large terminal teeth.

Pleopods (Figure 10L): Terminal endopodal setal row distinct from lateral setae. Setal formula (0,0) (3,8,3) (0,1;0,10,1).

Uropods (Figure 6A): With 9 endopodal articles on each side.

DESCRIPTION OF SECONDARY COPULATORY MALE ALLOTYPE (male AP from WHOI B. Sta. 64).—*Body* (Figures 2A, 3A): 8.1 mm long and 5.9 times longer than wide.

Carapace: 1.4 times longer than wide. Narrower anteriorly than in other stages, giving appearance
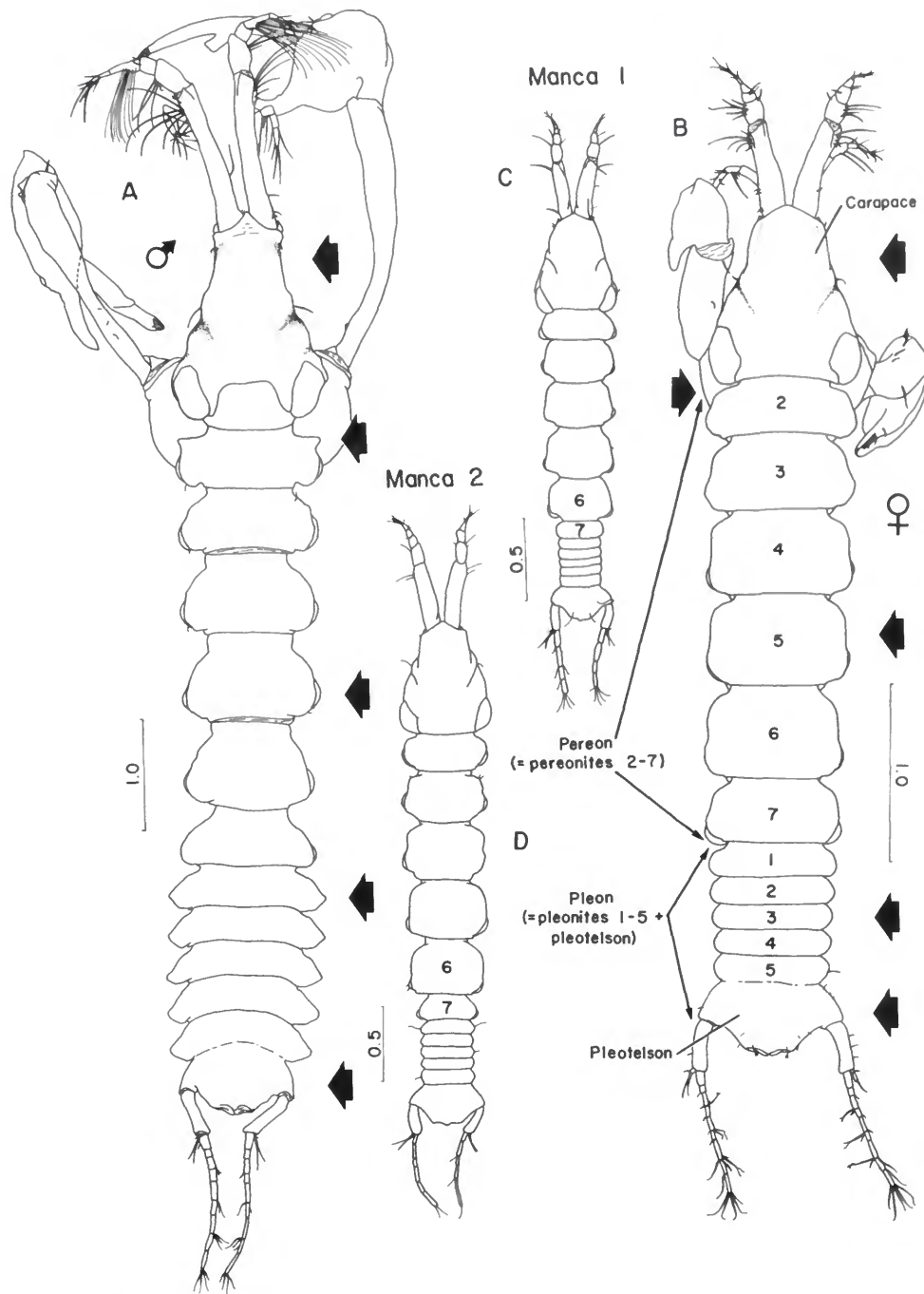
FIGURE 3.—*Neotanais micromopher*, new species (all specimens from WHOI Benthic Station 64): A, dorsal view, copulatory male allotype; B, preparatory female 2 L; C, manca 1 CL; D, manca 2 CD. This figure illustrates terminology used for major body divisions and basic differences in body morphology at various stages of development.

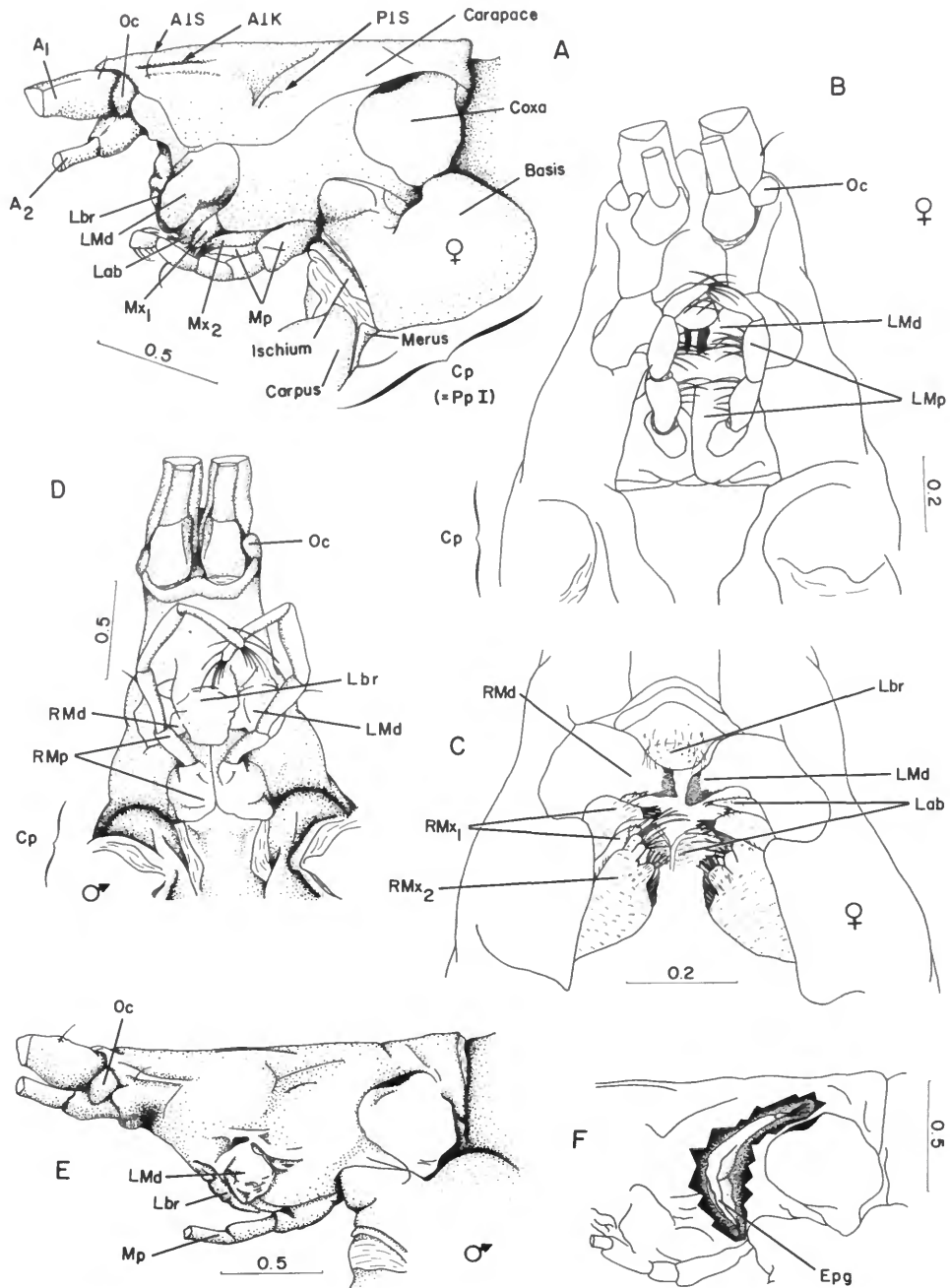FIGURE 4.—The neotanaid cephalosome (all figures are of *Neotanais micromopher*, new species): A, lateral view, stages other than copulatory male; B, C, ventral view of same, with and without maxillipeds, respectively; D, same view of copulatory male (note reduction of mouthparts and their fusion with carapace); E, lateral view of same; F, same, with parts of carapace removed to reveal epignath.
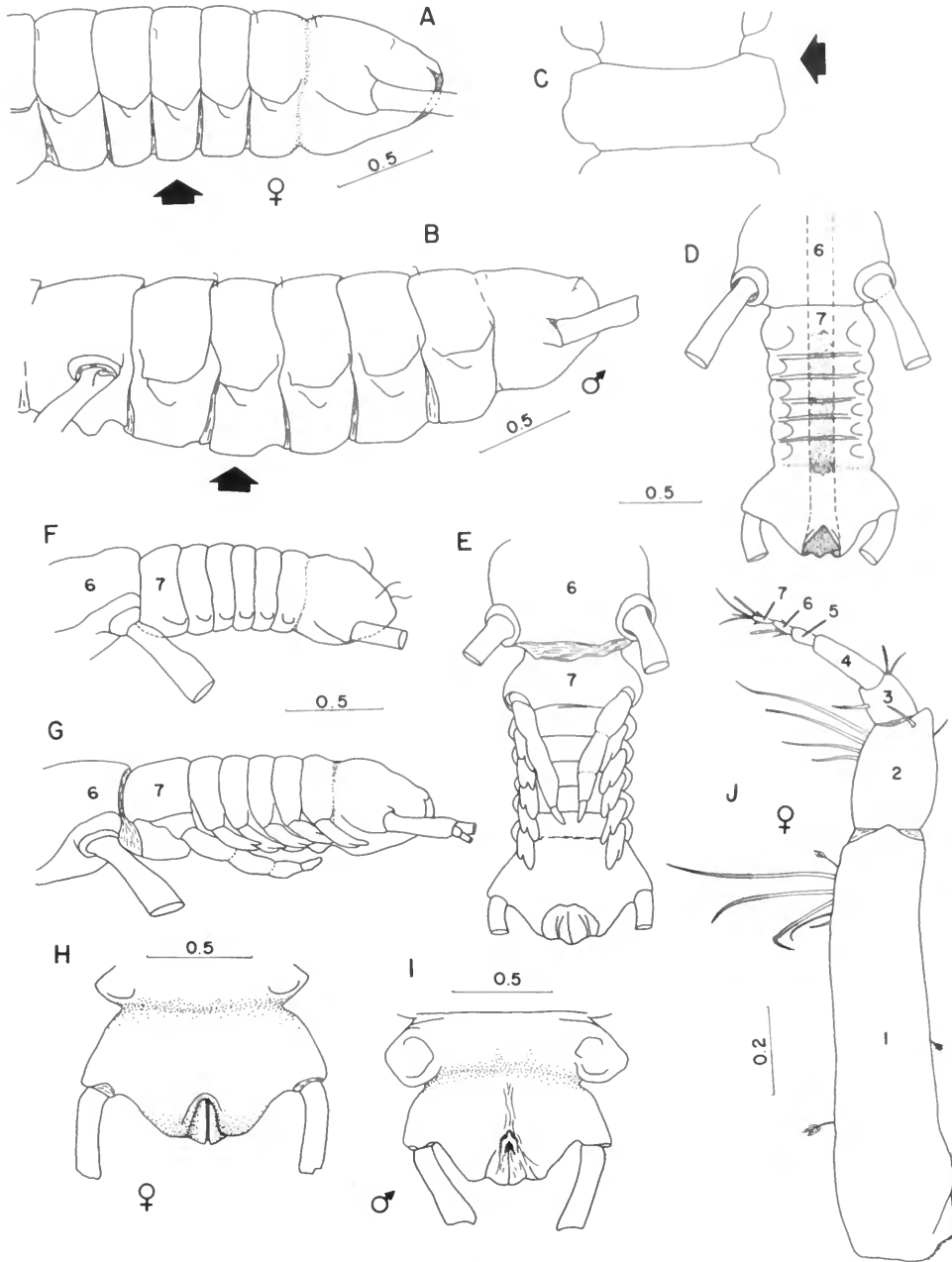
FIGURE 5.—*Neotanais micromopher*, new species (all animals from WHOI Benthic Station 64): A, pleon, lateral view, intermediate (?) female, holotype; B, same, copulatory male, allotype; C, pereonite 2, dorsal view, showing fullest development of anterolateral "shoulders," copulatory female AB; D, pleon, ventral view, manca 1 CL (6 and 7 refer to pereonites 6 and 7); E, same, manca 2 CD; F, pleon, lateral view, manca 1 CL; G, same, manca 2 CD; H, pleonite 5 and pleotelson, ventral view, holotype (anal membranes functional); I, same, allotype (anal membranes calcified, fused); J, left first antenna, dorsal view, holotype (also see Figure 6c for enlargement of distal end).
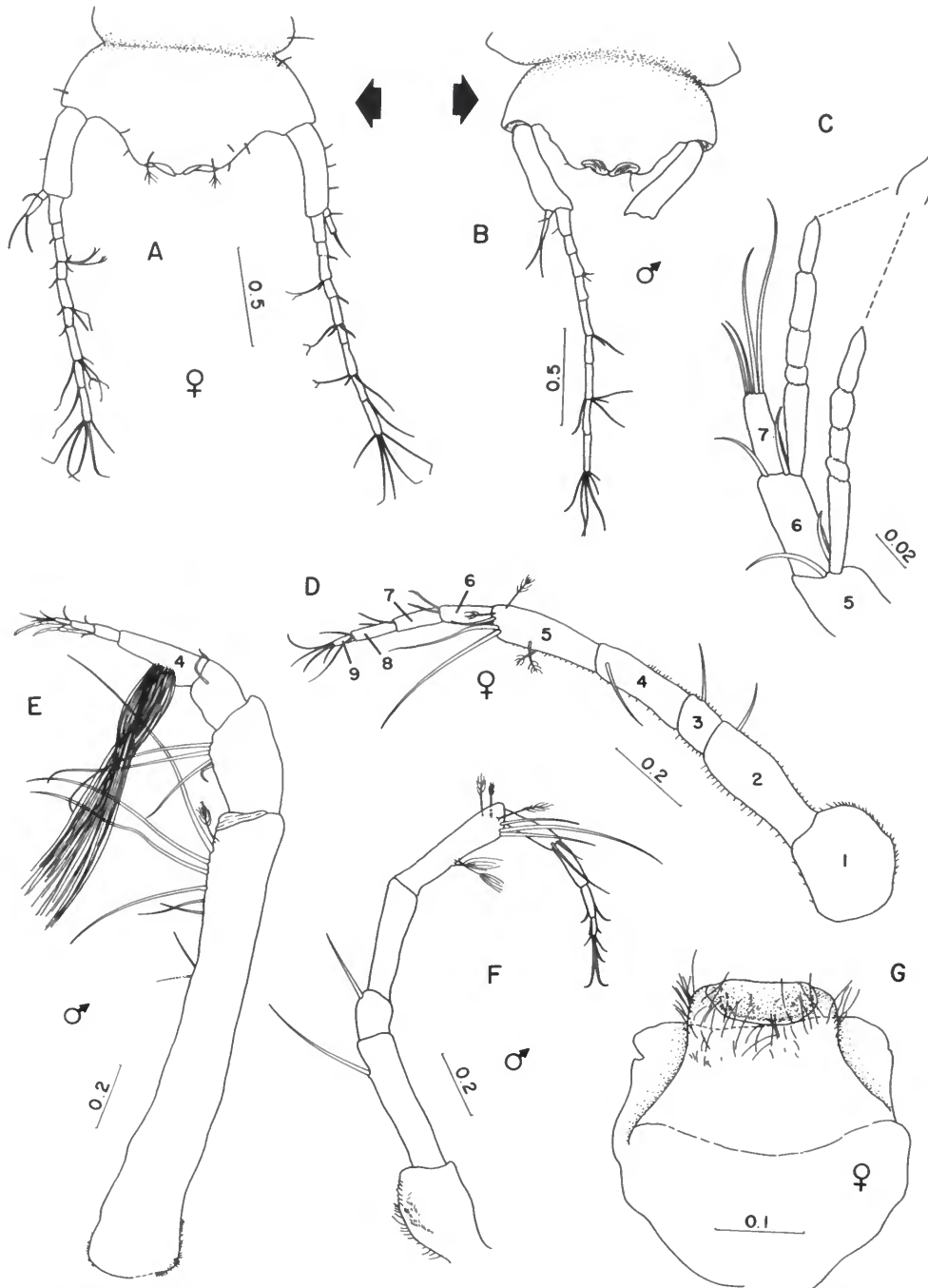
FIGURE 6.—*Neotanais micromopher*, new species (all figures except c are of holotype and allotype from WHOI Benthic Station 64): A, pleotelson and uropods, dorsal view, holotype; B, same, allotype; C, distal tip of first antenna, ventral view, showing the two large annulated esthetascs of articles 5 and 6, female FA, Sta. 76; D, right second antenna, ventral view, holotype; E, left first antenna, dorsal view, allotype; F, left second antenna, ventral view, allotype; G, labrum, anterior view, holotype.
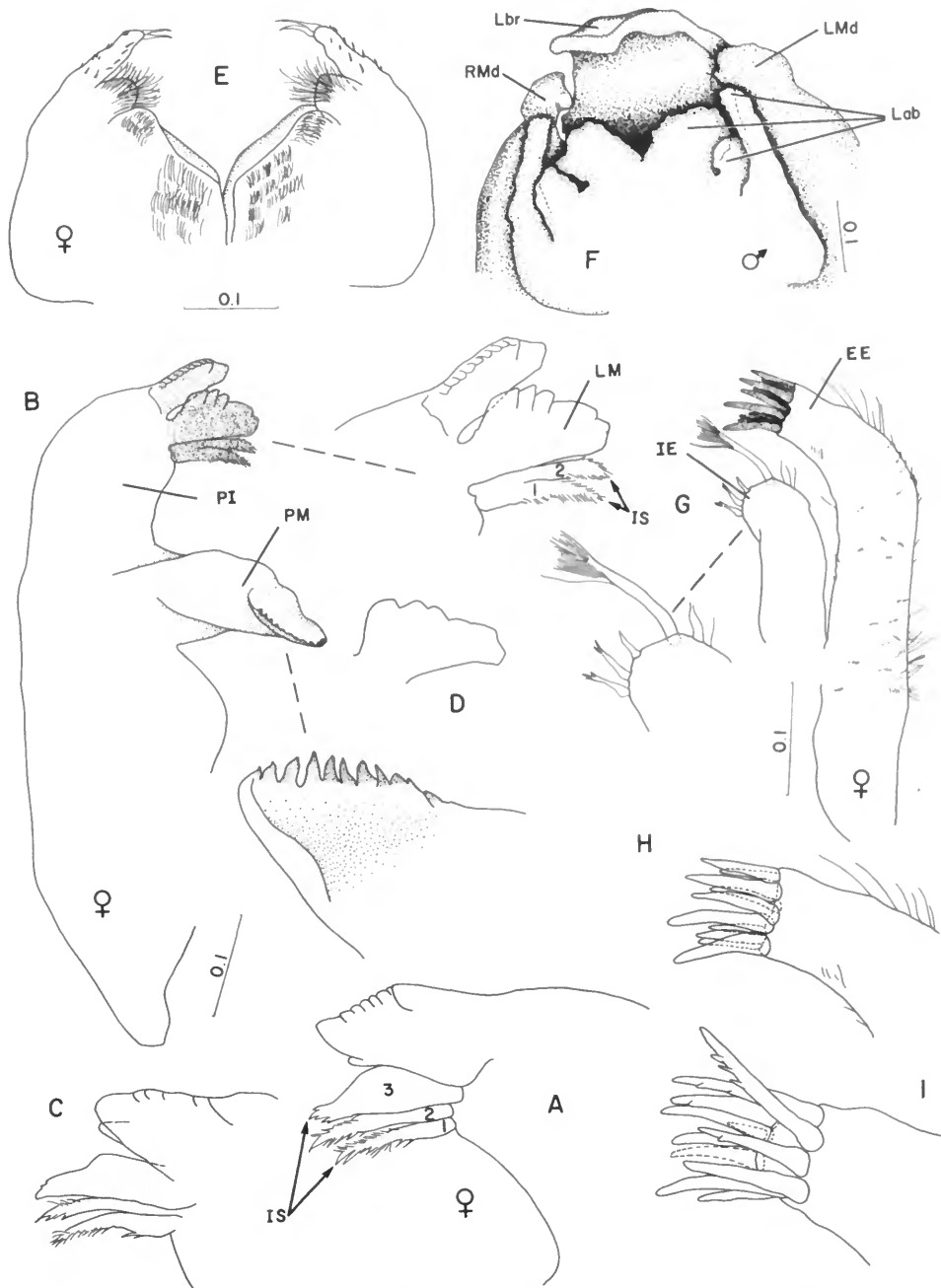
FIGURE 7.—*Neotanais micromopher*, new species (all figures except F are of animals from WHOI Benthic Stations): A, pars incisiva of right mandible, anterior view, female, holotype, Sta. 64; B, left mandible, anterior view, with enlargements of pars incisiva and molar teeth, holotype; C, pars incisiva of right mandible, female FC, Sta. 76; D, lacinia mobilis of left mandible, anterior view, same animal; E, labium, anterior view, holotype; F, anterior mouthparts, posterior view, copulatory male, CMS Sta. 2154; G, left first maxilla, posterior view, holotype; H, enlargement of distal portion of external endite from first maxilla in E; I, same, more commonly observed spine pattern with teeth, right maxilla, anterior view, female FA, Sta. 76.
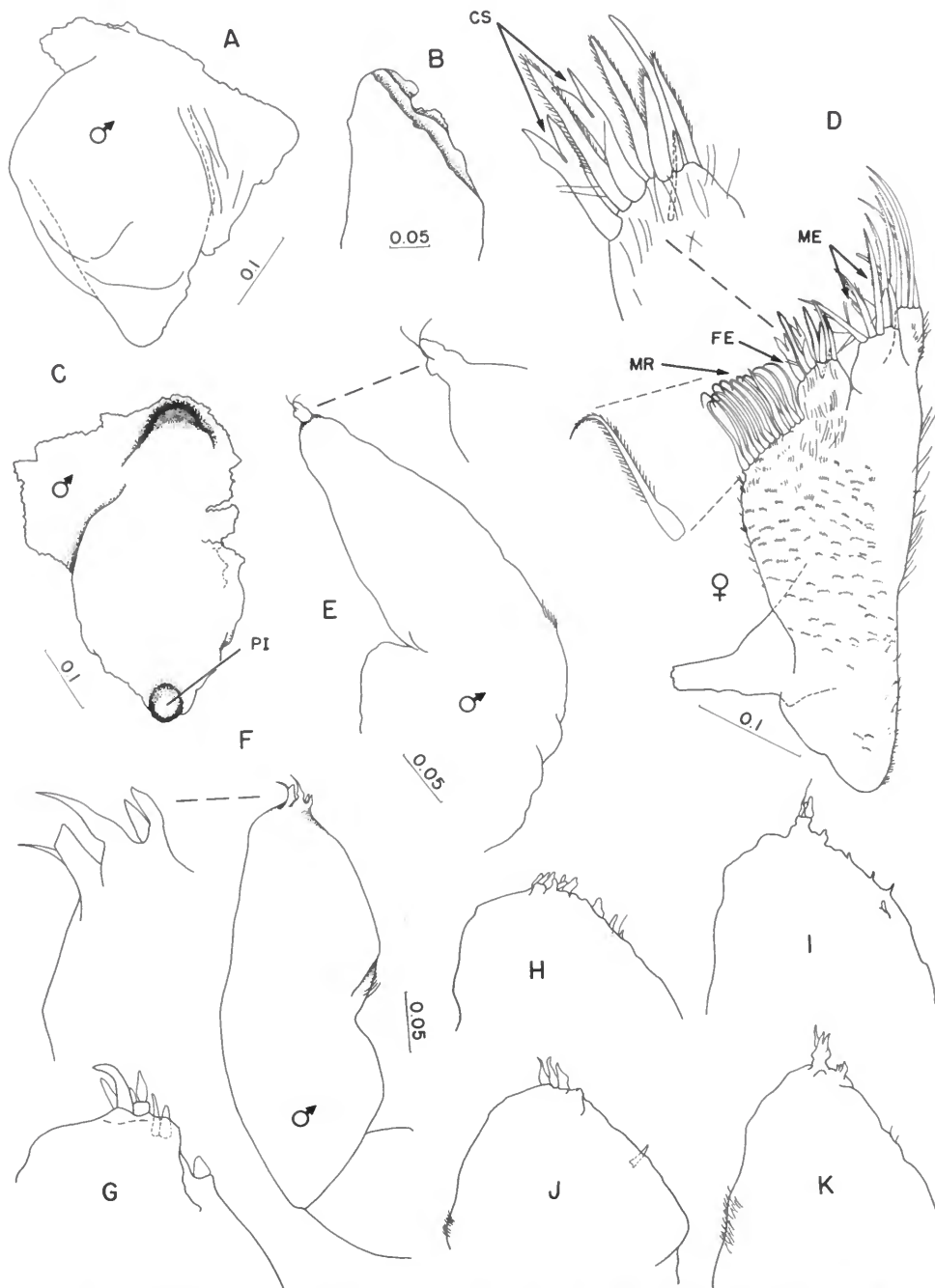
FIGURE 8.—*Neotanais micromopher*, new species (all animals from WHOI Benthic Station 64): A, right mandible, lateral view, copulatory male, allotype; B, same, viewed posteriorly, obliquely, and inverted; C, left mandible, medial view, copulatory male AS; D, right second maxilla, anterior view, female, holotype; E, same, lateral view, allotype; F, same, viewed anteriorly; G, left maxilla, posterior view, allotype; H, I, left and right second maxillae viewed anteriorly and posteriorly, respectively, copulatory male AR; J, K, right and left second maxillae viewed posteriorly and anteriorly, respectively, copulatory male AS.
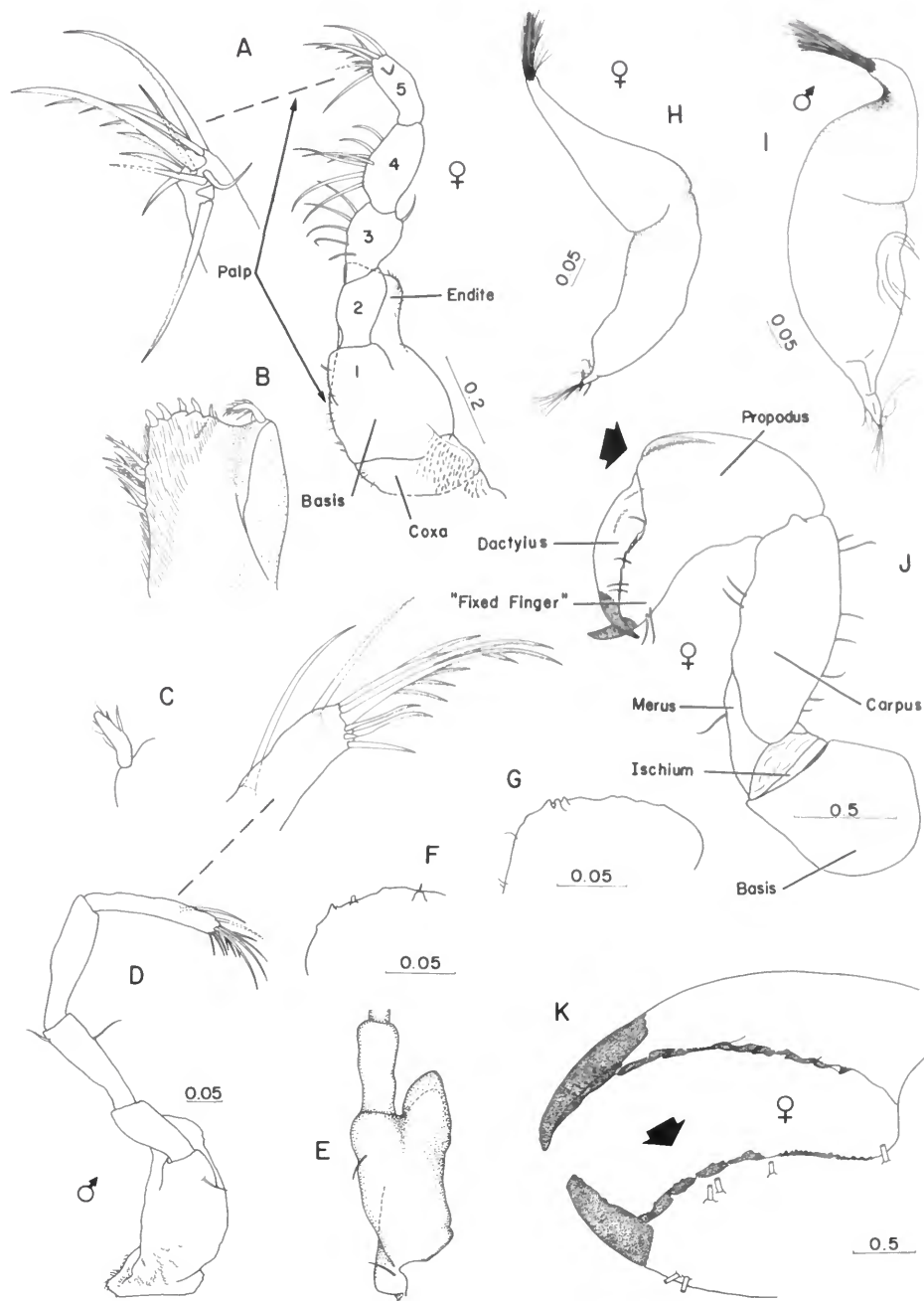
FIGURE 9.—*Neotanais micromopher*, new species (maxillipedal and chelipedal terminology labeled; all figures are of animals from WHOI Benthic Stations except F and G): A, left maxilliped, posterior view, female, holotype, Sta. 64; B, endite of same, posterior oblique view; C, distal medial spine from female FA, Sta. 76; D, right maxilliped, posterior view, copulatory male, allotype, Sta. 64; E, coxal and basal portion of same, medial view, showing relief; F, G, distal margin of endites of left and right maxillipeds viewed anteriorly and posteriorly, respectively, copulatory male, CMS Sta. 2154; H, right epignath, posterior view (not inverted), holotype; I, left epignath, same position, allotype; J, left cheliped, holotype; K, left chela, holotype.
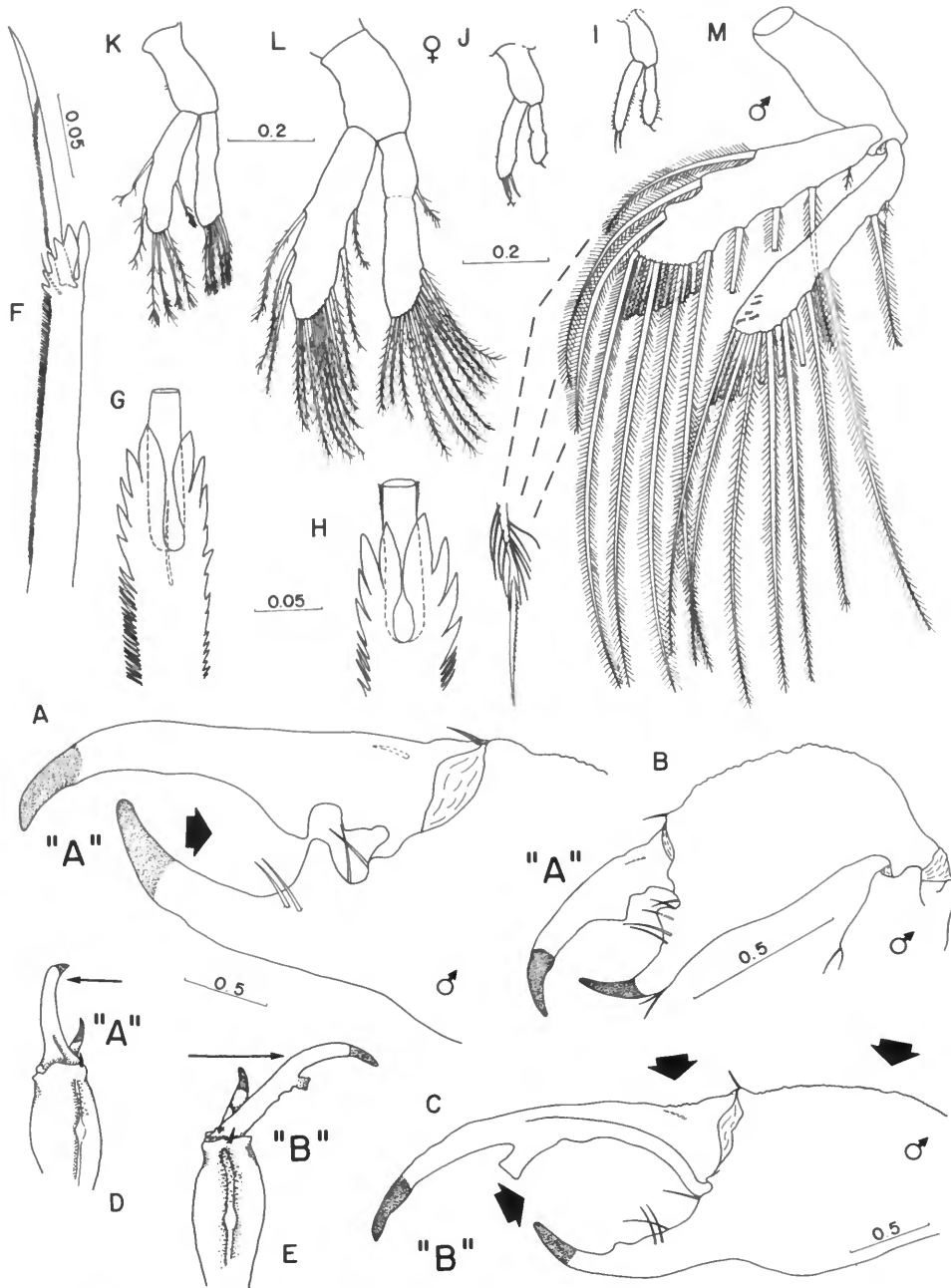
FIGURE 10.—*Neotanais micromopher*, new species (all figures are of animals from WHOI Benthic Stations): A, chela type A, primary copulatory male HA, Sta. 76; B, same, AU, Sta. 64; C, chela type B, secondary copulatory male, allotype, Sta. 64; D, E, chelae types A and B, respectively, in dorsal view, showing horizontal orientation of dactyli (D actually slightly oblique); F, distal tip of dactylus of pereopod VI, posterior oblique view of female FD, Sta. 76; G, dorsal view of same; H, same for pereopod V. I–M, development of pleopods (all from Sta. 64): I, juvenile BE; J, preparatory female 1 BF; K, preparatory female 2 P; L, intermediate (?) female, holotype; M, secondary copulatory male, allotype, with enlargement of tip of medial endopodal seta.

of being more elongated. Respiratory chambers moderately, and chelipedal coxae strongly, expanded laterally. Rostrum strongly pointed, much more so than in other stages, and with sides markedly concave. Oblique furrows moderately deep. An inverted U-shaped line connects posteromedial angles of chelipedal coxae. Height of carapace proportionately shallower anteriorly than in female, probably due to rudimentary nature of the mouthparts (Figure 4E). Anterolateral keels small and difficult to see in dorsal view; 1 anterolateral and 1 posterolateral seta present.

Pereonites: Although wider than long as in other stages, decidedly not quadrangular; pereonites 3–7 gradually rounded anteriorly on each side, areas over pereopods widest. Anterior margin of pereonite 2 straight on each side and prolonged laterally into prominent, acutely angled "shoulders."

Pleonites (Figures 3A, 5B,I, 6B): Pleonite 1 considerably wider than pereonite 7 and somewhat wider than pleonite 5. Pleonite 5 considerably wider than pleotelson. Epimeres markedly angular and somewhat tapered laterally in dorsal view. Sternites rounded or slightly anteriorly flattened midventrally in lateral view.

Pleotelson (Figures 3A, 5B,I, 6B): Short, similar to that of other stages; 1.7 times wider than long. Posterior margin convex rather than concave as in other stages. Ventral surface bearing a raised, horseshoe-shaped protuberance below anal fusion.

First Antenna (Figure 6E): Article 1, 5.6 times longer than wide.

Second Antenna: As in Figure 3F.

Labrum (Figures 4D,E, 7F): Without hairs.

Mandibles (Figures 4D,E, 7F, 8A–C): Both similar in form; strongly reduced. Fused with carapace dorsally and posteriorly. Pars incisiva remains as small ventromedial protuberance. Pars molaris absent.

Labium (Figure 7F): Very flat, apparently more so than in other stages. Although strongly reduced, all 3 lobes clearly recognizable.

Second Maxilla (Figure 8E–G): Strongly reduced; a few irregular and variable hairs, spines, and knobs present.

Maxilliped (Figure 9D,E): Coxa fused to basis. Coxa and basis, including endite, without setae. Setal formula of palp, (1,0,1+1,0,12).

Cheliped (Figures 2A, 3A, 10C,E): Carpus slender, strongly but gradually curved; with at least 3 or 4 short dorsal setae centrally and 1 or 2 moderately

long, slender ventral setae distally. Chela (type B): Dorsal surface of propodus finely crenate in lateral view or slightly scaly in dorsal view. A very slight dorsal depression centrally located on propodal crest (characteristic of all copulatory males of this species). Fixed finger with 1 low tooth about midway along its length. Dactylus with a low rise just proximal to a large, distally directed tooth with slightly expanded flat tip; tooth located about midway along dactylus. Dactylus strongly medially directed (in Figure 10C both fingers are drawn in the same plane, hence dactylus appears much longer—its true length—than in life).

Pereopods II–VII (Figure 13A–G): Anterior propodal setae of pereopods II–IV moderately slender and bearing numerous fine setules. Setal formulae of pereopods II–IV, (5,4,5,4), (7,7,3,5), and (7,8,3,5). Long, terminal propodal spine single, present on pereopods II–IV (cf. holotype), and bearing 15 to 20 moderately large, irregular teeth on one side and about 3 such teeth on the other. Short, terminal propodal spine of pereopods II–IV slender, practically straight, and bearing very fine teeth or setules. Short, subterminal carpal spine of pereopod II stout and almost straight. Short, subterminal propodal spines of pereopod VII absent as in other stages.

Pleopods (Figure 10M): Setal formula, (0,0) (3,11,5) (0,2;0,9,5).

Uropods (Figure 6B): With 9 endopodal articles on each side.

INTRASPECIFIC VARIATION.—*Neotanais micromopher* provided the basis for a detailed study of intraspecific variation in the genus *Neotanais*. The differences among many individuals are discussed at length below (p. 175); however, a description of chela type A of primary copulatory males is given here for purposes of identification. (Body lengths of individuals at WHOI Benthic Stations 64 and 76 are listed in Tables 16 and 17). Chela Type A (primary copulatory males; Figure 10A,B,D): Similar to chela type B, but one large tooth present on fixed finger. One small to moderately large, proximal tooth and one large, more distally located tooth on dactylus. Dactylus more or less parallel to fixed finger in lateral view although directed outward in dorsal view (chela in Figure 10D tipped to right, hence minimizing the latter angle).

Male AQ (body length, 7.6 mm) from Sta. 64 has a normal type A chela on the left side. But the

dactylus on the right side bears a flat-tipped, distally directed tooth (Figure 11A) similar to that of a secondary male. However, the tooth is short and the overall length of the dactylus relative to the fixed finger is similar to that of the left side. The two low protuberances proximal to the large dactylar tooth are more distinct than those on primary males (cf. Figure 10A,B).

A male (body length, 7.0 mm) from WHOI B. Sta. 66 is very similar in all respects, but the two proximal dactylar protuberances are even more distinct and both chelae have the same aberrant form. A third specimen (body length, 8.4 mm), from *Noratlante* Sta. 019, has chelae in which the fixed finger resembles that of a primary male (Fig-
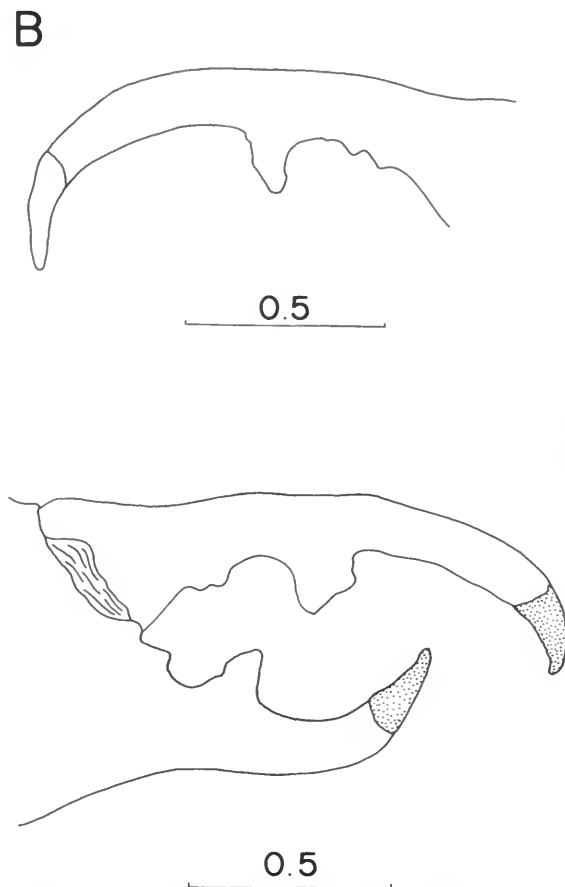

FIGURE 11.—*Neotanais micromopher*, new species (copulatory male AQ from WHOI Benthic Sta. 64): A, right cela; B, dactylus of left chela.

ure 10A) and the dactylus that of the secondary male in all respects (Figure 10c). The significance of these unusual males is discussed under "Development."

A single individual, a manca 2, has been collected from eastern Atlantic waters (*Noratlante* Sta. 111, B016). This specimen (body length, 3.5 mm) is identical with western Atlantic specimens except for a somewhat convex posterior pleotelsonal border in dorsal view. This difference is not unreasonable, however, since the animal is very young, and this much variation has been observed over long distances in other species. This animal was also found at a depth (4729 m) considerably greater than the deepest western Atlantic collection (3828 m) of this species.

REMARKS.—This species was described by Beddard (1886a, 1886b) as *Neotanais americanus*. Beddard apparently based his description on a specimen collected in South American waters. His second specimen, collected off Delaware Bay, New Jersey, actually is *N. micromopher*.

Although the two species apparently are not closely related, Beddard has not been the only one to confuse them. I originally considered them to be conspecific (they often are collected together off eastern North America). Hansen worked on three specimens of "*Neotanais serratispinosus*," conspecific with *N. americanus*, collected by the *Ingolf* Expedition (Hansen, 1913). One of these specimens is *N. micromopher*. Apparently Wolff (1956a) did not notice the difference when examining Hansen's material in connection with his study of *Neotanais*. Finally, several specimens of *N. micromopher* identified as *N. americanus* by H. Richardson were in the collections of the United States National Museum.

A comparison of the figures illustrating these two species will demonstrate their disparate nature (e.g., pereonite shape and posterior border of pleotelson in dorsal view, shape of teeth on fixed finger of cheliped, midventral shape of pleonites in lateral view, and, of course, the pubescent cuticle of *Neotanais micromopher* and the fusion of its pleotelson with pleonite 5—the pleotelson of *N. americanus* is always clearly articulated). The copulatory males of these two species, unknown prior to this study, exhibit even more marked differences.

Although Beddard (1886b) describes his specimen as a male, it is clearly a preparatory female 2

FIGURE 12.—*Neolanais micromopher*, new species. Pereopods of female, holotype, from WHOI Benthic Station 64: A–F, left pereopods II–VII viewed posteriorly; G, enlargement of tip of propodus of pereopod II (in A), dorsal view. Enlargement on basis in A represents silhouette of the fine cuticular pubescence found on these appendages.
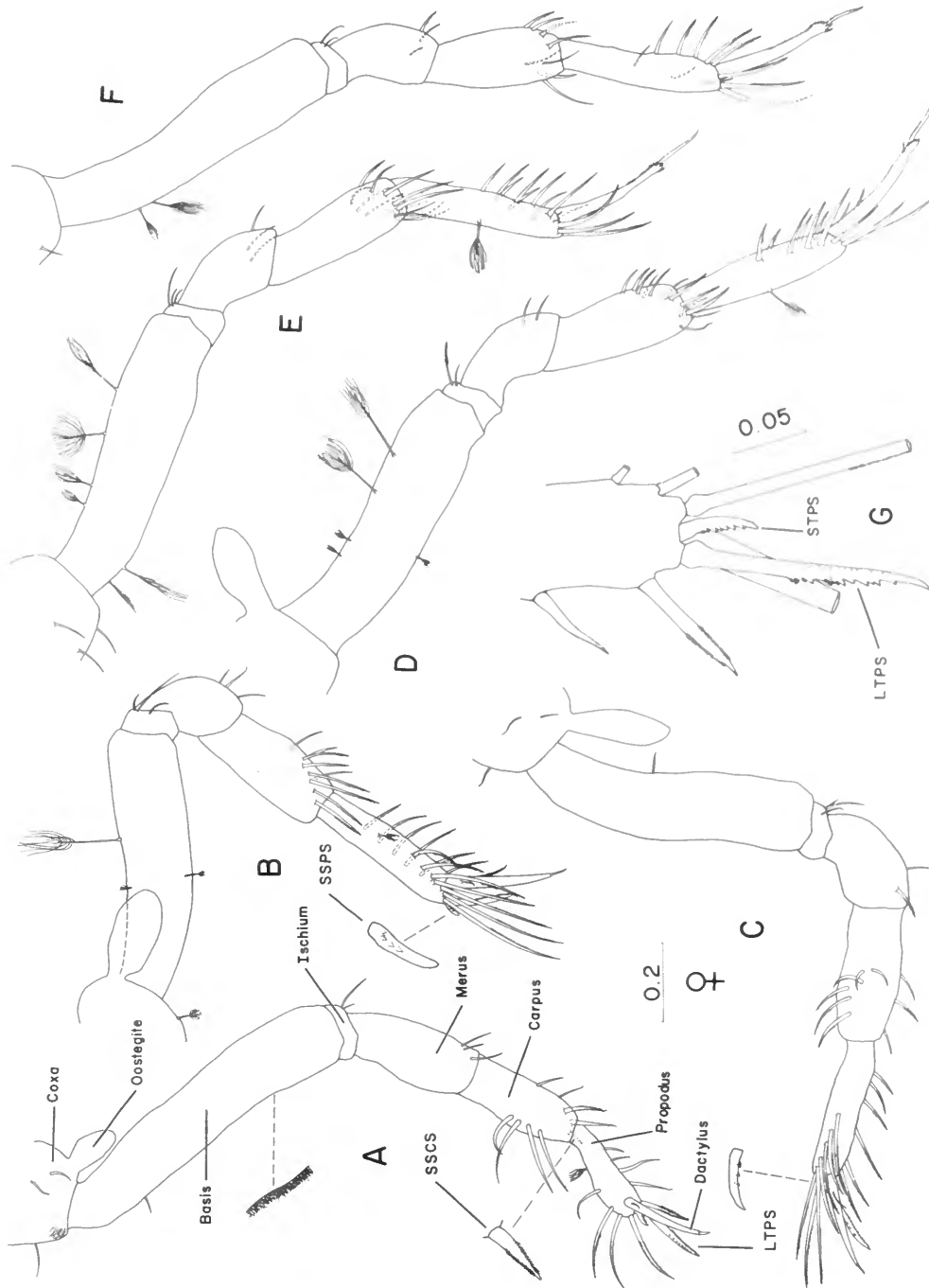
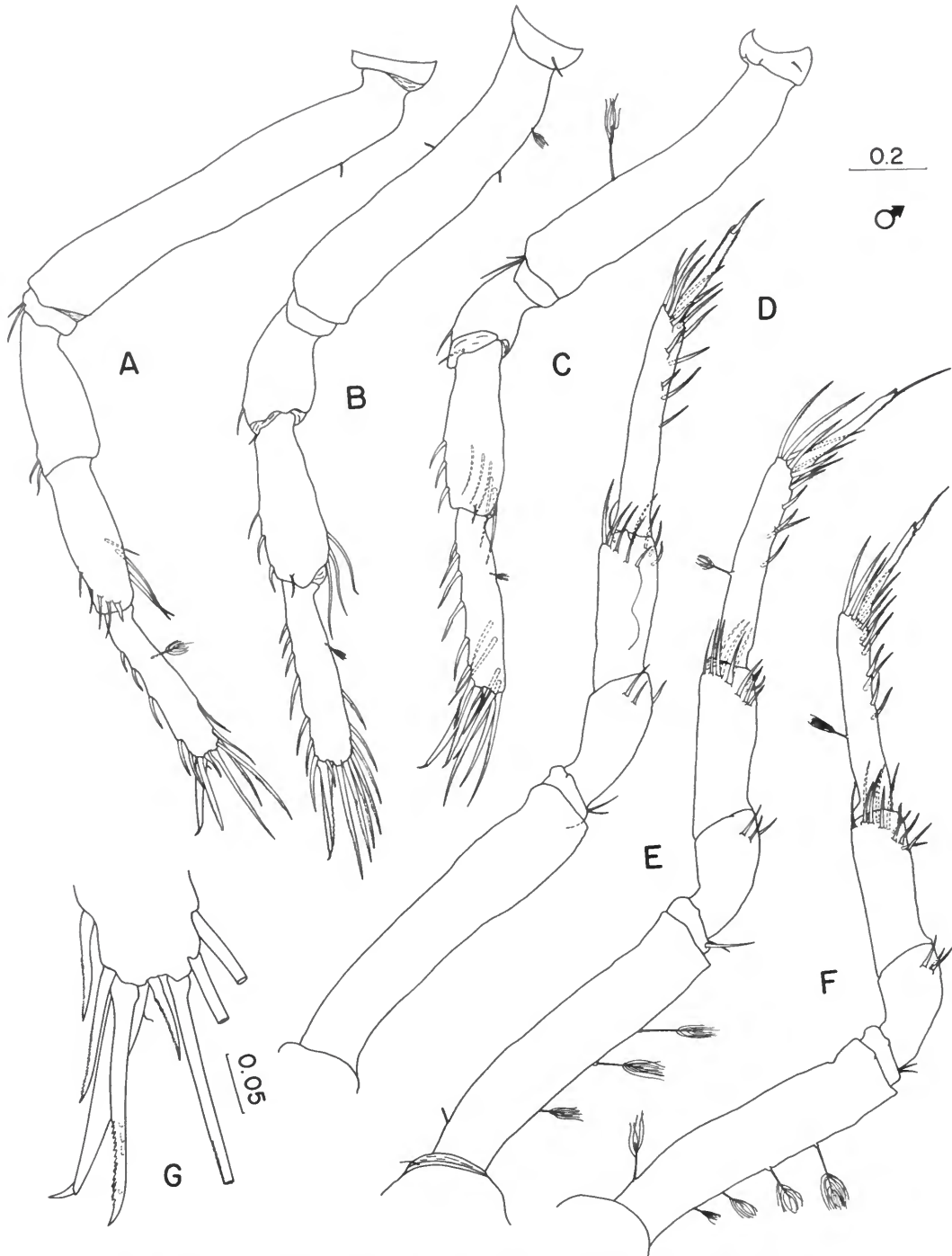FIGURE 13.—*Neotanais micromopher*, new species. Pereopods of copulatory male, allotype, from WHOI Benthic Station 64: A–F, left pereopods II–VII viewed anteriorly or anterior obliquely; G, distal tip, propodus of pereopod II (in A) in dorsal view.

and bears easily visible rudimentary oostegites. This specimen is mounted on a microslide and is missing parts of several appendages. Hence, intermediate female A is described here. Secondary copulatory male AP, from the same sample, has been chosen as the allotype.

In his descriptions, Beddard (1886a, 1886b) variously refers to the depth of *Challenger* Sta. 45 as 1250 fms (1886a:118; 1886b:126), 1240 fms (1886b:

127), and 1252 fms (1886b:124). The official station list for the expedition (Tizard et al., 1885:1007) cites the depth as 1240 fms (=2268 m).

Neotanais micromopher was the species most abundant in all collections available for this study. Consequently, it has formed the basis for the studies of intraspecific variation and postmarsupial development. Many of the figures representing the morphology of this species also have been utilized

TABLE 2.—*Examined material of* Neotanais micromopher, *new species*

Program or ship	Station no.	General location	Depth (meters)	Material
WHOI Benthic	HH 1	Gay Head-Bermuda Transect	2873	1 P♀1
	HH 3		2900	3 Ml, 1 Juv, 1 P♀1
	63		2891	1 Juv, 1 fgmt.
	64		2886	2 Ml, 7 M2, 13 Juv, 17 P♀1 (incl. 2 fgmts.), 17 P♀2, 2 ?1♀1 (incl. holotype), 5 Cop ♀, 7 P♂, 3 1°Cop ♂, 4 2°Cop ♂ (incl. allotype)
	65		2891	1 Ml, 1 P♀1, 1 P♀2
	66		2802	4 Ml, 2 M2, 4 Juv, 4 P♀1, 1 P♀2, 1 Cop ♀, 1 P ♂, 2 2° Cop ♂, 1 Cop ♂ (unid. stage)
	72		2864	2 M2, 1 P♀1, 4 P♀2, 4 Cop ♀, 1 P♂, 1 1° Cop ♂, 1 fgmt.
	76		2862	15 Juv, 18 P♀1, 31 P♀2, 11 Cop ♀, 10 P♂, 5 1°Cop♂, 3 2°Cop ♂, 2 Cop ♂ (unid. stage), 9 fgmts.
	78		3828	1 Cop ♀
	85		3834	4 M2, 1 Juv, 4 P♀1, 3 P♂, 1 unid. fgmt.
	95		3753	1 M2, 1 Juv, 1 Cop ♀
	112		2900	1 P♀2, 1 Cop ♀, 1 P♂, 1 1°Cop ♂, 1 2° Cop ♂
	126		3806	1 Ml
Albatross	2221	S of Martha's Vineyard, Massachusetts	2789	1 P♀2
	2570	S of Georges Bank	3316	1 Ml, 2 M2, 5 Juv, 1 P♀2, 1 Cop ♀
Challenger	45	E of Delaware Bay, New Jersey	2268	1 P♀2
CMS	2072	Off North Carolina	2725	1 P♀2, 2 2°Cop ♂
	2073		2610	1 ?Cop ♀
	2118	Off Delaware	2975	1 2°Cop ♂
	2125	E of Cape May, New Jersey	2682	1 1°Cop ♂
	2144	SW of Cape Cod, Massachusetts	2850	1 2°Cop ♂
	2145	S of Cape Cod, Massachusetts	2925	1 Cop ♀, 1 1°Cop ♂
	2154	SE of Cape Cod, Massachusetts	2840	2 P♀2, 1 1°Cop ♂
	2164	SW of Georges Bank	3015	1 P♀2
	2188	S of Georges Bank	2715	1 ?Cop ♀, 1 ?P♂
Eastward	2756	E of Cape Hatteras, North Carolina	3017	1 Juv
	5491	SE of Cape Hatteras	3825	1 Juv
	6228		3057	1 M2, 1 P♀1
Ingolf	22	SW of Greenland	3474	1 Juv
Noratlante	019, E003	E of Labrador	4120	6 Juv, 1 P♀1, 1 P♀2, 1 Cop ♀, 1 1°Cop ♂, 2 2°Cop ♂
	042, E006	Labrador Sea	3430	8 Ml, 6 M2, 3 Juv, 1 P♀2, 2 Cop ♀, 1 ?1♀, 2 1°Cop ♂, 8 nonmale fgmts.
	111, B016	Bay of Biscay, N of Santander, Spain	4729	1 M2

to illustrate basic neotanaid structure and the terminology relating thereto.

DISTRIBUTION.—*Neotanais micromopher* has been collected in the western North Atlantic from the Greenland area to the Cape Hatteras, North Carolina, region at depths of about 2270 to 3830 m. A single collection has been made in the eastern Atlantic—in the Bay of Biscay, at 4729 m.

MATERIAL.—See Table 2.

LOCATION OF MATERIAL.—NMNH: holotype (USNM 143132); allotype (USNM 143133); WHOI 64 developmental series including MI (CL, CM), M2 (CF, CG), Juv (BD, BG, BL, BX), P ♀ 1 (E, BH), P ♀ 2 (B, D), ?I ♀ (C), Cop ♀ (AB, BA), P ♂ (AA, AD), 1°Cop ♂ (AV, AQ), 2°Cop ♂ (AR, AS, AT) (USNM 143134); *Albatross* 2221 (USNM 43234); *Albatross* 2570 (USNM 141450); CMS 2072 (USNM 143135); CMS 2073 (USNM 143136); CMS 2118 (USNM 143137); CMS 2125 (USNM 143138); 2144 (USNM 143139); CMS 2145 (USNM 143140); CMS 2154 (USNM 143141); CMS 2164 (USNM 143142); CMS 2188 (USNM 143143); *Noratlante* 019, E003 (USNM 143145); *Noratlante* 042, E006 (USNM 143144); *Noratlante* 111, B016 (USNM 143146). BMNH: *Challenger* 45 (Reg. No. 1889.4. 2'/107, microslide). UCZM: *Ingolf* 22; WHOI 66; WHOI 72.

DERIVATION OF NAME.—Referring to the anterolateral spurs borne on pereonite 2 of the copulatory males. From the Greek *mikros* (little), *omos* (shoulder), and *phero* (to bear).

Neotanais dinotomer, new species

FIGURES 14–16, *96*

DIAGNOSIS.—*Stages Other Than Copulatory Male*: *Pleotelson markedly wider than long, more so than in any other known species of *Neotanais*, width-length ratio 2.3 to 2.4; *fused to pleonite 5. *Pereonites generally rounded in dorsal view, appearing wider than long, width-length ratio of pereonite 5, 1.3 to 1.4; relatively long and heavy hairs borne laterally on pereonites; each segment bearing a low, acute, midventral convexity in the posterior one-third of segment. Pleon tapering noticeably anteroposteriorly in dorsal view and becoming more slender posteriorly in lateral view. *Pleonites with a noticeable blunt spur on posterior border of each sternite in lateral view. Carapace without prominent dorsal surface features; *several long setae present anterolaterally below weak keels; one long posterolateral seta. Chelipedal carpus with up to 14 dorsal setae in preparatory female 2. Specialized pereopodal spines as follows: *short, subterminal propodal spine row of pereopod VII absent; short, terminal propodal spines of pereopods II–IV straight, heavy, and bearing 10 to 15 prominent triangular teeth in II but about 6 or 7 such teeth in III and IV.

Copulatory Male (only one type known): *Pleotelson similar to that of other stages. *Pereonites obviously wider than long, width-length ratio of pereonite 5 about 1.7; *anterior margin rounded in dorsal view; *posterior border almost straight across. *Pleonites similar in shape to those of other stages; often bearing 2 feathered setae dorsally on epimeres. *Carapace with anterolateral borders parallel; *bearing setae as on female; surface without marked features. Chelipedal carpus bearing up to about 13 long, thin dorsal hairs similar to those of other stages although somewhat shorter; *2 ventral setae very long and a single, shorter midventral seta present distally; *a prominent distomedial spur present, unlike most species; both fingers twisted and turned medially; *dentition as in Figure 16F.

DESCRIPTION OF PREPARATORY FEMALE 2 HOLOTYPE (WHOI Sta. 118).—*Body* (Figure 14A): 6.2 mm long and 6.2 times longer than wide.

Carapace: 1.4 times longer than wide. Almost devoid of surface relief dorsally except for short and very weakly developed anterolateral keels; oblique furrows almost imperceptible. Chelipedal coxae narrow when viewed from above and closely pressed to carapace. Three or four long, relatively widely spaced, anterolateral setae present, followed by 1 posterolateral seta of similar shape. Rostral area not especially prominent; sides slightly concave.

Pereonites (Figures 14F, 15A): Fifth pereonite 1.3 times wider than long but giving appearance of greater length relative to width due to marked rounding of corners and deep depressions between pereonites. Dorsal surfaces perfectly smooth, several relatively long thick hairs located laterally. Areas of pereopodal attachment not prominent in dorsal view. Pereonites each with a low convexity midventrally in posterior one-third of each sternite.

Pleonites (Figures 14C,D, 15A): Epimeres rounded laterally in dorsal view, not prominent, and bearing several hairs including at least one long, feathered
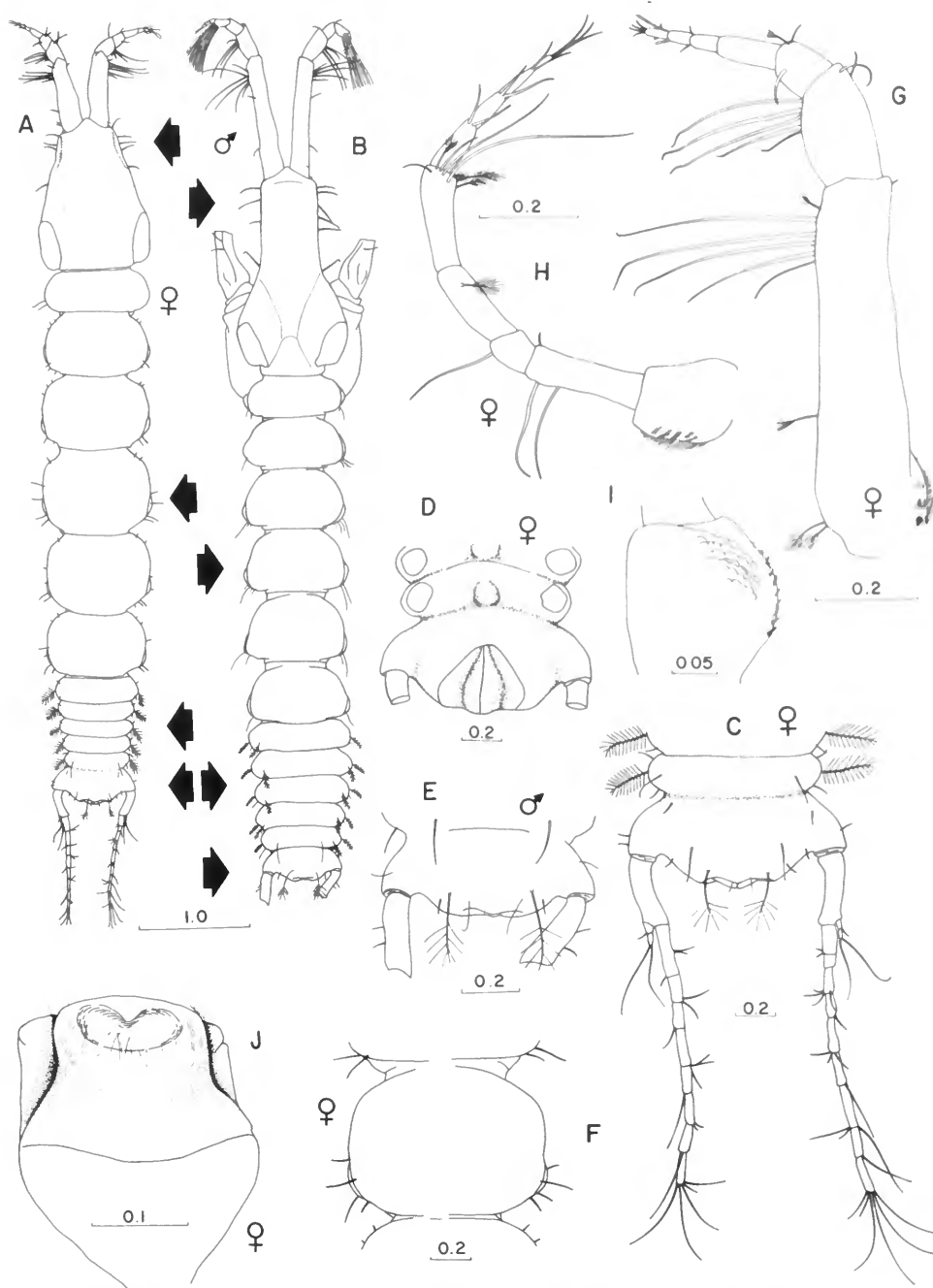
FIGURE 14.—*Neotanais dinotomer*, new species: A, dorsal view, preparatory female 2, holotype, Sta. 118; B, same, copulatory male, allotype, Sta. Ber. 8; C, pleonite 5, pleotelson, and uropods, dorsal view, holotype; D, pleotelson, ventral view, holotype; E, same, dorsal view, allotype. F–J, all holotype: F, pereonite 5, dorsal view; G, left first antenna, dorsal view; H, left second antenna, ventral view; I, first article of same, dorsal view; J, labrum, anterior view.
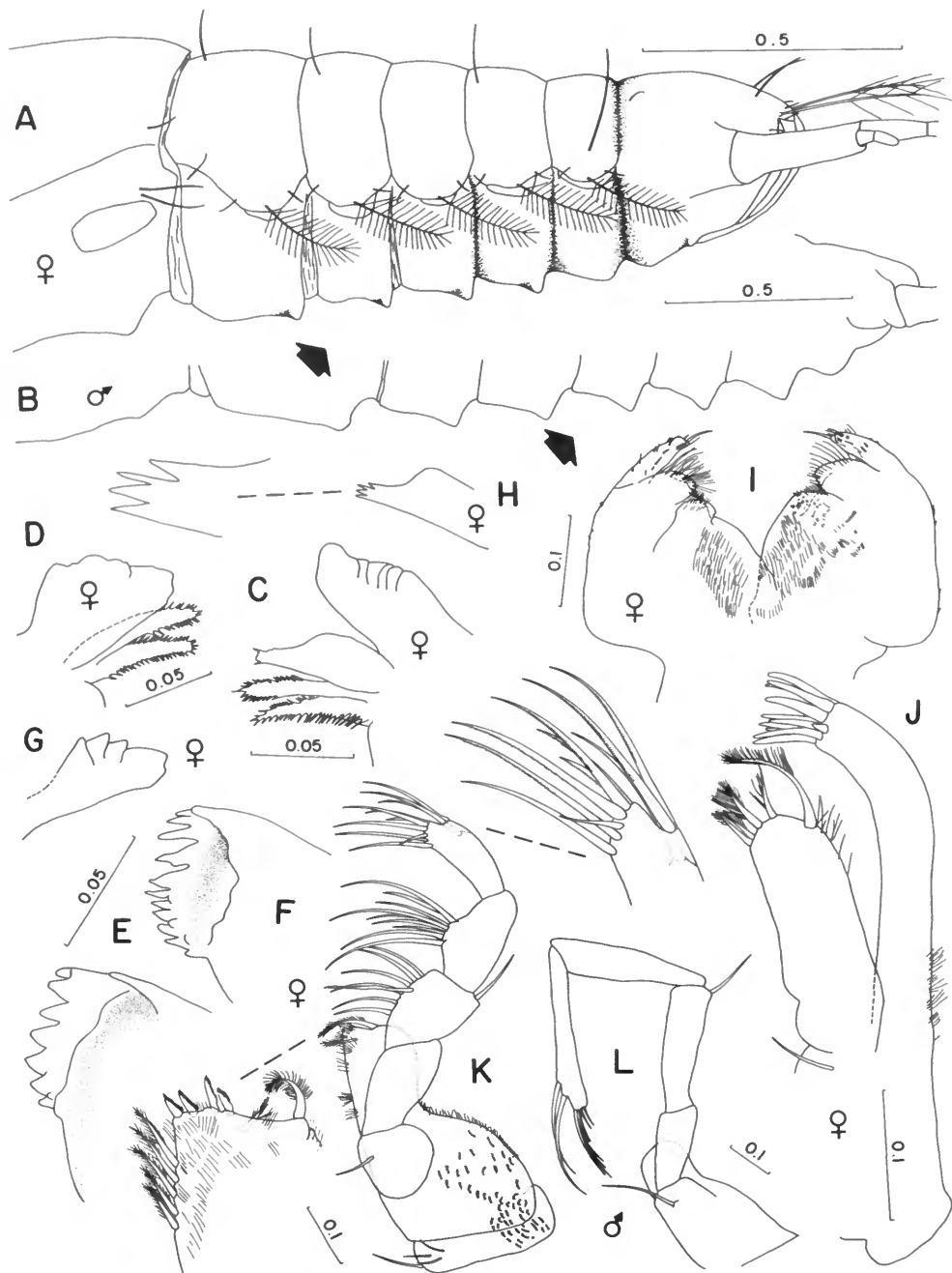
FIGURE 15.—*Neotanais dinotomer*, new species: A, pereonite 7 and pleon, lateral view, preparatory female 2, holotype, Sta. 118; B, ventral silhouette of same, copulatory male, allotype, Sta. Ber. 8; C, pars incisiva of right mandible, holotype; D, incisive spines and lacinia mobilis of left mandible, anterior view, holotype; E, F, molar teeth of right and left mandibles, respectively, holotype; G, lacinia mobilis of preparatory female 2 B, Sta. 118; H, third incisive spine, same animal; I, labium, posterior view, holotype; J, left first maxilla, posterior view, holotype; K, left maxilliped, posterior view, with enlargements of basal endite and last palpal article; L, same, allotype.
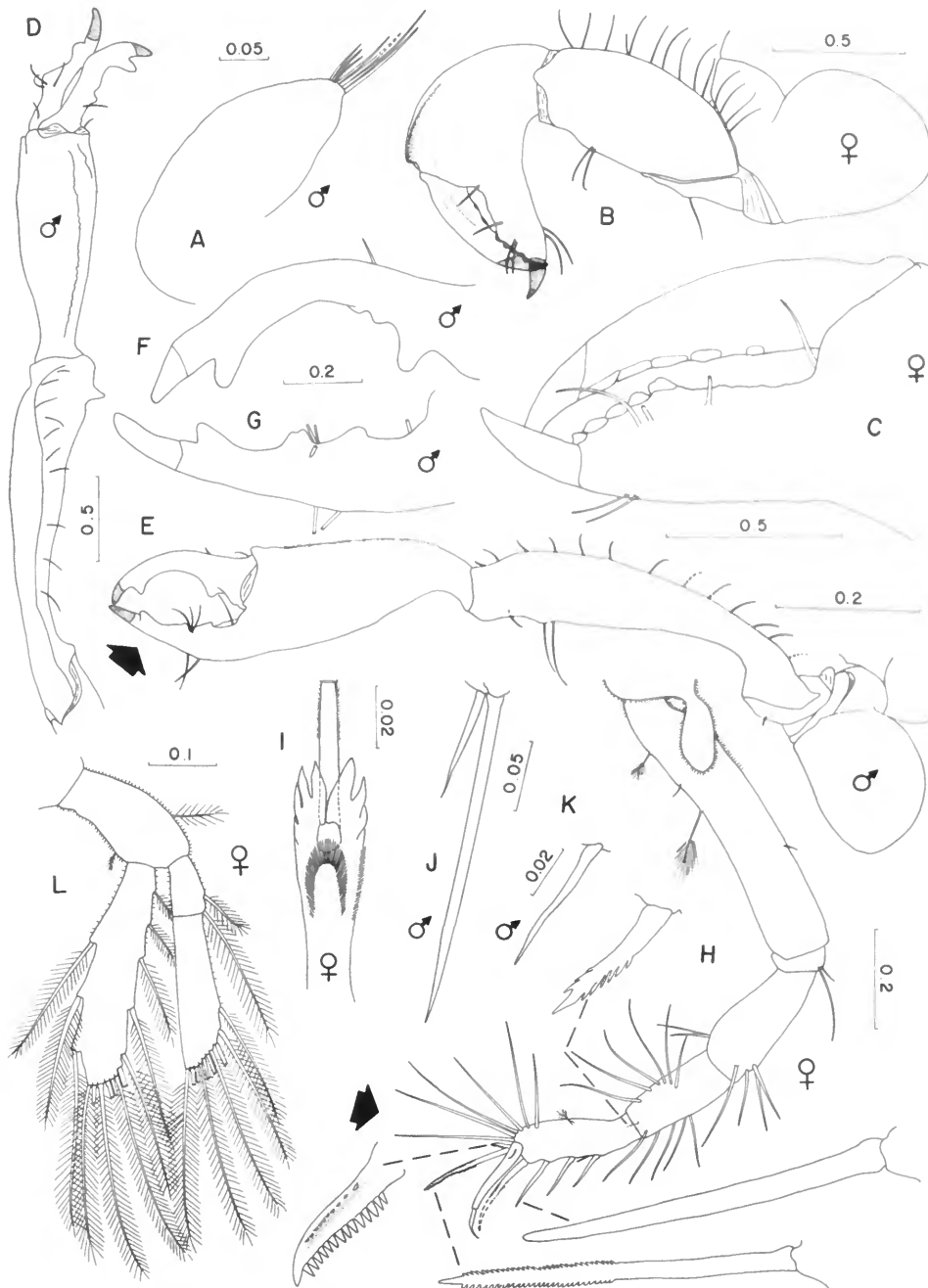
FIGURE 16.—*Neotanais dinotomer*, new species: A, left second maxilla, copulatory male, allotype, Sta. Ber. 8; B, left cheliped, preparatory female 2, holotype, Sta. 118; C, left chela, same; D, left cheliped, dorsal view, allotype; E, same, lateral view; F, G, enlargements of dactylus and fixed finger of same; H, left pereopod II, posterior oblique view, holotype; I, dorsal view of dactylar tip, pereopod V of a preparatory female 2 at Sta. 118; J, long and short, terminal propodal spines of pereopod II, allotype; K, short, subterminal carpal spine of pereopod II, allotype; L, left pleopod 1, anterior view, holotype.

seta on each side. Pleon tapering noticeably antero-posteriorly, pleonite 1 being 1.3 times wider than pleonite 5. Posterior margins of sternites each bearing a low, midventral spur. Articulations of segments increasingly obscure posteriorly, that of pleonites 4 and 5 often very difficult to observe.

Pleotelson (Figures 14c,d, 15a): 2.5 times wider than long and hence much shorter relatively than any other known species of *Neotanais*. Bearing several hairs or setae of various lengths including two very long broom setae near posterior margin. Borders convex both anterior and posterior to uropods. Fused to pleonite 5; fusion most clear ventrally.

First Antenna (Figure 14g): Article 1, 3.5 times longer than wide.

Second Antenna: As in Figure 14h,i.

Labrum: As in Figure 14j.

Right Mandible (Figure 15c,e): Proximal 2 incisive spines serrate on both sides, the second only along the distal one-third of its length. Third spine serrate at its tip although broken (cf. preparatory female B, Figure 15h).

Left Mandible (Figure 15d,f): Incisive spines as on right side. Distal border of lacinia mobilis irregular and teeth indistinct; large posterior lobe also irregular and uncleft.

Labium: As in Figure 15i.

First Maxilla: As in Figure 15j.

Second Maxilla: Medial setal row with 17 long, naked setae in addition to 2 stout spines with pointed tips.

Maxilliped (Figure 15k): Setal formula of palp, (1,0,7 + 1,9,10).

Cheliped (Figure 16b,c): Carpus bearing 14 long dorsal setae. Dorsal crest of propodus very shallow, almost resembling a low ridge. Fixed finger with no proximal denticles although this area is irregular; distal teeth prominent and more or less rounded. Dactylus bearing 5 smooth, low teeth of markedly unequal size; 3 proximal teeth separated from each other.

Pereopods II–IV (Figure 16h,i): Bearing varying amounts of pubescence proximally, usually on upper part of basis and on coxa. Proximal ventral surface of propodus often with small spurs or denticles. Anterior setae on propodus considerably shorter and stouter than posteriorly. Merus with an unusual pair of dorsal setae in addition to the usual ventral groups. Short, terminal propodal spines straight and bearing a characteristic num-

ber of irregular teeth—11 and 14 on pereopods II, and 6 or 7 each on pereopods III and IV. Long, terminal propodal spine single and with many fine teeth; present only on pereopod II. First seta in anterior row almost as long as long spine, and bearing much heavier setules than other setae in that row in pereopods II and III. Such setae and long spine missing on pereopod IV. Short, subterminal carpal spine of pereopod II straight and bearing long but fine teeth. Anterior setae usually naked, heavy (see enlargement, Figure 16h). Setal formula of pereopod II, (4,6,6,6); dactylar spine very slender and curved distally, at least 0.25 times as long as dactylus.

Pereopods V–VII (Figure 16i): All dactyli bear large terminal teeth. Short, subterminal propodal spines absent from pereopod VII.

Pleopods: As in Figure 16l. Terminal endopodal setae 0.87 times the endopodal length. Setal formula, (1,1) (3,7,5) (0,2;0,8,2).

Uropods (Figure 14a,c): 8 and 9 articles in left and right endopods respectively.

DESCRIPTION OF COPULATORY MALE ALLOTYPE (WHOI Sta. Ber. 8).—*Body* (Figure 14b): 6.5 mm long and 6.4 times longer than wide.

Carapace: 2.1 times longer than wide. Anterolateral borders parallel; a shallow, transverse furrow located just posterior to rostral area. Anterolateral setae similar to those of other stages in shape, number, and arrangement. Oblique furrows very shallow, connected with other posterior lines as in Figure 14b. Posterior border extended into a narrow "neck" behind chelipedal coxae. The latter not well developed laterally in dorsal view.

Pereonites: More obviously rectangular in dorsal view than in other instars, but similarly rounded anteriorly in dorsal view and with long posterolateral hairs. Fifth pereonite 1.7 times wider than long (other stages about 1.3 times wider than long). Posterior one-third of each sternite with a convexity as in other stages (Figure 15b).

Pleonites (Figures 14b, 15b): Very similar in shape to those of other stages dorsally and ventrally, although midventral spurs better developed. Anteroposterior taper (in dorsal view) similar to that of other stages, pleonite 1 again being 1.3 times wider than pleonite 5.

Pleotelson (Figure 14b,e): Shape close to that of other stages, but only 1.8 times as wide as long (female holotype, 2.5). Setae and hairs similar to

those of other stages. Most distinctly fused to pleonite 5 ventrally.

First Antenna: First article 6.1 times longer than wide (female holotype, 3.5).

Mandibles: Each bearing a simple, medially directed, distal protuberance representing pars incisiva.

Second Maxilla: As in Figure 16A.

Maxilliped (Figure 15L): Setal formula of palp, (1,0,1,0,10).

Cheliped (Figure 16E–G): Ischium particularly prominent and heavily calcified. Carpus bearing 13 prominent dorsal setae of moderate length, 2 ventrally in the usual position, and 1 midventral seta anteriorly where carpus flattens ventrally. Carpus bearing a prominent, medially directed spur just proximal to articulation of propodus. Propodus bearing 3 moderate teeth, the center tooth irregularly tipped, the distalmost tooth distally directed. A tuft of 3 brown setae originates at base of middle tooth and proximal to it. Dactylus with 4 teeth: 2 very prominent teeth (one at either end of article) and 2 very low, rounded teeth located just distal to large proximal tooth. Both fixed finger and dactylus bent medially and twisted (Figure 16D). This chela possibly represents type A belonging to primary males (see "Postmarsupial Development," below.)

Pereopods: Short, terminal propodal spines on pereopods II–IV needle-like and devoid of teeth (Figure 16J) in marked contrast to those of other stages. Long, terminal propodal spine similar to the latter but much longer (same figure) and present only on pereopod II as in other stages. Short, subterminal carpal spine of pereopod II also needle-like and naked but not completely straight, similar to those of other stages (Figure 16K). Setal formulae of pereopods II and III, (6,6,6,6) and (9,9,9,8), respectively; of pereopod VII, (8,9,8,7). As in other stages, merus of pereopod II observed to have 1 dorsal seta distally in addition to 4 other setae below. No short, subterminal propodal spines present on pereopod VII.

Pleopods: With 9 terminal endopodal setae which are 1.5 times longer than endopod.

Uropods: With 9 endopodal articles on each side.

INTRASPECIFIC VARIATION.—*Body Lengths*: The lengths of the animals at Sta. Ber. 8 and Sta. 118 are presented in Table 3. Three animals collected at Sta. Ber. 1 each differed in body size from those of the same developmental stage at the other two

TABLE 3.—*Representative body lengths, in millimeters, for specimens of* Neotanais dinotomer, *new species*

Stage	At WHOI B. Sta. Ber. 8	No. animals	At WHOI B. Sta. 118	No. animals
M1	2.1 to 2.3	5	2.2	1
M2	2.6 to 3.0	3	2.8 to 2.9	3
Juv	3.4 to 3.8	2	3.4 to 3.9; 4.8*	3
P♀2	4.9 to 5.0	2	5.3 to 6.2	2
Cop ♀	5.3 to 6.3	3	—	0
Cop ♂	4.8 to 6.6	3	—	0

* "Juvenile" E, with body length much greater than that of the other juveniles (see "Postmarsupial Development," below).

stations. In each case, the animals were considerably smaller; the manca 2 was 2.2 mm, the preparatory female 2 was 4.4 mm, and the copulatory female was 4.9 mm (cf. Table 3). Such a consistent difference at this station is interesting; however, small sample size ($N=3$) at Sta. Ber. 1 prevents further inferences from being drawn. All three samples come from practically the same location and depth and the forementioned difference probably is due to chance alone.

Stages Other Than Copulatory Male: The lacinia mobilis of the left mandible in preparatory female 2 B from the same station (118) as the holotype had three distinct teeth and a partly divided posterior lobe (Figure 15G). The right mandible of the same animal illustrates what was probably the original condition of the distalmost incisive spine of the holotype before being broken (Figure 15H).

Copulatory Males: The chelae of the smallest male (AV, from Sta. Ber. 8) have only one small dactylar tooth between the two larger teeth.

POSTMARSUPIAL DEVELOPMENT.—None of the specimens possessed male gonopore anlagen.

The pleopods attain the proportions found in the copulatory females at the juvenile stage, although they continue to add a few setae later. Terminal setal length/endopodal length ratios for juveniles D, E, and F (Sta. 118) are 1.4, 1.1, and 0.99, respectively, and each of these animals has four or five terminal endopodal setae. Copulatory females AD and AE at Sta. Ber. 8 have ratios of 1.1 and 1.2, comparable to preparatory females 2 at the previous station, and six or seven setae. Copulatory males at Sta. Ber. 8 have ratios of 1.9 and 1.5, respectively, higher than any of the female stages.

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Mancas 1 have 4 segments in the uropodal endopods; mancas 2, 6; juveniles, 7 or 8; preparatory females 2 and copulatory males, 8 or 9.

The fact that copulatory male AV (Sta. Ber. 8) is so much smaller (4.8 mm) than the other males at that station (AT, 6.6 mm, and allotype, 6.5 mm) is evidence for a third, small, class of males (see under "Development"). AV surely is a primary male, so its chelae represent chela type A. The allotype and male AT then must be very large primary copulatory males, considerably larger than some of the copulatory females and probably at the high end of the body length distribution for their developmental stage.

"Juvenile" E is much larger (4.8 mm) than the other juveniles (3.4 mm and 3.9 mm) at Sta. 118. It may represent a preparatory male without observable male gonopore anlagen. In any event, it resembles similar animals occasionally noted in other species as well (see "Development").

REMARKS.—*Neotanais dinotomer* is closely allied to *N. micromopher.* The similarities and differences of these species are discussed under the *micromopher* group above.

Neotanais dinotomer is known to range from 1000 to 1700 m on the Bermuda Slope. All records are from depths more shallow than for *N. micromopher.* However, the rough topography of the Bermuda slope prevented adequate sampling in that area, and *N. dinotomer* probably ranges more widely. Nevertheless, the mean depth of its distribution is almost certainly more shallow than that of *N. micromopher.*

The similarity of pleopodal development in *Neotanais dinotomer* to that of other species in the genus is interesting in view of its close affinity to *N. micromopher.* The latter apparently exhibits a unique type of pleopodal development.

MATERIAL.—This species is known only from Bermuda; all stations are WHOI Benthic Stations. Sta. Ber. 1, 1000 m, 1 M2, 1 Juv, 1 P ♀ 2, 2 Cop ♀; Sta. Ber. 2, 1700 m, 1 unid. (not Cop ♂, dried out); Sta. Ber. 4, 1700 m, 2 unid. (not Cop ♂, dried out); Sta. Ber. 6, 1500 m, 1 Juv; Sta. Ber. 8, 1000 m, 5 M1, 3 M2, 2 Juv, 3 P ♀ 2, 5 Cop ♀, 3 Cop ♂ (including allotype); Sta. 118, 1135 to 1153 m, 1 M1, 3 M2, 3 Juv, 3 P ♀ 2 (including holotype).

LOCATION OF MATERIAL.—NMNH: holotype (USNM 143147); allotype (USNM 143148); WHOI Ber. 6 (USNM 143150); WHOI Ber. 8 (USNM 143149); WHOI 118 (USNM 143151). UCZM: WHOI Ber. 1.

DERIVATION OF NAME.—Referring to the uniquely rounded appearance of the pereonites in dorsal view. From the Greek *dinotos* (rounded) and *meros* (part).

The *americanus* Group of Species

This group comprises *Neotanais americanus, N. sandersi, N. laevispinosus, N. hadalis,* and *N. mesostenoceps.* It is, for the most part, noted for a lack of distinctive morphologic features compared to other groups (*N. hadalis* and *N. mesostenoceps* are more distinct and differ from the rest of the group in several characters). It is this lack of outstanding characters, particularly when distinguishing among members of the group, which has made correct identification of these species so difficult over the years. Indeed, *N. americanus, N. sandersi,* and *N. laevispinosus* can be considered sibling species (Mayr, 1963). The chelae of the copulatory males provide more easily usable taxonomic characters than those available in other stages. Unfortunately, only certain male stages are known.

STAGES OTHER THAN COPULATORY MALE (unknown for *Neotanais mesotenoceps*).—Uniquely lacking in easily noticeable identifying characters. Carapace with poorly developed anterolateral keels, oblique furrows, respiratory chambers, and chelipedal coxae. Pereonites plain, square, or slightly rectangular in dorsal view, without unusual features. Pleonites evenly rounded laterally or nearly so in dorsal view. Chela not remarkable: dorsal crest present and of various heights, five large distal teeth on fixed finger prominent and with generally rounded tips; dactylus evenly curved and about as long as fixed finger. Dactylar spines of pereopods II–IV always less than 0.3 times as long as article (unknown for *N. laevispinosus*).

COPULATORY MALES.—These males differ from other males in those nondimorphic characters listed above for other stages. In addition, the following characters are apparently distinct: chelipedal carpus stout and notably bent proximally, almost at right angles at times; ventral, distal seta of the same article thick and often of brown coloration but of about the same length as the slender proximal seta (in contrast with the *pfaffi* group of species). Short,

subterminal spines on the propodus of pereopod VII lacking serrations or, if serrate, imperfectly so, and often malformed and present in reduced numbers compared with those of other developmental stages.

REMARKS.—For additional information see the following key and the individual species diagnoses and accompanying figures. When dealing with "sibling" species, it is very difficult to construct a key which will transcend geographic variation and be usable by someone without detailed knowledge of the group.

Key to Species of the *americanus* Group

STAGES OTHER THAN COPULATORY MALE

1. Pleotelson long, width-length ratio only about 1.5; uropodal endopod stout and only two-thirds as long as pleon ....*N. hadalis*
   Pleotelson short, width-length ratio about 1.8 to 2.0; uropodal endopods slender and longer than pleon 2
2. Midventral surface of pleonites only barely, if at all, expanded into very low projections; pleonite 1 slightly narrower than pereonite 7 in dorsal view; pleonites apparently never bearing feathered hairs laterally. (Frequently serrations present on dactyli of pereopods II–IV.) ....*N. americanus*
   Midventral surface of pleonites clearly expanded into moderately large spurs; pleonite 1 about as wide as pereonite 7; pleonites bearing feathered hairs laterally. (Serrations never observed on dactyli of pereopods II–IV.) 3
3. Rostrum very low, scarcely, if at all, pointed; midventral pleonal spurs moderately long, but not sharply pointed and never recurved posteriorly, pleonite 1 being especially broad and low; short, subterminal carpal spine on pereopod II amply serrate ....*N. sandersi*
   Rostrum prominently pointed; midventral pleonal spurs relatively sharply pointed, at times recurved posteriorly, and pleonite 1 being especially elongate and pointed; short, subterminal carpal spine on pereopod II naked, except for about 2 irregular low teeth distally ....*N. laevispinosus*

COPULATORY MALES

1. Pleotelson comparatively long in dorsal view, width-length ratio about 1.5; articles of uropodal endopod stout, and endopod only about two-thirds as long as pleon; *or* anterior part of carapace expanded laterally and pleonites flared laterally in dorsal view and extended downward as relatively long, pointed, midventral spines 2
   Pleotelson comparatively short in dorsal view, width-length ratio about 1.8 to 2.0; articles of uropodal endopod slender, and endopod longer than pleon; sides of carapace parallel or of decreasing width anteriorly; pleonites more or less evenly rounded in dorsal view 3
2. Pleotelson relatively long in dorsal view, width-length ratio about 1.5; articles of uropodal endopod stout and endopod only about two-thirds as long as pleon; pleonites rounded midventrally in silhouette or extended midventrally as short blunt spurs, and evenly rounded laterally in dorsal view; carapace with sides markedly parallel or sloping slightly anteromedially in dorsal view in area of anterolateral keels ....*N. hadalis*
   Pleotelson relatively short in dorsal view, width-length ratio about 1.8 or more; articles of uropodal endopod slender and endopod longer than pleon; pleonites extended downward as long, pointed, midventral spines and flared laterally in dorsal view; carapace noticeably expanded laterally in area of anterolateral keels ....*N. mesostenoceps*
3. Carapace with sides parallel in area of anterolateral keels anterior to oblique furrows when viewed from above ....*N. sandersi*
   Carapace with sides sloping slightly anteromedially in area of anterolateral keels anterior to oblique furrows 4
4. Pleonites extended as bluntly tipped, downwardly directed midventral spurs; short, terminal propodal spine and subterminal carpal spine on pereopod II each bearing a row of teeth ....
   ....*N. americanus*
   Pleonites extended as low, moderately sharply tipped, posteriorly directed midventral spurs; short, terminal propodal spine and subterminal carpal spine on pereopod II both naked ....
   ....*N. laevispinosus*

Neotanais americanus Beddard, 1886

FIGURES 17-20, *97*

Neotanais americanus Beddard, 1886a:118 [in part, South American specimen only]; 1886b:124, pl. 26: figs. 4–6 [in part, South American specimen only].

Neotanais serratispinosus Norman and Stebbing.—Hansen, 1913:18, pl. 1: figs. 6a,b; pl. 2: figs. 1a–c [in part, only manca 2 and copulatory female].

Neotanais serratispinosus (Norman and Stebbing).—Lang, 1956b:469, figs. A1–14 [in part, female only].

Alaotanais serratispinosus Norman and Stebbing, 1886:111, pl. 23: fig. 1 [in part, specimen from *Valorous* Sta. 15 only].

DIAGNOSES (Atlantic populations only; see section on Pacific specimen under intraspecific variation below).—*Stages Other Than Copulatory Male*: *Pereonites 4–6 almost square in dorsal view (depending on degree to which animal is stretched), with areas of pereopodal attachment sometimes being visible from above. *Pleotelson short, about twice as wide as long, border slightly convex on either side posterior to uropods (in marked contrast to *Neotanais micromopher*. *Pleonites with low, posteriorly directed, and often rounded midventral spurs in lateral view; rounded laterally in dorsal view and bearing occasional short hairs laterally on epimeres. Cheliped with about 10 dorsal carpal setae; *propodus with substantial dorsal crest; the distal teeth generally rounded (cf. teeth in *Neotanais micromopher*); dactylus with about 3 brownish convexities or teeth pointed to various degrees. *Carapace with few prominent features: anterolateral keels, oblique furrows, respiratory chambers, and chelipedal coxae in dorsal view insignificantly developed; 1 or 2 short anterolateral and posterolateral setae present. Propodal and carpal setae of pereopods II–VII strongly developed and spinelike, at least those of pereopods II–IV with easily visible teeth; dactyli of pereopods II–IV often bearing slender distal teeth ventrally (in North Atlantic populations) similar to those of pereopods V–VII, the only instance of such serration known in the Neotanaidae (teeth sometimes invisible from certain angles); long, terminal propodal spines of pereopods II–IV very often with fewer widely spaced teeth than in other species; *short, terminal propodal spine of same legs with curved tip and 4 to 6 large, triangular teeth borne almost at right angles to axis of spine; *short, subterminal carpal spine of pereopod II almost straight and bearing 4 or 5 teeth of moderate size.

Copulatory Males (Gay Head–Bermuda Transect): *Pereonites 4–6 sloping gradually anteromedially from area of pereopodal coxae in dorsal view. *Pleonites rounded laterally with sides sloping forward from epimeres more gradually anteriorly than posteriorly as seen from above; *sternal spurs more pronounced midventrally than in other stages and slightly less posteriorly directed. *Carapace bearing relatively sharp rostrum, very distinct oblique furrows, and a series of other furrows (see Figure 17E); *chelipedal coxae prominent, anterior sides not quite parallel; number of setae on carapace and *shape of pleotelson shared with other stages. *Chelipedal carpi strongly bent but heavy, those of males with chela type B having a pronounced posterior hook at bend; bearing about 10 dorsal setae; *posterior ventral carpal seta thin and posteriorly directed, anterior seta straighter and thick, brown, and with broad base. Chela type A (primary male) with *dorsal keel of propodus thin and frayed along its distal half; *both fingers moderately bent medially; *dentition as in Figure 19E. Chela type B (secondary male) as in type A except *fixed finger strongly bent medially and *dentition as in Figure 19F.

DESCRIPTION OF PREPARATORY FEMALE 2 A (WHOI B. Sta. 76).—*Body* (Figure 17E): 6.9 mm long and 6.5 times longer than wide.

Carapace: Smooth, devoid of appreciable relief dorsally, lateral keels not flared dorsally, and oblique furrows faint. Anterolateral setae not observed (see "Intraspecific Variation," below); 2 posterolateral setae present on each side.

Pereonites: Appearing relatively square in dorsal view (many specimens appear much more nearly square than shown in Figure 17E); attachments of pereopods barely visible dorsally (see "Intraspecific Variation," below); bearing only occasional very short hairs laterally. Sternites with faint ridge midventrally.

Pleonites (Figures 17A, 18A): Rounded laterally in dorsal view; width of pleonites decreasing anteroposteriorly, giving slightly tapered appearance to pleon in dorsal view; short, scattered, epimeral hairs present dorsally. Sternites each gradually sloping downward posteriorly (in lateral view), forming very low spurs.

Pleotelson (Figure 17H): Considerably wider than long, width-length ratio, 2.0.
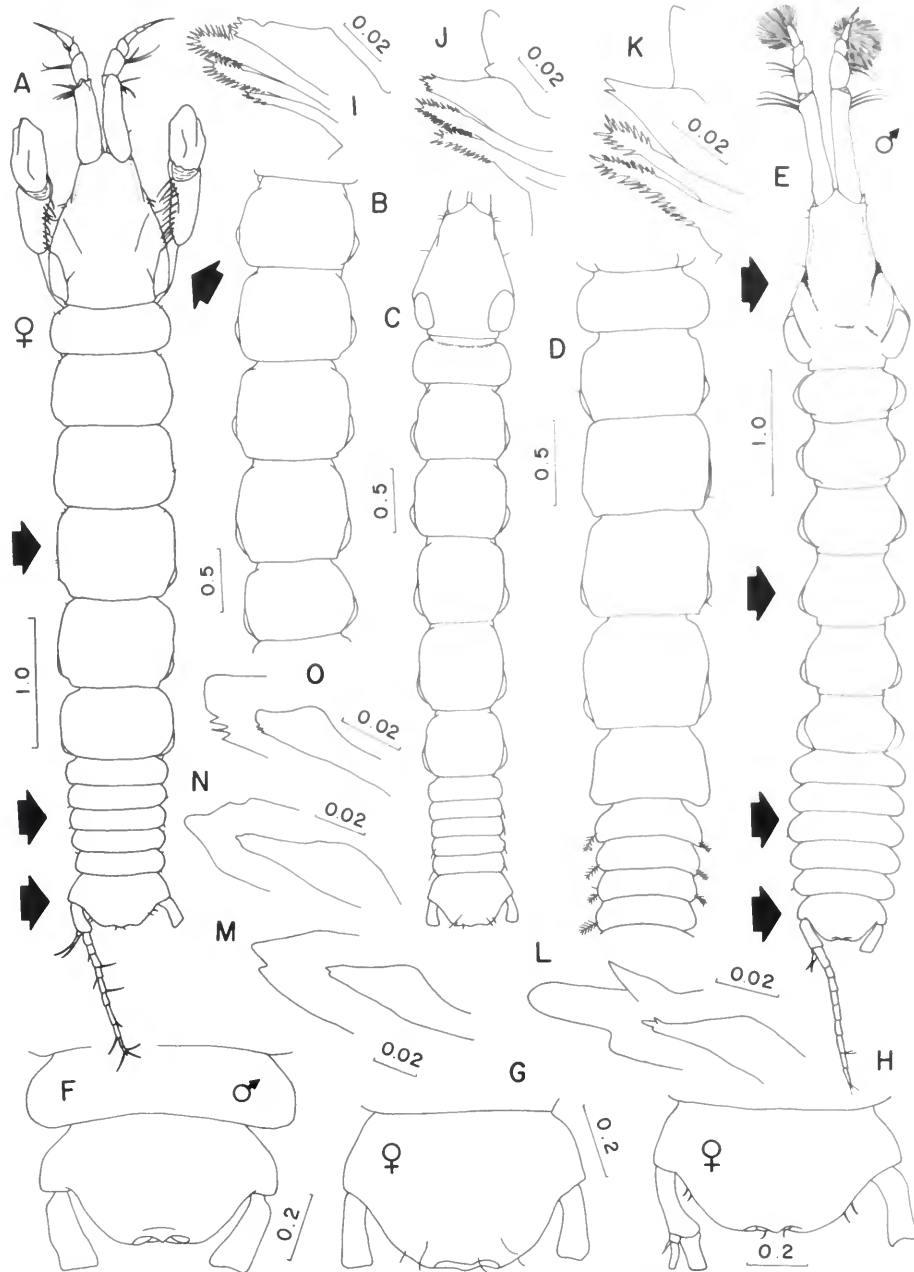
FIGURE 17.—*Neotanais americanus* Beddard: A, dorsal view, described preparatory female 2 A, North America, WHOI B. Sta. 76; B, same, a copulatory female, same station; C, juvenile, holotype, off Uruguay, *Challenger* Sta. 323; D, preparatory female 2, off Peru, *Anton Bruun* Sta. 179; E, described secondary copulatory male, WHOI B. Sta. 76; F, pleonite 5 and pleotelson, dorsal view, same animal; G, pleotelson, dorsal view, holotype; H, same, female A; I, incisive spines, right mandible, anterior view, preparatory female 2 C, same station; J, same, preparatory female 2 D, same station; K, same, holotype; L-N, most distal incisive spine, right mandible, anterior view, three specimens of various stages from the Argentine Basin, *Vema* Sta. 17-81; O, same, preparatory female 2, *Anton Bruun* Sta. 179.

FIGURE 18.—*Neotanais americanus* Beddard: A, molar teeth, right mandible, described prepara-
tory female 2 A, North America, WHOI B. Sta. 76; B, left mandible, same animal; C, left first
maxilla, posterior view, same animal; D, representative terminal spines of external endite, a
preparatory female 2, WHOI B. Sta. 84; E, pleon, lateral view, female A; F, same, juvenile,
holotype, off Uruguay, *Challenger* Sta. 323; G, same preparatory female 2, off Peru, *Anton Bruun*
Sta. 179; H, described copulatory male, WHOI B. Sta. 76; I, left cheliped, female A.
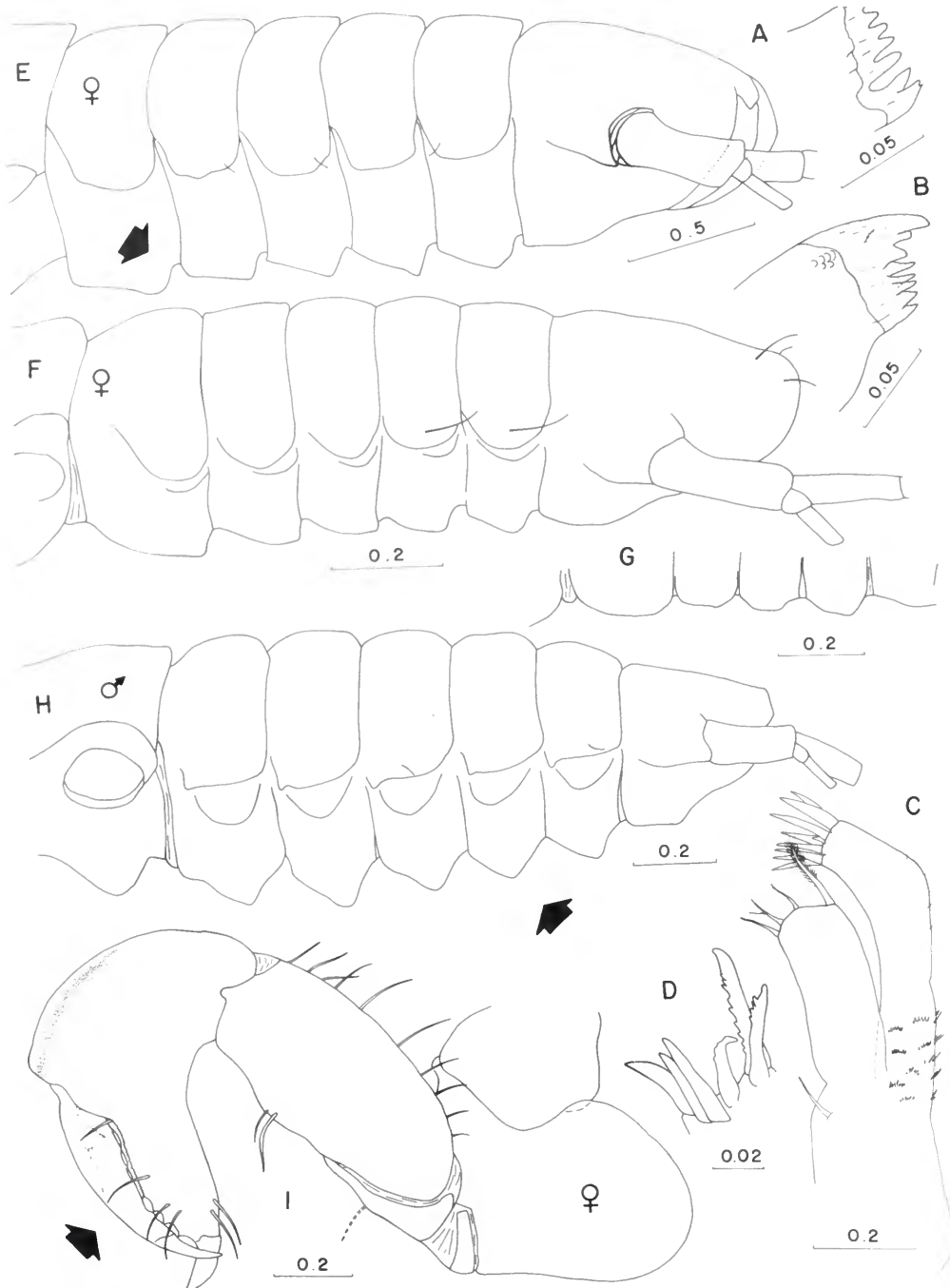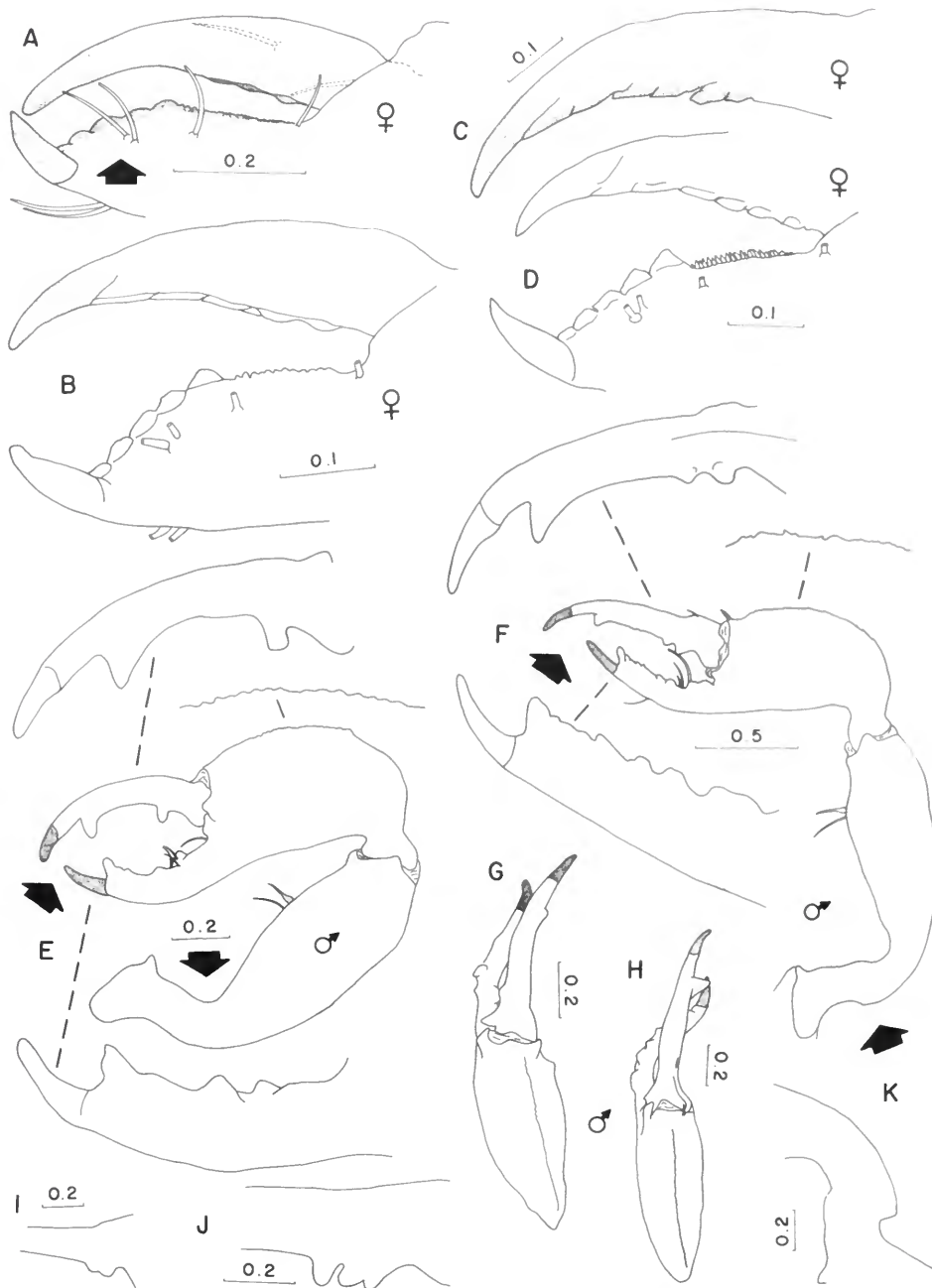
FIGURE 19.—*Neotanais americanus* Beddard: A, left chela, described preparatory female A, North America, WHOI B. Sta. 76; B, same, juvenile, holotype, off Uruguay, *Challenger* Sta. 323; C, chelipedal dactylus, preparatory female 2 C, WHOI B. Sta. 76; D, left chela, copulatory female, WHOI B. Sta. KK 3; E, same, with slightly oblique enlargements of fingers, primary copulatory male, WHOI B. Sta. 76 (see also K); F, same, described secondary copulatory male, same station; G, dorsal view of chela type A, male in E above; H, same, chela type B, described male; I, proximal dactylar teeth, secondary copulatory male, North America, *Eastward* Sta. 2756; J, same, WHOI B. Sta. 83; K, proximal bend in chelipedal carpus, slightly oblique, same animal.
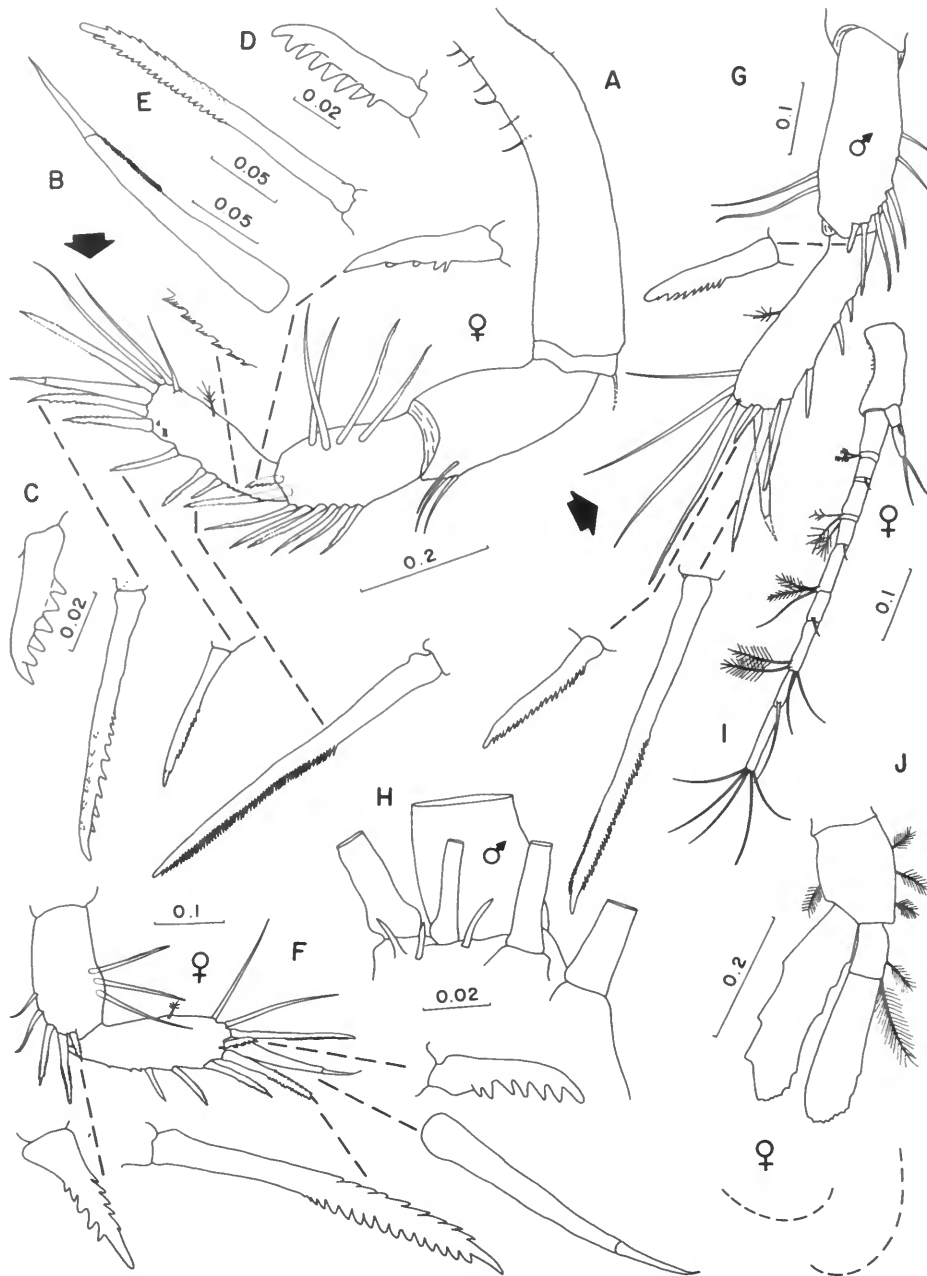
FIGURE 20.—*Neotanais americanus* Beddard: A, left pereopod II, posteroventral view, described preparatory female 2 A, North America, WHOI B. Sta. 76; B, dactylus of same, different view; C, short, terminal propodal spine, same appendage; D, same, a preparatory female 2, WHOI B. Sta. 70; E, distalmost long, terminal propodal spine, same appendage; F, distal portion of left pereopod II, anterior view, juvenile, holotype, off Uruguay, *Challenger* Sta. 323; G, same, right pereopod II, anterior view, described secondary copulatory male, WHOI B. Sta. 76; H, distal portion of propodus, right pereopod VII, posterior view, same animal; I, right uropod, lateral oblique view, preparatory female 2 C, WHOI B. Sta. 76; J, left pleopod, anterior view, female A.

First Antenna: First article 3.7 times longer than wide.

Right Mandible (see Figures 17I,J; 18A): First 2 incisive spines serrate on both sides, third spine with "comb" of teeth distally.

Left Mandible (Figure 18B): Incisive spines as in right mandible. Lacinia mobilis with 3 large, pointed teeth; posterior lobe uncleft.

First Maxilla: As in Figure 18C.

Second Maxilla: Forked spines on fixed endite bifid. Twelve setae present in medial row along with 2 stout spines.

Maxilliped: 6 setae on coxa. Setal formula of palp, (1,0,6+1,4+4,8).

Cheliped (Figures 18I, 19A): Carpus bearing 10 long dorsal setae. Propodal crest of appreciable size. Fixed finger bearing about 30 denticles anteriorly on cutting edge; distal teeth rounded and brown. Setae on chela long and thick. Dactylus with only 3 low, brown swellings proximally on cutting edge. Dactylar seta long and thick.

Pereopod II (Figure 20A,B): Setae generally low in number and large in size, anterior setae of propodus and carpus spinelike. Setal formula, (3,3,7,4). Short, terminal propodal spine strongly curved distally and bearing 4 or 5 heavy, triangular teeth oriented at right angles to axis of spine. Two long, terminal propodal spines with teeth large and scattered along spine. First (distal) seta in anterior propodal row long, heavy, spinelike, and bearing sizable teeth; remaining setae with somewhat smaller teeth. Short, subterminal carpal spine straight, thick, and with about 4 irregular teeth on either side. First seta in anterior row especially thick and dentate. Dactylus bearing slender teeth or setules on either side distally and ventrally; spine 0.4 times as long as article.

Pereopods III–VII: Pereopods III and IV also with 2 long, terminal propodal spines identical to those of pereopod II. Setae of pereopods V–VII also thick. Setal formula of pereopod V, (6,4,5,7). Row of short, subterminal propodal spines on pereopod VII not observed in this specimen; 2 other specimens (same stage) from this station with 5 and 7 spines; dentition of these spines similar to those of most species.

Pleopods (Figure 20J): Setal formula, (1,3) (3,5,5) (0,2;0,8,2). Protopodal setae short and slender.

Uropods (Figure 20I): Endopods slender; exopods 0.9 times length of first endopodal article.

DESCRIPTION OF SECONDARY COPULATORY MALE A (WHOI B. Sta. 76).—*Body* (Figure 17E): 5.9 mm long and 6.0 times longer than wide.

Carapace: 1.6 times longer than wide. Rostral area acute, anterolateral keels moderately developed; oblique furrows deep and proceeding posteriorly to a deep transverse furrow; 2 short furrows extending lateral to transverse furrow on either side. Anterolateral setae 1 and 2 in number on either side; posterolateral setae of similar number but of greater length.

Pereonites: 3–7 narrow anteriorly, sloping gradually anteromedially anterior to pereopods and sloping abruptly posteriorly to legs. Genital cones prominent.

Pleonites (Figures 17E, 18H): Rounded laterally in dorsal view. Pleonite 1 wider than pleonite 5, giving pleon a slightly tapered appearance. Dorsal epimeral hairs scattered, single, and short. Sternites expanded into bluntly tipped midventral spurs considerably longer than those of other stages.

Pleotelson (Figure 17F): 1.9 times wider than long in dorsal view. Anal area distorted. Ventral surface with median angularity.

First Antenna: First article 5.2 times longer than wide.

Mandibles: Incisive tips elongate, pressed closely to labrum, and with rudimentary incisive spines.

Second Maxilla: Bearing prominent setulated setae representing movable endite and 2 or 3 groups of smaller and irregular setae.

Maxilliped: Four setae on coxa; setal formula, (0,0,0,10,9).

Cheliped (Figures 19F,H): Carpus strongly bent (right angle) with a slight posterior convexity just below bend; proximal ventral seta weak and recurved, distal seta strong, brown, and with expanded base; about 8 to 10 dorsal setae present (broken in this specimen). Dorsal keel of propodus thin and with irregularly serrate edge. Median propodal seta stout and brown. Fixed finger strongly medially bent. Most proximal tooth flat-topped, wide, and followed by about 5 variously shaped blunt teeth, the last of which is taller and leans distally. Setae as in Figure 19F. Dactylus relatively straight in dorsal view; proximal teeth 2 in number and moderate in size. Distal tooth much larger, triangular, and strongly medially bent; medial seta weak. Surface of dactylus "beaded" lightly in places.

Pereopods II–VII (Figure 20G,H): Pereopod II similar to that of female but setae not as stout; setal formula, (3,4,6,2). Long, terminal propodal spines 2 in number and with sharp, fine, tightly packed teeth. Short spines on both propodus and carpus different from those of other stages: short, terminal propodal spine of pereopods II–IV slender, straight, and with a row of many, moderately sized teeth along one entire side; short, subterminal carpal spine of pereopod II also straight and with similar teeth along distal two-thirds of spine only. Dactylus of pereopods II–IV without distal serrations (cf. other stages). Pereopod VII with 3 exceedingly short, thin, rudimentary spines distally on propodus (remnant of short, subterminal spine row of other stages).

Pleopods: Setal formula, (2,1?) (3,7,5) (0,2;0,7,3). Terminal endopodal setae 1.6 times longer than endopod.

Uropods: With 9 endopodal articles (one side only, other broken). First endopodal article bearing a number (about 15) of broom setae on dorsolateral side (not figured).

INTRASPECIFIC VARIATION IN THE NORTH ATLANTIC.—*Stages Other Than Copulatory Male*: a. Specimens from Gay Head–Bermuda Transect (WHOI B. Sta. 64): Representative body lengths (numbers of individuals considered are in parentheses): manca 1 (1), 2.3 mm; juvenile (9), 3.5 to 6.2 mm; preparatory female 2 (8), 5.8 to 6.6 mm; copulatory female (10), 6.3 to 7.9 mm; preparatory male (1), 6.7 mm. The anterolateral and posterolateral setae on the carapace both vary between one and two. Some animals have a few heavily toothed spines on the external endite of the first maxilla (Figure 18D). The number of spines (8) as found on female A described above is aberrant (Figure 18c); other individuals have 10. The denticles on the propodal finger of the cheliped vary considerably in height (Figure 19A,B,D); the teeth on the dactylus often are anteriorly directed, pointed, and of variable number (Figure 19A–D). The dactyli of pereopods II–IV sometimes lack setules. The long, terminal propodal spines of these legs sometimes have more closely packed teeth than those of female A (Figure 20E). There is some indication that lack of dactylar setules and the presence of more closely packed teeth may be common at deeper stations.

b. Copulatory Female from *Ingolf* Sta. 22, Davis Strait: The length is 6.7 mm. The midventral

points of the pleonites are more blunt than those of other specimens. All significant features, however, are similar to female A described above. The *Noratlante* specimens from the same general area lack the dactylar setules on pereopods II–IV.

c. Juvenile from *Valorous* Sta. 15, Southeast of Greenland: This animal was one of three specimens on which Norman and Stebbing (1886) erected *Neotanais serratispinosus*. It is the one illustrated in their plate 23 and apparently it was used as the basis of their written description. It agrees with female A down to the smaller details such as the presence of distal serrations on the dactyli of pereopods II–IV. Its body length is 4.2 mm. See "Remarks," below.

d. Preparatory Female from the Bay of Biscay: This preparatory female (length 7.2 mm) almost perfectly resembled the described female from the Gay Head–Bermuda Transect in all details including carapace setation; shapes of carapace, pereonites, pleonites, and pleotelson; and dentition of the long and short specialized spines and the dactyli of pereopods II–IV. It differed in having two small feathered hairs on each pleonal epimere.

e. Specimens from the Canary Islands: Two specimens were collected by the *Discovery* in the vicinity of the Canary Islands. These have been assigned to *Neotanais americanus* because they resemble this species more closely than others. It is difficult to say much about the manca 1 (body length, 4.5 mm). The juvenile (body length, 7.2 mm) differs from the holotype (off Uruguay) in having more pronounced spurs midventrally on the pleon, similar to the North American animals. It differs from most North American specimens in lacking dactylar serrations on pereopods II–IV, and the proportions of the pleotelson more nearly resemble those of the South American holotype. The body lengths of both specimens are longer than for equivalent stages of North American populations. The long, terminal propodal spines of pereopods II–IV have small and more numerous teeth that are set more closely together than in other populations examined. The setal formula of pereopod II is (1,4,3,3). The short, terminal propodal spine of pereopod II bears only a couple of pointed teeth on each side. The carapace bears a single anterolateral seta and a single posterolateral seta. The penultimate dorsal seta on the chelipedal carpus is much longer than the other setae in this

row. The depths at which these animals were collected are within the range in which one would expect to find *Neotanais americanus*.

Copulatory Males: Representative Body Lengths (WHOI B. Sta. 64; numbers of individuals considered are in parentheses): Primary copulatory male (3), 5.7 to 7.2 mm; secondary copulatory male (4), 7.7 to 8.6 mm.

Cheliped Type A (primary male B, WHOI B. Sta. 76): The carpus is similar to that of animals with chela type B but lacks the posterior convexity below the proximal bend. The fixed finger is strongly bent medially and bears two moderate teeth proximally, the first of which is medially directed, and one high, narrow tooth distally following two low convexities. The dactylus bears two prominent teeth: the proximal tooth is narrow and round-tipped, the distal tooth triangular and bluntly tipped.

Cheliped Type B: The posterior convexity of the carpus is often more prominent than in the described male (e.g., Figure 19κ). The fixed finger always has a broad proximal tooth separated from the other teeth by a gap, but the other teeth vary in shape and in size. The proximal dactylar teeth are sometimes fused (Figure 19ι) and usually are two in number but occasionally there are three (Figure 19ϳ).

Carapace: The posterolateral setae are notably longer and heavier in some specimens than in the described male (e.g., WHOI B. Sta. 80 and *Eastward* Sta. 5474 from deep water).

Pereopods II–IV: Dactylar setae are sometimes present as in the other stages at WHOI B. Sta. 76.

INTRASPECIFIC VARIATION IN THE SOUTH ATLANTIC.—*Juvenile Holotype from Challenger Sta. 323*: The length of this specimen is 6.1 mm. Several figures of this specimen, inadequately illustrated by Beddard (1886b), are presented here. The pereonites are not as square in dorsal view as in female A (described above), but the variation is not appreciably greater than that among the other animals from WHOI B. Sta. 76 (cf. Figure 17A–C). Pereonite 2 has a more marked anterior depression than female A. The pleonal hairs are longer but this condition was also observed on the *Ingolf* specimen from the Davis Strait. The pleotelson is only 1.6 times wider than long. The pleonal sternites are blunt medially, but this also was noted

in the *Ingolf* specimen from the North Atlantic (Figure 18F).

The tip of the most distal incisive spine on the right maxilla is cleft only once (Figure 17κ). In the Antarctic specimen from IWSOE Sta. 44 (see under specimen from Weddell Sea, below), which in all other respects is identical with the holotype, this spine is serrate terminally, similar to the North Atlantic specimens; however, the animals from the Argentine Basin (*Vema* 17–81) are closer to the holotype in this feature than to North Atlantic specimens or to the Antarctic specimen (Figure 17L–N).

The chela is like that of the North Atlantic populations (Figure 19B), as is peropod 11 (Figure 20F), except that the dactylar spines on some legs are longer. The dactylus is without serration distally and the teeth on the long, terminal propodal spines are not widely spaced. The pleopodal setal formula is (2,2) (2,3,4) (0,2;0,4,2). The shape of the pleopods is like that of female A, described above.

Specimens from Argentine Basin: Four additional specimens are known from *Vema* 17–81 at 5330 m. They agree with the *Challenger* holotype in almost all characters. The third right incisive mandibular spine of the three oldest specimens were compared (Figure 17L–N) and found to be consistently similar to that of the holotype but unlike the North Atlantic and Weddell Sea specimens. There are two or three anterolateral setae and two posterolateral setae on the carapace of these animals.

The specimens include a preparatory female 1 with faint male gonopore anlagen, a manca 1, and an animal with no secondary sexual characters except very faint gonopore anlagen and a length almost as great as that of the preparatory female 1.

Specimens from Weddell Sea, Antarctica: The specimens from IWSOE Sta. 0008 resemble the holotype in the midventral shape of the pleonal sternites (lateral view) and in the shape of the pleotelson (dorsal view). Pereonites 4–6 are notably square in dorsal view, and each of the pleonal epimeres bears one or two feathered setae. The setal formula of pereopod II of the copulatory female is (5,5,6,7), with the short, terminal propodal spine bearing three large, slightly forwardly directed teeth; the two long terminal spines have slender teeth. There are 12 short, subterminal propodal spines on pereopod VII. The carapace

bears a single long anterolateral and posterolateral seta on each side.

The third incisive spine of the right mandible is serrate terminally in the juvenile at IWSOE Sta. 44 as in North Atlantic populations. That of the copulatory female from IWSOE Sta. 0008 is similar terminally but also has serrations similar to those of the other incisive spines along the outer third of the inner side.

The specimen from IWSOE Sta. 0019 has two long anterolateral and three posterolateral setae on its carapace. The areas over the pereopods on the pereonites are wider than in the other specimens, and the pereonites bear long, lateral hairs. This specimen has feathered pleonal hairs as do the others. Whether it belongs to the same species as the other specimens is not clear. More material will be required to determine its relationships clearly.

INTRASPECIFIC VARIATION IN THE PACIFIC.—*Preparatory Female 2 from* Anton Bruun *Sta. 179 (4823 to 4925 m), off Peru*: This animal resembles *Neotanais americanus* from the Gay Head–Bermuda Transect in the following ways: (1) pereonite shape in dorsal view; (2) carapace shape; (3) shape of chela; (4) third incisive spine of right mandible with same serrations distally (Figure 17o); (5) pereopod II with 2 long, terminal propodal spines and the teeth loosely spaced; (6) short, terminal propodal spine with 3 or 4 large, triangular teeth; (7) short, subterminal carpal spine similar (if with only 2 or 3 somewhat smaller teeth); (8) 1 dactylus apparently bearing a few setules distally, but cuticle blistered and difficult to determine this precisely.

The following differences from the North Atlantic specimens were observed: (1) the midventral silhouette of the pleonites is much smoother (but not round—Figure 18G); (2) the pleonites bear feathered setae laterally (Figure 17D); (3) the distalmost setae in the anterior rows of pereopods II–IV are not as thick or the setules as long; and (4) the dactylar spines on pereopods II–IV sometimes are considerably longer and more tapered distally.

These differences, especially the first three, may be significant; however, in light of the large number of similarities to North Atlantic populations, this specimen is assigned to *Neotanais americanus*. Unfortunately, the pleotelson and uropods are missing.

REMARKS.—Descriptions of both the primary and secondary copulatory males of *Neotanais americanus* and diagnoses for both sexes are presented here for the first time.

Neotanais americanus was first described in February 1886 by Beddard (1886a) from a juvenile collected by the *Challenger* off Uruguay in 1876. Beddard's original description, a single paragraph, contains little useful information, being rather a list of generic characters. His description was amplified in a longer paper (Beddard, 1886b), published in the *Challenger* Reports, wherein he presents several figures in support of his description.

The following corrections or additions are made to Beddard's (1886b) description. (1) Beddard claimed that the holotype was a male when in fact it is a juvenile. (2) On page 125 and figure 5 of plate 16 he indicates that the first antennae have three esthetascs distally, whereas there are only two. (3) He did not examine the mouthparts of the holotype because it was mounted in balsam; but it now has been dismounted and the mandibles studied and drawn (Figure 17κ). (4) In his discussion of the cheliped, Beddard overlooks the ischium and states that the carpus articulates directly with the basis. Although the ischium and merus are small, the carpus does not articulate with the basis. (5) The basis is taken to be the first article in pereopods II–IV in Beddard's description. (6) In figure 4 of his plate 16, Beddard shows a symmetrical, transverse dorsal furrow two-thirds of the way back on the carapace. This is not a furrow but an obvious break in the carapace. (7) The second specimen mentioned by Beddard from *Challenger* Sta. 45 is *Neotanais micromopher* (q.v.).

In October of the same year, Norman and Stebbing (1886) described *Alaotanais serratispinosus* on the basis of three specimens collected in 1875 at *Valorous* Sta. 15. Two of these specimens, one a fragment, actually are *Neotanais peculiaris* (q.v.). The third, on which a number of figures (on plate 23) and apparently most of their text were based, is *N. americanus*. It is discussed under intraspecific variation above. *Neotanais serratispinosus* is therefore a junior synonym of *N. americanus*.

The depth and position given for *Valorous* Sta. 15 by Norman and Stebbing (1886:113) are at variance with those presented by Carpenter (1877) and Jeffreys (1877) in their papers summarizing the general results of the expedition. Norman himself, in a section in Jeffrey's paper dealing with the

TABLE 4.—*Examined material of* Neotanais americanus *Beddard*

Program or ship	Station no.	General location	Depth (meters)	Material
		NORTH ATLANTIC		
WHOI Benthic	HH 3	Gay Head–Bermuda Transect	2900	1 M1, 1 M2, 1 P♀2
	KK 3		4758	1 ?Cop ♀
	63		2891	1 M1, 2 Juv, 1 Juv or P♂, 1 P♀2
	64		2886	1 M1, 10 Juv, 10 P♀2, 11 Cop ♀, 1 P♂, 3 1°Cop ♂, 4 2°Cop ♂
	65		2891	7 M1, 1 Juv
	66		2802	6 M1, 3 M2, 5 Juv, 1 ?Juv or P♂, 2 Cop ♀, 1 1°Cop ♂, 2 2°Cop ♂
	69		4663	1 Juv
	70		4680	2 P♀2
	76		2862	7 Juv, 12 P♀2, 6 Cop ♀, 2 P♂, 3 ?P♂, 3 1°Cop ♂, 4 2°Cop ♀, 1 fgmt.
	78		3828	1 Cop ♂ (fgmt.)
	80		4970	1 P♀2, 1 1°Cop ♂, 1 Cop ♂ (fgmt.)
	83		5000	1 2°Cop ♂
	84		4749	2 Juv, 1 P♀2
	92		4694	1 P♀2
	95		3753	3 Juv
	109		4750	1 P♂
	120		5018–5023	1 M2
	121		4800	1 Juv, 1 P♂
	122		4833	1 P♂
	126		3806	2 Juv, 1 P♀1
Albatross	2570	SE of Georges Bank	3316	4 Juv, 1 P♀2, 1 Cop ♀
Discovery	6710	S of Gran Canaria Is.	2670	1 M1
	6711		2988	1 Juv
Eastward	2756	E of Cape Hatteras, North Carolina	4460	2 Juv, 2 P♀2, 3 Cop ♀, 1 P♂, 1 2°Cop ♂
	5474		5340	1 2°Cop ♂ (fgmt.)
	5481		5080	1 Juv
	6228	SE of Cape Hatteras	3057	1 P♀2, 1 Cop ♀
	7547		3780	1 Juv
Ingolf	22	SW of Greenland	3474	1 M1, 1 Cop ♀
Noratlante	019, E003	E of Labrador	4120	1 M1, 1 M2, 3 Juv, 1 P♀1, 2 Cop ♀
	026, E004		3680	1 M1
	042, E006	Labrador Sea	3430	2 M1, 2 Juv, 1 P♀2, 1 fgmt.
	111, B016	Bay of Biscay	4729	1 P♀2
Valorous	15	SE of Greenland	2715	1 Juv (see "Remarks")
		SOUTH ATLANTIC		
Challenger	323	Off Rio de la Plata, Uruguay	3475	1 Juv (holotype)
IWSOE	44	Weddell Sea, Antarctica	3995	1 ?Juv (fgmt.)
	0001		513	1 M1
	0008		570	1 M2, 3 Juv, 1 Cop ♀
	0019		1447	1 ?Juv
Vema	17–81	Argentine Basin	5329–5332	1 M1, 1 Juv, 1 P♀1, 1 P♂
		PACIFIC		
Anton Bruun	179	Off Peru	4832–4925	1 P♀2

Crustacea, agrees with these, and they are presented in Table 4.

Norman and Stebbing described *Alaotanais laevispinosus* in the same paper in which they described *A. serratispinosus*. *A. laevispinosus* is based on a copulatory male collected off the coast of Ireland at *Porcupine* Sta. 1. Lang (1956b; 1968) has indicated that this animal represents the copulatory male of *Neotanais serratispinosus* (=*N. americanus*), which is unlikely (see remarks under *N. laevispinosus*).

In his monograph on the Tanaidacea collected by the *Ingolf* Expedition, Hansen (1913) gives a partial description of one of three specimens—referred by him to *Neotanais serratispinosus* (=*N. americanus*)—collected at Sta. 22. In fact, only two of these specimens are *N. americanus*: a copulatory female, described by Hansen, and a manca 2. The third specimen, a juvenile, is *N. micromopher* (q.v.). The confusion of these two species has occurred commonly, and the differences between them are discussed under *Neotanais micromopher*.

In 1956 Lang (1956b) described the two pairs of antennae and mouthparts of the holotype of *Alaotanais serratispinosus*, the latter for the first time. In the same year, Wolff (1956c) described *Neotanais serratispinosus hadalis*, here referred to as *N. hadalis*, from the *Galathea* collections in the Kermedec Trench. These animals definitely are not conspecific with *N. americanus* (see *N. hadalis*).

Kudinova–Pasternak (1965a) described a single female from the Bougainville Trench which she refers to *Neotanais serratispinosus*. This specimen almost certainly is not *N. americanus* (see *N. hadalis*).

Some authors have made much of the supposedly wide geographic and vertical distribution of this species. It was thought to range from Ireland in the North Atlantic to the Bougainville Trench in the South Pacific and to have a vertical distribution from about 680 m off Ireland to 8300 m in the Kermedec Trench. These animals actually represent a number of species which, along with others, comprise the *americanus* group of species.

With regard to the distribution of *Neotanais americanus*, further collecting in the Pacific probably will show that the specimen from off Peru (*Anton Bruun* Sta. 179) belongs to a species distinct from *N. americanus*.

MATERIAL.—See Table 4.

LOCATION OF MATERIAL.—BMNH: holotype (Reg. No. 1889.4.2′/108, formerly microslide, now dismounted); *Valorous* 15 (Reg. No. 1903.5.20.73, microslides 1911.11.8.375 and 376). AMNH: *Vema* 17–81 (AMNH 14.888). UCZM: *Ingolf* 22; WHOI 63. NMNH: *Albatross* 2570 (USNM 41860); *Anton Bruun* 179 (USNM 143156); *Discovery* 6710 (USNM 143157); *Discovery* 6711 (USNM 143158); IWSOE 44 (USNM 143163); IWSOE 0001 (USNM 143164); IWSOE 0008 (USNM 143165); IWSOE 0019 (USNM 143166); *Noratlante* 019, E003 (USNM 143159); *Noratlante* 026, E004 (USNM 143160); *Noratlante* 042, E006 (USNM 143161); *Noratlante* 111, B016 (USNM 143162); WHOI 64 (USNM 143152); WHOI 66 (USNM 143154); WHOI 76 (USNM 143153); WHOI 84 (USNM 143155).

DISTRIBUTION.—*Neotanais americanus* has been found from Greenland to the Antarctic in the western Atlantic and from the Bay of Biscay and Canary Islands in the eastern Atlantic. On the Gay Head–Bermuda Transect it is a deepwater species, having been collected from about 2800 to 5020 m. In the Antarctic, at IWSOE Stas. 0001 and 0008, it has been found in depths as shallow as 513 m. One specimen collected off Peru has been assigned to this species.

Neotanais sandersi, new species

FIGURES 21-24, *102*

DIAGNOSES (Atlantic populations only; see intraspecific variation below).—*Stages Other Than Copulatory Male*: *Pereonites 3–7 rectangular in dorsal view, wider than long; bearing 2 relatively long hairs above pereopodal coxae, the widest section of each pereonite. *Pleotelson appreciably wider than long. *Posteriorly directed midventral spurs on pleonites similar to those of *Neotanais americanus* but longer and more easily visible; 1 or 2 lateral, feathered hairs on each pleonal epimere. Cheliped almost identical to that of *Neotanais americanus*; about 10 long, dorsal carpal setae present; chela appearing a little shorter relatively than in *N. americanus*; distal teeth on fixed finger somewhat angular but generally rounded; dactylus with about 3 brownish convexities of variable sharpness and degree of separation from dactylus along cutting edge. Carapace smooth along sides posteriorly in dorsal view, respiratory chambers
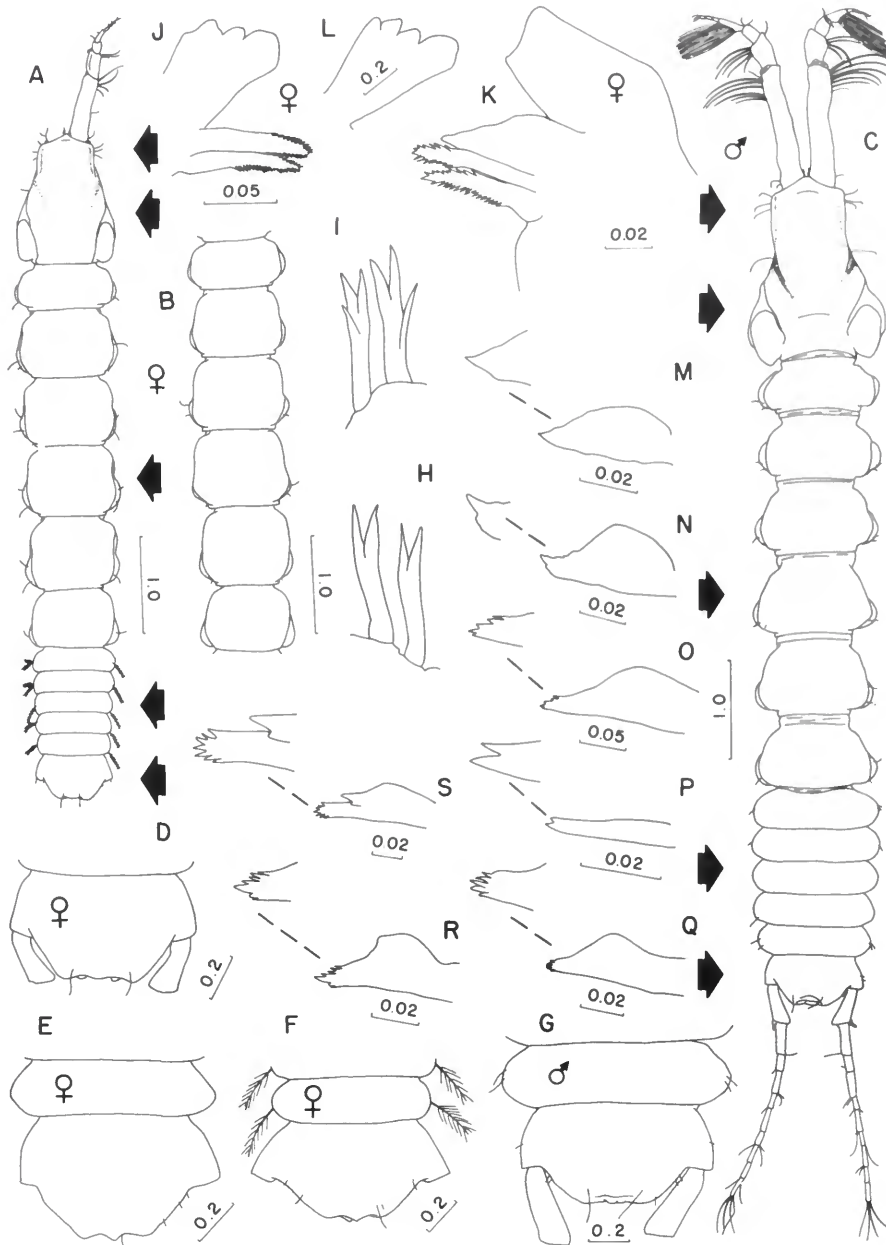
FIGURE 21.—*Neotanais sandersi*, new species: A, dorsal view, preparatory male, holotype, WHOI B. Sta. 62; B, same, copulatory female B, off Chile, *Vema* 17–5; C, same, described copulatory male, Sta. 62; D, pleotelson, dorsal view, holotype; E, same, copulatory female, Bay of Biscay, *Sarsia* Sta. 44; F, same, female B; G, same, described copulatory male; H, cleft spine of fixed endite on right second maxilla, holotype; I, same, left side; J, incisive spines and lacinia mobilis, left mandible, anterior view, holotype; K, pars incisiva, right mandible, holotype; L, lacinia mobilis, female B; M, distalmost spine, right mandible, copulatory female, Sta. GH 3; N, same, juvenile, Sta. F 1; O, same, a female, Sta. 103; P, same, manca 1, Sta. 128; Q, same, female B; R, same, female A, off Chile, *Vema* Sta. 17–5; s, same, female from Bay of Biscay.
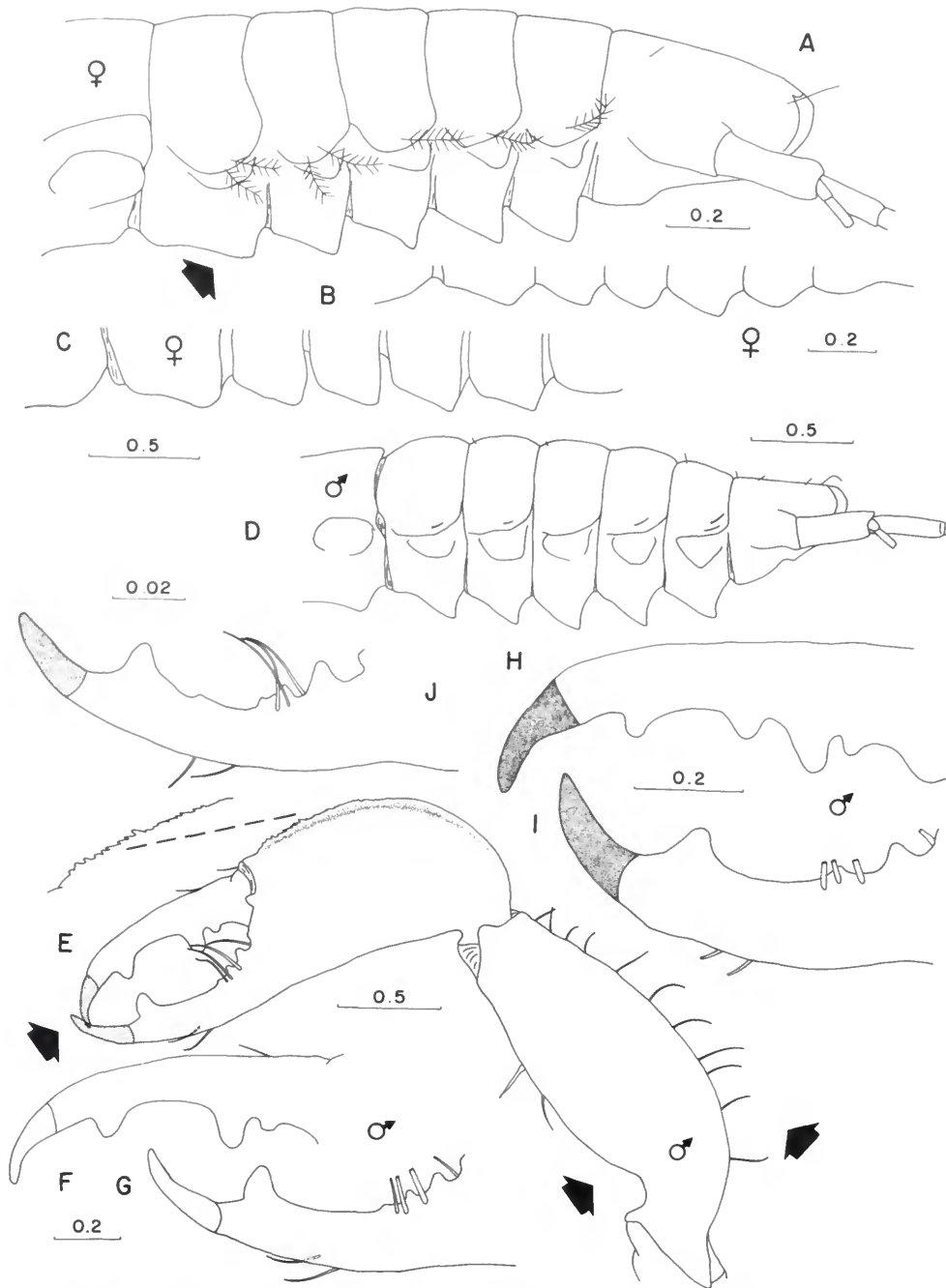
FIGURE 22.—*Neotanais sandersi*, new species: A, pleon, lateral view, preparatory male, holotype, WHOI B. Sta. 62; B, same, copulatory female, Bay of Biscay, *Sarsia* Sta. 44; C, same, copulatory female B, off Chile, *Vema* Sta. 17–5; D, same, described copulatory male, Sta. 62; E, left cheliped, same animal; F, G, enlargements of dactylus and fixed finger, same animal (E); H, I, same, copulatory male, *Eastward* Sta. 2756; J, fixed finger, copulatory male, CMS Sta. 2146.

and chelipedal coxae not outstanding; oblique furrows faint; 2 or 3 anterolateral setae and a single posterolateral seta usually present; rostrum low, anterior margin on either side only slightly concave. Propodal and carpal setae of pereopods II–VII heavy and spinelike; those of pereopods II–IV with prominent teeth; short, terminal propodal spine with curved tip and about 8 large, forwardly directed teeth; short, subterminal carpal spine slender, straight, and bearing about 7 slender, forwardly directed teeth.

Copulatory Male (only one type known): *Pereonites 4–7 appearing much wider than long, anterior sides sloping gradually anteromedially from pereopods to anterior margin. *Pleonites rounded laterally; each epimere bearing 1 or 2 unfeathered dorsal hairs; *sternites strongly pointed midventrally, spurs slightly recurved. *Pleotelson similar to, but shorter than, that of other stages. *Carapace with blunt rostrum with only slightly concave sides; *anterolateral keels prominent, parallel, and proceeding posteriorly to the deep, oblique furrows which nearly meet medially; respiratory chambers and chelipedal coxae prominent in dorsal view. Pereopods II–VII with stout setae toothed similar to those of other stages. *Chelipedal carpus very stout, bent relatively little, and with up to 10 or more dorsal setae; *proximal ventral seta fine and posteriorly directed, distal seta brown, straight, stiff, and swollen basally; *dorsal propodal crest very thin and with edge frayed along distal half; neither finger strongly bent; *teeth as in Figures 22E–J, 23.

DESCRIPTION OF PREPARATORY MALE HOLOTYPE (WHOI B. Sta. 62).—Body (Figure 21A): 6.8 mm long and 6.8 times longer than wide.

Carapace: 1.3 times longer than wide, oblique furrows moderate in depth, not prominent. Anterolateral setae moderately long and 3 in number; followed by a single posterior seta. Slight transverse depression present behind rostral area. Respiratory chambers and chelipedal coxae not prominently inflated as viewed from above.

Pereonites: Seemingly wider than long in dorsal view, width-length ratio of pereonite 5, 1.3. Each pereonite bearing 2 slender hairs laterally above each pereopod.

Pleonites (Figures 21A, 22A): Rounded laterally in dorsal view, pleonite 5 only slightly more narrow than pleonite 1. Epimeres bearing 1 or 2 feath-

ered hairs laterally. Sternites, especially 2 through 5, with marked, posteriorly directed midventral spurs.

Pleotelson (Figures 21A,D, 22A): Short, width-length ratio, 1.8. Sides posterior to uropods slightly convex but almost straight. Posterior edge wide and almost parallel to anterior edge. Clearly articulated with pleonite 5.

First Antenna: Length-width ratio of article 1, 3.6.

Right Mandible (Figure 21K): Proximal two incisive spines serrate on both sides. Third spine pointed distally and not serrate.

Left Mandible (Figure 21J): Incisive spines as on right mandible. Lacinia mobilis with 2 blunt teeth and uncleft posterior lobe.

Second Maxilla (Figure 21H,I): Medial row with 15 feathered setae and 2 spines with split tips. Forked spines of fixed endite both trifid on left side and bifid on right side.

Maxilliped: Setal formula of palp, (1,0,5+1,6,8).

Cheliped (Figure 24A,B): Carpus with 11 long dorsal setae. Propodus with dorsal crest prominent. Fixed finger bearing about 25 low denticles proximally; distal teeth rounded and with irregular crests. Dactylus with 3 irregular, rounded teeth; seta large. All teeth, denticles, and distal "claws" of chela are brown.

Pereopods II–VII (Figure 24D): Dactylar spine straight, 0.4 times as long as article. Anterior propodal and carpal setae (particularly distal anterior setae of latter article) heavy, spinelike, and with toothlike setules. Short, terminal propodal spine
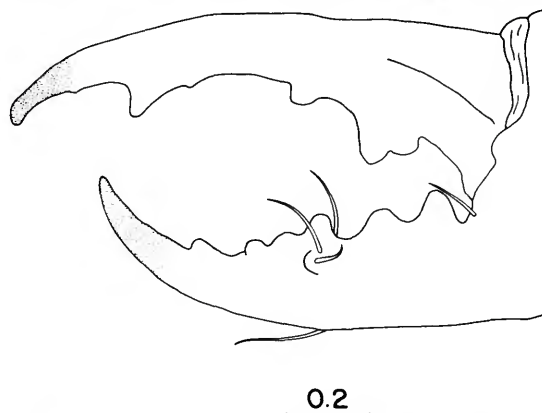

0.2

FIGURE 23.—Neotanais sandersi, new species: left chela of copulatory male from the eastern Atlantic (Noratlante Sta. 003, E001).

of pereopods II–IV curved at tip and with 8 large teeth; 2 long, terminal propodal spines with moderately closely set teeth. Stout, subterminal carpal spine of pereopod II straight and bearing 7 distally directed teeth. Pereopod VII with row of 7 short, subterminal propodal spines.

Pleopods: Terminal endopodal setae in a distinct row. Setal formula, (2,2) (3,7,5) (0,3;0,7,4). Setules very long. Tips of medial endopodal setae very long, finely serrate on at least distalmost seta. Generally very similar to those of *Neotanais americanus*.

Uropods: Each endopod with 9 articles. Exopod 0.8 times the length of first endopodal article.

DESCRIPTION OF COPULATORY MALE (WHOI B. Sta. 62).—It is not known whether this male is primary or secondary.

Body (Figure 21c): 8.3 mm long; 6.1 times longer than wide.

Carapace: With blunt rostrum, slightly concave anteriorly on either side of rostrum. Anterolateral keels slightly raised but long, dropping abruptly into deep, oblique furrows posteriorly, and parallel along most of their length. Anterolateral setae moderately long and 3 in number; single posterolateral seta long. Respiratory chambers and chelipedal coxae prominent and swollen in dorsal view.

Pereonites 4–7: Wide, gradually sloping inward anteriorly, but less so than in *Neotanais americanus*. Genital cones on pereonite 7 prominent.

Pleonites (Figures 21c, 22d): Rounded laterally in dorsal view, epimeres bearing simple, unbranched hairs of moderate length. Sternites elongated into posteriorly directed midventral spurs of considerable size.

Pleotelson (Figures 21c,g, 22d): Short, width-length ratio, 1.9. All sides convex. Anal area slightly distorted and with a short midventral protuberance.

First Antenna: Article 1, 6.5 times longer than wide.

Mandibles: Remnants of incisive spines present.

Second Maxilla: Movable endite with 3 and 6 long setae present on exterior and interior lobes, respectively, and 1 short spine more proximally.

Maxilliped: Setal formula of palp, (1,0,1+1,0,9).

Cheliped (Figure 22e–g): Carpus stout, only very slightly bent, with about 12 moderately long dorsal setae on medial side. Proximal ventral seta thin; distal seta stout, light brown, and with expanded base. Propodus with thin dorsal crest irregular and frayed along distal half. Fixed finger with 3 small, round-tipped teeth of decreasing height proximally and 1 moderately large tooth distally. Dactylus bearing 2 round-tipped teeth proximally, the first shorter than the second, and 1 distal tooth of moderate size. Fingers only slightly bent medially, both in same plane.

Pereopods II–VII (Figure 24e,g): Setae somewhat more slender than in other stages and with less prominent setules. Setal formula of pereopod II, (5,5,6,4). Long, terminal propodal spines 2 in number and with small, closely packed teeth. Short, terminal propodal spine relatively long, slender, and without apparent dentition; short, subterminal carpal spine similar. Short, subterminal propodal spine row of pereopod VII composed of about 8 weak, naked, rudimentary spines.

Pleopods: Ratio of terminal endopodal setal length to length of endopod, 1.4. Setal formula, (2,3) (3,11,6) (0,4;0,11,4).

Uropods: With 9 articles in each endopod. First endopodal article bearing a number (about 15) of broom setae dorsolaterally (not figured).

INTRASPECIFIC VARIATION.—*Stages Other Than Copulatory Male*: a. North American Continental Slope: Representative body lengths (WHOI B. Sta. 62): juvenile, 4.2 mm; copulatory female, 5.4 mm.

The anterior carapace setae vary from one to three in number. The pereonites vary somewhat in shape, so that the swellings above the pereopods are relatively prominent. The midventral sternal spurs of the pleonites differ slightly as in most species. Much variation was noted in the third right mandibular spine (Figure 21m–p), but the terminal serration usually was more limited than in *Neotanais americanus*. The stout spines along the medial setal row of the second maxilla may be entire or cleft distally. The two forked spines of the fixed endites are simply bifid in two other specimens examined (WHOI B. Stas. 61 and 72). The dentition of the chela shows the usual amount of dactylar variation; some animals have sharp, forwardly directed teeth; several teeth are fused to the dactylus along their entire lengths. Propodal teeth are occasionally 6 in number—as is the case in other species (Figure 24c)—and the proximal denticles vary in height. Pereopods II–IV have one or two long, terminal propodal spines. The teeth

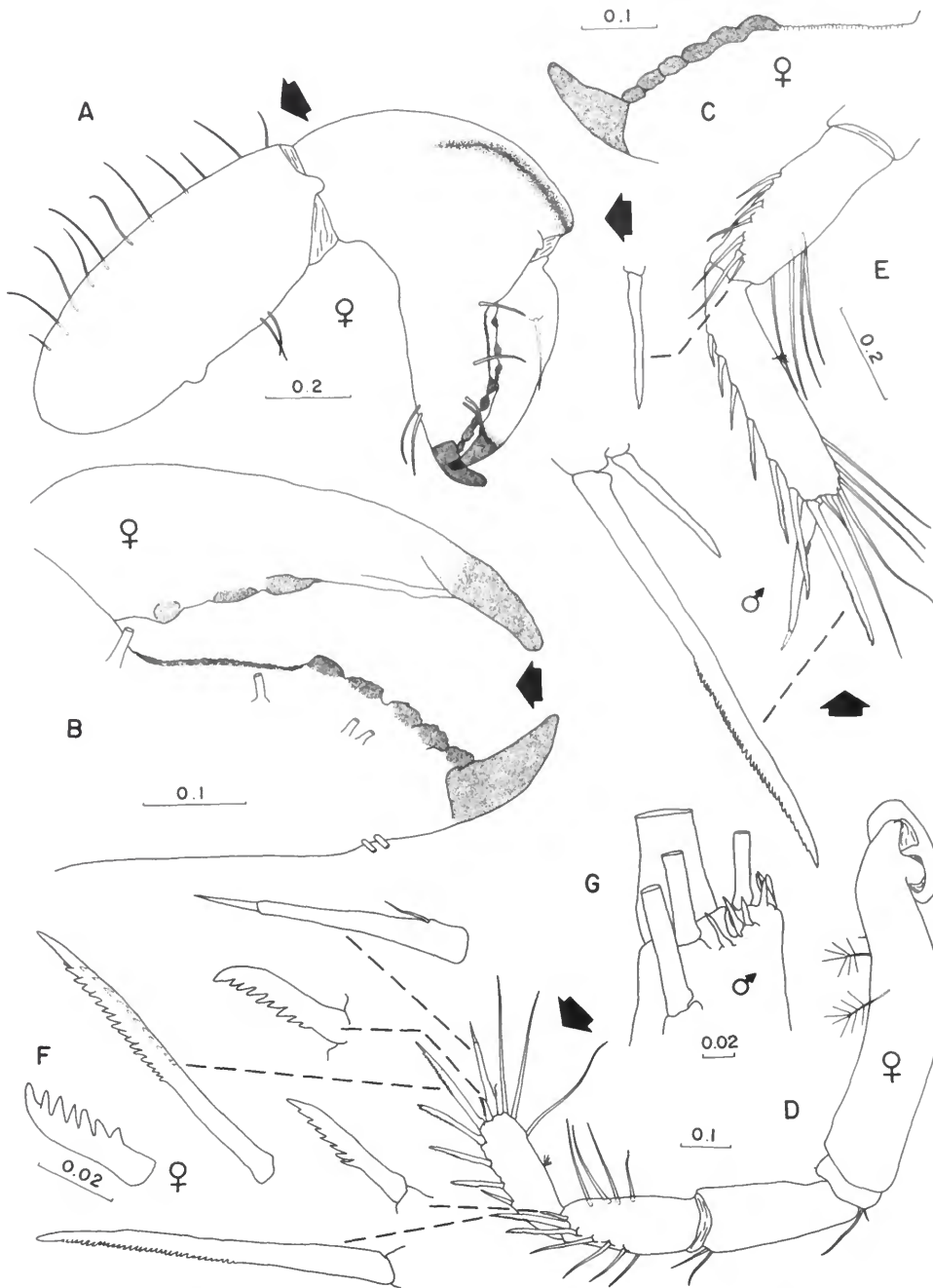FIGURE 24.—*Neotanais sandersi*, new species: A, right cheliped, preparatory male, holotype, WHOI B. Sta. 62; B, chela of same; C, fixed finger, copulatory female, CMS Sta. 2162; D, right pereopod II, holotype; E, terminal portion of left pereopod II, described male; F, short, terminal propodal spine, pereopod II, another animal (not a copulatory male) from Sta. 62; G, propodus of left pereopod VII, described male.

on these spines vary somewhat in size. The short terminal spines of the propodi occasionally resemble those of *Neotanais americanus* (Figure 24F).

b. Specimens Collected West of Ireland: The animals collected by the *Noratlante* are very similar to western Atlantic specimens. The differences noted are: (1) pleonites somewhat more pointed midventrally, (2) absence of pleonal epimeral hairs, (3) less pointed rostra, and (4) generally larger body lengths (4 juveniles, 5.3 to 6.3 mm; and 2 copulatory females, 8.3 and 9.3 mm).

c. Copulatory Female from the Bay of Biscay (*Sarsia* Sta. 44): A number of differences from the holotype were noted, and of these the following are the most significant. (1) The pleotelson and the ventral surface of the pleonites are of slightly different shape (cf. Figures 21D,E, 22A,B). (2) The third incisive spine of the right mandible is unusual (Figure 21s), its tip serrate as in *Neotanais americanus* (but see Figure 21o); the extra branch is probably abnormal. (3) The pleonites are without feathered epimeral hairs. (4) The pleonites are not quite rounded laterally and are slightly flared anteriorly. (5) Pereopod VII bears only four short propodal spines.

This animal may represent a new species; however, the number of similarities with *Neotanais sandersi* easily warrants its inclusion here—at least for the time being—in view of the degree of variability noted in other species.

d. Copulatory Females from *Vema* Sta. 17–5, off Chile: The following differences were noted between this population and the North American holotype: (1) the pereonites appear slightly longer with respect to width, although the width-length ratio is 1.3, identical with the holotype; (2) the midventral spurs of the pleonites are shorter; (3) the lacinia mobilis has three teeth rather than two (Figure 21L); (4) the cheliped is relatively longer; (5) perhaps most significantly, the pleotelson appears considerably wider with respect to length (but the width-length ratio is 2.0 compared with 1.8 for the holotype); (6) the tip of the third incisive mandibular spine is serrate as in *Neotanais americanus* (Figure 21Q,R, but see Figure 21o of animal from WHOI B. Sta. 103).

These differences are not significant enough to warrant erection of a new species for these specimens at this time.

Copulatory Males: All specimens are very sim-

ilar. The anterolateral setae on the carapace are two or three in number, usually three. The midventral sculpturing on the pleon is slightly variable as in other stages. The dentition of the chela showed the following variation: the fixed finger of the animal from CMS Sta. 2146 has the first tooth larger and the second and third teeth more clearly joined (Figure 22J); the distal tooth is shaped slightly differently and a low protuberance is present between the proximal and distal teeth; the male from *Eastward* Sta. 2756 lacks the third proximal tooth (Figure 22I), but this animal bears an additional, third dactylar tooth (Figure 22H).

Apparently all of the copulatory males from the North American Slope belong to the same developmental type. The variations noted in the specimen from *Eastward* Sta. 2756 probably are not sufficient to distinguish it from the others as one of the two major types established for the genus. On the other hand, this animal may be analogous to the one or two deviant animals noted in the developmental study of *Neotanais micromopher*, and it may represent a third male developmental pathway.

The male from the eastern Atlantic (*Noratlante*), however, displays a greater degree of variation in the dentition of the chelae (Figure 23). In other respects, it displays only minimal variation from North American populations; viz., the pleonal epimeres appear to be slightly less rounded laterally when seen from above.

COMPARISONS.—*Differences between* Neotanais sandersi *and* N. americanus: *Neotanais sandersi* is very similar morphologically to *N. americanus*, and both species are found in the same geographic region although they barely overlap vertically. The similarities among the copulatory males of these species are not nearly as pronounced as those among other instars. On the basis of the latter, these species may be considered as "sibling" species (Mayr, 1942). Significant differences between these stages of the two species are listed below.

(1) Shape of pereonites almost square in dorsal view in *Neotanais americanus* but more nearly rectangular (wider than long) in *N. sandersi* (this difference not always apparent when examining one or two specimens but always noticeable with careful examination of additional material). (2) Midventral pleonal spurs of *N. sandersi* longer than in *N. americanus*. (3) Dorsal hairs on pleonal epimeres much longer and more distinctly feathered

in *N. sandersi*. (4) Dorsal pereonal hairs much longer in *N. sandersi*. (5) Rostral area of carapace more acute in *N. americanus*; anterolateral keels more prominent in *N. sandersi*; anterolateral setae 1 or 2 in number in *N. americanus* and 2 or (usually) 3 in *N. sandersi*. (6) Short, terminal propodal spine on pereopods II–IV with 4 to 6 very large, triangular teeth borne at right angles to axis of spine in *N. americanus*; in *N. sandersi* spine bears about 8 smaller and more forwardly directed teeth. (7) Short, subterminal, carpal spine of pereopod II with about 4 or 5 somewhat irregular, moderately large teeth in *N. americanus*; in *N. sandersi* up to about 7 relatively evenly shaped, forwardly directed teeth present. (8) Dactylus of pereopods II–IV frequently bearing distal setules in *N. americanus*. (This character apparently disappears in the lower part of the depth distribution of *N. americanus* but usually is present where the two species come into contact.) (9) Long, terminal propodal spines on pereopods II–IV generally

bearing loosely spaced teeth; this character apparently distributed as in (8). (10) Tip of third incisive mandibular spine usually serrated as in a comb in *N. americanus* but usually pointed or only poorly cleft in *N. sandersi* (this character variable).

REMARKS.—*Neotanais sandersi*, easily confused with other members of the *americanus* group of species, is amphi-Atlantic in its distribution and displays little morphological variation over this range. This species is most closely related to *N. laevispinosus* and possibly is conspecific with it (see the discussion of affinities under *N. laevispinosus*, below).

MATERIAL.—See Table 5.

LOCATION OF MATERIAL.—NMNH: holotype (USNM 143167); allotype (USNM 143168); WHOI 62 (USNM 143169); WHOI 103 (USNM 143170); CMS 2146 (USNM 143171); CMS 2162 (USNM 143172); Sarsia 44 (USNM 143173); *Noratlante* 003, E001 (USNM 143174). AMNH: 17–5 (AMNH 14.893). UCZM: WHOI 72; WHOI 73.

TABLE 5.—*Examined material of* Neotanais sandersi, *new species*

Program or ship	Station no.	General location	Depth (meters)	Material
		WESTERN ATLANTIC		
WHOI Benthic	E 3	Gay Head–Bermuda Transect	824	1 Cop ♀
	F 1		1500	1 Juv, 1 fgmt.
	G 1		2000	1 M1, 1 Juv., 1 P♀2, 4 unid.
	G 3		2478	1 Juv
	G 9		2021	1 M2, 2 ?Cop ♀
	G 13		2036	1 ?Cop ♀
	GH 3		2478	1 ?Cop ♀
	61		2000	1 P♀1
	62		2496	2 M2, 1 Juv, 1 P♀1, 1 Cop ♀, 1 P♂ (holotype), 1 Cop ♂ (allotype)
	72		2864	1 P♀2
	73		1330–1470	1 Cop ♂
	103		2022	1 M1, 1 Juv, 1 P♀2, 1 Cop ♀, 2 fgmts.
	128		1254	1 M1
	131		2178	1 P♀2, 1 Cop ♀
CMS	2146	S of Cape Cod, Massachusetts	2645	1 Cop ♂
	2162	SE of Cape Cod	2295	1 Cop ♀
Eastward	2756	E of Cape Hatteras, North Carolina	3017	1 Cop ♂
		EASTERN ATLANTIC		
Noratlante	003, E001	W of Ireland	2460	5 Juv, 2 Cop ♀, 1 Cop ♂, 1 fgmt.
Sarsia	44	Bay of Biscay off Spain	1739	1 Cop ♀
		PACIFIC		
Vema	17–5	Off Chile	3739–3824	2 Cop ♀

DISTRIBUTION.—This species is known from both the eastern and western North Atlantic. One specimen from the Bay of Biscay and two from Chile have been assigned to this species with some reservation. *Neotanais sandersi* ranges in depth from about 825 to 2860 m along the Gay Head–Bermuda Transect. One collection was obtained in the same general area at about 3020 m.

DERIVATION OF NAME.—In honor of Dr. Howard L. Sanders of the Woods Hole Oceanographic Institution.

Neotanais laevispinosus (Norman and Stebbing, 1886)

FIGURES 25, 26, 97

Alaotanais laevispinosus Norman and Stebbing, 1886:114, pl. 24 (II).

Neotanais Edwardsi Dollfus, 1898:77 [in part, only specimen not figured].

[non] *Neotanais serratispinosus* (Norman and Stebbing).— Lang, 1956b:469, fig. B1–3.

DIAGNOSES.—*Stages Other Than Copulatory Male*: *Pereonites wider than long when viewed from above and generally of quadrangular shape; area of pereopods widest. *Pleonites somewhat expanded and slightly flared laterally, each epimere bearing 1 or 2 feathered hairs; *sternites extended into posteriorly directed and sometimes hooked midventral spines. *Pleotelson short and rounded posteriorly. *Chelipedal carpus bearing only about 5 relatively short dorsal setae, and chelae similar to those of other species in the *americanus* group of species. Short, terminal propodal spine of pereopod II bearing about 6 large, triangular teeth; propodal setae stout and with prominent setules. *Rostrum of carapace pronounced.

Copulatory Male (only one type known): *Pereonites 4 and 5 rounded appreciably anteriorly in dorsal view (cf. *Neotanais americanus*) and wider than long. *Pleonites generally rounded laterally and extended ventrally into posteriorly directed spurs. *Pleotelson short, much wider than long, and generally rounded posteriorly. *Chelipedal carpus stout, bent almost at right angles proximally, and bearing about 10 slender dorsal setae; the distal ventral seta shorter and slightly stouter basally than the proximal seta; *chela with dorsal crest thin and frayed, fingers not appreciably bent, and dentition as in Figure 25G.

DESCRIPTION OF PREPARATORY FEMALE 2 (Bay of Biscay, *Sarsia* Sta. 50).—*Body* (Figure 25A): 7.5 mm long and 7.0 times longer than wide.

Carapace: 1.3 times longer than wide with moderate anterolateral keels and oblique furrows. Respiratory chambers and chelipedal coxae not especially pronounced in dorsal view.

Pereonites: Almost quadrangular in dorsal view and wider than long, width-length ratio of pereonite 5, 1.4. Pereonite 2 with very slight anterior swellings laterally (Figure 25A).

Pleonites (Figures 25C, 26A): Decreasing slightly in width posteriorly. Epimeres more attenuated and flared laterally than in most species and bearing 1 or 2 fine, feathered, dorsal hairs. Sternites drawn out into posteriorly curved spines.

Pleotelson (Figures 25C, 26A): Short, 1.8 times wider than long, and rounded posteriorly when viewed from above.

First Antenna: First article 3.9 times longer than wide.

Right Mandible (Figure 25E): Proximal 2 incisive spines serrate on both sides. Third spine irregular, and serrate terminally.

Left Mandible (Figure 25F): Incisive spines as on right side. Lacinia mobilis bearing 3 large teeth; posterior lobe unequally cleft.

Second Maxilla: Medial setal row with 18 setae and 2 spines. Two forked spines on fixed endite simply bifid.

Cheliped (Figure 26C,D): Carpus bearing only about 5 short dorsal setae. Propodus with strong dorsal crest; fixed finger without proximal denticles along somewhat irregular cutting edge; distal teeth irregularly rounded. Dactylus bearing only about 3 very low, irregular, rounded teeth proximally.

Pereopods II–VII (Figure 26E): Mostly missing or broken. At least 2 long, prominently toothed terminal spines on propodi of pereopods II–IV; short, terminal propodal spine with 6 extremely large, triangular teeth. Short, subterminal carpal spine of pereopod II broken (see Figure 26F of this spine from *Travailleur* specimen). Anterior propodal setae of pereopods II–IV heavy and with heavy setules but not notably stout. Posterior setae very long, slender, and acutely tipped. Setal formula of pereopod II, (5,4,8,4). Pereopod VII bearing 9 short, subterminal spines on propodus.

Pleopods: Setal formula, (2,2) (3,8,6) (0,2;0,8,5). Endopod with terminal setal row distinct.

FIGURE 25.—*Neotanais laevispinosus* (Norman and Stebbing): A, dorsal view, preparatory female 2, Bay of Biscay, *Sarsia* Sta. 50; B, same, copulatory male, holotype, off Ireland, *Porcupine* Sta. 1; c, pleonites 4 and 5 and pleotelson, dorsal view, described female; D, same, holotype; E, pars incisiva, right mandible, anterior view, described female; F, same, left mandible; G, left cheliped, holotype; H, tip of propodus, left pereopod VII, holotype.
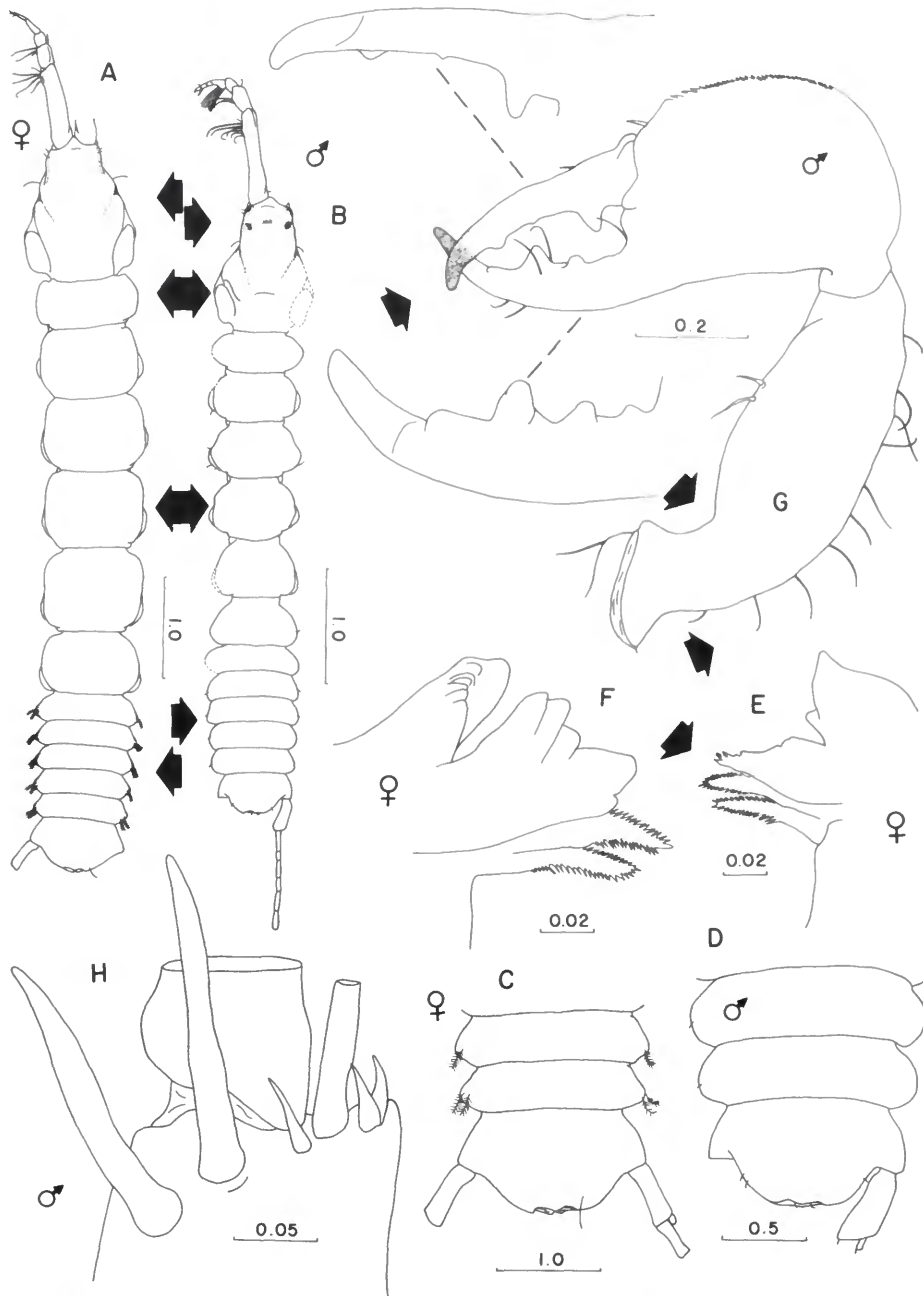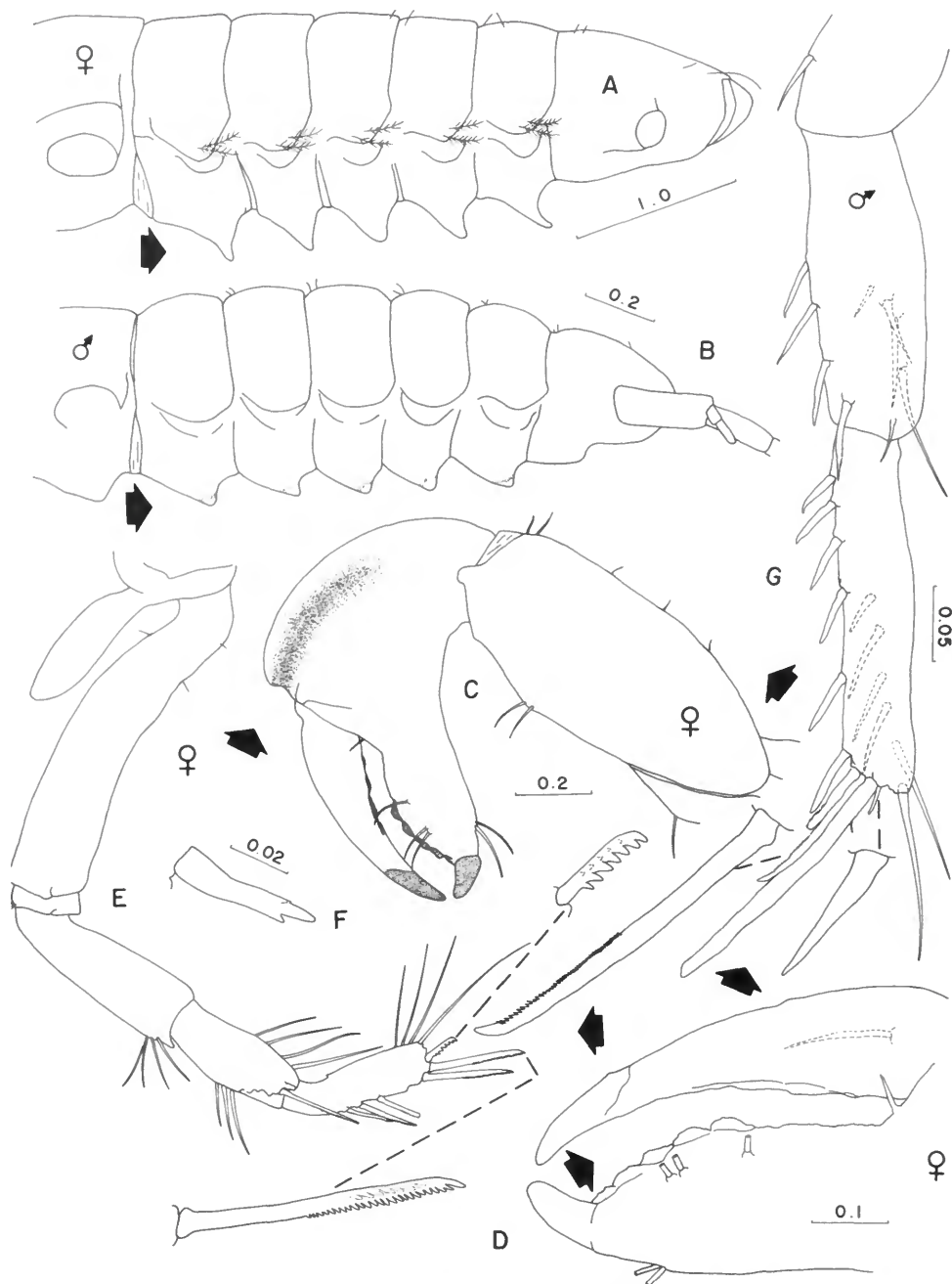
FIGURE 26.—*Neotanais laevispinosus* (Norman and Stebbing): A, pleon, lateral view, described female, Bay of Biscay, *Sarsia* Sta. 50; B, same, holotype, off Ireland, *Porcupine* Sta. 1; C, left cheliped, allotype; D, chela, same; E, left pereopod II, anterior view, described female; F, short, subterminal carpal spine, pereopod II, a preparatory female 2 from Bay of Biscay, *Travailleur* Dredge 10; G, left pereopod II, anterior view, holotype.

Uropods: Broken (on all specimens) but, judging from fragments remaining, probably slender, similar to *Neotanais americanus* and *N. sandersi*.

DESCRIPTION OF COPULATORY MALE HOLOTYPE (from *Porcupine* Sta. 1, southwest of Ireland, the only copulatory male known for this species).—*Body* (Figure 25B): 5.3 mm long and 6.1 times longer than wide.

Carapace: Rostral area not prominently pointed; anterolateral keels without dorsal longitudinal depression but deflected anteriorly and entire carapace somewhat depressed across laterally constricted anterior area. Oblique furrows moderate. Two anterolateral setae and 1 posterolateral seta present. Respiratory chambers moderately expanded in dorsal view, and area of chelipedal coxae slightly concave posterolaterally.

Pereonites: Wider than long, with pereonites 4 and 5 exhibiting moderate anterolateral expansions anterior to pereopods.

Pleonites (Figures 25D, 26B): Generally rounded in dorsal view and each bearing a single, short epimeral hair on either side. Sternites forming posteriorly directed spurs midventrally.

Pleotelson (Figures 25D, 26B): Considerably wider than long, width-length ratio, 1.8. Generally rounded posteriorly when viewed from above.

First Antenna: About as illustrated by Lang (1956b, fig. B1) except that the first article bears about 6 lateral setae distally.

Second Maxilla: Setae of movable endite prominent (see Lang, 1956b, fig. B2).

Cheliped (Figure 25C): Carpus stout, bent almost at right angles proximally, and bearing 10 long, slender dorsal hairs. Ventral carpal hairs similar to those of other species in the *americanus* group of species, the proximal seta being long and slender, although somewhat thicker at its base, the distal seta shorter and considerably thickened basally. Propodal crest thin and frayed into weak, distally directed "serrations." Fixed finger with 3 teeth of increasing height toward distal end and a fourth, lower tooth, just before the brown claw. Dactylus with 1 long tooth proximally, 1 tiny tooth centrally, and a third, inwardly directed, tooth distally. Neither finger markedly twisted.

Pereopods II–VII (Figures 25H, 26G): Setae very stout, spinelike, and notable for their lack of prominent setules. Setal formula of pereopod III, (6,6,4,4) (both pereopods II mounted on deterio-

rated slide); apparently 2 long, terminal propodal spines bearing very fine teeth. Short terminal propodal spine thin, naked, and very short. Short subterminal propodal spines in row on pereopod VII very short, pointed, and 3 in number. Short subterminal carpal spines of pereopods II unknown.

Pleopods: Setal formula, (2,2)(3,9,6)(0,2;0,9,4). Endopod with distinct terminal row of setae.

Uropods: Broken. Six endopodal articles remaining on one side. First endopodal article apparently lacking dorsolateral broom setae.

INTRASPECIFIC VARIATION.—No significant differences were noted between the *Travailleur* specimens and the described female. The former specimens were in too poor condition to permit a detailed analysis. The preparatory female 2 collected by the *Travailleur* is 10.3 mm long.

COMPARISONS.—*Differences between the Copulatory Males of* Neotanais laevispinosus *(Holotype) and* N. americanus *(the Described Male)*: (1) Shape of pereonites in dorsal view, (2) midventral silhouette shape of pleonites, (3) carapace shape, (4) chela shape, (5) shape and presence of dorsal setae on the chelipedal carpus, and (6) shapes of propodal and carpal setae and of specialized spines on pereopods II–VII.

The holotype of *Neotanais laevispinosus* was found at 677 m, whereas *N. americanus* has never been found at depths of less than 2670 m in the North Atlantic and frequently is found at much greater depths, one record being 5340 m (see "Vertical Distribution" under "Ecology").

Differences between the Holotype of Neotanais laevispinosus *and the Copulatory Males of* N. sandersi: a. Allotype (Gay Head–Bermuda Transect): (1) The shape of the chela (although only one type of chela is known for each species), (2) the shapes of the propodal and carpal setae on pereopods II–VII, (3) the shapes of the specialized spines on pereopods II–IV, (4) the number of short spines in the propodal row on pereopod VII (3 and 8 respectively), (5) the shape of the carapace, and (6) the midventral silhouette of the pleonites (may not be significant). b. Male Collected West of Ireland: This male of *Neotanais sandersi* was almost identical to the males of that species from North America.

Although the two species are very similar, particularly in the shape of the pereonites in dorsal view and the shape of the chelipedal carpus, the following differences were noted: (1) in *Neotanais*

laevispinosus the pleonal epimeres are more rounded in dorsal view, (2) the midventral pleonal spurs are more posteriorly directed, (3) the rostrum is more prominent, (4) the chelipedal carpus bears up to 13 short dorsal setae compared to only 9 long setae in the other, much larger animal, and (5) the pleotelsons vary slightly in dorsal view.

Affinity of Neotanais laevispinosus *and* N. sandersi: *Neotanais laevispinosus* is much closer to *N. sandersi* than to *N. americanus* and may be conspecific with it, although this is improbable. This affinity is indicated by the shapes of the pereonites in dorsal view, the pleon, and the shape and setation of the chelipedal carpus. Also, the depth at which *N. laevispinosus* is found is consistent with the known North American depth range of *N. sandersi.*

The stages other than copulatory male of this species closely resemble an animal herein referred to *Neotanais sandersi* that was collected in the Bay of Biscay at *Sarsia* Sta. 44 and were at first thought to be conspecific with it. However, in view of differences in the following characters and the geographical proximity of the collections, it is almost certain that these specimens represent a species distinct from *N. sandersi*: (1) The length and shape of the midventral spurs or spines on the pleonites (cf. Figures 22B, 26A), (2) the shape of the pleonal epimeres, (3) the shape of the pleotelson (Figures 21E, 25C), (4) the dorsal setae on the chelipedal carpus (Figures 24A, 26C), (5) the shape of the rostrum and the anterolateral keels of the carapace, (6) a much darker brown coloration of the claws of the chela in the animal from *Sarsia* Sta. 44, (7) a much lower dorsal crest on the chela in the same specimen, and (8) the shape of pereonite 2 (Figures 21A, 25A). Referenced figures of the holotype of *Neotanais sandersi* closely resemble the specimen from *Sarsia* Sta. 44.

Conspecificity of the Holotype and of the Described Female of Neotanais laevispinosus: Differences between these specimens are: (1) although the midventral pleonal spurs or spines are usually longer in copulatory males than in other stages within a species, the reverse is true here; (2) the pleonal epimeres are more pronounced in the females than in the holotype, whereas the epimeres of males usually are as well expanded as in other stages in many species if not more so; (3) the setae of pereopods II–VII are smooth or practically so

on the holotype, whereas they are setulate in other stages; (4) the posterior propodal setae on pereopod VII are short, stout, and bluntly tipped in the holotype, whereas they are long, slender, and pointed in the other specimens; (5) the rostrum of the holotype is not elongated, whereas it is pronounced in the female, (6) the row of short, propodal spines of pereopod VII is composed of only 3 spines whereas there are 8 on the female, and the male might be expected to have a similar or greater number than other stages; (7) the short, terminal propodal spine on pereopods II–IV of the holotype is naked, whereas such spines on the other specimens are heavily dentate.

Differences (3), (4), (6), and (7) are typical sexual dimorphisms for the *americanus* group of species. Differences (1) and (5) are relatively minor, as is (2), which may be due to mechanical damage in handling. The geographic locations of all specimens are very close, and their depth range is within that observed for other, better known species.

The following characters indicate most clearly the conspecific status of these animals in view of their very close geographic origins: (1) the midventral, posteriorly directed, and slightly hooked spurs on the pleonal sternites, (2) the shape of the pereonites in dorsal view (similar in their relationship to the sexes in *Neotanais sandersi,* and (3) the similar shape and setation of the carapace.

REMARKS.—In 1886 Norman and Stebbing described this species as *Alaotanais laevispinosus,* based on a single copulatory male collected off Ireland by the *Porcupine* Expedition at a depth of 677 m. They contrasted it with their *Alaotanais serratispinosus* (=*Neotanais americanus*)—collected south of Greenland at a depth of 2715 m—by, among other things, the relatively smooth spines on its pereopods II–VII. Lang (1956b:471, fig. B1–3) described and figured the first antennae, second maxillae, and maxillipeds of the holotype and stated that "no doubt *laevispinosus* is the male of *serratispinosus.*" He did not indicate, however, why he believed this to be true other than to say that the dactylar armament of pereopods V–VII is the same in the two species. (Norman and Stebbing had used this character as a major distinguishing feature.)

In my opinion, the specimen collected by the *Porcupine* represents a species distinct from *Neo-*

tanais americanus for the reasons cited above and, in addition, is distinct from all other described species. Therefore, *N. laevispinosus* must be retained as the name for this species.

In 1898 Dollfus described *Neotanais edwardsi*, collected by the *Travailleur* from the Bay of Biscay, and noted that two specimens had been collected. The specimen which he figured and upon which he apparently based his description is, in fact, conspecific with *N. hastiger*, and the second specimen and a third, also collected by the *Travailleur* and identified as *N. edwardsi*, are not *N. hastiger* but *N. laevispinosus*.

The station data given by Dollfus in his description of *Neotanais edwardsi* are incorrect (see "Remarks" under *N. hastiger*). The label for the second specimen collected by the *Travailleur* (Paris Museum) gives the following data: 1910 m, No. 10, 16 July, 43°39′ N., 5°52′ W., mud. The official cruise reports of M. A. Milne–Edwards (1882a:126; 1882b, cruise track) gives the date and location as 26 July 1880, lat. 43°39.05′ N., long. 5°48.00′ W., off Santana, Spain, in 1960 m. The third specimen in the Paris Museum bears no date or location data; however, since the label indicates that it was collected by the *Travailleur* in 1880 at "1910 m"—data identical to those of the other two specimens—presumably it was collected at the same station.

The holotype is redescribed in detail herein; females are described for the first time; and diagnoses are presented for both.

MATERIAL.—*Porcupine* Sta. 1, southwest of Ireland, 677 m, 1 Cop ♂ (holotype); *Travailleur* Dredge No. 10, Bay of Biscay off Spain, 1960 m, 1 P ♀ 2, 1 fgmt.; *Sarsia* Sta. 50, Bay of Biscay off Spain, 2379 m, 1 P ♀ 2 (described).

LOCATION OF MATERIAL.—BMNH: holotype (Reg. No. 1903.5.20.70 and microslide Reg. No. 1911.11. 8.372). FNMNH: *Travailleur* Dredge No. 10. NMNH: *Sarsia* 50 (described female; USNM 143175).

Neotanais mesostenoceps, new species

FIGURES 27, 28, *102*

DIAGNOSIS.—*Copulatory Male* (all other stages unknown): *Carapace narrow anteriorly with prominent, pointed rostrum; *anterolateral keels expanded laterally, oblique furrows relatively deep, and chelipedal coxae greatly expanded in dorsal

view; 2 anterolateral setae and 1 prominent posterolateral seta present. Pereonites wider than long and pereonites 4–7 appearing to be more rounded anteriorly than posteriorly in dorsal view. *Pleonites flared and slightly tapered laterally; *sternites long and spinelike midventrally. *Pleotelson short, about 1.8 times wider than long. *Chelipedal carpus robust, bent proximally, and bearing about 6 dorsal setae; first ventral carpal seta slender, second brown, thick, and swollen basally; *propodus of chela frayed along dorsal edge and dentition as in Figure 28B. Uropodal exopod about 0.4 the length of first endopodal article; endopod very slender distally, first article bearing about 16 broom setae on its dorsal surface. Dactylar spines of pereopods II–IV 0.3 times the length of dactylus; short, naked propodal spines of pereopod VII about 13 in number.

DESCRIPTION OF COPULATORY MALE HOLOTYPE.— *Body* (Figure 27A): 10.8 mm long and 5.8 times longer than wide.

Carapace: Length-width ratio, 1.3; anterior end narrow and elongate. Anterolateral keels expanded anteriorly over 2 anterolateral setae; 1 relatively long posterolateral seta present. Rostrum very prominent and bluntly pointed, oblique furrows pronounced, and chelipedal coxae greatly expanded in dorsal view.

Pereonites: Appearing wider than long in dorsal view, pereonites 4–6 seemingly relatively straight across posteriorly and with sides rounded anteriorly. Genital cones prominent.

Pleonites (Figures 27A,B, 28A): Slightly depressed middorsally and successively narrower. Flared and slightly attenuated laterally. Sternites drawn out into long spines midventrally. One or 2 slender dorsal hairs present on each epimere.

Pleotelson (Figures 27A,B, 28A): Short, 1.8 times wider than long. Articulated with pleonite 5.

First Antenna: First article 6.4 times longer than wide.

Second Maxilla: Movable endite with 3 and 6 well-formed setae on external and internal lobes respectively. Two additional, more medial clumps of 2 and 5 setae present respectively.

Maxilliped: Endite with 2 terminal setae. Setal formula of palp, (1,0,1+1,1,13).

Cheliped (Figure 28B): Carpus stout, moderately curved proximally, and bearing about 6 dorsal setae. First ventral seta on carpus slender and
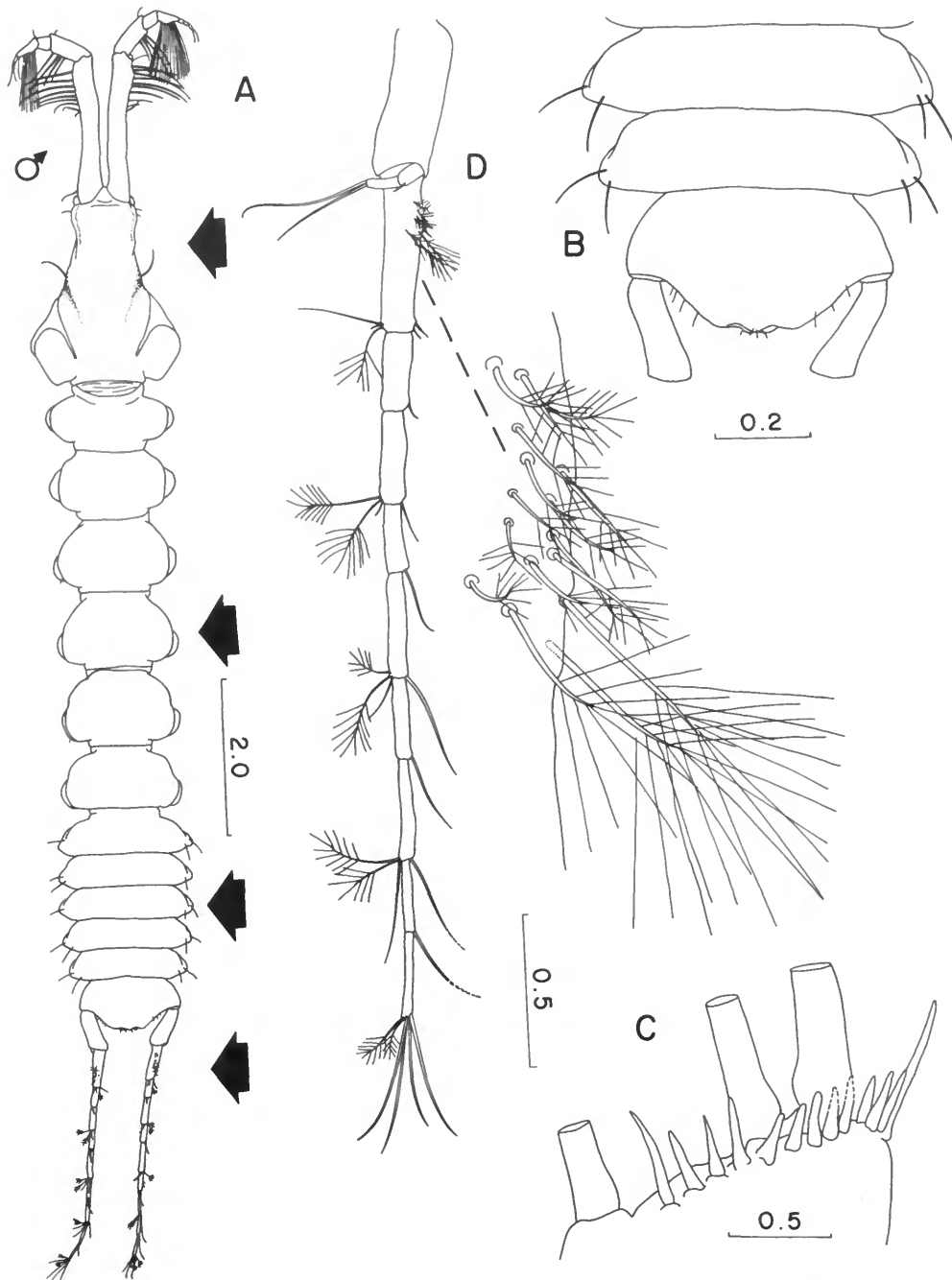
FIGURE 27.—*Neotanais mesostenoceps*, new species (all figures are of copulatory male, holotype, off West Africa, WHOI B. Sta. 147): A, dorsal view; B, pleonites 4 and 5 and pleotelson, dorsal view; C, tip of propodus of left pereopod VII, posterior view; D, left uropod, lateral view with enlargement of dorsolateral surface of first endopodal article.

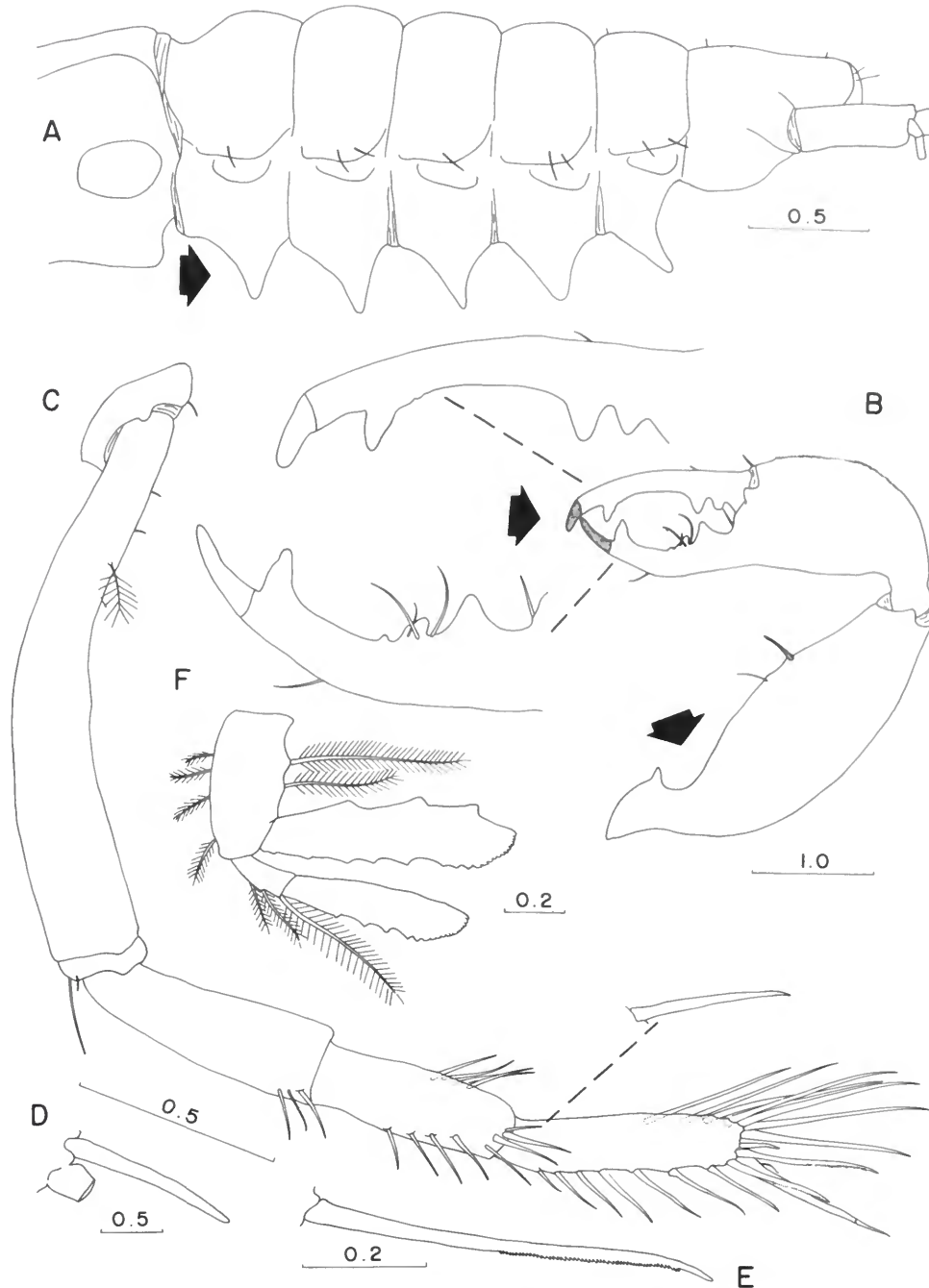FIGURE 28.—*Neotanais mesostenoceps*, new species (all figures are of copulatory male, holotype, from off West Africa, WHOI B. Sta. 147): A, pleon, lateral view; B, left cheliped with enlargements of dactylus and fixed finger of chela; C, left pereopod II, anterior oblique view; D, short, terminal propodal spine, same leg; E, first long, terminal propodal spine anterior to short spine; F, right pleopod, anterior view.

recurved; second seta thick, swollen at base, and brown in coloration. Fixed finger bearing a large, proximal tooth followed by 2 others of greatly decreasing size. One large, distal tooth located just before claw. Dactylus with 2 proximal teeth of increasing size and 1 large, distal tooth.

Pereopods II–VII (Figures 27c, 28c–e): Dactylar spines of pereopods II–IV 0.3 times as long as article. Setal formula of pereopod II, (7 or 9,7,7,4), depending on whether the 2 anteriormost propodal setae represent long terminal spines (serration often reduced in copulatory males). Short, terminal propodal spine of pereopods II–IV and short, subterminal carpal spine of pereopod II both slender and naked. Short, subterminal propodal spines of pereopod VII naked, of varying length, and 13 in number.

Pleopods (Figure 28f): Setal formula, (2,4)(3,13,7) (0,3;0,13,5).

Uropods (Figure 27a): Each endopod very slender at tip and composed of 9 articles. Exopod 0.4 times length of first endopodal article and strongly bent downward. First endopodal article bearing a group of about 16 broom setae of varying lengths dorsally on proximal half.

REMARKS.—*Neotanais mesostenoceps* differs noticeably from the other known copulatory males of the *americanus* group in the lateral and midventral shape of its pleonites.

MATERIAL.—WHOI B. Sta. 147, off Guinea, West Africa, 2934 m, 1 Cop ♂ (holotype).

LOCATION OF MATERIAL.—NMNH: holotype (USNM 143176).

DERIVATION OF NAME.—Referring to midlateral constriction of the copulatory male carapace in dorsal view. From the Greek *mesostenos* (narrow in the middle) and Latin affix *-ceps* (denoting head).

Neotanais hadalis Wolff, 1956, new rank

FIGURES 29–32, *102*

Neotanais serratispinosus hadalis Wolff, 1956a:210, figs. 21–34.
Neotanais serratispinosus (Norman and Stebbing).—Kudinova-Pasternak, 1965a:75, figs. 1–3; 1970:344. [Synonymy with *N. hadalis* uncertain; see "Remarks."]

DIAGNOSES.—*Stages Other Than Copulatory Male:* *Pleonites rounded laterally in dorsal view, but at times somewhat flattened laterally, and each curving medially more gradually anteriorly than pos-

teriorly; *generally smooth and rounded below in lateral view or with only slight midventral protuberances. *Pleotelson relatively long, 1.5 times wider than long. *Uropods short, usually only about two-thirds as long as pleon; *composed of relatively few, stout endopodal articles with unusual setation. *Pereonites 3–6 generally square in dorsal view. Carapace with moderately well-developed anterolateral keels, shallow oblique furrows; respiratory chambers and chelipedal coxae not appreciably expanded in dorsal view. Carpus of cheliped with up to about 17 dorsal setae, dentition of chela as in Figure 29k. Short, terminal propodal spine of pereopods II–IV stout, curved at tip, and bearing about 9 strong, triangular teeth; *dactylar spines less than 0.2 times as long as article.

Copulatory Male: Pereonites 3–7 tapering anteromedially, gradually, and evenly in dorsal view, from pereopodal coxae to anterior borders. Pleonites decreasing in width from pleonite 1 to pleonite 5 in dorsal view; *ventrally bearing very low to moderately blunt spurs. *Anterolateral keels of carapace sharp laterally and parallel. *Chelipedal carpus moderately bent and bearing numerous dorsal setae; chela variable (cf. Figure 30f and Wolff, 1956c:215, fig. 32). Uropods bearing up to about 20 broom setae on surface of first endopodal article. Chelipedal coxa with posteroventral margin very close to bulbous portion of basis and area of proximity decidedly concave, fitting around curve.

DESCRIPTION OF "ADULT FEMALE" HOLOTYPE AND COPULATORY MALE ALLOTYPE.—See Wolff, 1956a: 210 ff.

COMPARISONS.—*Differences between Wolff's Kermedec Trench Specimens and the North Atlantic Specimens of* Neotanais serratispinosus (=N. americanus): Most of the similarities between these animals are shared to a greater or lesser extent by all of the species in the *americanus* species group.

Wolff made a comparison for intraspecific variation on the basis of the specimens described by Norman and Stebbing (1886)—including the holotype of *Neotanais laevispinosus* which Lang (1956b) had transferred to *N. serratispinosus*—and the copulatory female described by Hansen (1913) from the *Ingolf* Expedition. Of the former specimens, none was available to Wolff personally, but they were studied with the aid of the published descriptions and personal communications with Lang,
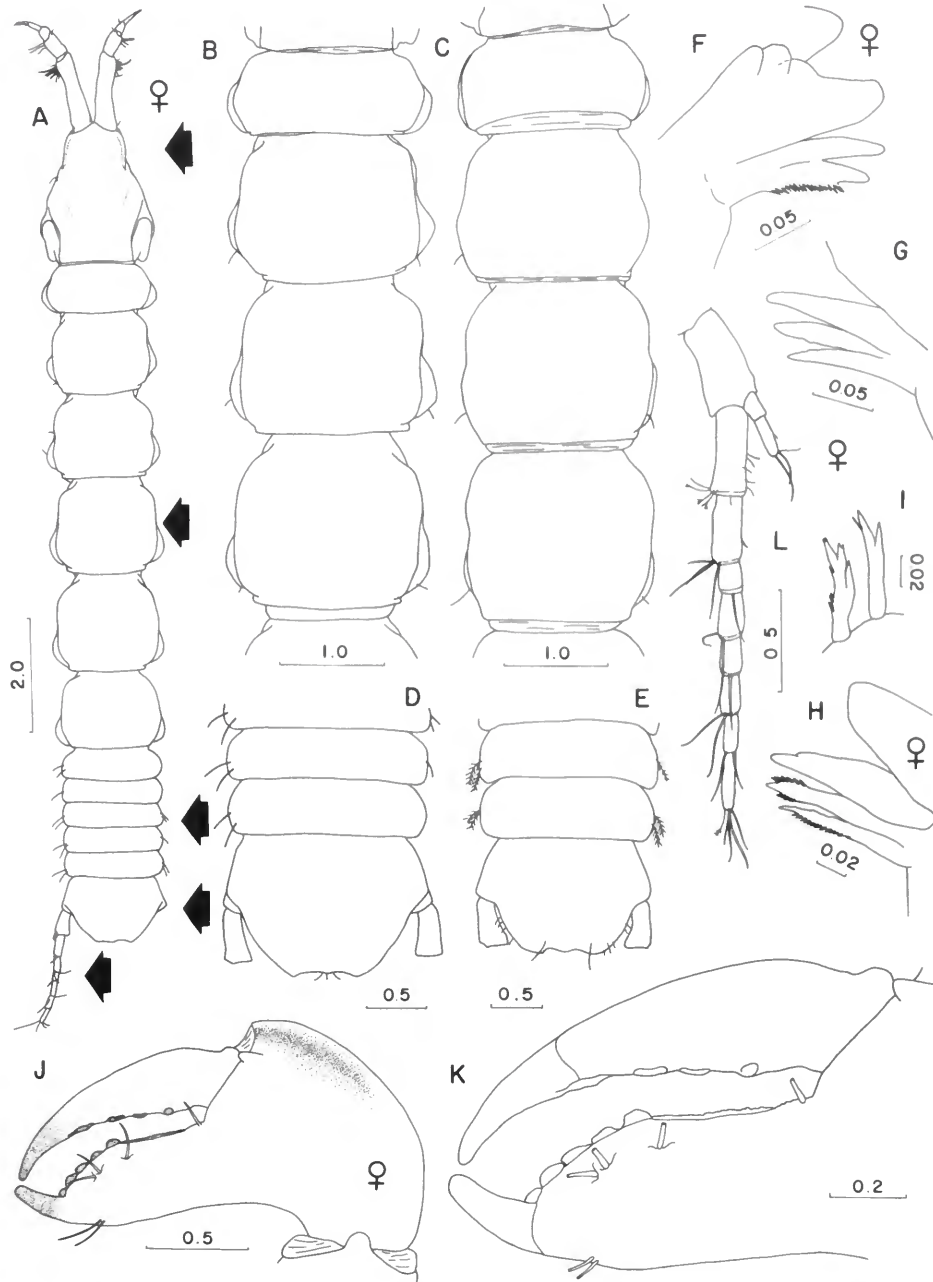
FIGURE 29.—*Neotanais hadalis* Wolff: A, dorsal view, preparatory female 2 A, Argentine Basin, *Vema* Sta. 17–81; B, enlargement of pereonites 2–5 of same animal; C, pereonites 2–5 of preparatory male from Kermedec Trench, *Galathea* Sta. 649; D, pleonites 4 and 5 and pleotelson, dorsal view, female A; E, same, preparatory male, Kermedec Trench; F, incisive spines and lacinia mobilis, left mandible, anterior view, female A, Argentine Basin; G, incisive spines, right mandible, same animal; H, same, preparatory female B, same station; I, stout cleft spines on fixed endite of right second maxilla, preparatory male, Kermedec Trench; J, left chela, female A, Argentine Basin; K, same, enlargement; L, right uropod, dorsal view, preparatory male, Kermedec Trench.
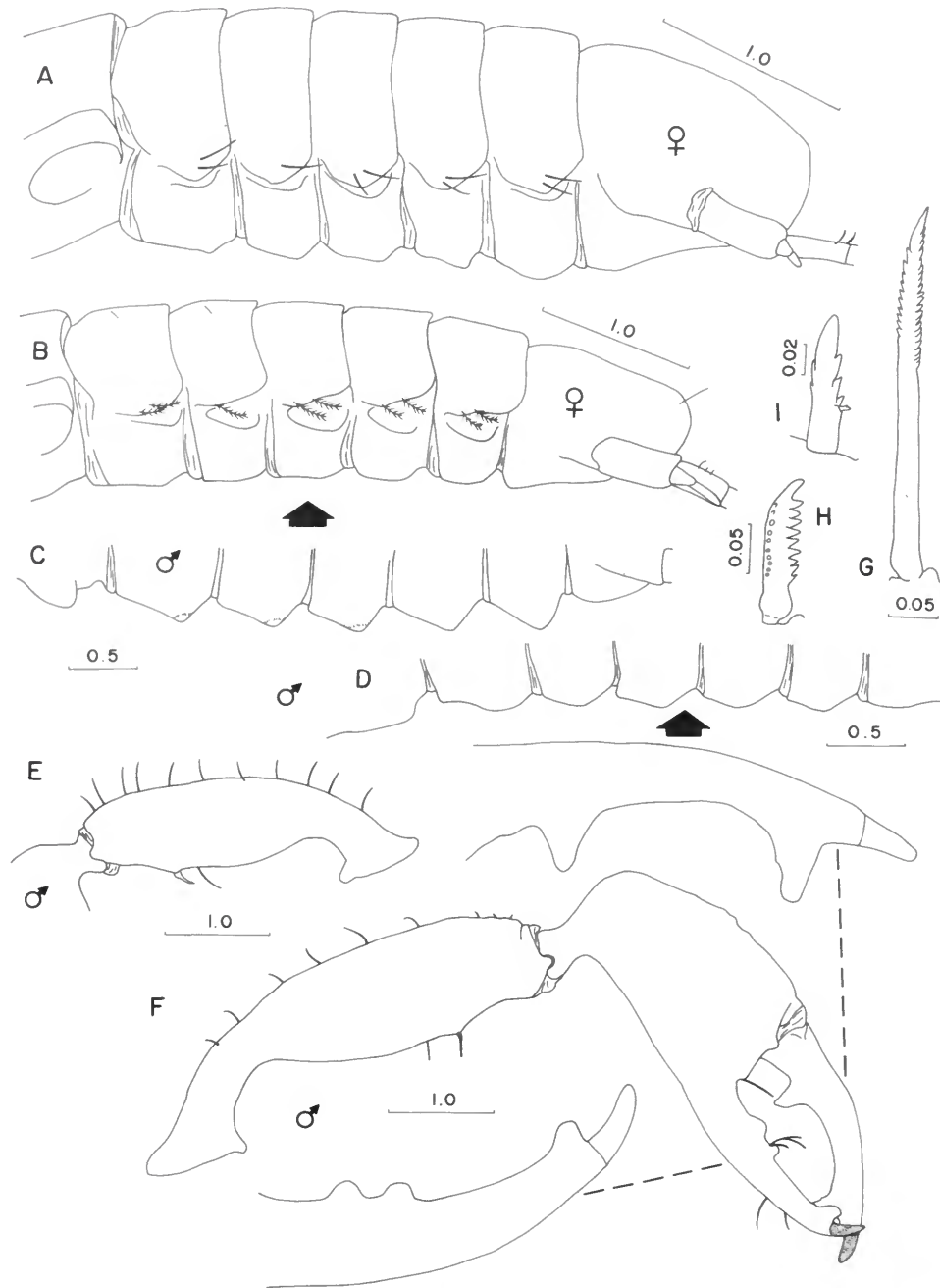
FIGURE 30.—*Neotanais hadalis* Wolff: A, pleon, lateral view, preparatory female A, Argentine Basin, *Vema* Sta. 17–81; B, same, preparatory male, Kermedec Trench, *Galathea* Sta. 649; C, same, midventral profile, copulatory male, same station; D, same, Wolff's copulatory male, allotype, Kermedec Trench, *Galathea* Sta. 649; E, carpus of left cheliped, same animal; F, right cheliped of copulatory male from Argentine Basin, *Vema* Sta. 17–81; G, long, terminal propodal spine of pereopod III, preparatory male in B; H, short, terminal propodal spine, same leg; I, short, subterminal carpal spine of pereopod II, female A, Argentine Basin.

FIGURE 31.—*Neotanais hadalis* Wolff (all figures are of copulatory male from Argentine Basin, *Vema* Sta. 17–82): A, dorsal view; B, pleonites 4 and 5 and pleotelson, dorsal view; C, left cheliped with enlargements of dactylus and fixed finger; D, right uropod, anterior view; E, enlargement of terminal tip of one medial endopodal seta.
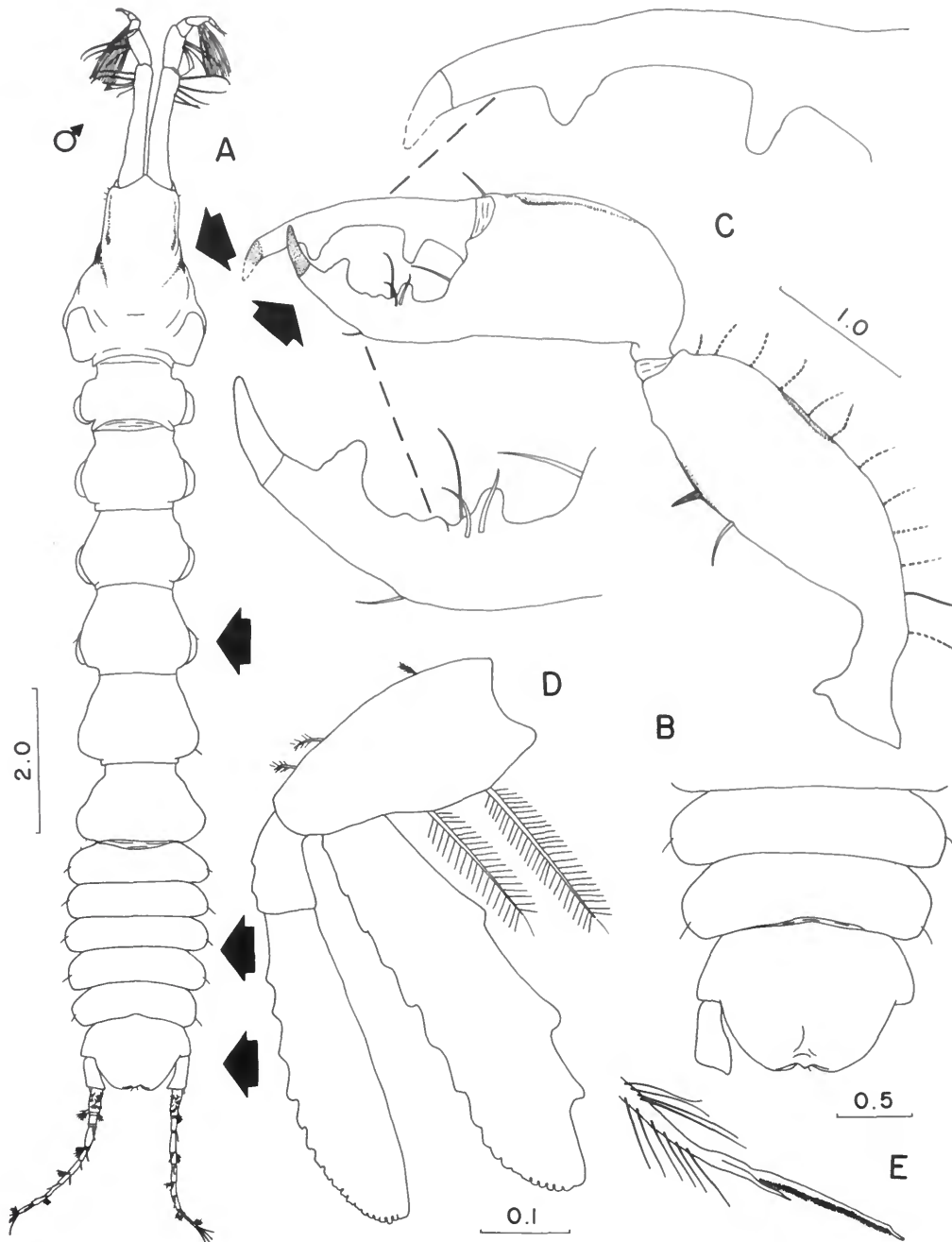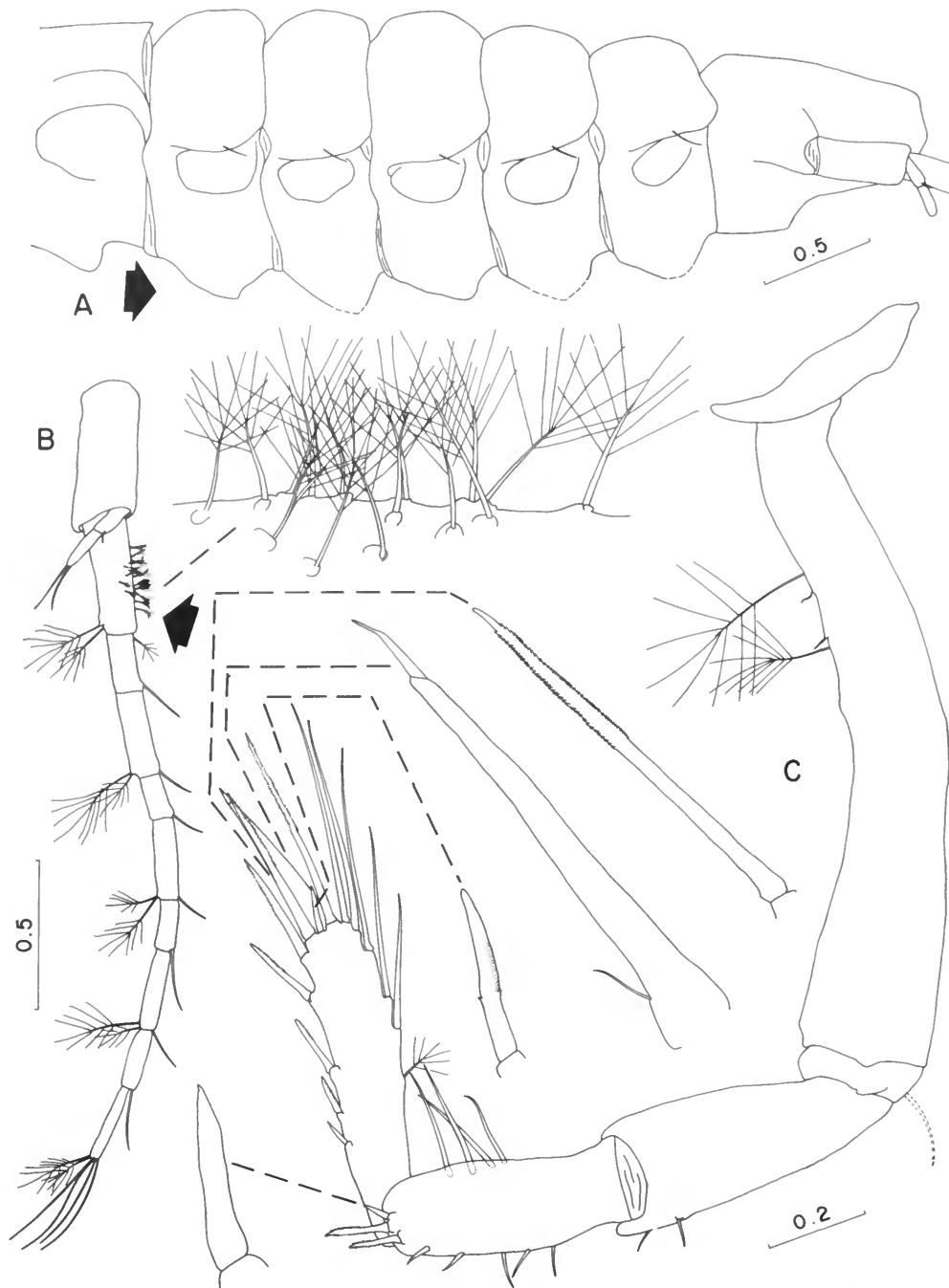
FIGURE 32.—*Neotanais hadalis* Wolff (all figures are of copulatory male from Argentine Basin, *Vema* Sta. 17–82): A, pleon, lateral view; B, left uropod, lateral view, with enlargement of dorsolateral surface of first endopodal article; C, right pereopod II, anterior oblique view, with enlargements of specialized spines.

who had the specimens at the time. I have examined all of these specimens and have found them to represent four different species (see p. 28); hence, the validity of Wolff's comparison is severely compromised.

a. Stages Other Than Copulatory Male: A comparison of the descriptions and figures of these two species will demonstrate their distinct status (see Wolff's figures 22 and 23). The most notable differences are in (1) body length; (2) shape of pleotelson; (3) more pronounced keels, furrows, chelipedal coxae, and larger number of posterolateral setae on the carapace of *Neotanais hadalis;* and (4) the relative length of the uropodal endopod and shapes of its articles.

b. Copulatory Males: Those characters shared by the copulatory males with other stages (e.g., pleotelsonal shape and shape of pleonites) differ from the copulatory males of *"serratispinosus"* in the same ways as do the other stages. Other differences, not noted by Wolff, have mainly to do with the dentition of the chelae (see Wolff's figures 32a and 32b) and the shape and dorsal setation of the chelipedal carpi (see Figures 19e,f,k, 30e), neither mentioned nor figured by Wolff. The carpus of a second male from the Kermedec Trench is similar to that of the described animal but slightly shorter and stouter.

Wolff (1956a:216) discusses this second "male," which has the body of a female and, among other features, the genital cones, first antennae, and chelipeds of a copulatory male. At the time Wolff wrote, the status of this individual in the life history of the species was unknown. After having examined hundreds of specimens of *Neotanais,* I have not seen any other combination of characters such as exhibited by Wolff's "male." The animal is probably abnormal, an aberration of heredity or environment. Whether the two types of chelae found on these two males represent types A and B of primary and secondary males, respectively, cannot be determined because of the uncertain developmental status of "male" B.

Similarities and Differences between the Bougainville Trench Specimen and the Kermedec Trench Specimens: Similarities: (1) Large body length (14 mm); (2) serration of the setae on pereopods V–VII; (3) number of short, subterminal propodal spines on pereopod VII; (4) length and relative thickness of the uropodal endopods; (5) uropodal

exopod only 0.62 times as long as first endopodal article; (6) pleotelson 1.5 times wider than long; (7) midventral surface of the pleonites smooth and rounded in lateral view; (8) two relatively long epimeral hairs or setae borne laterally on each pleonite (it is not clear whether these are feathered); and (9) the shapes of the three incisive mandibular spines.

Differences: Kudinova–Pasternak (1965a) describes the following differences between her specimen and Wolff's specimens. (1) She figures the labium of her animal and describes it as having only a single inner lobe bearing hairs (Kudinova–Pasternak, 1965a:77, fig. 2c). 1 have not observed this degree of variation even among the different genera in the Neotanaidae. If the labium of this animal has this structure it is probably abnormal. (2) The stout cleft spines on the fixed endite of the second maxilla bear four points, in marked contrast to the bifid spines of Wolff's holotype (Wolff, 1956a, fig. 25b; Kudinova–Pasternak, 1965a, fig. 3c). I have figured another animal from Wolff's collection that has many-cleft spines (Figure 29i); however, the proportions of the latter differ markedly from those in Kudinova–Pasternak's figure. In fact, I have never observed such slender spines on this endite in any species of neotanaid. (3) In a figure of the distal crest of the chela that Kudinova–Pasternak sent to me, the four dorsal teeth appear to be of appreciable size. (4) There are two anterolateral and two relatively long posterolateral setae present on the carapace. These are the only differences of substance that I could detect. The other differences described by Kudinova–Pasternak are relatively minor.

Similarities and Differences between the Argentine Basin Specimen and the Kermedec Trench Specimens: Similarities: (1) The body size is very large: at *Vema* Sta. 17–81, the figured preparatory female 2 is 14.7 mm in length, the other preparatory female 2, 14.8 mm, and the copulatory male, 16.1; the copulatory male from *Vema* 17–82 is 12.5 mm long. (2) The uropods are composed of a relatively small number of articles, (6,–), (6,6), (7,7), and (9,9), respectively; and total uropodal length is only about two-thirds the length of the pleon and is of similar unusual setation (see Figure 29l). Other similarities are (3) the long pleotelson (Figure 29d,e); (4) the shape of the pleonites midventrally and in dorsal view (Figures 29d,e; 30a–d); (5) the

very large number of dorsal carpal setae on the cheliped in stages other than copulatory males; (6) the shape and dentition of the chela in the same stages (Figure 29J,K); (7) the general shape of the incisive mandibular spines (Figure 29F–H); (8) the shapes of the setae and spines of peropods II–VII (both sexes); (9) a similar depth distribution (deep abyssal–hadal); and (10) the pleopods being almost identical, with the setal formulae as follows: the Kermedec holotype with (2,3) (3,9,5) (0,3;0,12,7) and the preparatory female 2 from the Argentine Basin with (2,2) (3,9,9) (0,2;0,10,7).

Differences: Stages Other Than Copulatory Male: (1) The shape of the pereonites viewed from above (Figure 29A–C; Wolff, 1956a, fig. 22a); (2) the midventral silhouette of the pleonites (Figures 30A,B); (3) the apparent lack of pleonal hairs in the Atlantic population (Figures 29D,E, 30A,B); (4) the length of the uropodal exopod relative to the first endopodal article is about 0.5 for the figured preparatory female 2 from the Argentine Basin and 0.8 for the figured preparatory male from the Kermedec Trench (Figure 29A,L; Wolff, 1956a, fig. 23); (5) the articles of the uropodal endopods are slightly more slender in the Atlantic population; (6) the anterolateral and posterolateral carapace setae of the holotype are 2 and 4 in number, respectively, but for the figured preparatory female 2 from the Argentine Basin both are 3 in number; (7) the fixed finger of the chela is slightly longer with respect to total propodal length in the latter animal (0.5 compared to 0.4 for the holotype); (8) the chelipedal basis is proportioned slightly differently between the two; (9) the Atlantic population is of brownish coloration with darker brown claws on the chelae, the Pacific specimens are brightly cream-colored; and (10) there are eight short, subterminal spines in the propodal row on pereopod VII in the figured preparatory female 2 from the Atlantic and 13 in the Pacific holotype, an "adult female" of unknown age.

Differences: Copulatory Males: (1) The male differs in the following above-listed characters: (2) [see Figure 30C,D], (4), (5), (6), (8), and (9) ; (2) the dactylus of the chela is similar, but the fixed finger has two teeth of equal size proximally and another just before the claw in the specimen from Vema Sta. 17–81 (Figure 30F; Wolff, 1956a, fig. 32a) and two small protuberances set between two larger teeth in the male from Sta. 17–82 (Figure

31C); (3) the dorsal setae of the chelipedal carpus are shorter (especially the first three) but of similar number (Figure 30E,F); and (4) the same article is more slender proximally.

Differences between the Specimen Collected off Portugal and Other Populations.—The specimen collected off Portugal is very similar to the other specimens and most differences observed are slight: (1) The pleotelson is more angular, with more distinctly straight rather than curved margins in dorsal view and appears to be longer with respect to width; (2) the chelipedal coxae are oblique posterolaterally in dorsal view; (3) the pleonites are sharper midventrally in silhouette than in the Argentine population; (4) the body length of this preparatory male is 20.0 mm, considerably greater than that of the two largest copulatory males known (Kermedec Trench, 15.7 mm; Argentine Basin, 16.1 mm); (5) the number of anterolateral and posterolateral hairs on the left and right sides of the carapace are, respectively, 3 and 8 and 3 and 6; and (6) the third incisive spine of the right mandible has four or five tiny, slender teeth on either side of its relatively blunt tip.

There are at least two characters in which the Portugal specimen resembles the Pacific rather than the Argentine population: the shape of the pereonites in dorsal view, and the presence of three feathered hairs on the pleonal epimeres.

REMARKS.—In 1956 Wolff (1956a:210) described this species "with some hesitation" as subspecies hadalis of Neotanais serratispinosus (=N. americanus), previously known only from the North Atlantic. He referred all other known specimens to the subspecies serratispinosus (see under "Use of the Subspecies Category for the Deep-Sea Fauna").

The above-discussed differences between the animals from the Kermedec Trench and the North Atlantic specimens demonstrate the specific distinctness of the former, conclusively shown by the discovery of both species living together at Vema Sta. 17–81 at 5330 m in the Argentine Basin. In addition, one specimen of Neotanais hadalis is known from the North Atlantic (Noratlante Sta. 096, B014), an area where the neotanaid fauna is relatively well known. The Atlantic specimens assigned to N. hadalis share most of their major morphologic differences from N. americanus, perhaps the best of which is the shape of the uropods. Future collections may indicate additional specific

status for the Atlantic animals; however, they are much more closely related to *N. hadalis* than any other presently known species.

Several years after Wolff's work, Kudinova–Pasternak (1965a:75) described a single "female with oostegites" from the Bougainville Trench. On the basis of a comparison between that specimen and Wolff's work she assigned that animal to *Neotanais serratispinosus* but discounted the need for separate subspecific status for the Pacific specimens. Unfortunately, it was not possible to obtain that specimen for comparison; however, Dr. Kudinova–Pasternak kindly sent me additional descriptive material that included a number of figures. On the basis of these data and of her published description, a comparison was made between the Bougainville and Kermedec animals (see above). The former specimen is here assigned to *N. hadalis*. It clearly is not *N. serratispinosus* (=*N. americanus*).

As this work was nearing completion I received Kudinova–Pasternak's 1970 paper in which she reports three other specimens that she assigns to *Neotanais serratispinosus* from *Vitjaz* collections in the area of the Kurile–Kamchatka trench; Sta. 3166 (44°43′ N., 153°49′ E., 5876 m, grab), two females with oostegites (12.2 and 17.5 mm), and Sta. 5620 (44°06′ N., 155°54′ E., 4895 m, grab), one manca 2 (6.5 mm). Because these records are unaccompanied by a description, the affinity of these specimens cannot be determined until they are examined. They are here tentatively assigned to *N. hadalis*.

Kudinova–Pasternak (1965a) described her single animal as a "female with oostegites." According to the additional descriptive material she sent to me, these oostegites are "thick, heavy, and opaque." In other words, the oostegite sheaths are unopened. The unusual thing about them is that they occur only on the pereopods II. Because they are at the stage when they have not yet opened, it is unlikely that the others have been broken off. Both male genital cone and gonopore anlagen are present ventrally on pereonite 7, which indicates that this animal probably, although not necessarily, is a copulatory female. It probably is the product of aberrant development.

MATERIAL.—*Galathea* Sta. 649, Kermedec Trench, 8210 to 8300 m, "adult female" holotype (not examined), 1P ♂, 1 Cop ♂, 1 "intersex" (see below); *Galathea* Sta. 651, Kermedec Trench, 6960 to 8300

m, 1 fgmt. (not Cop ♂); *Noratlante* Sta. 096, B014, southwest of Lisbon, Portugal, 4707 m, 1 P ♂; *Vitjaz* Sta. 3655, Bougainville Trench, 6920 to 7657 m, 1 "female with oostegites" (not examined); *Vema* Sta. 17–81, Argentine Basin, 5329 to 5332 m, 2 P ♀ 2, 1 Cop ♂; Sta. 17–82, Argentine Basin, 5139 to 5148 m, 1 Cop ♂.

LOCATION OF MATERIAL.—UCZM: *Galathea* collections, including holotype. AMNH: *Vema* 17–81 (AMNH 14.892); *Vema* 17–82 (AMNH 14.889). MZM: *Vitjaz* collection. NMNH: *Noratlante* 096, B014 (USNM 143177).

The *robustus* Group of Species

This group comprises *Neotanais robustus* and *N. antarcticus*. It is recognized mainly on the basis of male characters which are more notably distinct than those of other stages (see "Remarks" under *N. bulbodens* for similarities of that species to the *robustus* group).

STAGES OTHER THAN COPULATORY MALE.—The pleotelson is long, about 1.4 times wider than long. The pereonites generally are square or slightly rectangular in dorsal view. The pleonites are rounded laterally in dorsal view and midventrally in silhouette. The dorsal crest on the chela is low and inconspicuous, and the dactylus is curved relatively more strongly than in other species. The uropodal exopods are only about 0.5 times as long as the first endopodal article.

The two species differ in the following ways: The body length of *Neotanais antarcticus* is about 8 mm for a preparatory female 2, whereas it is about 18 mm for the same stage in *N. robustus*; the ratio of body length to width is 7.0 for the former species compared to about 5.8 for the latter; there are only four distolateral setae on the first article of the first antenna (preparatory female 2) in *N. antarcticus* but seven or eight in *N. robustus* (preparatory males); and in *N. antarcticus* there are about 14 short subterminal spines on the propodus of pereopod VII compared to 25 to 30 in *N. robustus* (same stages).

COPULATORY MALES (two stages known for *Neotanais robustus* and one for *N. antarcticus*).—The male stages vary from those of other species in the nondimorphic characters listed above for other stages. In addition, the fixed finger of the chela bears a large clump of teeth proximally (q.v.)

which is separated from a single large distal tooth by a notch formed by the marked upward bending of the finger. The distal ventral carpal seta of the cheliped is very much thickened and is brown in coloration. The dactylus of the chela bears one small proximal tooth and another larger distal tooth. The chelipedal carpus is slender, gradually bent, and bears various protuberances or keels. The anterolateral areas of the carapace are expanded or flared laterally. The short, subterminal propodal spines on pereopod VII bear moderately fine teeth similar to those of other instars.

The two species differ in the nondimorphic characters listed above for other developmental stages. In addition, the shape of the pereonites in dorsal view is different (q.v.). The rostrum in *Neotanais antarcticus* is considerably more pointed than in *N. robustus*. The chela is remarkably different in *N. robustus*, exhibiting a series of large protuberances lacking in *N. antarcticus*. The chelipedal carpus differs in a number of ways. It bears distal lateral and/or medial protuberances in *N. robustus*. The distal ventral seta in *N. robustus* is spinelike and borne on a protuberance but is more slender, longer, and lacking the protuberances found in *N. antarcticus*. The dorsal setae are few and exceedingly short in the former, whereas they are up to 5 in number and relatively long in the latter species.

Neotanais robustus Wolff, 1956

FIGURES 33–35, *100*

Neotanais robustus Wolff, 1956c:41–43, fig. 1, pl. 1: figs. 7–10.

DIAGNOSES.—*Stages Other Than Copulatory Male*: *Pereonites appearing generally rectangular in dorsal view, but each slightly wider in area above pereopods; without significant dorsal relief. *Pleonites rounded laterally in dorsal view and without prominent epimeral hairs; pleonite 5 almost as wide as pleonite 1; *rounded and smooth midventrally in lateral view. *Pleotelson long relative to many species, about 1.4 times wider than long. *Chelipedal propodus with low dorsal crest; large distal teeth irregular and sometimes fused; dactylar teeth distally directed, some sharp with pointed tips, others fused. *Carapace considerably expanded posteriorly; *anterolateral keels prominent; a single anterolateral seta and a single posterolateral

seta on each side. First article of first antenna about 4.1 times longer than wide. Uropodal exopod strongly deflected downward; endopod slender compared to many species. *Pereopod VII with a remarkably long row of short, subterminal propodal spines, about 25 to 30 being present in preparatory males.

Copulatory Males: *Pereonites appreciably wider in area over pereopods, rounded and sloping forward medially anterior to this point; without significant dorsal relief. *Pleonites rounded and slightly flared laterally in dorsal view with a slight longitudinal furrow dorsally; *sternites rounded midventrally in lateral view; pleon only moderately tapered, pleonite 5 being nearly as wide as pleonite 1. *Pleotelson long, similar to other stages. *Anterolateral keels on carapace pronounced and expanded laterally; lateral setae single as in other stages; oblique furrows noticeable, continuing posteriorly to area of chelipedal coxae where joined by a faint transverse furrow; *respiratory chambers and coxae expanded laterally and exhibiting considerable relief. *Chelipedal carpus strongly curved and not especially stout; *proximal ventral seta very slender and posteriorly directed, distal seta replaced by a huge, posteriorly directed, brown-colored spine borne on a blunt projection. *Chela type ?A (primary copulatory male) with a large ventral spur and a large lateral spur borne on wide area of propodus; dorsal propodal surface irregular and with fine undulations; fixed finger somewhat twisted, with dentition as in Figure 35B. *Chela type ?B (secondary copulatory male) with only 1 ventral propodal spur and dorsal surface of propodus without fine undulations but with distally directed prominence midway along dorsal surface; fixed finger strongly twisted, with dentition as in Figure 35A.

DESCRIPTION OF PREPARATORY MALE E (*Galathea* Sta. 664).—This animal is described rather than a female due to the limited material available. The holotype also is a preparatory male.

Body (Figure 33A): 19.2 mm long and 5.8 times longer than wide.

Carapace: 1.1 times longer than wide; anterolateral keels prominent; only 1 anterolateral seta and 1 posterolateral seta present. Oblique furrows moderately well developed and chelipedal coxae strongly expanded laterally in dorsal view.

Pereonites: Generally rectangular in dorsal view

but appearing only slightly wider than long; rounded anteriorly. Width-length ratio of pereonite 5, 1.5 (Figure 33c). No obvious surface relief. Ventral surface of pereonite 7 bearing slit-shaped male gonopore anlagen (Figure 33c); genital cone primordia not visible.

Pleonites (Figure 33A,D,E): Epimeres rounded laterally in dorsal view, and pleonite 1 about as wide as pereonite 7 or pleonite 5. Sternites smooth and rounded midventrally in lateral view.

Pleotelson (Figure 33A,D,E): Long, about 1.4 times wider than long.

First Antenna: First article 4.1 times longer than wide.

Left Mandible: Second incisive spine serrate only at tip on both sides; first spine similar on its outer side but serrate along about the outer two-thirds on its inner side. [Holotype (Figure 33I) agrees in all details.] Lacinia mobilis with 6 teeth; posterior lobe notched. Pars molaris with about 22 teeth.

Right Mandible: Proximal 2 incisive spines as on left side (holotype also).

Second Maxilla: Stout cleft spines of fixed endite with 3 and 4 points (Figure 33J). Medial row composed of 23 feathered setae and 4 naked spines, 1 of which is slightly cleft at tip.

Maxilliped: Setal formula of palp, (1,0,5+1,8,20).

Cheliped (Figure 34A,B): Carpus bearing 9 dorsal setae of moderate length. Dorsal crest of propodus shallow and narrow. Proximal cutting edge of fixed finger with about 50 denticles; 6 irregular distal teeth partially fused. Dactylar teeth irregular and generally slightly pointed distally.

Pereopods II–VII (Figure 34D): Setal formulae of pereopods II and III, (10,13,15,13) and (18,27, 19,27). Posterior propodal and carpal setae extremely long and fine. Short, terminal propodal spine of pereopods II–IV with curved tip and about 10 moderately large teeth (Figure 34E). Short, subterminal carpal spine, pereopod II, apparently naked (Figure 34C). Long, terminal propodal spines of pereopods II–IV, 4, 5, and 3 in number, respectively; teeth varying in size from relatively large to moderately small. Pereopod VII with 27 short, subterminal propodal spines. Dactylar spine of pereopod II, 0.3 times as long as article. Dactyli of pereopods V and VI with coarse terminal teeth, dactylus of pereopod V with very fine teeth.

Pleopods: Terminal and lateral rows of endopodal setae appear continuous. Former setae 0.97

times as long as endopod. Setal formula, (1,4) (3,18,11) (0,5;0,16,11).

Uropods: Each endopod with 9 articles; exopod about 0.5 times as long as first endopodal article and strongly deflected downward (Figure 33H). Endopod relatively slender.

DESCRIPTION OF COPULATORY MALE K (*Galathea* Sta. 664).—*Body* (Figure 33B): 21.3 mm long and 5.7 times longer than wide.

Carapace: 1.3 times longer than wide. Anterolateral keels very pronounced and expanded laterally, overhanging lower areas of carapace. Oblique furrows markedly well developed and extending posteriorly, almost to rear margin of carapace; a short, shallow, transverse furrow lying between former at level of chelipedal coxae. Coxae markedly expanded laterally in dorsal view.

Pereonites: Generally appearing wider than long, with area over pereopods expanded laterally. Pereonites 4–6 rounded anteriorly and gradually sloping medially. Width-length ratio of pereonite 5, 1.6. No marked dorsal surface relief present.

Pleonites: Tapering moderately anteroposteriorly, pleonite 1 slightly wider than pleonite 5. Pleonite 1 considerably wider than pereonite 7. Epimeres rounded and flared laterally in dorsal view (Figure 33B); a slight longitudinal depression running the length of pleon middorsally. Sternites rounded midventrally in lateral view as in other stages, but midventral convexities more pronounced (Figure 33F).

Pleotelson: Long in dorsal view, similar to that of other stages; width-length ratio, 1.5.

First Antenna: Article 1, 5.9 times longer than wide.

Second Maxilla: Bearing a number of long setae. Movable endite recognizable, bearing 3 and 7 setae on external and internal lobes respectively. Two long setae and 2 short, triangular or wedge-shaped spines present in area of fixed endite and 3 longer setae in area of medial setal row.

Maxilliped: Endite naked. Setal formula of palp, (0,0,4+1,11,19).

Cheliped (Figure 35A,H): Carpus moderately strongly curved and not especially stout; 3 weak hairs borne middorsally and centrally. Ventral surface bearing 2 low convexities in proximal half. Centrally, long, thin, recurved seta followed by an immense, brown-colored, posteriorly directed spine (much modified second carpal seta). A broad, distal
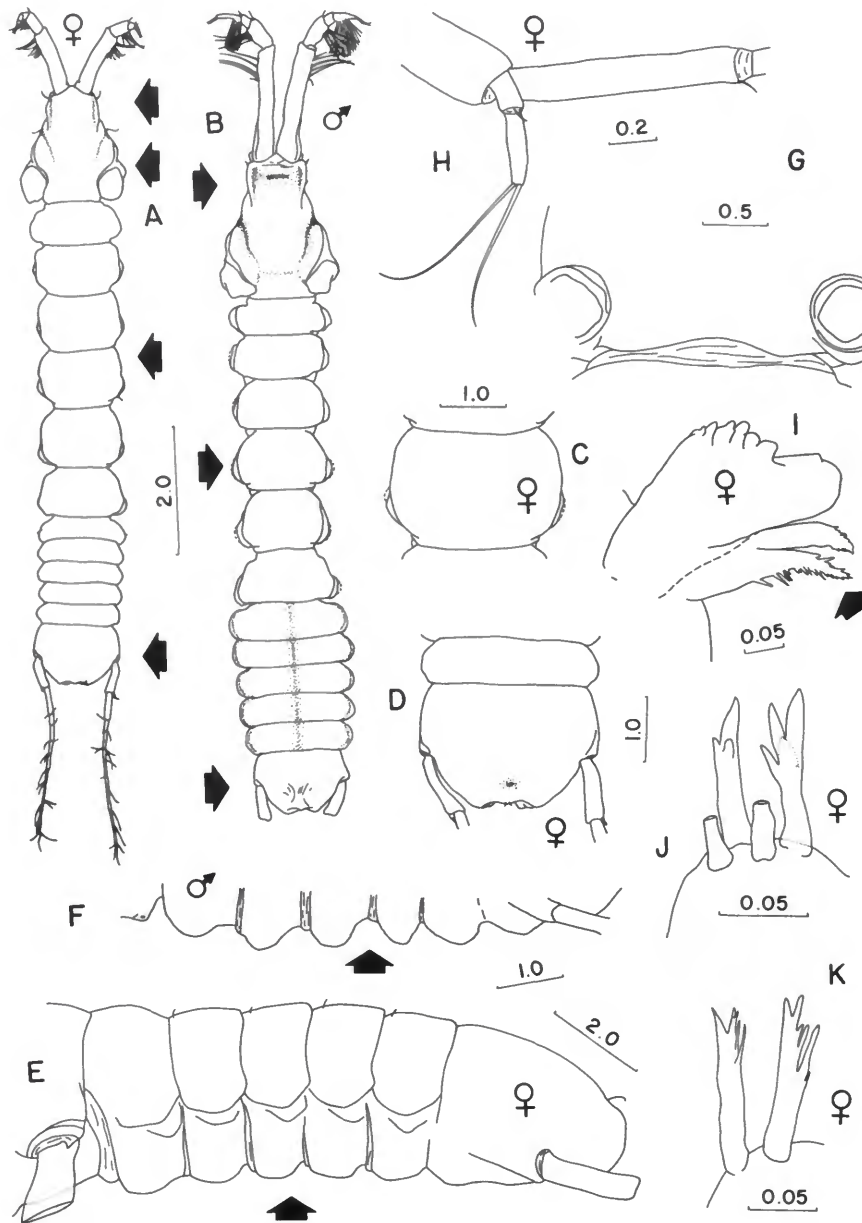
FIGURE 33.—*Neotanais robustus* Wolff, *Galathea* collections (preparatory males are designated by ♀ because they also represent female stages): A, preparatory male E, dorsal view, Sta. 664; B, copulatory male K, dorsal view, same station; C, pereonite 5, dorsal view, preparatory male E; D, pleonite 5 and pleotelson, dorsal view, same animal; E, pleon, lateral view, same animal; F, pleon, lateral view, copulatory male K; G, pereonite 7, ventral view, preparatory male E; H, left uropodal exopod and first endopodal article, lateral view, same animal; I, pars incisiva, left mandible, preparatory male, holotype, Sta. 663; J, forked spines of fixed endite, right second maxilla, preparatory male E; K, same, left side, holotype.
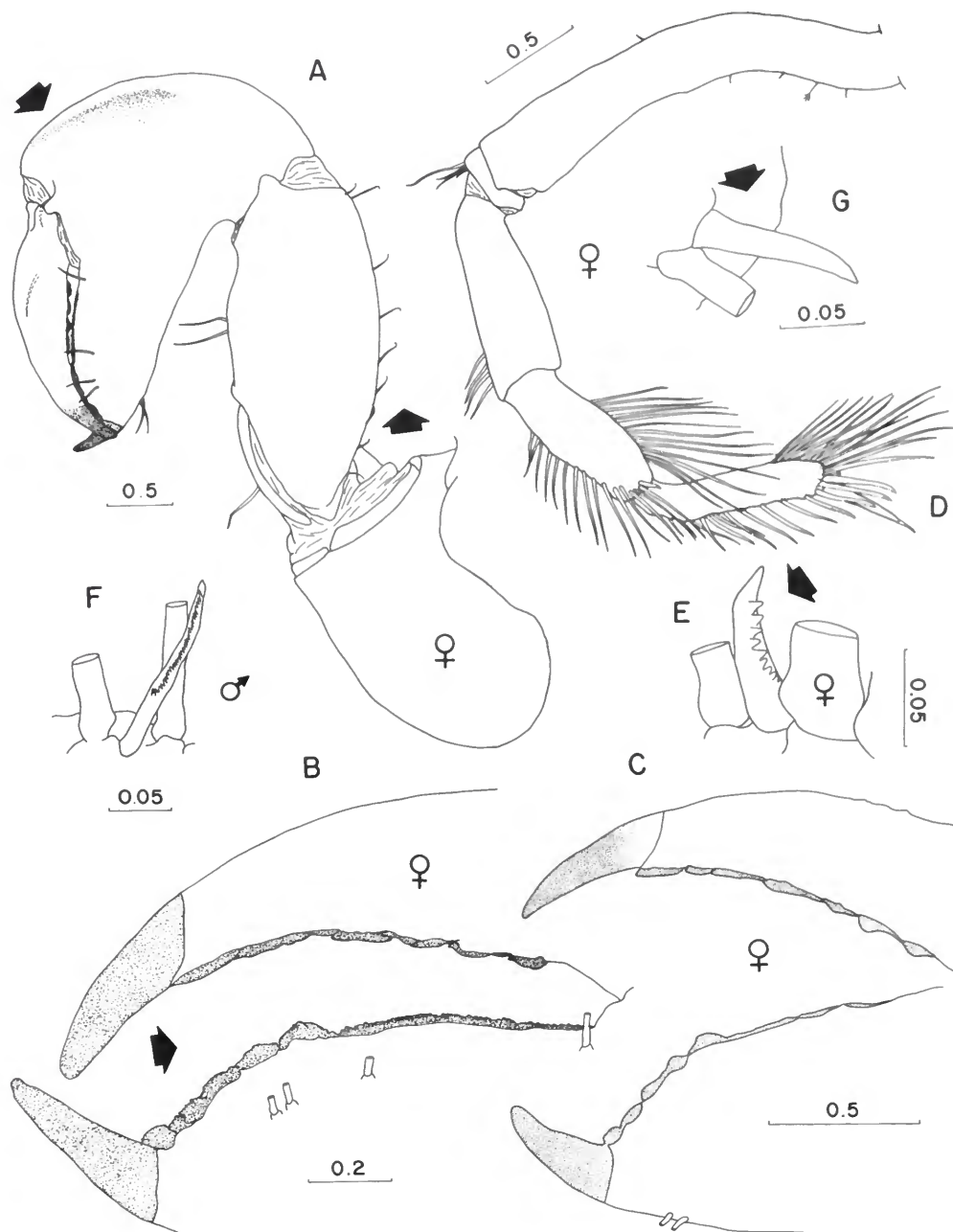
FIGURE 34.—*Neotanais robustus* Wolff, *Galathea* collections: A, left chela, preparatory male E, Sta. 664; B, chela, same appendage; C, same, preparatory male G, same station; D, left pereopod II, preparatory male E; E, short, terminal propodal spine, same appendage; F, same spine, copulatory male K, same station; G, short, subterminal carpal spine, male E.
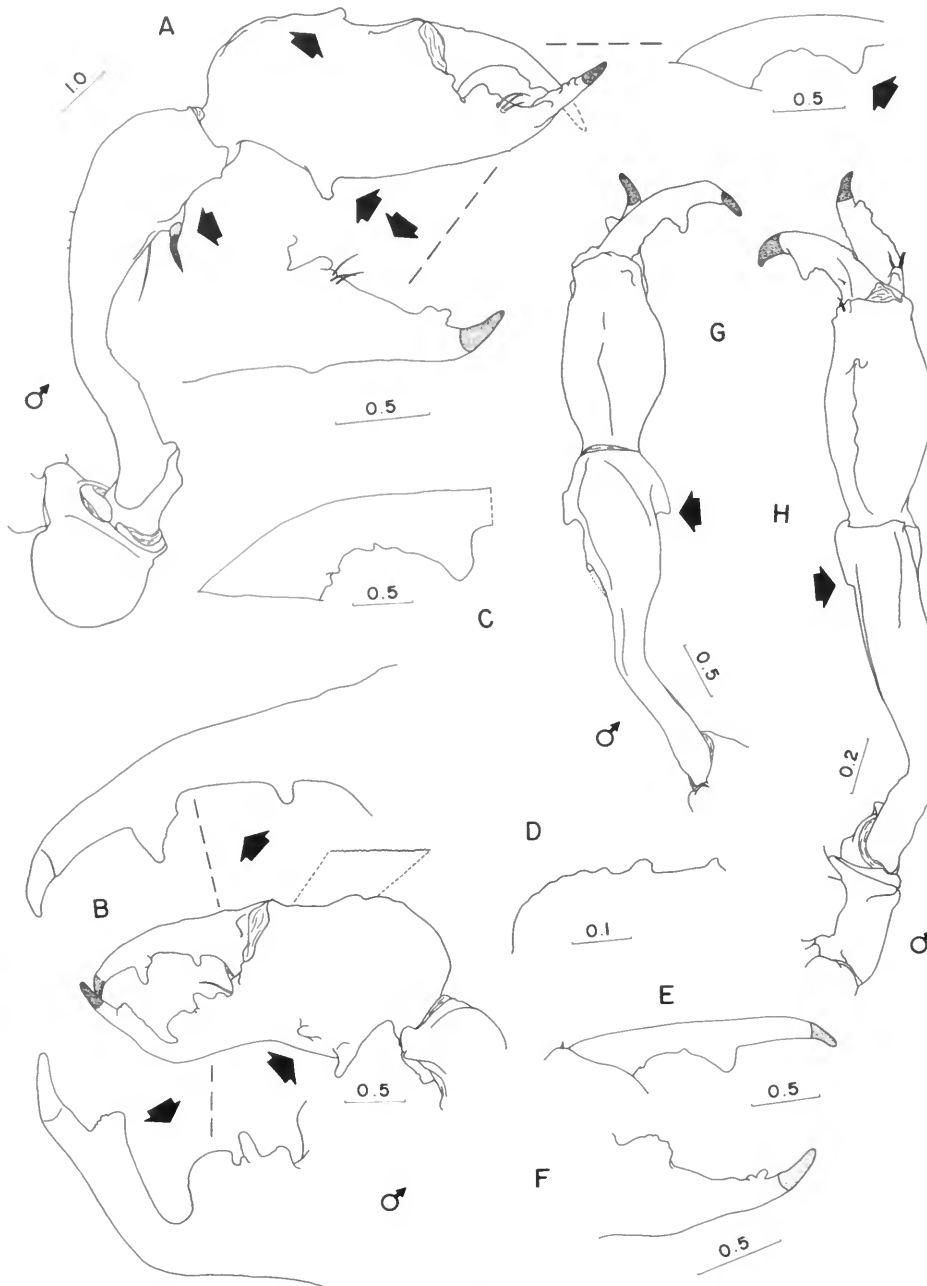
FIGURE 35.—*Neotanais robustus* Wolff. Chelipeds of copulatory males, *Galathea* collections: A, right cheliped with slightly oblique enlargements of "fingers," male K, Sta. 664; B, left cheliped, with enlargements, male D, Sta. 663; C, dactylus, right chela, lateral view, male C, same station; D, dorsal propodal crest, same chela; E, F, dactylus and fixed finger, right chela, male B described by Wolff, same station; G, dorsal view of left cheliped, male D; H, same, right side, male K.

medial projection present on carpus. Dorsal propodal surface irregular and bearing a rounded, forwardly directed protuberance centrally which slightly overhangs surface below. One long, rounded, somewhat anteriorly directed spur borne ventrally and followed by a tiny protuberance less than one-third of the distance from the end (on fixed finger). Distal end of fixed finger twisted strongly, teeth facing laterally although axis remains relatively straight. Three setae located between low, rounded, closely appressed teeth proximally and 1 bilobed tooth distally. Dactylus turned strongly medially and bearing 2 small protuberances proximal to 1 very large, triangular distal tooth.

Pereopods II–VII: Setal formula of pereopod II, (12,15,14,17). Pereopods II–IV with 3, 4, and 4 long, terminal propodal spines respectively (fourth spine in pereopod II may be enlarged first seta in anterior row; teeth very fine on pereopod IV). Short, terminal propodal spines relatively straight and more slender than in other stages and with more numerous teeth (Figure 34E). Short, subterminal carpal spine of pereopod II similar to that of other stages. Short, subterminal propodal spines of pereopod VII 34 in number and similar in shape to those of other stages.

INTRASPECIFIC VARIATION.—*Stages Other Than Copulatory Male*: The width-length ratio of pereonite 5 is 1.9 in the holotype, possibly due to the anteroposterior compaction of the segments. The width-length ratio of the pleotelson is 1.6. The stout cleft spines of the fixed maxillary endite of the holotype have more points than those of the animal described above (six and four versus three and four; cf. Figure 33J,K). There are three stout spines next to the medial row of 22 setae in the holotype. The chela of preparatory male G (Figure 34C) bears five propodal teeth (typical of most specimens) and an irregular proximal denticular area; the three proximal dactylar teeth are rounded. The terminal dactylar teeth of pereopods V–VII bear the following types of teeth (preparatory male J, Sta. 664): both pereopods V and right pereopod VI, coarse; left pereopod VI and both pereopods VII, fine.

Copulatory Males: Cheliped: Of the four copulatory males examined, three (K, described above, Sta. 664, and B and C, Sta 663) share one type of chela, whereas male D, Sta. 663, has another type.

The distribution of body sizes may indicate that B, C, and K, larger animals, have chela type B and are secondary males, whereas male D is a primary male and has chela type A. Variation in type B cheliped is illustrated in Figure 35A,C–F,H. The body lengths of the copulatory males are as follows: B, 22.0 mm; C, 21.7 mm; K, 21.3 mm; and D, 20.4 mm (estimated). In male D (Figure 35B,G), with cheliped type A, the carpus is somewhat less strongly bent and the distal medial projection is more pronounced than in male K. A lateral projection also is present, with an additional lateral spur just distal to a spur homologous with that of male K. The fixed finger bears a large, proximal cluster of four teeth of irregular size and shape. One large, distally directed tooth with an irregular margin lies distally near the claw. The dactylus bears two prominent teeth, the distal one bearing a lateral protuberance.

POSTMARSUPIAL DEVELOPMENT.—Preparatory males have eight or nine articles in the uropodal endopod; copulatory males have nine or ten (data available from these stages only). The terminal endopodal seta length/endopod length ratios of the pleopods are as follows: preparatory female 1F, 1.1; preparatory male E, 0.97; and copulatory male K, 1.4. The number of terminal endopodal setae is 10, 18, and 19 respectively.

REMARKS.—*Neotanais robustus* was described briefly in 1956 by Wolff from 13 specimens collected by the *Galathea*. It is redescribed here in detail and diagnoses are given for all stages. Primary and secondary copulatory males are distinguished for the first time.

MATERIAL.—*Galathea* Sta. 663, Kermedec Trench, 4410 m, 1 P ♂ (holotype), 3 cop ♂ (including Wolff's allotype); *Galathea* Sta. 664, same area, 4510 to 4570 m, 1 P ♀ 1, 1 P ♀ 2, 1 Cop ♀, 3 P ♂, 1 Cop ♂.

LOCATION OF MATERIAL.—UCZM: all material.

Neotanais antarcticus Kussakin, 1967

FIGURES 36, *101*

Neotanais antarcticus Kussakin, 1967:320–323, figs. 59–61.

DIAGNOSES.—*Stages Other Than Copulatory Male* (based on examination of female paratype): *Pereonites 4–6 generally square or slightly rectangular in dorsal view with parallel sides. *Pleotelson relatively long in dorsal view, only 1.4 times wider

than long; *sides anterior to uropods more or less parallel, posterior to uropods sloping evenly medially and not especially rounded. *Pleonites rounded laterally in dorsal view and without prominent dorsolateral hairs; *sternites smoothly rounded midventrally in lateral view. Uropodal exopods about 0.5 times as long as first endopodal article. *Carapace bearing relatively well-developed rostrum; *anterolateral keels relatively prominent; *chelipedal coxae not especially expanded laterally; oblique furrows not prominent. *Cheliped similar to that in the *americanus* group of species; a number of substantial dorsal and two relatively long ventral carpal setae present; propodus with moderate dorsal crest.

Copulatory Male (only one type known): *Pereonites 4–6 generally square or rectangular in dorsal view but with areas over pereopods much wider than anterior parts of somites. *Carapace with prominent rostrum and anterolateral keels; oblique furrows pronounced and leading posteriorly into depressed lines; a single, short anterolateral and a single, relatively long posterolateral seta present on either side. *Pleonites rounded and flared laterally in dorsal view and bearing 2 or 3 short hairs dorsolaterally; sternites generally rounded in lateral view but more angular than in other stages. *Pleotelson about 1.6 times wider than long. *Chelipedal carpus not strongly bent but expanded distally into a low, ventrolateral keel bearing the 2 long ventral setae; *distalmost seta very long, thick, and brown; about 7 moderately long dorsal setae present. Chela with dorsally serrate propodus of ordinary form; *propodal finger strongly bent; *dentition as in Figure 36c.

MISCELLANEOUS OBSERVATIONS ON SPECIMENS EXAMINED.—*Preparatory Female 2 Paratype*: Body 7.8 mm long and 7.0 times longer than wide. Pereonite 7 with no trace of male genital anlagen. Pleotelson 1.4 times wider than long in dorsal view. First antenna with first article 4.9 times longer than wide. Setal formulae of two pleopods, (2,1)(3,9,5)(0,2;0,9,4) and (1,1)(3,8,6)(0,2;0,10,3). [Formula of the holotype is (0,0)(3,9,6)(0,3;0,6,4) according to Kussakin's (1967) figure 61.] Terminal endopodal setae of paratype female 1.4 times longer than endopod. Uropodal exopod 0.5 times as long as first endopodal article.

Copulatory Male Allotype: Body 8.5 mm long and 7.0 times longer than wide. Pleotelson 1.6

times wider than long. First antenna with first article 7.0 times longer than wide. Pereopod II with setal formula (5,6,6,5); dactylar spine only about one-fourth as long as article. Pereopod VII with short, subterminal propodal spines dentate as in other stages; number not reduced. Setal formula of pleopods, (3,0)(3,7,6)(0,3;0,9,3).

DATA FROM KUSSAKIN'S PAPER.—A number of items are repeated here from Kussakin's original description (in Russian) of the "female" holotype. The left mandible has serrations on both sides of both incisive spines; the lacinia mobilis bears three irregular teeth, and the large lobe has two shallow terminal depressions. No mention is made of the right mandible. The two forked spines of the fixed endite on the maxillae apparently are bifid; the medial setal row is composed of 13 setae and two spines. The proximal cutting edge of the fixed finger on the chela bears proximal denticles. The length of the uropods is considerably longer than that of the pleon; the exopod is three-fourths as long as the first endopodal article.

REMARKS.—It was possible to examine the copulatory male allotype and the preparatory female 2 paratype but not the holotype. Appendages were not dissected and many legs were broken or missing. The results of my examination are presented above in text and figures and are intended to supplement the description of Kussakin (1967). The places at which the holotype and allotype were collected were accidentally interchanged in the original published description (Kussakin, personal communication). The correct locations are given below, under material.

The conspecificity of the holotype and the other specimens could not be verified here because the former was unavailable. The two specimens examined were collected from locations in close geographical proximity and at similar depths. My examination showed that they shared significant similarities in the following: (1) body size, (2) pleotelsonal shape in dorsal view, (3) shape of pleonites midventrally, (4) number of distolateral setae on article 1 of the first antenna, and (5) similar numbers of propodal and carpal setae on pereopods II–VII. No reason was found to doubt their conspecificity.

Neotanais antarcticus, N. robustus, N. bulbodens, and *N. peculiaris* are similar in having the distal ventral carpal seta on the copulatory male cheli-

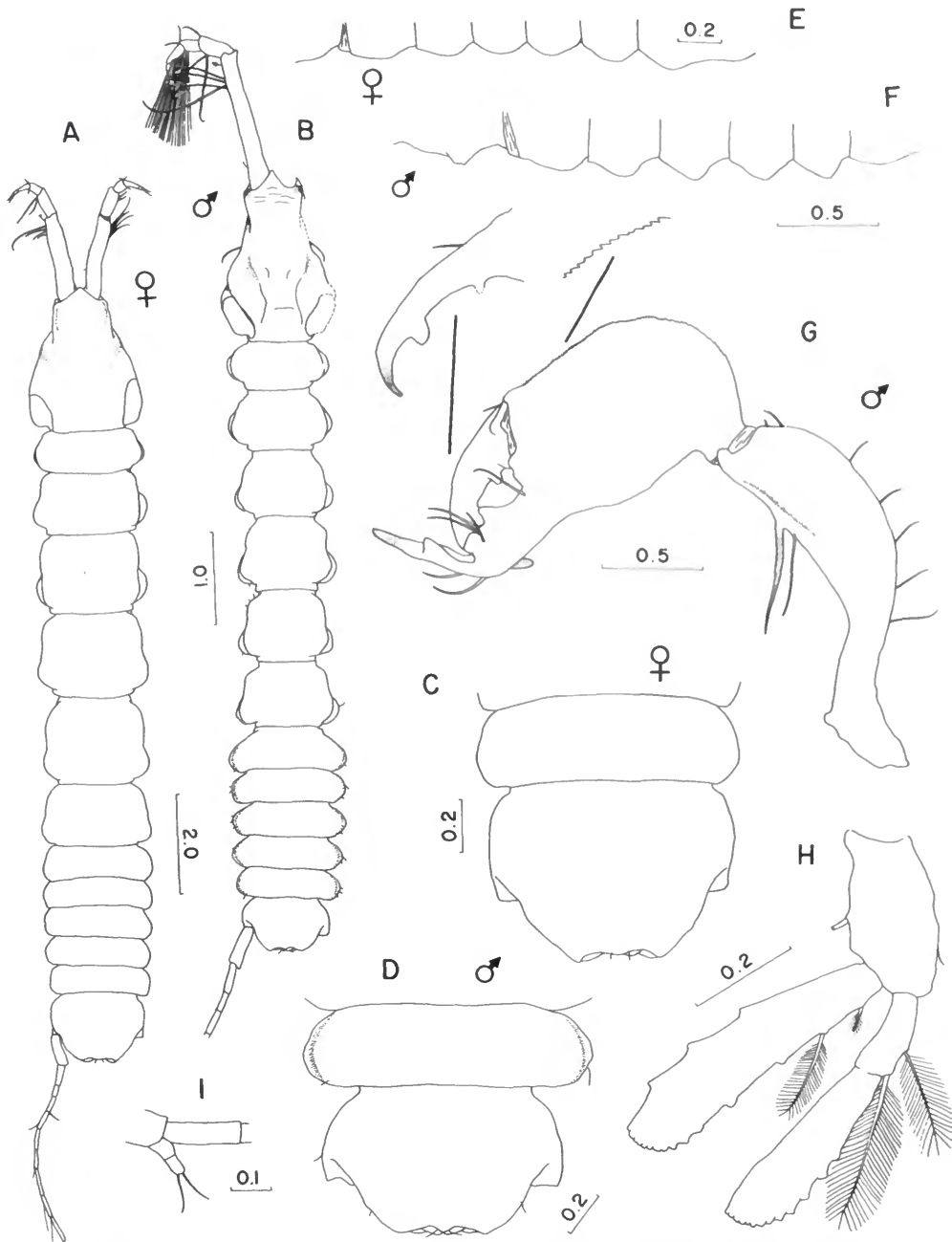FIGURE 36.—*Neotanais antarcticus* Kussakin: A, dorsal view of preparatory female 2 from *Ob* Sta. 331; B, dorsal view of copulatory male allotype; C, pleonite 5 and pleotelson in dorsal view, female in A; D, same, allotype; E, ventral silhouette of pleon in lateral view, female in A; F, same, allotype; G, left cheliped of allotype; H, pleopod of female in A; I, uropodal exopod and first endopodal article, female in A.

peds much enlarged and colored brown. This character differentiates them from all other species for which adult males are known. However, the affinities of *N. antarcticus* must await further collections.

MATERIAL.—All from Antarctica. *Ob* Sta. 14, along Banzare Coast, 223 m, 1 Cop ♂ allotype; *Ob* Sta. 41, along Princess Astrid Coast, 397 m, 1 " ♀ " holotype (not examined); *Ob* Sta. 331, along Banzare Coast, 390 to 410 m, 1P ♀ 2.

LOCATION OF MATERIAL.—ZIASL: *Ob* 14, allotype (No. 3/50208); *Ob* 41, holotype (No. 1/46988); *Ob* 331 (No. 2/49998).

Neotanais bulbodens, new species

FIGURES 37, 38, *98*

DIAGNOSES.—*Stages Other Than Copulatory Male:* *Body narrow, about 8 times longer than wide. *Pereonites 3–6 square or somewhat bell-shaped in dorsal view due to widening over pereopods. *Chelipedal carpus with about 6 to 8 long dorsal setae, the penultimate seta being especially long; *most-proximal tooth of fixed finger extremely prominent, larger than the others; *dactylar "teeth" are isolated brown swellings, about 3 in number. *Pleotelson appearing relatively short in dorsal view; sides convex both anterior and posterior to uropods. Pleon and pleotelson about as wide as pereonite 7; *pleonal sternites expanded ventrally into blunt, posteriorly directed spurs of moderate size. Carapace simple, oblique furrows almost imperceptible, and single anterolateral and posterolateral setae present. Uropodal exopod 1.3 times as long as first endopodal article.

Copulatory Male (only one type known): *Pereonites similar to other stages but slightly wider proportionately. *Chelipedal carpus stout, scarcely curved at all, and bearing a few dorsal setae; *distalmost ventral seta modified into a strong, brown-tipped spine reminiscent of that of *Neotanais robustus*; dorsal border of propodus serrate; dentition of fingers as in Figure 38B,C; dorsal surface of dactylus finely and irregularly crenate; neither finger appreciably twisted or bent.

DESCRIPTION OF PREPARATORY FEMALE 1 HOLOTYPE (*Anton Bruun* Sta. 95).—*Body* (Figure 37A): 7.6 mm long and 8.0 times wider than long.

Carapace (Figure 37A): 1.3 times longer than wide. Anterolateral keels moderately well devel-

oped; oblique furrows almost imperceptible; area of chelipedal coxae moderately swollen in dorsal view. Only single anterolateral and posterolateral setae present.

Pereonites (Figure 37A,B): Pereonites 3–6 square in dorsal view or bell-shaped due to lateral expansion of area over pereopods; width-length ratio of pereonite 5, 1.0.

Pleonites (Figure 37A,C,D): Epimeres sloping gradually laterally and posteriorly in dorsal view. Pleonite 1 as wide as pereonite 7 and only very slightly wider than pleonite 5. Sternites drawn out midventrally into large, posteriorly directed, and bluntly tipped projections.

Pleotelson (Figure 37C,D): Short; margins convex anterior and posterior to uropods; lateral angles acute. Anal membranes not visible from above.

First Antenna: First article 4.3 times longer than wide.

Right Mandible (see Figure 38A): First incisive spine entirely serrate on inner side and along distal third of outer side; second spine serrate on distal third of both sides. Tip of third spine broken (see "Intraspecific Variation," below).

Left Mandible: Incisive spines as in right mandible. Lacinia mobilis with 3 low, rounded teeth; large posterior lobe rounded and partially flattened centrally.

Second Maxilla: Fixed endite with 2 stout, bifid spines. Medial setal row with 11 setae with setules and a single spine.

Maxilliped: Only 2 medial filter setae present on endite. Setal formula of palp, $(-,-,4+1,6+1,11)$.

Cheliped (Figure 37F,G): Carpus bearing 7 relatively long dorsal setae; penultimate seta extremely long. Dorsal crest of propodus not prominent. Distal claws of both fingers set off from rest of finger (tips slightly expanded) in contrast to most species. Propodal teeth irregular, most proximal tooth greatly enlarged, brown area of tooth extending proximally; proximal cutting edge of fixed finger smooth. Dactylus bearing 3 large convexities separated from each other and lying proximal to the 4 distalmost propodal teeth.

Pereopods II–IV (Figure 38D): With setal formulae (1,4,4,4), (3,7,5,5), and (3,8,5,4) respectively. Proximal ventral area of propodi with several small, distally directed spurs. Short, terminal propodal spine with several large teeth (Figure 38E). Three large, terminal propodal spines present on
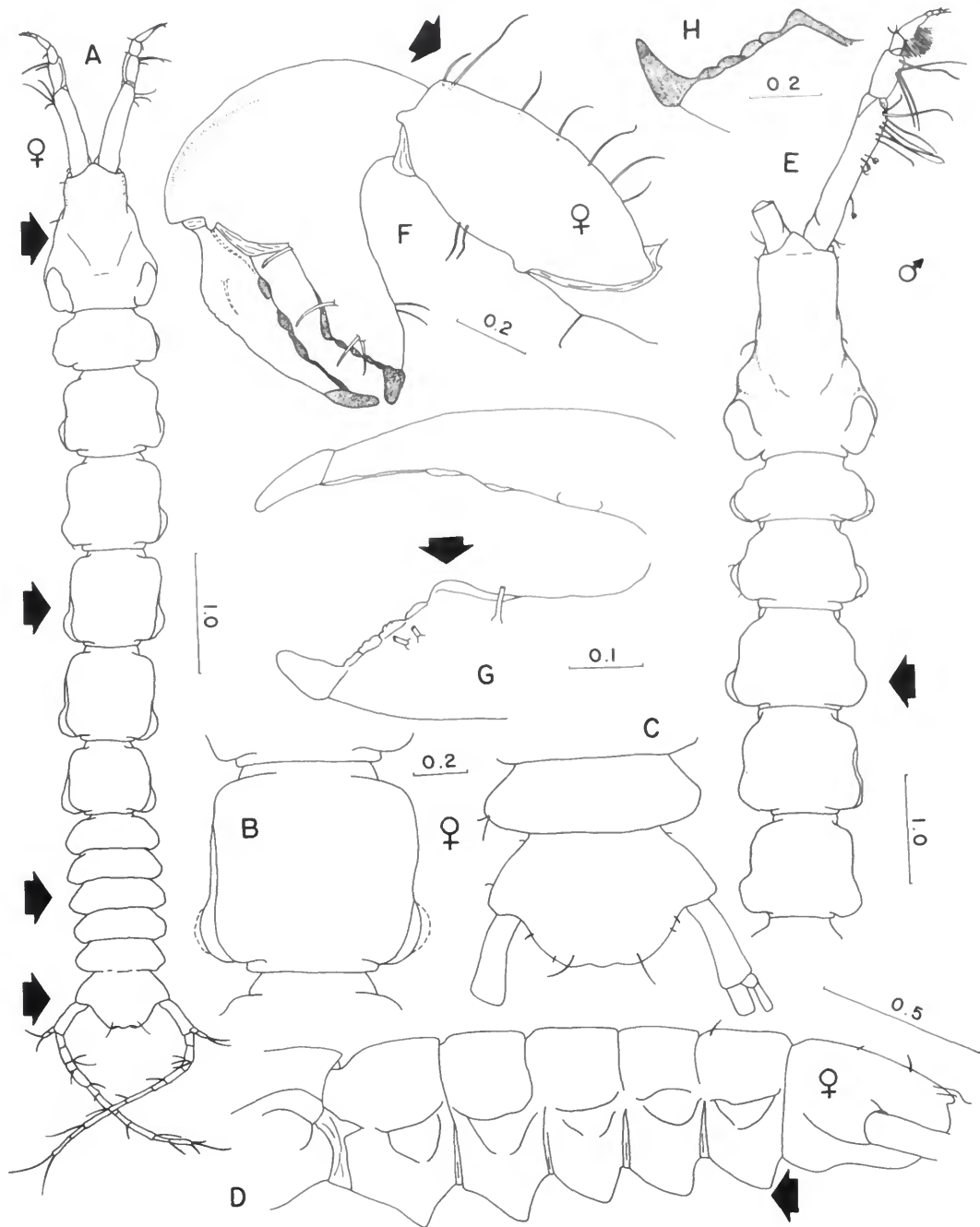
FIGURE 37.—*Neotanais bulbodens*, new species (all except E and H are of preparatory female 1, holotype, *Anton Bruun* Sta. 95): A, dorsal view; B, pereonite 5; C, pleonite 5 and pleotelson; D, pleon, lateral view; E, dorsal view, described copulatory male, same station; F, left cheliped; G, same, chela slightly oblique to F; H, same, preparatory female 1 D, same station.
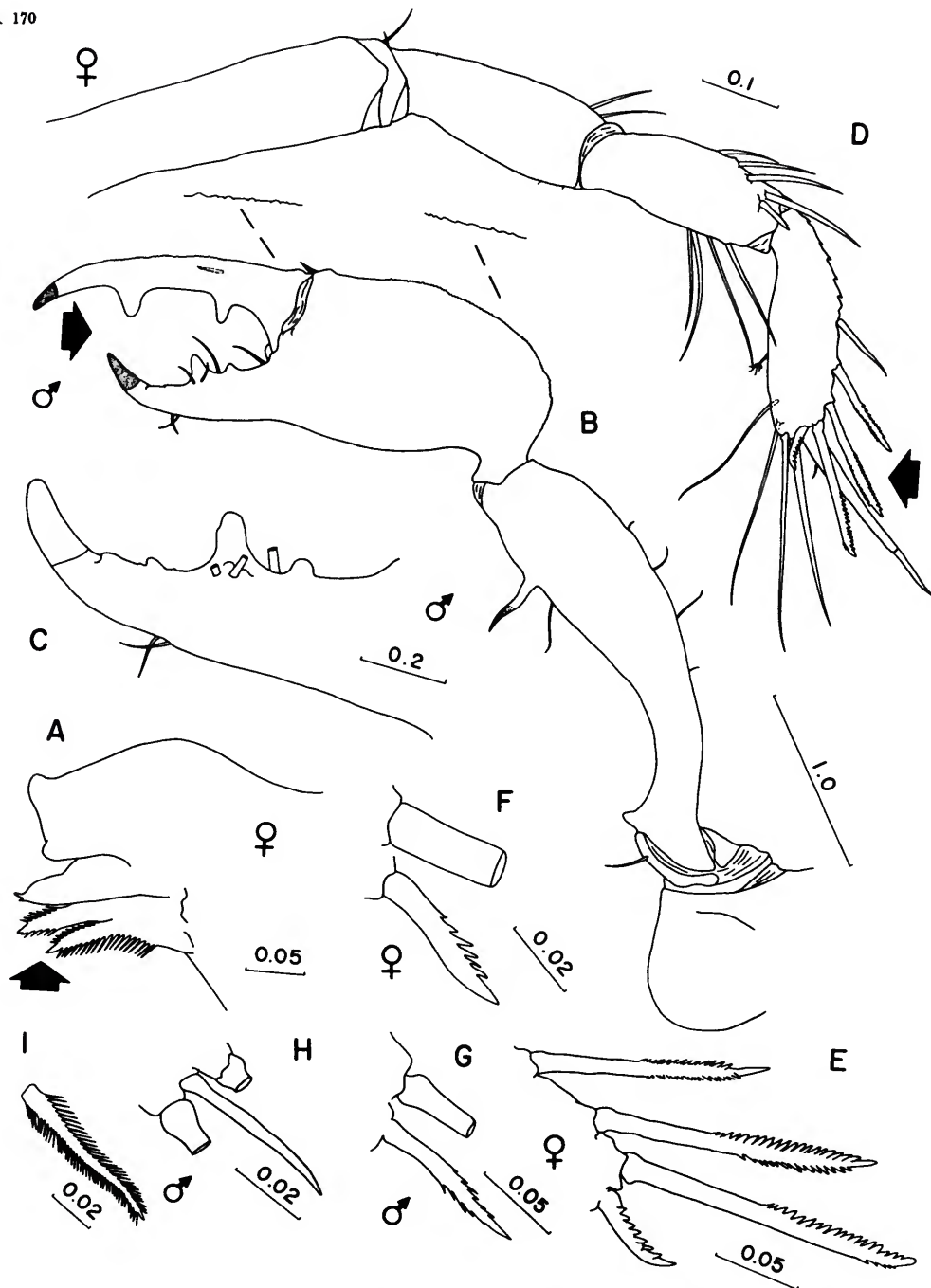
FIGURE 38.—*Neotanais bulbodens*, new species: A, pars incisiva, right mandible, preparatory female 1, *Anton Bruun* Sta. 95; B, left cheliped, described male, same station; C, enlargement of fixed finger, same animal, slightly oblique to B; D, right pereopod II, anterior view, holotype, same station; E, terminal propodal spines, same appendage; F, short, subterminal carpal spine, same appendage; G, same spine, described male; H, short, terminal propodal spine, pereopod II, same animal; I, same spine, pereopods III and IV, same animal.

each of these legs (Figure 38E). Short, subterminal carpal spine of pereopod II bearing several narrow, acute teeth on at least 1 side (Figure 38F). Dactylar spine of pereopod II 0.4 times as long as article.

Pereopods V–VII: With setal formulae (6,5,5,5), (6,5,5,5), and (5,5,4,5) respectively. Dactylar teeth all coarse. Nine short, subterminal propodal spines present on pereopod VII.

Pleopods: Setal formula, (2,2) (3,7,6) (0,3;0,7,5). Terminal endopodal setae 1.7 times as long as endopod.

Uropods: 10 articles in each endopod. Exopod 1.3 times longer than first endopodal article.

DESCRIPTION OF COPULATORY MALE ALLOTYPE (*Anton Bruun* Sta. 95; only one type of copulatory male known).—*Body* (Figure 37E): Pleon missing; 7.8 mm in length from rostrum to posterior edge of pereonite 7.

Carapace: 1.5 times longer than wide. Rostrum relatively acute; lateral setation as in female holotype; oblique furrows only moderately well developed.

Pereonites: Showing clear resemblance to those of other stages (q.v.), although appearing relatively wider; pereonite 5, 1.1 times wider than long.

First Antenna: First article 5.7 times longer than wide.

Second Maxilla : Bearing 3 and 5 relatively long setae on external and internal lobes of movable endite, respectively.

Maxilliped: Setal formula of palp, (1,0,1,0,11).

Cheliped (Figure 38B,C): Carpus stout and little curved. Propodus bearing tiny, distally directed teeth along its dorsal surface. Fixed finger considerably shorter than dactylus; neither finger greatly twisted or bent. Propodus with 1 large, central, round-tipped tooth preceded by a similar but smaller one and followed by several irregular distal convexities. Dactylus with 2 large, round-tipped, and equally spaced teeth; dorsal surface bearing tiny irregular crenations along proximal half.

Pereopods II–VII: Setal formulae of pereopods II–IV and VII, (3,6,5,4), (11,10,6,8), (5,13,6,7), and (7,9,5,6), respectively. Short, terminal propodal spine on pereopod II straight and apparently naked (Figure 38H); same spine on pereopods III and IV bearing long setules or teeth on both sides (Figure 38I). Long, terminal propodal spines variable, dentition varying from teeth resembling those of other stages (Figure 38E) to very long teeth.

Short, subterminal carpal spine of pereopod II longer than in other stages, slender, practically straight, and bearing acute teeth on both sides (Figure 38G). Ten short, subterminal propodal spines, serrate as in other stages, on pereopod VII. Dactylar teeth of pereopod VII of moderate size and sharply pointed.

Pleopods: Terminal endopodal seta length/ endopodal length ratio, 1.5. Setal formula, (2,3) (3,12,5) (0,3;0,13,2). The 2 medial protopodal setae long; the lateral setae tiny.

INTRASPECIFIC VARIATION.—*Stages Other Than Copulatory Male*: The body length of the manca 2 from *Anton Bruun* Sta. 95 is 4.1 mm long. The other specimens are broken. The right mandible of the second preparatory female 1 has the tip of the third and largest incisive spine divided (Figure 38A). The second maxilla of the same animal bears two stout spines (rather than one) along the media setal row. The pleopods of the juvenile from *Anton Brunn* Sta. 95 has four terminal endopodal setae. These are 1.8 times longer than the endopod. The manca 2 has six endopodal articles, the juvenile, eight. The juvenile collected at *Vema* Sta. 17–4 corresponds closely to the holotype. It is 4.6 mm long.

REMARKS.—*Neotanais bulbodens* resembles the species of the *robustus* group primarily in the possession of a very heavy distal ventral seta on the chelipedal carpus in the copulatory male. The male also has serrate short spines subterminally on the propodus of pereopod VII. The other stages resemble *N. antarcticus* most closely in the shape of the pereonites in dorsal view. The relationships among these species are unclear at present.

As this work was nearing completion I received Kudinova–Pasternak's (1970) paper on the tanaidaceans of the Kurile–Kamchatka Trench. She describes *Neotanais tuberculatus* from three *Vitjaz* stations: (1) Sta. 5634 (44°17'N., 149°37'E., 4840 m, grab), two "females" (7.3 mm, with oostegites, holotype; 8.9 mm, without oostegites) and one copulatory male (8.5 mm); (2) Sta. 3154 (41°02'N., 167°22'E., 5666 m, grab), two "females" (11.8 mm, one pair of oostegites; 7.4 mm, without oostegites); and (3) Sta. 3212 (36°10'N., 145°32'E., 5876 m, grab), one female (12 mm, with oostegites), and one copulatory male (14 mm).

Neotanais tuberculatus resembles *N. bulbodens* in the following characters. Females: (1) square

shape of several pereonites with posterior expansions over pereopods in dorsal view, (2) midventral expansions of pleonal sternites, (3) narrow body. Copulatory male: (4) the structure (dentition, dorsal serration) of the chela of the animal from Sta. 3212 is very similar. Body length, number of uropodal articles, and depth at which the two species are found are similar.

The most striking differences between the two species are the following. Females: (1) the pleotelson in *Neotanais bulbodens* is short, whereas that of *tuberculatus* is long (according to Kudinova-Pasternak, longer than that of *pfaffioides*, which I have examined and which is clearly longer than in *bulbodens*); (2) the carapace of *bulbodens* is simple, the oblique furrows almost imperceptible, whereas in *tuberculatus* the carapace is similar to that of *pfaffioides*, in which the furrows are prominent; (3) the proximal chelipedal propodal tooth in *tuberculatus* apparently is not notably larger than the others, as in *bulbodens*, and the dactylar teeth, unusual in *bulbodens*, are not mentioned; (4) the distal claws of the chela in *tuberculatus* apparently are not prominently offset from the "fingers" as they are in *bulbodens*. Copulatory male from Sta. 5634: (5) the chelipedal carpus is strongly bent whereas it is slightly bent in *bulbodens*, and (6) the stout second ventral seta, so prominent in *bulbodens*, is lacking.

These species should be considered distinct until the specimens of *Neotanais tuberculatus* can be examined.

MATERIAL.—*Anton Bruun* Cruise 11, Sta. 95, off Peru, 4332 to 4423 m, 1 M2, 1 Juv, 2 P ♀ 1 (including holotype), 1 Cop ♂ (allotype); *Vema* Sta. 17–4, off Chile, 4116 m, 1 Juv.

LOCATION OF MATERIAL.—NMNH: Holotype (USNM 143178); allotype (USNM 143179); remainder of *Anton Bruun* 95 (USNM 143180). AMNH: *Vema* 17–4 (AMNH 14974).

DERIVATION OF NAME:—Referring to swollen condition of first tooth on fixed chelipedal finger among stages other than copulatory males. From the Latin *bulbus* (a swelling) and *dens* (tooth).

The *affinis* Group of Species

This group comprises three species: *Neotanais affinis, N. vemae,* and *N. peculiaris.*

Stages Other Than Copulatory Male.—Dactylus of chela obviously longer than fixed finger, dorsal propodal keel shallow and not prominent, and a low lateral keel present on fixed finger of chela. First article of first antenna very slender, about 4.5 to 5.5 times longer than wide. Peotelson long, width-length ratio about 1.2 to 1.5. Dactylar spines on pereopods II–IV exceedingly slender distally.

Key to Species of the *affinis* Group

STAGES OTHER THAN COPULATORY MALE

1. Pleonites bearing moderately long midventral spurs; ventral setae on merus and carpus, medial dorsal seta on propodus, and medial dactylar seta of cheliped all exceptionally long; articles of uropodal endopod stout compared to those of most species, first article being about 2.4 to 2.7 times longer than wide ....*N. peculiaris*
   Pleonites rounded midventrally and lacking spurs of any type; length of chelipedal setae similar to that of most species; articles of uropodal endopod relatively slender, certainly no stouter than in most species, first article being about 3.5 to 5.0 times longer than wide .2

2. Rostrum unusually blunt; body about 6 times longer than wide; distal teeth on fixed finger of chela usually more or less rounded; anterior setae of propodus and carpus on pereopods II–IV very long, much more slender and numerous than in most species, setal formula for pereopod II variable, but about (6,11,9,14) (preparatory female 1 holotype) to (14,12,13,13) (preparatory female 2, Labrador Sea); short, subterminal carpal spine on pereopod II heavily set with rows of about 8 regular teeth ....*N. affinis*
   Rostrum pronounced; body about 7 times longer than wide; distal teeth on fixed finger of chela with irregular tips; anterior setae of propodus and carpus on pereopods II–IV slender but not particularly long or numerous, setal formula for pereopod II of holotype (preparatory female 1), (2,4,5,4); short, subterminal carpal spine on pereopod II almost naked ......
   ....*N. vemae*

COPULATORY MALES.—Only one type of male is known for *Neotanais peculiaris*. It has several characteristics similar to those of the *robustus* group, including an enlarged, brown, second ventral seta on the chelipedal carpus. The males of *N. affinis* and *N. vemae* probably have this enlarged seta also.

Neotanais affinis Wolff, 1956

FIGURES 39–41, *98*

Neotanais affinis Wolff, 1956c:51, pl. 2: figs. 11, 12.

DISTRIBUTION.—*Neotanais affinis* has been collected on both sides of the North and South Atlantic as well as from the Mid-Atlantic Ridge, and from the Labrador Sea to the Antarctic. It has been found at depths of about 1860 m in the Labrador Sea to 5330 m in the Argentine Basin. Because it is known from eastern South Africa, it probably ranges through parts of the Indian Ocean as well.

DIAGNOSIS.—*Stages Other Than Copulatory Male* (copulatory males unknown): *Cheliped most distinctive: dactylus slender, tip very acute, and considerably longer than fixed finger; *fixed finger with a prominent ventrolateral keel; carpus bearing about 5 to 8 short dorsal setae. *Pereonites generally rectangular in dorsal view, widest part being area over pereopods; pereonite 5, 1.4 to 1.6 times broader than long (shape slightly different in manca stages—see Figure 39B). *Pleotelson noticeably longer than in many species, about 1.4 to 1.6 times wider than long. *Pleonites rounded midventrally in lateral view; epimeres usually bearing 1 to 3 relatively long, feathered dorsal setae. *First article of first antenna relatively narrow, about 4.7 to 4.9 times longer than broad. Uropodal exopod long, 0.9 to 1.2 times as long as first endopodal article; endopod slender. Pereopodal setae numerous, noticeably long, slender, and smooth; propodus of pereopod VII with about 10 to 15 short, subterminal spines in older stages. *Carapace with 1 very long anterolateral seta and 1 similar posterolateral seta.

DESCRIPTION OF PREPARATORY FEMALE 2 (WHOI B. Sta. 76).—*Body* (Figure 39A): 9.5 mm long and 6.1 times longer than wide.

Carapace (see Figure 39C): 1.3 times longer than wide; with prominent anterolateral keels. One very

long anterolateral seta and a similar posterolateral seta present. Oblique furrow, respiratory chambers, and chelipedal coxae all moderately well developed.

Pereonites 4–7 (Figure 39D): Generally rectangular in shape in dorsal view; widest point at articulation of pereopods, gradually narrowing anteriorly. Pereonite 5, 1.4 times wider than long.

Pleonites (Figures 39A,E, 40A): Pleonite 1 slightly (1.2 times) wider than pleonite 5. Generally rounded midventrally in lateral view. Epimeres rounded laterally in dorsal view and slightly flared and bearing various short hairs. Due to poor condition of specimen other hairs probably broken (see Figure 39G and "Intraspecific Variation" below).

Pleotelson (Figures 39E, 40A): Width-length ratio 1.5. Borders anterior and posterior to uropods evenly rounded; relatively prominent median posterior convexity bounded laterally on both sides by concavities in posterior margin.

First Antenna (Figure 39H): First article 4.9 times longer than wide.

Second Antenna: As in Figure 39I.

Labrum: As in Figure 39J.

Right Mandible (Figure 40D): Incisive spines 1 and 2 serrate on both margins. Third spine naked and bifid distally (possibly abnormal).

Left Mandible (Figure 40H): Incisive spines as on right side. Lacinia mobilis with 4 low rounded teeth; posterior lobe uncleft.

Labium: As in Figure 40J.

First Maxilla: As in Figure 40K.

Second Maxilla: Fixed endite with 2 stout, simply bifid spines. Medial setal row with 13 curved setae with setules in addition to 2 sharply pointed, naked spines.

Maxilliped: Setal formula of palp, (0,0,5,6,13).

Cheliped (Figure 41A,B): Carpus with 3 short dorsal hairs (others broken; right side with 2). Propodus with marked keel along ventral edge of finger. Distal teeth on fixed finger low, rounded, and irregular; about 30 denticles located proximally along cutting edge. Dactylus considerably longer than propodus and with about 5 low, irregular teeth along cutting edge.

Pereopods II–VII (Figure 41E–I): Pereopods II–IV with extremely long, smooth, slender setae posteriorly on propodus and carpus; anteriorly, setae shorter and thicker, those of propodus considerably thicker than posteriorly but slender and smooth. Setal formulae for pereopods II and III, (14,12,13,13)
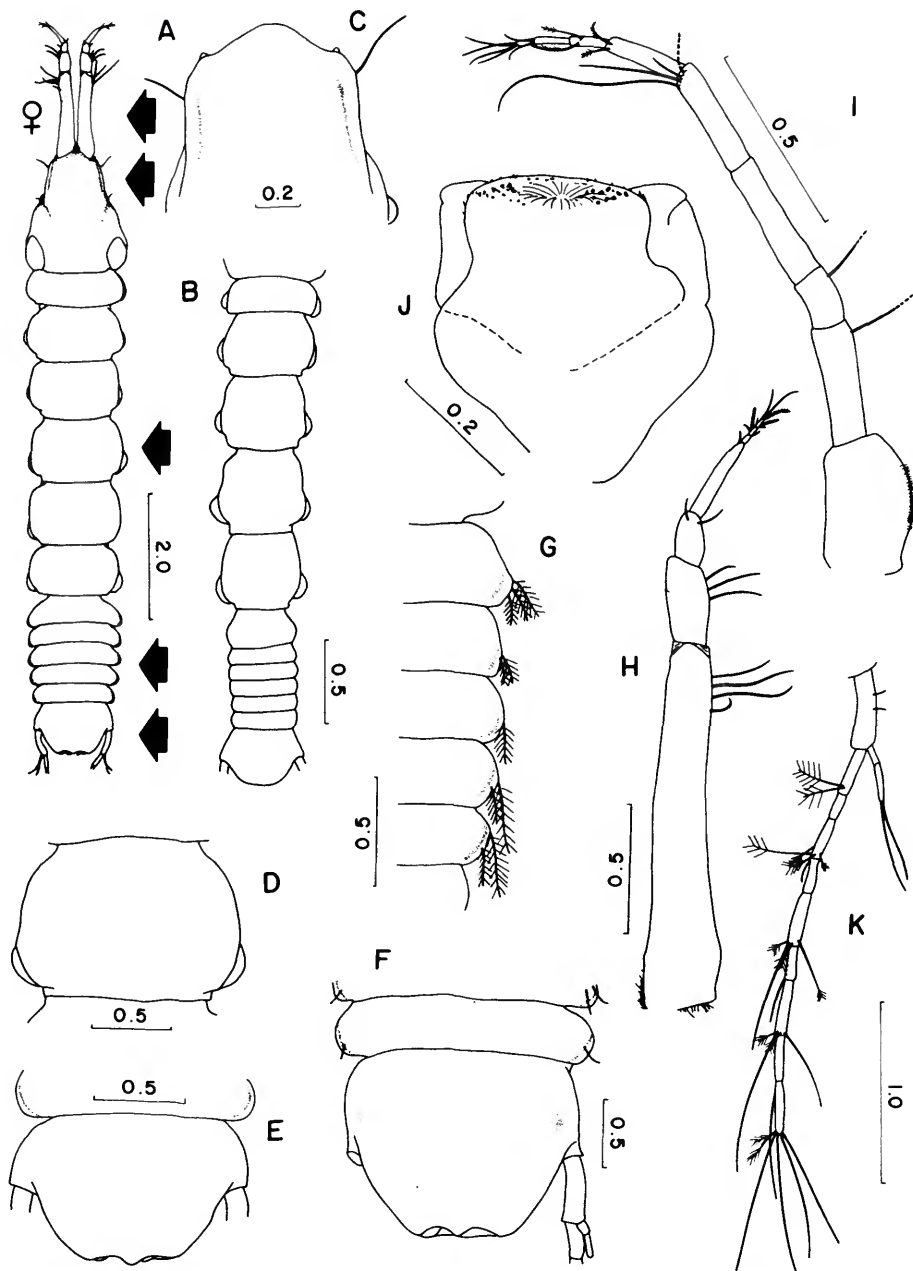
FIGURE 39.—*Neotanais affinis* Wolff: A, dorsal view of female from WHOI B. Sta. 76; B, dorsal view of manca 1 from *Eastward* Sta. 5494; C, anterior area of carapace in dorsal view, female from CMS Sta. 2152; D, pereonite 5 in dorsal view, female in A; E, pleonite 5 and pleotelson in dorsal view, female in A; F, same, ?juvenile from Argentine Basin (*Vema* Sta. 17-81); G, pleonites 1–5 in dorsal view, female from Labrador Sea (*Vema* Sta. 16–55); H, right first antenna in dorsal view, female in A; I, right second antenna in ventral view, female in A; J, labrum in anterior view, female in A; K, right uropod in lateral view, female from WHOI B. Sta. G 13.
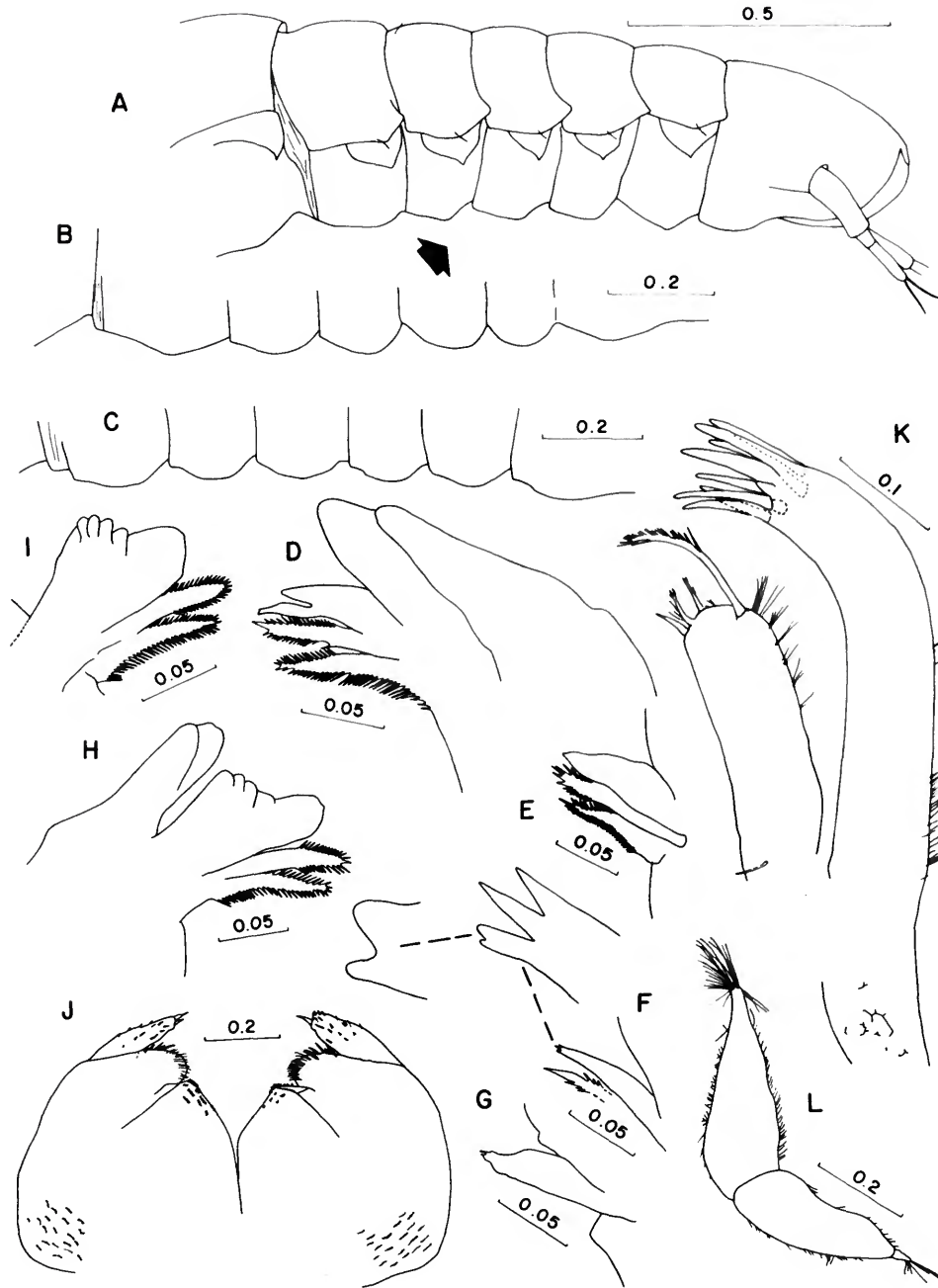
FIGURE 40.—*Neotanais affinis* Wolff: A, pleon in lateral view, female from WHOI B. Sta. 76; B, same, CMS Sta. 2152; C, same, female from Bay of Biscay (*Sarsia* Sta. 50); D, pars incisiva of right mandible, female in A; E, incisive spines of right mandible, female at CMS Sta. 2152; F, second and third incisive spines of female from Labrador Sea (*Vema* Sta. 16–55); G, third incisive spine of female from Weddell Sea (IWSOE Sta. 0023); H, pars incisiva of left mandible, female in D; I, incisive spines and lacinia mobilis of left mandible of female from CMS Sta. 2152; J, labium (posterior view) of female from WHOI B. Sta. 76; K, left first maxilla of same female; L, epignath of same female.
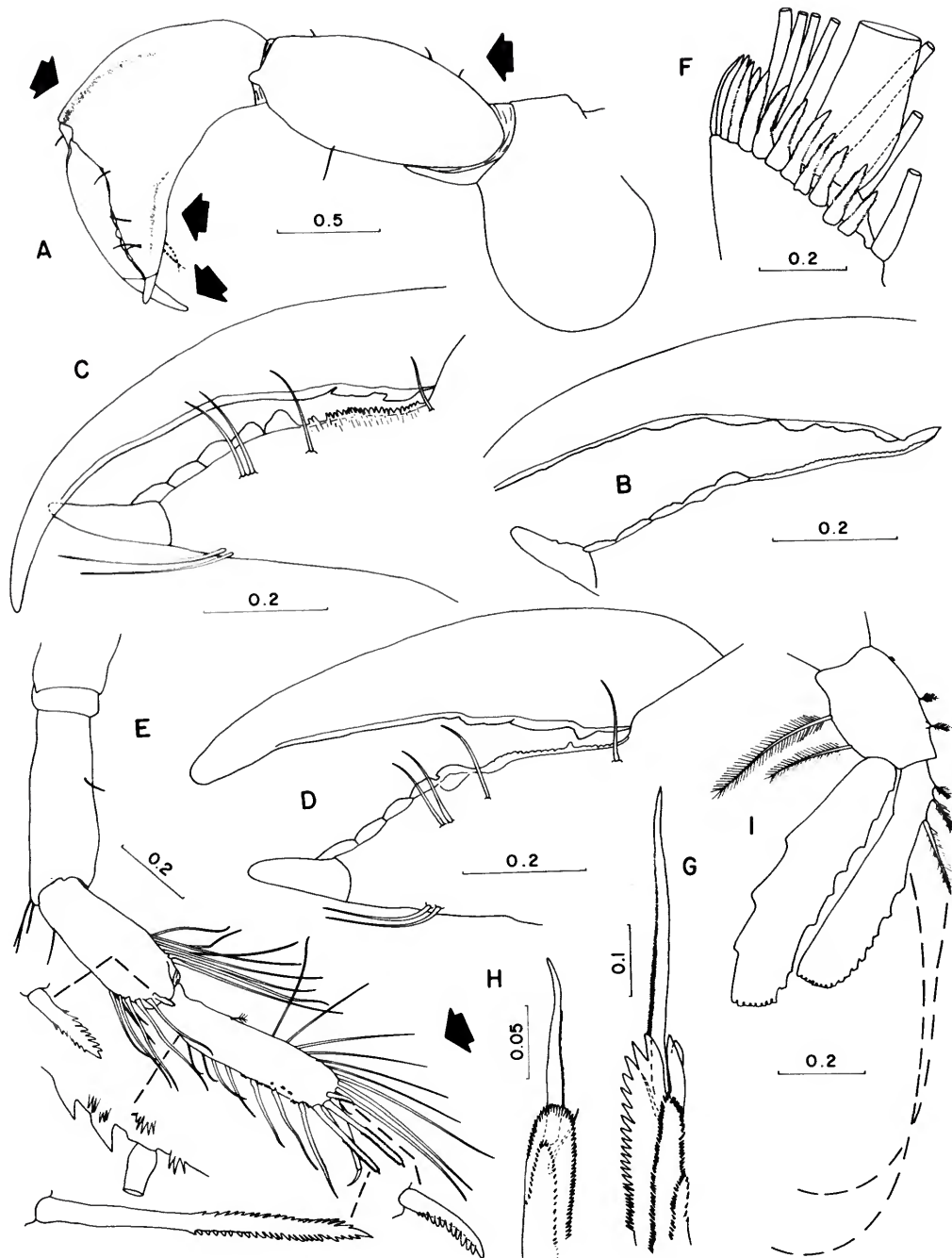
FIGURE 41.—*Neotanais affinis* Wolff: A, left cheliped of female from WHOI B. Sta. 76; B, chela of same; C, same, female from WHOI B. Sta. 103; D, same, female from WHOI B. Sta. G 13; E, right pereopod II of female from CMS Sta. 2152; F, distal tip of propodus, posterior view, right pereopod VII of female at WHOI B. Sta. 76; G, tip of dactylus in dorsal view, pereopod V, female, holotype (*Galathea* Sta. 193); H, same, pereopod VII from *Vema* Sta. 16–55; I, left pereopod in anterior view, female from WHOI B. Sta. 76.

and (20,21,16,16). Two long, heavily toothed, ter-
minal propodal spines present, and short, terminal
propodal spine also with large teeth. Short, subter-
minal carpal spine of pereopod II similar to the
latter. Propodus bearing numerous tiny denticles
dorsally and distally along its sides, a few larger
denticles present more proximally just distal to
articulation with carpus. An unusual small seta is
found laterally and above the usual distomedial
cluster of setae on merus of pereopod II only.
Dactyli of pereopods V and VI bearing relatively
large terminal teeth (Figure 41G), but those of
pereopod VII are small (Figure 41H). Fourteen
short, subterminal propodal spines borne on pereo-
pod VII; setules relatively prominent.

Pleopods: As in Figure 41I. Eight well-developed
terminal setae on endopod. Setal length/endopodal
length ratio, 0.92. Setal formula, (2,2) (3,8,8)
(0,3;0,9,8).

Uropods: Missing (see Figures 39K, 40A). In
other specimens endopod uniformly slender, and in
figured specimen from WHOI B. Sta. G 13 com-
posed of 8 articles on each side. Exopod long, 1.2
times longer than first endopodal article in same
specimen.

INTRASPECIFIC VARIATION.—Stages Other Than
Copulatory Male: Representative Body Lengths
(mm): WHOI B. Sta. 155, Mid-Atlantic Ridge on
the Equator: 4 M1, 3.2–3.6; 1 M2, 4.0; 2 Juv, 5.1–
6.5; 1 P ♂, 10.8. WHOI B. Sta. 156, same area:
2 M1, 3.2–3.3; 1 M2, 4.2; 3 Juv, 5.3–5.4; 1 P ♀ 1,
7.6. CMS Sta. 2152, North American Slope, 1 P ♀ 2,
9.3. Vema 16–55, Labrador Sea, 1 P ♀ 2, 8.4 Sarsia
Sta. 50, Bay of Biscay, 1 Cop ♀, 11.0. Galathea
Sta. 193, P ♀ 1 holotype, 9.9. Vema Sta. 17–81,
Argentine Basin, 1 M1, 4.9; 1 ?Juv, 12.2 (see "Post-
marsupial Development," below). IWSOE Sta. 0023,
Weddell Sea, 1 P ♀ 1, 8.6.

Carapace (Figure 39C): The anterolateral and
posterolateral setae are almost uniformly single
and long. Carapace shape is uniform.

Pereonites 4–7: In the animals from the south-
ern South Atlantic each segment apparently is
slightly narrower anteriorly. Mancas (North At-
lantic) are more nearly square in dorsal view than
are older stages (cf. Figure 39A,B).

Pleonites: Although there is some variation in
epimeral setation, most animals have one or more
long, feathered lateral setae (Figure 39C). Ventrally,

the pleonites are rounded in various degree, but all
are similar (cf. Figure 40A–C).

Pleotelson: Specimens from the South Atlantic
appear to be slightly longer with respect to width
and have their uropods borne more ventrally (Fig-
ure 39F), width-length ratio, 1.2. The specimen
from the Labrador Sea (Vema Sta. 16–55) bears
two long dorsal and posterior broom setae setu-
lated at their tips only.

Right Mandible: The third incisive spine varies
from straight, pointed, and naked (CMS Sta. 2152,
North America; Sarsia Sta. 50, Bay of Biscay; ?Juv,
Vema Sta. 17–81, Argentine Basin—Figure 40E) to
variously irregular in shape (Vema 15–55, Labra-
dor Sea; IWSOE Sta. 0023, Weddell Sea—Figure
40F,G). The spine in the described female from
WHOI B. Sta. 76 (Gay Head–Bermuda Transect)
probably is aberrant.

Left Mandible (Figure 40H,I): The lacinia mo-
bilis always bears four or five teeth and its posterior
lobe is always uncleft.

Pereopods II–IV: Setal formulae vary consider-
ably. Pereopods II and III: preparatory female 2,
Labrador Sea, (13,11,15,13), (20,20,16,16); copula-
tory female, Bay of Biscay, (5,7,8,7), (10,15,11,9);
preparatory female 1 holotype, off South Africa,
(6,11,9,14), (14,20,–,20). The number of long, termi-
nal propodal spines varies from one to three but is
most often two. Tooth size also varies to some ex-
tent but generally is large. The female from the
Bay of Biscay has fine teeth on its short, subtermi-
nal carpal spine (pereopod II).

Summary: All animals in the North Atlantic
were remarkably similar in major body features.
The three South Atlantic populations (east of
South Africa, Argentine Basin, and Antarctic) all
appear slightly heavier and longer and have a
somewhat longer pleotelson. Otherwise they appear
identical with North Atlantic populations. Hence,
this species shows notably little variation.

POSTMARSUPIAL DEVELOPMENT.—The pleopodal
setae show a considerable level of development in
the juvenile at WHOI B. Sta. 76 (seven ter-
minal endopodal setae present and a setal length/
endopodal length ratio of 1.4). The preparatory
male at the same station had eight setae and a
ratio of 1.3, although apparently more setules were
present on the setae than in the juvenile. The
preparatory female 2 at WHOI B. Sta. 76 had
eight setae and a ratio of 1.1, whereas the copula-

TABLE 6.—*Examined material of* Neotanais affinis *Wolff*

Program or ship	Station no.	General location	Depth (meters)	Material
		NORTH ATLANTIC		
WHOI Benthic	G 1	Gay Head–Bermuda Transect	2000	1 M1, 2 P♀2, 1 Cop ♀, 1 fgmt. (all dried out)
	G 7		2158	1 Cop ♀ (dried out)
	G 9		2021	1 M2, 1 fgmt. (dried out)
	G 13		2036	1 P♀2 (dried out)
	64		2886	1 M2
	70		4680	1 P♀1
	76		2862	1 ?Juv, 1 P♀2 (described), 1 P♂
	103		2022	1 M1, 1 P♀2
	126		3806	1 M1
	131		2178	1 M1
	155	Equator near Sts. Peter's and Paul's Rocks	3730–3783	4 M1, 1 M2, 2 Juv, 1 P♂, 1 fgmt.
	156		3459	2 M1, 2 M2, 3 Juv, 1 P♀1
CMS	2152	SE of Cape Cod, Massachusetts	1865	1 P♀2
	2201	SE of Georges Bank	2451	2 fgmts.
Eastward	2756	E of Cape Hatteras, North Carolina	3017	1 ?Juv
	5494	S of Cape Hatteras	3620	2 M1
Noratlante	042, E006	Labrador Sea	3430	1 M1? (fgmt.)
	063, E008	S of Azores	1940	1 M1
Sarsia	50	Bay of Biscay N of Bilboa, Spain	2379	1 Cop ♀
Vema	16–55	Labrador Sea SW of Greenland	2452	1 P♀2
		SOUTH ATLANTIC		
Galathea	193	SE of Durban, South Africa	3680	1 P♀1 (holotype)
IWSOE	0023	Weddell Sea N of Filchner Ice Shelf	3658	1 P♀1
Vema	17–81	Argentine Basin	5329–5332	2 M1, 1 M2, 1 ?Juv

tory female from the Bay of Biscay (*Sarsia* Sta. 50) had 10 setae and the longest were 1.4 times longer than the endopod. Hence, in *Neotanais affinis* the pleopodal setae bear about the same relationship of length to endopodal length throughout life (stages other than copulatory male).

The uropods of mancas 1 are composed of four articles, mancas 2 have six articles, juveniles have seven or eight articles, and older stages have up to ten articles.

In addition to the preparatory males, only the copulatory female from the Bay of Biscay was found to have male gonopore anlagen.

REMARKS.—*Neotanais affinis* was described briefly in 1956 by Wolff from a single broken specimen collected by the *Galathea* Expedition off eastern South Africa. Since then it has been collected at many locations (Table 6). It is redescribed here in detail and a diagnosis is given for stages other than copulatory males. The latter are still unknown.

MATERIAL.—See Table 6.

LOCATION OF MATERIAL.—UCZM: holotype. AMNH: *Vema* 16–55 (AMNH 14.891); *Vema* 17–81 (AMNH 14.890). NMNH: CMS 2152 (USNM 143182); IWSOE 0023 (USNM 143186); *Noratlante* 042, E006 (USNM 143183); *Noratlante* 063, E008 (USNM 143184); *Sarsia* 50 (USNM 143185); WHOI 76 (USNM 143181); WHOI 155 (USNM 143187).

Neotanais vemae, new species

FIGURES 42, 43, *98*

DIAGNOSIS.—*Stages Other Than Copulatory Male* (copulatory males unknown): *Chela bearing very long, slender dactylus, longer than fixed finger; propodus with shallow keels dorsally and ventro-laterally on fixed finger; distal propodal teeth very irregular. *Pleotelson long, with rounded posterior margin; *uropods borne posterior to midlateral

point. *Pereonites 4–6 generally square in dorsal view, but areas over pereopods expanded laterally. *Pleonites generally rounded midventrally in lateral view. *Carapace laterally compressed, chelipedal coxae poorly expanded laterally in dorsal view; a single anterolateral and posterolateral seta present.

DESCRIPTION OF PREPARATORY FEMALE 1 HOLOTYPE.—*Body* (Figure 42A): 7.0 mm long and 7.1 times longer than wide.

Carapace: Bearing a single short anterolateral seta and a similar posterolateral seta. Anterolateral keels prominent; rostrum prominent, blunt, and with margin of carapace concave on either side. Respiratory chambers poorly developed and chelipedal coxae flattened laterally in dorsal view, giving carapace a narrow appearance. Oblique furrows modest.

Pereonites (Figure 42B): Pereonites 4–6 generally square in dorsal view, but area above pereopods swollen laterally. Pereonite 5, 1.3 times wider than long.

Pleonites (Figure 42A,D): Rounded laterally in dorsal view and curving posteriorly on either side. Single short hairs located dorsolaterally. Sternites low and variously rounded midventrally.

Pleotelson (Figure 42C,D): Long, 1.5 times wider than long. Posterior border evenly convex except for wide anal area containing small middorsal posterior convexity. Uropods borne posterior to midlateral point.

First Antenna: First article slender, 4.8 times longer than wide. Shapes of articles very similar to those of *Neotanais affinis* (Figure 39H).

Right Mandible (Figure 42E): Incisive spines 1 and 2 serrate on both sides, the second spine along distal one-third only. Third spine with an irregular tip.

Left Mandible (Figure 42F): Incisive spines as on right side. Lacinia mobilis apparently bearing 3 rounded teeth, the first of which is subdivided into 3 smaller, round teeth; posterior lobe only slightly divided.

Second Maxilla: Fixed endite with 2 stout bifid spines. Medial row containing 11 setae and 2 sharply pointed spines.

Maxilliped: Setal formula of palp, (1,0,5+1,6,13). Left endite with only 2 medial filter setae; 3 on right side.

Cheliped (Figure 42G–I). Dactylus longer than

propodus and bearing about 5 or 6 low, flattened, and irregular teeth. Propodal teeth very irregular; proximal area of propodal cutting edge containing irregular denticles. Carpus bearing about 6 short dorsal setae; a prominent ventral convexity located at articulation with merus.

Pereopods II–IV (Figure 43A): Setae slender, apparently smooth; those in anterior rows shorter and stouter than those in posterior rows. Setal formulae, (2,4,5,4), (5,8,6,9), and (6,9,6,8) respectively. Two long, terminal propodal spines bearing relatively large teeth on each leg. Short, terminal propodal spine almost straight and bearing about 9 similarly shaped teeth. Short, subterminal carpal spines (2 in number) straight and naked. (Presence of 2 such spines probably aberrant.)

Pereopods V–VII (Figure 43B–D): Short, subterminal propodal spines on pereopod VII 9 in number and bearing fine setules. Dactyli of pereopods V and VI with large terminal teeth; dactylus of pereopod VII with fine teeth.

Pleopods (Figure 43E): Terminal endopodal setae 1.5 times the length of endopod, thus showing considerable development. Setal formula, (2,1) (3,6,7) (0,2;0,9,4).

Uropods (Figures 42A,C): Similar to those of *Neotanais affinis;* 9 articles in right endopod, left side missing. Exopod long, 1.1 times the length of first endopodal article.

COMPARISONS.—*Significant Differences between* Neotanais vemae *and* N. affinis: (1) The body of *vemae* is much more slender and delicate and its length-width ratio is 7.1 compared to 6.1 for *affinis*. (2) Pereonites 4–6 are much more nearly square than in *affinis*. (3) The uropods are attached more posteriorly in *vemae* and perhaps slightly more dorsally than South Atlantic specimens of *affinis*. (4) The carapace is laterally compressed in dorsal view in the area of the chelipedal attachment in *vemae*. (5) The numbers of propodal and carpal setae of pereopods II–IV are considerably less in *vemae* than in *affinis*. (6) The dorsal and ventral keels on the chela are less prominent in *vemae*.

REMARKS.—This specimen originally was thought to be a Pacific representative of *Neotanais affinis;* however, closer examination showed that, although it has close affinities with that species, it differs from it in several significant characters.

MATERIAL.—*Vema* Sta. 15–84, off Chile 5657 m, 1 P ♀ 1 holotype.
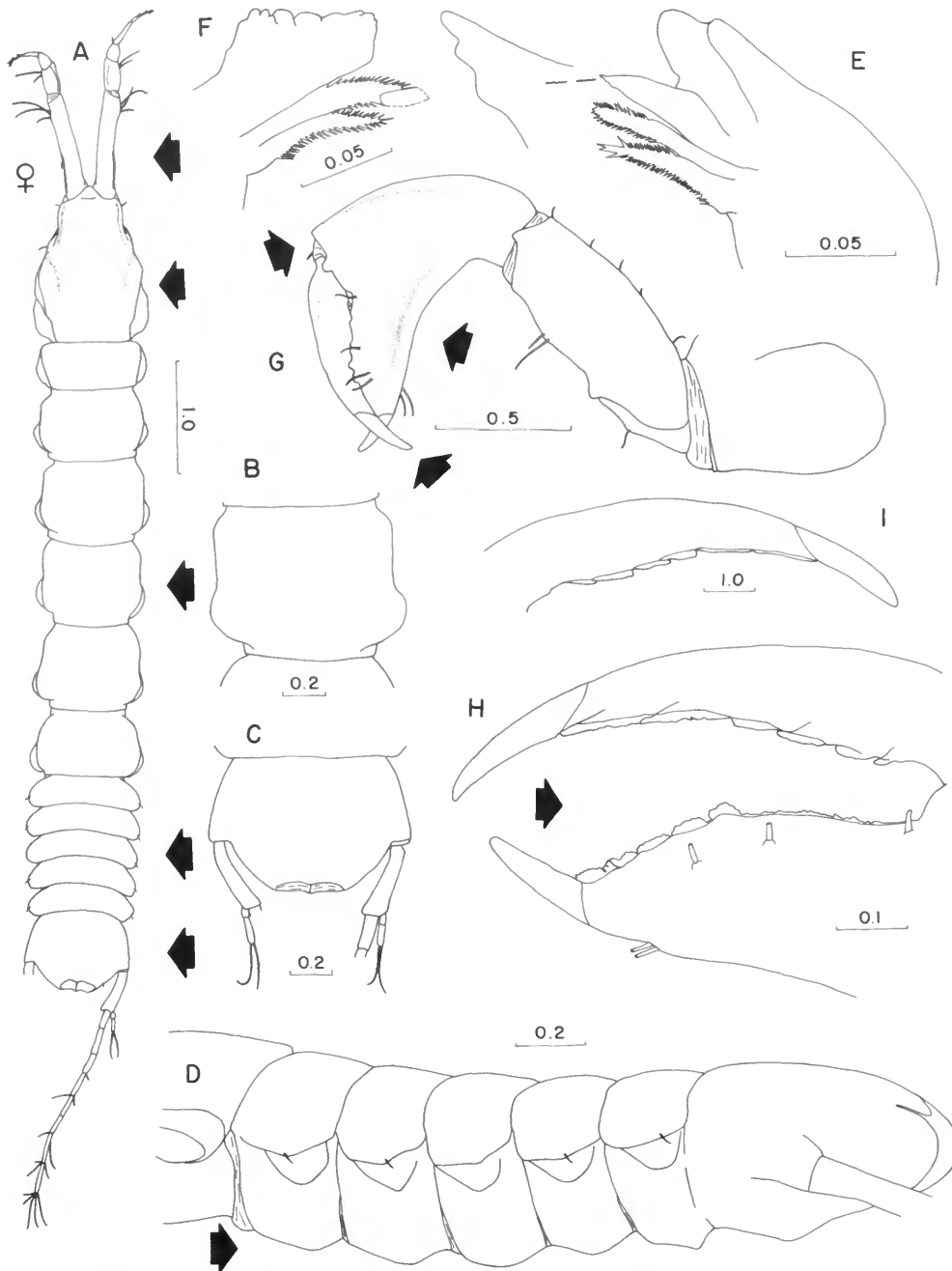
FIGURE 42.—*Neotanais vemae*, new species (all figures are of preparatory female 1, holotype, from Chile): A, dorsal view; B, enlargement of pereonite 5 in dorsal view; C, enlargement of pleotelson in dorsal view; D, pleon in lateral view; E, pars incisiva of right mandible; F, incisive spines and lacinia mobilis of left mandible; G, left cheliped; H, left chela; I, dactylus of right cheliped.
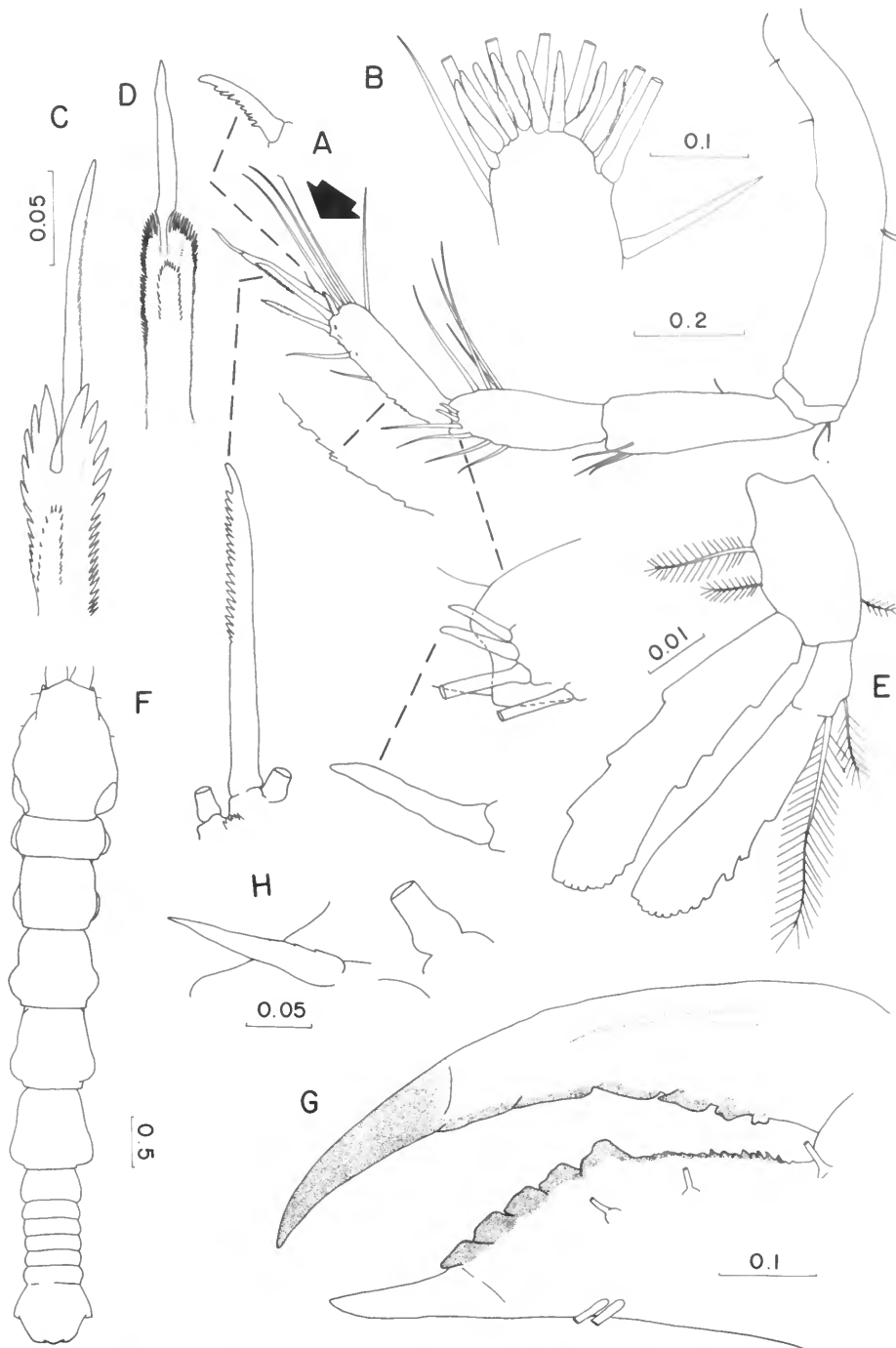
FIGURE 43.—*Neotanais vemae*, new species (all figures are of preparatory female 1, holotype, from Chile): A, right pereopod II, anterior view; B, distal tip of propodus of left pereopod VII in dorsal view; C, distal tip of dactylus of pereopod VI; D, same, pereopod VII; E, right pleopod in posterior view. *Neotanais peculiaris* Lang: F, dorsal view of manca 1 from Bay of Biscay (*Sarsia* Sta. 65); G, right chela of same animal; H, short, subterminal carpal spine of ?juvenile from same station.

LOCATION OF MATERIAL.—AMNH: Holotype (AMNH 14975).

DERIVATION OF NAME.—From R/V *Vema* of the Lamont Doherty Geological Observatory of Columbia University.

Neotanais peculiaris Lang, 1968

FIGURES 43, 44, *98*

Alaotanais serratispinosus Norman and Stebbing, 1886:111, pl. 24 (1) [in part, specimens from *Porcupine* Stas. 19 and 30 only].
Neotanais peculiaris Lang, 1968:147, figs. 89–93, pl. 6c,d.

DIAGNOSES.—*Stages Other Than Copulatory Male*: *Pereonites 5 and 6 square in dorsal view, area above pereopods barely widest. *Pleotelson very long, only about 1.3 times wider than long, and sides anterior to uropods almost parallel with rest of body. *Pleonites rounded laterally and expanded midventrally into triangular, slightly posteriorly directed spurs located in posterior half of each sternite. *Chelipedal dactylus longer than fixed finger and bearing irregularly pointed and spaced teeth; fixed finger denticulate proximally, distal teeth more or less flat-topped and slightly distally inclined; *ventral meral and carpal, dorsal propodal, and dactylar setae all very long and attenuated. Endopodal articles of uropods relatively stout. *First article of first antenna about 4.5 times longer than wide. *Dactylar spine of pereopods II–IV long (about 0.5 times as long as article and very slender distally); short, subterminal carpal spine of pereopod II straight and only slightly setulated at most.

Copulatory Male (only one type known): *Pleotelson long compared to many species, width-length ratio about 1.3. *Pereonites 4–6 appearing wider than long in dorsal view and area over pereopods much wider than anteriorly; *margin not sloping evenly posterolaterally but with a moderate lateral expansion located midway from pereopods to anterior border. *Pleonites rounded laterally in dorsal view and bearing single, moderately long epimeral hairs; *sternites expanded into bluntly tipped midventral spurs of moderate length. *Carapace very slender anteriorly with relatively prominent rostrum; anterolateral keels relatively prominent; oblique furrows shallow; *a single, long antero-lateral and posterolateral seta present on either

side. *Chelipedal carpus stout and strongly curved proximally, so much so as to form a sharp angle on the lower surface; a few setae of medium length present dorsally; *first ventral seta very slender, the second thicker, relatively long, and brown; *carpus flat distally on lower side; dorsal propodal crest straight, thin, and lined with small, rounded denticles; *fingers twisted and varying in shape (see Fig. 44D–H). *Dactylar spine of pereopods II–IV about one-third to one-half as long as article and strongly attenuated along distal half of its length. Pereopod VII bearing a row of about 8 short, subterminal propodal spines with slender teeth of substantial length compared to many species.

DESCRIPTION OF COPULATORY MALE (stage unknown; from *Noratlante* Sta. 003, E001).—*Body* (Figure 44A): 9.2 mm long and 6.9 times longer than wide.

Carapace: 1.6 times longer than wide and very slender anteriorly in dorsal view. Rostrum prominent, oblique furrows shallow and leading posteriorly into a series of superficial lines. Chelipedal coxae swollen laterally and flattened posterolaterally in dorsal view. Anterolateral keels shallow and slightly swollen anteriorly. Anterolateral and posterolateral setae, on either side, single and very long.

Pereonites: Pereonites 4–6 wider than long in dorsal view. Areas over pereopods considerably expanded and forming widest area of each pereonite. A second, smaller lateral expansion present anterior to pereopods.

Pleonites (Figure 44B,C): Rounded laterally in dorsal view and occasionally bearing a single epimeral seta. Sternites expanded into blunt midventral spurs of substantial length.

Pleotelson (Figure 44A–C): Long, width-length ratio being only 1.3. Posterolateral margin rounded.

First Antenna: First article 6.6 times longer than wide.

Cheliped (Figure 44D–F): Carpus stout and strongly bent; dorsal setae of moderate length and only 3 in number; first ventral seta very slender; the second seta considerably longer, thicker, and light brown in coloration; carpus flat below distally. Dorsal margin of propodus relatively straight; dorsal crest shallow, thin, and bordered by low, rounded denticles; fixed finger strongly bent and bearing two low teeth proximally and another, taller, tooth distally. Dactylus very strongly bent
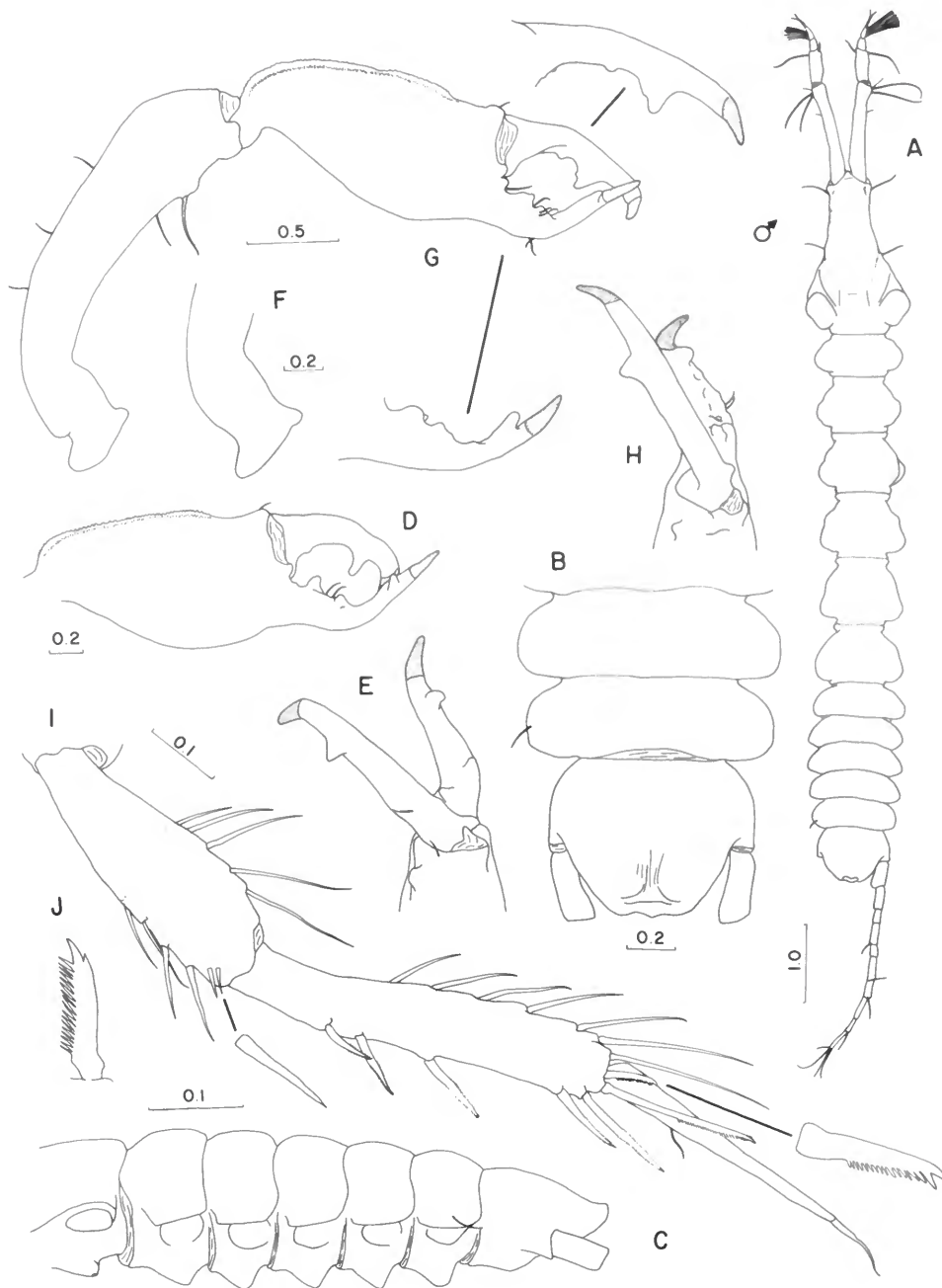
FIGURE 44.—*Neotanais peculiaris* Lang (all copulatory males): A, dorsal view of male described in this work (*Noratlante* Sta. 003, E001); B, pleonites 4 and 5 and pleotelson of same animal; C, pleon in lateral view, same animal; D, right chela of the same animal; E, dorsal view of same; F, proximal area of chelipedal carpus of same animal; G, cheliped of male from *Noratlante* Sta. 126, E016; H, dorsal view of same; I, carpus, propodus, and dactylus of left pereopod II in anterior view, male described in this work; J, a representative short, subterminal propodal spine from pereopod VII of same male.

inward; bearing 2 very small teeth proximally and a large triangular tooth midway along its length.

Pereopods II–IV (Figure 44I): Setal formula of pereopod II, (5,7,4,5). Short, terminal propodal spine bearing many fine teeth; long, terminal propodal spine also finely toothed. Short, subterminal carpal spine of pereopod II represented by 2 straight, naked spines on both sides of body. Anterior propodal setae stout and sharply pointed. Dactylar spine 0.4 times as long as article and tapering abruptly midway along its length.

Pereopod VII (Figure 44J): Short, subterminal propodal spines 8 in number and bearing strong, slender teeth.

Pleopods: Setal formula, (1,2) (3,11,4) (0,3;0,10,4).

Uropods (Figure 44A): Nine endopodal articles; articles short and stout as in other stages. Exopod 0.6 times as long as first endopodal article.

INTRASPECIFIC VARIATION.—*Stages Other Than Copulatory Male*: Of the specimens of *Sarsia* Sta. 65, the manca 1 (Figure 43F) has a body length of 4.8 mm and the juvenile (?) 6.9 mm.

The first article of the first antenna varys somewhat in shape, usually being much more slender than that figured by Lang (1968), the length-width ratio being about 4.8 to 5.4.

The juvenile (?) at *Sarsia* Sta. 65 has the following characteristics. The left mandible is similar to that of the holotype, but the large lobe of the lacinia mobilis is considerably more pointed. One of the forked spines of the fixed endite on the second maxilla is bifid, the other is trifid (according to Lang the holotype has two bifid spines on the right side and two trifid spines on the left). Dentition of the chela is slightly different from that of the holotype (Figure 43G). The setae in the anterior propodal rows on pereopods II–IV are stout and sharply pointed. The short, terminal propodal spines are as figured by Lang (1968, figs. 91, 92); the short, subterminal carpal spine of pereopod II is straight and setulated (Figure 43H). The propodus of pereopod II has two long, toothed spines (on the left side one of these is very short and deformed). Pereopods III and IV have four and three such spines respectively (Lang states that the holotype has two of these spines on each leg). Pereopod VII has 13 short spines in the subterminal propodal row (Lang figures nine for the holotype). The uropods have nine relatively thick endopodal articles (the manca 1 has four articles).

Copulatory Males: A single additional anterior fragment of a copulatory male was collected from the Bay of Biscay (*Noratlante* Sta. 126, E016). It resembles the described male very closely except for the cheliped. Instead of being smoothly rounded proximally, both carpi (Figure 44G) bear a posteriorly directed protuberance near their articulation with the meri. The dactylus is not so strongly bent medially (Figure 44G,H). The dentition of both fingers is different from that of the described male (cf. Figure 44D,E). It is not clear whether this male represents a developmental stage different from the described male.

IMPORTANT SIMILARITIES BETWEEN COPULATORY MALES AND OTHER STAGES.— (1) Shape and proportions (length) of pleotelson and low uropodal attachment; (2) rounded pleonal epimeres; (3) general shape of midventral pleonal spurs; (4) proportions (stout) of endopodal articles of uropods; (5) presence of single, long anterolateral and posterolateral setae on the carapace; and (6) length and distal tapering of dactylar spines on pereopods II–IV.

REMARKS.—Lang described this species from one preparatory female 2 from the Bay of Biscay. Previously, Norman and Stebbing (1886:111, pl. 23: fig. 1; pl. 24: fig. 1) described three specimens which they assigned to *Alaotanais serratispinosus* (=*Neotanais americanus*). One of these, a preparatory female 2 from *Porcupine* Sta. 19, clearly is *N. peculiaris*. Although two of the specimens were figured, the textual description accords with the specimen from *Valorous* Sta. 15, and this leaves the former specimen without a name. Hence, Lang's name, *N. peculiaris*, is retained for this species. The third specimen of Norman and Stebbing, a fragment from *Porcupine* Sta. 30, apparently also is this species.

Because many additional species of *Neotanais* and a number of additional specimens of *N. peculiaris* are now known, and all known species have been compared, it is possible to write diagnoses for *N. peculiaris* for the first time. The copulatory male is described here for the first time.

Neotanais peculiaris shares a number of characters with the *affinis* group of species, the most notable being the presence of a very long chelipedal dactylus in stages other than copulatory males. The significance of this character is uncertain because it appears elsewhere in the genus (*N.*

giganteus). For the time being, however, *N. peculiaris* is placed in association with the other species in the *affinis* group.

MATERIAL.—*Galathea* Sta. 773, Bay of Biscay, 1680 m, 1 P♀2 (holotype); *Noratlante* Sta. 003, E001, west of Ireland, 2460 m, 1 P♀2, 1 Cop ♂ (described), 1 unid. fgmt.; *Noratlante* Sta. 126, E016, southwest of Brest, France, 1913 m, 1 M2, 1 ?Juv, 1 P♀2, 1 Cop ♀, 1 Cop ♂ (fgmt.); *Porcupine* Sta. 19, west of Ireland, 2487 m, 1 P♀2; *Porcupine* Sta. 30, northwest of Ireland, 2523 m, 1 P♀2 (fgmt.); *Sarsia* Sta. 65, Bay of Biscay off Spain, 1922 m, 2 M1, 1 ?Juv.

LOCATION OF MATERIAL.—UCZM: Holotype. BMNH: *Porcupine* 19 (Reg. No. 1911.11.8.7357–7358); *Porcupine* 30 (Reg. No. 1903.5.20.71–2 and microslides 1911.11.8.372–374?). NMNH: *Noratlante* 003, E001 (USNM 143188); *Noratlante* 126, E016 (USNM 143189); *Sarsia* 65 (USNM 143190).

The *pfaffi* Group of Species

This group comprises *Neotanais pfaffi, N. giganteus, N. pfaffioides,* and *N. armiger.* The grouping is based primarily on characters of stages other than copulatory male. The males are unknown for *N. pfaffioides,* and only a single copulatory male stage is known for *N. giganteus* and for *N. pfaffi.* For distinction of species, refer to the diagnoses of the respective species.

STAGES OTHER THAN COPULATORY MALE.—*All Species*: Areas of pereonal tergites over pereopods raised, showing distinct surface relief in contrast to the surrounding area or (in *Neotanais pfaffioides*) these areas modified to form shallow depressions dorsally. Pleonites extended laterally and flared in various degree, not evenly rounded in dorsal view. Propodal and carpal setae of pereopods II–IV long, very slender, and numerous. Representative setal formulae for pereopod III: *N. pfaffi* (copulatory female), (14,23,11,16); *N. giganteus* (preparatory female 2), (30,22,13,23); *N. pfaffioides* (copulatory female), (16,21,10,13); and *N. armiger* (copulatory female), (19,15,9,17).

All Species Except Neotanais pfaffioides: Chela large in proportion to remainder of cheliped compared to other species. Fourth article of first antenna longer than twice the length of articles 5–7 together.

All Species Except Neotanais armiger: Body very large, preparatory female 2 or copulatory female about 17 to 22 mm long. Uropodal endopodal articles very stout, first article only about 2.5 to 3.0 times longer than wide. Dactylar spine of pereopod II very short, only 0.2 times as long as article, or less. Lateral setal row of pleopodal endopod arranged in a continuous row from tip to protopod; i.e., a terminal setal row not differentiated from a lateral row. Incisive spines of right mandible as follows: first spine serrate on proximal side only, second and third spines naked (*N. armiger* similar but with some additional serrations on first two spines).

COPULATORY MALES (unknown in *Neotanais pfaffioides*).—These males differ from other males in those nondimorphic characters listed above for other stages. In addition, both dorsal and ventral chelipedal carpal setae are very slender and often extremely short; carpus is relatively stout but not greatly bent.

REMARKS.—Individual species sometimes differ from the rest of the group in several prominent characters; e.g., the shape of the chela and the fusion of the pleotelson with the fifth pereonite in *Neotanais longimanus.* *Neotanais armiger* is the most disparate species of the group. However, because of the large number of similarities among them, the species are here considered collectively as a group. Other similarities besides those mentioned here were noted; however, such similarities were not so widely shared among the species. This species group is much less homogeneous than the *micromopher, hastiger,* and *americanus* groups.

The collection of additional copulatory males of these species will go far toward clarifying their relationships with one another.

Neotanais pfaffi Wolff, 1956

FIGURES 45–47, 97

Neotanais pfaffi Wolff, 1956c:45–47, fig. 2c,d; pl. 2: figs. 17–20.

DIAGNOSES.—*Stages Other Than Copulatory Male*: *Chela large, with spaces between distal propodal teeth; *3 low, rounded dactylar teeth proximally. *Pereonite 5 with area above pereopods markedly expanded laterally; *surface of both carapace and pereonites showing marked relief. *Epimeres of pleonites tapered and acute laterally, each with

several feathered hairs; *pleonal sternites bearing blunt midventral projections. Carapace with up to 8 anterolateral setae; chelipedal coxae greatly swollen laterally. *Pleotelson moderately long, posterior margin straight across with wide anal opening. Uropodal exopods about 0.4 to 0.6 times the length of first endopodal article and markedly deflected ventrally. Article 4 of first antenna more than twice as long as articles 5 through 7 combined. *Dactylar spines of pereopods II–IV very short and feeble, only about 0.1 as long as dactylus.

Copulatory Male (only one type known): *Chela toothed as in Figure 47A,B; propodus with obvious but shallow and smooth dorsal crest; irregular lines or furrows inscribed on lateral surface of propodus just below crest; *carpus stout and with up to 10 fine, short dorsal setae. Carapace with markedly expanded respiratory chambers and chelipedal coxae in dorsal view; *anterolateral keels not raised dorsally but greatly expanded laterally above 8 or 9 long setae on either side. First article of first antenna over 5 times longer than wide. Genital cones markedly raised on a single protuberance.

DESCRIPTION OF COPULATORY FEMALE H (*Galathea* Sta. 716).—*Body* (Figure 45A): 21.4 mm long and 6.5 times longer than broad. Setae and hairs borne on body generally apparently finer or more slender than in many species.

Carapace: 1.3 times longer than wide. Anterolateral keels pronounced and with up to 8 setae below each. Respiratory chamber and chelipedal coxae considerably expanded. Oblique furrows prominent; shallow transverse furrows present just behind rostral area and posterior to and almost connecting oblique furrows. One pair of curved furrows lateral to latter transverse furrow.

Pereonites: Exhibiting some low surface relief (Figure 45A). Pereonite 5 (Figure 45c) 1.3 times wider than long, generally square in appearance in dorsal view but with area over pereopods expanded laterally. Pereonite 7 bearing prominent male gonopore and genital cone anlagen ventrally (Figure 45H).

Pleonites (Figure 45A,E,F): Tapered laterally, first pleonite considerably wider than pereonite 7. Epimeres bearing 2 to 4 fine, feathered hairs dorsally. Midventral projections of sternites generally triangular in lateral view. A very fine, middorsal, longitudinal depression present in each pleonite.

Pleotelson (Figure 45E,F): 1.8 times wider than long, posterior border almost straight across, anal opening very wide. Ventral surface bearing a slight swelling anteriorly.

First Antenna (Figure 45J): Article 1, 4.6 times longer than wide. Article 4 more than twice as long as articles 5–7 combined.

Right Mandible (Figure 46A): Third incisive spine bifid terminally, second spine naked, and first spine serrate along basal two-thirds of inner side but naked on outer side.

Left Mandible (Figure 46B): Distal incisive spine naked on both sides with irregular tip (abnormal). Proximal 2 spines as on right side. Lacinia mobilis with 4 low, blunt teeth; large lobe blunt and somewhat irregularly shaped.

Second Maxilla: Fixed endite (Figure 46F) with 2 stout, irregularly cleft spines. Medial setal row with 26 finely feathered setae and 4 spines with variably cleft tips.

Maxilliped: Setal formula of palp, (1,0,5+1+1, 8,16).

Cheliped (Figure 46J,K): Carpus bearing 7 weak dorsal setae. Low dorsal keel present on propodus; fixed finger with a vague lateral keel. Five brown, round propodal teeth separated by spaces. Proximal area of cutting edge almost straight and without denticles. Dactylus with 3 rounded, widely spaced proximal teeth and a trace of 1 or 2 distal teeth merging with brown border.

Pereopods II–VII: Setal formulae for pereopods II–IV, VI, and VII, (6,11,10,9), (14,23,11,16), (16,23,10,14), (14,18,16,14), and (15,15,10,12). Two relatively straight, short, terminal propodal spines, bearing moderately large teeth, present on pereopod II (Figure 47D). Three long, terminal spines with relatively small teeth also on same article (Figure 47F). Pereopods III and IV each bearing one of these spines. Row of 14 short, serrate subterminal spines present on propodus of pereopod VII (Figure 47J). Two short, subterminal carpal spines present on pereopod II, medial member of pair needle-shaped and without armament (Figure 47D). Presence of paired short spines on propodus and carpus of pereopod II is probably abnormal (see "Intraspecific Variation," below). Dactyli of pereopods II–IV with exceedingly short, feeble, and strongly curved terminal spines; dactylus of pereopod II only 0.1 times the length of dactylus (Figure 47C).

Pleopods: With an almost continuous row of
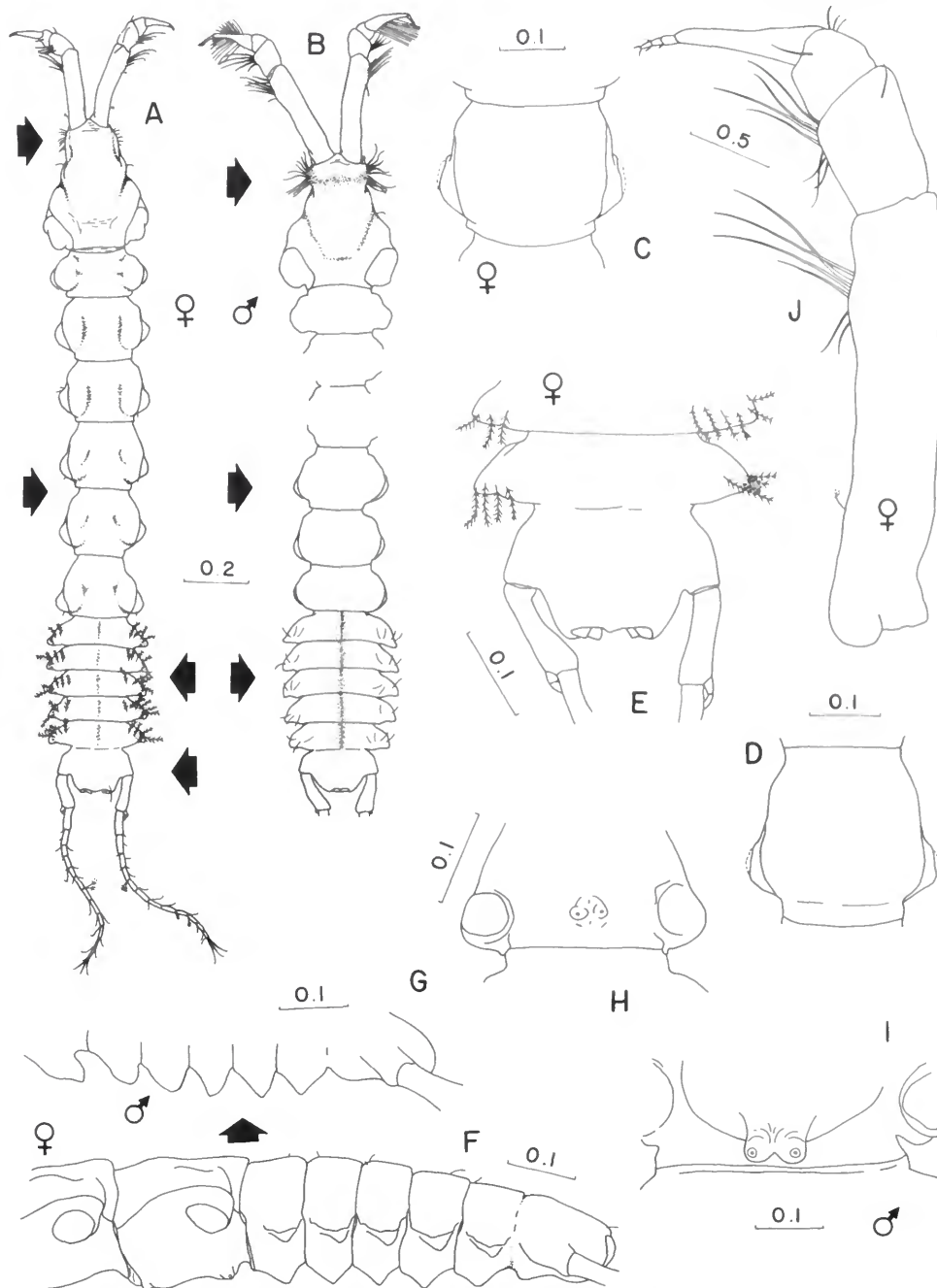
FIGURE 45.—*Neotanais pfaffi* Wolff: A, dorsal view, copulatory female H, *Galathea* Sta. 716; B, dorsal view, copulatory male Y, same station; C, pereonite 5 from above female H; D, pereonite 5, juvenile D, same station; E, pleotelson from above, female H; F, pleon, lateral view, female H; G, pleon, male Y; H, pereonite 7, ventral view, female H, showing male genital cone anlagen; I, pereonite 7, ventral view, male Y; J, left first antenna, dorsal view, copulatory female L, same station.
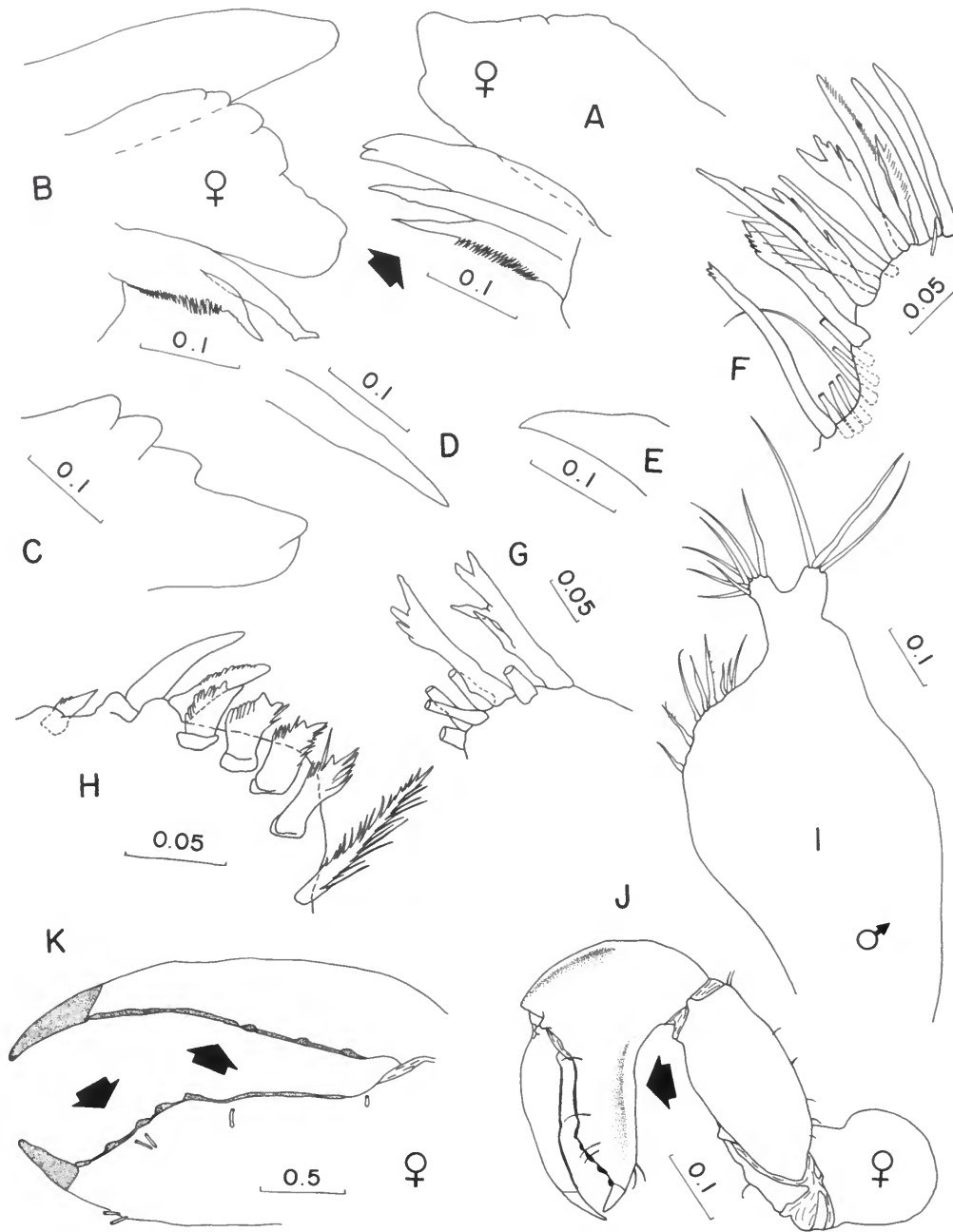
FIGURE 46.—*Neotanais pfaffi* Wolff: A, pars incisiva of right mandible, anterior view, copulatory female H, *Galathea* Sta. 716; B, pars incisiva of left mandible, anterior view, same animal; C, lacinia mobilis, copulatory female F, same station; D, distal incisive spine, left mandible, female F; E, distal (3rd) incisive spine, right mandible, female F; F, fixed endite, left second maxilla, posterior view, female H; G, fixed endite, right second maxilla, posterior view, holotype (copulatory female), same station; H, distal medial tip of endite, left maxilliped, posterior view, female H; I, left second maxilla, posterior view, male Y; J, left cheliped, female H; K, left chela, same animal.
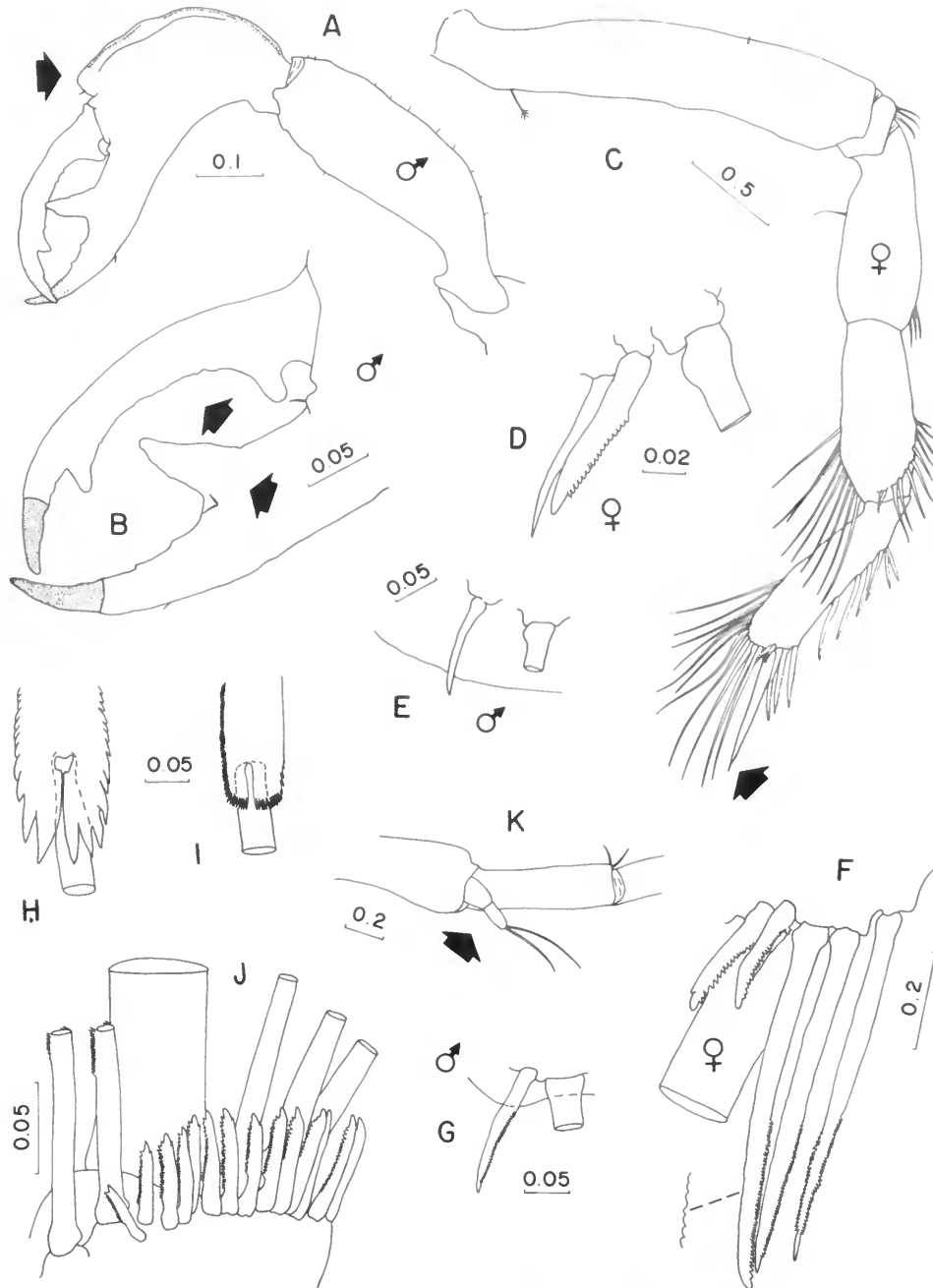
FIGURE 47.—*Neotanais pfaffi* Wolff: A, left cheliped, copulatory male Y, *Galathea* Sta. 716; B, left chela, same animal; C, right pereopod II, anterior view, copulatory female H, same station; D, short, subterminal carpal spine (s), same appendage; E, same spine, right pereopod II, male Y; F, long and short terminal propodal spines, same appendage as in C; G, short terminal propodal spine, right pereopod II, male Y; H, I, tip of dactyli, pereopods VI and VII respectively, dorsal view, holotype, same station; J, tip of propodus, pereopod VII, posterior oblique view, female H; K, left uropodal exopod, lateral view, female H.

setae around the end and lateral side of endopod. Setal formula, (5,7) (3,17,13) (0,8;0,17,9).

Uropods (Figure 45A): Exopods 0.4 times as long as first endopodal article and markedly ventrally deflected.

DESCRIPTION OF COPULATORY MALE ALLOTYPE (from *Galathea* Sta. 716.—*Body* (Figure 45A): 5.6 times longer than wide (estimated from decalcified animal—all copulatory males largely decalcified).

Carapace: Only 1.2 times longer than broad. Anterior area expanded laterally but not raised appreciably. Nine long anterolateral setae present. Oblique furrows moderately well developed; respiratory chambers and chelipedal coxae expanded laterally in dorsal view.

Pereonites: Clearly wider than long. Decalcified and distorted nature of cuticle prevented accurate measurements. Genital cones pominent on pereonite 7; directed ventrally and posteriorly on a common raised base (Figure 45G,I).

Pleonites: Longitudinal furrow on dorsal surface of pleonites deeper than in female. Epimeral hairs apparently not feathered.

Pleotelson: Of slightly different shape but similar to that of other stages.

First Antenna: First article 5.3 times longer than wide.

Second Maxilla: As in Figure 46I.

Maxilliped: Setal formula of palp, (1,0,5+1,5,16).

Cheliped (Figure 46A,B): Carpus stout, not very strongly curved, and bearing 10 tiny dorsal setae. Propodus with very low dorsal crest below which lie 1 or more fine, lateral furrows or lines. Fingers not markedly twisted. Fixed finger with 1 very large, distally directed tooth proximally; this preceded by a small protuberance at the base of the finger and followed distally by 2 tiny, equally spaced protuberances. Dactylus with 2 large teeth, one near each end of article, and separated by a number of very small irregularities.

Pereopods II–VII: Setal formula of pereopod II, (9,10,11,10). Short, terminal propodal spine of pereopods II–IV slender, almost straight, and bearing small teeth along at least one side (Figure 47G). Two long, terminal propodal spines on pereopods II–IV bearing fine teeth (finer than in other stages); short, subterminal carpal spine on pereopod II slender, naked, and almost straight (Figure 47E). Pereopod VII with 11 short, subterminal propodal spines in posterior row; spines serrate as in other

stages. Terminal dactylar teeth of pereopods V–VII relatively fine, coarse, and fine, respectively, but never large.

INTRASPECIFIC VARIATION.—*Stages Other Than Copulatory Male*: Body Length: At *Galathea* Sta. 716 ranges were as follows (numbers of individuals considered are in parentheses): preparatory females 2 (2), 18.1 to 19.5 mm; copulatory females (20), 16.5 to 22.1 mm; preparatory males (3), 17.8 to 19.7 mm; and copulatory males (3), 18.8 to 20.5 mm. The preparatory female 2 from *Vema* 15–55 was 18.6 mm long.

Mandibles: The third incisive spine of the holotype and copulatory female F are straight. These structures probably are abnormal in female H (cf. Figure 46F,G).

Second Maxilla: The number of stout spines associated with medial row varies between 3 and 4.

Pereopods II–VII: The setal formula for pereopod II in copulatory female F is (8,12,17,7). Much variation was noted in the number and length of the short and long terminal propodal spines. The following arrangements were noted in these copulatory females (the number of short spines is followed by the number of long spines for pereopods II–IV, respectively): Female B, 1,3,1,2,1,1; F, 1,2,1,1,1,0; M, 1,2,1,2,1,1; and R, 1,3,1,2,1,0. Two short, subterminal carpal spines, as described for female H (Figure 47D), also are found in female F. All other animals investigated have only one, finely toothed, spine present. The terminal dentition of the dactyli on pereopods V–VII vary between the two types, coarse and fine, described for female H, all combinations being present on the three pairs of legs; however, in no case do all three pereopods have either coarse or fine dentition. No correlation is apparent between type of dentition and age or sex.

Uropods: Another copulatory female had exopods 0.55 times as long as the first endopodal article.

POSTMARSUPIAL DEVELOPMENT.—Juveniles have 10 to 12 endopodal articles in the uropod; copulatory females and males have 12 to 14.

The terminal setae of the pleopodal endopods vary in number and in setal length to endopodal length ratio as follows: 2 juveniles, 7 and 10, 1.1 and 1.3; 2 copulatory females, 15 and 17, 1.1 and 1.2; and the copulatory male described above, 18 and 1.1 Thus, the relative proportions of setae and

endopod remain constant throughout life after the juvenile stage.

Almost all of the copulatory females have faint traces of what may be male genital cone anlagen. The ventral surface of pereonite 7 is slightly constricted and raised and/or scored medially. This situation was not noted in juveniles or in preparatory females. Three copulatory females (F, H, W) have both prominent genital cone and gonopore anlagen (Figure 45H). These structures appear to be better developed than those of preparatory males.

REMARKS.—*Neotanais pfaffi* was described briefly in 1956 by Wolff from about 40 specimens collected by the *Galathea* Expedition off the Pacific coast of Costa Rica. Since then it has been collected by several other groups. It is redescribed here in detail, and diagnoses are presented for all stages.

DISTRIBUTION.—*Neotanais pfaffi* is known to range from the Pacific coast of El Salvador and Honduras to Peru, and has been found at depths of 2599 to 3950 m.

MATERIAL.—*Anton Bruun* Cruise 11, Sta. 111, off Peru, 3086 to 3202 m, 1 P ♀ 2; *Anton Bruun* Cruise 11, Sta. 149, off Peru, 3117 to 3177 m, 1 M2, 1 P ♀ 2, 2 Cop ♀ , 1 P ♂ , 1 Cop ♂ , 1 unid. fgmt. (Juv or P ♂); *Eltanin* Sta. 50, off Peru, 2599 to 2858 m, 1 Juv; *Galathea* Sta. 716, off Pacific coast of Costa Rica, 3590 m, 4 Juv, 4 P ♀ 2, 21 Cop ♀ (including holotype), 5P ♂ , 3 Cop ♂ (including described ♂), 3 unid. fgmts.; *Vema* Sta. 15–55, off Pacific coast of El Salvador and Honduras, 3777 to 3950 m, 1 P ♀ 2.

LOCATION OF MATERIAL.—UCZM: *Galathea* collection, including holotype. AMNH: *Vema* 15–55 (AMNH 14.894). NMNH: *Anton Bruun* 111 (USNM 143191); *Anton Bruun* 149 (USNM 143192).

Neotanais giganteus Hansen, 1913

FIGURES 48–50, 99

Neotanais giganteus Hansen, 1913:20, pl. 2: figs. 2a–h.—Wolff, 1956a:208, figs. 19, 20.
Neotanais longimanus Wolff, 1956c:49, fig. 4.
Neotanais deflexirostris Lang, 1968:135, figs. 79–83, pl. 5: figs. e, f.

DIAGNOSES.—*Stages Other Than Copulatory Male*: *Chela distinctive, propodus with narrow dorsal keel and long, prominent lateral keel on fixed finger; *propodal teeth rounded and widely spaced

along distal half of fixed finger; *dactylus longer than propodus and with about 15 to 20 low, rounded, undulating lobelike teeth along cutting edge. *Carapace bearing prominent anterolateral keels, each above a row of about 15 to 20 long setae. *Pereonites showing considerable dorsal relief, being slightly bulbous over pereopods and widest at this point as well, narrowing gradually anteriorly, abruptly posteriorly. *Pleonites expanded laterally, sides tapering forward gradually, edges of epimeres slightly flared and each bearing a single simple hair; pleon tapering anteroposteriorly, pleonite 1 being wider than pleonite 5; sternites rounded ventrally and in lateral view. *Pleotelson often appearing concave posteriorly in dorsal view; about twice as wide as long; *fused to pleonite 5. Fourth article of first antenna over twice as long as articles 5 through 7 together. *Uropods with numerous (up to 12 in copulatory female) stout endopodal articles; exopod about 0.5 the length of first endopodal article. Pereopods with many (up to 30 on a side) long, extremely finely setulated setae on propodi and carpi; *dactylar spines of pereopods II–IV only about 0.2 times as long as dactyli. *Pleopods with 5 medial endopodal setae in contrast to the 3 characteristic of all other species in genus.

Copulatory Males: *Pleotelson convex laterally anterior to uropods and straight or slightly concave posterior to uropods with abrupt corners and strongly concave posterior margin. *Chela with 2 proximal lobes on fixed finger, the second larger than the first and bearing a distal angularity, and a very long, slender, round-tipped tooth midway along finger; *dactylus with very small teeth of various shapes proximally and a somewhat larger tooth distally. *Pleontes each with a low, sternal convexity midventrally which bears a rounded projection divided longitudinally into 2 parts (see "Remarks"). Pereopods II–IV apparently without long, toothed propodal spines and bearing many fine smooth setae on propodi and carpi; dactyli of pereopods V–VII without distal teeth.

DESCRIPTION OF PREPARATORY FEMALE 2 A (WHOI B. Sta. 62).—*Body* (Figure 48A): 9.9 mm long and 5.7 times longer than wide.

Carapace: With prominent oblique furrow; articulation between chelipedal coxa and carapace depressed into obvious furrow. Length-width ratio, 1.1. Anterolateral keels marked and with a row of

about 20 anterolateral setae located just below on each side (Figure 48D); 1 or 2 posterolateral setae located posteriorly and ventrally to these. Respiratory chambers moderately and chelipedal coxae considerably swollen laterally in dorsal view. Rostral area relatively blunt anteriorly in dorsal view due to strongly decurved point (Figure 48D).

Pereonites (Figure 48A): Pereonites 4–7 appear to widen gradually from anterior edge to widest area, above the pereopods; constricted behind pereopods; lengths of individual pereonites much more similar than in many species.

Pleonites (Figure 48A,F,G): Sloping gradually posterolaterally; edges of epimeres flared slightly upwards to horizontal plane and each with a single dorsal hair. Segments progressively narrower from pleonites 1 to 5. Sternites rounded midventrally and very slightly laterally compressed, but not forming a marked ridge or thin points.

Pleotelson (Figure 48E,F,G): A little narrower than pleonite 5 and 2.1 times wider than long. Posterior edge slightly concave in dorsal view; a slight median protuberance present posteriorly. Fused to pleonite 5.

First Antenna (Figure 48I): First article 4.4 times longer than wide. Article 4 over twice as long as articles 5–7 combined.

Second Antenna: As in Figure 49A.

Right Mandible (Figure 49F): Third incisive spine stout, but not basally swollen; sharp and naked. Second spine similar; first spine naked on outer edge and serrate on the inner edge.

Left Mandible (Figure 49C): Incisive spines as on right side. Lacinia mobilis with 4 large teeth in addition to partially divided posterior lobe.

Labium: As in Figure 49B.

First Maxilla: As in Figure 49H.

Second Maxilla (Figure 49I): Fixed endite with 1 stout bifid and 1 stout trifid spine. Medial row with 11 feathered setae and 2 stout, slightly setulated spines terminally.

Maxilliped (Figure 50A,B): Setal formula of palp, (0,0,4,6,17).

Cheliped (Figure 50C,D): With 8 short dorsal setae. Propodus with low dorsal keel and long, prominent lateral keel on fixed finger. Propodal teeth rounded and widely spaced along distal half of fixed finger. Dactylus longer than propodus and bearing about 17 low, rounded, and undulating lobelike teeth along cutting edge.

Pereopods II–VII: With propodal and carpal setae numerous, finely setulated, long, and thin (Figure 50I). Setal formulae of pereopods II–VII, (20,14,13,14), (30,22,13,23), (26,26,16,23), (11,12, 13,12), (12,12,13,10), and (10,10,9,9). Long, terminal propodal spines on pereopods II–IV absent. Short, terminal propodal spines of same appendages relatively slender, straight, and bearing up to about 15 moderately large teeth on each side (Figure 50E). Short, subterminal carpal spines on pereopod II straight, with sharp or blunt tips, and apparently naked (Figure 50F). Short, subterminal propodal spines of pereopod VII 8 in number and bearing easily visible teeth of moderate size (Figure 50J). Dactylar spines of pereopods II–IV very short, only about 0.2 as long as dactylus (Figure 50I). Terminal dactylar teeth of pereopods V–VII not significantly different from those of other species.

Pleopods (Figure 50K): Terminal endopodal row of setae continuous with lateral row; about 15 terminal endopodal setae; setal-endopodal length ratio, 1.1. Setae on protopod very small; setal formula, (2,2) (5,15,10) (0,6;0,15,10).

Uropods (Figure 48A,E,H): Composed of 9 and 10 endopodal articles on left and right sides respectively; exopod 0.5 times as long as first endopodal article. Endopodal articles stout; first endopodal article bearing 1 or 2 dorsal broom setae centrally.

INTRASPECIFIC VARIATION.—*Stages Other Than Copulatory Male*: See "Remarks" under *Neotanais deflexirostris*, below. Following are the body lengths of various specimens (numbers of animals considered are indicated in parentheses): WHOI Benthic Sta. 62: manca 2 (2), 3.4 and 4.6 mm; juvenile (14), 5.2 to 12.0 mm; preparatory female 1 (2), 13.8 mm; preparatory female 2 (1), 16.8 mm; copulatory female (4), 16.7 to 17.7 mm. *Galathea* Sta. 65: copulatory female (3), 18.4 to 19.2 mm.

The measurements given for specimens from WHOI B. Sta. 62 are representative of specimens elsewhere in the North American Basin. Wolff's specimens indicate a larger body length in the eastern Atlantic. The copulatory female collected off Guinea (WHOI B. Sta. 151) was immense (22.3 mm) compared to all other copulatory females (12), 15.6 to 17.7 mm.

The rostrum may appear to be relatively pointed or flat anteriorly in dorsal view depending on its angle of curvature (Figure 48D). Although article 1
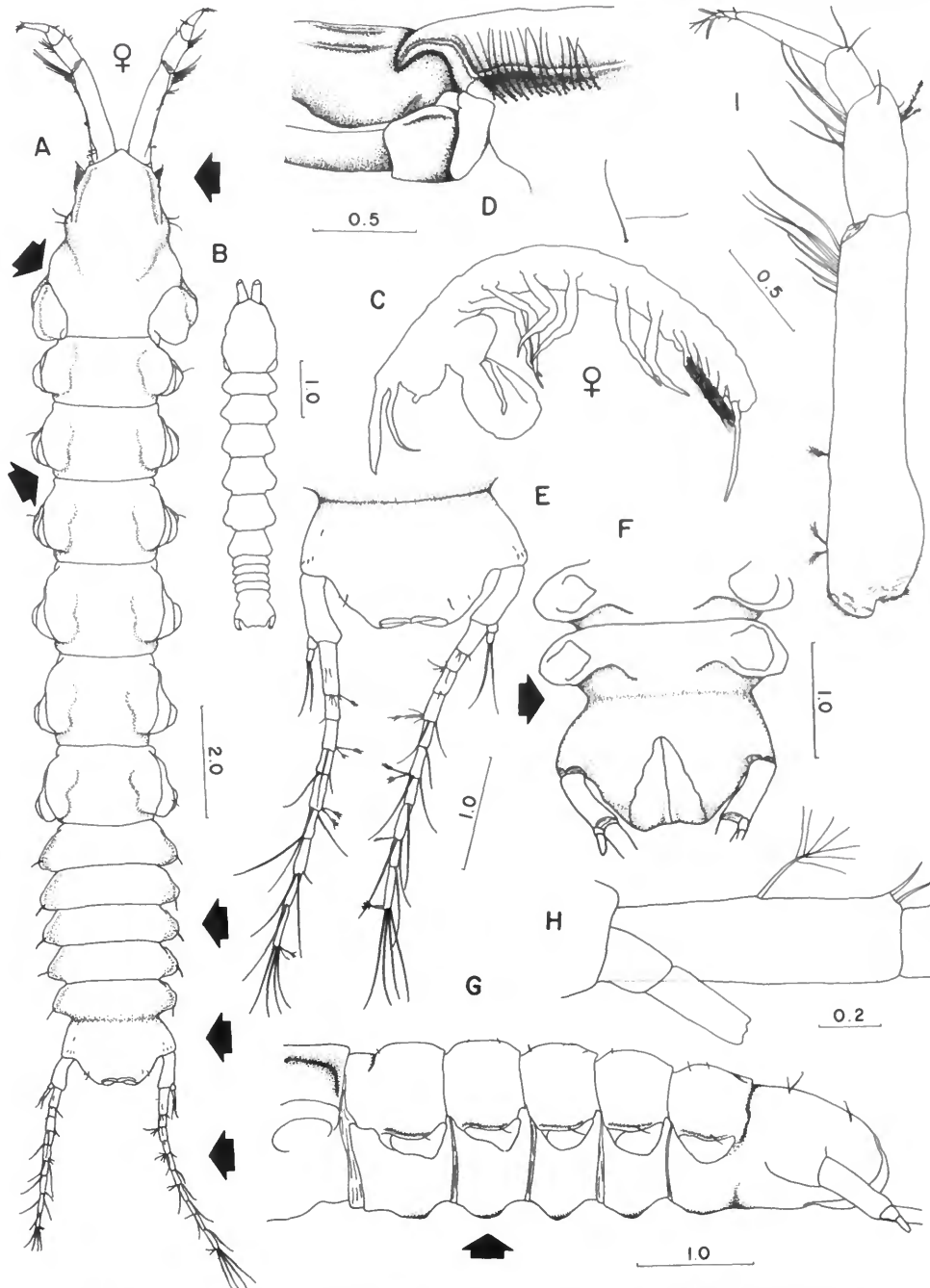
FIGURE 48.—*Neotanais giganteus* Hansen: A, preparatory female 2 A, dorsal view, WHOI B. Sta. 62; B, a juvenile, same station (dorsal outline)—note differences in shape; C, configuration when preserved, lateral view; D, lateral view of carapace, female A, left first and second antennae removed; E, pleotelson and uropods, dorsal view, same animal; F, same, ventral view; G, pleon, lateral view, same animal; H, uropodal exopod and article 1 of endopod, lateral view, same animal; I, left first antenna, dorsal view, same animal.

FIGURE 49.—*Neotanais giganteus* Hansen: A, left second antenna, from below, preparatory female 2 A, WHOI B. Sta. 62; B, labium, same animal; C, left mandible, anterior view, with enlargements of lacinia mobilis (upper) and molar teeth (lower), same animal; D, lacinia mobilis, copulatory female R, same station; E, incisive blade and spines of left mandible, same animal (also see G, below); F, right mandible anterior view, with enlargements of pars incisiva (upper) and molar teeth (lower), female A; G, incisive spine, right mandible, anterior view, female R (note extra spine, see also E, above); H, left first maxilla, posterior view, female A; I, left second maxilla, posterior view, with enlargements of fixed endite and medial seta, female A; J, enlarged forked spines of fixed endite, left second maxilla, female R; K, same spines, holotype (copulatory female), *Galathea* Sta. 65.
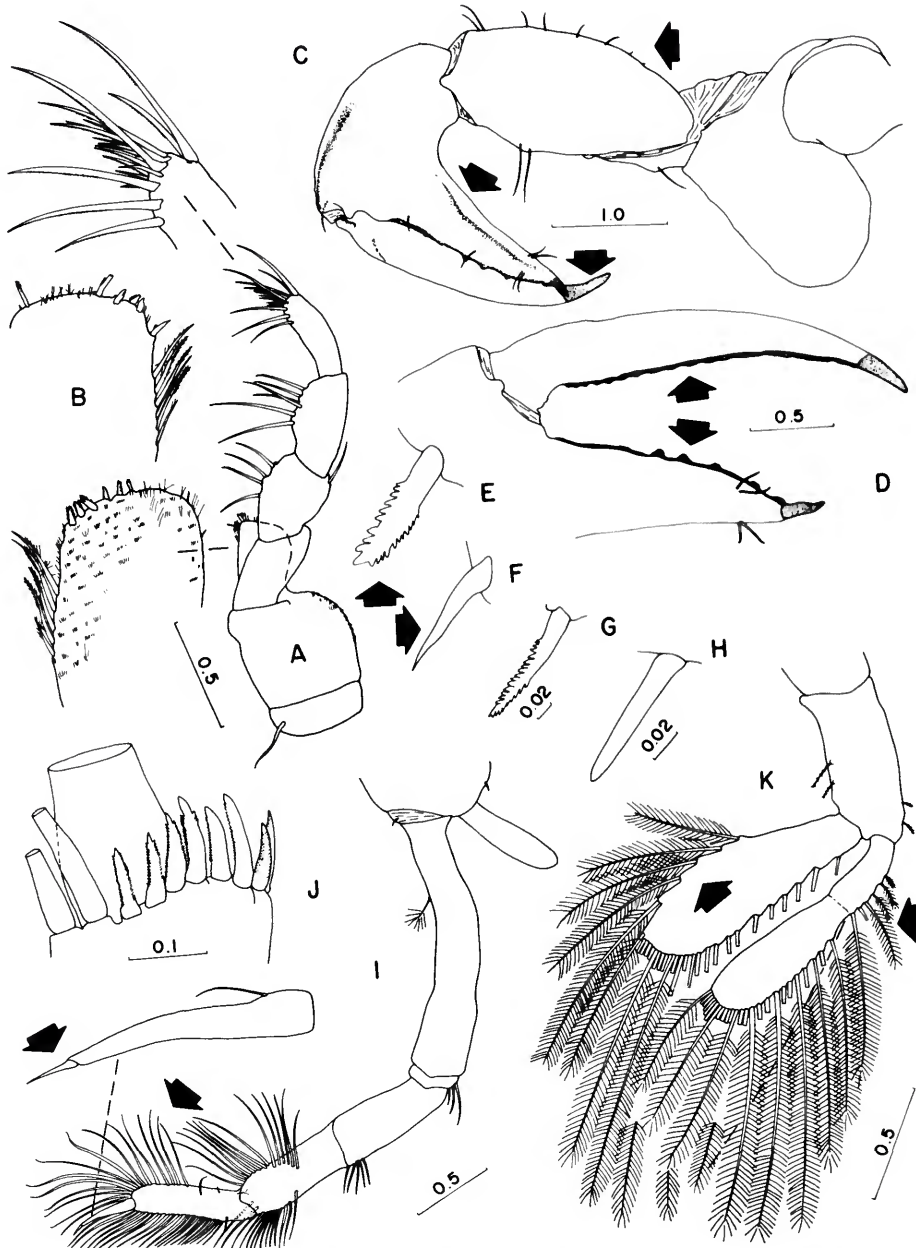
FIGURE 50.—*Neotanais giganteus* Hansen: A, left maxilliped, posterior view, with enlargements of endite and terminal palpal article, preparatory female A, WHOI B. Sta. 62; B, enlargements of right maxillipedal endite, same animal; C, left cheliped, same animal; D, right chela, same animal; E, short, terminal propodal spine, left pereopod II, dorsal view, same animal; F, short, subterminal carpal spine, same appendage; G, short, terminal propodal spine, right pereopod II, holotype, female; H, short, subterminal carpal spine, same appendage; I, left pereopod II, with enlargement of dactylus, posterior oblique view, female A; J, tip of propodus, left pereopod VII, posterior oblique view, same animal; K, left pleopod, anterior view, same animal.

of the first antenna is usually about 4.4 times longer than wide, that of copulatory female T (WHOI B. Sta. 62) has a ratio of only 3.9. The pleotelsonal width-length ratio varies from 1.6 to 2.1.

Of the three copulatory females of which the mouthparts were examined, the lacinia mobilis was almost identical in two, but copulatory female R (WHOI B. Sta. 62) had six teeth in addition to the large cleft lobe (Figure 49D). Also, the second incisive spine of the left mandible in R has an irregularly spinous tip (Figure 49E). The second spine on the right mandible of R also differs from that of the other specimens in having a few subterminal setules (Figure 49G) and an extra spine which is probably abnormal.

The fixed endite of the second maxilla varies in the shape of the stout cleft spines. Although there are always two of these present, one bifid and one trifid spine are present in females A and T (WHOI B. Sta. 62, Figure 49I), one trifid and one with four points in R (same station, Fig. 49J), and one bifid and one with four points on both sides in a female from Galathea Sta. 65 (Figure 49K).

The differences in pereopodal setal counts sometimes were appreciable within animals of the same stage; setal formulae for pereopods II–IV of female R are (26,22,17,10), (25,26,20,14), and (20,29,14,14). Female R apparently is aberrant in many characters.

The numbers of dorsal setae on chelipedal carpi varied from eight to twelve among copulatory females. The growth of uropods with age (WHOI B. Sta. 62): mancas 2, four articles; juveniles, usually six, occasionally seven or eight; preparatory females and older stages, nine to twelve.

POSTMARSUPIAL DEVELOPMENT AND VARIATION IN PLEOPODS (based on animals from WHOI B. Sta. 62).—Several animals from Sta. 62 have body lengths between 7.9 and 12.0 mm, but none of these show traces of oostegites or of male gonopore anlagen. On the basis of the developmental pattern of Neotanais micromopher they would be juveniles; however, the variation in their body lengths indicates that they probably belong to other groups. A group of ten individuals with body lengths between 5.2 and 6.6 mm probably represents a stage equivalent to the juveniles in Neotanais micromopher.

The larger individuals can be separated into two groups: (1) D and F, with lengths of 7.9 and 8.0 mm respectively, and (2) S, U, and W which are, respectively, 9.5, 10.2, and 12.0 mm in length. These groups probably represent two different developmental stages, although the possibility that animals D and F are extreme variants of either the upper or lower (juvenile) group cannot be ruled out. Development of the pleopods, characteristic of the developmental stages in Neotanais micromopher, may shed additional light here.

Mancas 2 have only a single terminal stub on their rudimentary pleopods. In contrast to Neotanais micromopher, they have not yet developed the primordia of both rami. The cluster of small juveniles also exhibits a rudimentary pleopodal structure, although the rami are present and indistinctly articulated with the protopod. The next larger animals, D and F, have one or two terminal endopodal setae of considerable length, and the ratio of setal length to endopodal length is about 0.60. The largest animals, S, U, and W, have five, six, and seven setae, respectively, and ratios of 1.3, 1.0, 1.1. A, a preparatory female 2, has 15 setae and a ratio of 1.1. The development of the female pleopods has been nearly completed; copulatory females R and T have only 17 and 16 setae and ratios of 1.2 and 1.1, respectively. Although setae are added continuously up until the copulatory female instar, they have already attained their adult proportions relative to the length of the endopod in the case of animals S, U, and W.

The animals of dubious developmental status differ from each other as groups and fall between the small juveniles and the preparatory females 1 with respect to pleopodal development. D and F may be precocious juveniles, perhaps on the way to becoming preparatory males as suggested for certain large juveniles of Neotanais micromopher; however, the size gap is large. S, U, and W may be preparatory males, none of which has otherwise been identified at WHOI B. Sta. 62. But in N. micromopher this instar approximates copulatory females in pleopodal development, and evidence either of male gonopore anlagen—so clear in the preparatory males of other species of the genus—or of faint genital cone anlagen would be expected. A further possibility is that development in Neotanais varies, and that two or three juvenile stages are present in N. giganteus; however, considering the extreme conservatism of this genus in other respects, this suggestion is not appealing.

COMPARISON OF HOLOTYPE WITH OTHER SPECI-

MENS.—The copulatory male holotype resembles the other specimens in the following important characteristics: (1) carapace with long rows of about 20 anterolateral setae and marked dorsal relief; (2) presence of dorsal relief and swellings on pereonites above attachments of pereopods; (3) shape of pleotelson in dorsal view (relatively straight sides posterior to uropods and concave posterior margin); (4) shape of lateral margins of pleonites in dorsal view (sloping outward posteriorly); (5) uropods with a large number (13) of relatively stout endopodal articles, first endopodal article bearing setae along its length, similar length relative to pleon, and exopod of similar length compared to first endopodal article; (6) pereopods II–VII bearing many fine propodal and carpal setae and pereopods II–IV without long, toothed spines; (7) pleopods with relatively long protopods, wide endopods, and five medial endopodal setae.

The body length of the *Ingolf* specimen (holotype), 20 mm, is within the range expected for a copulatory male. As figured by Hansen (1913, pl. 2: fig. 2g) and mentioned by Wolff (1956a:209), the dactyli of pereopods V–VII are without distal dentition. (This is the only known case within the genus where dentition is not found in all stages; however, *N. giganteus* is unique in a number of other features in which it stands apart from all other known species of *Neotanais*.)

The pleotelson is clearly delimited from pereonite 5 in the now largely decalcified holotype. This arthrosis may be obscured in life, similar to other specimens.

Wolff (1956a:209, fig. 19a) described low, midventral convexities on the pleonites, each of which is "split into two halves by a longitudinal cleft." This division may be an artifact of decalcification.

REMARKS.—*Neotanais giganteus* was described by Hansen (1913) from a single copulatory male collected by the *Ingolf*. Later, Wolff reexamined the specimen and described its mouthparts and made various comments on its morphology. *Neotanais longimanus* was described briefly by Wolff (1956c) from four female specimens collected by the *Galathea* off Gabon. Since then it has been collected at many other locations. Because of the great number of similarities between these two species, they are here considered to be conspecific. Stages other than those of copulatory males are described in detail and diagnoses are presented for all stages.

Lang (1968) described *Neotanais deflexirostris* from a single preparatory female from *Galathea* Sta. 575 in the Tasman Sea. He noted that it was very similar to *N. longimanus* Wolff, and he was uncertain whether it represented a new species or a subspecies of *N. longimanus*. He erected the new species on the basis of differences noted in the shapes of the carapace, pereonites, pleotelson, and midventral surface of the pleonites.

Having examined the much larger collection of *Neotanais giganteus* now available from several localities in the North and South Atlantic, it is my opinion that the differences in pereonites and pleotelson together with the fact that the midventral protuberances on the pleonites are slightly split, are all relatively minor differences, and are accountable for on the basis of individual or geographic variation. The differences in carapace are that (1) the chelipedal coxae appear shorter (cf. Lang, 1968, pl. 5f,h) and (2) the rostral area is curved ventrally to the extent that, in dorsal view, the carapace appears flattened anteriorly. With regard to (1), chelipedal coxae in specimens of *N. giganteus* from the Atlantic sometimes resemble those of the specimen from *Galathea* Sta. 575; therefore, this is an unimportant difference. The rostrum is strongly deflected but not directly downward (Figure 48D and Lang, 1968, fig. 79b). Not all individuals of *N. giganteus* have as pronounced a rostrum as the animals examined by Lang. These individuals also have the rostrum strongly deflected but not to the same extent as in the specimen from the Tasman Sea.

In view of the apparently trivial nature of their differences, these species are here considered conspecific. When the southwest Pacific fauna has become better known, and if additional individuals are found bearing the same deviant characters as *Neotanais deflexirostris* Lang, they may be considered typical of that local population but not necessarily representative of a new species or even of a namable subspecies (see discussion of subspecies, p. 18).

The esthetascs on articles 5 and 6 of antenna 1 in Lang's specimen are annulated and shaped as in other species, and not as figured in the original description (Lang, 1968, fig. 79d). The tips of the medial endopodal setae on the pleopods are specialized, thus resembling those of all other species of the genus.

TABLE 7.—*Examined material of* Neotanais giganteus *Hansen*

Program or ship	Station no.	General location	Depth (meters)	Material
		EAST COAST OF NORTH AMERICA		
WHOI Benthic	GH 3	Gay Head–Bermuda Transect	2478	1 P♀2
	62		2496	2 M2, 15 Juv, 2 P♀1, 1 P♀2, 4 Cop ♀, 2 fgmts.
	64		2886	5 Juv
	72		2864	1 M2, 2 Juv, 3 P♀1, 1 P♀2, 3 Cop ♀
	78		3828	1 P♀2
CMS	2157	SW of Georges Bank	2460	1 P♀2
	2163		2695	1 Cop ♀
	2169	S of Georges Bank	2870	1 P♀1, 1 Cop ♀
Eastward	2756	E of Cape Hatteras, North Carolina	3017	1 P♀1, 1 Cop ♀
Ingolf	36	Davis Strait	2702	1 Cop ♂ (holotype)
		WEST COAST OF AFRICA		
Galathea	65	Off Gabon, West-Central Africa	2770	1 P♀2, 3 Cop ♀
WHOI Benthic	151	Off Guinea, West Africa	3861	1 Cop ♀
		PACIFIC OCEAN		
Galathea	575	Tasman Sea	3710	1 P♀2 (described by Lang as holotype of N. deflexirostris)

MATERIAL.—See Table 7.

LOCATION OF MATERIAL.—UCZM: Holotype; *Galathea* collections. NMNH: CMS 2157 (USNM 143197); CMS 2163 (USNM 143198); CMS 2169 (USNM 143199); *Eastward* 2756 (USNM 143196); WHOI 62 (USNM 143193); WHOI 72 (USNM 143194); WHOI 151 (USNM 143195).

Neotanais pfaffioides Lang, 1968

FIGURE 102

Neotanais pfaffioides Lang, 1968:152, figs. 94–97, pls. 6e,f, 7a,b.

DIAGNOSIS—*Stages Other Than Copulatory Male* (copulatory males unknown): *Pereonites 4–6 generally square in dorsal view with area over pereopods prominently expanded laterally; *each pereonite with shallow dorsal depressions. *Pleonites of similar width, each bearing up to 7 relatively long, feathered epimeral hairs in a row running dorsally on each side, sides gradually sloping posterolaterally; *each pleonite with a moderately sized, acutely tipped, midventral protuberance posteriorly located on each sternite. Pleotelson convex both anterior and posterior to uropods in dorsal view and bearing a small, pointed ventral protuberance anteriorly. Chelipedal carpus with at least 12 dorsal setae (copulatory female);

fixed finger with uneven inner border without distinct teeth; *dactylar border only slightly uneven or undulate and without teeth. First article of first antenna 4.2 times longer than wide. Pereopodal carpal and propodal setae slender and with very fine setules; long, terminal propodal spines apparently absent. Pereopod VII with about 20 short, subterminal propodal spines in row (copulatory female).

REMARKS.—The following observations can be added to the description given by Lang. A slightly raised ridge runs along the midventral line of the pereonites. The pereonites have pairs of slight dorsal depressions roughly parallel to the level of pereopodal attachment but, with the exception of pereonite 2, these do not accentuate the area of coxal attachment as in *Neotanais armiger, N. giganteus,* and *N. pfaffi.* Pereonite 2 bears a transverse ridge behind and parallel to the posterior margin of the carapace and separated from it by a depressed area. The pleotelson bears a small, pointed midventral protuberance anteriorly. The esthetascs borne on the fifth and sixth articles of the first antennae are annulated (5 sections) as in other species in contrast to Lang (1968, fig. 94d). Each of the uropodal endopods is composed of 11 articles.

The holotype is a copulatory female without oostegites but with oostegite scars and gonopores

(not a female with rudimentary oostegites—Lang, 1968:152).

A diagnosis for *Neotanais pfaffioides* is presented above for the first time.

MATERIAL.—*Galathea* Sta. 471, Sunda Trench, 2780 m, 1 Cop ♀ (holotype).

LOCATION OF MATERIAL.—UCZM: Holotype.

Neotanais armiger Wolff, 1956

FIGURES 51–55, 99

Neotanais armiger Wolff, 1956c:47, fig. 3, pl. 2: figs. 13–16.

DIAGNOSES.—*Stages Other Than Copulatory Male*: Pleonal epimeres often drawn out into blunt spurs or rounded laterally (see "Intraspecific Variation," below); *sternites projecting downward, forming long, attenuated midventral spurs. *Chela very large relative to remainder of cheliped; dorsal carpal setae of cheliped scattered, hairlike; ventral carpal setae slender. *Carapace seeming almost triangular in dorsal view, about as long as wide, and very narrow anteriorly. Pleotelson short, often with obtuse angles in margins anterior and posterior to uropods. *First antenna with long slender first article, about 5 times longer than wide and 1.4 times longer than carapace; *article 4 very long, over twice as long as articles 5–7 combined. *Second antenna very slender. Pereopods apparently longer relative to body length than in many other species; *short, terminal propodal spine of pereopods II–IV characteristic: strongly arched and often projecting prominently distally and dorsally in anterior or posterior view; propodal and carpal setae of same legs numerous, slender, and with exceedingly fine setules. Pereonites considerably wider than elsewhere in area over pereopods in dorsal view; *surface generally raised in this area; tapering gradually forward, often being somewhat bell-shaped in dorsal view, especially pereonites 5–7 (see "Intraspecific Variation").

Copulatory Males (see also "Intraspecific Variation," below): *Pleonites (epimeres and sternites), pleotelson, second antenna, and pereopods much the same as in other stages. *First article of first antenna slightly longer than carapace. Carapace with prominent rostrum with markedly concave sides; oblique furrows, respiratory chambers, and chelipedal coxae markedly developed in dorsal

view; a relatively deep, transverse furrow lying between chelipedal coxae dorsally. *Chelipedal carpus with a few very slender, hairlike setae dorsally and 2 such setae ventrally (for details of chelae see description of allotype and "Intraspecific Variation," below). *Pereonites 4–6 similar to, but appearing somewhat longer with respect to width than, those of other stages.

DESCRIPTION OF COPULATORY FEMALE (No. 33, *Vema* Sta. 15–40).—*Body* (Figure 51A): 9.3 mm long and 5.8 times longer than wide.

Carapace: Short, only 1.1 times longer than wide. Rostrum moderately well developed with markedly concave sides. One anterolateral seta and 1 posterolateral seta present on each side. Anterolateral keels not well developed. Oblique furrows relatively deep. Respiratory chambers and chelipedal coxae well developed in dorsal view, giving carapace a triangular appearance.

Pereonites (Figure 51E): Pereonites 4–6 wider than long and somewhat "bell-shaped" in dorsal view. Areas over pereopods prominently expanded laterally and swollen dorsally.

Pleonites (Figures 51F, 52A): Pleonite 1 a little wider than pleonite 7. Epimeres greatly expanded and tapered laterally. Sternites extended midventrally into long, sharply pointed spurs, some being slightly posteriorly directed. Bearing occasional long, dorsal epimeral setae, some of which are feathered (all probably feathered originally).

Pleotelson (Figures 51F, 52A): Short, 1.8 times wider than long, and much narrower than pleonite 5. Shape characteristic (but different from animals with short pereonal epimeres—see "Intraspecific Variation," below).

First Antenna (Figure 52E): First article 4.9 times longer than wide, 1.4 times longer than carapace, and bearing a number of very long lateral setae. Fourth article over twice as long as articles 5–7 combined.

Second Antenna (Figure 52F): Very slender. Second article 4.3 times longer than the third.

Right Mandible (Figure 53K): Third incisive spine naked, slightly irregular at tip, and not swollen basally. Second spine with only a few scattered setules on distal half. First spine fully setulated on both sides.

Left Mandible (Figure 54O): Second incisive spine serrate along entire inner side and distal half of the other. First spine serrate on both margins.
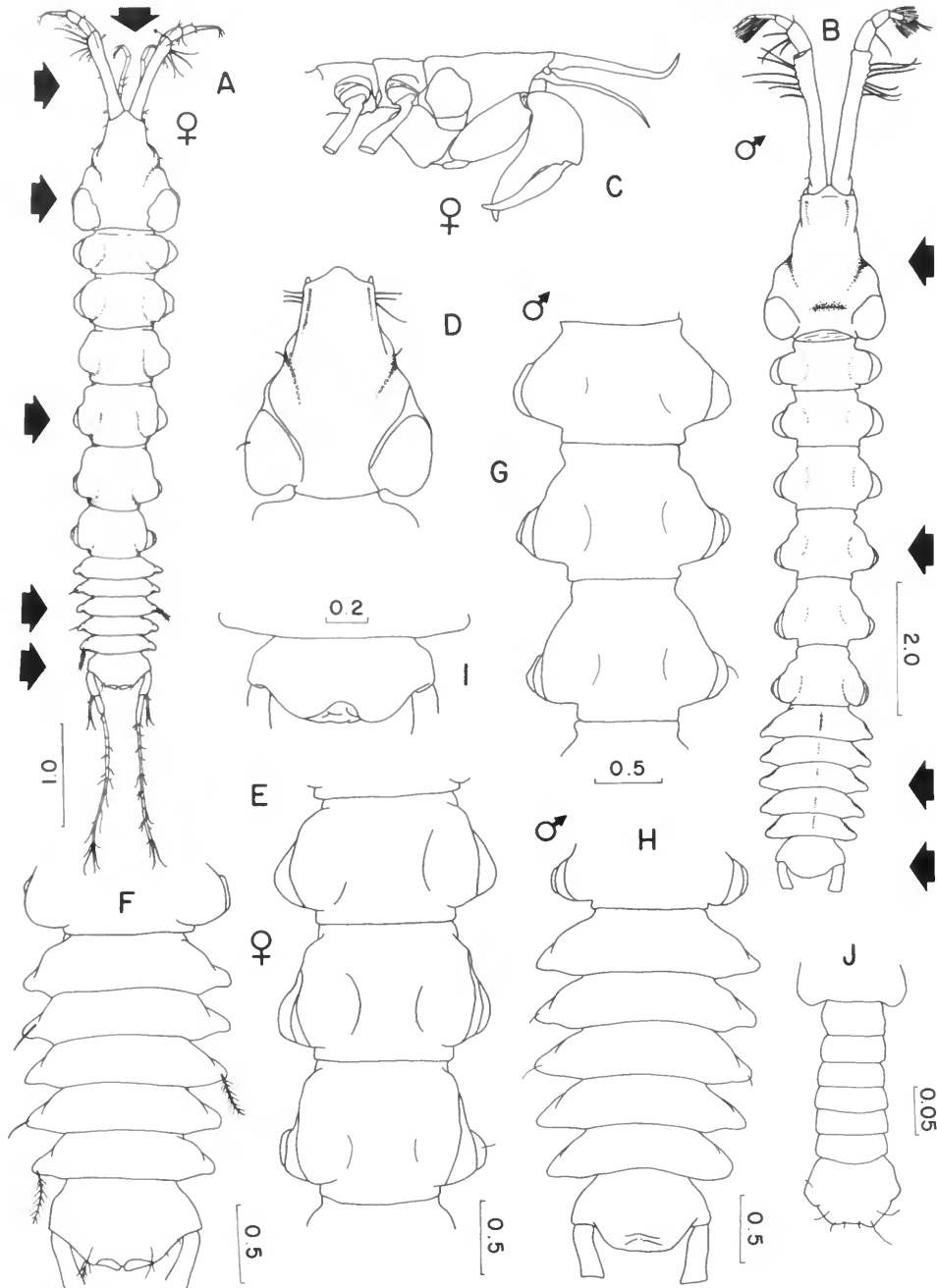
FIGURE 51.—*Neotanais armiger* Wolff: A, dorsal view of copulatory female 33 from *Vema* Sta. 15–40; B, secondary copulatory male, allotype, *Galathea* Sta. 726; C, lateral view of anterior area of body showing chelipedal proportions, stages other than copulatory male; D, carapace of copulatory female, CMS Sta. 1597 off Florida Keys; E, pereonites 4–6 in dorsal view, female in A; F, pleon of same animal; G, pereonites 4–6 in dorsal view, copulatory male in B; H, pleon of same animal; I, pleotelson in dorsal view, copulatory male 31, *Vema* Sta. 15–21 in the Caribbean Sea; J, pleon in dorsal view, manca 1 from OSU Sta. 163.
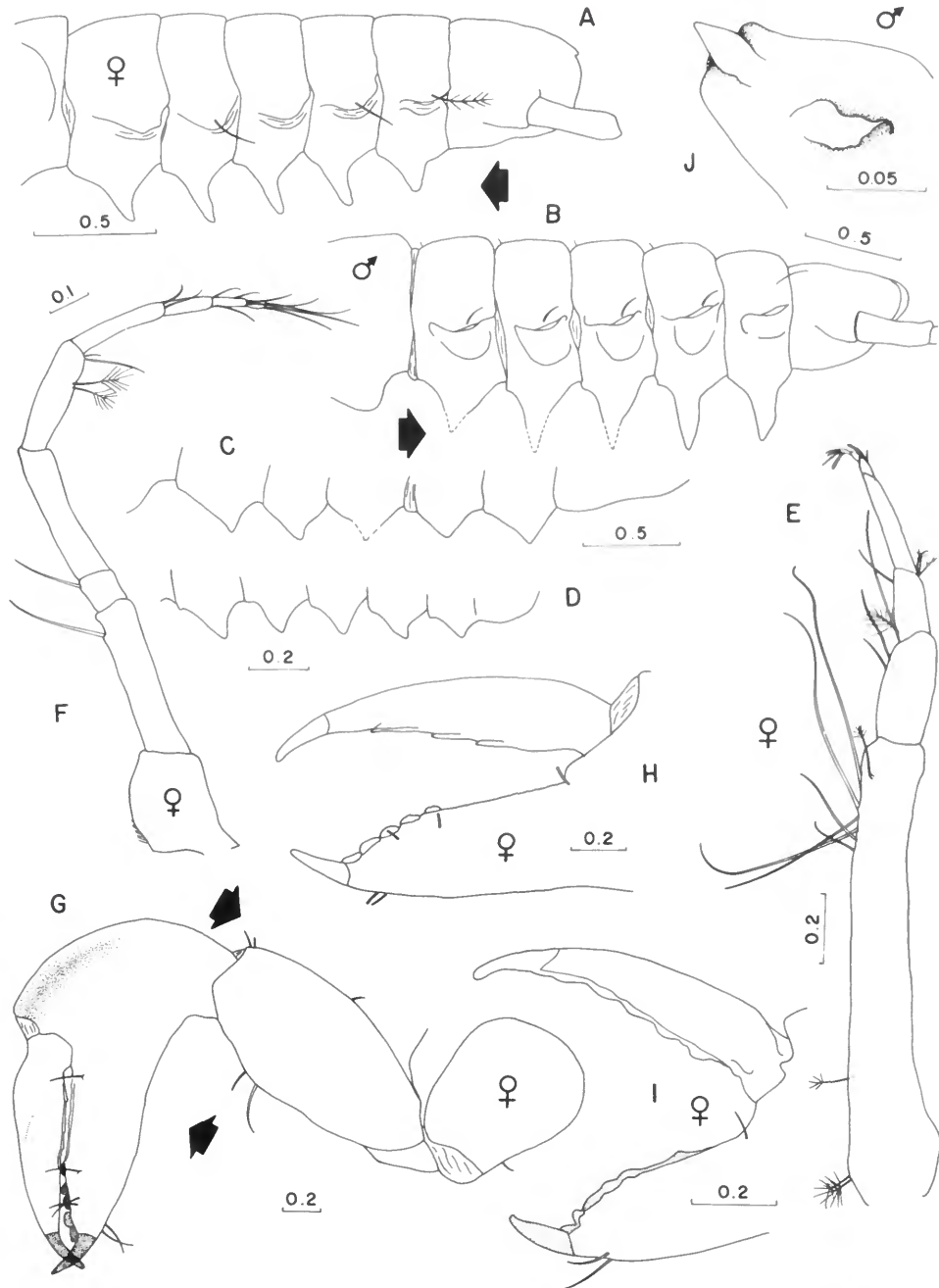
FIGURE 52.—*Neotanais armiger* Wolff: A, lateral view of pleon of copulatory female 33, *Vema* Sta. 15–40; B, same, secondary copulatory male allotype, *Galathea* Sta. 726; C, same, copulatory female 1, *Galathea* Sta. 716; D, same, preparatory male 46, *Vema* Sta. 15–21 in the Caribbean Sea; E, left first antenna in dorsal view, female 33; F, left second antenna in ventral view, same animal; G, left cheliped of same animal; H, enlargement of chela of same; I, left chela of preparatory male 46 (Caribbean Sea); J, distal tip of right mandible in oblique medial view, copulatory male 47 from same station.

Lacinia mobilis with 3 prominent teeth and 1 large irregular posterior lobe.

Second Maxilla: Fixed endite with 2 large, stout bifid spines. Medial setal row composed of 16 (left) and 17 (right) feathered setae and 2 (left) and 3 (right) unfeathered, stout spines.

Maxilliped: Setal formula of palp, (0,0,4 + 1,7,13). Endite with 6 (left) and 7 (right) medial setae.

Cheliped (Figure 52g,h): Carpus with only about 3 very short, fine dorsal setae. Chela noticeably larger in comparison to rest of appendage than in most species, carpus being only 0.7 times as long as propodus (Figure 51d). Dorsal propodal keel moderately well developed. Five large distal teeth on fixed finger brown and rounded; about 40 to 45 small denticles located proximally. Dactylus bearing 4 low, partially fused, and distally directed teeth on cutting surface.

Pereopods II–VII (Figure 55a,e). Propodal and carpal setae numerous, long, slender, and with extremely fine setules visible only with difficulty. Setal formulae of pereopods II and III, (15,12,18,17) and (19,15,19,17). Two long, heavily toothed propodal spines present on pereopod II, whereas pereopods III and IV bear only 1 each. Short, subterminal carpal spine of pereopod II slightly curved and very faintly setulated. Short, terminal propodal spine of pereopods II–IV very stout, strongly curved, bearing numerous strong teeth, and arched upward. Fifteen short, prominently setulated, subterminal spines present on the propodus of pereopod VII.

Pleopods (Figure 55g): Rami long and slender. Protopod bearing 4 small setae. Lateral setae of first exopodal article relatively long and stout. Setal formula, (2,2) (3,9,7) (0,3;0,11,6). Endopodal setae noticeably longer (1.4 times) than article and 11 in number.

Uropods: Slender and longer than pleon. Endopod with 10 and 11 articles on left and right sides, respectively. First article of endopod longer and wider with respect to the succeeding ones than in some species. Exopod about 0.9 times as long as first endopodal article on left side (longer than in many specimens).

DESCRIPTION OF SECONDARY COPULATORY MALE ALLOTYPE (*Galathea* Sta. 726).—*Body* (Figure 51b): 10.8 mm long and 5.8 times longer than wide.

Carapace: Bears pronounced and pointed rostrum with strongly concave sides. A single anterolateral and posterolateral seta present on the left side. Ocular lobes prominently visible from above. Anterolateral keels shallow and short. Oblique furrows prominent and a marked transverse crease or furrow present posterior to these. Respiratory chambers and chelipedal coxae strongly developed laterally in dorsal view.

Pereonites (Figure 51g): Very wide in area over pereopods. Sides of pereonites 4–7 sloping gradually posterolaterally with a slight convexity anterior to pereopods.

Pleonites (Figures 51h, 52b): Very similar to those of other stages. Lateral setae not observed (possibly broken).

Pleotelson (Figures 51h, 52b): Similar to that of other stages but posterior margin generally rounded due to fusion of anal area.

First Antenna (Figure 51b): First article 8.7 times longer than wide and about as long as carapace.

Cheliped (chela type B; Figure 54a): Carpus almost straight, only very slightly bent; very swollen centrally; bearing about 6 very slender, hairlike setae dorsally and 2 similar but longer setae ventrally. Dorsal propodal crest finely serrate distally. Fixed finger with 2 rounded teeth on a single eminence proximally, another single tooth slightly distally followed by a very small tooth, and 1 larger tooth distally just before claw. Dactylus with 2 posteriorly directed teeth proximally, followed by 3 small, evenly spaced convexities of decreasing size distally.

Pereopods II–VII: Setae similar to those of other stages. Setal formula of pereopod II, (15,10,17,17). Short, terminal propodal spine of pereopods II–IV similar to that of other stages, strongly curved and serrate on both sides (Figure 55d). Long, terminal propodal spines of same legs bearing prominent teeth on pereopod II (Figure 55d), absent from pereopod III, and bearing finer teeth on pereopod IV. Pereopod VII bearing 14 short, smooth spines subterminally on propodus (Figure 55f).

Uropods: With 10 and 9 endopodal articles on left and right sides, respectively.

INTRASPECIFIC VARIATION.—*Variation in Body Length* (numbers of individuals considered are in parentheses): *Galathea* Sta. 726 (Gulf of Panama): preparatory female 1 (1), 6.6 mm; preparatory female 2 (1), 8.8 mm; copulatory female (6), 9.0 to 9.6 mm; copulatory male, chela type A (1), 9.1
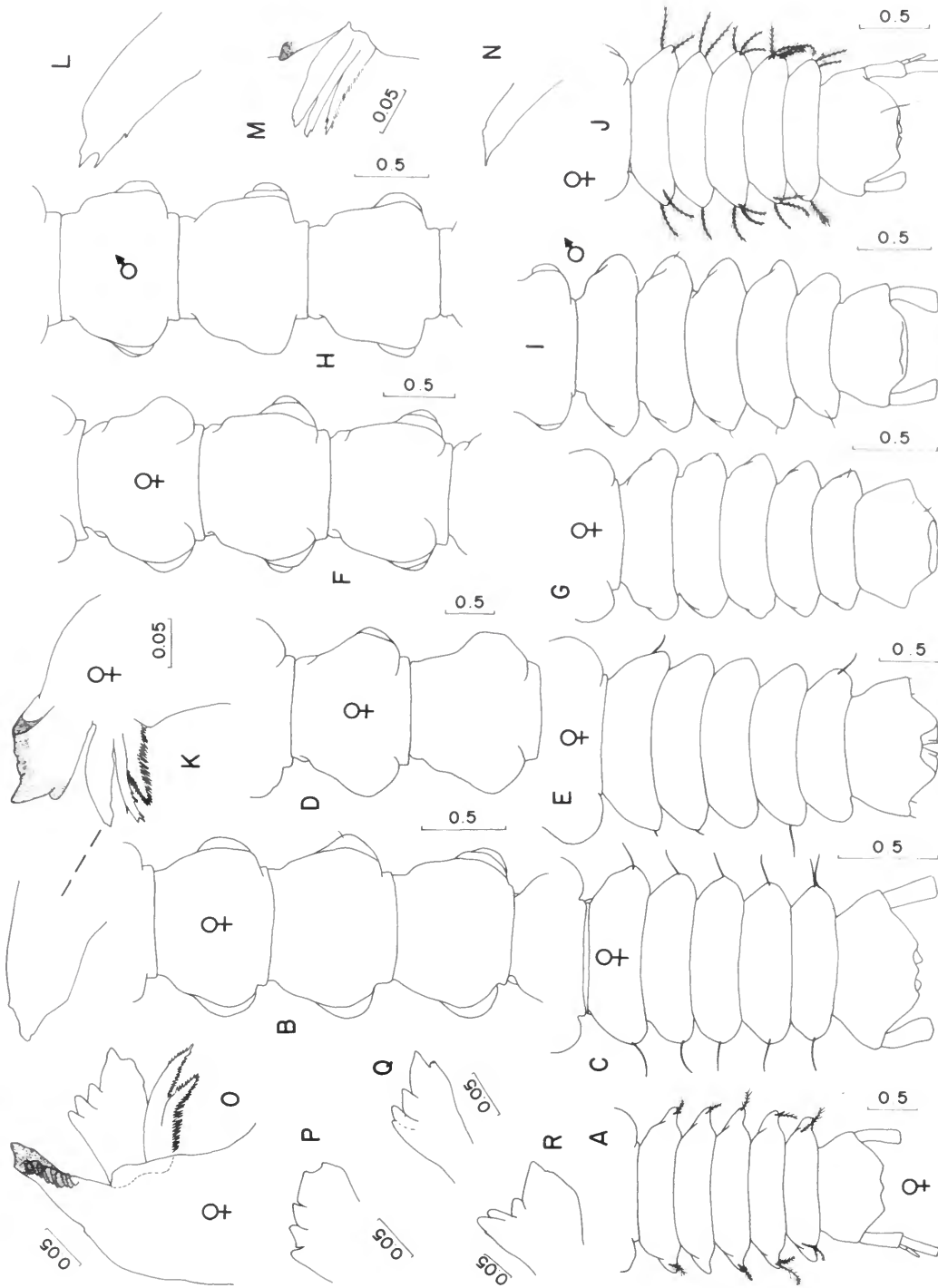
FIGURE 53.—*Neotanais armiger* Wolff: A, dorsal view of pleon, copulatory female from OSU Sta. 155; B, peronites 4–6 in dorsal view, copulatory female from OSU Sta. 155; C, pleon of same animal; D, peronites 4 and 5 of copulatory female from OSU Sta. 33; C, pleon of same animal; D, peronites 4 and 5 of copulatory female 1, *Galathea* Sta. 716; E, pleon of same animal; F, peronites 4–6 of a copulatory female from *Anton Bruun* Sta. 111; G, pleon of same animal; H, peronites 4–6 of a copulatory male from *Anton Bruun* Sta. 111; I, pleon of same animal; J, pleon of copulatory female from CMS Sta. 1597 (off Florida Keys); K, pars incisiva of right mandible, anterior view, female 33 from *Vema* Sta. 15–40; L, tip of third incisive spine of right mandible, female 34 from same station; M, incisive spines of right mandible, female 39 from *Vema* Sta. 17–7; N, tip of third incisive spine of preparatory male 46 from *Vema* Sta. 15–21 (Caribbean Sea); O, pars incisiva of left mandible, female 33; P, lacinia mobilis of left mandible, female 34 from *Vema* Sta. 15–40; Q, same, female 35 from *Vema* Sta. 15–40; R, same, female from OSU Sta. 155.

mm; copulatory male, chela type B (5), 9.7 to 10.8 mm. *Vema* Sta. 17–7 (off Chile): Juvenile? (1), 5.8 mm; preparatory female 2 (1), 7.2 mm; copulatory female (1), 8.3 mm; copulatory male (1), 9.0 mm.

Animals collected off Oregon (except for the copulatory female from OSU Sta. 155) were about half as large as equivalent stages of more southerly populations (see below). Copulatory males (6) from Peru and Chile varied from 6.1 to 9.1 mm in length. Specimens from the Atlantic and Gulf of Mexico were smaller than those from the Gulf of Panama (see below).
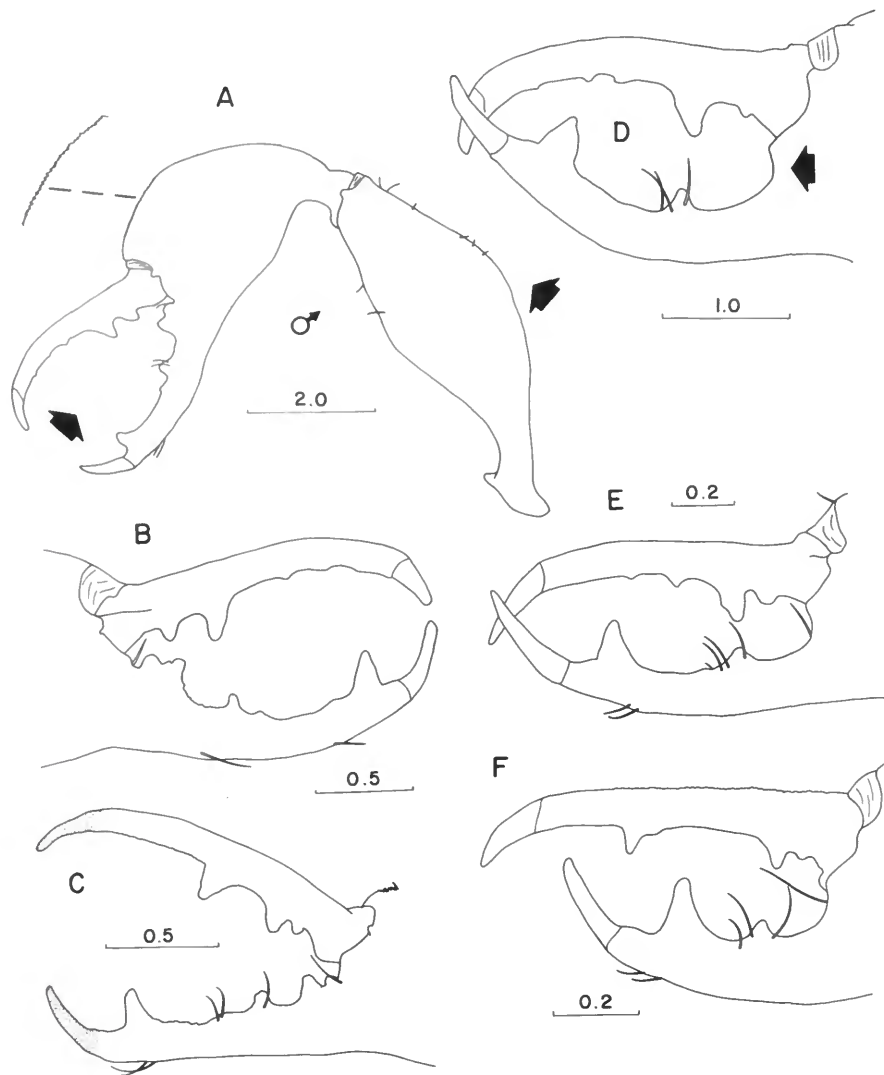
FIGURE 54.—*Neotanais armiger* Wolff: A, left cheliped of secondary copulatory male, allotype, *Galathea* Sta. 726; B, right chela of secondary copulatory male 31, *Vema* Sta. 15–39; C, left chela of secondary copulatory male from *Anton Bruun* Sta. 111; D, same, primary copulatory male 24 from *Galathea* Sta. 726; E, same, primary copulatory male 32 from *Vema* Sta. 15–39; F, same, copulatory male 31 from *Vema* Sta. 15–21 (Caribbean).
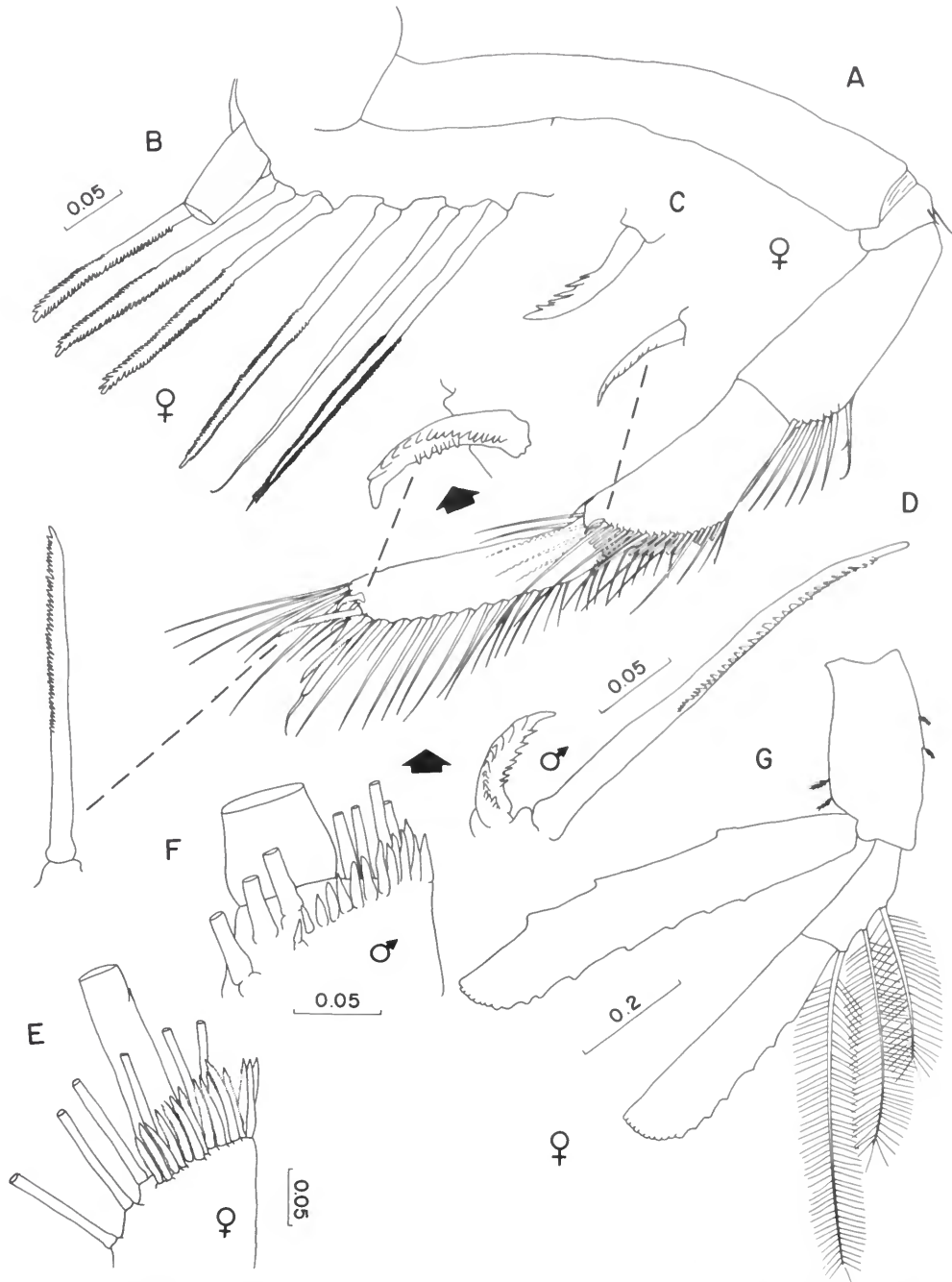
FIGURE 55.—*Neotanais armiger* Wolff: A, right pereopod II of female 33 from *Vema* Sta. 15–40; B, long, terminal propodal spines of pereopod II, female 39 from *Vema* Sta. 17–7; C, short, subterminal carpal spine of pereopod II, female from OSU Sta. 164; D, short and long, terminal propodal spines of left pereopod II, copulatory male allotype from *Galathea* Sta. 726; E, short, subterminal propodal spines of left pereopod VII, female 33 from *Vema* Sta. 15–40; I, same, of copulatory male, allotype.

Pacific Populations: The pleonal sternites vary in length but usually are long. Occasionally short examples have been noted (Figure 52c,d).

The long, terminal propodal spines of pereopod II usually are two in number; however, occasionally only one is found and, in some populations (e.g. at *Anton Bruun* Sta. 111), one-third to one-half of the animals have three, and occasionally four are found (Figure 55b). The long spines of pereopods II and III usually are present only singly or are absent. No correlation was observed between the number of these spines and the types of pleonal epimeres or other characters described below.

A major difference among the animals was in the shape of the pleonal epimeres in dorsal view. This difference was first noted among the animals from Oregon, one of which, a copulatory female from OSU AD 155, was very large (10.4 mm), heavily calcified, and bearing long epimeral extensions similar to those of the holotype (Figure 53a). The others were shorter (AD 33, copulatory female, 4.4 mm; AD 164, copulatory female, 5.4 mm; AD 118, ?juvenile, 5.8 mm; AD 163, manca 1, 1.8 mm, five juveniles, 2.9 to 3.3 mm, and a copulatory female, 5.2 mm). They also had much shorter pleonal epimeres (Figure 53c) and differently shaped pleotelsons. The setal formulae for pereopods II and VII are as follows: large copulatory female from AD 155, (15,12,20,22) and (6,14,13,11); small copulatory female from AD 33, (10,8,10,13) and (5,8,6,5); and copulatory female from AD 164, (8,6,10,10) and (7,7,6,4). The large female had a single anterolateral seta on either side of its carapace, whereas the others often had two such setae.

A similar difference in pleonal epimeral shape was noted all along the Pacific coast, some stations containing only animals with long epimeres, others with all short epimeres, and still others were mixed. Generally, the animals with short epimeres also were considerably smaller than the others, were less well calcified, and had slightly differently shaped pleotelson and pereonites (cf. Figures 51d–h, 52a–i). The dorsal relief of their pereonites was less pronounced, possibly due to differences in size and/or calcification. Two very large animals were noted with these characters differently shaped and with shorter pleonal sternites as well (copulatory female, 11.3 mm, and copulatory male, 11.4 mm, *Galathea* Sta. 716—Figures 52c; 53d,e).

The chelae of the copulatory males fell into three categories: (1) those of the largest males (body lengths 9.7 to 11.0 mm—Figure 54a,b); (2) those of smaller males (*Galathea* Sta. 726, length 9.1 mm, and *Vema* Sta. 15–39, length 7.1 mm—Figure 54d,e) with chelae types B and A of secondary and primary males respectively and found on males with long pleonal epimeres; and (3) those found on males with short epimeres. The latter type is assumed to be unique to such males (*Vema* Sta. 15–67, *Anton Bruun* Sta. 111, and *Eltanin* Stas. 40 and 75—Figure 54c). These males usually were small in comparison with the other males; however, one male with short epimeres had chela type B described above (body length 9.0 mm, from *Vema* Sta. 17–7 off Chile).

At first it seemed appropriate to erect a new species for those animals with short pleonal epimeres, short body length, and pereonites and pleotelsons differing from those of the holotype and allotype; however, in view of the very close similarity of other characters among these individuals—the decalcified and broken condition of many important specimens, the presence of one copulatory male with short pleonal epimeres but with chela type B, and the presence of the two very large animals (copulatory female, 11.3 mm, and copulatory male, 11..4 mm, both from *Galathea* Sta. 716) with short pleonal epimeres and sternites and other slight morphological differences—the situation has become so confused that even after a very extensive study it seems best for the present to retain them all within *Neotanais armiger*.

With the collection of additional materials, the situation may be clarified. That the animals with short pleonal epimeres are not variants in which the epimeral tips have been eroded is indicated by the presence of dorsolateral epimeral setae (which would have been lost in any such erosion, cf. Figure 53a,c) and by what appears to be a significant difference in the body sizes of the two groups when animals of equivalent age (stage) are compared. The argument that they are not geographic variants is based on the close proximity of the two types off Oregon and their sympatric occurrence at Central American stations.

In chela type A (primary copulatory males—Figure 54d,e) the propodal crest is finely serrate as in chela type B. The fixed finger bears only two teeth: one small tooth proximally and a much

larger one distally. The dactylus has a small proximal tooth followed by a much larger one which is followed, in turn, by two or three very small convexities (body lengths: *Galathea* Sta. 726, 9.1 mm, and *Vema* Sta. 15–39, 7.1 mm).

The third type of chela (animals with short pleonal epimeres—Figure 54c) is similar to that of the secondary male with long epimeres, but the midsection of the fixed finger is without distinct teeth and is irregular. The dactylus bears a single large, triangular tooth centrally, replacing the three small convexities found in the type A chela. This third type of chela would represent chela type B (secondary male) of the animals with short pleonal epimeres if these animals do in fact represent a distinct species. The body lengths of these males are as follows: *Anton Bruun* Sta. 111, 7.4 and 8.5 mm; *Eltanin* Sta. 40, 9.1 mm; and *Eltanin* Sta. 75, 6.1 mm.

Atlantic Specimens: Four specimens were examined from the Atlantic Ocean and ancillary waters: a copulatory female (7.6 mm) from CMS Sta. 1597, east of the Florida Keys at 598 m; a copulatory female (6.9 mm) from *Alaminos* Sta. 5, south of Alabama at 1550 to 1740 m; and a preparatory male (3.9 mm) and a copulatory male (5.7 mm) from *Vema* Sta. 15–21, on the Caribbean Slope of Panama at 938 m.

All of these individuals have short pleonal epimeres and their body lengths also are appropriately short compared to the holotype and allotype. The animals collected off Florida and Alabama share dorsal pereonite shape with most of the Pacific animals and have long pleonal sternal spines. The Panamanian animals more closely resemble the unusual animals at *Galathea* Sta. 716 (Figure 53D) in these characters but are, of course, much smaller.

The Florida and Alabama animals have three long, feathered setae on each pleonal epimere (Figure 53J). The Panamanian animals do not have these setae, but they may have been broken off. The female from Florida has the longest anterolateral keels on its carapace of any specimen examined, and it has three long anterolateral setae on each side of the carapace (Figure 51D). The other specimens have the following anterolateral setation on the left and right sides respectively: *Alaminos*, 2,1; preparatory male from Panama, 1,0; and copulatory male at the same station, 1,1.

The chelae of the Alabama animal and the

preparatory male from Panama have a slight convexity midway along the proximal area of the fixed finger, and proximal denticles are absent. The fixed finger of the Florida specimen is straight proximally and lacks such a convexity.

The depths at which these animals are found are relatively shallow, about 600 to 1700 m. In fact, this range includes one of the shallowest records for the family (see "Vertical Distribution" under "Ecology"). In addition, all of these collections of *Neotanais armiger* are shallower than any Pacific collection; however, other specimens—not available for examination but identified by Dr. Gilbert T. Rowe of the Woods Hole Oceanographic Institution—apparently were collected at 3375 m in the Gulf of Mexico west of Cuba.

Because these animals show such striking similarities to the Pacific populations and because of the impossibility of dividing the Pacific collections into more than one species, these specimens are here assigned to *Neotanais armiger*.

POSTMARSUPIAL DEVELOPMENT.—*Uropods*: The endopods contain four articles in mancas 1, seven in juveniles, and nine in preparatory and copulatory females and copulatory males. Occasionally 11 or 12 articles are present in the copulatory stages.

Pleopods: The terminal endopodal setae reach their full length, relative to article length, by the juvenile stage.

Male Gonopore Anlagen: Of 19 recognizable copulatory females with pereonite 7 present, only one specimen had visible gonopore anlagen, and these were very faint. This situation is in marked contrast to this instar in some species where the anlagen frequently are visible, or are visible on other female stages as well.

Male Oostegites: In addition to one juvenile from *Anton Bruun* Sta. 111 that bore a tiny oostegite on its left pereopod V, both copulatory males at that station bore small rudimentary oostegites on all pereopods II–V. The plates were about the size of those found on preparatory females 1. This is a very unusual circumstance (see p. 225 under "Development").

REMARKS.—*Neotanais armiger* was described briefly by Wolff (1956c) from specimens collected in the Pacific by the *Galathea* Expedition at two stations off Central America. Since then it has been collected in both the Atlantic and—in appreciable

numbers—the Pacific. Here, it is redescribed in detail and diagnoses are given.

This species is very difficult to understand in light of appreciable differences in the shapes of the pleonal epimeres and pleotelson. Most of the other differences among the specimens were minimal. Future work on larger collections at single stations may show that the animals with long pleonal epimeres and those with short epimeres are other species. In fact, *Neotanais armiger* actually may represent an *armiger* group of species, some members of which may be sympatric. The depth distribution of these animals apparently is very wide, but whether this is due solely to geographic varia-

TABLE 8.—*Examined material of* Neotanais armiger *Wolff*

Program or ship	Station no.	General location	Depth (meters)	Material	Pleonal epimeres (long or short)
PACIFIC					
Anton Bruun	111	Off Peru	3086–3202	2 Juv, 5 P♀1, 3 P♀2, 5 Cop ♀, 3 P♂, 2 Cop ♂, 3 fgmts.	Short
	113		5986–6134	1 P♀1, 1 fgmt.	Short
	157		3994–4364	1 Juv, 1 P♀1, 1 P♀2, 1 Cop ♀	Short
Eltanin	25	Off Colombia	2489	1 Ml, 1 P♀1	Short
	40	Off Peru	3404–3495	2 P♀1, 1 Cop ♂	Short
	75	Off Chile	1932–3142	1 Cop ♂	Short
Galathea	716	Off Costa Rica	3590	1 P♀1, 2 Cop ♀, 1 2°Cop ♂ (long pleonal epimeres), 1 Cop ♂ (short epimeres)	Long and short
	726	Gulf of Panama	3710	1 P♀1, 2 P♀2, 12 Cop ♀ (including holotype), 1 1°Cop ♂, 6 2°Cop ♂ (including allotype), 3 Cop ♂ fgmts.	Long
OSU	AD33	Off Oregon	2800	1 Cop ♀	Short
	AD118		2800	1 ?Juv	Short
	AD155		2840	1 Cop ♀	Long
	AD163		2400	1 Ml, 5 Juv, 1 Cop ♀	Short
	AD164		2400	1 Cop ♀	Short
Vema	15–39	Off Colombia	3859	1 1°Cop ♂, 1 2°Cop ♂	Long
	15–40		3700–3757	1 Ml, 3 Cop ♀	Long
	15–41	Off Panama	2270	2 unid. fgmts.	Long
	15–46	W of Costa Rica	3517–3528	1 2°Cop ♂	Long
	15–67	Off Peru	2816–2846	3 P♀1, 1 Cop ♂	Short
	17–2	Off Chile	4030–4036	1 fgmt.	Short
	17–7		3089–3279	1 ?Juv, 2 P♀2, 2 Cop ♀, 1 ?2°Cop ♂, 1 fgmt.	Short
ATLANTIC					
Alaminos	66–A–5, Sta. 5	S of Alabama	1550–1740	1 Cop ♀	Short
CMS	1597	E of Florida Keys	598	1 Cop ♀	Short
Vema	15–21	Caribbean slope of Panama	938	1 P♂, 1 Cop ♂	Short

tion cannot be determined at this time because of the limited number of specimens on hand from critical areas.

DISTRIBUTION.—*Neotanais armiger* has been collected from Oregon (45°N.) to Chile (40°S.) along the Pacific coasts of North and South America and in the Gulf of Mexico–Caribbean Sea area. Its known depth range in the former is from less than 2000 to over 6100 m and in the latter is from about 600 to 1740 m. More than one species may be included in this material (see above under "Intraspecific Variation" and "Remarks").

MATERIAL.—See Table 8.

LOCATION OF MATERIAL.—UCZM: *Galathea* collections including holotype. AMNH: *Vema* 15–21 (AMNH 14976); *Vema* 15–39 (AMNH 14977); *Vema* 15–40 (AMNH 14978); *Vema* 15–41 (AMNH 14979); *Vema* 15–46 (AMNH 14980); *Vema* 15–67 (AMNH 14981); *Vema* 17–2 (AMNH 14982); *Vema* 17–7 (AMNH 14983). NMNH: *Alaminos* 5 (USNM 143205); *Anton Bruun* 111 (USNM 143200); *Anton Bruun* 157 (USNM 143201); CMS 1597 (USNM 143206); *Eltanin* 40 (USNM 143207); *Eltanin* 75 (USNM 143208); OSU 33 (USNM 143202); OSU 155 (USNM 143203); OSU 163 (USNM 143204).

The *hastiger* Group of Species

This group comprises only two species, *Neotanais hastiger* and *N. tricarinatus*.

STAGES OTHER THAN COPULATORY MALE.—The cheliped is unique: the chela is shorter than usual, thus having a "fist-shaped" appearance. The propodal and dactylar teeth are rounded, variable in size and shape, and brown in coloration. The cheliped is borne generally perpendicular to the axis of the body when preserved, with the animal resembling a cross from above. A notch is present on either side of the carapace between the ocular lobe and the anterolateral keel.

Neotanais tricarinatus differs from *N. hastiger* in being only about half as large, in having its chelipedal coxae extending posterior to the rear margin of the carapace, and in having relatively long, feathered hairs on each pleonal epimere.

COPULATORY MALES.—Only one type of male is known for each species. The single male known for *Neotanais hastiger* is from the Bermuda slope, and there is reason to believe that this male may represent a third species in the group; therefore, only

the most general characters can be of use in distinguishing this group.

These males differ from other males in the nondimorphic characters listed above for other stages. In addition, the medial side of the chelipedal carpus bears one or more low, rounded protuberances and the ventral chelipedal carpal setae are slender and widely separated in contrast to every other copulatory male known.

The males of *Neotanais tricarinatus* differ from those of *N. hastiger* in the following characters: the carapace bears a single middorsal ridge and a midlateral ridge on either side running anteroposteriorly along the anterior half of the carapace. The chelipedal carpus is gradually and evenly curved rather than being bent at right angles. The dorsal propodal margin of the cheliped is turned upward distally rather than being straight.

Neotanais hastiger (Norman and Stebbing, 1886)

DIAGNOSES.—*Stages Other Than Copulatory Male:* *Chela "fist-shaped," very unusual; *carpus, propodus, and dactylus all very short and "stubby" in appearance; carpus with row of 7 to 12 dorsal setae in postjuvenile stages; *position of cheliped when preserved is characteristic, animal resembling a cross when viewed dorsally, chelipeds being held more or less perpendicular to long axis of body. *Pereonites 4–6 generally square or rectangular in dorsal view. *Pleonal epimeres rounded or slightly acute laterally; *sternites with prominent midventral spurs appearing triangular in lateral view. *Pleotelson relatively longer than in many species. *Carapace bearing a notch laterally on either side at forward end of anterolateral keels; 2 to 4 anterolateral setae present.

Copulatory Males: See "Description of Copulatory Male O," below.

DESCRIPTION OF PREPARATORY FEMALE 1 A (Gay Head–Bermuda Transect; WHOI B. Sta. 95).— *Body* (Figure 56A): 7.6 mm long and 6.8 times longer than wide.

Carapace (Figure 56A,D): 1.3 times longer than wide. Anterolateral keels and oblique furrows both
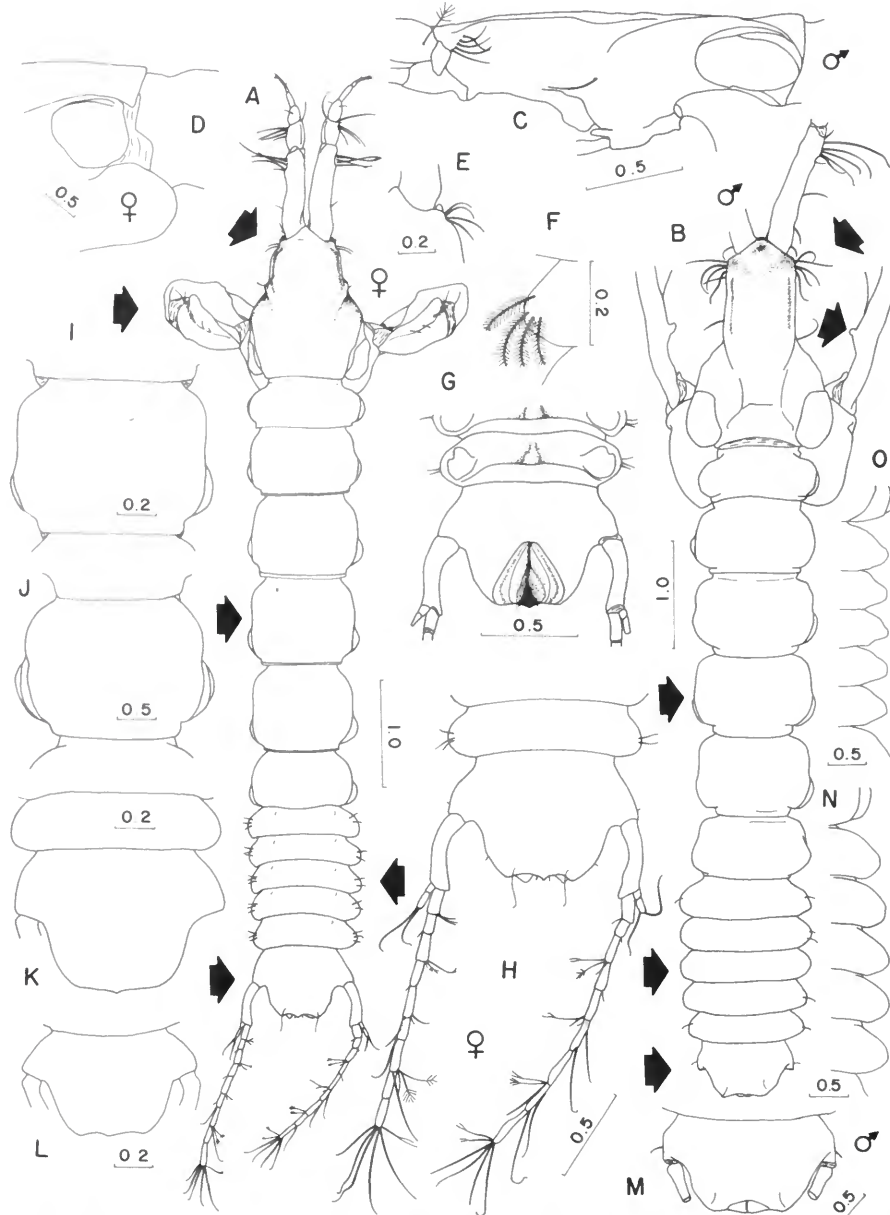
FIGURE 56.—*Neotanais hastiger* (Norman and Stebbing): A, dorsal view, preparatory female 1 A (described here), North America, WHOI B. Sta. 95; B, dorsal view, copulatory male O (described here), Bermuda, WHOI B. Sta. Ber. 7; C, lateral view of carapace, same animal; D, left lateral view, posterior area of carapace, preparatory female 2 N, same station; E, anterolateral setae of carapace, dorsal view, same animal; F, left lateral border of pleonite, same animal; G, pleonite 5 and pleotelson, ventral view, female A; H, same, including uropods, dorsal view; I, pereonite 5, dorsal view, female A; J, same, copulatory female described by Dollfus, Bay of Biscay; K, pleonite 5 and pleotelson, dorsal view, holotype; L, pleotelson, dorsal view, copulatory female F, Bay of Biscay, *Sarsia* Sta. 44; M, same, copulatory male O, Bermuda (see B); N, right side of pleonites, setae omitted, female A (see A); O, same, female F, Bay of Biscay.
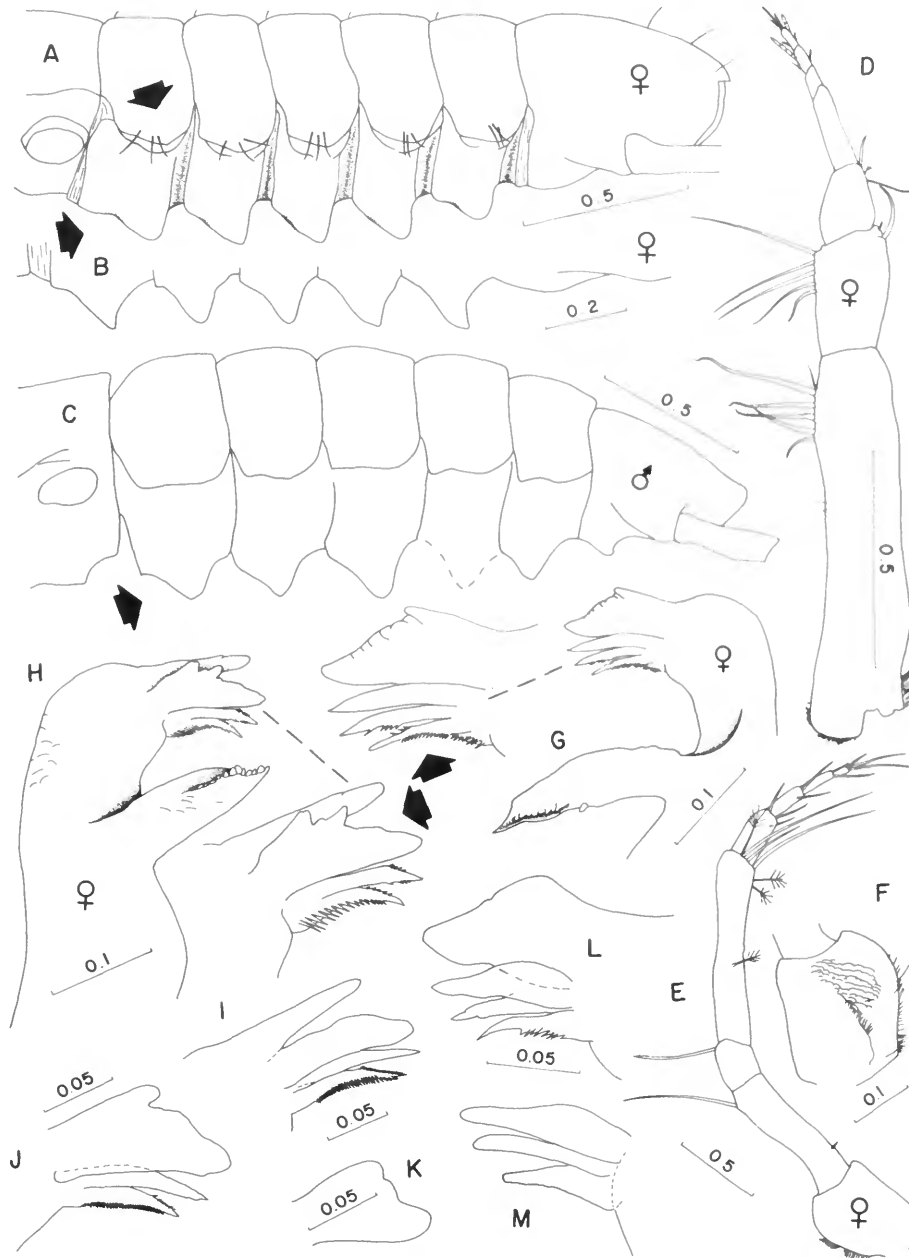
FIGURE 57.—*Neotanais hastiger* (Norman and Stebbing): A, pleon, lateral view, preparatory female 1 A, North America, WHOI B. Sta. 95; B, same, copulatory female F, Bay of Biscay, *Sarsia* Sta. 44; C, same, copulatory male O, Bermuda, WHOI B. Sta. Ber. 7; D, left first antenna, dorsal view, female A; E, left second antenna, ventral view, female A; F, first article of same appendage, dorsal view; G, right mandible, anterior view with enlargement of pars incisiva, female A; H, left mandible, female A; I, same, juvenile C, same station; J, pars incisiva, copulatory female D, same station; K, lacinia mobilis, left mandible, female F; L, pars incisiva, right mandible, same animal; M, incisive spines right mandible, preparatory female 2 N, Bermuda, WHOI B. Sta. Ber. 7.
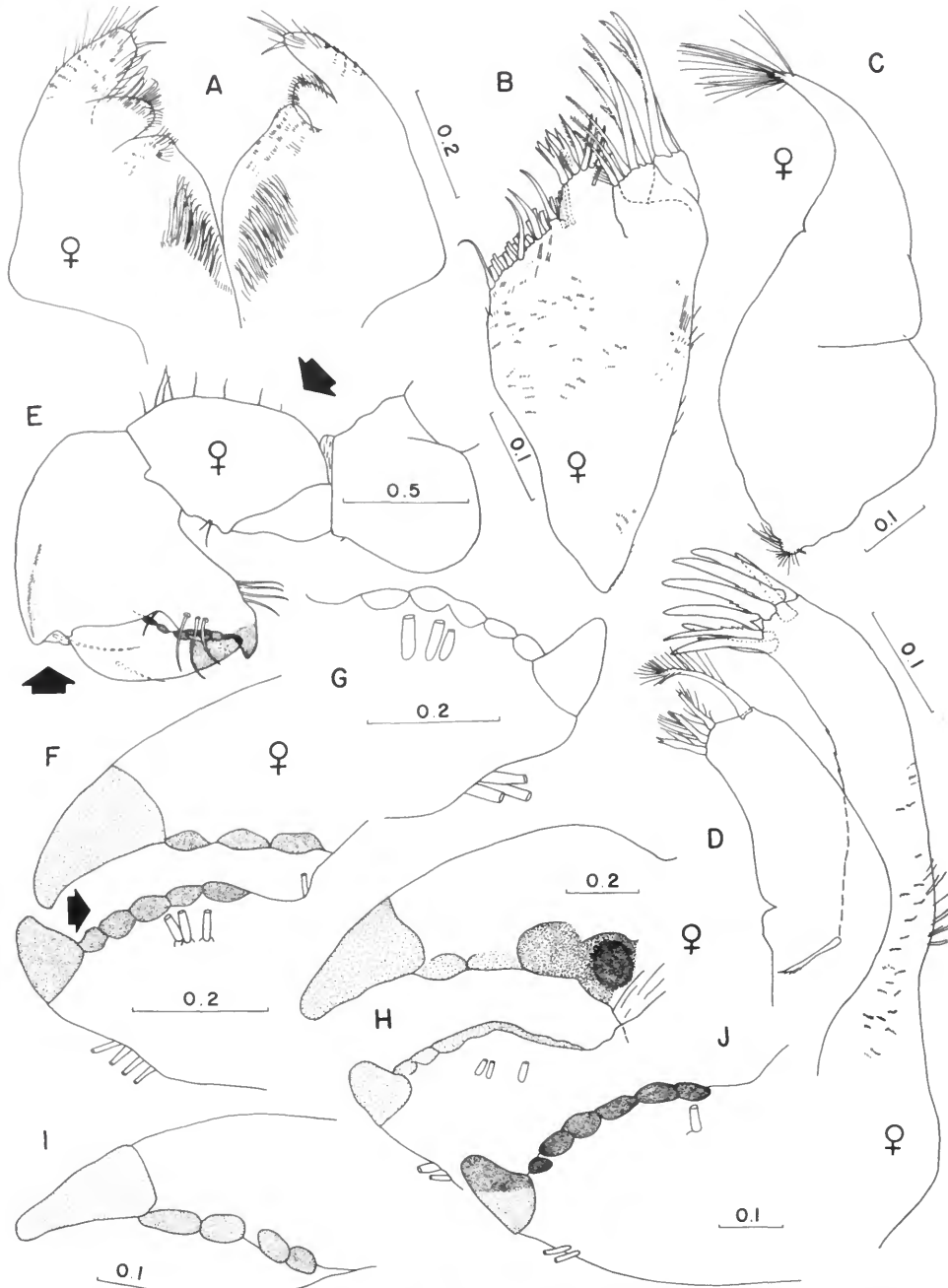
FIGURE 58.—*Neotanais hastiger* (Norman and Stebbing). A–F, Preparatory female 1 A described here, North America, WHOI B. Sta. 95: A, labium, posterior view; B, left second maxilla, posterior view; C, epignath; D, left first maxilla, posterior view; E, left cheliped; F, dentition of left chela. G, Fixed finger, right chela, preparatory female 2, holotype, Labrador Sea, *Valorous* Sta. 9. H, Left chela, preparatory female N, Bermuda, WHOI B. Sta. Ber. 7. I, Left chelipedal dactylus, copulatory female F, Bay of Biscay, *Sarsia* Sta. 44. J, Fixed finger, left chela, copulatory female G, Bay of Biscay, *Sarsia* Sta. 44.

prominent. Two anterolateral setae and one posterolateral seta present. Notch present in keel on each side of carapace over setae. Anterior margins of carapace on each side of rostrum concave in dorsal view; rostrum prominent.

Pereonites (Figure 56A,I): Pereonites 5 and 6 generally quadrangular with moderate expansions above pereopods. Pereonite 5, 1.2 times wider than long.

Pleonites (Figures 56A,G,H, 57A): Rounded and somewhat flared laterally; each epimere bearing 2 or 3 slender hairs of moderate length dorsally. Hairs apparently not feathered as in Bermudan female but with at least a few irregular setules visible under high magnification. Sternites expanded into blunt, posteriorly directed, midventral spurs. Sternites separated ventrally by relatively deep furrows.

Pleotelson (Figure 56A,G,H): Long in comparison to many species; width-length ratio, 1.4. Edges anterior to and posterior to uropods convex, a relatively prominent concavity lying on either side of median posterior prominence. A long, very fine hair located posteriorly on either side over these concavities.

First Antenna (Figure 57D): First article 4.2 times longer than wide.

Second Antenna: As in Figure 57E,F.

Right Mandible (Figure 57G): Third incisive spine sharply pointed, second spine only serrate for a short distance distally along inner side, and first spine similarly toothed on outer side but serrate along entire inner margin.

Left Mandible (Figure 57H): Incisive spines as on right side. Lacinia mobilis composed basically

of 2 large teeth and a long, pointed posterior lobe.

Labium: As in Figure 58A.

First Maxilla: As in Figure 58D.

Second Maxilla (Figure 58B): Fixed endite with 2 bifid terminal spines. Medial setal row with 21 apparently naked setae and 3 smooth, stout, pointed spines.

Maxilliped (Figure 59B): Setal formula of palp, (1,0,5+1,6,10). Five medial filter setae present on endite.

Epignath: As in Figure 58C.

Cheliped (Figure 58E,F): Carpus very short relative to propodus, only 0.6 times the length of the latter; bearing 8 dorsal setae. Fixed finger of chela with 5 low, rounded, brown teeth; proximal denticles absent, teeth taking up most of the length of the cutting edge; claw short, blunt, and brown. A cluster of 4 setae present ventrally; dorsolateral setae grouped together to form a cluster of 3. Dorsomedial propodal seta at articulation of dactylus unusually long. Medial dactylar seta with fine setules. Dactylus with 3 low, rounded, and smooth teeth; shorter than fixed finger. Chela resembles a clenched fist and is generally held more or less perpendicular to body when preserved.

Pereopods II–IV (Figure 59C,D): Short, terminal propodal spine slightly curved, very stout, and with 3 large teeth on one side and 9 smaller ones on the other. Long, terminal propodal spines not present. Setae moderately stout, tapered to fine points, and bearing fine but prominent setules. Setal formulae of pereopods II–IV, (4,4,8,7), (9,10,8,10), and (10,10,10,10). Proximal end of propodus of at least pereopods II and IV bearing a few large, ventrolateral serrations. Short, subterminal carpal spine slender, straight, and devoid of any armament (see Figure 59E).

Pereopods V–VII: Setal formulae, (9,7,7,9), (8,8,8,8), and (8,8,6,6) respectively. Dactyli of all 3 appendages fringed with very small terminal teeth (Figure 60D) continuing proximally and merging imperceptibly with more proximal lateral rows of denticles. Distal dactylar cleft very wide. Propodus of pereopod VII lacking short subterminal spines.

Pleopods (Figure 59L): With 8 terminal endopodal setae; seta length 1.7 times that of endopod. Setal formula, (2,1) (3,8,7) (0,2;0,8,8). Endopod with a distinct row of terminal setae.

Uropods (Figure 56A,H): Each with 9 endopodal articles. Exopods of left and right sides 1.1 and 0.9

FIGURE 59.—*Neotanais hastiger* (Norman and Stebbing): A, left cheliped with enlargements of fingers, copulatory male O, Bermuda, WHOI B. Sta. Ber. 7; B, left maxilliped, posterior view, with enlargements of terminal palpal setae and endite (anterior oblique view), preparatory female 1 A, North America, WHOI B. Sta. 95; C, cuticular surface, showing pattern of cuticular prisms, basis of pereopod, same animal; D, left pereopod II with enlargement of short, terminal propodal spine, posterior oblique view, same animal; E, short, subterminal carpal spine, copulatory female D, same station; F, same, preparatory female 2 E, Bay of Biscay, *Sarsia* Sta. 44; G, second distal anterior seta, propodus, preparatory female 2 N, Bermuda, WHOI B. Sta. Ber. 7; H, same seta, female E; I, short, terminal propodal spine, female D; J, same spine, female E; K, propodus, right pereopod VII, posterior view, copulatory female G, Bay of Biscay, *Sarsia* Sta. 44; L, left pleopod, anterior view, female A.

times longer, respectively, than first endopodal article.

DESCRIPTION OF COPULATORY MALE O (Bermuda Slope; WHOI B. Sta. Ber. 7).—This is the only known copulatory male of the species. Caution should be exercised in using this description for comparative purposes because the Bermuda female differs from North American populations (as well as from others), and it can be assumed that the male varies as well (see "Intraspecific Variation," below).

Body (Figure 56B): 8.1 mm long; width-length ratio, 6.0.

Carapace (Figure 56B,C): Rostrum blunt and anterior border almost straight on either side. Keels straight and parallel, leading into deep oblique furrows posteromedially. Anterolateral setae 5 in number, posterolateral seta single. Respiratory chambers and chelipedal coxae greatly inflated laterally in dorsal view.

Pereonites: Pereonites 3–7 rectangular in dorsal view.

Pleonites (Figures 56A, 57C): Generally rounded laterally and bearing one or two setae without setules. Sternites similar to described female midventrally.

Pleotelson (Figures 56A,M, 57C): Appearing considerably shorter and more angular than that of described female and bearing a low midventral prominence anteriorly.

First Antenna: First article 4.8 times longer than wide.

Cheliped (Figures 56B, 59A): Carpus strongly bent proximally and bearing a row of about 9 very small dorsal setae, 2 slender and very widely separated ventral setae, and a sizable medial protuberance at level of bend. Propodus straight dorsally with proximal two-thirds forming an irregularly edged keel. Fixed finger about as long as dactylus and bearing a large tooth proximally and several low irregularities on grasping surface beyond. Dactylus with a very small, proximal tooth and an extremely large, triangular distal tooth. Fingers neither twisted nor bent.

Pereopods II–VII: Setal formula of pereopod II, (5,3,7,5). Long, terminal propodal spines of pereopods II–IV absent. Short, terminal propodal spine of pereopods II–IV and short, subterminal carpal spine of pereopod II both short, slender, and apparently naked or with only very fine setules.

Propodus of pereopod VII bearing row of 8 short, prominently serrate, subterminal spines. Dactylar spines of pereopods II–IV long, slender, and bent at tips. Dactyli of pereopods V–VII all bearing very fine terminal teeth (see Figure 60c).

Uropods: Each with 9 endopodal articles.

INTRASPECIFIC VARIATION.—*Stages Other Than Copulatory Male*: In addition to the usual intrapopulational variations expected in *Neotanais*, noticeable and consistent differences were observed among the six populations of which representatives were available for study. These differences are described and intraspecific relationships are summarized here.

Holotype, Preparatory Female 2 (Labrador Sea): This animal is almost identical with the described female A from the Gay Head–Bermuda Transect. The pleotelson (Figure 56K) and the dental arrangement on the chelipedal propodus (Figure 58G) are slightly different.

The following are additions or corrections to the description given by Norman and Stebbing (1886). The body length from rostrum to tip of pleotelson is 7.8 mm and not 5 mm as published. The carapace is illustrated very poorly in the original description and closely resembles Figure 56A except that there are three anterolateral setae on either side. Norman and Stebbing correctly observed that the large, toothed terminal spines are absent on the propodi of pereopods II–IV. Short terminal spines on the same articles are similar to Figure 59D (enlargement) and the subterminal carpal spine of pereopod II resembles Figure 59E.

Norman and Stebbing do not mention a row of short propodal spines on pereopod VII, and these legs could not be examined. The dactyli of the posterior pereopods are not unique as suggested by these workers but are typical of the genus.

Other Populations: Following are representative body lengths (number of animals considered indicated in parentheses). WHOI B. Sta. 95: juveniles (2), 4.7 and 5.2 mm; copulatory female (1), 9.6 mm. WHOI B. Sta. 85: preparatory female 1 (1), 6.7 mm. *Sarsia* Sta. 44: manca 2 (2), 3.9 and 4.0 mm; preparatory female 1 (1), 4.9 mm; preparatory female 2 (2), 7.3 and 7.6 mm; copulatory female (2), 7.1 and 7.4 mm. WHOI B. Sta. Ber. 7: preparatory female 2 (1), 7.1 mm; copulatory male (1), 8.1 mm.

The long anterolateral and posterolateral setae

on the carapace are, respectively, 4 or 5 and 1 in number in the Bermudan specimens (Figure 56B,E) as contrasted with 2 and 1 for North American Slope populations (Figure 56A). The specimen collected by the *Noratlante* in the Bay of Biscay exactly resembles the Bermudan population in this character.

The pereonites (Figure 56I,J) of the animals collected off North America and Bermuda were more nearly quadrangular in dorsal view than those from Europe and Africa. The latter appeared to be relatively wider. This difference, not reflected in width-length ratio, is due to the configuration of the anterior and posterior areas of the pereonites.

The pleonites of some European specimens (Bay of Biscay) have more expanded and flared epimeres in dorsal view than do western North Atlantic populations (Figure 56H,N,O). The Bermudan female has at least three strikingly long and heavily feathered hairs or setae on each epimere (Figure 56F), whereas in North American specimens they appear shorter and have few setules (Figure 56H; but see Bermudan male, Figure 56B). The midventral spurs vary, some being relatively blunt and others pointed (Figure 57A,B). One specimen from the Bay of Biscay has midventral spines of appreciable length.

The pleotelson (Figure 56H,K,L) usually appears shorter with respect to width in dorsal view in specimens from European populations than in those animals from the North American Slope and Bermuda.

In female C (North America) the two proximal incisive spines of the right mandible are serrate on both sides of the tip only (Figure 57G,L,M); female F (Bay of Biscay) has a slightly irregularly tipped second spine and the first spine bears teeth only proximally on the inner side.

The number of setae in the medial row of the second maxilla varies from 18 to 22 in three individuals examined, but the number was 33 in female F (Bay of Biscay), a remarkable difference. In no case were setules observed on these setae. Stout spines associated with this row were two or three in number, sometimes on the same animal.

See Figure 58F–J for the variation in number, size, shape, location, and color of propodal and dactylar teeth on the chela. The variation illustrated is the maximum encountered and many animals showed much less variation. The dactylus

is slightly longer than the propodus in the female from Bermuda.

No notable variations in numbers of carpal and propodal setae were observed for pereopods II–VII. The short, terminal propodal spines of pereopods II–IV vary considerably in shape (Figure 59D,I,J) but are always prominently toothed. The row of short, subterminal propodal spines on pereopod VII is absent from North American populations but present in populations from the Bay of Biscay (Figure 59K) and Bermuda. Long, terminal propodal spines are misssing from all populations investigated. Short, subterminal carpal spines of pereopods II are always naked; however, in the European populations they are more slender than in others (Figure 59E,F). The anterior propodal setae of pereopods II–IV were considerably more bluntly tipped in the Bermudan female than in any other population (Figure 59G,H).

The dactyli of pereopods V–VII exhibit interesting differences. In all animals examined from North American populations, the dentition is the same as for female A above: all three dactyli have very fine teeth (Figure 60D). Specimens from the Bay of Biscay have relatively large teeth on all three pereopods with some variation among them (Figure 60E,F). Female N from Bermuda has coarse teeth on the dactyli of pereopods V and VI, whereas fine teeth are present on pereopod VII (Figure 60A–C). (Copulatory male O from Bermuda, however, has fine teeth on all of these dactyli.)

In summary, there are various combinations of characters shared among the six populations sampled. The Bermuda Slope and Biscay populations shared the presence of a row of short propodal spines on pereopod VII. North American animals and *Neotanais tricarinatus* (q.v.) lack such a row. All animals from the western North Atlantic have relatively square pereonites in dorsal view, whereas the more anteriorly tapered shape is shared by Biscay and West African populations (and *Neotanais tricarinatus*). Western Atlantic populations have truly blunt pleonal epimeres, whereas in Biscay and African animals these structures are slightly attenuated.

The presence of these overlapping combinations of morphologic features shared among the populations and the limited sample size make it difficult to recognize specific differences, if present, among these populations.
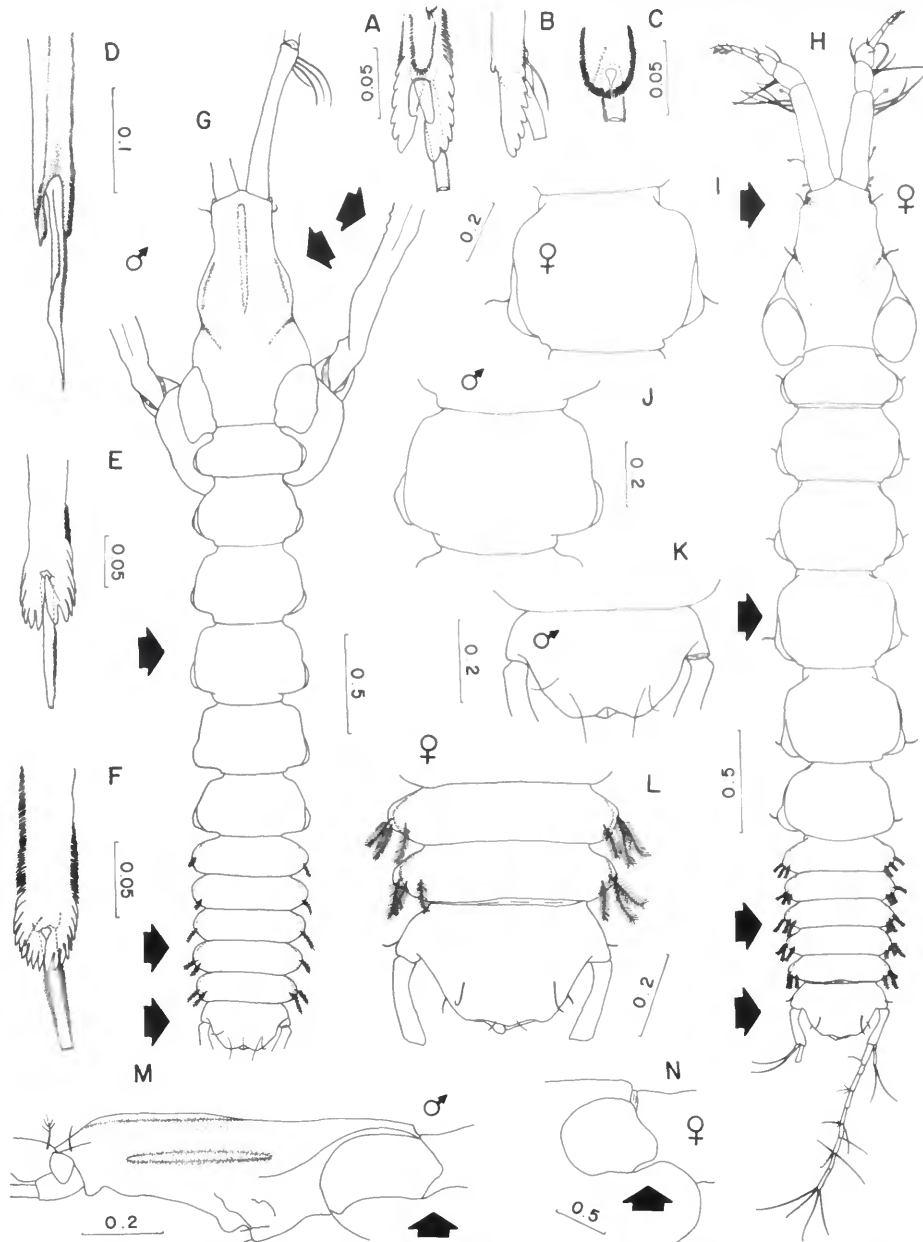
FIGURE 60.—A–F, *Neotanais hastiger* (Norman and Stebbing): A, dactylus, pereopod V, dorsal view, preparatory female 2, Bermuda, WHOI B. Sta. Ber. 7; B, same, lateral view, same scale; C, same, pereopod VII, dorsal view, same animal; D, same, pereopod V, ventral oblique view, preparatory female 1 A, North America, WHOI B. Sta. 95; E, same, dorsal view, preparatory female 2 E, Bay of Biscay, *Sarsia* Sta. 44; F, same, pereopod VII, copulatory female G, same station. G–N, *Neotanais tricarinatus,* new species (all from WHOI B. Sta. 169 off Brazil): G, dorsal view, copulatory male, allotype; H, dorsal view, copulatory female, holotype; I, dorsal view, pereonite 5, holotype; J, same, allotype; K, dorsal view of pleotelson, allotype; L, dorsal view of pleonites 4 and 5 and pleotelson, holotype; M, lateral view of carapace, allotype; N, lateral view, posterior area of carapace, holotype.

The Bermudan female differs from North American speicmens mainly in the dentition of its chelae; the presence of a row of short, subterminal propodal spines on pereopod VII; the number and length of anterolateral setae on the carapace; and the feathering of its pleonal epimeral setae. The anterior propodal setae of pereopods II–IV are bluntly tipped in the Bermudan female, whereas they are pointed in North American animals (and all others). These are considerable differences for populations separated by only a few hundred miles, and the Bermudan population eventually may be determined to be distinct.

The single animal from West Africa is almost certainly conspecific with the European populations with which it was most similar in examinable characters: pereonite and pleonite shape and midventral configuration of the pleotelson; the dactylus of the chela bears four round teeth; and the propodus has five low, slightly raised, round teeth. In dorsal view, however, the pleotelson was most similar to the North American populations. The dactyli on pereopods V and VI had coarse teeth. The carapace and the pereopods VII were missing, preventing comparison of these structures.

The European specimens differ from North American populations most significantly in the presence of a row of short, subterminal propodal spines on pereopod VII. The populations on the North American Continental Slope are almost identical with the holotype population near Greenland. If the eastern Atlantic populations are later determined to represent a distinct species, the name *Neotanais edwardsi* will be reinstated for them with the *Travailleur* specimen as the holotype.

POSTMARSUPIAL DEVELOPMENT.—*Male Gonopore Anlagen*: Of the 13 specimens of this species examined (excluding mancas and copulatory males), three had evidence of male gonopore anlagen as clear, decalcified spots. These were a copulatory female, a preparatory female 1, and a preparatory female 2. In *Neotanais*, preparatory females infrequently display these anlagen so clearly.

Uropods: Mancas 1 have four endopodal articles; mancas 2, six; juveniles, seven; and copulatory males and females, nine.

Pleopods: The pleopods continue to increase in number of terminal endopodal setae from five in the juveniles (B and C, WHOI B. Sta. 95) to eight in the preparatory females 1 (A, same station), to

12 in the copulatory female (D, same station), the largest number observed. The ratio of terminal setal length to endopodal length remains about the same through development (juveniles B and C, 1.7 and 2.0 respectively; preparatory female 1 A, 1.7; copulatory female D, 1.7). The ratios of preparatory female 2 N and copulatory male O, WHOI B. Sta. Ber. 7, were 1.9 and 1.7 respectively.

REMARKS.—After the original description of this species by Norman and Stebbing (1886), a specimen of *Neotanais hastiger* collected by the *Travailleur* in the Bay of Biscay was described by Dollfus (1898) as *N. edwardsi*. In addition to adding to confusion in the taxonomic literature, the description by Dollfus, including figures, is totally inadequate and bears little resemblance to the specimen described.

Dollfus states that two males were collected on 24 July 1880 in the Gulf of Gascony (Bay of Biscay) from a muddy bottom at a depth of 1960 m. He gives the location as 43°39'N., 50°48'W. In fact, the specimen he described is a preparatory female 2 with large rudimentary oostegites. The second specimen, also labeled as a type, is not a member of this species. I have assigned it, as well as a third specimen (see p. 28), to *Neotanais laevispinosus*, also erected by Norman and Stebbing (1886).

Among other data, the museum label indicating the "type" specimen gives the following information: No. 10, 16 July, 1910 m, long. 5°52'W.; hence, the published description and the museum label do not agree on date or place of collection. In his official reports on the 1880 cruise of the *Travailleur*, M. A. Milne–Edwards (1882a:126; 1882b, cruise track) gives the following information: 26 July 1880, dredge No. 10, lat. 43°39.05'N., long. 5°48.00'W., off Santana, Spain, at 1960 m on a muddy bottom.

In his description, Dollfus states that the ocular lobes are pigmented. In fact, they are not pigmented and are similar to all other known species of the Neotanaidae. Dollfus states that the length of the "holotype" is 9 mm. In actuality, the length is 7.6 mm.

The species is redescribed here in detail, and a description of a copulatory male is presented for the first time. A diagnosis of the stages other than those of copulatory males is presented together with an analysis of the geographic variability of the species. A diagnosis of the copulatory males must

TABLE 9.—*Examined material of* Neotanais hastiger *(Norman and Stebbing)*

Program or ship	Station no.	General location	Depth (meters)	Material
		WESTERN ATLANTIC		
WHOI Benthic	85	Gay Head–Bermuda Transect	3834	1 P♀1
	95		3753	2 Juv, 1 P♀1, 1 Cop ♀
	Ber. 7		2500	1 P♀2, 1 Cop ♂
Noratlante	019, E003	E of Labrador	4120	2 Juv, 1 P♀2
	026, E004		3680	1 M2, 1 Juv, 1 P♀2
	042, E006	Labrador Sea	3430	2 M1, 1 P♀1, 1 P♀2, 1 Cop ♀
Valorous	9	Labrador Sea SW of Greenland	3200	1 P♀2 (holotype)
		EASTERN ATLANTIC		
WHOI Benthic	146	Off Guinea, West Africa	2842–2891	1 P♂
Noratlante	109, B015	Bay of Biscay, NW of Santander, Spain	1856	1 Cop ♀
Sarsia	33	Bay of Biscay, off Spain	1784	1 M1
	44		1739	2 M2, 2 P♀1, 2 P♀2, 2 Cop ♀
Travailleur	Dredge 10	Bay of Biscay, off Spain (Gulf of Gascony)	1960	1 P♀2 (Dollfus holotype of *N. edwardsi*)

await collection of additional specimens from continental populations for comparison with the single male known from Bermuda.

DISTRIBUTION.—*Neotanais hastiger* is known from the western Atlantic, including the Bermuda Slope, from depths of 2500 to more than 4100 m. In the eastern Atlantic it has been collected in the Bay of Biscay from about 1740 to 1960 m, and off West Africa from about 2840 to 2900 m.

MATERIAL.—See Table 9.

LOCATION OF MATERIAL.—BMNH: holotype, *Valorous*. FNMNH: *Travailleur* collection. NMNH: *Noratlante* 019, E003 (USNM 143212); *Noratlante* 026, E0004 (USNM 143213); *Noratlante* 042, E006, (USNM 143214); *Noratlante* 109, B015 (USNM 143215); *Sarsia* 33 (USNM 143216); *Sarsia* 44 (USNM 143217); WHOI 95 (USNM 143209; WHOI Ber. 7 (USNM 143210); WHOI 146 (USNM 143211).

Neotanais tricarinatus, new species

FIGURES 60–62, *100*

DIAGNOSES.—*Stages Other Than Copulatory Male:* *Chela very broad, fixed finger short with short distal claw and bearing 4 irregular teeth of varying shapes usually preceded proximally by a large protuberance on cutting edge; *dactylus with 3 low, rounded, brown teeth distally, each separated

from the next; carpus of cheliped short and bearing about 6 relatively long, dorsal hairs; merus proportionately larger than in other species; *chelipeds held almost perpendicular to long axis of body when preserved and resembling a cross in dorsal view. Carapace with low rostrum; *a notch present on either side over ocular lobe just forward of anterolateral keels; 1 relatively large anterolateral seta and posterolateral seta present; *chelipedal coxae extending caudad to posterior edge of carapace. Pereonites wider than long as seen from above, with sides curving anteromedially relatively abruptly in pereonites 3–7. Pleonites flared laterally and bearing about 3 long, feathered epimeral setae; *sternites elongated ventrally into large, blunt, posteriorly directed spurs. *Pleotelson relatively short, sides posterior to uropods almost straight; bearing a midventral protuberance anteriorly. Uropodal exopods slightly longer than first endopodal article. Row of short, subterminal propodal spines on pereopod VII absent. Dactylar spines of pereopods II–IV slender, bent at tip, and about one-third as long as article.

Copulatory Male (only one type known): *Carapace unique in having a large midlateral keel located along each of its sides and another middorsal keel extending from just behind rostral area to level of moderately deep, oblique furrows; *respiratory chambers moderately and chelipedal coxae greatly expanded, the latter extending caudad to

posterior margin of carapace; rostrum very low. *Chelipedal carpus long, slender, and evenly arched; propodus with straight dorsal edge, upturned distally, and thin, frayed, and irregular proximally; *fixed finger less than half as long as dactylus; *dentition as in Figure 61A–C; *proximal two-thirds of dactylus bearing lateral keel. Pereonites more pronouncedly rectangular in dorsal view than other stages.

DESCRIPTION OF COPULATORY FEMALE HOLOTYPE (WHOI B. Sta. 169).—*Body* (Figure 60H): 4.4 mm long and 5.8 times longer than wide.

Carapace (Figure 60H,N): 1.3 times longer than wide. Rostrum low in dorsal view; anterolateral keels truncated anteriorly and beginning behind a notch in carapace over single anterolateral seta; 1 posterolateral seta present. Oblique furrows shallow; respiratory chambers only slightly developed but chelipedal coxae very pronounced in dorsal view, extending caudad beyond posterior margin of carapace.

Pereonites (Figure 60H,I): Wider than long in dorsal view, area over pereopods widest; sides bending inward abruptly anteriorly in pereonites 4–7 as seen from above. Single pereopodal coxal setae visible from above.

Pleonites (Figures 60H, 61D): Markedly flared laterally; each epimere bearing about 3 feathered hairs dorsally. Pleonite 1 slightly wider than pleonite 5. Sternites elongated into large, bluntly tipped, posteriorly directed, midventral spurs.

Pleotelson (Figures 60H,L, 61D): Short, width-length ratio, 1.6. Sides almost straight posterior to uropods; median prominence on posterior margin low and wide in dorsal view. Dorsal hairs much thicker than in other species. A midventral protuberance with a nearly vertical posterior border in lateral view is present anteriorly.

First Antenna: First article 4.0 times longer than wide.

Right Mandible: Lost. Two other specimens had incisive spines 1 and 2 serrate on both sides; third spine naked, sharply pointed (see Figure 61H).

Left Mandible (Figure 61G): Incisive spines as in right mandible. Lacinia mobilis unusual (all 3 of the compared specimens agree) in having large lobe deeply cleft into 2 long lobes directed away from the other 3 teeth.

Second Maxilla: Two bifid spines present on fixed endite; medial setal row with 18 setae and 2 spines.

Cheliped (Figure 62A,B): Carpus about 0.6 times length of propodus and bearing 5 long dorsal setae. Propodus with a large protuberance proximally on fixed finger followed by 4 brown, irregularly tipped teeth; these structures occupying almost entire length of finger. Propodal setae heavy and long. Dactylus bearing 3 rounded, brown lobes ("teeth") of increasing size centrally along cutting edge. Distal claw very large, reaching from last tooth to end of article.

Pereopods II–VII (Figure 62D–G): Setal formula of pereopod II, (5,3,5,4). Carpal and propodal setae long but relatively thick and bearing fine setules of moderate length. Long, terminal propodal spines of pereopods II–IV absent. Short, terminal propodal spine on same legs curved distally and bearing 3 or 4 large teeth. Short, subterminal carpal spine of pereopod II slender, needle-like, and naked. Dactylus bearing very long terminal spine, curved distally, and 0.3 times the length of dactylus. Pereopod VII lacking row of short, subterminal spines on propodus.

Pleopods (Figure 62J,K): Setal formula, (2,1) (3,5,5) (0,2;0,5,5); with distinct row of terminal endopodal setae.

Uropods (Figure 60H): Nine articles in each endopod. Exopod 1.1 times the length of first endopodal article.

DESCRIPTION OF COPULATORY MALE ALLOTYPE (WHOI B. Sta. 169).—*Body* (Figure 60G): 4.6 mm long and 6.3 times longer than wide.

Carapace (Figure 60G,M): Rostrum very low in dorsal view; a single anterolateral seta present on each side. Respiratory chambers not greatly expanded but chelipedal coxae prominent in dorsal view and extending posteriorly beyond rear margin of carapace; oblique furrows of appreciable depth. Three extraordinary keels present anteriorly: a midlateral keel on either side and a third keel extending upward middorsally and reaching from just behind rostrum to a level even with ends of lateral keels just anterior to oblique furrows.

Pereonites (Figure 60G,J): Appearing rectangular, with sides turning abruptly anteromedially in dorsal view in pereonites 4–7.

Pleonites (Figures 60G, 61F): Flared laterally and bearing 1 or 2 long, feathered dorsal hairs on each epimere. One stout dorsal hair located anteriorly
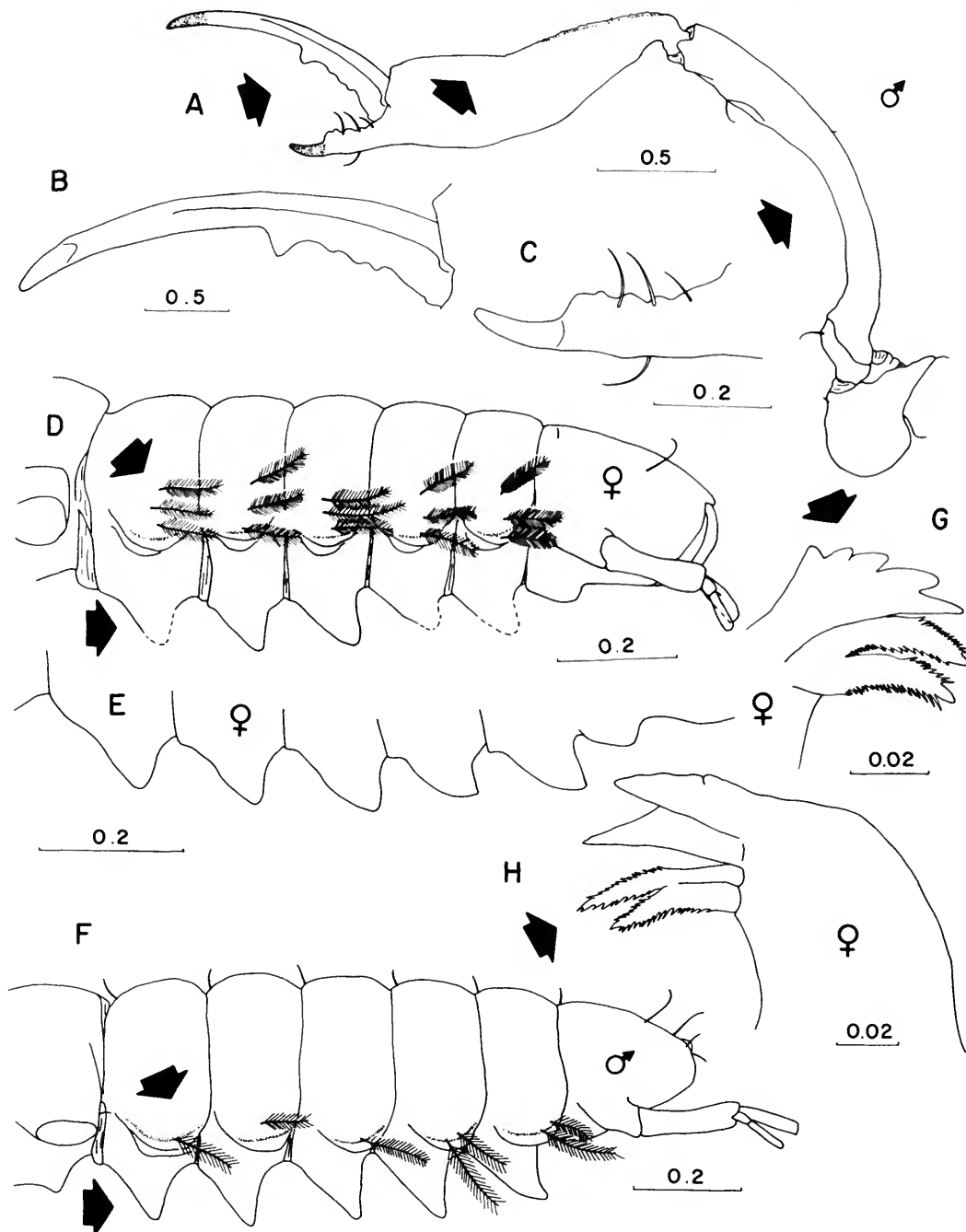
FIGURE 61.—*Neotanais tricarinatus*, new species (all from WHOI B. Sta. 169 off Brazil): A, left cheliped, copulatory male, allotype; B, same, dactylus; C, fixed finger, same; D, pleon, lateral view, copulatory female, holotype; E, same, preparatory female 2 BC; F, same, allotype; G, pars incisiva, left mandible, anterior view, holotype; H, same, right mandible, another female.
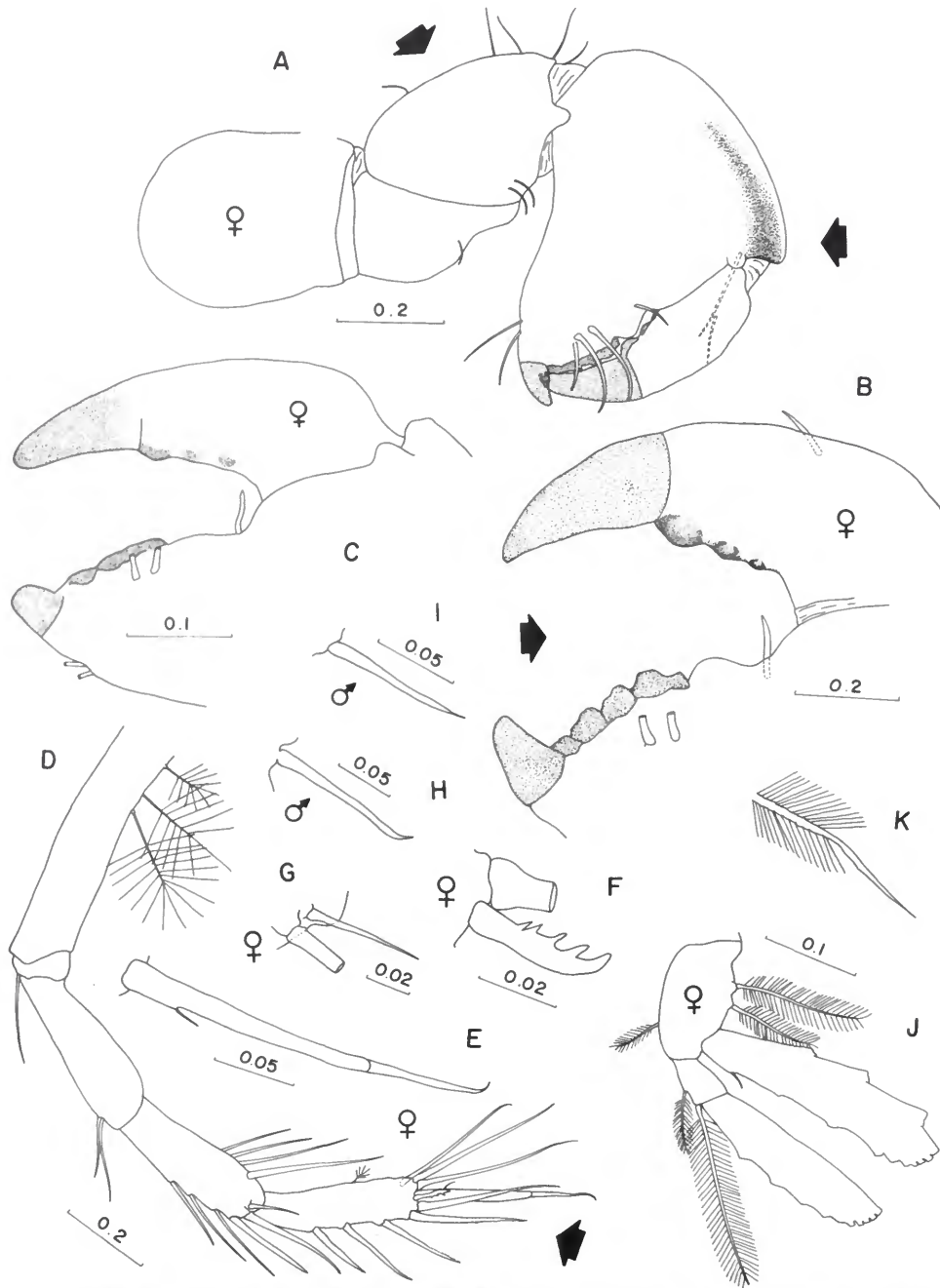
FIGURE 62.—*Neotanais tricarinatus*, new species (all from WHOI B. Sta. 169 off Brazil): A, right cheliped, copulatory female, holotype; B, left chela, holotype; C, same, another female; D, left pereopod II, anterior oblique view, holotype; E, dactylus and spine, pereopod II, holotype; F, short, terminal propodal spine, pereopod II, posterior view, holotype; G, short, subterminal carpal spine, pereopod II, dorsal oblique view, holotype; H, short, terminal propodal spine, pereopod II, allotype; I, short, subterminal carpal spine, pereopod II, allotype; J, right pleopod, anterior view, holotype; K, tip of medial endopodal seta, same pleopod.

on each pleonite. Sternites elongated into long midventral spurs as in other stages but longer and more pointed.

Pleotelson (Figure 60G,K): Similar to that of other stages but with a more prominent angle along sides posterior to uropods in dorsal view.

First Antenna: First article 6.6 times longer than wide.

Cheliped (Figure 61A–C): Carpus long, gently curved, and bearing a single seta of moderate size ventrally and a very small seta dorsally. Propodus bent upward distally; dorsal crest straight, with irregular margin, extending along proximal half of dorsal side. Fixed finger less than half as long as dactylus and bearing 4 teeth of various shapes. Dactylus with several irregular, rounded teeth followed by a larger tooth on proximal half; distal half without dentition. A lateral keel runs along proximal two-thirds of article.

Pereopods II–VII (Figure 62H,I): Setal formula of pereopod II, (5,3,5,5). Long, terminal propodal spines absent on pereopods II–IV. Short, terminal propodal spines of same legs long, slender, straight except for curved tip, and totally devoid of dentition. Short, subterminal carpal spine of pereopod II similar but entirely straight.

Uropods: Bearing 8 and 9 endopodal articles on left and right sides, respectively.

INTRASPECIFIC VARIATION.—The dentition of the chela from another female is as illustrated in Figure 62C.

Following are the various body lengths (numbers of individuals considered are indicated in parentheses). Dredge 12: manca 1 (8), 1.7 to 1.8 mm; manca 2 (2), 2.0 to 2.2 mm; juvenile (1), 2.4 mm; preparatory female 1 (3), 3.0 to 3.6 mm; preparatory female 2 (1), 3.7 mm; copulatory female (1), 4.1 mm; copulatory male (1), 3.4 mm. WHOI B. Sta. 169; manca 1 (2), 1.8, 1.9 mm; manca 2 (1), 2.3 mm; juvenile (2), both 3.0 mm; preparatory female 1 (4), 3.3 to 3.6 mm; preparatory female 2? (1), 4.5 mm; copulatory female (3), 3.9 to 4.4 mm; copulatory male (4), 4.0 to 4.6 mm.

REMARKS.—This species is very closely related to *Neotanais hastiger*. In addition to those characters listed in the introduction to the *hastiger* species group, *N. tricarinatus* differs from *N. hastiger* in the following ways. Stages other than those of copulatory males: (1) Carapace: anterolateral setae and shape of ocular lobes and rostrum; (2) midventral

shape of pleonites; (3) shape of pereonites in dorsal view; (4) hairs and ventral shape of pleotelson; (5) dentition of chela; and (6) shapes of specialized spines on pereopods II–IV. Copulatory males: The differences between the copulatory males of the two species are considerably more marked than among other stages: (1) anterior depression of carapace in *N. tricarinatus;* (2) number of anterolateral setae on carapace; (3) number and location of medial protuberances on chelipedal carpus; (4) dentition of chelae and; (5) length-width ratios of article 1 of first antenna.

Neotanais tricarinatus has been found only at depths of about 600 to 800 m, whereas *N. hastiger* has been collected only from about 1750 to 3800 m, possibly indicating greatly different depth ranges for the two species.

MATERIAL.—*Chain* Cruise 35 (*Equalant*), Dredge 12, off Recife, Brazil, 770 to 805 m, 8 M1, 3 M2, 1 Juv, 3 P ♀ 1, 1 P ♀ 2, 1 Cop ♀ , 1 Cop ♂ ; WHOI B. Sta. 169, same area, 587 m, 2 M1, 1 M2, 2 Juv, 4 P ♀ 1, 1 P ♀ 2, 3 Cop ♀ (including holotype), 4 Cop ♂ (including allotype).

LOCATION OF MATERIAL.—NMNH: WHOI 169, holotype (USNM 143219); WHOI 169, allotype (USNM 143220); WHOI 169, other specimens (USNM 143221); *Chain* Dredge 12 (USNM 143218).

DERIVATION OF NAME.—Referring to the three keels on the carapace of copulatory males. From the Greek *trias* (in threes) and the Latin *carina* (keel).

Ungrouped Species

Neotanais calcarulus, new species

FIGURES 63, 64, *100*

DIAGNOSIS.—*Stages Other Than Copulatory Male* (copulatory males unknown): *Carapace with about 6 anterolateral and about 8 posterolateral feathered setae (less in some populations); rostrum relatively prominent; oblique furrows and anterolateral keels moderately well developed. *Pereonites generally a little wider than long, with rounded sides; area over pereopods widest. *Pleonites with epimeres rounded laterally, each bearing a U-shaped row of about 12 long, feathered setae on outer edge; *sternites with relatively long, pointed, vertically directed spurs. *Pleotelson 1.4 to 1.7 times wider
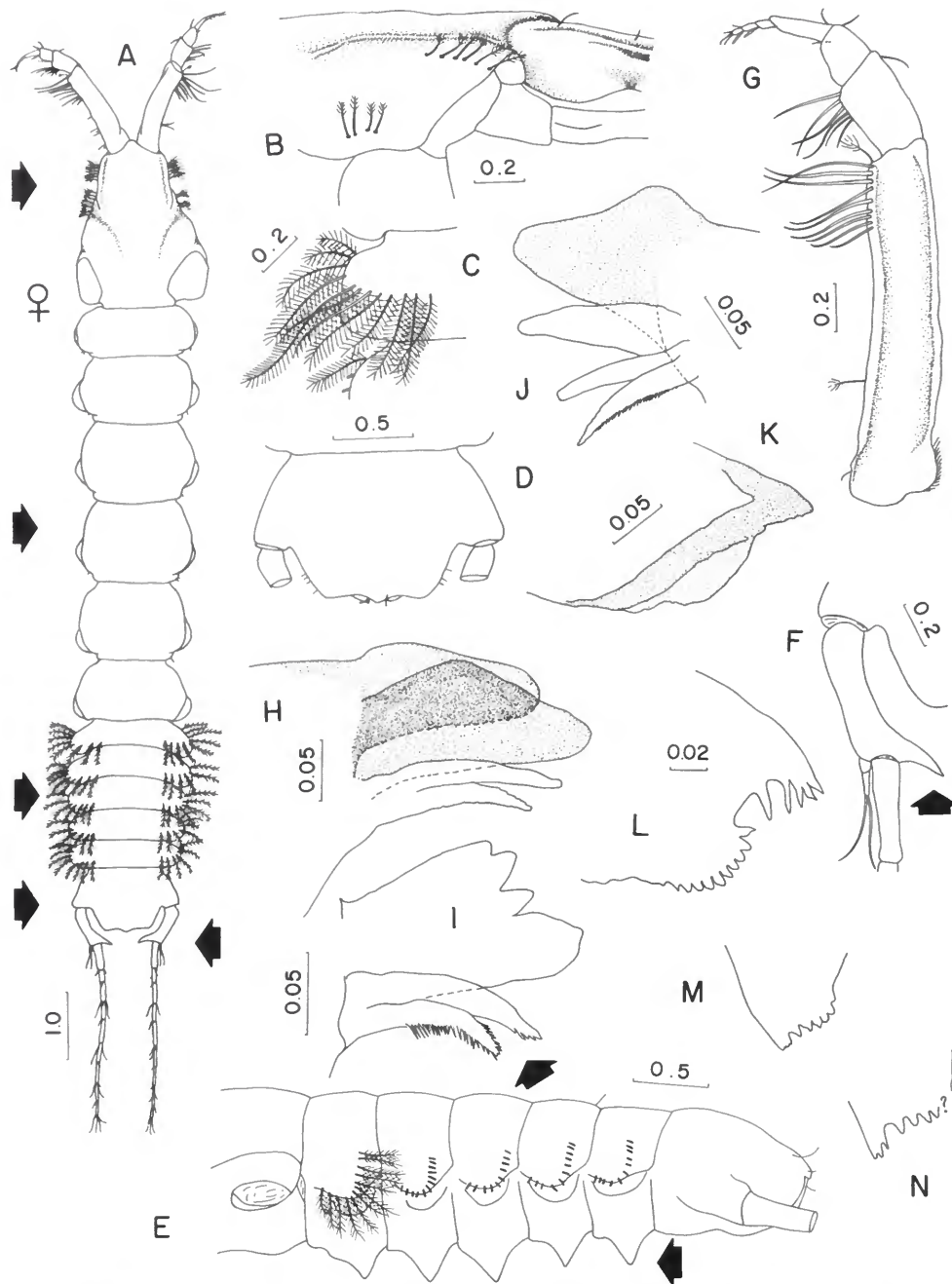
FIGURE 63.—*Neotanais calcarulus*, new species (A–H, J, K, all copulatory female, holotype, OSU AD 156, off Oregon): A, dorsal view; B, lateral view of carapace; C, pleonal epimere, dorsal view; D, pleotelson, dorsal view; E, pleon, lateral view; F, left uropodal protopod, exopod, and first endopodal article; G, left first antenna, dorsal view; H, pars incisiva, left mandible, anterior view; I, same, copulatory female C, *Vema* Sta. 17–2, off Chile; J, pars incisiva, right mandible, anterior view; K, pars molaris, same mandible (broken?); L, same, copulatory female C; M, N, same, manca 2B, OSU AD 156. (L–N, same scale.)

than long, angular in dorsal view. *Cheliped distinctive: propodus with high, thin dorsal keel and low lateral keel on fixed finger; *dentition clearly distinct from that of other species (see Figure 64I); teeth and borders of fingers brown, sometimes relatively dark. *Pleopods much more setose and rami broader than in most species, protopod bearing 2 very long, thick medial setae and about 11 slender, lateral setae (copulatory female). *Uropods distinctive, protopods each bearing a large, distal, medially directed spur; endopod slender.

DESCRIPTION OF HOLOTYPE (copulatory female A, OSU AD 156).—*Body* (Figure 63A): 12.0 mm long and 6.2 times longer than wide.

Carapace: Length-width ratio 1.3. Oblique furrows and anterolateral keels well developed. Six anterolateral and 4 and 8 posterolateral feathered setae present on either side (Figure 63A,B). Anterior margin concave lateral to rostrum. Ocular lobes noticeably smaller than in some species (cf. Figures 4A, 48D, 63B).

Pereonites: Generally wider than long and rounded laterally.

Pleonites (Figure 63A,C,E): Pleonite 1 slightly wider than pereonite 7; successive pleonites becoming progressively narrower, giving pleon a slightly tapered appearance. Prominent row of about 12 long, feathered setae arising from epimeres dorsally. Sternites expanded midventrally into moderately large, ventrally directed, pointed spurs.

Pleotelson (Figure 63A,D,E): 1.5 times wider than long. Sides anterior and posterior to uropods almost straight in dorsal view; posterior median projection bordered on each side by a wide, shallow concavity. Anterior and posterior margins almost parallel.

First Antenna (Figure 63G): First article 3.9 times longer than wide and with a low, rounded dorsal keel running along each side.

Right Mandible (Figure 63J): Third incisive spine bluntly tipped (broken?); second spine entirely naked with truncate tip (broken?); first spine finely serrate all along inner side and on distal third of outer side (teeth broken off latter side). Molar process (Figure 63K) completely lacking in terminal teeth (broken?—see "Intraspecific Variation").

Left Mandible (Figure 63H): Incisive spines as on right side. Lacinia mobilis without dentition (abnormal?—cf. Figure 63I).

Labium: As in Figure 64A.

First Maxilla: See Figure 64B,C.

Second Maxilla: Fixed endite (Figure 64E) with the usual 5 heavy terminal spines and a slender subterminal seta. A bluntly tipped bifid spine and a trifid spine present on left side; right member bears 2 bifid spines. Medial setal row composed of 32 setae; 4 long, relatively straight spines with irregular tips lying along row.

Maxilliped: Left endite with 9 medial filter setae (Figure 64F). Setal formula of palp, (-,-,6,5,11).

Cheliped (Figure 64H): Carpus with about 10 moderately long, dorsal setae. Dorsal keel of propodus high and thin; a low lateral keel lying along fixed finger. Dentition clearly distinct from that of other species; a very long and high tooth (Figure 64I) located centrally along fixed finger followed by 4 other teeth, the first 2 being much larger than the distal 2. No proximal denticles present, margin of finger smooth. Dactylus bearing 4 oval, lateral teeth decreasing in size distally. All teeth and borders of both fingers dark brown.

Pereopods II–VII (Figure 64K–Q): Setal formulae of pereopods II–IV, (9,8,9,7), (13,11,11,11), and (14,17,11,13) respectively. Anterior and posterior propodal and carpal setae relatively long and slender and with very fine setules. Short, terminal propodal spine of pereopods II–IV straight but with bent tip and bearing about 16 teeth (Figure 64N—spine missing on left pereopod II). Long, terminal propodal spines apparently absent on these legs. First 2 long, propodal setae in anterior row of pereopod II with very fine teeth (Figure 64L,M—these found in the position normally occupied by long, toothed spines of other species and may be homologous with them). Pereopod VII with row of 13 relatively long, "short" subterminal propodal spines with prominent serrations (Figure 64Q). Short, subterminal carpal spine of pereopod II naked, straight, and pointed (Figure 64O). Dorsomedial, subterminal setae on carpi of pereopods III and IV very short and thick. Dactylar teeth of pereopods V–VII as in Figure 64P.

Pleopods (Figure 64R): Much more setose than in most species. Terminal endopodal setal row not well differentiated from lateral row; terminal setae 1.1 times longer than endopod. Protopod notable for presence of 2 long, medial setae and 11 shorter, more slender, lateral setae. Setal formula, (2,*11*) (3,14,10) (0,7,0,16,13).
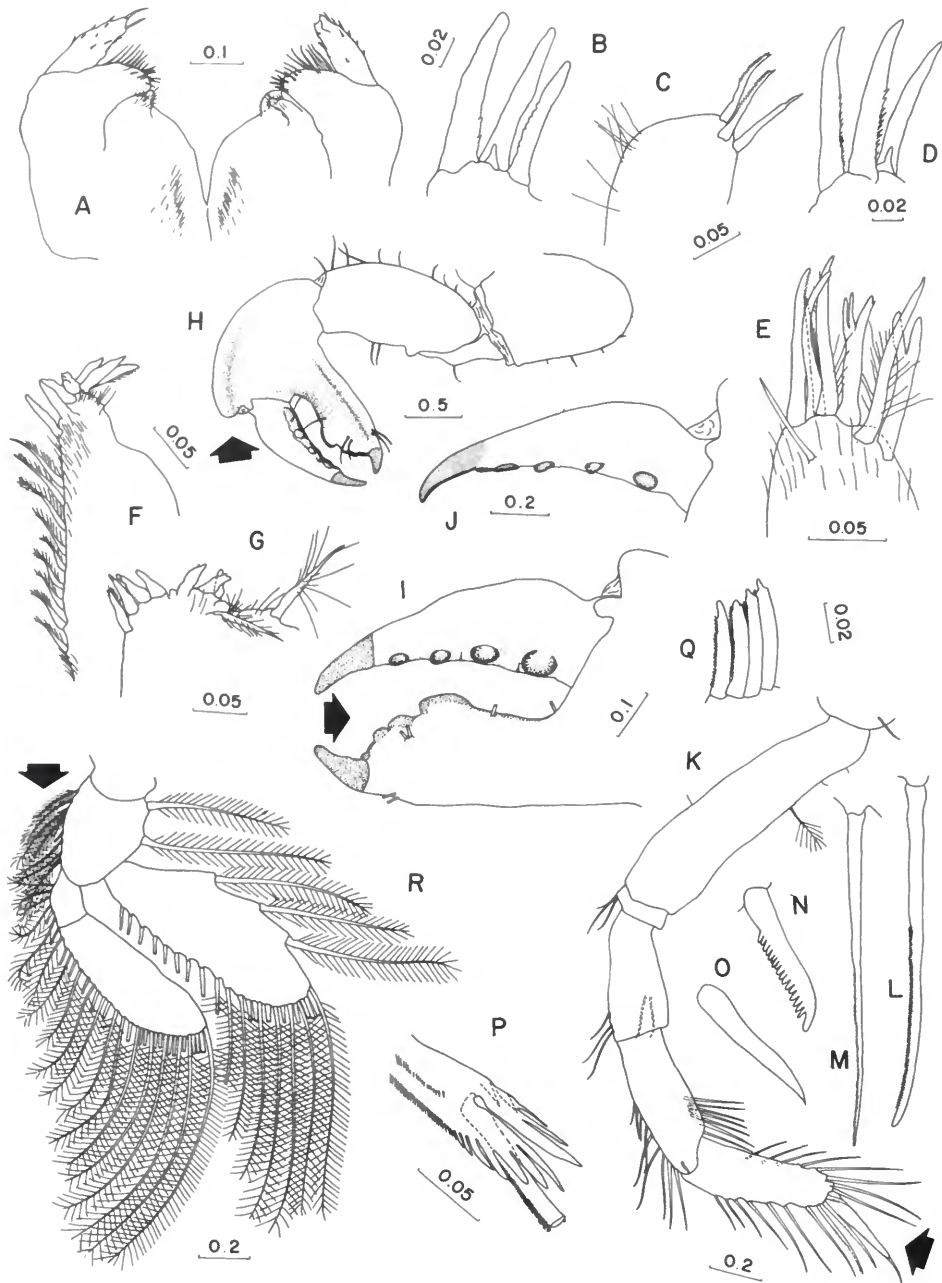
FIGURE 64.—*Neotanais calcarulus*, new species (D, J, copulatory female C, *Vema* Sta. 17-2, off Chile; all others, copulatory female, holotype, OSU AD 156, off Oregon): A, labium, anterior view; B, representative terminal spines, external endite, right first maxilla; C, tip of internal endite, left first maxilla; D, representative terminal spines, external endite, left first maxilla; E, fixed endite, left second maxilla, posterior view; F, endite of left maxilliped, medial view; G, same, posterior view; H, left cheliped; I, same, chela; J, dactylus of cheliped; K, left pereopod II, anterior view; L, first antenna propodal seta in K; M, second anterior propodal seta in K; N, short, terminal propodal spine in K; O, short, subterminal carpal spine in K; P, dactylus, left pereopod V; Q, representative short, subterminal propodal spines, pereopod VII; R, pleopod.

Uropods (Figure 63A,F): Protopod with extraordinary distomedial spur; exopod less than one-half length of first endopodal article. Each endopod composed of 9 articles.

INTRASPECIFIC VARIATION.—*Stages Other Than Copulatory Male*: Carapace: Copulatory female C from Chile has fewer lateral setae on the carapace (about four in each group) than the holotype, and these lack setules distally. *Anton Bruun* specimens are similar but have only about two anterolateral setae. Female C is smaller (10.8 mm) than the holotype.

Mandibles: The second incisive spine of the right mandible is not bluntly tipped in female C as in the holotype (latter probably broken). The lacinia mobilis of the left mandible has three prominent teeth in addition to the posterior lobe in C (Figure 63I). The distal incisive spine has a number of terminal teeth. The pars molaris bears 15 teeth (Figure 63L) in marked contrast to that of the holotype (Figure 63H), which has no teeth (probably abnormal). Examination of manca 2 B from Oregon (Figure 63M,N) demonstrated that teeth are present in this population.

Cheliped: Dentition of the dactylus is somewhat different in female C (Figure 64J).

REMARKS.—*Neotanais calcarulus* exhibits a remarkable number of features distinguishing it from all other known species. Note should be taken of the closeness with which the shape and setation of the pleopods resemble those of *N. pfaffioides* and, to a lesser extent, those of *N. giganteus*.

DISTRIBUTION.—*Neotanais calcarulus* is known to range from Oregon to Chile and has been collected at depths of about 2800 to 4400 m.

MATERIAL.—*Anton Bruun* Cruise 11, Sta. 95, off Peru, 4332 to 4423 m, 2 Juv; OSU AD 156, off Oregon, 2838 m, 1 M2, 1 Cop ♀ (holotype); *Vema* Sta. 17-2, off Chile, 4030 to 4036 m, 1 M2, 1 Juv, 1 Cop ♀ ; *Vema* Sta. 17-6, off Chile, 4303 to 4323 m, 1 P ♀ 1?.

LOCATION OF MATERIAL.—NMNH: OSU 156, holotype (USNM 143223); OSU 156 (remainder) (USNM 143224); *Anton Bruun* 95 (USNM 143222). AMNH: *Vema* 17-2 (AMNH 14984); *Vema* 17-6 (AMNH 14985).

DERIVATION OF NAME.—Referring to the small, distomedial spurs on the uropodal protopods. From the Latin *calcarulus* (little spur).

Neotanais barfoedi Wolff, 1956

FIGURES 65–67, *99*

Neotanais barfoedi Wolff, 1956c:44, fig. 2a,b, pl. 2: figs. 3–6.

DIAGNOSES.—*Stages Other Than Copulatory Male:* *Pereonites 4-6 square, about as long as wide. *Pleotelson short compared to most species, about twice as wide as long, and sides forming acute angles laterally. *Pleonal epimeres rounded laterally in dorsal view and each with 1 to 3 weak, feathered hairs; *sternites with moderately developed, posteriorly directed, midventral protuberances. *Carapace with 4 or 5 short anterolateral setae and 5 or 6 posterolateral setae. *Chela with high dorsal crest; dactylar teeth low, rounded, and irregular. Uropodal endopods relatively heavy, articles stout, some relatively short. Anterior setal rows of propodi and carpi of pereopods II–IV composed of relatively stout spines with heavy teeth. Article 1 of first antenna with a length-width ratio of about 3. Ischia of pereopods each with at least 1 long, thick seta and about 2 very short, weak setae.

Copulatory Male (only one type known): *Pleotelson, *carapace setae, ischial setae of pereopods, and uropods similar to those of other stages. *Chelipedal carpus very strongly S-shaped proximally and bearing about 5 short, weak dorsal setae and 2 slender and equal ventral setae; *dorsal surface of propodus nearly straight, without pronounced crest, and with fine, anteriorly directed serrations; fixed finger twisted but not lying in a plane very different from that of dactylus; dentition of fingers as in Figure 66A,B. Row of short, subterminal propodal spines on pereopod VII about 17 in number and tiny, naked, and triangular.

DESCRIPTION OF PREPARATORY MALE D (*Galathea* Sta. 665).—See "Remarks" below.

Body (Figure 65A): 17.3 mm long and 7.4 times longer than wide.

Carapace: 1.4 times longer than wide. Anterolateral keels moderately well developed; 4 or 5 anterolateral setae and 5 or 6 posterolateral setae occurring in rows on each side. Oblique furrows moderately deep and appearing to converge posteriorly in a fine, incomplete, U-shaped line. Respiratory chambers and chelipedal coxae relatively well expanded in dorsal view.

Pereonites: Peronites 4-6 generally square in dorsal view, pereonite 5 (Figure 65c) only 1.2 times
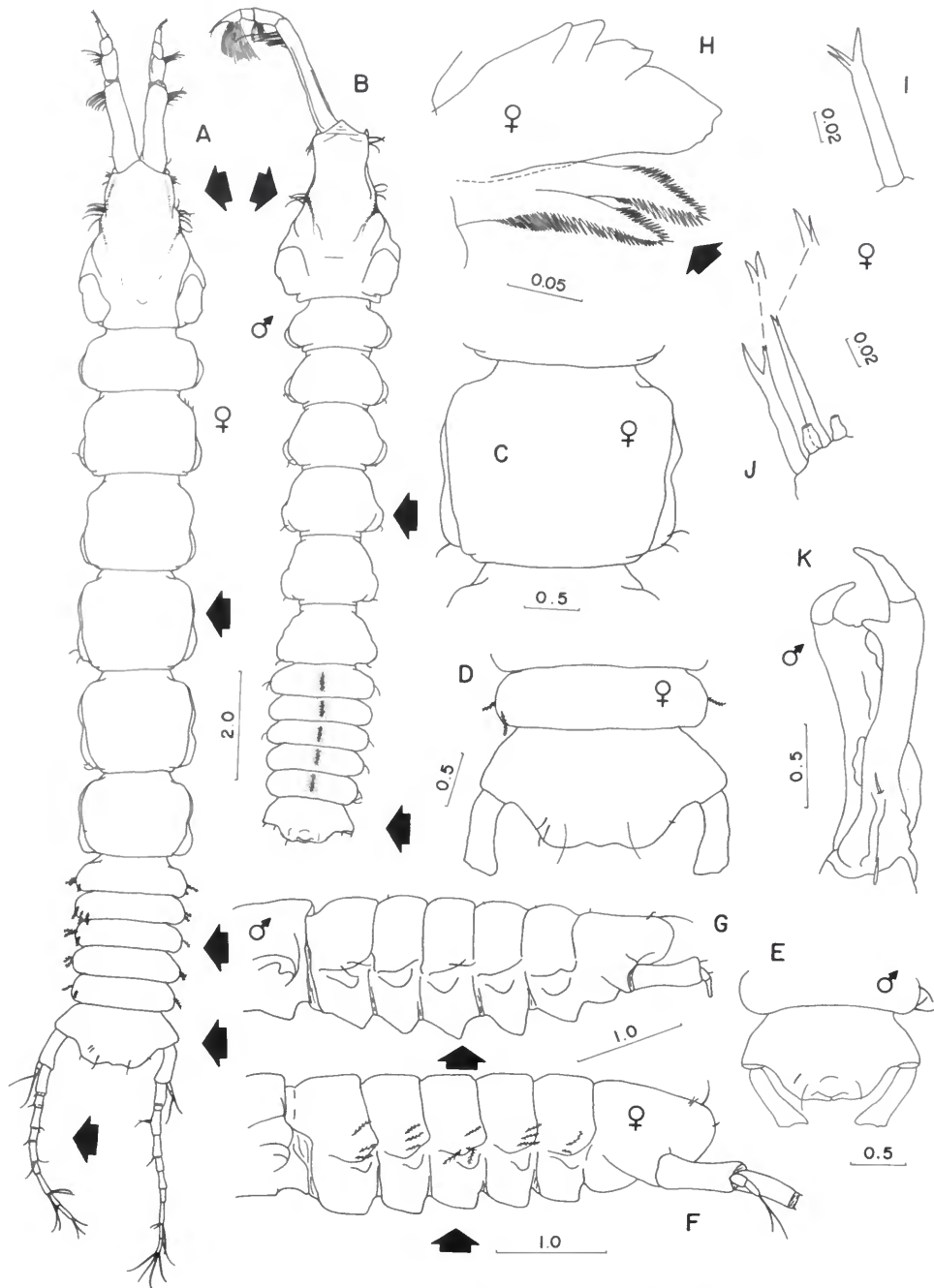
FIGURE 65.—*Neotanais barfoedi* Wolff: A, preparatory male D, dorsal view, *Galathea* Sta. 665 (see "Remarks"); B, copulatory male F, dorsal view, *Galathea* Sta. 668; C, pereonite 5, dorsal view, preparatory male D; D, pleonite 5 and pleotelson, same animal, dorsal view; E, same, copulatory male F; F, pleon, lateral view, preparatory male D; G, same, copulatory male F; H, pars incisiva, left mandible, anterior view, preparatory male, holotype, *Galathea* Sta. 665; I, forked spine, fixed endite of maxilla 2, preparatory male D; J, same, holotype; K, left chela, dorsal view, copulatory male F.
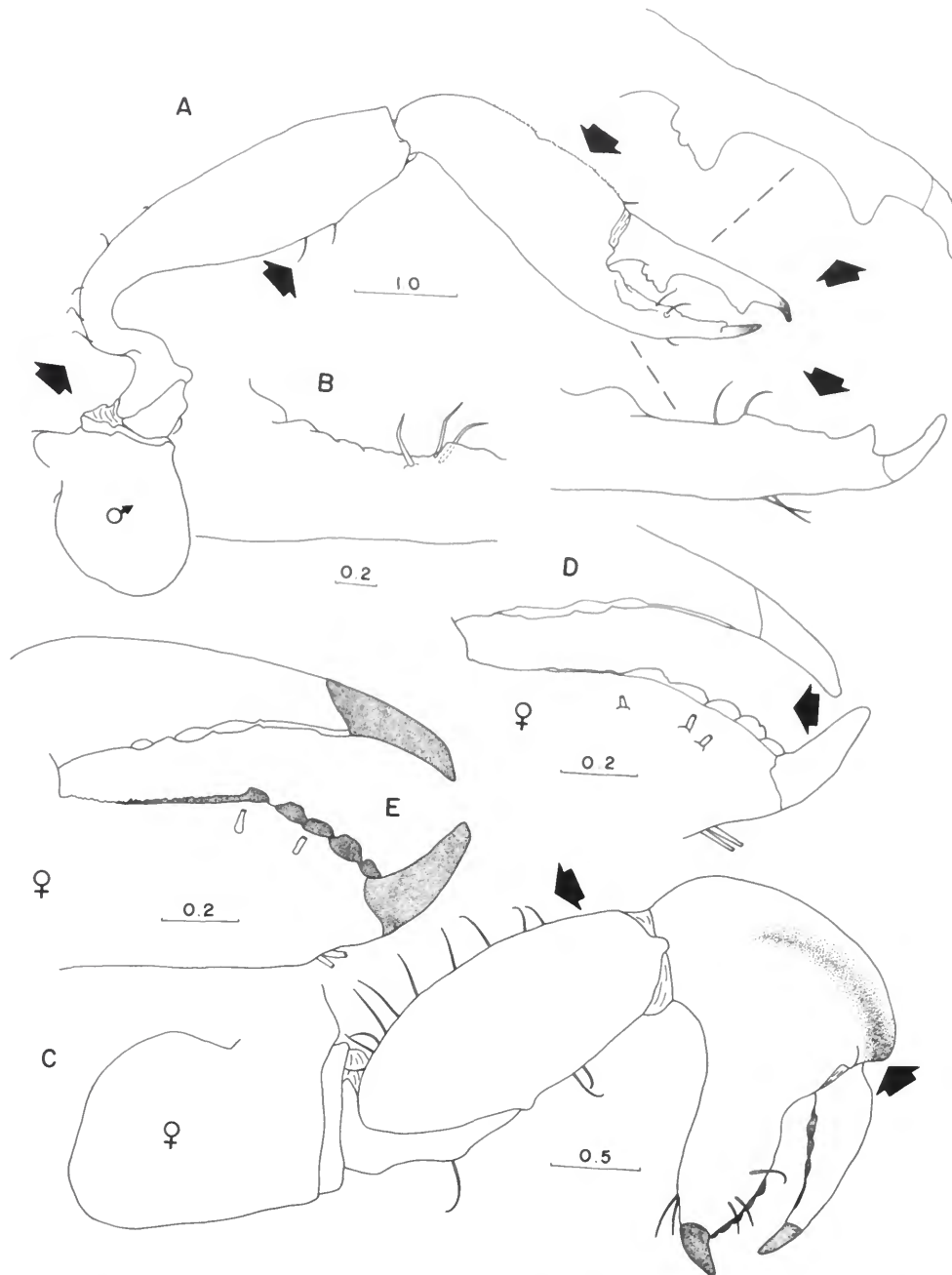
FIGURE 66.—*Neotanais barfoedi* Wolff: A, right cheliped with enlargements of fingers of chela (both slightly oblique with respect to major figure), copulatory male F, *Galathea* Sta. 668; B, enlargement of proximal area, fixed finger of chela, copulatory male G, *Galathea* Sta. 668; c, right cheliped, preparatory male D, *Galathea* Sta. 665; D, enlargement of chela in c; E, right chela, preparatory male, holotype, *Galathea* Sta. 665.
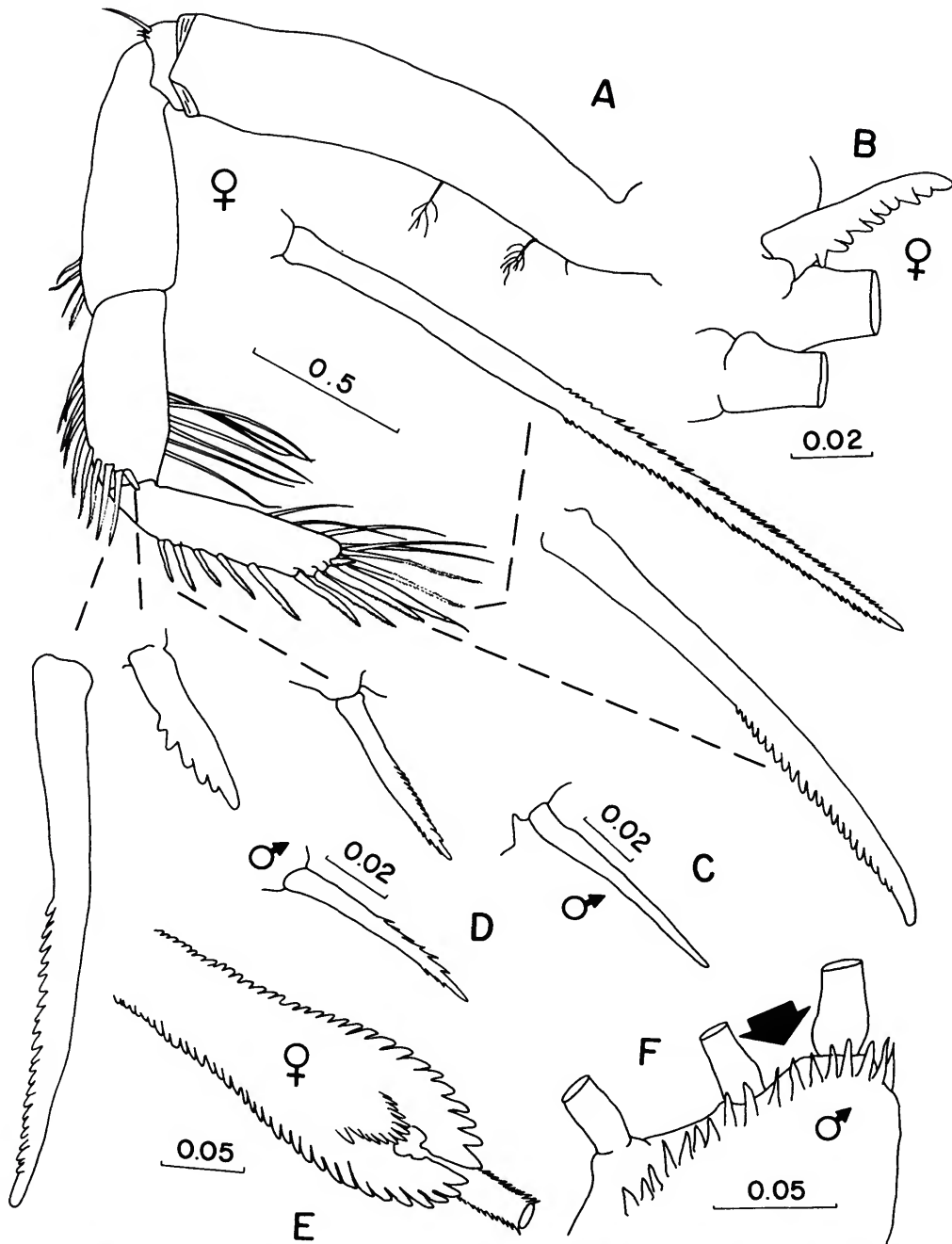
FIGURE 67.—*Neotanais barfoedi* Wolff: A, left pereopod II, anterior view, with enlargements of various setae and spines, preparatory male D, *Galathea* Sta. 665; B, short, terminal propodal spine, same appendage; C, same spine, copulatory male F, *Galathea* Sta. 668; D, short, subterminal carpal spine, same animal; E, dactylus, pereopod V, dorsal view, preparatory male C; F, distal tip of propodus, pereopod VII, posterior oblique view, copulatory male F.

wider than long; area over pereopods not always the widest part of somite. Pereonite 7 with 2 small, uncalcified male gonopore anlagen borne on slightly raised, ventral, genital cone anlagen.

Pleonites (Figure 65D,F): Rounded laterally in dorsal view and bearing 1 to 3 fine, feathered dorsal hairs on epimeres. Pleonite 1 about as wide as pereonite 7 and not appreciably wider than pleonite 5. Sternites bearing posteriorly directed, midventral protuberances.

Pleotelson (Figure 65D,F): Noticeably short compared to many species, only 2.1 times wider than long.

First Antenna: First article 3.2 times longer than wide.

Left Mandible: Mandibles of this specimen in very poor condition; holotype described here (Figure 65H). Lacinia mobilis with 3 sharp teeth; posterior lobe pointed (preparatory male D with a small notch in lobe). Second spine serrate on outer half of both sides; first spine serrate on distal half of outer side and almost entirely serrate on inner side.

Right Mandible (holotype): Third incisive spine with short point; first two spines and pars molaris as in left mandible.

Second Maxilla: Fixed lobe with forked spines variable, only one observed clearly due to poor condition of specimen. This one (Figure 65I) with 3 points (see holotype, Figure 65J). Medial row composed of 22 setae with long setules and three setulated spines.

Maxilliped: Setal formula of palp, (1,0,5+1,8,12).

Cheliped (Figure 65C,D): Carpus with 10 relatively long dorsal setae. Dorsal propodal crest prominent. Cutting edge of fixed finger irregular proximally but without denticles. Distal teeth rounded and somewhat irregular. Dactylar teeth irregular, low, rounded, and about 4 in number.

Pereopods II–VII: Dactylar spine of pereopod II is 0.2 times as long as dactylus. Short, terminal propodal spine on same leg relatively straight and bearing 9 large teeth (Figure 67B). Short, subterminal carpal spine of same leg straight, stout, and with 5 large teeth. Posterior propodal setae long, thin, and very finely setulated except for distalmost 1 or 2 setae which have much larger setules (Figure 67A). Anterior propodal setal row composed of very stout, heavily toothed spines, the first three of which are especially heavy. Anterior carpal setae

heavy and serrate as in propodus (same figure). Ischia each with at least 1 long, thick seta and about 2 very short, weak setae. Setal formulae of pereopods II–VII respectively: (8,7,9,8), (9,9,8,9), (10,11,9,9), (7,7,11,8), (9,8,9,10), and (7,7,8,9). Short, subterminal propodal spines of pereopod VII shaped as in other species and 17 in number. Dactylar teeth of pereopods V–VII moderate in size, bluntly tipped, and continuous, with relatively large proximal denticular rows; dorsal, U-shaped denticular row short, composed of comparatively large denticles (Figure 67E).

Pleopods: Terminal endopodal setal row distinct from lateral row. Terminal setae 0.66 times as long as endopod. Setal formula, (2,3) (3,15,7) (0,6;0,11,9).

Uropods: Endopodal articles stouter than in many species; 9 and 10 articles present on left and right sides, respectively. Exopod 0.6 times as long as first endopodal article.

DESCRIPTION OF COPULATORY MALE F (*Galathea* Sta. 668).—*Body* (Figure 65B): 13.5 mm long and 6.1 times longer than wide.

Carapace: 1.5 times longer than wide with 3 anterolateral setae below well-expanded keels and 3 or 4 posterolateral setae. Oblique furrows relatively pronounced. Transverse lines present behind rostrum and between chelipedal coxae.

Pereonites: Appear wider than long in dorsal view, pereonite 5 is 1.4 times wider than long; sides gradually widen posteriorly to area of pereopodal attachment, which is considerably wider than anterior end.

Pleonites (Figure 65B,E,G): Rounded laterally in dorsal view as in other stages, each bearing a few apparently unfeathered hairs and with a middorsal longitudinal depression. Pleonite 1 slightly wider than pereonite 7 and pleonite 5. Sternites extended into longer midventral spurs than in other stages.

Pleotelson (Figure 65E,G): About as wide as last pleonite and 1.8 times wider than long, appearing short as in other stages.

First Antenna: First article 5.7 times longer than wide.

Maxilliped: Palp very long and thin; setal formula (1,0,1+1,2+1,ca. 6).

Cheliped: Carpus remarkably twisted into an S-shape proximally and bearing 5 weak dorsal setae in area of twist and 2 thin and equal ventral setae (Figure 66A). Propodus with dorsal surface not

especially crested but relatively straight and with fine dorsal serrations or cuticular extensions. Fixed finger twisted but both fingers lying in nearly the same plane (Figure 65κ). Fixed finger bearing 2 dorsal setae and 1 ventral seta. Proximal surface expanded and relatively flat dorsally following a large, rounded protuberance; two small, more distally located bumps followed by a tooth just proximal to claw. Dactylus with a large, proximal, ventral protuberance bearing 3 rounded, successively longer teeth and a large, triangular distal tooth.

Pereopods II–VII: Setal formulae (8,6,8,8), (10,17,7,10), (10,16,7,10), (8,8,11,8), (8,9,9,10), and (7,7,8,7). Setae in anterior rows without marked teeth in contrast to those of other stages, but with much finer setules. Ischial setation as in other stages. Short, terminal propodal spines of pereopods II–IV slender and naked (Figure 67c). Short, subterminal carpal spine of pereopod II slender but with a few teeth (Figure 67d). Dactylar teeth of pereopods V–VII as in other stages (Figure 67e). Short, subterminal spines of pereopod VII are 17 in number, but very tiny and triangular in contrast to other stages (Figure 67f).

Pleopods: Setal formula, (2,3) (3,15,8) (0,4;0,11,10). Terminal endopodal setae 1.4 times longer than article.

Uropods: With 9 articles in each endopod; exopod 0.48 times the length of first endopodal article.

INTRASPECIFIC VARIATION.—*Stages Other Than Copulatory Male*: Body Length: Sta. 665: juvenile, 9.5 mm (estimated) and 9.7 mm; preparatory female 2, 11.8 mm; preparatory male, 15.8 mm (holotype), 17.3 mm.

Second Maxilla: The two forked spines of the fixed endite in preparatory female 2 E, Sta. 665, are bifid as in most species. The holotype has one bifid and one uncleft spine (Figure 65н); however, each of these has one secondarily split point. In both female E and the holotype, only two spines are present along the medial row, in both cases with fine setules of moderate length on at least one side.

Chela: The chela of the holotype (Figure 66e) has proximal denticles along the cutting edge of the fixed finger. Its dactylar teeth are more distinct than in the animal described above.

Pereopods II–VII: The setal formula of pereopod II of the holotype is (7,6,8,7). Pereopod VII bears 15 short propodal spines in the posterior row.

Copulatory Males: Body Length: Sta. 668: copulatory male, 13.5 mm (described specimen), 15.6 mm (another of same developmental stage).

Chela: The "cutting edge" of the dactylus is irregular proximal to the first tooth in male G (Sta. 668), and it is not expanded as in the described male F (cf. Figure 66a,b).

POSTMARSUPIAL DEVELOPMENT.—Surprisingly enough, the uropods of all stages, juveniles through copulatory males, have nine endopodal articles. Juvenile C has two male gonopore anlagen on the ventral surface of pereonite 7. It is not possible to say whether the two copulatory males are primary or secondary. They do not come from the same station as the other specimens, and hence their body lengths cannot, with certainty, be compared with the latter.

REMARKS.—*Neotanais barfoedi* was described briefly by Wolff in 1956 from seven specimens collected by the *Galathea* Expedition north of New Zealand. It is redescribed here in detail, and diagnoses are given. Due to limited material, preparatory male D is decribed rather than a female. Its general morphology is, of course, almost identical with that of the females; the holotype also is a preparatory male.

The holotype and the copulatory males do not come from the same station; however, there is little doubt that they are conspecific. The most obvious characters shared are the short pleotelson, the midventral silhouette of the pleonites, and the relatively large number of anterolateral and posterolateral setae on the carapace.

MATERIAL.—*Galathea* Sta. 665, north of New Zealand and southwest of the Kermedec Trench, 2470 m, 2 Juv, 1 P ♀ 2, 2P ♂ (including holotype and a specimen described here); *Galathea* Sta. 668, near same locality, 2640 m, 2 Cop ♂ (including specimen described here).

LOCATION OF MATERIAL.—UCZM: All material.

Neotanais bacescui Lang, 1968

FIGURE 102

Neotanais bacescui Lang, 1968:141, figs. 84–88, pl. 6a,b.

DIAGNOSIS.—*Stages Other Than Copulatory Male* (copulatory males unknown): *Pereonites 4–6 about as long as wide in dorsal view (poor condition of specimen prevents further comment). *Pleonites

progressively narrower, forward edge of epimeres sloping gradually posteriorly; epimeres bearing about 3 small hairs. *Pleotelson long, about 1.4 times wider than long; uropods borne close to body of pleotelson; sides convex anterior and posterior to uropods. *Chelae with large fingers; *fixed finger with large, distinct, and somewhat flat-topped distal teeth; dactylar teeth 2 or 3 in number, partially fused with dactylus, and anteriorly directed. Pereopodal setae slender, with very fine setules; short, terminal propodal spines slightly curved distally and with relatively large teeth, at least on pereopods III and IV; long terminal propodal spines absent. Pereopod VII with only a few short, subterminal propodal spines (4 in Lang's (1968) figure 87g). Pleopods with distinct terminal row of endopodal setae. Both proximal incisive spines of mandibles setulated on both sides.

REMARKS.—The esthetascs borne on the fifth and sixth articles of the first antennae are annulated (5 sections) as in other species and not smooth as in Lang's (1968) figure 84c.

Because many additional species of *Neotanais* are now known and all species have been compared, it has been possible to write a diagnosis for *N. bacescui*. It should be used in conjunction with Lang's (1968) figures.

MATERIAL.—*Galathea* Sta. 282, southwest of Ceylon, 4040 m, 1 P ♀ 1 (holotype, completely decalcified and broken).

LOCATION OF MATERIAL.—UCZM: holotype.

Neotanais hessleri, new species

FIGURES 68, 99

DIAGNOSIS.—*Stages Other Than Copulatory Male*: *Pereonites 4–6 bell-shaped in dorsal view, area over pereopods markedly wider than anteriorly. *Pleotelson relatively long, about 1.4 times wider than long. Uropodal exopod only about 0.3 times as long as first endopodal article. *Carapace not appreciably expanded laterally in areas of respiratory chambers and chelipedal coxae in dorsal view. *Dactylus of chela longer than fixed finger. Pereopods II–IV with dactylar spines about 0.4 times as long as article; short, terminal propodal spine almost straight, pointed, and bearing 7 or 8 sharply pointed teeth; *short, subterminal carpal spine straight, sharply pointed, and practically naked.

DESCRIPTION OF HOLOTYPE (manca 1).—*Body*

(Figure 68A): 3.8 mm long and 7.1 times longer than wide. Rostrum blunt in dorsal view; oblique furrows, chelipedal coxae, and respiratory chambers not prominent in dorsal view; a single anterolateral and posterolateral seta present on each side.

Pereonites: Pereonites 4–6 bell-shaped in dorsal view, widest in area of pereopods.

Pleonites: Typical of all mancas 1 but with occasional, relatively long hairs dorsolaterally.

Pleotelson: Long, about 1.4 times wider than long in dorsal view.

First Antenna: Composed of 6 articles, typical of all mancas 1 in this genus; first article 4.1 times longer than wide.

Mouthparts: Not dissected.

Cheliped (Figure 68B,C): Bearing only scattered dorsal setae on carpus. Propodal crest low, dactylus longer than propodus. Most proximal propodal tooth prominent and rounded.

Pereopod II (Figure 68D): Setal formula (1,3,3,3). Two long, terminal propodal spines present; short, stout subterminal propodal spine only slightly curved and bearing about 8 sharp teeth. Dactylar spine long, about 0.4 times as long as article. Anterior ventral surface of propodus bearing numerous clumps of spinelets.

Uropods (Figure 68A): Each uropod composed of 4 articles. Exopod 0.3 times as long as first endopodal article.

COMPARISONS.—The length of the pleotelson in this species immediately distinguishes it from many others. Because this species is established upon a single young individual, significant differences from other species with relatively long pleotelsons are listed below.

Neotanais affinis: Shape of chela (dentition, length of dactylus, and shape of fixed finger), shape of pereonites in dorsal view, and shape of article 1 of first antenna.

N. antarcticus: Shape of pleotelson in dorsal view; relative lengths of uropodal exopod and first endopodal article, and relative length of dactylar spines of pereopods II–IV.

N. bacescui: Shape of carapace (posterolateral expansion, rostrum), shape of chela and relative lengths of dactylar spines of pereopods II–IV.

N. hadalis: Body length, relative lengths of uropods and pleon, proportions of endopodal segments of uropods, shape of chela (dentition and length of dactylus).
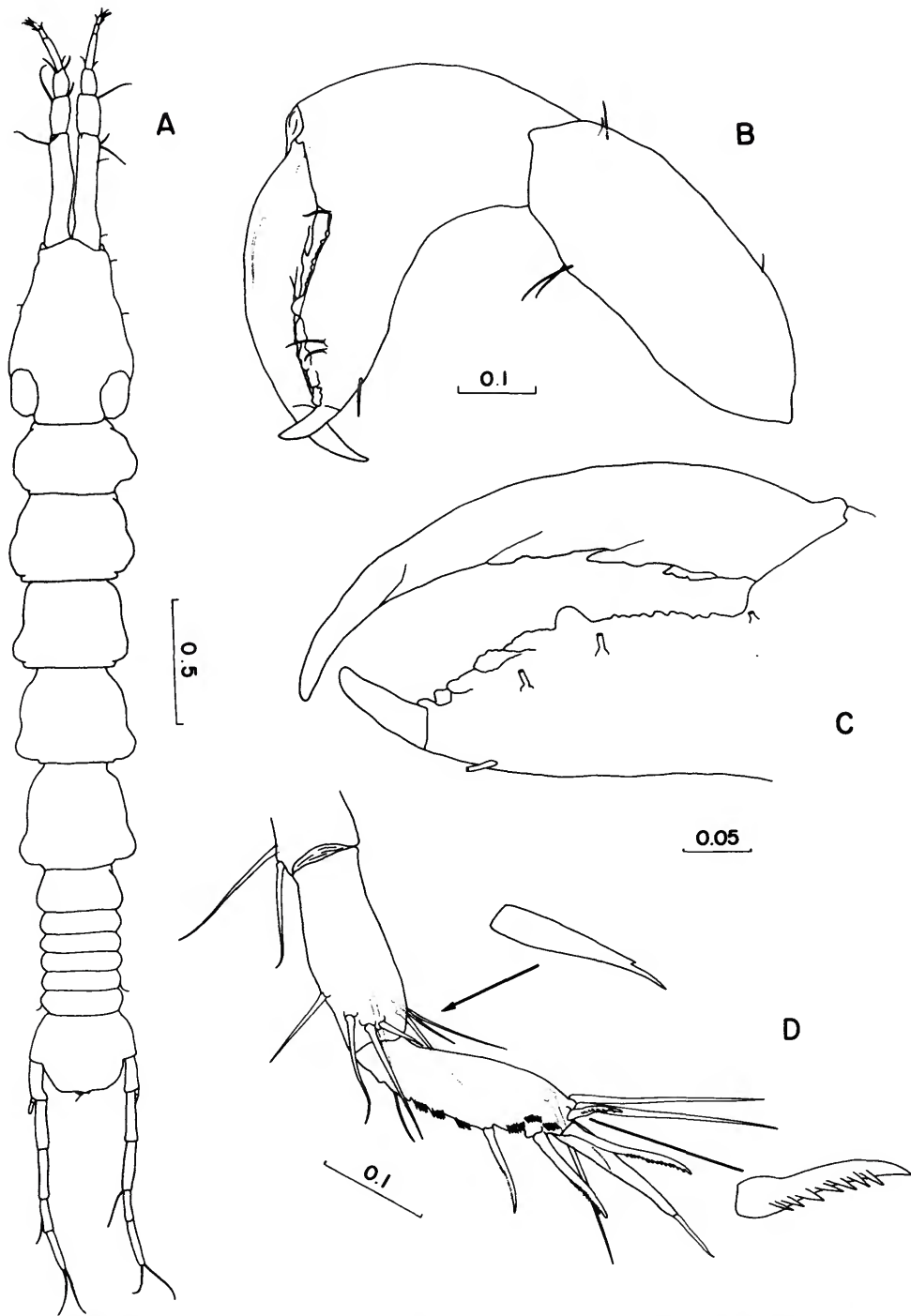
FIGURE 68.—*Neotanais hessleri,* new species, manca 1, holotype: A, dorsal view; B, left cheliped; C, left chela; D, left pereopod II in anterior view.

N. hastiger and *N. tricarinatus*: Shapes of chela and carapace and relative lengths of uropodal exopod and first endopodal article.

N. peculiaris: Shape of chela (dentition and length of dactylus) and shape of dactylar spines of pereopods II–IV.

N. pfaffioides: Body length, shape of carapace (rostrum, respiratory chambers), and dentition of chela.

N. robustus: Shape of pleotelson and pereonites in dorsal view, degree of lateral expansion of the carapace posteriorly, and the relative lengths of the articles of the first antenna, particularly article 4.

N. insolitus: Point of uropodal attachment to pleotelson, shape of pereonites in dorsal view, and height of dorsal crest on chela.

N. bulbodens: Pereonites more nearly square in dorsal view, shape of chela (crest, length of dactylus, dentition), relative length of pleon, and relative lengths of uropodal exopod and first endopodal article.

N. vemae: Shape of pleotelson and chela (length of dactylus, shape of fixed finger, and dorsal crest).

REMARKS.—Although this species is known only from a single manca, the holotype is distinct enough from other known species to warrant its description as a new species.

MATERIAL.—*Eltanin* Sta. 366, Cruise 25, southeast of Bounty Island (South Pacific), 5340 m, 1 M1, holotype.

LOCATION OF MATERIAL.—NMNH: holotype (USNM 143225).

DERIVATION OF NAME.—In honor of Dr. Robert R. Hessler of Scripps Institution of Oceanography of the University of California.

Neotanais insolitus, new species

FIGURES 69, 99

DIAGNOSIS.—*Stages Other Than Copulatory Male* (copulatory males unknown): *Pleotelson unusual, having sides broadest anteriorly and sloping smoothly posteromedially, and uropods attached ventrally, point of attachment not being visible from above. *Body slender, about 9.0 times longer than wide. *Chela with very large dorsal crest which overhangs dactylus slightly; 5 distal propodal teeth large, irregular, and sometimes fused together; 3 large, proximal, irregular, forwardly directed teeth

partially fused to dactylus. *Pereonites 3–6 more or less square in dorsal view, 3 and 4 appearing longer than wide, and area above pereopods hardly, if at all, wider than other parts. *Carapace almost devoid of relief dorsally; chelipedal coxae not appreciably expanded laterally in dorsal view. Uropodal exopod 1.5 times longer than first endopodal article.

DESCRIPTION OF HOLOTYPE (juvenile?).—*Body* (Figure 69A): 5.6 mm long and 9.1 times longer than wide.

Carapace: 1.6 times longer than wide. Rostrum pointed, anterolateral keels moderately well developed, oblique furrows very unobtrusive, and chelipedal coxae not appreciably expanded laterally in dorsal view. Dorsal and lateral relief generally very limited. Two anterolateral setae and a single posterolateral seta present.

Pereonites: Relatively square in dorsal view, 3 and 4 appearing longer than wide but length-width ratio of pereonite 4, 1.1. Area above pereopods not appreciably wider than other parts. (Shapes possibly distorted somewhat by decalcification and mechanical damage.)

Pleonites (Figure 69A,G,H): Rounded laterally with epimeres bearing 1 or 2 long feathered setae. Each sternite with a posteriorly directed midventral spur. First pleonite about as wide as pereonite 7 and just slightly wider than pleonite 5. Pleon strongly curved downward (may be artifactual).

Pleotelson (Figure 69F–H): Long, width-length ratio 1.1; widest anteriorly with sides smoothly curving posteromedially. Posterior border concave in dorsal view except for small median convexity. Anal membranes visible dorsally, points of attachment of uropods not visible from above. Uropods borne on ventral protuberances located on either side of anal opening unlike any other known species of *Neotanais*.

First Antenna (Figure 69A): Article 1, 3.1 times longer than wide.

Second Antenna: Similar to that of other species.

Right Mandible (Figure 69B): With molar teeth distinct, strong, and 6 in number. Incisive spines 1 and 2 both serrate along distal half of both edges. Third spine exceedingly broad proximally and with row of 7 small, acute teeth terminally.

Left Mandible: With incisive spines as on right side. Lacinia mobilis with 3 acutely tipped teeth; posterior lobe with slight median depression at tip.

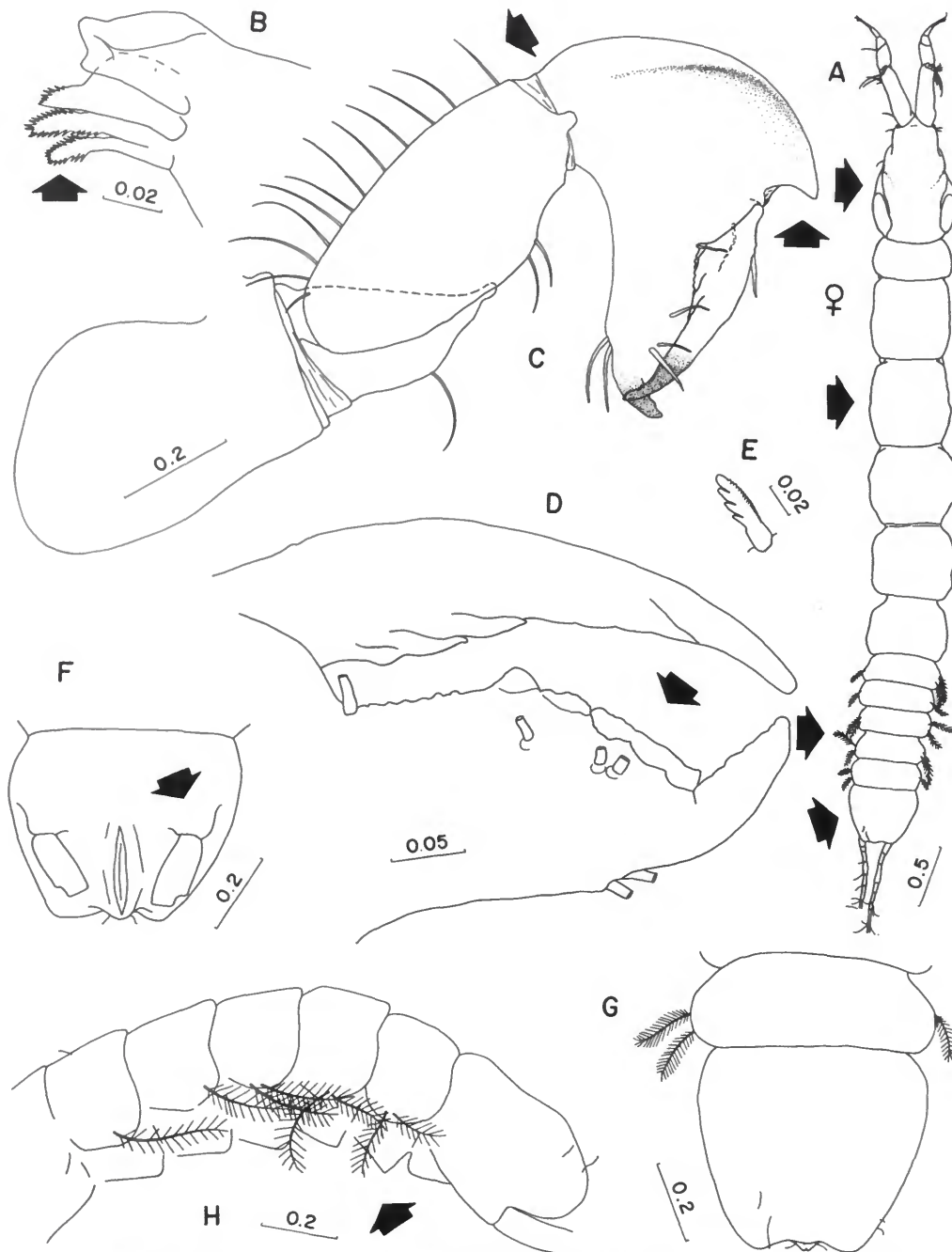FIGURE 69.—*Neotanais insolitus*, new species, juvenile, holotype: A, dorsal view; B, pars incisiva of right mandible; C, right cheliped; D, right chela showing dentition; E, short, terminal propodal spine, pereopod IV, from below; F, ventral surface of pleotelson showing points of attachment of uropods; G, dorsal surface of pleotelson and pleonite 5; H, lateral view of pleon with sternites reconstructed (note uropodal attachment).

First Maxilla: With 9 terminal spines on external endite, about 3 of which bear fine teeth.

Second Maxilla: With 3 and 6 setae on external and internal lobes, respectively, of movable endite. Fixed endite with the usual 5 terminal spines, 2 stout bifid spines, and 1 slender subterminal seta.

Maxilliped: Setal formula of palp, (1,0,5+1,3+4,9). Endite with only 2 medial filter setae.

Cheliped (Figure 69C,D): Basis not as rounded posteriorly as in many species. Carpus bearing 13 substantial dorsal setae. Propodus with very accentuated dorsal crest, of which the distal extremity actually forms an acute projection overhanging the dactylus. Setae of chela strong. Fixed finger with 5 large, irregular distal teeth; first tooth high and rounded, 3 distalmost teeth fused together. Proximally about 7 large and somewhat separated denticles. Dactylus bearing 3 large, irregularly pointed, and distally directed proximal teeth all fused to article.

Pereopods II–VII (these appendages almost worthless for examination): Setal formula of pereopod III, (6,7,5,7); propodus of pereopod IV, (5,5). Short, terminal propodal spine of pereopod IV bearing 3 large, dull, distally directed teeth on one side and a row of tiny, blunt teeth on the other (Figure 69E). No long, terminal propodal spines observed. At least 6 (?) short, subterminal propodal spines present in row on pereopod VII. Dactylar spines of pereopods II–IV about one-third to one-half the length of their articles, dactylar spine of pereopod VII long and curved and dactylus with exceedingly fine terminal teeth.

Pleopods: Terminal endopodal setae merging with lateral setal row. Terminal seta length/endopodal length ratio, 1.8. Setal formula, (2,1)(3,7,6)(0,2;0,11,3). Protopodal setae long.

Uropods (Figure 69A): Broken; endopods with 7 and 8 remaining articles, respectively, on left and right sides. Exopod 1.5 times the length of first endopodal article.

REMARKS.—This species departs markedly from all other known species of *Neotanais* in the structure of the pleotelson and the ventral attachment of the uropods. This character possibly is indicative of distinct generic status; however, the species has been included in *Neotanais* for the present. The single, small, juvenile? specimen available is decalcified, its body broken, and its appendages either broken or missing.

In the future, when additional specimens become available, the following characters may be of generic significance and may justify the inclusion of this species in a new genus: (1) shape of pereonites in dorsal view, (2) shape of pleonites, (3) narrow length-width relationship of body, (4) shape of first antenna, (5) height of chelal crest, (6) shape of incisive mandibular spines, and (7) structure of pereopods. In any event, *Neotanais insolitus* represents a separate phyletic line within the genus, equivalent to the *americanus* or *hastiger* groups.

MATERIAL.—*Eastward* Sta. 7530, Cruise 27, off North Carolina, 4460 m, 1 Juv? holotype.

LOCATION OF MATERIAL.—NMNH: holotype (USNM 143226).

DERIVATION OF NAME.—Referring to the obscure affinities of this species. From the Latin *insolitus* (unusual; strange).

Neotanais wolffi Kudinova-Pasternak, 1966

FIGURE 100

Neotanais wolffi Kudinova-Pasternak, 1966:522–524, fig. 5.

CHARACTERS POTENTIALLY USEFUL IN IDENTIFICATION.—*Stages Other Than Copulatory Male* (copulatory males unknown): From described animal, undesignated stage and without further identification. Body length unknown (about 12 to 16 mm), 6.7 times longer than wide. Pereonites decidedly quadrangular in dorsal view, wider than long, and with marked corners; areas over pereopods not appreciably wider than anteriorly. Pereonites 5 and 6 each twice as long as pereonite 2. Pleonites decreasing in width from pleonite 1 to pleonite 5 giving pleon tapered appearance in dorsal view; sternites bearing "small spines" midventrally. Pleotelson 1.6 times wider than long. Incisive spines of right mandible all (?) without teeth, whereas first spine of left mandible bears teeth along proximal border. Pereopodal setae less strongly serrate than in *Neotanais americanus*. According to Kudinova-Pasternak's (1966) text and figure 5, dactyli of pereopods III and IV (II also?) bear stout projections terminally (dorsally?) at insertion of spine. Uropods about as long as pleon and with 10 endopodal articles.

REMARKS.—Unfortunately, it was not possible to obtain specimens of this species for examination. Several important structures (e.g., cheliped) are

not figured, and it is not possible to write a diagnosis or to determine clearly the affinities of this species. The original description does not designate a holotype.

MATERIAL.—*Vitjaz* Sta. 3214, east of Honshu, Japan, 6156 to 6207 m, 1 "♀" without oostegites (body length 15.6 mm), 1 ♀ with oostegites (12.5 mm), and 1 M (?2) (5.1 mm); *Vitjaz* Sta. 3232, same general area, 6126 m, 1 M (?1) (4 mm). None of the material was examined.

LOCATION OF MATERIAL.—MZM: possibly all.

"Neotanais sp." of Kudinova-Pasternak

FIGURE 100

"*Neotanais* sp." Kudinova-Pasternak, 1966:521, 522, figs. 3, 4.

CHARACTERS POTENTIALLY USEFUL IN IDENTIFICATION.—*Copulatory Male* (other stages unknown): Carapace not especially narrow anteriorly, with about 4 anterolateral hairs, and only moderately pronounced respiratory chambers and chelipedal coxae in dorsal view. Pereonites wider than long and not markedly tapered anteriorly. First article of first antenna about 4.8 (?) times longer than wide. Chelipedal carpus strongly bent; propodus with serrate dorsal crest and additional serrations proximally on fixed finger which also bears 1 small proximal tooth, the latter followed by 2 small teeth and a distally directed tooth just before claw; dactylus with dorsal serrations proximally and 2 large, widely spaced, ventral teeth. Pereopods II–IV with heavy, strongly setulated setae; setal formula of pereopod II, (8,6,6,6); dactylar spine very short.

REMARKS.—Unfortunately, it was not possible to obtain this specimen for examination. The limited published description does not permit a diagnosis to be written or to identify the specimen as definitely new to science.

Kudinova–Pasternak (1970) states that this animal is similar to *Neotanais tuberculatus,* which she described in that paper. I doubt, however, that the two forms are conspecific because of differences in (1) shape of the carapace and pereonites as illustrated by Kudinova–Pasternak, (2) degree of chelipedal carpal expansion, (3) dentition of the fixed chelipedal finger, and (4) presence in Kudinova–Pasternak's "*Neotanais* sp." of proximodorsal serrations on both chelipedal fingers.

MATERIAL.—*Vitjaz* Sta. 3849, New Hebrides

Trench, 6680 to 6830 m, 1 Cop ♂ (described ♂, body crushed posterior to pereonite 5—not examined).

LOCATION OF MATERIAL.—MZM.

Genus *Herpotanais* Wolff, 1956

Herpotanais Wolff, 1956a:218, figs. 35–52.

TYPE-SPECIES.—*Herpotanais kirkegaardi* Wolff, 1956a. By monotypy and original designation.

DIAGNOSES.—*Stages Other Than Copulatory Male:* Pleopods uniramous in contrast to all other known neotanaid genera, being composed of only 2 articles and bearing relatively few feathered setae. Pereonites 5–7 longer than wide. Pleonites long, pleon making up about 30 percent of total body length. Uropods with long, thick protopod, a maximum of 6 endopodal articles (in type-species), and an extremely short exopod. Bases of pereopods V–VII about 4 times longer than wide. Chela with exceedingly low, almost imperceptible dorsal crest.

Copulatory Males: Cheliped not very dissimilar from that of other stages (in marked contrast to *Neotanais*) but with somewhat lengthened carpus. Gonopores located on very low protuberances differing from cones of *Neotanais.* First antenna composed of 8 articles. Pleopods, uropods, and pereonites similar to those of other stages.

REMARKS.—Since Wolff (1956a) originally described *Herpotanais,* many more species of neotanaids have been studied and described, including representatives of two additional genera. With this additional understanding of intrafamilial variation and the erection of new genera, it is appropriate to present a new diagnosis of *Herpotanais.* Additional observations on *H. kirkegaardi* are described below.

The pleotelsonal shape and naked dactylar spines of pereopods V–VII may be of generic significance for *Herpotanais.*

Insofar as can be determined, the legs of *Herpotanais* are adapted primarily for locomotion by walking as in *Neotanais.*

Herpotanais kirkegaardi Wolff, 1956

FIGURES 88, 103

Herpotanais kirkegaardi Wolff, 1956a:219, figs. 35–52, table 4.

DIAGNOSIS.—Because *Herpotanais* is monotypic,

those characters listed in the generic diagnoses are diagnostic for this species as well.

DESCRIPTIONS OF HOLOTYPE AND ALLOTYPE.—See descriptions and figures of Wolff (1956a:219 ff.).

REMARKS.—This species is known from a single station in the Kermedec Trench at a depth of about 7000 m. In examining this species a number of new observations were made.

The original description does not mention two small anterolateral setae borne on each side of the carapace behind the ocular lobe and a single posterolateral seta, also on each side. These are taxonomically significant in *Neotanais*. The pereonites have a noticeable groove laterally where the tergites meet the sternites.

Wolff (1956a:218, 224) states that the gonopores in copulatory male Z are located on low, short keels. These keels are not prominent in other specimens, where they might be described as low, slightly oblique cones, but they are not especially keellike. The gonopores are oval.

The pleonites of copulatory males are expanded laterally at the points of attachment of the pleopods; however, in other stages they are almost cylindrical, in marked contrast to *Neotanais*. The pleotelson in copulatory males has its sides flaring outward posteriorly to a greater extent than in other stages.

Both Wolff (1956a:218) and Lang (1968:133) state that the first antenna has eight articles (five in the "flagellum"). These statements fail to take age into consideration. In reviewing Wolff's discussion and from additional observations, it seems that mancas 1 and 2 have six articles each; juveniles, seven; and all other stages, eight (for a more detailed discussion see page 200).

Of those animals examined, there usually were one to three long, slender annulated esthetascs, depending on the stage of development. These were borne on each of the three penultimate articles of the first antenna. Their shape resembled that already established for *Neotanais* (four or five sections) and not exactly as figured by Wolff (1956a, figs. 38a, 45b).

A very low dorsal crest is present on the chelae as in *Neotanais*. Some of the long hairs mentioned as being on the pereopodal setae actually may be detritus that has become caught on the setules. In any event, these setae are not feathered as might be inferred from Wolff's (1956a) figure 44a,b and his

statement (p. 223) concerning the holotype (pereopod III and, presumably, IV).

The pleopods (Figure 88) provide what is perhaps the most significant difference between this genus and others in the family. The setulation observed was considerably more extensive than that figured by Wolff (1956a, fig. g), surely enough to indicate retention of the natatory function of these appendages, at least in the older stages. The fact that the ramus is composed of only a single article and that it bears a medial seta distally (Figure 88c) may indicate that it represents the endopod, and that it is the exopod which is missing. In the other genera the exopod is composed of two articles, neither of which ever bears medial setae.

The setation on the uropods is as follows: the protopod bears several small distal setae, the endopod an alternating pattern of relatively undistinguished setae, and the exopod a short seta distally on the first article, as often found in *Neotanais*, and three (rather than two) terminal setae on the second article.

MATERIAL.—*Galathea* Sta. 651, Kermedec Trench, 6960 to 7000 m; 41 specimens, including 2 not listed by Wolff (1956a) in his table 4, and 3 fragments. I have examined all except the holotype (preparatory female) and animals O, P, LL, OO, TT, V, and Z. For the ages of the animals see page 200.

LOCATION OF MATERIAL.—UCZM: holotype, allotype, and most of the remainder of material from *Galathea* 651. JNM: P. MOI: TT. NMNH: R (USNM 105891).

Venusticrus, new genus

TYPE-SPECIES.—*Venusticrus glandurus*, new species. By monotypy and present designation.

DIAGNOSIS.—*Stages Other Than Copulatory Male* (copulatory males unknown): Cheliped bearing an extremely large, thin, brown-bordered dorsal crest. Pleotelson acorn-shaped in dorsal view; articulations of uropods ventral and not visible from above. Pereonites 3–6 longer than wide; attachments of pereopods not visible from above. Pleon short, composing only about 20 percent of total body length compared to other genera (*Neotanais micromopher*, 25 percent; *Herpotanais kirkegaardi*, 31 percent; *Carololangia mirabunda*, 26 percent). Antenna 1 of bizarre shape, highly sculptured, bearing brown

lateral and medial keels dorsally on first article and an undulating lateral brown keel on second article, in contrast to all other known genera. Uropods containing very long setae of decreasing size distally in numbers up to 6 at alternate articulations, many of these setae bearing fine, long hairs. Pereopods V–VII bearing long rows of very long, flexible, feathered setae on ventral surfaces of propodi, carpi, and meri and on dorsal surface of carpus; vertical anterior rows of straight, lightly setulated spines present on carpi and meri; these articles constricted laterally near spines; propodi of pereopods III and IV much longer than propodus of pereopod II and bearing slightly recurved, spatulate spines anteriorly; pereopods V and VI bearing an exceedingly long propodal broom seta dorsally; very long posterolateral rows of short broom setae present on bases.

REMARKS.—The following characters may also be diagnostic for *Venusticrus*: (1) irregularly shaped lacinia mobilis; (2) presence of a row of ventral setae on chelipedal merus; (3) relatively short length, shape of distal teeth, and absence of terminal dorsal slit and opening on dactylus of pereopod VII; and (4) presence of chromatophores.

DERIVATION OF NAME.—Referring to the elaborate structure of pereopods V–VII. From the Latin *venustus* (lovely; beautiful) and *crus* (leg; shank). *Venusticrus* is masculine.

Venusticrus glandurus, new species

FIGURES 70–73, *103*

DIAGNOSIS.—Because *Venusticrus* is monotypic, those characters listed in the generic diagnosis are diagnostic for this species as well. Copulatory males are unknown.

DESCRIPTION OF PREPARATORY FEMALE 2 HOLOTYPE (WHOI B. Sta. NN 1).—*Body* (Figure 70A): 8.9 mm long and 9.1 times longer than wide. Originally heavily calcified, obscuring scattered, black chromatophores, especially abundant in head region (see "Chromatophores" below); pleon short, only 0.19 times length of entire body.

Carapace (Figure 70A,B): Rostrum pointed; surface relief minimal. Chelipedal coxae poorly developed laterally; coxae fused to carapace dorsally. Anterolateral keels not prominent compared to *Neotanais*; anterior dorsal surface sloping down-

ward slightly from center to sides and thence ventromedially downward below rounded lateral border. Length 1.6 times greater than width. Four fine anterolateral setae of moderate length followed by 5 posterolateral setae, each group present in a row on each side.

Pereonites: Pereonites 3–6 markedly longer than wide, width-length ratio of pereonite 5 being 0.77. Sides of pereonites almost parallel, in each a slight concavity present about two-thirds of the distance from anterior edge. Ventral surface deeply concave posteriorly on either side, making sides appear bulbous anteriorly (Figure 70c,D). A few small, naked setae borne ventrally anterior to pereopodal coxae (Figure 70D).

Pleonites: Short; each sloping posterolaterally in dorsal view, the widest point of each being the posterior border. Pleonite 1 longer than usual with respect to the others; all of about the same width, pleonite 1 only slightly wider than pleonite 5. Each epimere with 6 to 8 long, feathered setae laterally. Pleonites 2–5 each bearing a slightly posteriorly directed, midventral spur (Figure 71A); spur on pleonite 1 much less prominent than spurs of other segments.

Pleotelson (Figures 70A,E,F, 71A): Notably long with respect to pleonites, equaling pleonites 3–5 and one-half of pleonite 2 in length. Clearly articulated with pleonite 5. Widest anteriorly, width-length ratio, 1.2. Acorn-shaped in dorsal view; anal opening large but not visible from above; posterior margin with prominent middorsal convexity. Attachments of uropods ventral on 2 lateral protuberances, not visible from above. Slight ventral concavity present between uropods and anal opening.

First Antenna (Figure 70G): First article longest, but only 1.4 times longer than second and only 2.8 times longer than wide. Second article 2.6 times longer than the third, which, in turn, is less than one-half as long as the fourth. Last 3 articles very short; articles 5 and 6 each bearing a long, annulated esthetasc. First article with raised, brown, lateral keels dorsally; second article with similar brown keel laterally only; the latter flaring laterally and ventrally at its proximal end. Distal tip of appendage actually curving medially.

Second Antenna (Figure 70H): First article very much expanded by dorsolateral keels. Hair more abundant on article 1 than in other genera. Shapes
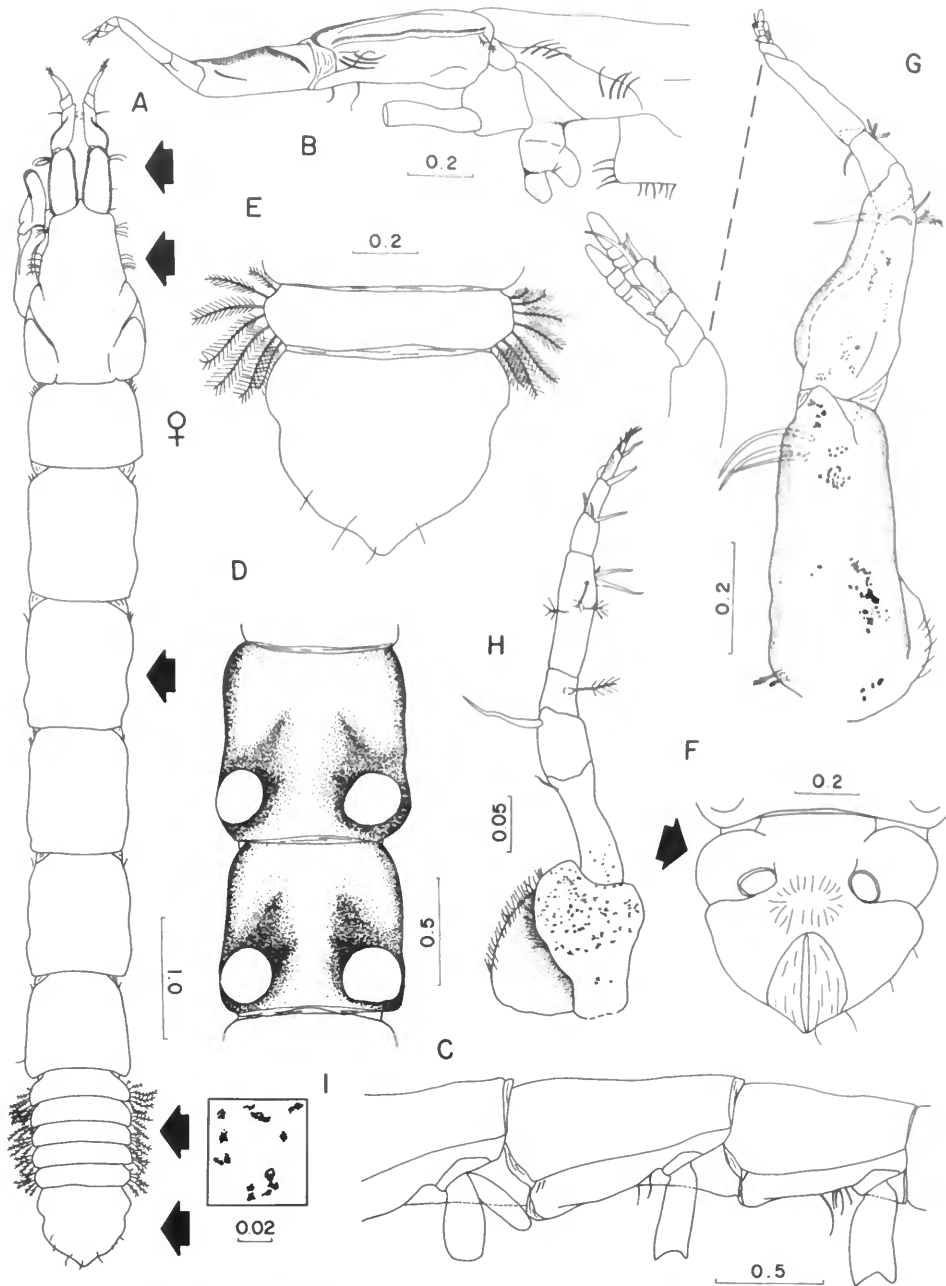
FIGURE 70.—*Venusticrus glandurus,* new genus, new species: A, dorsal view, preparatory female 2, holotype, WHOI B. Sta. NN 1; B, left first antenna and anterior portion of carapace, preparatory female 2, WHOI B. Sta. 70; C, pereonites 5–7, lateral view, same animal; D, pereonites 6 and 7, ventral view, same animal; E, pleonite 5 and pleotelson, dorsal view, holotype; F, same, ventral view; G, left first antenna, dorsal view, with enlargement of tip in ventral view, holotype; H, left second antenna, median view (dorsal side is to the left), holotype; I, representative section of first article of second antenna to show chromatophores (partially decalcified, showing subsurface chromatophores).

FIGURE 71.—*Venusticrus glandurus*, new genus, new species (all figures are of preparatory female 2, holotype, WHOI B. Sta. NN 1): A, pleon, lateral view; B, left mandible; C, representative terminal spines, external endite of the left first maxilla; D, left maxilliped, posterior view, with enlargement of basal endite in anterior view; E, left cheliped; F, left chela.

FIGURE 72.—*Venusticrus glandurus*, new genus, new species (all figures are of preparatory female 2, holotype, WHOI B. Sta. NN 1): A, left pereopod II, anterior view; B, left percopod IV without setae (to illustrate shapes of articles); C, propodus and dactylus of same; D, left uropod, lateral view.

of articles and setation as in figure. Generally stout.

Labrum: Similar to that of other genera.

Left Mandible (Figure 71B): Terminal portion of pars incisiva almost perpendicular to main axis of mandible. First incisive spine serrate on both sides, second spine smooth except irregular and possibly bearing a few teeth along distal one-third on proximal sides. Lacinia mobilis highly irregular, apparently with 4 large teeth. Pars molaris with 9 triangular teeth.

Right Mandible: First two incisive spines as on left side. Third spine smooth, pointed, and wide at base. Eleven molar teeth present.

Labium: Similar to that of *Neotanais*.

First Maxilla (Figure 71c): External endite with 9 spines, at least 2 of which bear sharp teeth along 1 side on basal half of spine. Internal endite as in *Neotanais*, 3 short spines and a long seta being present.

Second Maxilla: Fixed endite bearing 5 simple terminal spines, 1 slender subterminal spine, and 2 stout bifid spines. Medial row containing 15 setae and 2 smooth spines with uncleft tips.

Maxilliped (Figure 71D): Coxae with 2 setae on each. Endite with 5 filter setae (both maxillipeds), shape of these similar to those of *Carololangia mirabunda* (Figure 76B), with setules of decreasing length along one side only. One long terminal seta with long setules and 3 long and 2 stout spines (3 on right side) present terminally on endite. Setal formula for palp, (1,0,6+1,7,8).

Epignath: As in *Neotanais*.

Cheliped (Figure 71E,F): Basis more elongate and angular than in *Neotanais*. Merus large, bearing 5 small setae ventrally (1 found in *Neotanais*). Carpus bearing 2 setae ventrally, just anterior to a convexity, and 18 dorsal setae; distolateral convexity with brown border. Propodus uniquely shaped, bearing an immense crest with a thin, brown border dorsally. Setae as in most species of *Neotanais*. Propodal teeth 5 in number, vary large, fused together, and with a single, smooth crest. Proximal area of cutting edge smooth and with brown border. Dactylar teeth smooth, rounded, and 4 in number, the proximal 3 separated by small spaces, and the first located at the propodal-dactylar junction.

Pereopods II–VII: All pereopods very slightly pubescent proximally. Setation of pereopods II–IV markedly different from that of pereopods V–VII.

Pereopod II (Figure 72A): Dactylar spine 0.4 times as long as article. Propodus very small, bearing 2 long, toothed spines distally. Short terminal spine relatively straight and bearing 4 immense teeth on anterior side and 4 smaller teeth posteriorly. Anterior setal row composed of 5 heavy spines toothed on both sides and decreasing markedly in length proximally. Posterior row bearing 2 long, thin setae with prominent but sparse setules; these followed proximally by a short broom seta. Short, subterminal carpal spine with 6 to 10 scattered teeth on each side. Proximal to this lie 2 very long, toothed spines bearing irregularly triangular teeth on one side and more acutely tipped and forwardly directed teeth on the other. Eight anterior and 8 posterior setae all sparsely setulated as in posterior propodal row. Merus long and bearing a row of 7 anterior setae (plus a small distal seta) and 10 posterior setae, all similar to those of previous articles except distal seta, which is naked. Ischium with 4 long setae, 1 of which is sparsely setulated. Basis short and bearing a short, lateral broom seta and a row of 8 broom setae (see description of posterior legs). Coxa with 2 naked setae; rudimentary oostegite large, over two-thirds the length of basis.

Pereopods III and IV (Figure 72B,C): Articles differing in shape from those of pereopod II. Propodus much larger, merus not nearly as elongated (as usual in the Neotanaidae), basis shorter, and oostegite longer than basis, giving basis appearance of being very short. Propodi again bearing 2 long terminal spines and a short terminal spine with immense teeth. Anterior row of spines much better developed than in pereopod II, 9 and 8 in number respectively for pereopods III and IV; spines apparently with round-tipped setules or teeth only on one side. Posterior row of 15 and 13 setae respectively; setae shaped as in pereopod II. Carpi without terminal spines; setae shaped as in pereopod II, setal formulae being (7,8) and (8,8) respectively for pereopods III and IV. Meri each with only 4 anterior setae. Ischia with 2 and 3 setae respectively and bases bearing about 4 lateral and 4 or 5 medial broom setae.

Pereopods V–VII (Figure 73A): Articles of these legs differing somewhat in shape from the foregoing due to remarkable differences in setation. Most prominent differences are presence of dense rows of long, thin, feathered setae on propodi, carpi,
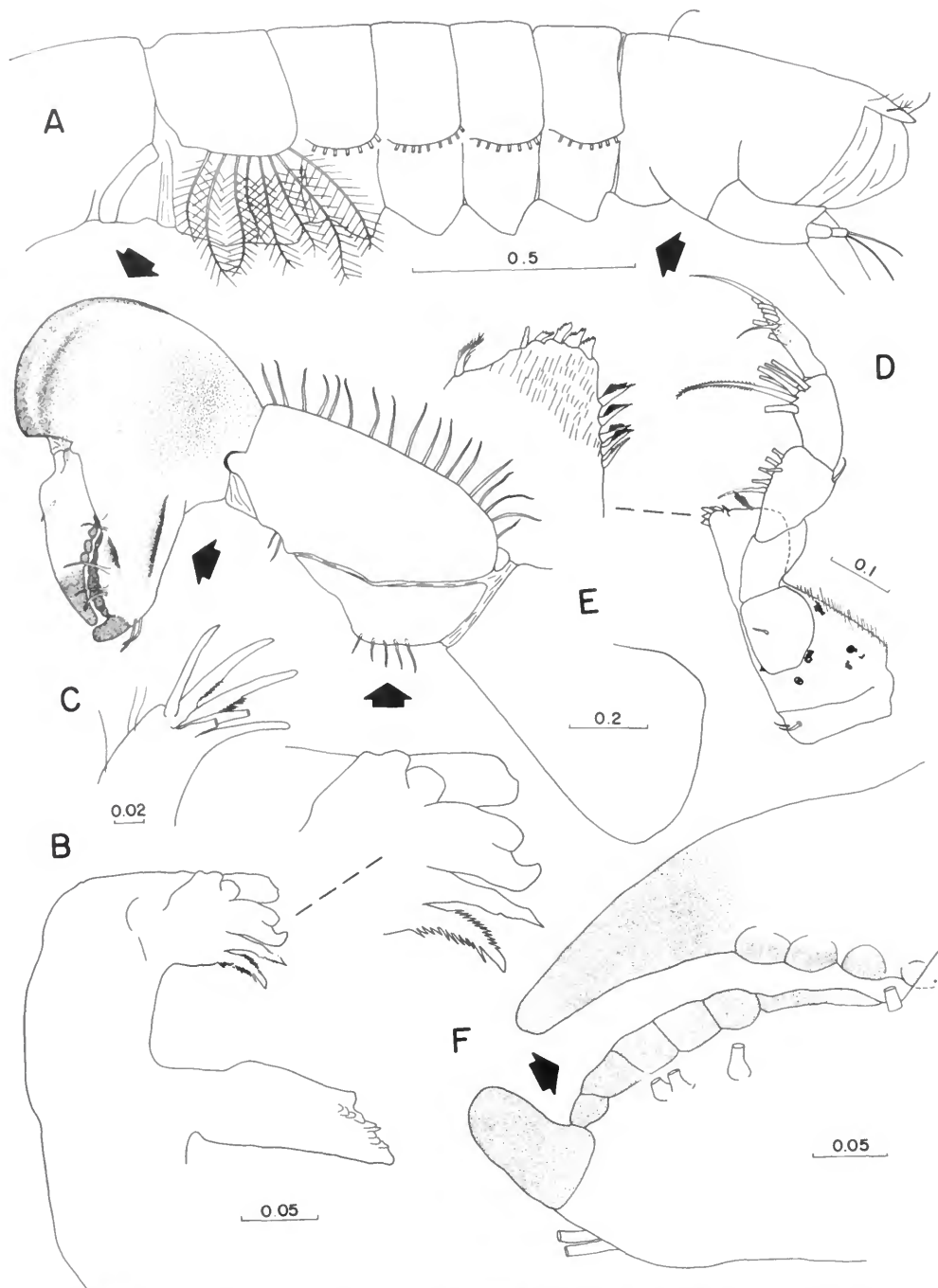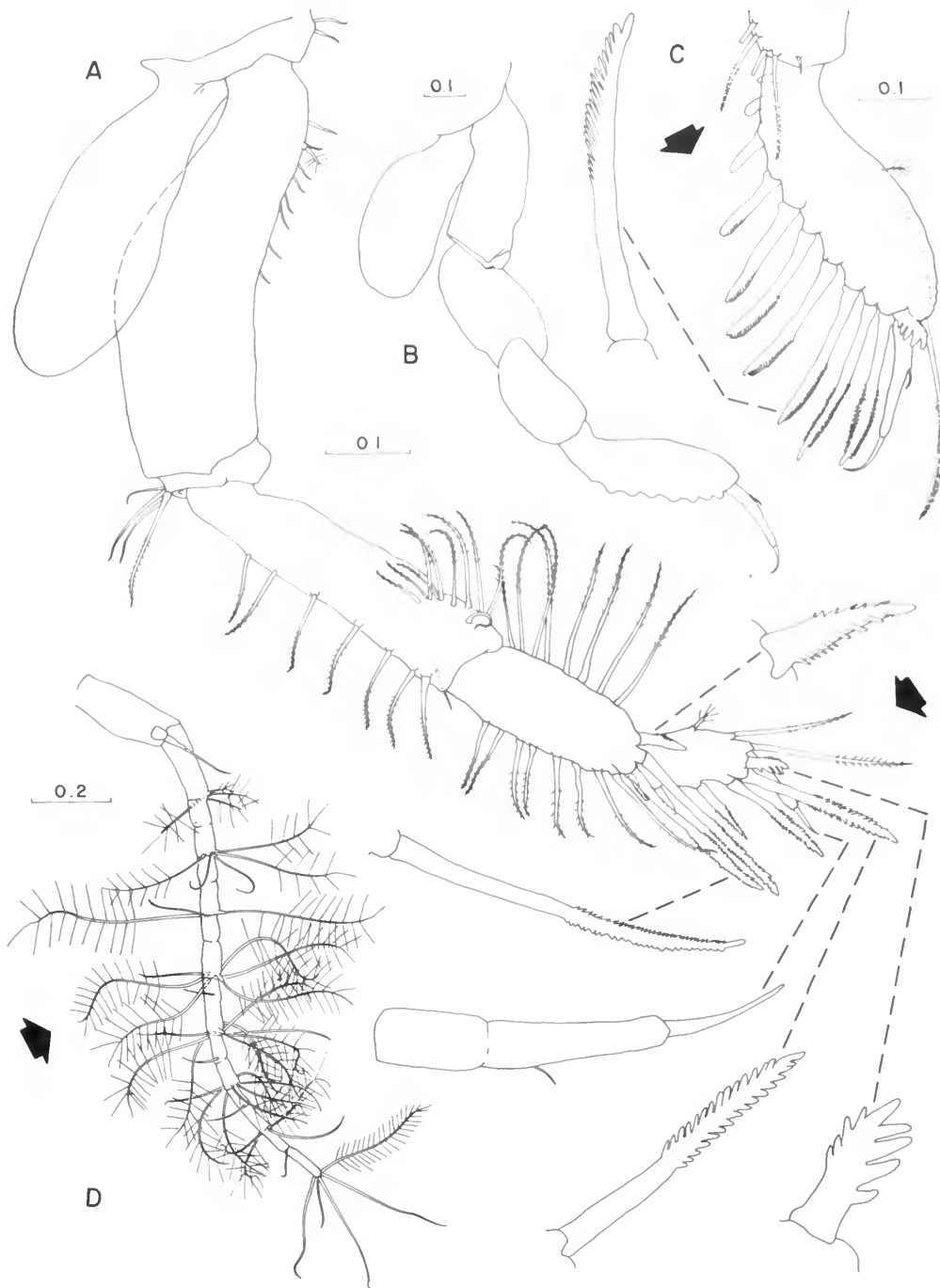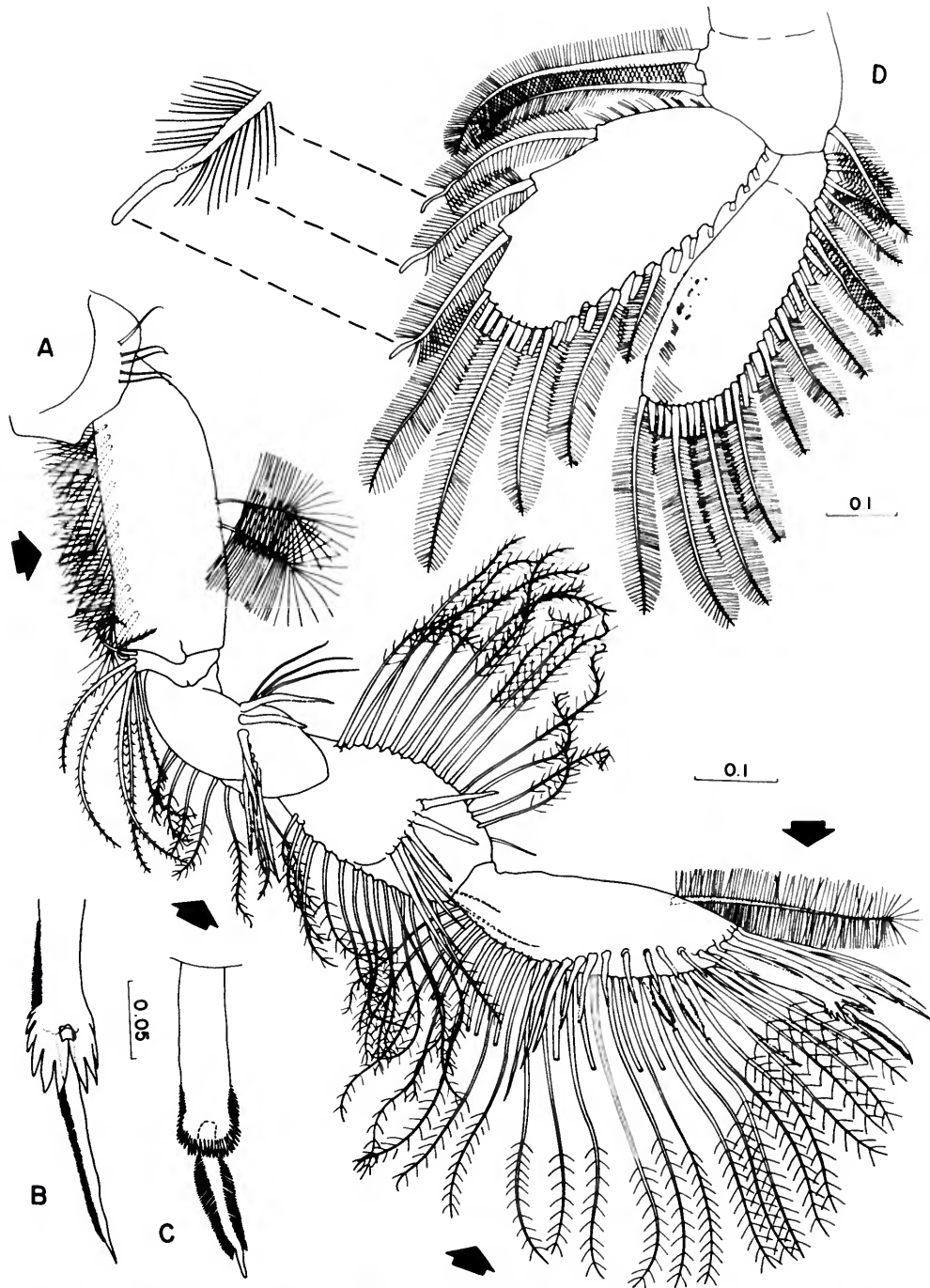
FIGURE 73.—*Venusticrus glandurus*, new genus, new species (all figures are of preparatory female 2, holotype, WHOI B. Sta. NN 1): A, left pereopod VI, anterior view; B, distal end of dactylus of same, dorsal oblique view; C, dactylus of left pereopod VII, dorsal view.

and meri and of transverse rows of stout, pointed spines on carpi and meri. Dactyli of pereopods V and VI with coarse and sharply pointed terminal teeth (Figure 73B), long spine with long setules, and subterminal ventral seta. Dactylus of pereopod VII much shorter than dactyli of V and VI and with very fine teeth (Figure 73C). Broom seta on propodi of V and VI dorsal and less than one-third of distance back from distal tip of article, exceedingly long and with long, dense hairs arranged around axis. This seta apparently absent on pereopod VII. Setal formulae of anterior and posterior setal rows (really one long U-shaped row) composed of sharply tipped, moderately setulated setae of varying lengths, (9,7), (16,6), and (24,14) on pereopods V–VII respectively. Running down midventral area between these 2 "rows" are 25, 30, and 25 extremely long, thin setae feathered along the distal one-half to one-third of their lengths. In addition to these setae, pereopod VII bears the usual row of 10 short, subterminal propodal spines, setulated or toothed as usual in most members of *Neotanais*. Carpi with rows of similar setae dorsally and ventrally, their numbers on pereopods V–VII being (6,12), (15,17), and (28,21) respectively. Carpi with 6, 7, and 11 stout, pointed spines in a vetrical anterior row. Meri with 6, 8, and 5 such anterior spines and 2 to 5 thin, apparently naked setae dorsally. Ventrally these pereopods bear 5, 8, and 12 thin, feathered setae respectively. Ischia with 8, 8, and 5 relatively long, feathered setae medially. Bases each with 2 large, lateral broom setae and 11 and 14 shorter, stout broom setae (pereopods V and VI) in a long, dense posterolateral row. The latter setae apparently are absent on pereopod VII. Coxae bearing 2 and 5 setae respectively on pereopods V and VI.

Pleopods (Figure 73D): Arrangement of setae, all densely feathered, similar to *Neotanais*; setal formula, (2,1) (3,8,13) (0,6;0,11,15). Protopodal setae very large. Slender hairs, some of considerable length, located proximally along medial edge of endopod and distomedial surface of exopod. Medial setae of endopod with tips differing from all others as in *Neotanais* and *Carololangia*; however, these are distinct in having their ends swollen, devoid of setules, slightly bent, and bluntly tipped.

Uropods (Figure 72D): Similar in general form to those of *Neotanais* and with 15 endopodal articles on each side. Most characteristic feature is

presence of many extremely long setae bearing very long and fine setules and each borne on and apparently articulated with an elongated basal article. As many as 7 of these occurring in a whorl around alternate articulations in combination with at least 1 shorter, naked seta. Terminal cluster of 5 setae containing only 1 seta with long setules. Each alternate articulation bearing a short naked seta. Exopod about 0.5 times the length of first endopodal article.

INTRASPECIFIC VARIATION.—The second specimen (body length 8.1 mm) was not dissected because of the limited amount of material. No significant differences from the holotype were noted.

CHROMATOPHORES.—Although I have examined well over 10,000 deep-sea tanaids, I have never before noted the presence of pigment, somatic or ocular, in specimens found at depths below about 500 or 600 m. Darkly colored chromatophores are scattered across the body surface of both specimens of *Venusticrus glandurus*. Notable accumulations occur on the dorsal surfaces of the pleotelson and the anterior part of the carapace. Other chromatophores are scattered throughout the interior surfaces of the body and are especially apparent in the oral area and along the large muscle bundles of the cheliped. With the exception of the two pairs of antennae and the maxillipeds (Figures 70G–I, 71D), other appendages do not possess chromatophores.

The chromatophores are variously shaped, usually punctate, punctostellate, or of various types of ringlike forms. Their color is deep black (or brown), presumably due to contained melanin. Sometimes a slight reddish tinge can be detected, possibly indicating the presence of more than one pigment, a common occurrence among crustaceans. Chromatophores containing black pigment usually lie in the endocuticle (Dennell, 1960).

The fact that chromatophores are visible at all is very probably an artifact of decalcification, and it is improbable that they are normally visible exteriorly when highly calcified. This was suggested by the difficulty of finding them at first in the specimen from WHOI B. Sta. 70, a specimen which was much more heavily calcified than the holotype.

It has been surprising to discover chromatophores in these deep abyssal animals, and their function, especially in a lightless environment, is unknown. It is even more surprising because they probably

are not visible externally when the specimens are fully calcified.

FUNCTIONAL MORPHOLOGY OF PEREOPODS II–VII.— The structure of the armament on pereopods II–VII is unique for the Neotanaidae. All legs resemble those of *Neotanais* in having specialized long and short terminal spines as well as long rows of setae on the propodi and carpi, at least on pereopods II–IV. But modifications are present which indicate specialization for functions in addition to walking.

It was observed above that the anterior row of propodal setae present in most species in *Neotanais* is here represented by stout spines in pereopods II–IV (Figure 72A,C). Pereopods III and IV differ markedly from pereopod II in the development of the propodus—or at least in the substantial reduction of this article in pereopod II—and in the presence of many more anterior spines in the former two appendages. In addition, these spines are uniquely shaped, being spatulate distally, with a row of closely set, round-tipped teeth forming the lateral edge along the distal half of each spine. The spines of pereopod II are armed with pointed teeth along both sides, similar to the usual long, toothed spines present in *Neotanais*. In addition, the carpus of pereopod II bears two exceptionally long subterminal spines of similar structure. The short axes of the propodi of pereopods III and IV are distinctly vertically oriented; that is, the anterior margin is turned downward, and the spatulate spines on that edge curve slightly posteriorly and medially.

One is immediately impressed by the similarity between the general structure of these articles and those of the second pereopod of many monokonophorans such as *Sphyrapus*. It is well known that these appendages are fossorial; that is, they are used in excavating the sediment. In the case of *Venusticrus* there are two such pairs of appendages, and they possibly serve a similar function. The curvature of the spines suggests a posteriorly directed digging stroke. The elongated body of *Venusticrus glandurus* resembles the cylindrical form of many tubicolous dikonophorans and would be consistent with life in an excavation of some sort.

A number of species of *Neotanais* have their propodal setae modified as stout spines; however, none is spatulate as is the case here. Somewhat different spatulate setae are found in *Carololangia*

mirabunda (Figure 77E), but in neither *Neotanais* nor *Carololangia* are the propodi vertically oriented. In *Carololangia* the spatulate spines are located in the posterior row, in *Venusticrus* in the anterior row. Hence, the paddle-like shape of this article is unique among the Neotanaidae and, insofar as known, among the Dikonophora.

The posterior three pairs of pereopods (Figure 73A) also are specialized, but for a different function. The usual neotanaid setal rows are present but, in this case, only on the propodi. These setae are well setulated, some with relatively long setules. However, between the two arms of the U-shaped rows—that is, along the ventral surface of the propodus—each leg bears a dense row of extremely long, thin setae, moderately well feathered distally and apparently articulated at their bases. Each row reaches along the entire length of the article. A similar row is not present in any other neotanaid, or, in fact, in any other dikonophoran of which I am aware.

The carpi of pereopods V–VII likewise are greatly modified. In other neotanaid genera there are usually an anterior and a posterior row of setae rising obliquely as one moves distally along the article. Most often the anterior setae are relatively thin and those of the posterior row even more slender. Between the distal terminal setae of these rows there is a slender, usually naked, median seta. The carpi of *Venusticrus glandurus* are remarkably different. There is a vertical row of six to eight stout spines with small setules borne centrally on the anterior side of the article. A similar row of spines is borne in an analogous position on the merus. On the carpus this row of spines is properly related to the slender dorsomedial seta and not far from the position in which it would be found in *Neotanais*. In addition, the shapes of these spines generally resemble those of the anterior propodal spines, the usual case for the anterior carpal setae in neotanaids. I interpret this ventral row as homologous with the anterior carpal row in other genera. However, a similar row is not present on the posterior side of the article, presumably a modification to suit the unique adaptive function of this appendage.

In addition to the spines described above, two rows of long, thin, distally feathered setae are present, one ventrally directed as in the propodus, but here, there is a vertical row as well. These

long rows of setae also are unknown in other neo-tanaid taxa.

The meri are similar to the carpi in having an anterior vertical row of heavy setae, possible homologous with the few setae usually present here in other genera. There is a long row of feathered setae distally and ventrally as in the previous two articles. These setae are present only distally, that is, distal to the upward curve of the meri. Hence, they form a continuation of the long bank of feathered setae on the carpus and propodus. More proximal setae would be medially directed.

There are up to eight long, feathered setae on the ischia. In *Neotanais* and *Herpotanais* they are only one to four in number and never feathered. In *Carololangia* they have longer setules than in *Venusticrus*.

It is tempting to speculate that these setae aid in locomotion by swimming in conjunction with the particularly well-developed pleopods. However, it is difficult to imagine how the setae would be "feathered" (as one "feathers" oars in rowing) on alternate strokes. Also, there appears to be no modification in the shapes of the pereopodal articles as might be expected for a natatory limb. The pleopodal articles, for instance, are flat, and their surfaces undoubtedly function in concert with their setae.

Another possibility is that the posterior pereopods function in moving water in and out of a tube or excavation. This suggestion is appealing in view of a possible fossorial habit for this genus. Again, both legs and pleopods probably would function in the aeration of such a cavity. However, many tubicolous tanaids aerate their tubes satisfactorily without such structures and, in some cases, without pleopods as well.

There are two notable sensory adaptations which parallel these specializations. The first of these is the immense development of the dorsal, propodal "broom" seta, here more closely resembling a laboratory bottle brush. The second modification is the presence of a dense bank of up to 14 stout broom setae on the posteromedial surface of the bases of pereopods V and VI; a smaller number of similar setae are to be found on pereopods II–IV as well. These sensory devices may be related to monitoring the quality or quantity of the water being moved by the pereopods if, in fact, this is their function.

The stout anterior spines on the carpi and meri of pereopods V–VII undoubtedly are specialized for some function. Possibly the carpi and meri of these appendages touch the substrate only on the anterior side. If so, and if these spines are homologous with the anterior setae of *Neotanais*, the posterior row, at least of the carpus, has disappeared, no longer being of functional significance.

REMARKS.—Two specimens of this species are known. Both have large rudimentary oostegites but not the anlagen of male gonopores. If development is similar to that of *Neotanais*, they probably are preparatory females 2.

MATERIAL.—WHOI B. Sta. NN 1, Gay Head–Bermuda Transect, 4950 m, 1 P ♀ 2 (holotype); WHOI B. Sta. 70, same area, 4680 m, 1 P ♀ 2.

LOCATION OF MATERIAL.—NMNH: holotype (USNM 143227); WHOI 70 (USNM 143228).

DERIVATION OF NAME.—Referring to the acorn-like shape of the pleotelson in dorsal view. From the Latin *glans* (acorn) and the Greek *oura* (tail).

Carololangia, new genus

TYPE-SPECIES.—*Carololangia mirabunda*, new species. By monotypy and present designation.

DIAGNOSIS.—*Stages Other Than Copulatory Male* (copulatory males unknown): Presence of a number of feathered setae of various lengths in lateral and dorsal rows on pereonal tergites, pleotelson (dorsal row), uropod (protopod and both rami), chelipedal carpus, pereopods, and maxillipedal palp. Pleotelson very short, only about half as long as wide; posterior edge expanded upward as 2 semicircular keels, each bearing a fan of about 20 to 25 stiff, feathered setae (all other known genera are without setae on pleotelson, but fine hairs or an occasional broom seta may be present); articulation of uropods located ventrally. Carapace short, about as wide as long. Uropodal endopod composed of short, stout articles, exopod as long as first 2 endopodal articles and setated as noted above. Second maxilla with a clump of about 15 long, bluntly tipped, naked setae terminally on lateral side of fixed endite (other known genera with only 1 or 2 such setae).

REMARKS.—The following additional characters also may be determined, later, to be of diagnostic value at the generic level: (1) chela totally devoid of dorsal crest; (2) distal claw of fixed finger (chela)

straight or actually decurved rather than curving upward; (3) expanded shape of meri and carpi of pereopods V–VII; (4) short dactyli without terminal dorsal cleft or opening on pereopods V–VII (cf. *Venusticrus glandurus*); and (5) specific pattern of pereopodal setation.

The structure of the pleotelson and uropods of genus *Carololangia* are so radically different from those of other tanaidaceans as to suggest the erection of a new family for the genus. However, close examination of the uropod reveals a number of articles in the rami typically found in the Neotanaidae although the setation differs from all other known species in the family. In addition, the structure of the body, antennae, mouthparts, pereopods, and pleopods are typically neotanaid. Indeed, some of these structures are almost identical with those of other neotanaid genera, and they clearly indicate the affinity of the genus.

DERIVATION OF NAME.—In honor of Professor Dr. Karl Lang, of the Swedish State Museum of Natural History, whose extensive work on the order Tanaidacea has made the completion of this study infiinitely easier. *Carololangia* is feminine.

Carololangia mirabunda, new species

FIGURES 74–77, *103*

DIAGNOSIS.—Because *Carololangia* is monotypic, the characters listed in the generic diagnosis are diagnostic for this species as well.

DESCRIPTION OF PREPARATORY MALE HOLOTYPE (*Eastward* Sta. 7542).—Assuming a developmental pattern similar to that of *Neotanais*, this specimen probably is a preparatory male. Oostegites or their scars and female gonopore scars are absent, and prominent male genital cone and gonopore anlagen are present.

Body (Figure 74A): 11.8 mm long and 7.2 times longer than wide. Surface ornamented by 100 to 200 long, feathered setae.

Carapace: Very short compared to that of other species, being 1.1 times wider than long and only 0.13 times as long as body. Oblique furrows very shallow, anterolateral keels not pronounced. A single anterolateral seta is followed by another single, lateral seta somewhat posteriorly. Several (4 or 5) long, feathered, anteriorly directed setae located in a vertical row ventrally on carapace next to tips of mandibles and first maxillae.

Pereonites: Pereonites 3–6 generally square in dorsal view, but widest over pereopods. Pereonite 5 (Figure 74c) 1.1 times wider than long. Each pereonite with numerous feathered setae in a lateral row on each side and several more in an anterior, dorsal row. Pereonites rounded ventrally and without significant midventral sculpture. Pleonite 7 bearing marked genital cone and gonopore anlagen ventrally.

Pleonites (Figure 74B,E,F): With 10 to 20 feathered setae dorsally in a long row stretching from one side to the other. Lateral margin of each tergite sloping gradually posterolaterally; epimeres rounded in dorsal view. Pleonite 1 about as wide as pereonite 7 and only very slightly wider than pleonite 5. Sternites smooth and rounded midventrally in lateral view.

Pleotelson (Figure 74B,D–F): Short, width 2.1 times greater than length, widest point being at attachments of uropods midway along lateral margin. Uropods attached to pleotelson ventrally (Figure 74F). Compressed laterally behind point of uropodal attachment but again expanding posteriorly into a raised ridge bearing 2 semicircular rows of stiff, feathered setae; setal rows not meeting middorsally. Between 15 and 20 long, feathered setae located in a transverse row similar to those of pleonites. Viewed laterally, dorsal surface of pleotelson rises posteriorly to form a crest bearing stiff setae; this is the highest point in pleon. Anal aperture large, below crest but protruding posterior to it and hence visible from above (Figure 74D). Two wide, slightly raised areas present ventrally. Pleotelson clearly articulated to pleonite 5.

First Antenna (Figure 75A): Length of first article 3.6 times greater than width. Article 1 longer than article 2, which, in turn, is longer than article 3. Article 4 much longer than article 3 and almost twice as long as articles 5–7 combined. Large esthetascs 2 in number and bearing several circumferential constrictions; tips slightly tapered. Articles 4–6 markedly oblique distally, each overlapping and surrounding next distal article. Setation as in figure; not remarkably different from that of *Neotanais*.

Second Antenna (Figure 75B): Slender. Setation as in figure. Generally not remarkably different from that of *Neotanais* except for presence of occasional feathered setae. Dorsal surface of first article with scales as in *Neotanais*.

FIGURE 74.—*Carololangia mirabunda*, new genus, new species (all figures are of preparatory male, holotype, off North America, *Eastward* Sta. 7542): A, dorsal view (pleotelson bent downward showing articulation with pleonite 5); B, pleon, lateral view; C, pereonite 5, dorsal view; D, pleotelson without setae, dorsal view; E, same, with setae; F, same, ventral view; G, left uropod, lateral oblique view.

FIGURE 75.—*Carololangia mirabunda*, new genus, new species (all figures are of preparatory male, holotype, off North America, *Eastward* Sta. 7542): A, left first antenna, dorsal view, with enlargement of tip; B, left second antenna, ventral view; C, right mandible with enlargement of incisive spines, anterior view; D, incisive spines of left mandible, anterior view; E, labium, posterior view; F, right first maxilla, posterior view; G, left second maxilla, posterior view, with enlargement of fixed endite; H, cleft spines, fixed endite of right second maxilla, same view.

Right Mandible (Figure 75c): First incisive spine serrate on inner side and naked on outer side. Second spine naked on both sides of part remaining (about two-thirds of spine missing). Third spine broad basally and apparently entirely naked, similar to that in *Neotanais;* tip broken. Pars molaris bearing about 7 teeth.

Left Mandible (Figure 75d): Overall shape similar to that of *Neotanais.* Proximal incisive spine serrate on inner side; outer side naked, as are both sides of second spine. Tips of both spines broken. Lacinia mobilis with only 2 rounded teeth; large posterior lobe very much elongated but bluntly tipped. Pars molaris with about 10 teeth.

Labium (Figure 75e): Similar to that of *Neotanais.*

First Maxilla (Figure 75f): Similar to that of *Neotanais.* Nine long, terminal spines and a short, slender, naked spine on external endite of both sides. At least 3 of these spines with long rows of round-tipped teeth.

Second Maxilla (Figure 75g): Similar to that of *Neotanais.* Movable endite with 3 and 8 setae on external and internal endites respectively. Fixed endite of left appendage with 3 terminal spines bearing long setules; 1 slender, subterminal spine; 2 stout, bifid spines; and an extraordinary cluster of 14 long, bluntly tipped, naked spines. Right side similar except for stout, forked spines, one of which is probably trifid (one branch broken) and the other bifid but with an unusual unilateral row of about 10 long, pointed teeth or spines (Figure 75h). Medial row composed of 35 setulated setae and 6 stout, irregularly tipped spines. A number of stout "hairs" lie proximal to the latter.

Maxilliped (Figure 76a): Coxa rounded and rising along lateral curve of basis and bearing 3 short setae medially. Palp shaped as in *Neotanais* with following setal formula (f=feathered setae): (1,0,5f+3f+1f,4+4,18). Feathered setae on article 3 arranged as follows: row of 5 medially, row of 3 posteriorly, and 1 seta laterally on distal corner. Endite (Figure 76b) with long, terminal seta laterally as in *Neotanais* and 4 slender and 2 stout spines more medially. Nine filter setae present along medial margin; these differing in shape from *Neotanais,* each having a long spine medially and a long row of fine setules unilaterally along axis from spine to distal tip of seta.

Cheliped (Figure 76c,d): Generally as in *Neotanais.* Three or 4 feathered setae borne laterally on coxae. Ventral setae of merus and carpus very long and brown. Those of latter article of very disparate length and thickness. Dorsal carpal setae 13 in number; all are fully feathered. Distolateral articulating protuberance of carpus with brown border. Propodal teeth 5 in number, connected, with or without distinct crowns, and often merging with each other. Claw deflected downward with a ventral convexity at its base. Brown border continuing proximally from base along ventral surface of propodus for over one-half its length. Cutting edge smooth proximal to teeth. Dactylar teeth 5 in number, rounded or flat, and fused with dactylus; an irregular, brown area present proximal to teeth. Setal arrangement as follows: 2 ventromedially, 1 pair and a single seta laterally on fixed finger; 1 long seta dorsally and medially on propodus at articulation of dactylus; dactylus with 1 medial, distally directed seta.

Pereopods II–VII: Setation and shape of articles often considerably different from those of other genera. Legs give marked impression of being shorter because of relatively shorter bases.

Pereopod II (Figure 77a): Dactylar spine 0.4 times length of article, shaped as in *Neotanais.* Fine, proximal dactylar seta present as in *Neotanais.* Propodus with short terminal spine in same position as in all other genera; spine curved and with massive teeth on both sides. In anterior setal row, next to this spine, stand 3 very large, toothed spines. Proximally in anterior row are 4 spines of similar structure but of increasingly reduced size. Posterior row composed of 7 very long, slender, feathered setae. One small broom seta present proximal to this row. Carpus with subterminal spine very short, curved, and with a few slender teeth. Anterior row composed of 5 feathered setae, posterior row of 3 feathered setae of much greater length. Two long, feathered setae on merus, 3 on ischium, 1 on basis. One large broom seta also present on basis. Coxa without armament.

Pereopod III (Figure 77b–d): Short and long terminal propodal spines as in pereopod II. Anterior row not as in pereopod II but with distal side setulated and proximal side with short, parallel-sided, bluntly tipped teeth as illustrated for pereopod V (Figure 77e). The two distalmost setae of posterior row long and feathered; remainder of row composed of short spines as in anterior row. Anterior carpal row made up of 7 feathered setae, with
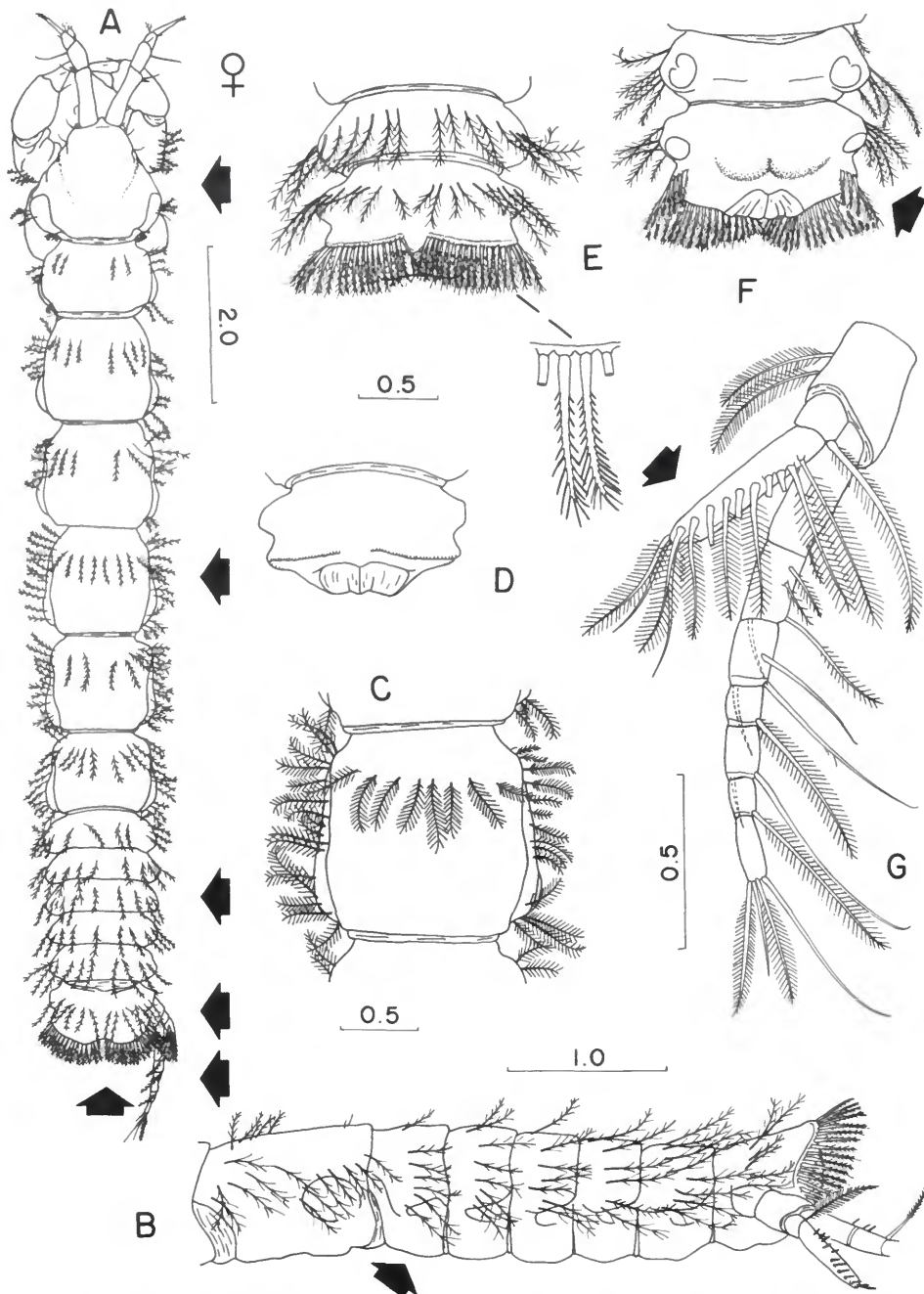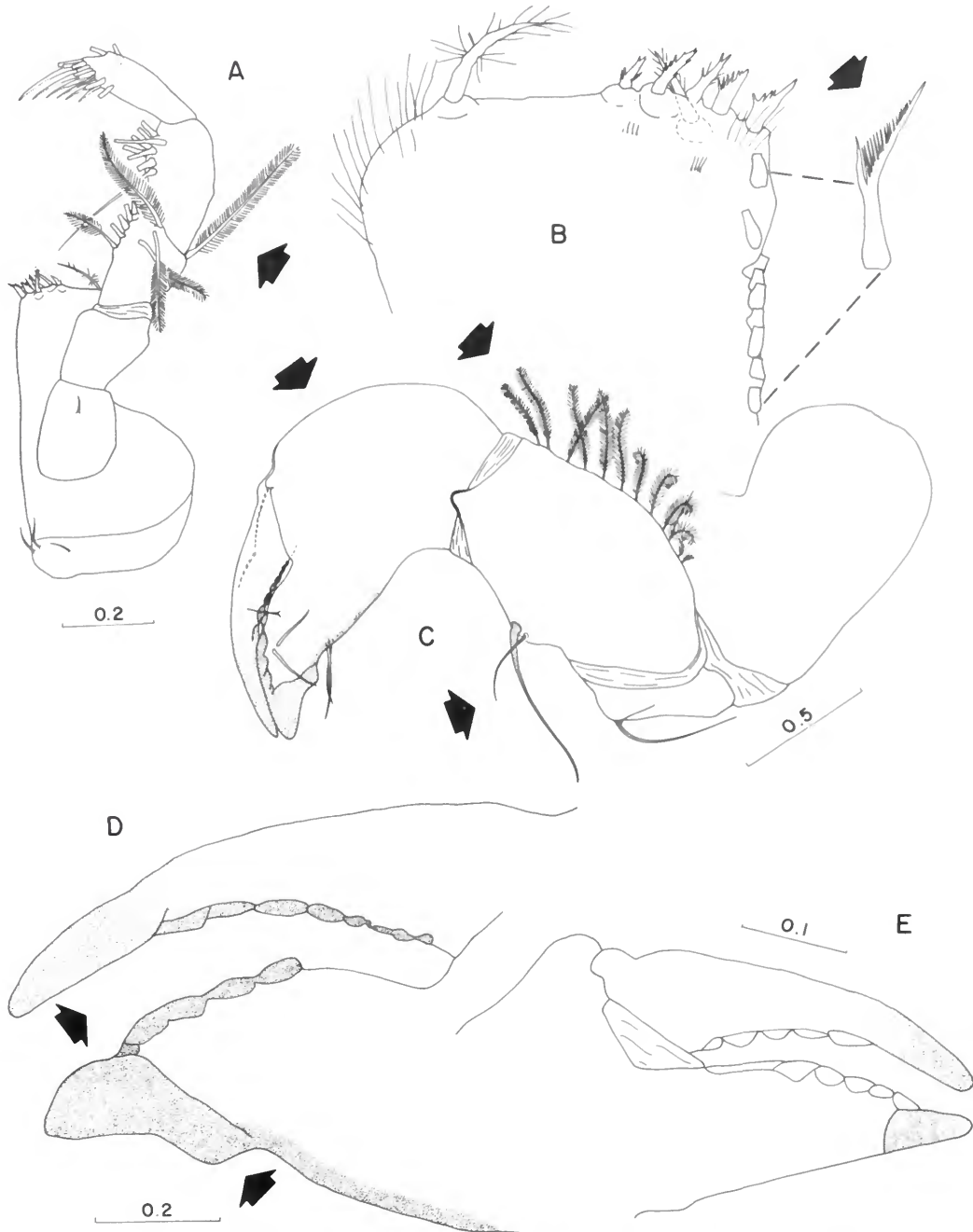
FIGURE 76.—*Carololangia mirabunda*, new genus, new species (all except E are of preparatory male, holotype, off North America, *Eastward* Sta. 7542): A, left maxilliped, posterior view; B, basal endite of same, anterior view, with enlargement of medial seta; C, left cheliped; D, left chela (without setae); E, right chela (without setae) of juvenile from Bermuda, WHOI B. Sta. Ber. 5.
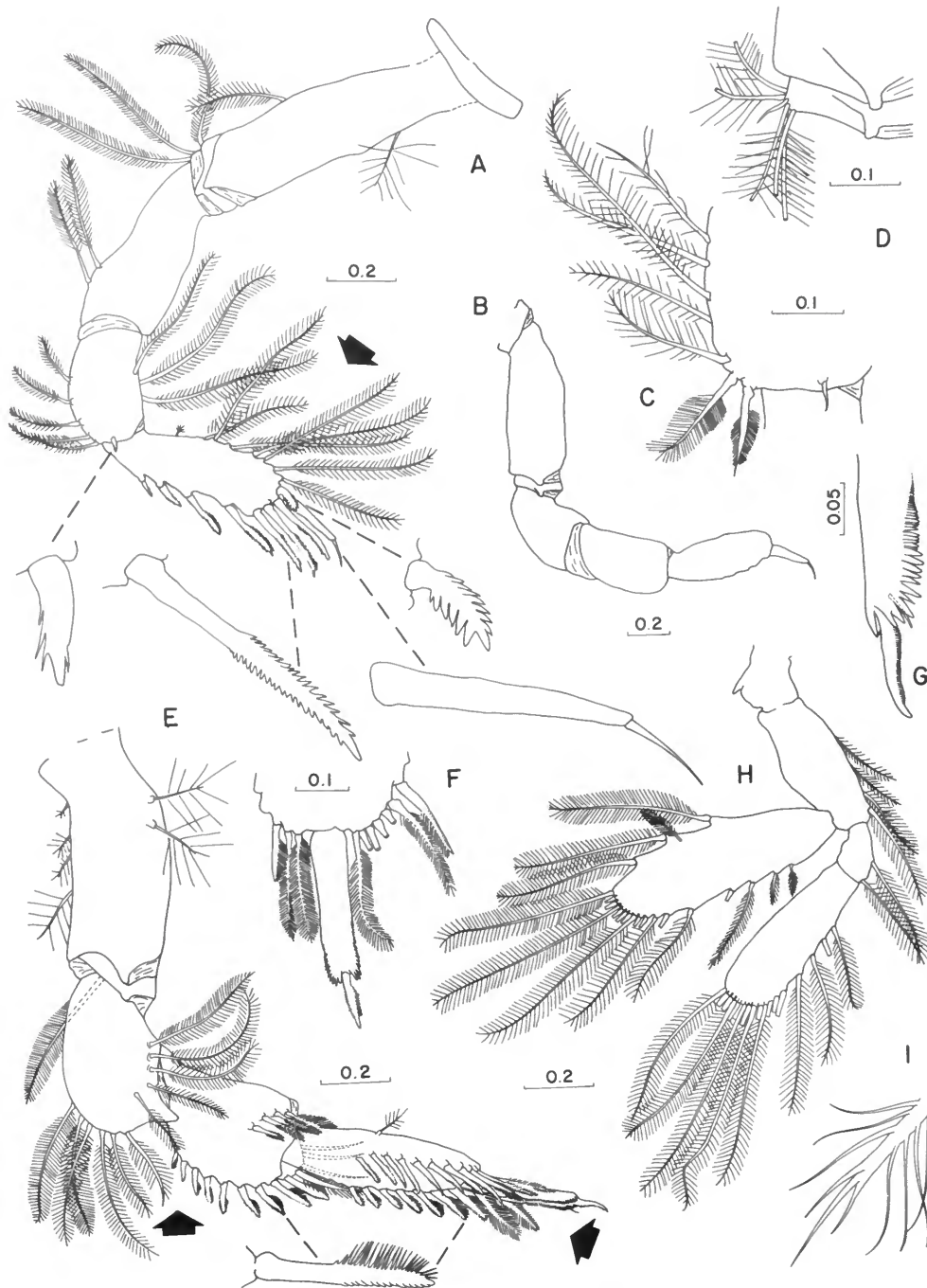
FIGURE 77.—*Carololangia mirabunda*, new genus, new species (all figures are of preparatory male, holotype, off eastern North America, *Eastward* Sta. 7542): A, left pereopod II, anterior view; B, left pereopod III, without seta (to illustrate shape of articles), anterior view; C, carpal setae of same leg; D, ischial setae of same; E, left pereopod V, anterior oblique view; F, distal tip of same; G, dactylus and spine of same, lateral oblique view; H, left pleopod 1, anterior view; I, enlargement of distal tip of a medial endopodal seta.

MATERIAL.—*Eastward* Cruise 27–67, Sta. 7542, southeast of Cape Hatteras, North Carolina, 4690 m, 1 P ♂ holotype; WHOI B. Sta. Ber. 5, Bermuda Slope, 2000 m, 1 Juv.

LOCATION OF MATERIAL.—NMNH: holotype (USNM 143229); WHOI Ber. 5 (USNM 143230).

DERIVATION OF NAME.—Referring to the highly unusual and ornate appearance of this species. From the Latin *mirabunda* (full of wonder).

Intraspecific Variation

VARIATION WITHIN POPULATIONS

Chance genetic or environmentally induced, developmental, and sexual differences all introduce variation within a population. When working with a poorly known taxon, it is important to establish the limits of intraspecific variation before preceding with the classification of specimens. Failure to recognize the range of variation within a taxon may result in synonymy. For example, on these grounds Lang (1955) has synonymized *Apseudopsis* (Norman, 1899) with *Apseudes* and *Apseudopsis ostroumovi* (Băcescu and Cărăuşu, 1947) with *Apseudes acutifrons*. Many authors have been able to give little, if any, information on the amount of variation that one can expect to encounter in deepsea tanaidacean species.

A detailed study of intraspecific variation in *Neotanais* was carried out for the first time on *Neotanais micromopher* from relatively closely located stations on the Gay Head–Bermuda Transect. This study was based primarily on animals from WHOI Benthic Sta. 76. Data from Stas. 64 and 66 were added where stages were missing from Sta. 76 and where deemed to be appropriate without biasing the results. *N. micromopher* was chosen because of the large amount of material available; these specimens also formed the basis of the developmental study. Most of the other species in the Neotanaidae in which variation could be observed—i.e., those species known from a number of specimens—vary about as much as *Neotanais micromopher*. *Neotanais armiger* (q.v.) apparently is a notable exception.

Characters determined to be of some taxonomic significance among the species of *Neotanais* are discussed; other characters, used by previous workers but found here to be useless because of their change with age or their uniformity among species, have not been included. Because of limited material, usually not more than five individuals were selected to represent a developmental stage. Most counts, measurements, and ratios are presented in the tables, and the data are summarized and discussed here. Dashes or blank spaces in the tables indicate that data are missing, usually because a structure is missing or broken.

SHAPE OF BODY IN DORSAL VIEW.—The frequently cited and important body-length/carapace-width ratio provides a measure of overall bodily shape. The ratio is slightly less in the manca 1, 5.2, than in older stages, 5.7 to 5.8, primarily because of the incomplete development of the last pereonite and of the pleonites in the former. Among older stages the ratio usually is very stable in *Neotanais micromopher* (but considerably different for copulatory males in some species).

SHAPE OF CARAPACE IN DORSAL VIEW.—The carapace length-width ratio, an indicator of carapace shape, remains practically the same throughout life: mancas 1, 1.3; copulatory females, 1.2; preparatory males, 1.2; and copulatory males, 1.4. In some species (e.g., *N. dinotometer*), the copulatory males may vary substantially from all other stages. This pattern contrasts with Lang's (1958) report that there is a steadily progressive change in the shape of the carapace from preparatory females to protogenous males in *Tanais stanfordi*. Moreover, in *Neotanais* the different types of males all have the same carapace shape, contrasting with the findings of Bückle Ramírez (1965:765, fig. 42) for *Heterotanais oerstedi*, where the different types of copulatory males have greatly divergent carapace shapes.

SHAPE OF PLEOTELSON IN DORSAL VIEW (Figure 3).—The width-length ratio describes pleotelsonal shape. In early stages the pleotelson is slightly longer than in later stages (manca 1, 1.6; preparatory female 2, 2.1; intermediate female, 2.0), but the specific configuration of the pleotelson usually permits recognition of the species to which the mancas belong. In the copulatory male the pleotelson usually has a shape similar to that of the other stages (ratio, 2.1).

The amount of variation in *Neotanais* is far less than that described for some other tanaidaceans such as the shallow-water *Apseudes acutifrons* by Lang (1955:66, fig. 5).

FIRST ANTENNA (=ANTENNULE) (Figures 5J,

6c,e.—The terminal (seventh) article first appears in the juvenile stage. The number of articles is then fixed at seven and does not increase. This contrasts both with the Monokonophora (e.g., Wolff, 1956:198), where the flagellum is composed of many articles and in which there is appreciable growth, and with many dikonophorans in which there is no growth in early stages. Lang (1957:7) states that the articles of the first antennae of male *Leptochelia* increase in number with age.

Lang (1958) has noted a progressive change in the length of the first article with age in *Tanais stanfordi*. The first articles of older females more closely resemble those of copulatory males where they are proportionately longer than in other stages. The ratio of carapace length to length of first article indicates that this article remains about the same length relative to the length of the carapace (1.6 to 1.8) throughout life in *Neotanais micromopher* except for copulatory males, where it increases in relative length, the ratio decreasing to 1.4.

The shape of the first article, an important taxonomic character in some species of *Neotanais*, varies greatly among species; however, intraspecific variation is limited. A relative increase in length is apparent with age, the ratio of article length to width varying as follows: mancas 1, 3.8; mancas 2, 4.0; and females, 4.2. The preparatory males have a ratio of 4.4, relatively longer than any other stage except the adult male in which the ratio is 5.9.

The number of setae on the first antenna is very constant, with most increase occurring in setal rows on articles 1 and 2 during the manca instars.

The esthetasc of the penultimate article is missing in the manca instars, but an esthetasc is present on article 5 in all stages. The fourth article is naked except for a dense clump of long, slender, smooth esthetascs in the copulatory males.

SECOND ANTENNA (=ANTENNA OF SOME AUTHORS) (Figure 6D,F).—No significant variation of any type was observed.

MANDIBLES.—The number of molar teeth (Figure 7F) is almost identical on both mandibles. There is an increase in numbers of teeth with age, mancas 1 having about eight and older stages ten or eleven. The molar processes are absent in copulatory males.

No difference was observed in number of incisive spines (Figure 7A–C), and their form is gen-

erally about the same in both mandibles. Some minor variation in the lacinia was noted among the individuals of a species. The mandibles of the copulatory males are greatly reduced and nonfunctional.

SECOND MAXILLA (=MAXILLA OF SOME AUTHORS) (Figure 8D).—The only noticeable variation in armament was in the number of setae in the medial row. This was substantially lower in the manca 1 (six to eight) than in older stages (ten to twelve). Variability is much greater in copulatory males; this appendage is greatly reduced and the different parts are not always identifiable.

MAXILLIPED (Figure 9A–C).—The armament of the maxilliped is very stable. The only appreciable differences were found in the numbers of medial setae on the endite and in the setae of the fourth and fifth palpal articles, all of which increase in number with age, especially early in life. Many setae are missing in the copulatory males because of the reduction of this appendage.

CHELIPED.—The number of dactylar teeth and proximal denticles on the propodal finger (Figure 9K) increases with age. The large, distal, propodal teeth remain five in number throughout life (not copulatory males). Some species, such as *Neotanais hastiger*, demonstrate more variation than *N. micromopher*.

Copulatory males show little variation in dentition in *Neotanais micromopher* as illustrated by Figures 10A–E, 11 (see discussion, page 32). This sort of variation is analagous to that established for *Heterotanais oerstedi* (Bückle Ramírez, 1965:765, fig. 42).

The ratio of propodal length to width remains constant at about 2.1 in stages other than copulatory males. Copulatory males, in which the chelae are strongly dimorphic, display a length-width ratio of about 2.4.

The number of setae in the dorsal row of carpal setae (Figure 9J) increases with age: there are three or four setae in mancas 1 and up to seven in the preparatory female 2.

These results differ from Lang's (1953a:348) findings in the shallow-water *Apseudes spectabilis*, a species which varies considerably in the armament and proportions of the cheliped.

ARMAMENT OF PEREOPODS II–VII (Figures 12, 13; Table 19).—Each seta and spine on pereopods II–VII was counted in several representatives of most

developmental instars. Where more than one representative of an instar was examined, each row of setae (anterior and posterior) of each propodus and carpus was compared among all individuals. The most frequently occurring number in each row was taken as representative for that stage, and these counts are summarized in Table 25. When two different counts co-occurred the same number of times, both counts, separated by a hyphen, are listed.

A distinct pattern of pereopodal setal addition emerges from the summary in Table 25. Zero to two setae, often one seta, are added to each row with each successive molt. Wolff (1956a:198, 205) has demonstrated similar setal addition with age in *Apseudes* (=*Leiopus*) *galatheae* and *A.* (=*Leiopus*) *gracillimus*.

Occasionally, a larger number of setae was present in a given row in one stage than in the next older stage. This is presumably due to natural variability and has been observed to occur in *Apseudes* by Lang (1953b:420).

The individuals chosen for examination were, when possible, selected to reflect maximum variation in body size within each instar. The results show little correlation with body length and indicate a close dependence of pereopodal setation on the number of ecdyses through which an animal has passed rather than on body length alone.

The "short" terminal spines on the propodus (pereopods II–IV) and carpus (pereopod II only) do not increase in number with growth in *Neotanais micromopher*. They remain constant in number from manca 1 through copulatory male. Although constant in *N. micromopher*, the number of "long" terminal propodal spines varies in certain other species; for example, from one to three in *N. armiger*. The variation usually is not more than one spine on either side of the most commonly occurring number of spines in those species showing variation. In some species the number of spines differs in a regular fashion on each of the three pereopods—for example, pereopod II having two spines and pereopods III and IV each bearing only a single spine.

The amount of variation in numbers of setae present within a given instar increases markedly with age. This is clearly shown by a comparison of the counts for the mancas 1. All four individuals counted are identical with the exception of three

setal rows (out of 24 rows) in one animal. In Table 19 the increase in variation is obvious, as indicated by increasing indecision as to a "typical" setal count for each instar.

Variation in setation between the left and right members of a pair of appendages is minimal; if the setae in a row are not identical in number, they differ by only a single seta or two setae at the most.

The setae on the bases, ischia, and meri vary appreciably in number, probably because of mechanical damage. Broom setae, found only on the bases and propodi, vary considerably on the bases (zero to four), and from limb to limb; only a single broom seta is ever present on the propodus. The broom setae are very slender and apparently are more fragile than other setae; no clear pattern of setal distribution was detected for the bases.

The form of the distal dactylar serrations on pereopods V–VII has been used by some authors (e.g., Norman and Stebbing, 1886) as a taxonomic character. In some species they are coarse, in others fine, and in still others they vary from one appendage to another. Considerable variation was noted within a population in *Neotanais hastiger*, where one female had coarse teeth on pereopods V and VI but fine teeth on pereopod VII. A male from the same station had fine teeth on all three pereopods. Other populations varied from these animals in this regard. The amount of variation within and between populations compromises the taxonomic usefulness of this character.

PLEOPODS (Figure 10k–m).—Pleopodal length generally increases along with body length between instars (Figure 79).

The relative length of the pleopodal setae as measured by the ratio of terminal endopodal setal length to endopodal length increases markedly with age; that is, the setae grow more rapidly than the articles. In the juvenile the ratio is between 0.3 and 0.4; in the preparatory female 2 it has risen to almost 0.6; in the preparatory male it is 0.8; and by the time a copulatory male has been formed it is 1.5. There is no observable pattern of variation with body length within an instar. This sort of marked setal growth among various instars, except for the formation of copulatory males, appears to be unique to *Neotanais micromopher* in this genus.

The number of setae also increases with age: juveniles and preparatory females 1 have about two to four terminal endopodal setae; preparatory

females 2, four to six; copulatory females, eight to ten; preparatory males, eight; and copulatory males about eight to twelve. There seems to be some relationship, although not constant, between body size and the number of setae within an instar.

In addition to increasing in number and length, the setae increase in degree of setulation in *Neotanais micromopher* (Figure 10i–M). There are essentially no setules in juveniles and preparatory females 1. Setules are first present in appreciable numbers in preparatory females 2 and are first found at the tips of the setae. In copulatory and intermediate females and in preparatory males (Figure 10L) the setules appear almost all the way to the bases of the setae, and in copulatory males setulation is complete.

The pleopods are the main neotanaid swimming organs. Increase in setal number and length and in the number of setules obviously keeps pace with the growing need of the animal for more thrust in swimming, especially in the probably highly motile copulatory males.

The number of setae on the various pleopods of an animal does not vary significantly and certain rows are invariable.

LENGTH OF UROPOD (Figure 6A,B; Table 28).— The endopod increases in length with age: all mancas 1 have four articles and mancas 2 have six. The increase continues, but an animal adds either a single article or none at each ecdysis thereafter. (See discussion of small primary copulatory males, p. 198.)

Age-related increase in the length of the uropodal endopod is known for species of *Leptochelia* (Lang, 1957:7), *Tanais stanfordi* (Lang, 1956c:255), *Apseudes* (=*Leiopus*) *galatheae* (Wolff, 1956a:198), and there is an indication of a slight increase in *Herpotanais kirkegaardi* (Wolff, 1956a:227). In *Leiopus galatheae* (Wolff, 1956a:227) the uropodal exopod can increase in length. Lang (1957:5) states that the exopod can be composed of either one or two articles in *Tanaissus liljeborgi*. In *Neotanais* the exopod is always composed of two articles.

Lang (1957:5) goes on to say that the articulation between the first and second exopodal articles in *Tanaissus* is sometimes obscure. This is often true for the first two endopodal articles in the Neotanaidae.

SUMMARY.—Meristic variation with age occurs in the molar teeth of the mandibles, the uropodal

endopodal articles, the proximal denticles on the fixed chelipedal finger, and setae in various places. Setae showing progressive increase in numbers are found laterally on the first and second articles of the first antenna, the medial row of the second maxilla, the dorsal chelipedal carpal surface, the fifth palpal article of the maxilliped, the carpi and propodi of pereopods II–VII, and the pleopods. In each of these cases, the setae are arranged in a row and generally are similar in structure. Variation in the same row between members of a pair of appendages is very low; often the two are identical in number. Broom setae and specialized spines usually are constant in number throughout life in *Neotanais micromopher* and some are constant throughout the genus.

Meristic variation usually is not correlated with body size alone but with the number of ecdyses through which an animal has passed. For example, the larger animals within a developmental instar will not necessarily have a greater number of setae than smaller individuals. For absolute measurements of those body parts which increase in size with body size, the use of ratios removes the effect of differences in body size within an instar. These ratios may change with age, but this change reflects variation among instars.

The amount of variation among individuals within an instar increases with age; for example, young animals are more nearly alike in numbers of setae than older animals.

The overall impression gained from this study of *Neotanais micromopher* is that the numbers and dimensions of some structures display appreciable nongeographic variation within a species. Variation may be less in certain other Dikonophora because their appendages are less complex than in the Neotanaidae and there are fewer parts to show variation. For example, among the Tanaidae and Paratanaidae the number of articles in both antennae is less and pereopodal setation often is markedly reduced. Indeed, within the genus *Neotanais*, the larger the species the more frequently a greater number of setae is found in a row or articles in a uropod and the greater the range of variation.

The morphological differences observed in *Neotanais* ordinarily are not random and usually are correlated with age or increasing body size in a regular way. If this pattern of age-related change is borne in mind, in addition to using characters

which are invariable certain variable characters can be used for taxonomic purposes because they vary predictably. For example, numbers of pereopodal setae may be a good taxonomic character for a row which varies from zero to 5 setae in *Neotanais micromopher*, 7 to 12 in *N. robustus*, and 15 to 23 in *N. giganteus*; identification of the instar being examined is all that is necessary. Assumption of this degree of confidence in dealing with variation has not been possible previously when working with the Neotanaidae.

SEXUAL DIMORPHISM

Sexual dimorphism is the rule among the Tanaidacea, and it expresses itself in various ways in different groups. This dimorphism often is hidden during stages earlier than the sexually mature instars, and, in many forms, all stages other than adult males resemble each other closely (e.g., Bückle Ramírez, 1965; Lang, 1953b). Adult neotanaid males differ from other stages in the following ways (a detailed description of this variation for each taxon is presented in the generic and specific diagnoses):

Carapace elongate and, because of reduced mouthparts, shallow.

Pereonites differently shaped in dorsal view, each pereonite usually narrower anteriorly and wider posteriorly. Seventh pereonite bearing two posteriorly directed genital cones on its sternite.

Pleonites differently shaped in dorsal and lateral view; setulation of pleonal epimeral setae frequently different.

Pleotelson slightly different in dorsal view; differences usually related to fusion of anal opening.

First antenna differently shaped and bearing a dense clump of nonannulated esthetascs on a protuberance of the fourth article.

Mouthparts variously reduced or missing and fused to carapace.

Cheliped much modified, especially in *Neotanais;* carpus and chela greatly developed.

Pleopods much better developed, with longer setae.

Many meristic differences are present—such as the numbers of setae on the first antennae or the pereopods and the number of articles in the uropodal endopods; the specialized pereopodal spines may be reduced or otherwise modified in form depending on the species (see infrageneric species groups or species diagnoses presented earlier).

Dimorphic male characters arise suddenly in neo-

tanaid development. The primary male assumes his shape following the maturation molt, the secondary male following the final molt of a copulatory female.

Presumably their highly developed pleopods aid the males in swimming to the females, and their specialized first antennae are important in detecting the presence of the females. This function probably is especially important in the deep sea where the density of females (or any other stage) probably is relatively low compared to that in shallow water. Hansen (1913:6) notes that the males of *Leptochelia* and *Paratanais* (littoral forms) have much larger eyes than the females, presumably another adaptation that serves a similar function.

It is difficult to propose plausible uses for the remainder of the dimorphic characters. One would assume that the highly modified chelae are important in courtship or copulation; however, the males of other taxa, such as *Agathotanais, Paranarthrura,* and *Strongylura,* apparently get along well without such modifications. Indeed, in *Heterotanais oerstedi,* a species in which the chela is radically modified in the adult males, Bückle Ramírez (1965) found that fertilization of the females was accomplished satisfactorily in spite of single or double experimental amputation of the chelipeds.

Bückle Ramírez found that the chelae were important in tearing open the tubes containing the females, but the neotanaids probably do not build tubes (see "Tube-Building" under "Ecology"). The chelae may function in species recognition, but this would have to be tactile because the neotanaids are blind.

The male mouthparts vary greatly from individual to individual and from one side of an animal to the other. This is in marked contrast to the mouthparts of other stages in which the basic shape and the armament are very stable within a species. Being nonfunctional and the precise shape probably having little direct survival value for the animal, there is likely to be little if any selective pressure maintaining the genetic mechanisms controlling structural constancy of the mouthparts. Defective mutants may have been allowed to accumulate in population gene pools, and time has brought about a slow loss of structural and functional constancy. This stability ordinarily would be maintained by continued selection pressure eliminating defective mutants (Dobzhansky, 1951).

Geographic Variation

Numerous studies have demonstrated that careful observation almost always reveals some type of variation among animal populations, especially those that are widely separated (Mayr, 1963).

Geographic variation is of pragmatic interest to the taxonomist because only by adequately conceiving of the degree of variation among the populations with which he is working can he satisfactorily appraise the systematic position of organisms from different populations. This is particularly important 'in a group such as the Neotanaidae where species often resemble each other closely.

Geographic variation also is of theoretical interest from a genetic or evolutionary point of view. The fact that populations vary phenotypically may itself be evidence for genotypic variation, that these populations are not collectively panmictic, and that there is a genetic lag within the species. These conclusions lead to questions concerning the factors causing the genetic lag, the degree in which widely separated populations are conspecific, and the rate at which gene flow is occurring. These questions are of special interest when dealing with the deep-sea fauna as compared with the faunas of other, much better understood environments.

Although variations in certain characters result from the pleiotropic effects of genes being selected for their effects on other, cryptic characters, much variation, although apparently minimal, is actually adaptive in nature according to Mayr (1963). However, the adaptive significance of most of the variations observed in this study is not obvious.

Considerable morphological variation with distance is known for some tanaidacean species. For example, Lang (1955) has described wide variation in the shapes of the rostrum, pereonites, and pleonites; the length of the uropodal exopod; and the number of spines on the pereopods in *Apseudes acutifrons*—the latter two characters being unrelated to size or sex. These populations came from the Black Sea, Adriatic Sea, Tyrrhenian Sea, and widely separated points in the Atlantic off Africa, and they were all collected at depths less than 100 m. In addition, Lang (1957:15) has reported appreciable variation in *Leptognathia gracilis*, also in shallow water.

Among the Neotanaidea, a number of species lend themselves to an analysis of geographic variation. These are species which have been collected from populations in widely separated locations but which are represented in sufficient numbers at each location for a true idea of intrapopulational variation to be obtained. This sort of analysis has not been possible previously due to limited material. Ideally it would have been desirable to examine geographic variation in *Neotanais micromopher*, the species in which intrapopulational variation is best known; however, only one specimen of this species is known from outside the North American area.

A number of species have had included with them isolated individuals from widely scattered locations (e.g., Pacific specimens of *Neotanais americanus* and *N. sandersi*). But where these specimens have differed appreciably from the better known populations their conspecific status is still subject to question, and they are not included in the discussion below. (Morphological variation is discussed in detail following each species description.)

Neotanais armiger is known from the Pacific Slope of the Americas from Oregon to Chile (Figure 99). It also is known from the western Atlantic–Gulf of Mexico area. Unfortunately, the highly confused pattern of variation in this species (see "Intraspecific Variation" under *Neotanais armiger*) precludes a detailed geographic analysis. Suffice it to say that certain specimens at the extreme ends of the Pacific distribution resembled each other almost exactly.

Neotanais calcarulus also ranges from Oregon to Chile (Figure 100). *Neotanais americanus, N. affinis, N. hastiger, N. sandersi, N. hadalis,* and *N. giganteus* are all known from several widely scattered locations in the Atlantic (Figures 97–100, 102). *Neotanais hadalis* and *N. giganteus* also are known from the South Pacific. The discussion below is based primarily upon these species, and it summarizes the observations recorded in the sections on these species.

Body Length.—Body lengths exhibit some differences among populations within a developmental stage. Unfortunately, the data available for most species of *Neotanais* are insufficient for definitive study of size variation. (Adequate numbers of animals are needed at each station in order to understand variation within each population before populations can be compared.)

From a comparison of the mean body lengths for *Neotanais micromopher* at WHOI B. Stas. 64 and 76 it is clear that there is a small but consistent difference in many instars for which the data are adequate. For example, preparatory females 1 are 5.3 ± 0.26 and 4.8 ± 0.21 mm and preparatory females 2 are 6.3 ± 0.14 and 5.9 ± 0.09 mm respectively. The population mean estimates do not overlap for either stage.

Although the data are limited, the same sort of slight difference in body length is apparent between the three copulatory females of *Neotanais giganteus* collected off Gabon (*Galathea* Sta. 65), with body lengths 18.4 to 19.2 mm ($\bar{x}=18.8$) and those from the Gay Head–Bermuda Transect (WHOI B. Sta. 62), with lengths of 16.7 to 17.7 mm ($\bar{x}=17.2$). Other copulatory females from stations in the same western Atlantic area have lengths of 15.6 and 16.1 mm (WHOI B. Sta. 72), 16.2 mm (CMS Sta. 2163) and 16.2 mm (CMS Sta. 2169), all in the same range. One exception is a third female from WHOI B. Sta. 72 which is 19.4 mm in length, longer than any of the *Galathea* specimens; however, this animal is so far outside the expected range of variation at its station that it may be a copulatory female which has raised a second brood (see under "Development").

A much more marked difference in size is displayed by the preparatory female 2 of *Neotanais giganteus* from the Tasman Sea (*Galathea* Sta. 575) that is 21.5 mm long and a copulatory female of 22.3 mm collected off Guinea (WHOI B. Sta. 151). It is unknown whether these specimens represent geographic variation or are, respectively, intermediate female and copulatory female 2 preparing to raise a second brood.

The examples cited above are those which illustrate variation in body length. But there are numerous instances where widely separated populations have similar body lengths. This is true of *Neotanais affinis*. Specimens from populations on the Gay Head–Bermuda Transect, the Labrador Sea near Greenland, the Mid-Atlantic Ridge near Sts. Peter's and Paul's Rocks, and the Weddell Sea (Antarctica) are all of similar lengths within their respective developmental groups.

In connection with a discussion of *Apseudes* (=*Leiopus*) *gracillimus*, Wolff (1956a:205) makes the following statement: "A considerable difference in size of adult specimens of the same tanaid species is often found in populations from various localities—e.g., females of *Neotanais serr. serratispinosus* from the North Atlantic, dredged by the Valourous [sic], the Porcupine, and by the Ingolf Expeditions." However, these examples are not valid. In the present work the specimens cited are assigned to three different species and include juveniles, preparatory females 2, and a copulatory female.

In summary, whereas the body length of a species varies among populations, it does not vary greatly—for example, by a factor of two. Greatly differing body lengths usually indicate the presence of different species.

OTHER CHARACTERS.—Most readily apparent are variations in the shapes of the pereonites, pleonal epimeres and midventral silhouette, and pleotelson when seen from above. Widely separated populations frequently display slight differences in these characters, which may or may not be reflected in width-length ratios.

Neotanais hastiger from the Bay of Biscay varies slightly from those populations on the North American Slope in pereonal (Figure 56I,J), lateral pleonal (Figure 56N,O), and pleotelsonal (Figure 49H,K,L) shape. The pleotelson of individuals of *N. affinis* from the Argentine Basin is relatively longer than that of animals from the North American Basin or from the equatorial Mid-Atlantic Ridge (Figure 39E,F). This is perhaps the most extreme variation of this sort observed in *Neotanais*. (Some individuals from northern populations were not as short as the one figured.)

The lengths of the midventral pleonal spurs vary in most species of *Neotanais* but usually scarcely more than within a population.

The pleonal epimeral hairs apparently vary among widely separated populations; sometimes they are short and thin, or they may be relatively longer and heavier; they may be feathered in some populations but not in others (Figure 39F,G). Considerable care must be exercised in examining them because the feathering is often difficult to observe and the setules are frequently broken.

The numbers of anterolateral and posterolateral setae on the carapace are relatively stable and, where only one to three are present (i.e., most species) variation is rarely more than a single seta, and usually the numbers of setae are identical. However, a copulatory female of *Neotanais calcaru-*

lus from Chile had only four posterolateral setae on each side, and these were without visible setules; the holotype of the same stage, collected off Oregon, had eight clearly setulated setae on one side and four on the other.

The individual of *Neotanais hadalis* collected off Portugal had eight posterolateral setae, the holotype from the Kermedec Trench, four, and a preparatory female 2 from the Argentine Basin, one (there should not be any developmental differences between these stages). The populations of *N. hastiger* from the North American Basin and near Greenland had one or two anterolateral setae; those from the Bermuda Slope and from the Bay of Biscay had four or five and these were comparatively longer in the Bermudan population. However, these are cases of extreme variation. In fact, the specimens of *N. hadalis* from the Argentine Basin later may be determined not to be conspecific with the other populations of *N. hadalis.* The same also may be true for the Bermudan specimens of *N. hastiger.*

The form of the cheliped, including the dentition of the chela, is very stable. There is appreciable variation between the dentition of the chelae of the male of *Neotanais hadalis* from the Argentine Basin and the males from the Kermedec Trench. A similar situation obtains between North American males of *N. sandersi* and a male of *N. sandersi* collected off Ireland. However, the relative scarcity of copulatory males in the samples and the presence of at least two different forms of male chelae during development prevent generalization regarding the relative morphological plasticity of this structure.

Usually the numbers of setae on pereopods II–VII are relatively stable within an instar, but occasionally one finds appreciable variations. In *Neotanais affinis* the setal formulae for pereopods II and III for three specimens are as follows: a preparatory female 2 from the Labrador Sea, (13,11,15,13) and (20,20,16,16), similar to a copulatory female from the Gay Head–Bermuda Transect; a copulatory female from the Bay of Biscay, (5,7,8,7) and (10,15,11,9); and the preparatory female 1 holotype collected off South Africa, (6,11,9,14) and (14,20,–,20).

The specialized spines on pereopods II–IV and VII do not vary greatly. This is particularly true for the short terminal or subterminal spines on the propodi or carpi of pereopods II–IV. An exception is a female of *Neotanais affinis* from the Bay of Bis-

cay on which the carpal spine is very finely toothed; this spine has moderately sized teeth in western Atlantic populations. The long, terminal propodal spines are more variable. However, variation usually is not greater than one spine, similar to that sometimes found within a single population. The position, shape, and number of teeth on these spines are more variable (Figure 20c,E,F).

The situation with the short, subterminal spine row on the propodus of pereopod VII is similar, but there is one known case where not all of the populations of a species have these spines. In *Neotanais hastiger* the populations on the North American Continental Slope and the Labrador Sea lack them, whereas the animals from Bermuda (possibly representing a distinct species) and from the Bay of Biscay have the spines.

The dactyli of pereopods II–IV in *Neotanais americanus* apparently may or may not be serrated (Figure 20b,F); however, this is also true of neighboring populations which are separated vertically (see "Variation with Depth," below).

SUMMARY.—Morphological variation with distance is low in *Neotanais* and species differ in the degree to which they vary and in the structures showing variation. Characters vary separately from each other. Therefore, several widely separated populations of a species such as *Neotanais hastiger* or *N. hadalis* share different combinations of variations with each other and do not grade uniformly away from each other in all characters. If as large a suite of characters as possible is utilized when identifying specimens, one or more characters may differ, but almost certainly not all.

Variation with Depth

Change in depth along the Continental Slope brings with it important changes in temperature, pressure, and light intensity as well as in other environmental parameters. Therefore, animals living at 3000 m will be subjected to environmental stresses dissimilar to those of other members of the same species living at 800 m or at 100 m. These populations may be adapting in somewhat different directions and may display discernible morphologic variations.

In order to detect this type of variation, if present, there should be available representatives of several populations of a species spread across as

large a range of depth as possible. Such specimens should come from an area where the deepest population is not far removed geographically from the most shallow population in order to eliminate the effects of horizontal geographic variation. The Gay Head–Bermuda Transect includes such an area.

Because of sampling difficulties, the uneven distribution of the deep-sea fauna, and the variable quality of the available specimens, there is only one species of neotanaid that can shed light on this question. Unfortunately, *Neotanais micromopher*, the best known species, only ranges from about 2800 to 3830 m along the Transect; however, *N. americanus* is known to range from about 2800 to 5020 m and has been collected from 13 stations.

Neotanais americanus displays practically no discernible variation—at least among the available specimens—with two exceptions. The distal serrations on the dactyli of pereopods II–IV were lacking in some specimens, and the teeth on the long, terminal propodal spines of pereopods II–IV were closely set in some animals in marked contrast to the arrangement in others. In both cases, these differences apparently are found in populations in very deep water on the Gay Head–Bermuda Transect. But, of the animals known from the area of Greenland and the Labrador Sea, those collected by the *Ingolf* (3474 m) and *Valorous* (2715 m) have the setules, whereas those obtained by the *Norllante* at a similar depth (3430 to 4120 m) do not.

The striking vertical morphological similarity among populations may indicate genetic uniformity due to unimpaired interbreeding along the Continental Slope (see "Distribution").

Phylogeny

Numerous authors have commented on the phylogenetic significance of various structures within the Tanaidacea, and Siewing (1953) has contributed greatly to our understanding of the relationships between the Tanaidacea and other peracaridan taxa. However, there have been few attempts to summarize knowledge of the relationships within the order and to reconstruct the pathways of evolutionary development through which the group has passed.

In 1956, Lang (1956b:473) divided the order into two suborders and proposed a scheme describ-

ing the relationships among the tanaidacean families in which he derived the Paratanaidae directly from the Neotanaidae. Lauterbach (1970) has published a detailed study of the head region of *Tanais* in which he proposes a series of relationships among the taxa based exclusively on characters of the head region and first free thoracic somite. He (p. 162) describes the head area of the hypothetical common ancestor of the two suborders in considerable detail. His phylogenetic scheme (p. 165) is similar to Lang's, but, justifiably, he no longer derives the paratanaids directly from the neotanaids.

The following phylogenetic reconstruction (Figure 78) is based on the works of Lang (1949–1968), Lauterbach (1970), others scattered through the literature, and—within the Neotanaidae—on the results of my study of this family. It is by no means exhaustive, but merely attempts to describe the major features of tanaidacean phylogeny and the probable position held by the Neotanaidae.

The Monokonophora apparently have diverged morphologically from the original tanaidacean considerably less than have the Dikonophora. The ancestral monokonophoran probably still retained pereopodal exopods, at least on the first two pereopods in adults and also on the last three in mancas. Both pairs of antennae retained much of their original length and were biramous as well. The uropodal endopods were long, and the exopods were made up of at least several articles. The mandibular palps were composed of three articles.

The Kalliapseudidae display greatly developed feeding filters on the modified second antennae, mandibles, maxillipeds, and chelipeds in various taxa. It is unclear whether possession of this feeding complex is primitive; it may be an increasingly developed specialization of original suspension-feeding mechanisms. Lang (1956a:224) and Lauterbach (1970:164) favor the view that the greatly developed pereopodal sensory organs of this family are primitive and tie the Tanaidacea to the Cumacea in which similar structures are known to occur. Lauterbach assumes, therefore, that the early tanaidacean bore such organs on all its pereopods.

The Apseudidae (in the sense prior to subdivision by Lang in 1970) demonstrate many primitive characters. However, in various taxa one can observe tendencies toward reduction of uropodal length, loss of the pleopods in certain stages and reduction of the number of pleonites, loss of the exopods of

the second antennae, and, in all known cases, pereopodal exopods, when present, are found only on the first two pereopods. Visual elements and, indeed, the ocular lobes themselves may or may not be present. Some of the same reductions are found in the Kalliapseudidae: ocular lobes and/or visual elements and the exopods of pereopods I and II may be missing, and the mandibles are reduced in some taxa.

The original dikonophoran probably was characterized by the following modifications: the first antenna had lost its second flagellum and the second antenna its articulated exopodal squama (scale); both appendages probably also had undergone substantial reduction in the lengths of their endopods; the mandibles no longer possessed a palp; and the exopods of all pereopods had disappeared and those of the uropods were reduced to two articles.

The question arises as to whether the Paratanaidae are derived from a common ancestor with the Tanaidae or with the Neotanaidae. The copulatory males of both the paratanaids and neotanaids display markedly reduced mouthparts (although the degree of reduction differs), whereas the male mouthparts of the Tanaidae resemble those of the females. On the other hand, both the Para-

tanaidae and Tanaidae possess thoracic cement glands and exhibit spinning behavior. Which of these characters, reduced mouthparts or tube-building, is most primitive, is problematical. It seems more likely that the reduction of mouthparts occurred separately among both the neotanaids and paratanaids, and that tube-building behavior was inherited in common (Lauterbach, 1970, also takes this position). If so, the ability to construct tubes would therefore have been a character possessed by ancestor 1 (Figure 78).

The early tanaid (ancestor 2) would, according to the scheme suggested here, have been specialized beyond the stem dikonophoran in having had the last two pleonites partly reduced and probably having already lost the last two pairs of pleopods. The rami of the remaining pleopods would each have been composed of a single article. The first antenna in the males would have been reduced to three articles, and the uropodal exopod in both sexes would have been lost and the endopod considerably shortened.

The three known genera of the Tanaidae—*Pancolus*, *Tanais*, and *Zeuxo*—presumably diverged at about the same time, although *Pancolus* might have arisen from a common stock with *Tanais*. The genera are not widely divergent today, and the
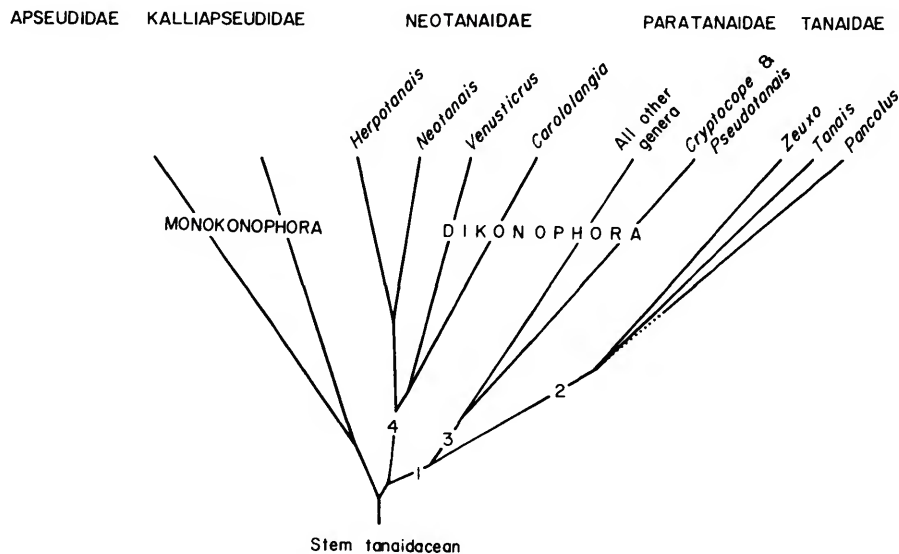
FIGURE 78.—Hypothetical phylogenetic relationships among the Tanaidacea. Apseudidae is used in its broad sense prior to its division by Lang in 1970. Dotted line indicates uncertain pathway.

major distinctions among them are the relative degrees of reduction of the pleonites and pleopods. Five pleonites are present in *Zeuxo*, but the last two are narrower and very much shorter than the others. In both *Zeuxo* and *Tanais*, three pairs of pleopods are present on the first three pleonites, but in the latter genus the pleonites are four in number, the last of these being somewhat narrower than the others. (Only three pleonites are present in *Zeuxo*). Lang (1961) has shown that the last of the three pairs of pleopods in *Pancolus* is rudimentary.

What is seen is an evolutionary trend in the degree of pleonal reduction from *Zeuxo* to *Pancolus*: from five to three pleonites. In *Pancolus* the last pair of pleopods also is reduced. There is a similar trend in uropodal reduction: there are four or five endopodal articles in *Zeuxo*, three in *Tanais*, and one in *Pancolus*. In addition, the terminal lobes of the labium are much reduced in *Pancolus*.

Ancestor 3 (Figure 78) probably was characterized by further shortening of the first antenna, the loss of the terminal labial lobes, the reduction of the first maxillary palp in the females to a single article bearing two setae, and the reduction of the male mouthparts until only the palp of the first maxilla and the maxillipeds and epignath remained.

In the family Paratanaidae, as presently conceived by Lang (1967), there are apparently two major lines, primarily distinguished by the number of pairs of oostegites in the females: *Cryptocope* and *Pseudotanais* are characterized by a single pair borne on the fifth pereopods similar to the situation observed in the Tanaidae; the remainder of the paratanaid taxa have four pairs borne on pereopods II–V.

There has been some question concerning the precise affinities of *Cryptocope* and *Pseudotanais*, and Lang (1949) originally assigned them to the Tanaidae on the basis of their single pair of oostegites. More recently, however, Lang (1967) has decided that they are paratanaids on the basis of their reduced male mouthparts. Moers-Messmer (1936) showed long ago that in *Pseudotanais* both oostegites contribute to the formation of a single marsupium (presumably this is also true in *Cryptocope*). This is the case elsewhere among the Paratanaidae where four pairs of oostegites are present. The Tanaidae, on the other hand, form one or two brood sacs ("ovisacs" of Lang, 1960).

Because the systematic relationships in the remainder of the family are not at all clear, it is pointless to attempt further phylogenetic reconstruction until these relationships are better understood. Suffice it to say that a number of generic groupings are present, and these may provide the basis for additional familial divisions. For example, *Agathotanais, Arthrura, Anarthruropsis, Paragathotanis,* and *Paranarthrura* are similar; and, among other similarities, *Heterotanais* and *Nototanais* share a subchelate male first pereopod, apparently unique among the Tanaidacea.

Within the Paratanaidae are a number of evident evolutionary tendencies: fusion of various parts of the pleon (also observed in the Monokonophora), fusion or other radical modification of the pleonites (also in the Tanaidae and Monokonophora), and the extreme modification of the uropods such as shortening of both rami in various degree and reduction of the exopod to a spur or even its loss (the latter also are observed in the Tanaidae).

The Neotanaidae are generally considered to be the most primitive dikonophorans (Lang, 1956b; Lauterbach, 1970). Ancestor 4 (Figure 78), the early neotanaid, probably would have been blind because visual elements on the ocular lobes had been lost; and the first maxilla, in stages other than copulatory males, would have lost its palp, and in copulatory males would have been missing altogether. Other male mouthparts would have been reduced.

There appear to be two different phyletic lines within the Neotanaidae: one includes *Neotanais* and *Herpotanais*, the other, *Carololangia* and *Venusticrus*. The second line differs from the first in the following characters: (1) the presence of numbers of feathered setae on pereopods V–VII, (2) the much stouter shapes of the pereopodal bases, (3) the position in which the legs are held, at least when preserved (see p. 174); (4) the attachment of the uropods below the pleotelson (but see *Neotanais insolitus*), and (5) the shapes of the medial brushing setae on the maxillipedal endite.

Originally I conceived of the two groups as subfamilies; however, the differences between *Carololangia* and *Venusticrus* are sufficiently great so that such a taxonomic division seems unwise, at least for the present.

Carololangia and *Venusticrus* are much more

specialized than *Herpotanais* and *Neotanais*. The latter retain pereopodal armament, pleotelsonal structure, uropodal structure and attachment, and maxillipedal brushing setae which resemble those of the relatively unspecialized apseudids (sensu lato) much more closely than do *Carololangia* and *Venusticrus*. Unfortunately, *Herpotanais, Carololangia,* and *Venusticrus* are monotypic and the copulatory males are unknown for the latter two genera. Discovery of additional species and the males of *Carololangia* and *Venusticrus* should add appreciably to our understanding of morphological diversity within these genera and, consequently, of intrafamilial relationships.

The great development of the chelipedal carpus and chela in copulatory males of *Neotanais* is a specialization which may be unique to that genus. In *Herpotanais*, these structures are not nearly so elaborately developed. The relative lengths of the pleon and (especially) of the pleotelson in this genus much more closely resemble those of many apseudid (sensu lato) genera (compared to all other neotanaids). This may or may not be a generalized trait. *Herpotanais* has become specialized through the marked reduction in the length of both the uropodal endopod and exopod and the loss of one pleopodal ramus.

Development

The postmarsupial development of the Tanaidacea has received relatively little attention since their discovery by Montagu in 1808. Müller (1864a, 1864b), Dohrn (1870), Smith (1906), and Roubault (1935, 1937) studied species of the dikonophoran genera *Heterotanais* and *Leptochelia*. They recognized the dimorphic character of the sexes, and several of them noted the presence of more than one form of male and discussed the significance of masculine dimorphim. All of these workers assumed that the animals were gonochoristic.

More recent investigators have suggested several patterns of sexual development. In 1953, Lang (1953a) discovered apparently simultaneous hermaphroditism in a species of the monokonophoran genus *Apseudes*. Later on, he suggested that protogyny also may be present among the Monokonophora (Lang, 1958); and Wolff (1956a) has speculated that some species of *Apseudes* may be protandrous. Morphological analysis and observa-

tions of animals in culture have shown that some members of the dikonophoran genera *Heterotanais* and *Tanais* are protogynous (Forsman, 1956; Lang, 1958; Bückle Ramírez, 1965). Wolff (1956a) thought that *Neotanais* might be a simultaneous hermaphrodite, but Kudinova–Pasternak (1965a, 1966b) has suggested that a final female phase succeeds protogynous males in this genus.

Insofar as is known, the study of Wolff (1956a) with species of *Apseudes* (=*Leiopus*), *Neotanais*, and *Herpotanais* has been the only investigation of development among the deep-sea Tanaidacea. Studies of deep-sea taxa are fraught with all of the difficulties encountered at lesser depths, but are further complicated by problems of sampling. Adult males usually occur in very small numbers, if present at all, in deep-sea samples, and it is difficult to relate them properly to other developmental stages. These stages, too, are present in limited numbers and frequently are all very similar to each other but very different from the adult males which may be present. For these reasons, developmental patterns among deep-sea taxa still remain obscure.

Postmarsupial Development and Systematics.— Sexton (1924:340) has pointed out that "many of the difficulties found in naming and classifying Crustacea are due to the extraordinary modifications caused by growth and sex, and the confusion arising from our lack of knowledge of these developmental stages has led to many errors." He states that, among the amphipods, developmental instars have been named as species and even genera, and he cites the case of *Jassa falcata* for which there are over 30 synonyms. An analogous situation exists among the Tanaidacea, a much more poorly known order. Some examples of developmentally related taxonomic difficulties follow.

Lang (1956b:471) considered the holotype of dae, the structure of animals beyond the manca stages changes with each ecdysis. Only the adult male stages of some paratanaid genera have reliable specific characteristics. But the male instars of a species sometimes are so different from each other that taxonomy is impossible until their developmental sequence has been clarified. This has been done infrequently because of the small numbers of individuals available for study.

The female of *Tanais stanfordi* gradually comes to resemble the male (Lang, 1958:538), and *T. fluviatilis, T. sylviae,* and *T. herminiae* are really

based on three different stages of this species (Lang, 1956c:255).

The description of the genus *Tanaiomera* (Brown, 1957:817) is based on a manca according to Lang (1967:344), and it is not clear to which genus this animal actually belongs. *Leptochelia profunda* is really an older stage of *L. filum* (Lang, 1957:7). Some of the characters used by Hansen (1913:13–16) to distinguish betweeen *Apseudes* (=*Leiopus*) *gracilis* and *A.* (=*Leiopus*) *gracillimus* are developmental stage characteristics (Wolff, 1956a:207).

Lang (1956b:471) considered the holotype of *Neotanais laevispinosus*, which is a copulatory male and the only specimen of this species known at the time, to be the male of *N. serratispinosus* (=*N. americanus*), of which only the female was then known. In fact, they are distinct species. Lang (1961:576) points out that, inasmuch as "preadult" males are often found more frequently than copulatory males, many male descriptions are based on immature specimens. For example, G. O. Sars (1896:40, pl. 17) did not know what the copulatory males of *Pseudotanais forcipatus* looked like. He described and figured an immature male as the adult, and then went on to base the generic diagnosis, in part, on this animal (Lang, 1953b:412). The males of most paratanaid genera are still unknown (Lang, 1967:344).

Claus (1888, pl. 2: fig. 15) figures the young *Apseudes latreillii* (=*A. acutifrons*) with functional eyes composed of seven rhabdomes. In one older specimen of *A. acutifrons* which had been identified as *A. latreillii* by Claus, Lang (1955:59) was unable to find visual elements but did discover small, rounded structures toward the rear of the ocular lobes; and he interpreted these as "aborted eyes." In other words, the young stages may have functional visual elements which become reduced during development. In a species where the presence or absence of eyes depends upon age, the use of this trait as an important taxonomic character will be the source of much confusion.

When the life history of a sexually dimorphic species is not known, different names probably will be assigned to each sex. Sexual dimorphism, so prominent among tanaidaceans, has been the cause of many taxonomic difficulties within the order. The differences between the males and the females of a species frequently are greater than between the males or the females of other species. G. O.

Sars (1896:15) points out that Krøyer gave the name *oerstedi* to the "female" of *Heterotanais oerstedi* but named the adult male *curculio*, and Müller later described the male as *rhynchites* and the "female" as *balthicus*. *Neotanais giganteus* Hansen, based on a copulatory male, and *N. longimanus* Wolff, based on females alone, are synonyms.

The presence of more than one type of male, sometimes differing appreciably in appearance, can be a further source of difficulties (see "Dimorphism among Males," p. 205).

DEVELOPMENT AND PHYLOGENY.—The study of external morphology has enabled investigators such as G. O. Sars, H. J. Hansen, and, more recently, Lang (e.g., 1949, 1956b) to deduce systematic and phylogenetic relationships among families and genera of the Tanaidacea. The resolution of developmental patterns may, in similar fashion, be useful in obtaining a better understanding of relationships within the order.

ENVIRONMENTAL IMPLICATIONS.—The deep-sea environment is markedly different from the shallow-water habitats familiar to many students of the Tanaidacea. Practically all studies of tanaidacean development have been conducted with shallow-water taxa. Detailed studies on the development of deep-sea forms may shed light on the ways in which these species meet their unique environmental challenges.

POSTMARSUPIAL DEVELOPMENT WITHIN THE NEOTANAIDAE

The most desirable method for investigating development in the Neotanaidae would have been to culture animals in the laboratory and then follow their development from the marsupium to death. This was the method of Bückle Ramírez (1965), who obtained excellent results with *Heterotanais oesterdi* in the most thorough study of a tanaidacean life history in the literature.

Unfortunately, present deep-sea collecting techniques do not permit living benthonic crustaceans to be returned to the laboratory in numbers adequate for this sort of study. Collecting and processing the animals subject them to severe mechanical, barometric, and thermal insult. Although many may be alive on arrival at the surface, extraction from the sediment is difficult and usually they soon die. Collecting often is difficult even with

shallow-water forms. Kjennerud (1950) remarked about the difficulty of finding large enough samples of the usually abundant isopod *Idotea* in one location for adequate experimental controls, particularly when dealing with a large number of developmental stages.

A second means of elucidating the developmental sequence is to compare the dimensions or the presence or absence of morphological features unique to various stages, placing a heavier reliance upon statistical techniques when distinguishing among the instars. In the past this has not been possible with deep-sea tanaidaceans. The very limited numbers of individuals in a sample prevented the recognition of many developmental stages. Previously, Wolff's *Galathea* samples of 41 specimens of *Neotanais pfaffi* (Wolff:1956c) and 41 individuals of *Herpotanais kirkegaardi* (Wolff:1956a) were by far the largest collections of the Neotanaidae ever made.

When very small samples are collected, most or all of the animals must be preserved for taxonomic purposes, making histological work virtually impossible. Improper fixation also frequently limits such investigations.

Using the collecting and processing procedures of Sanders, Hessler, and Hampson (1965) and of Hessler and Sanders (1967), adequate numbers of individuals have been obtained to resolve most of the major features of postmarsupial development in *Neotanais micromopher*. This study was carried out primarily on the samples from WHOI Benthic Stas. 64 and 76 on the Gay Head–Bermuda Transect. These contained the largest numbers of any neotanaid species ever collected, 75 and 95 (usable) individuals respectively. The material from Sta. 76 was analyzed most intensively, and Sta. 64 provided additional data in support of conclusions based on Sta. 76. Selected individuals from other stations were utilized to clarify certain aspects of the developmental sequence, and all species in the family were examined to detect departures from the developmental pattern of *N. micromopher*.

Detailed information about the stations is presented in Table 1. They are 209 km (113 nautical miles) apart, and their depths, 2886 m and 2862 m respectively, differ by only 24 m, or 0.84 percent of the shallower depth. Both samples were collected by the same technique, and seasonally they are only two months apart in consecutive years. Thus, it is

assumed that differential environmental effects between the two stations are minimal, an assumption borne out by the similarities of results obtained from the two samples.

The first step in understanding the development of *Neotanais micromopher* was to distinguish among the various intermolt stages or instars. The obvious method of doing this was to look for differences in external morphology among the individuals in a sample. In stages with pronounced differences (viz., manca stages, copulatory females with mature oostegites, and copulatory males) this was relatively easily accomplished. Other groups were more difficult to identify, and several unsolved problems remain.

The results obtained from external morphological analysis are described below. These are followed by additional evidence from an histological gonadal examination. Finally, there is a discussion of the development of sexual structures in the Neotanaidae and a comparative review of the literature dealing with postmarsupial development and sex among the Tanaidacea. The techniques used in handling and sectioning the animals are described under "Methods."

External Morphological Analysis

MANCA STAGE 1.—The smallest animals in the samples are distinct. Their body lengths are very short (Sta. 64, 2.6 mm; Sta. 66, $\bar{x}=2.75 \pm 0.21$ mm; see Figure 85 and Tables 16 and 18). The pleonites are narrower in relation to the pereonites than in older stages (cf. Figure 3b–d). The seventh pereonite is very small; its length approximates that of the pleonites, in marked contrast to older individuals. The seventh pereopods and the pleopods are missing (Figure 5d,f), and the uropodal endopods are composed of only four articles (Table 20).

MANCA STAGE 2.—Although longer than the first manca stage (Figure 85), these animals are much shorter than all others. No specimens were available from Sta. 76, but the seven specimens from Sta. 64 and the two from Sta. 66 are used for comparison. The pleonites are considerably narrower than the pereonites, compared to older stages (Figure 3d), and the seventh pereonite is better developed (longer) than in the mancas 1, but still considerably narrower than in older stages. The seventh pereopods are present, and although they are rudi-

metary (Figure 5E,G), some divisions between future articles are visible. Rudimentary pleopods also are present, but the borders between the future articles are not yet evident. No setae are present on either the pleopods or the seventh pereopods. Uropodal endopods are composed of six articles (Table 20).

FEMALES WITH MATURE OOSTEGITES.—See "Copulatory Females," below.

COPULATORY MALES.—Ten copulatory males are present in the material from Sta. 76 (Figure 85), and they range in length from 5.0 to 8.0 mm. This is a very large range (3.0 mm) in comparison with the ranges observed for other stages, usually not much greater than 1.0 to 1.5 mm. The copulatory

males include the largest animals present in the sample. However, one male, HE, is only 5.0 mm long, considerably smaller than the other males and only 0.2 mm longer than the largest juvenile (DN).

Although all males are very similar morphologically, the large range of body length indicates the presence of more than one instar. However, the only useful means found for identifying subgroups was the shape of the chelae. Two types of chelae are present, termed A and B respectively (Figure 10A–E), and they are described in detail under *Neotanais micromopher*. On the basis of the large range of body length and the consistent relation-
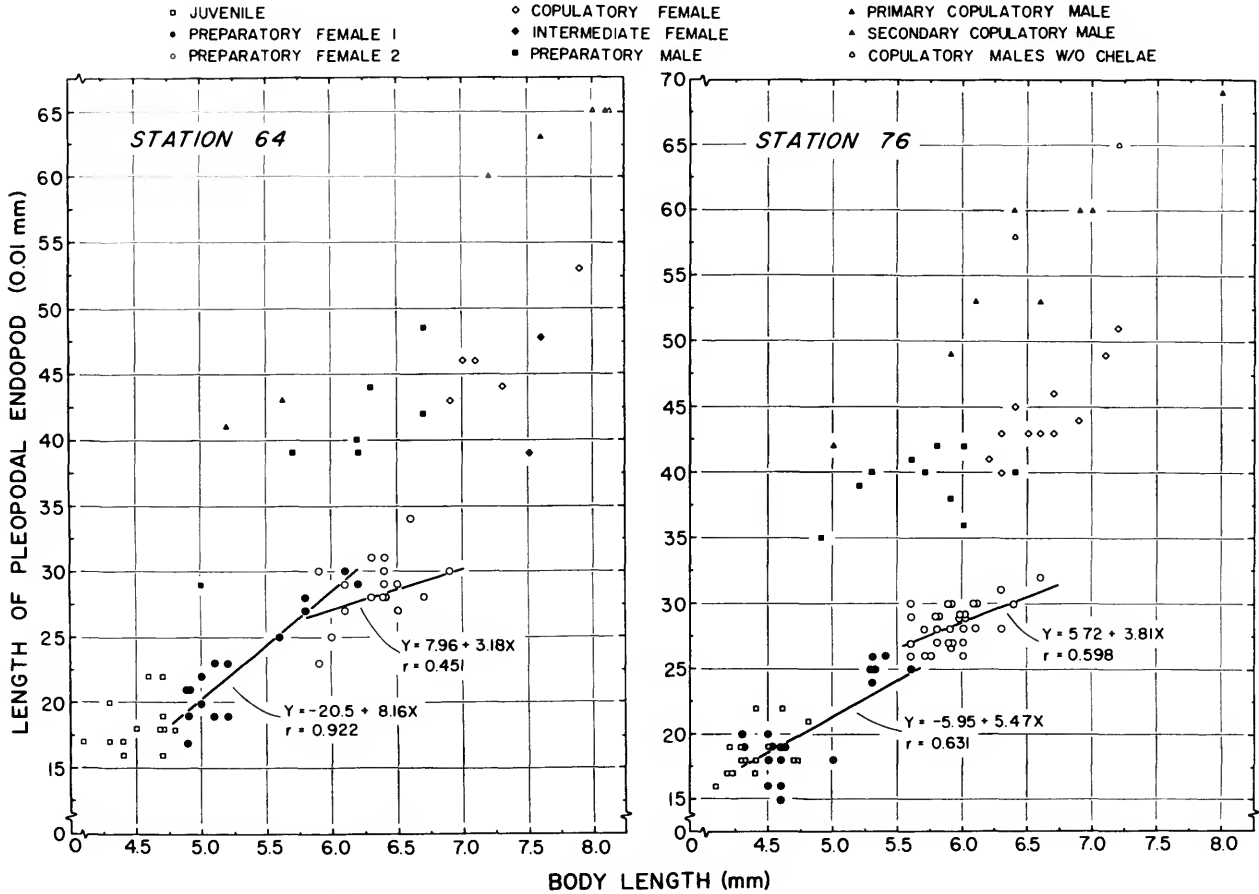
FIGURE 79.—Relationship between pleopodal length (represented by length of endopod) and body length in *Neotanais micromopher* at WHOI Benthic Stas. 64 and 76. The correlation coefficient is represented by "r."

ship of chela type with body length, there probably are at least two distinct groups of males in the sample, smaller ones with chela type A and larger ones with chela type B. The chelae were missing on HF and HG. HG (6.4 mm) might be expected to have type A chelae and HF (7.2 mm) type B chelae because these animals fall within the ranges of body length appropriate for these types of chelae.

The correlation of chela type and body length is supported by the evidence from Sta. 64 (Figure 85) where the seven copulatory males vary in length from 5.2 to 8.2 mm, a range of 3.0 mm. The smaller animals, with the exception of AQ, have chela type A, whereas the larger individuals have chela type B. AQ displays characters of both chelae A and B (Figure 11) and will be discussed later.

When the copulatory males of *Neotanais micromopher* found at other stations are examined, the number of specimens at any one station, often only one, does not permit a satisfactory comparison to be made of the relationship between body length and type of chela. But if all of these males are considered together, it is apparent that their lengths generally fall within the ranges expected from Stas. 64 and 76. The two types of males can be divided at a body length of about 7.0 mm, with males bearing type B chelae falling above this boundary and males with type A chelae remaining below. Of the 16 males with type B chelae, only three fall below 7.0 mm; three of the 15 males with chela A are longer than 7.0 mm. Individual and geographic variation probably can account for all of the exceptions noted, and it is safe to assume that these two groups of males represent two distinct developmental instars.

This conclusion is borne out by a similar chela type/body length relationship for *Neotanais americanus* at the same two stations (*N. americanus* is the species with the next largest number of males at a single station). Other species known to have copulatory males with two types of chelae are *N. armiger*, *N. robustus*, and *Herpotanais kirkegaardi*. Wolff (1956a) has also described two types of chelae for *N. serratispinosus hadalis* (=*N. hadalis*), but the significance of one of these is not clear.

All of the males of these species were compared, but no consistent pattern of dentition or degree of finger-twisting could be detected for the two types. Such a pattern may emerge when copulatory males are known for a larger number of species.

In addition to the very small male, HE (length 5.0 mm), at Sta. 76, there are two small males, AU and AV (5.2 mm and 5.6 mm) at Sta. 64. A fourth tiny male (5.1 mm) is known from *Noratlante* Sta. 042. Small males also are present in *Neotanais americanus* (two individuals at Sta. 64 and two at Sta. 76), *N. armiger* (one at *Vema* Sta. 15–39), *N. barfoedi* (one at *Galathea* Sta. 668), *N. dinotomer* (one at WHOI B. Sta. Ber. 8), and *N. tricarinatus* (one at *Chain* Dr. 12). Almost all of these individuals lie in the body-size range of juveniles, preparatory females 1, or of very small preparatory females 2 for their respective species (see Figure 85). The gap between these males and the smallest of the next larger group of males is almost always great (2.0 mm at Sta. 64 and 0.9 mm at Sta. 76).
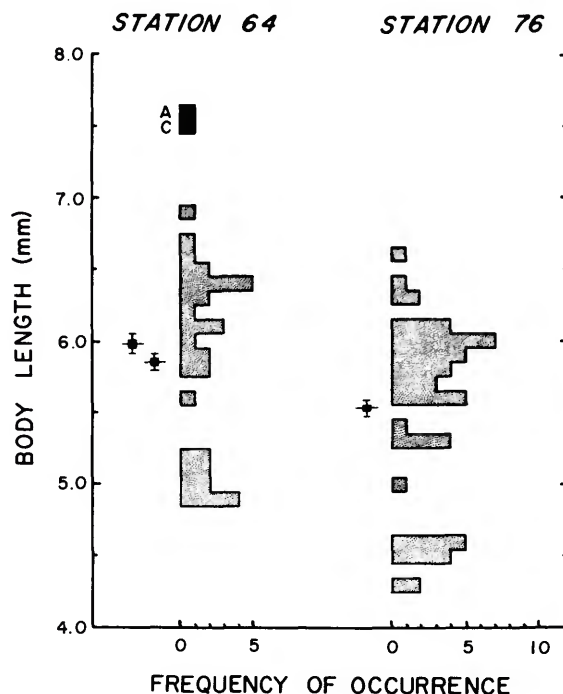
FIGURE 80.—Comparison of body lengths of females of *Neotanais micromopher* with rudimentary oostegites at WHOI Benthic Stas. 64 and 76. Represented are preparatory females 1 and 2 and intermediate females. Each square represents one animal. Mean body lengths are indicated by a horizontal line, the 95 percent confidence interval estimate of the mean by a vertical black bar, and sample standard deviation by a vertical line. For Sta. 64 the statistical symbol at the far left includes intermediate females A and C, the symbol on the right does not.

Pleopodal length often varies with body length (Figure 79), and the small males have shorter pleopodal endopods than do the other males. However, numbers of terminal pleopodal setae and the relative lengths of these setae are similar to those of some of the larger males. Possibly there is a lower critical level of pleopodal development necessary before a copulatory male can assume its function of actively swimming about in search of fertile females (these males are fully sexually mature—see "Gonodal Analysis").

Length of uropodal endopod is appreciably shorter than among the longer males (six or seven articles compared with eight or nine—Table 20).

These data are interpreted as very strong—even if not conclusive—evidence of the presence of a third type of copulatory male in *Neotanais*.

ANIMALS WITH RUDIMENTARY OOSTEGITES.—These animals are clearly distinguishable from all other stages by the presence of thick, oval, cuticular ooste-

gite sheaths borne posteromedially on the coxae of pereopods II–V (cf. Figure 94A–F).

The ranges of body length for these animals (Figure 80) are much greater than would be expected when compared with the other developmental stages (2.7 mm at Sta. 64 and 2.3 mm at Sta. 76—cf. Figure 85), an indication that these animals represent more than one stage. The break in body-length frequency distribution (Figure 80) at about 5.3 to 5.7 mm at Sta. 64 and 4.7 to 5.2 mm at Sta. 76 is not clean, and it is unclear whether it reflects a real discontinuity between instars or simply reflects the variability to be expected in small samples.

In order to detect possible subgroups, several additional measurements were made: the number of articles in the uropodal endopod (Tables 16, 17), the length of the pleopodal endopods (Figure 79), and the number and relative length of the pleopodal setae (Figure 10J,K). No unequivocal
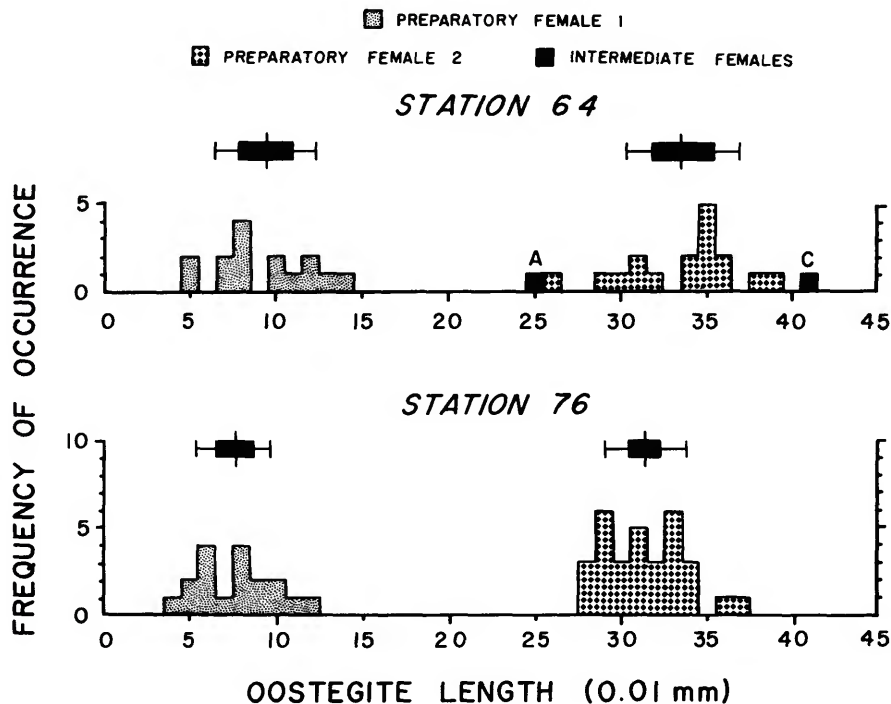
FIGURE 81.—Length distribution of rudimentary oostegite sheaths in *Neotanais micromopher* at WHOI Benthic Stas. 64 and 76. Statistical diagram: mean length of oostegite sheath, vertical line; 95 percent confidence interval estimate of mean, black bar; sample standard deviation, horizontal line. Specimens A and C at Sta. 64 are not included in the calculations.

discontinuities were found. However, Figure 81 shows that there are marked breaks in the distribution of oostegite sheath-length between animals with smaller and larger sheaths at each station.

The breaks occur at approximately the same place in the histograms for both stations and are of similar width. Variation in means and ranges between stations is easily accounted for on the basis of sample size or geographic differences, and the gaps between groups are almost as wide or even wider than the length range of either group of oostegites. A marked break is also present between

the distributions of sheath widths for the two groups at both stations (Figure 82). This clearly disjunct nature of the oostegite dimensions at each station is taken as definitive evidence for the existence of two stages in spite of some overlap in body length (Figure 83).

Shape relationships also differ between the two types of oostegites (Figure 82). Width varies relatively closely with length among the smaller oostegites; the coefficient of linear regression, b (Snedecor, 1956), is 0.603 and 0.567 at Stas. 64 and 76 respectively. However, among the larger oostegites,
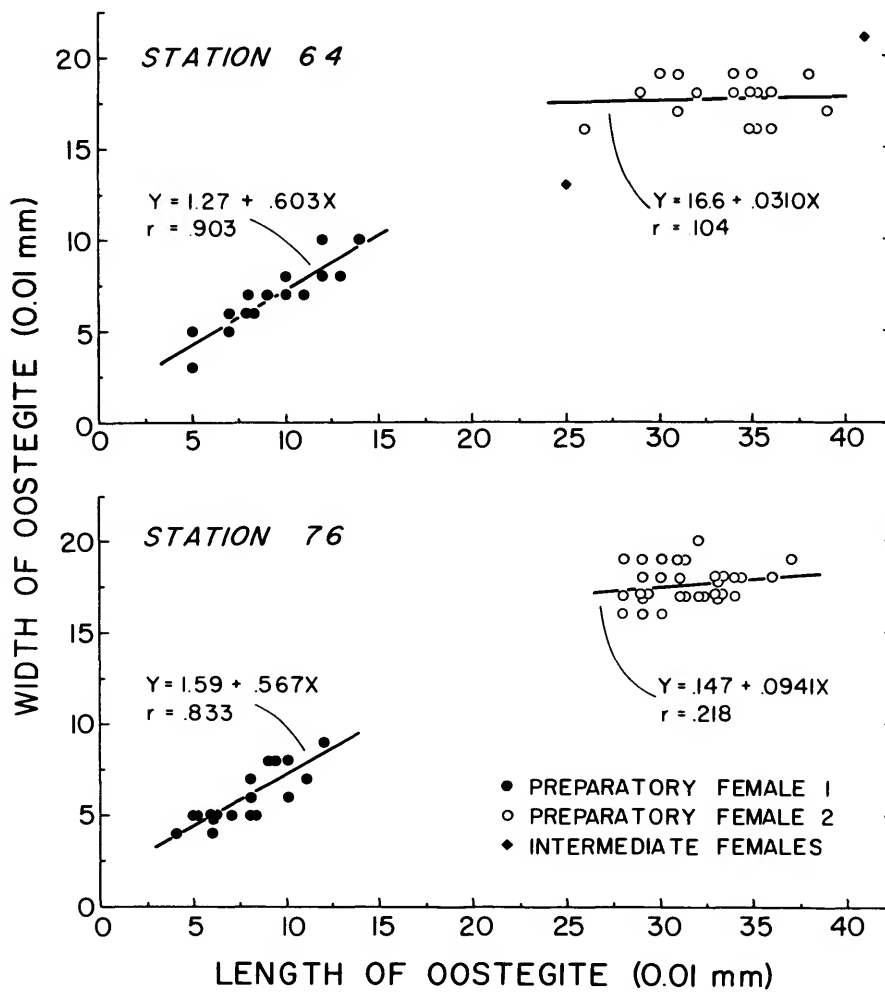
FIGURE 82.—Relationship of width to length of rudimentary oostegite sheaths in *Neotanais micromopher* at WHOI Benthic Stas. 64 and 76. The correlation coefficient is represented by "r."

there is little relationship between the two variables; $b=0.031$ and 0.094 (these slopes do not differ significantly from zero at the 0.05 level of risk); that is, oostegite sheath-width varies independently of length. Whereas among the smaller animals the longer oostegite sheaths will also be wider, among the larger animals this is not necessarily true. Therefore, sheath shape varies more among the larger animals than among the smaller ones (Figure 94L–O). The association between the variables is also indicated by the correlation coefficient (r) for the two groups of animals: $r=0.903$ and 0.833 for the smaller sheaths and 0.104 and 0.218 for the larger sheaths at Stas. 64 and 76 respectively.

Testing the significance of the differences among the regression coefficients (Brownlee, 1965), the differences between the groups of smaller animals and also between the groups of larger animals at both stations are nonsignificant at the 0.05 level of risk. However, the differences between the groups of small and large animals at each station are highly significant $(P < 0.01)$.

From the foregoing, it is clear that there are two instars represented among the animals with rudimentary oostegites, preparatory females 1 and 2 (see "Intermediate Females," below).

ANIMALS WITHOUT OOSTEGITES (=JUVENILES, PREPARATORY MALES, AND COPULATORY FEMALES LACKING OOSTEGITES).—A large number of animals (25 at Sta. 64 and 37 at Sta. 76) resemble females in all respects except that they do not bear oostegites. The wide ranges of body length, 3.8 mm and 3.1 mm respectively at the two stations, indicates that they represent more than one instar (see Figure 84).

The pleopods show marked differences in the degree of development among the animals. Figure 10I,L illustrates the difference in endopodal length together with the numbers and degree of develop-
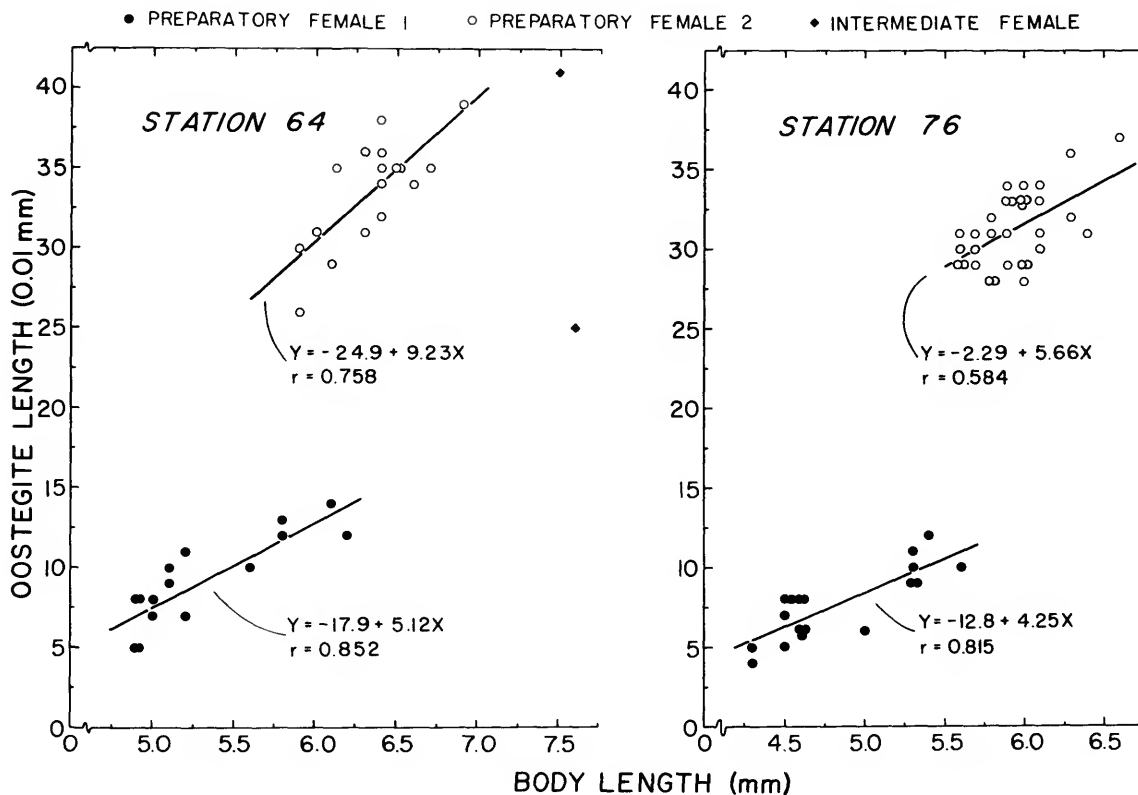
FIGURE 83.—Relationship of length of rudimentary oostegite sheath to body length for *Neotanais micromopher* at WHOI Benthic Stas. 64 and 76. The correlation coefficient is represented by "r."

ment of the terminal endopodal setae. Endopodal length is less than or equal to 0.22 mm for a group of smaller animals, and greater than or equal to 0.29 mm for the larger animals (Figure 84). The gap would be even greater except for specimen EH (Sta. 76) with a body length of 4.9 mm. On the basis of other data (see below), this animal has been assigned to the group of larger animals. The smaller animals have from zero to four poorly developed setae on the pleopodal endopod, whereas up to eight well-developed setae are present in the larger group. The terminal setae are no more than half as long relative to the endopod in the small animals compared to the larger ones.

Apparently this pattern of pleopodal development is unique to *Neotanais micromopher*. In other species for which adequate material was available, the pleopods assume their adult proportions (seta-length/endopodal-length ratio) by the juvenile *(N. affinis, N. armiger, N. hastiger, N. pfaffi, N. robustus, N. dinotomer,* and *N. calcarulus)* or by the preparatory female 1 *(N. giganteus)* instars. A sizable difference in ratio remains between copulatory males and all other stages, and the latter instars continue to show pleopodal growth and the addition of setae throughout life.

A comparison of the number of articles in the uropodal endopod showed a difference between the
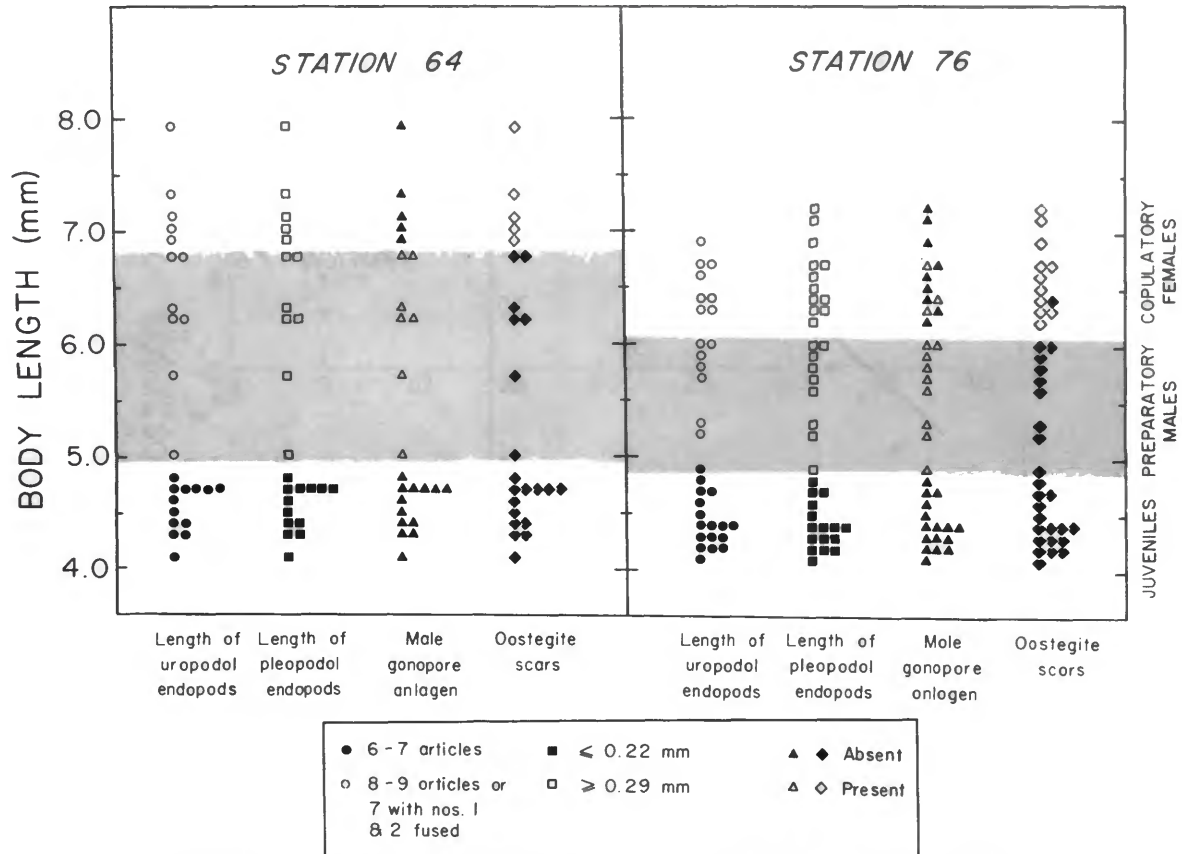
FIGURE 84.—Representation of five characters utilized in distinguishing juveniles, preparatory males, and copulatory females (without oostegites) in *Neotanais micromopher* at WHOI Benthic Stas. 64 and 76. The characters are the lengths of body, uropod, and pleopod and the presence or absence of male gonopore anlagen and oostegite scars. Missing symbols indicate lack of measurement due to defective specimens.

group of animals with poorly developed pleopods and the others (Figure 84, Table 20). The former had six or seven articles; the latter, eight or nine. (In some cases, animals in the latter group had articles 1 and 2 fused.)

Wolff (1956a:231, fig. 53; 1956c:49) noted the presence of "two scar-like marks" on the ventral surface of pereonite 7 in two females of *Neotanais giganteus*. Kudinova–Pasternak (1965a:81) observed "conical low protuberances" in a similar location on a specimen of *N. serratispinosus* (=*N. hadalis?*) with rudimentary oostegites. Because of limited sample size (four and one, respectively), neither author was able to understand adequately the significance of these markings or the place of these animals in the developmental series.

Each individual was examined for these marks or projections with the thought that they might be characteristic for a particular developmental stage. Certain animals do have a pair of spots on the ventral surface of pereonite 7; and in *Neotanais micromopher* they appear as small, decalcified areas in the cuticle (Figure 94P). In some specimens their slightly raised nature can be seen when they are sectioned vertically (Figure 91A).

Figure 84 illustrates the distribution of these decalcified spots among the animals without oostegites. Animals in the group with short body length, short uropodal endopods, and poorly developed pleopods lacked these spots. On the other hand, all animals longer than 4.9 mm and with longer uropodal and pleopodal endopods had clearly visible marks.

These structural differences clearly indicate that at least two different developmental instars are represented in this group of animals: (1) small animals lacking decalcified spots on the seventh pereonite, here referred to as juveniles, and (2) larger animals with or without decalcified spots.

Animal EH (length, 4.9 mm) at Sta. 76 shares characteristics of both groups. In body length and length of uropodal endopod it resembles the juveniles. However, at Sta. 64, where the mean body lengths of instars are slightly higher than at Sta. 76, animal AK (length, 5.0 mm) shares all characters of the upper group. Therefore, small body length in EH is probably due to natural variability. The presence of decalcified spots is taken to be more important than length of uropod in indicating

developmental stage, and therefore EH is placed in the upper group.

Animal EK at Sta. 76 (body length, 4.7 mm) has one tiny rudimentary oostegite on its left pereopod IV (see under "Morphological and Developmental Abnormalities").

The range in body length for the group of large animals (Sta. 64, 2.3 mm; Sta. 76, 2.3 mm) is still large enough to indicate the presence of more than one instar. Body length and length of pleopod are not useful in distinguishing additional groups; all animals are similar. Although a sufficiently clear break is present among the animals with and without decalcified spots at Sta. 64, there is some ambiguity at Sta. 76.

A careful examination of the specimens revealed that the coxae of pereopods II–V are differently shaped in some of the animals. The posteromedial area is somewhat distorted and apparently narrower than the rest of the article. On pereopod V, the entire posteromedial area of the coxa is decalcified (cf. Figure 94H,K).

The distribution of these aberrant coxae is identical to that of the oostegites in *Neotanais*, and these changes in coxal shape represent oostegite scars; they are found in animals that have had mature oostegites but later lost them—that is, in copulatory females. Shiino (1937:59) also noted the presence of similar oostegite scars on the monokonophoran *Apseudes nipponicus*. The wide coxal decalcification on pereopod V in *Neotanais* is the remainder of the closed female gonopore.

There is a strong negative correlation between the distribution of oostegite scars and the decalcified spots in pereonite 7 (Figure 84). Those individuals having clear evidence of decalcified spots never have any indication of oostegite or female gonopore scars. Those having oostegite scars usually do not have any indication of the decalcifications. Animal DV (body length, 6.4 mm) at Sta. 76 belongs with the lower group of animals (Figure 84), and easily falls within the size range observed for this group at Sta. 64. This is indicated by its lack of the scars both of oostegites and of female gonopores, infallible characters for identifying copulatory females.

The other exceptions to the pattern described are two animals from Sta. 76, EP (6.7 mm) and DJ (6.3 mm), both of which have oostegite scars, clearly placing them in the upper group. They also exhibit very faint subsurface discoloration or trans-

lucency at the sites of the ventral decalcifications found in smaller animals.

The animals of the middle group in Figure 84 are here referred to as preparatory males, and their ventral decalcifications are male gonopore anlagen. The frequency with which male gonopore anlagen appear in copulatory females apparently varies from species to species. Among 20 copulatory females of *Neotanais armiger* from several stations, only one had faint decalcifications. Of 16 similar females of *N. pfaffi,* also from several stations, only one did not have decalcifications of some sort.

JUVENILES.—The degree of pleopodal setal development varies considerably in number and length relative to the endopods among the juveniles. This variation is greater than that found in any other instar and is possible evidence of the presence of more than one type of individual within the group.

In several species there is a great range of body length among animals without oostegites, oostegite scars, or traces of male or female gonopores. Presumably these animals are juveniles, but their body lengths, relative to those of *Neotanais micromopher,* are distributed over a range of 3 mm or even 4 mm in certain species. These species are *N. affinis, N. americanus, N. giganteus, N. dinotomer,* and *Herpotanais kirkegaardi.* Juveniles of *N. giganteus* at WHOI B. Sta. 62 appear to be arranged in two or three groups (see discussion, p. 115).

It is possible that juveniles destined to become males have already started to diverge from incipient females, the former being larger than the latter, at least in some species. Differences observed in the ventral surface of the seventh pereonite and in the gonads are described under "Gonadal Development," below.

COPULATORY FEMALES.—These are animals with fully developed oostegites or with oostegite scars. Unfortunately, none of the former was present in the collections from Stas. 64 or 76. In fact, only five specimens with oostegites were present in all of the available collections of *Neotanais micromopher.* An oostegite measured on one of these animals was 0.50 mm long and 0.41 mm wide (cf. Figures 81, 82).

Although they do not have oostegites, there are animals in each sample that unquestionably are copulatory females. They compose the group with the largest body size in Figure 84, and they all bear oostegite scars. Their body length (Figure 85),

pleopodal length (Figure 80), pereopodal setation (Table 19), and length of uropods (Table 20) are larger than any other group except secondary copulatory males.

INTERMEDIATE FEMALES.—Specimens A and C at Sta. 64 are considerably larger than other individuals with rudimentary oostegites (Figure 80). Their pleopods are much longer than those of the preparatory females 2, which they most closely resemble, and they have a larger number of more well developed terminal endopodal setae on these appendages. There are nine articles in their uropodal endopods compared with seven or eight for the preparatory females 2. There are more pereopodal setae than usually found in the latter instar, and these are as large as those of some copulatory males (Table 19). Their oostegite sheaths are similar to those of the preparatory females 2, although slightly more swollen. In length, they fall in the extreme upper and lower tails of the distribution of those of the latter stage (Figures 81, 82), and they differ appreciably in oostegite width-length relationship (Figure 82) although they are almost identical in body length (Figure 80). The tentative interpretation made here is that these animals have already passed through a copulatory female stage and have molted, probably once, forming new oostegite anlagen in preparation for a second brood. This explains their greater body length and other characteristics of increased age.

It is not possible to determine at this time whether there are two instars between broods, analagous to the two preparatory female stages, even though the oostegites of these intermediate females are already of the same relative size as those of preparatory females 2. Judging from their body size, animals A and C have passed through only a single molt since the copulatory stage. If this is true, presumably only a single intermediate stage is present, and the oostegites would be large enough to serve their function following another molt.

COPULATORY FEMALES 2.—By means of culturing experiments, Bückle Ramírez (1965) has demonstrated that the copulatory females of *Heterotanais oerstedi* can, after raising a brood of young, molt and pass into an intermediate stage preparatory to a second copulatory stage. Shiino (1937) discovered copulatory females of *Apseudes nipponicus* without marsupia that had oostegite scars and whose ovar-

ies contained small developed ova in preparation for a second brood.

The evidence for the presence of intermediate females in *Neotanais* has already been presented. But copulatory females 2 were not present among the collections of *Neotanais micromopher*. If present, they would probably demonstrate some size increase over copulatory females 1, having passed through at least two additional molts.

Among 18 measurable females of *Neotanais pfaffi* from the collection at *Galathea* Sta. 716, body lengths range over 5.6 mm, a wide distribution even for a large species. Strangely enough, most of the animals (14) were clustered in the upper part of the range, far above the preparatory females 2 in the sample (4), but the smallest copulatory females were far smaller than the latter animals. Most copulatory females were larger than all of the copulatory males (3) in the sample. Although the disjunct distribution of copulatory females may be due to the presence of two copulatory instars, it is not absolutely certain that copulatory females 2 are present.

Among the samples of *Neotanais armiger* collected off Oregon there is one copulatory female similar in size to certain females collected off Central America but over twice as large as another female collected nearby at an Oregonian station. Ordinarily, such size variation at nearby stations would be clear evidence for two different copulatory stages. However, the confused taxonomy of *N. armiger* (q.v.) does not permit such a conclusion. Indeed, the two-fold difference in size between the two animals, a much greater difference than expected, in itself indicates that some other factor probably is involved.

Among the collections of *Neotanais giganteus*, there is an appreciable range of body length (4.8 mm) among the copulatory females (3) collected at WHOI B. Sta. 72. The two smaller animals (14.6 and 16.1 mm) do not have male gonopore or genital cone anlagen, whereas the largest animals (19.4 mm) has clear genital cone anlagen. However, copulatory females at nearby stations as well as at the type-locality on the other side of the Atlantic (*Galathea* Sta. 65) fall between these extremes in body length, thus confusing the interpretation.

One copulatory female of this species that was collected at WHOI B. Sta. 151 off West Africa has a body length of 22.3 mm and is far outside the size range found at any station, including the type-locality (also off the west coast of Africa). Although this is possibly a copulatory female 2, one cannot be sure because of the possibility of body length variation among widely separated populations. The nearest animal in body length (21.5 mm) is the female with rudimentary oostegites from the Tasman Sea (*Galathea* Sta. 575). It has been identified tentatively as a preparatory female 2, but it may be an intermediate female.

In summary, there are a number of indications that more than one brood can be produced in *Neotanais*, but because of limited material, the data are inconclusive.

Summary of Sequence of Postmarsupial Development in Neotanais micromopher

The sequence of instars composing the life history of *Neotanais micromopher* can be reconstructed, based on the morphological analysis above. This sequence may vary slightly within the genus, perhaps among the species groups. Thus, it may be possible to explain differences noted in the differing ranges of length for juvenile specimens, the presence of male gonopore anlagen on an occasional preparatory female, or the abundance of male genital cone anlagen in the females of some species.

The most important indicators of growth and placement in the developmental sequence are body length (Figure 85) and length of pleopod (Figures 79, 84), the ratio of terminal endopodal setal length to length of pleopodal endopod (Table 20), and, in certain cases, the presence or absence of certain secondary sexual characteristics (Figure 84). Figure 86 presents a summary flow diagram of development.

All animals pass from the first manca stage through the second manca into a juvenile instar. From this point the developmental pathway through which a female passes is clear. Juveniles which are incipient females pass through ecdyses which bring them successively to the preparatory female 1, preparatory female 2, and copulatory female stages. The last ecdysis is referred to as the maturation molt or "Reifungshäutung" of Forsman (1938). The eggs are shed and the young are brooded during the copulatory female instar.

More than a single brood probably is raised in *Neotanais*, although this is not certain. The copulatory female (actually copulatory female 1) would

undergo a molt to become an intermediate female with rudimentary oostegites. This animal would undergo at least one more molt to become a copulatory female 2 capable of raising a second brood.

The developmental sequence among the males is considerably more complex than among the females. There are at least two sources of mature copulatory males, and probably three. Juveniles molt to produce preparatory males, which, in turn, pass through a second molt to become primary copulatory males (chela type A). The smallest primary males almost certainly belong to a different developmental stage than the larger animals.

In order for them to increase in length proportionally to other groups following a molt (Figure 85) and to add an article to the uropodal endopod in common with other instars (Table 20), it is necessary to derive these small males directly from juveniles, following a molt. They may arise from the larger juveniles which display evidence of maleness (see "Gonadal Development") or perhaps they pass through two juvenile stages; however, the data are too limited to say more at this time.

The largest (secondary) copulatory males (chela type B) can be derived from the large primary copulatory males and account for a reasonable increase in body length between the two (Figure 85). However, pleopodal length, pleopodal setal length/endopodal length ratio, and the length of the uropodal endopods are identical betweeen the two stages. One might derive these secondary males from the smallest copulatory males, but such a development sequence would involve an increase in body length unknown elsewhere in neotanaid development together with an increase of two uropodal articles, twice that of normal growth.

If, however, the largest males are derived from copulatory females, there is a regular increase in mean body length, an increase in pleopodal setal length/endopodal length ratio ($\bar{x}=0.77$ to $\bar{x}=1.5$), and an increase in the length of the uropodal endopod (eight to nine articles). This interpretation is accepted here and is supported by the gonodal study (below). According to such an interpretation, the indications of male gonopores or genital cones on certain females are not scars from a previous male phase but the anlagen of secondary
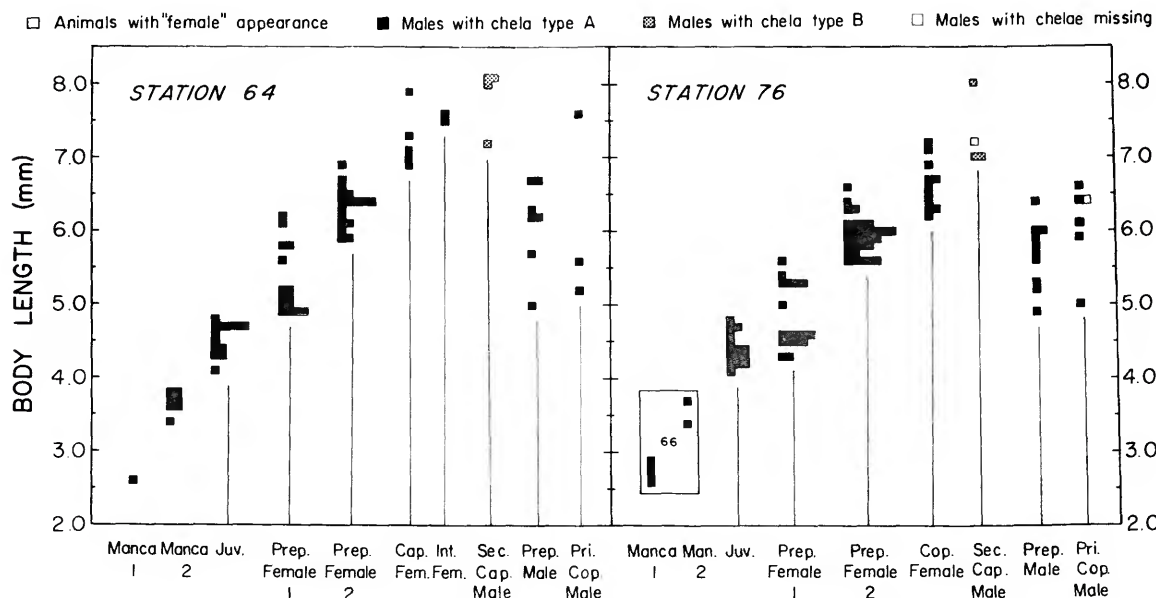
FIGURE 85.—Postmarsupial development in *Neotanais micromopher* at WHOI Benthic Stas. 64 and 76. Each instar is represented by a histogram of body-length frequency. The number of individuals increases horizontally to the right, each square representing one animal. Mancas from Sta. 66 are added under Sta. 76 for purposes of comparison (none present at Sta. 76).

sexual characters which will appear in full at the next molt. Bückle Ramírez (1965) found that 98 percent of the copulatory females of *Heterotanais oerstedi* which would later become males were of "blue" coloration prior to molting; however, no such external indications of an impending sexual change are present in *Neotanais*.

For these reasons, copulatory males have at least three possible origins: the two types of primary males are derived from different gonochoristic precursor stages; the secondary males are protogynous hermaphrodites. The rare males bearing aberrant chelae mentioned earlier (p. 32) may represent a fourth type of male occurring in lesser numbers

than the other three types or they may simply be developmental anomalies.

The copulatory males are the final instars in their respective lines of development. Animals larger than the males do not occur in the samples, and it is unlikely that the males continue molting and regain the food-processing devices of the mouth and gut which they once had. They probably do not pass into additional male stages because of energy limitations but mate for an unspecified period and then die.

Bückle Ramírez (1965) has shown that there are females of *Heterotanais oerstedi* which are truly gonochoristic and which never become males, and
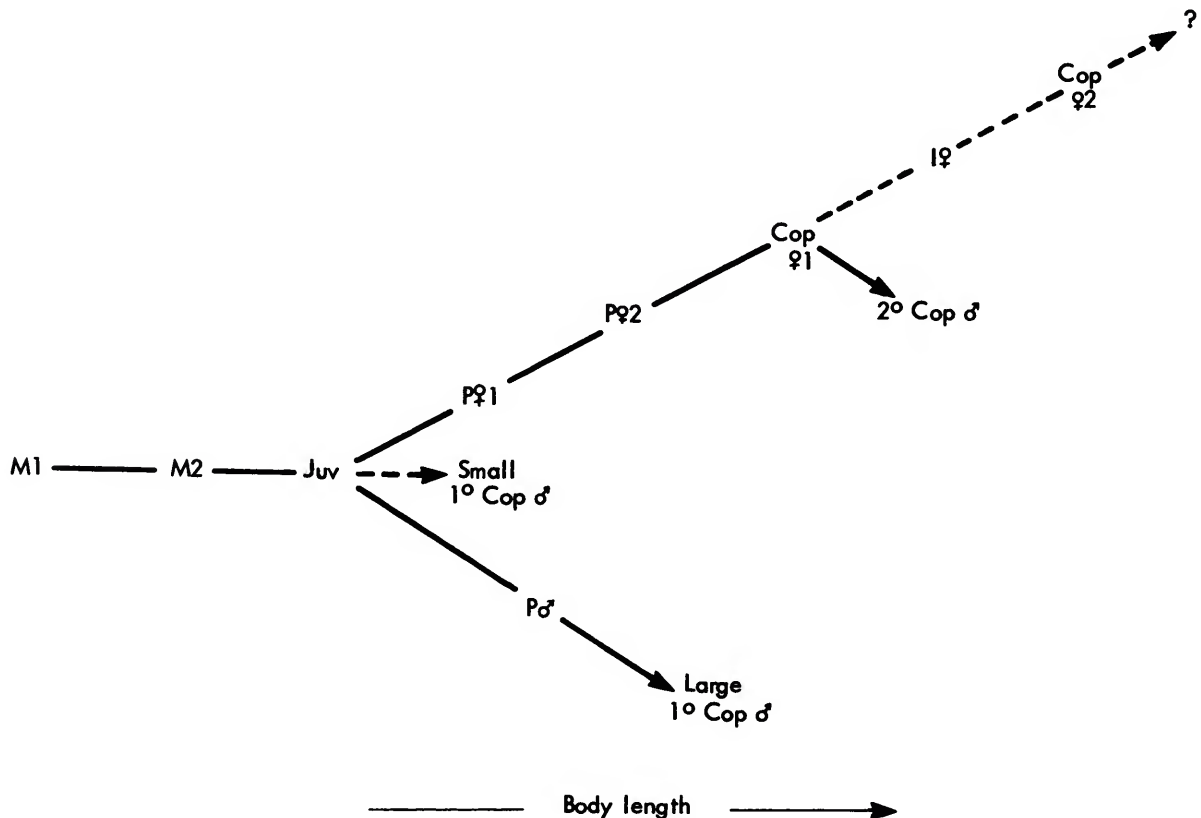
FIGURE 86.—Sequence of postmarsupial development in *Neotanais micromopher*. Only those developmental possibilities indicated by this study are included. Arrows indicate increasing age; solid lines, well-established steps; broken lines, steps for which the data are equivocal.

Lang (1958) has stated that this is true for *Tanais stanfordi*. Gonochoristic-females eventually may be shown to exist in *Neotanais* as well, but it is not possible to recognize them at present. If a large number of copulatory females were sectioned, several with "true" ovaries and not "ovotestes" might be found, the situation described by Lang for *Tanais*.

The ratio of copulatory males to copulatory females varies considerably in these relatively small deep-sea samples. But because there are consistently more secondary copulatory males than copulatory females large enough to have passed through an intermediate stage, more females probably become males in *Neotanais* than raise a second brood. How many die following release of their young is unknown.

Copulatory females at Stas. 64 and 76 comprise 6.7 and 11.6 percent of all animals collected there and 29.4 and 35.5 percent of the animals in the next previous stage (preparatory female 2) respectively. These percentages are roughly similar for most samples of neotanaids where a number of individuals were collected. An exception was the collection of *Neotanais pfaffi* at *Galathea* Sta. 716. Of a total of 37 animals which could be identified as to instar, 21, or 56.7 percent were copulatory females. This is probably due to chance or is an artifact of sampling procedure. WHOI B. Stas. 64 and 76 were collected on the Gay Head–Bermuda Transect (about 39° N) in August; *Galathea* Sta. 716 was collected in the Pacific off Costa Rica (about 9°30′ N) in May. Seasonal differences between the two areas probably should not account for these differences in female occurrence.

The copulatory males were also found in relatively low numbers. At WHOI B. Stas. 64 and 76 the numbers of individuals in all copulatory male stages of *Neotanais micromopher* were 9.4 and 10.5 percent respectively, typical for most neotanaid collections.

Low numbers of "males" or "adult males" have been reported in the literature a number of times. Of over 1000 specimens collected by the *Ingolf*, mostly in deep water, Hansen (1913) reports that only 14 were "adult" males. Smith (1906) had several thousand "female" specimens and only 80 males of the shallow-water *Leptochelia dubia*. Lang (1953b) remarked that he had no males among 300 specimens of *L. dubia*, and Forsman (1956) states

that the males are rare in *Heterotanais oerstedi*.

Unfortunately, statements on shallow-water populations are meaningless unless the dates of collection are provided. Bückle Ramírez (1965) has demonstrated that development and reproduction in the littoral *Heterotanais oerstedi* is strongly regulated seasonally. Thus, he found the percentage of copulatory males in his samples varying from 0 to 70 depending upon the date of collection. This explains the variation in his numbers of copulatory females as well. He often found less than 10 percent copulatory females, although the rate rose to 42.4 percent in one sample (Bückle Ramírez, 1965: 775). Presumably other, but not necessarily all, littoral forms are similarly responsive to seasonal fluctuations in their environments (reproductive periodicity in the Neotanaidae is discussed in the ecological section, p. 249).

Postmarsupial Development in Herpotanais *Wolff*

When describing *Herpotanais kirkegaardi*, Wolff (1956a:226) discussed the postmarsupial development of that species. He distinguished "adult" from "preadult" animals and adult males from adult females. At the time, the significance of the male gonopore anlagen was not understood, and preparatory males were considered to be females. Investigators had not utilized oostegite scars or female gonopores to identify copulatory females and could only recognize that stage if mature oostegites were present, which often was not the case.

Using the techniques developed in the study of *Neotanais*, the following assignments of developmental stages were made for Wolff's animals (cf. Wolff's table 4): mancas 1—A, B, and one animal not included by Wolff (body length, 8.5 mm); mancas 2—C and D; juveniles—E, F, one animal not included by Wolff (body length, 12.2 mm), G, H, and possibly K and N; preparatory females—holotype, *LL*, MM, NN, OO, PP, QQ, RR, SS, *TT*, and UU; copulatory females—Q, R, and perhaps S; preparatory males—I, J, L, and M; and copulatory males—V, W, X, Y, Z, and XX. The italicized specimens were not available for examination, but Wolff's data are sufficient to identify their developmental stage. Specimens O and P also were unavailable, but on the basis of body length and absence of oostegites they probably are preparatory males or copulatory females.

Wolff (1956a:229) comments on the differences in the chelae of copulatory males (Wolff's figure 47). Animal Z is longer than any of the other males and may represent a secondary copulatory male.

Specimens K and N lie considerably outside the body length range expected for juveniles, similar to the situation in *Neotanais* discussed earlier (p. 196).

Animal S, although not having oostegites or clear oostegite scars, does have slightly inflated inner coxal edges. It also has clear male gonopore anlagen. Its body length, 23.4 mm, lies in the length distribution of the copulatory females, far above that of the longest preparatory male (19.6 mm).

MORPHOLOGICAL CHANGES IN DEVELOPMENT.—The development of pereonite 7 and pereopod VII is similar to that of *Neotanais*: the pereonite increases gradually in size, and the pereopod is absent in mancas 1 and rudimentary in mancas 2. The pleo-

pods are absent in mancas I, but each is present as a single article with a distal, rudimentary seta in the manca 2 (Figure 88A). Each pleopod of juvenile E has two articles, the proximal article bearing one small lateral seta and the distal one bearing two rudimentary terminal setae (Figure 88B). In juvenile G each pleopod has a limited number of fully formed setae: the first article, one medial seta and three lateral setae; and the distal article, three setae terminally, one seta subterminally, and one lateral seta proximally. The pleopods of preparatory female MM, copulatory female Q, and preparatory male M are all similar to those of copulatory male X (Figure 88c) with respect to number, length, and setulation of the setae. Variation in number of pleopodal setae is as follows for preparatory male and female and older stages (not age related): proximal article on the medial side, one or two, and the lateral side, four or five; distal article on the medial side, one; the terminal and

Tanaidacea	Cumacea	Isopoda		
Heterotonois oerstedi	Diastylis r. rathkei	Jaera albifrons	Eugerdo tetarta	Chelator insignis
[Buckle Ramirez, 1965, p. 766]	[Forsman, 1938, p. 54]	[Forsman, 1944, p. 29]	[Hessler, 1970, p. 34]	[Hessler, 1970, p. 37]
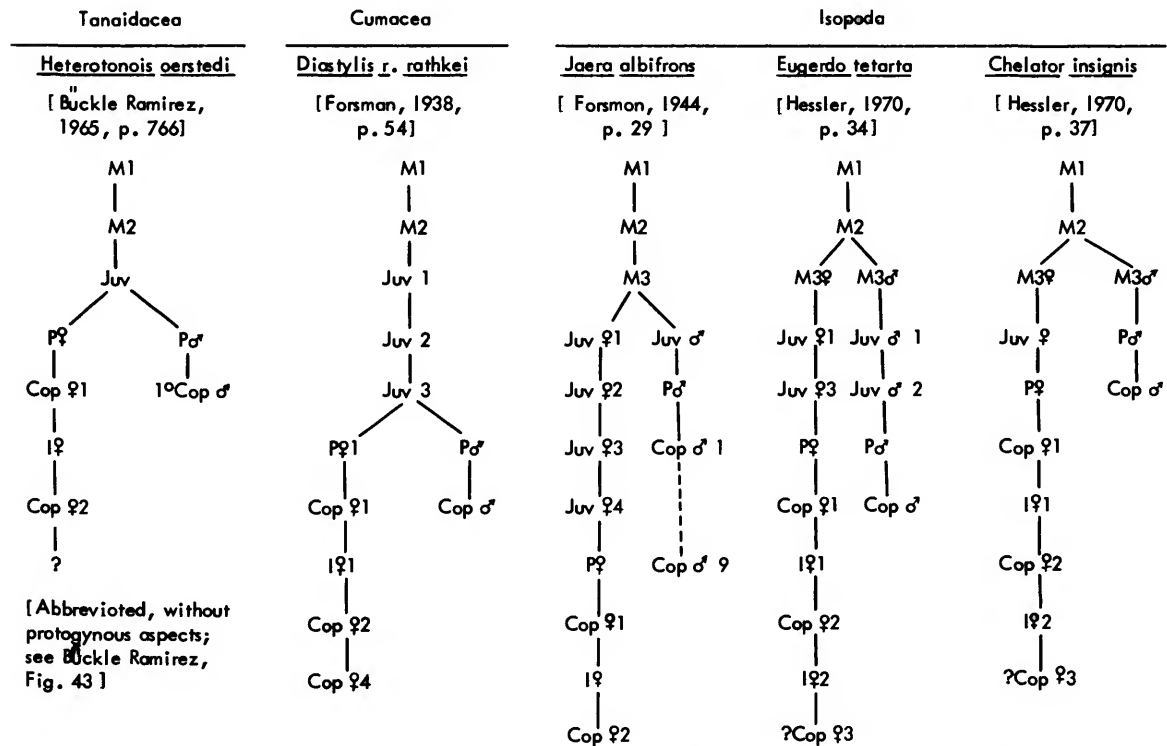
FIGURE 87.—Representative postmarsupial developmental sequences. The symbols are those used in this work, not necessarily those of the authors cited. Solid lines indicate well-established single molts; broken lines, uncertain or multiple steps.

lateral sides, seven to nine. Apparently the pleo-
pods are fully developed once the preparatory male
or female stage is reached; hence, pleopodal devel-
opment is not a useful tool in distinguishing among
older stages.

Male gonopore anlagen were clearly visible in
copulatory females (three individuals) and various-
ly visible in preparatory males (faint in L, clear
in M).

Female gonopores are in the same location and
apparently at the same stage as in *Neotanais* (copu-
latory female). Rudimentary oostegites in this
sample (six animals) are all of about the same size
(two, 0.43 mm; three, 0.46 mm; and one, 0.49 mm),
and presumably all these individuals belong to the
same instar. The oostegites are proportional to
those of preparatory females 2 in *Neotanais*. Judg-

ing from the gap in body length distribution be-
tween juveniles and the preparatory females 2, a
preparatory female 1 stage occurs in *Herpotanais*.
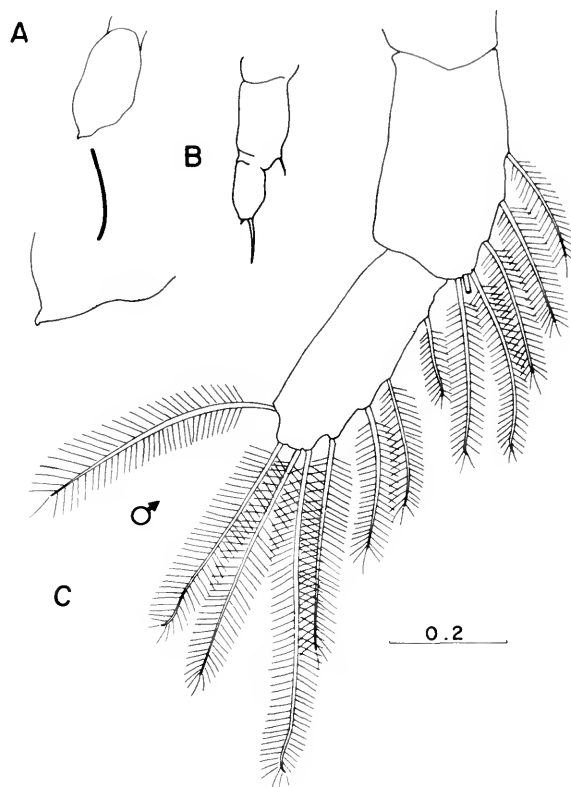
The first antennae show regular growth in the
early stages; both manca 1 and manca 2 have six
articles and one annulated esthetasc; juveniles have
seven articles and two esthetascs, and all other
stages have eight articles and three esthetascs.
Therefore, first antennal development is identical
with that of *Neotanais* except for a final total of
eight articles and three esthetascs rather than the
seven articles and two esthetascs present in the lat-
ter genus. Wolff's (1956c:224, 229) statements about
the number of first antennal articles in the copu-
latory male are not clear. Wolff seems to indicate
that male Z has eight articles, but he figures nine
and then states that all other males (except W and
XX in which the carapace is missing) are identical
to Z.

The second antenna is composed of nine articles
in all stages.

Each uropodal endopod is composed of four
articles in the manca stages (Wolff, 1956c, table 4),
but, unlike *Neotanais*, the length of the uropodal
endopods increases only to six articles and that by
at least preparatory female 2. Thereafter, four,
five, or six articles may occur. Hence, the number
of articles is not a useful clue to age among older
stages. (In *Neotanais*, the uropods increase in length
up to the copulatory male instars and may reach a
length of 14 articles.)

POSTMARSUPIAL DEVELOPMENT AMONG OTHER TAXA

Although there have been few studies of post-
marsupial development among the Tanaidacea, a
number of investigators have made observations
which shed light on developmental patterns within
the order. Some of these observations and those
made on other peracaridans are summarized below
in tabular form and in flow diagrams (Table 10;
Figure 87). Comparison with other, better known,
peracaridan taxa illustrates the basic similarity of
tanaidacean development—aside from its protogy-
nous aspects—to that of the Cumacea and Isopoda.
The names of the instars in the tables and flow
diagrams are those used in this study, not neces-
sarily those of the authors cited (see under "Nom-
enclature and Identification of the Developmental
Stages," below).

FIGURE 88.—Pleopodal development of *Herpotanais kirke-
gaardi* Wolff (all figures drawn to the same scale): A, manca
2 C; B, juvenile E; C, copulatory male X (preparatory female
MM, preparatory male M, and all copulatory females similar).

TABLE 10.—*Representative manca instars showing structural agreement with those of* Neotanais (terminology used is that of this study and not necessarily that of the authors cited)

Family	Species	Instar	Source
Apseudidae	*Apseudes galatheae* (=*Leiopus galatheae*)	M1	Wolff, 1956a:197
	A. gracillimus (=*Leiopus gracillimus*)	M1	Lang, 1953b:419
		M2	Wolff, 1956a:204
	A. latreillii (=*A. acutifrons*)	M1	Claus, 1888:201
	A. spinosus	M1	Wolff, 1956a:191
		M2	Lang, 1953b:419; Wolff, 1956a:191
	Leiopus wolffi	M2	Lang, 1968:117
Kalliapseudidae	*Psammokalliapseudes mirabilis*	?	Lang, 1956c:254*
Paratanaidae	*Anarthruropsis galatheae*	M2	Lang, 1968:188
	Exspina typica	M1	Lang, 1968:192
	Heterotanais antarcticus	M1, M2	Lang, 1953b:416
	H. oerstedi	M1, M2	Bückle Ramírez, 1965:744
	Leptochelia dubia	M1	Roubault, 1937:150
	Tanais dubius (=*Leptochelia dubia*)	M1	Müller, 1864b:4
	Leptochelia lifuensis	M1, M2	Lang, 1953b:418
	L. mirabilis	M1, M2	Lang, 1953b:418
	Leptochelia sp.	M1, M2	Lang, 1953b:418
	Leptognathia antarctica	M1, M2	Lang, 1953b:418
	"Leptognathia" oculata	M1, M2	Lang, 1953b:417
	Nototanais werthi	M1, M2	Lang, 1953b:417
Tanaidae	*Anatanais* (=*Zeuxo*) sp.	M2	Lang, 1953b:418

* Lang examined "zwei verschiedene Manca-Stadien. . . ." No further details were given.

The descriptions of all mancas to which reference has been found in the tanaidacean literature accord well with those described for the Neotanaidae (Table 10); that is, the last pair of pereopods and the pleopods are missing (manca 1) or poorly developed (manca 2). Perhaps more than two mancas occur in some taxa (as suggested by Lang, 1953b:419) for certain Monokonophora.

Apparently a single juvenile is known throughout the Tanaidacea, but additional juvenile stages are commonly reported for cumaceans and isopods (Figure 87). Some species of *Neotanais* (viz., *N. giganteus*) may later be shown to have more than one juvenile stage (see "Postmarsupial Development" and "Variation in Pleopods" under *Neotanais giganteus*).

A single preparatory stage in both male and female developmental pathways is typical, the females of *Neotanais* being an exception. In addition to those examples illustrated in the flow diagrams, Wolff (1962) states that there is a single preparatory female in the asellote isopod families Haploniscidae, Macrostylidae, Munnidae, and Nannoniscidae.

Copulatory females characteristically molt at some time following the loss of their larvae if they do not die, and additional broods often follow. The number of molts varies considerably.

Copulatory males are usually terminal. In *Heterotanais oerstedi* "the male never molts" (Bückle Ramírez, 1965); however, Forsman (1944) reports up to nine successive copulatory male stages in the isopod *Jaera albifrons* (Figure 87).

Sexual complications of this pattern are discussed below.

Patterns of Sexual Development

The Crustacea are generally bisexual, but they demonstrate widely differing developmental patterns and methods of sexual determination. This aspect of their biology has been reviewed by Charniaux-Cotton (1960).

There are a number of sexually "aberrant" groups in the malacostracan division Peracarida. Females of the isopod genus *Trichoniscus* produce broods of a single sex (Charniaux-Cotton, 1960). Menzies (1954) found rare individuals of the isopod

Limnoria that showed characteristics of both sexes (i.e., the male apophyses and the oostegites). He states that female sphaeromids have rudimentary testes connected to their ovaries, and Charniaux-Cotton (1960) notes that hermaphroditism is "general" in the parasitic family Cryptoniscidae as well as among some members of the Oniscoidea. Protandry is characteristic of the flabelliferan family Cymothoidae: the young are functional males but contain rudimentary ovarian tissue and progressively become functional females (Menzies, 1954).

Lang (1958) cites additional cases of hermaphroditism, mostly protandrous, among the isopods and amphipods. Most hermaphroditic malacostracans are protandrous, and the early gonad is composed of both ovarian and testicular primordia according to Charniaux-Cotton. Wolff (1962:223) reviews literature dealing with hermaphroditism and intersexes among the isopods. Charniaux-Cotton states that the isopod *Trichoniscus elisabethae* and the amphipod *Rhabdosoma* show geographic parthenogenesis; that is, populations from only certain areas are parthenogenetic.

The sexual pattern among the Tanaidacea has been confused. Gonochoristic development as well as simultaneous, protandrous, and protogynous hermaphroditism have all been suggested for various taxa. Forsman (1956) was the first to suggest that protogyny occurs among the Tanaidacea, and, according to Lang (1958:536), this was the first recorded instance of protogyny among the Crustacea. Forsman found a living male and a female exuvium in a dish which had originally contained only an adult female of *Heterotanais oerstedi*.

Lang (1958) reported that he had verified Forsman's hypothesis. In the same paper, he also reported discovering protogyny in *Tanais stanfordi*, and he stated that *Apseudes sarsi* Holthuis (= *A. holthuisi*) is protogynous, although without further discussion. Lang concluded that there were both protogynous hermaphrodites and gonochoristic males and females in both *Heterotanais* and *Tanais*. Bückle Ramírez (1965) maintains that, in such a case, species should be thought of not as protogynous hermaphrodites but as being potentially protogynous.

Lang (1966:551, 564) found that certain adult females of *Parapseudes latifrons* had eggs in their marsupia and a male genital cone on the seventh pereonite. But he suggested that this species is probably not hermaphroditic because the sexually dimorphic chelipeds are differentiated much earlier in life, and they continue to diverge with age. An examination of sections of similar females of *Apseudes spinosus* demonstrated no evidence of testes (Lang, 1966:564). Lang (1968:30) also reports a female of *A. grossimanus* with eggs in its marsupium and a genital cone as well developed as in the male, and he hypothesizes that this animal may be protogynous.

More recently than Forsman's (1956) work, Legrand and Juchault (1963) have established a protogynous pattern of sexual development in the isopod *Cyathura carinata*. Protogyny is a seasonal phenomenon in *Cyathura*. Among animals collected near Salses, in southern France, females took on external male characteristics; and their gonads were transformed into testes during January, February, and March. Legrand and Juchault cite other seasonal observations indicating that males become less frequent during the summer and are absent during the autumn and winter (at Roscoff and at Luc).

The androgenic gland appears to initiate male development in *Cyathura*. Apparently gonochoristic animals can exist along with the hermaphrodites. Legrand and Juchault report the occurrence of very large females and very small males.

This seasonal pattern of development closely parallels the sequence determined by Bückle Ramírez (1965) for populations of *Heterotanais oerstedi* in the North Sea–Baltic Sea Canal near Kiel, about 1300 km (800 miles) north of Salses. The first males were collected at the end of May, the maximum number at the end of June, and the last male on 21 September. A comparison of seasonal occurrence of males in these shallow-water forms with the regulation of male development among the deep-sea Tanaidacea will be very interesting (see discussion of reproductive periodicity under "Ecology").

Wolff (1956a:230) reports that the body lengths of the males of *Apseudes* (= *Leiopus*) *galatheae* and *A.* (= *Leiopus*) *gracillimus* which he examined were smaller than those of the "females." He interpreted this as strong evidence for protandry in these species. However, a maximum of only 18 specimens was available, making difficult the accurate estimation of size ranges for the various instars. The number of spines on the lower margin of the propodus of pereopod II was about the same

for both the males and females, and the numbers of articles in the two flagella of the first antenna were actually greater in the males. A gain in spines or articles is to be expected with increasing age.

The only detailed work on sexual development in the Monokonophora is that of Lang (1953a), in which he claims finding simultaneous hermaphroditism in *Apseudes hermaphroditicus* (=*A. spectabilis*). He reports finding mature ova and spermatozoa in the female and male portions of the gonads, respectively, at the same time. He points out that these animals may even be capable of self-fertilization. Băcescu (1961:155) has reported individuals of *Apseudes intermedius* which possessed the large, masculine chelipeds but which also carried eggs in the marsupium. Although his material was poorly preserved, he was able to determine that gonads of both sexes were present in the same individual.

Wolff (1956a) had at his disposal four specimens of *Neotanais serratispinosus hadalis* (=*N. hadalis*). The two male specimens were larger than the two females, and Wolff interpreted this fact as an indication that *Neotanais* probably was not protandrous. He also noted the improbability of regenerating complete mouthparts in a female instar following a male stage, a necessary modification if protandry were to occur. Because protogyny is relatively rare in the animal kingdom and seemed to be an unlikely explanation, Wolff postulated that *Neotanais* is normally gonochoristic but that simultaneous hermaphroditism may occur.

Wolff (1956c:49) discovered "scars" on the ventral surface of the seventh pereonite in two females of *Neotanais longimanus* (=*N. giganteus*). He interpreted these "scars" as vestiges of a previous simultaneous or purely male stage. However, the fact that the males of *N. hadalis* were longer than the females made protandry an unattractive hypothesis.

Wolff found that the "scars" were present only on the two larger animals but were absent in a smaller individual with mature oostegites. Kudinova–Pasternak (1965a, 1965b) hypothesized that there are alternating female-male-female stages in *Neotanais*; thus, the "scars" would be the remnants of a previous male stage.

However, simple protogyne hermaphroditism with possible concurrent gonochoristic development as demonstrated in this study explains the data

satisfactorily. The "scars" actually are male gonopore anlagen, and the slightly raised protuberances are genital cone anlagen. Some copulatory females have male anlagen, others do not. It is not clear whether those without them are gonochoristic and whether all of those with them are protogynous or potentially protogynous. All of Wolff's females fall within a single stage and, according to my measurements, are 18.4 mm (no scars), 18.7 mm, and 19.2 mm long.

DIMORPHISM AMONG MALES.—The first investigator to mention dimorphism among the males of a species of tanaid was F. Müller (1864a:20; 1864b:3). Müller studied *Tanais dubius*(?) Krøyer (=*Leptochelia dubia*?). He described two types of males—one characterized by small chelipeds similar to those of the females and the other by huge, powerful chelae (Müller, 1864a, figs. 3, 5). The former males occurred in a ratio of about 1 to 100 of the males, with large chelae among the thousands of individuals he collected. Müller was unable to find intermediate forms. Wolff (1956a:230) suggested that closer investigation would show that the two forms of males belonged to different species.

Later, Dohrn (1870) investigated dimorphic males in *Tanais savignyi* (=*Leptochelia dubia*). But G. O. Sars (1886:334) stated that Dohrn's males belonged to two different species, *L. dubia* and *Heterotanais anomalus*.

The findings of Müller and Dohrn were discussed first by Norman and Stebbing (1886:103) and then by Smith (1906:319) who carried out additional investigations. These authors compared the results of Müller and Dohrn with what was known for other crustaceans but did not clarify the status of these males in the developmental pattern. Smith claimed to have found differences among the males of *Leptochelia dubia* but such differences not as marked or as discontinuous as those described by Müller. Smith termed the two forms "high" and "low" males, and he found that their shapes overlapped each other; hence, for the Mediterranean specimens which he examined, there was no true dimorphism of the type described by Müller.

The only other author who has dealt with the question of dimorphism among the males of *Leptochelia dubia* has been Roubault (1935, 1937). He was unable to demonstrate clear dimorphism, and he states (Roubalt, 1937:150) that Smith's "low"

males are, in reality, "adolescent" males and his "high" males are adults.

In his morphological work on *Tanais* (=*Heterotanais*) *oerstedi*, Blanc (1884) commented that in all of the seasons during which he had collected this species in the Gulf of Kiel he had found only one type of male. However, referring to Müller's work (Müller, 1864a, 1864b) he predicted that another type would be found.

Two types of males were first reported for *Heterotanais oerstedi* by Monod (1924) who named them formae *oerstedi*, the previously known male, and *gurneyi*, described previously as the species *H. gurneyi* Norman. Monod designated the former as the "high" form and the latter as the "low" form, following Smith's (1906) practice with *Leptochelia*. Forma *oerstedi* was consistently larger than forma *gurneyi*, and its carapace was markedly elongated in front and broadened at the rear. The "processus polliciformis" on the chela was enlarged and club-shaped; the process had more or less parallel sides in forma *gurneyi* (Monod, 1924, fig. 1). The two forms also differed in the size of the anterior projection of the chelipedal carpus.

After raising *Heterotanais oerstedi* in the laboratory, Lang (1958:536) discovered that Monod's forma *oerstedi* was actually a protogynous secondary male that had arisen from a female following a molt. He does not comment on *gurneyi*. Bückle Ramírez (1965), the first to investigate thoroughly the life history of a tanaidacean in the laboratory, confirmed Lang's discovery and came to the following conclusions. Forma *gurneyi* corresponds to primary copulatory males which have arisen through an ecdysis from preparatory males (his "Neutrum II" stage) and secondary copulatory males type A, which had been females. These males agreed with *gurneyi* in the shapes of the processus polliciformis and of the carapace. Secondary copulatory male type C was, as Lang had found, equivalent to forma *oerstedi*, agreeing with the latter in the same two characters. Although secondary copulatory male type B resembled *oerstedi* in the shape of the processus polliciformis, the carapace of the former was similar to that of *gurneyi*. Bückle Ramírez aptly points out that the "forms" are of questionable usefulness.

The only other instance of male dimorphism reported for the Tanaidacea is that given by Lang (1958:538), who studied *Tanais stanfordi*. Lang describes two male forms, *typica* and *sylviae*. The former is smaller, ranging from 2.0 to 3.4 mm in length, and has the carapace strongly constricted anteriorly. Forma *sylviae*, on the other hand, is larger, 3.0 to 3.6 mm in length, and its carapace more nearly resembles that of the female, being only slightly constricted anteriorly. Both forms have true testes, but forma *sylviae* arises from a protogynous female whereas forma *typica* does not. Therefore, protogynous hermaphrodites as well as gonochoristic males and females are present as in *Heterotanais oerstedi*.

At least two, and almost certainly three, types of copulatory males have been demonstrated for *Neotanais micromopher* in the developmental analysis above. The smaller of the two, with chela type A (Figure 10A,B,D), is derived from a preparatory male (or, in some cases, possibly a juvenile) and is gonochoristic. The larger animals, with chela type B (Figure 10C,E), are protogynous hermaphrodites.

This is the first time that male dimorphism has been definitely demonstrated for the Neotanaidae. Wolff (1956a:217, fig. 32) described two forms of male chelae for *Neotanais serratispinosus hadalis* (=*N. hadalis*). The two specimens, A and B, differed from each other in the dentition of both the propodal finger and the dactylus as well as in the ornamentation of the wide portion of the propodus. However, the developmental status of "male" B is in question. Wolff also described two types of chelae for the males of *Herpotanais kirkegaardi* (Wolff, 1956a:229, fig. 47); but in this case the males apparently have the same propodal dentition and it is only the dactyli which vary. Because of his very small sample size, Wolff was able to describe these differences only as natural intraspecific variation.

DETERMINATION OF SEX.—The mechanisms determining sexual differentiation among invertebrates are not well understood. Many groups, including various crustacean taxa, have had little attention directed to their biology. The diversity of sexual patterns among the Crustacea has been indicated above, but there seems to be little overall pattern, and it is difficult to make generalizations concerning sexual development.

That the environment can have a marked effect in the determination of sex in the Crustacea is well known. As noted by Charinaux-Cotton (1960), overcrowding, high and low temperatures, and the

quality and abundance of food all can bring about the production of males or intersexes in certain Cladocera. The same author author points out that temperature can affect the sex ratio of broods in the amphipod *Gammarus duebeni;* high temperatures induce females. Vaquier and Belser (1965) have reported that an experimental increase of pressure on the pelagic marine copepod *Tigriopus* causes an abnormally large number of females to develop.

Fixation of larvae on adult females causes the larvae to develop into males in the epicaridean isopod families Boypridae and Entoniscidae, and another parasitic isopod, *Anilocra physodes,* is protandrous; isolated experimental males develop into females more rapidly than if both sexes are living together (Charinaux-Cotton, 1960). Presumably the female elaborates a pheromone of some sort which mediates the development of the larvae. Charinaux-Cotton points out that among the Crustacea that are fundamentally hermaphroditic, such as the cirripedes, sex chromosomes have not been found.

Bückle Ramírez (1965) conducted an elaborate series of laboratory experiments in an attempt to elucidate the pattern of sexual determination in *Heterotanais oerstedi.* Depending upon the experimental conditions, the development of mancas and copulatory females can be manipulated at will to bring about various results. If mancas 1 are placed in a dish with adult females, the mancas will develop into males. When kept with an adult male, they die as mancas 2 or juveniles, or they develop into adult females with marsupia and die in that stage (Bückle Ramírez, experiment 8, page 760). Apparently, then, sex is determined early in life and depends on certain factors in the environment of an animal.

If a copulatory male remains with a female throughout life, the latter remains a female (Bückle Ramírez, page 750); but if the male is removed when the larvae are in her marsupium, the female molts after brooding and changes into a copulatory male (Bückle Ramírez, experiment 1, page 755). Females with eggs in their ovaries but which are never fertilized can molt to become copulatory males, the eggs being reabsorbed (Bückle Ramírez, experiment 2, pages 756, 758).

A female which had raised young and was ready to molt again, presumably to become a male, did not, but—apparently due to the effect of the male with her—remained a female after the next molt, being fertilized and raising a second brood (Bückle Ramírez, experiment 1, page 755). Copulatory females ready to become males characteristically had a bluish coloration. When the male which was kept with such a female died while larvae were still in the female's marsupium, the female molted but did not become a male. Instead, she became an intermediate female with rudimentary oostegites and eggs in her ovaries; and following another molt, she became a copulatory female 2 and died in this stage (Bückle Ramírez, experiment 9, page 761).

Bückle Ramírez describes a female which formed a marsupium three times before dying. Neither eggs nor larvae ever appeared in the marsupium because no male was present (Bückle Ramírez, experiment 3, page 756).

According to Bückle Ramírez, there are four ways in which copulatory males can arise in *Heterotanais oerstedi.* Primary copulatory males originate from mancas which pass through the juvenile stage (his *"Neutrum* I") to become preparatory males (*"Neutrum* II"). These molt once again to become copulatory males. There are three sources of secondary copulatory males: (1) type A, copulatory females which have not been fertilized and which have reabsorbed their eggs and molted to become copulatory males; (2) type B, females which have had at least one brood and have molted to become copulatory males; and (3) type C, "blue" females which molt again after their larvae (at least one brood) leave the marsupium but still resemble females—they become copulatory males following one additional ecdysis. Secondary copulatory males types B and C are the largest, often having originated from females which have raised more than one brood. Their lengths, also more variable than those of type A males, depend on the number of broods they have raised. All of these males are able to fertilize females and produce larvae.

In summary, Bückle Ramírez was able to raise gonochoristic females which never became males although they had ample opportunity to do so. Gonochoristic primary males were produced as well as protogynous secondary males. That is why Bückle Ramírez (1965:768) refers to *Heterotanais oerstedi* as a potential hermaphrodite. Certain females are potential hermaphrodites; under the proper environmental conditions they will become

secondary males. Bückle Ramírez (1965:763) postu-lates a waterborne male pheromone as the causa-tive factor inducing sexual reversal. His experi-ments indicate that the basic developmental pattern in *Heterotanais oerstedi* is labile and subject to considerable variation depending on environmental conditions.

Primary, gonochoristic males were described for *Neotanais micromopher* in the developmental analysis above (p. 197). Such males probably are of more than one type: larger individuals which have arisen from preparatory males and very small animals which .have come from another source, perhaps directly from juveniles. The analysis of development also demonstrated the presence of secondary males, but it is not possible to distin-guish among different types without culturing the animals in the laboratory. Differentiation between gonochoristic and protogynous females also was impossible because of the limited number of fe-males available for sectioning.

The overall pattern of development of *Neotanais* is so similar to that of *Heterotanais* that it seems reasonable to assume that development is controlled and that sex is determined in much the same fashion in both groups.

Lang (1958:539) has suggested that large-scale environmental factors may determine whether ani-mals display protogyny. He was unable to find evidence of protogyny in a population of *Tanais stanfordi* from the Kurile Islands. From the results obtained with *Neotanais*, it is apparent that at least certain deep-sea taxa develop in much the same way as shallow-water forms. It will be of interest to see whether this pattern is generally true when other deep-sea tanaidacean genera are studied.

The functional usefulness of protogyny is of great interest, but the literature is notably lacking in convincing suggestions. The establishment of this developmental mode in both the shallow-water and deep-sea environments may indicate that its explanation does not reside in environmental con-ditions unique to either. On the other hand, if all protogynous tanaidacean taxa have arisen from protogynous deep-sea forms, it is then reasonable to speculate that, among the Tanaidacea, protogyny may have been an adaptation to the deep-sea environment and that it has been retained in cer-tain (or all) descendants, even though they may

have invaded other environments. Although gono-choristic males were retained by the deep-sea ances-tor, additional males were produced in order to fertilize the relatively scarce (compared to those of other environments) females. These males were formed by a potentially more energetically efficient method in the deep sea, an apparently nutritionally impoverished environment. Enough energy was stored in the copulatory female to support one additional, nonfeeding instar rather than raising the additional males from eggs. However, if this explanation is correct, it is not clear why primary males also do not feed.

GONADAL DEVELOPMENT

The major features of postmarsupial develop-ment in *Neotanais*, as reconstructed by external morphological analysis, have been described above. But some uncertainty concerning this interpreta-tion will remain unless verified by means of rearing experiments with cultured animals or by an analy-sis of gonadal development.

In addition to its usefulness in the elucidation of developmental patterns, an understanding of gonodal structure may be of future assistance in discerning systematic and phylogenetic relation-ships within the Tanaidacea. There appears to be considerable diversity of gonodal structure among those tanaidaceans that have been investigated (p. 219). The gonads of the Neotanaidae have never before been studied, usually because of the inade-quate preservation of collections or the necessity of retaining all available material intact for taxonomic purposes.

Rearing experiments with deep-sea tanaidaceans were not possible for the reason discussed earlier; however, the quality of preservation of the WHOI benthic samples was sufficient to permit the study of their gonadal structure, gametogenesis, and the structure of the gametes. A series of histological observations was carried out to observe the changes in gonadal development in the stages described earlier. These observations and their significance are described below. Neither time nor purpose per-mitted a complete morphological examination of the gonads; consequently only their grossest aspects are treated. Methods have been described in the introduction; and the basic data for the animals sectioned are presented in Tables 16–18.

Histological Observations on Neotanais micromopher

MANCA STAGE 1 (WHOI B. Sta. 65).—Discrete, continuous gonads were not found. However, from the level of pereopod III to the end of pereonite 5, fine, intermittent strands of cells (Ov, Figure 89A) can be seen in the position occupied by the ovaries in older animals. These strands lie on the dorsal side of the midgut (G) next to and closely pressed to the digestive glands (DG) and often are pear-shaped in cross section. The gonadal material could not be traced posterior to pereonite 5, and no evidence was found of either oviducts or vasa deferentia. The cells lying in the ovarian region are of two types: large, lateral primordial germ cells (Figure 89A) and smaller, medial, mesodermal cells (Scholl, 1963:533).

MANCA STAGE 2 (WHOI B. Sta. HH 3).—Gonads are clearly present. They begin midway through pereonite 4 and their cross-sectional shape is generally oval or cuneate (Figure 89A). No discrete swellings indicative of developing ova could be seen in the anterior, ovarian portion of the gonad, and the gonodal strands are not appreciably developed beyond those of the manca 1.

At the anterior part of pereonite 6 the strands become round in cross section and begin to move laterally and slowly downward between the gut and the digestive glands, the latter barely extending to this level. The strands end just before pereopod VII, having finally dropped precipitously toward the ventral surface of the pereonite. The round portion of each gonodal strand (in pereonites 6 and 7) represents the testicular portion. This descends to form a narrower and more ventral vas deferens. The vas deferens passes ventromedially under the ventral longitudinal muscles (see Figure 89c). Because of the superposition of several sections to show all parts of the male system, the gradual anteroposterior descent of the testes and slight forward turn of the vasa deferetia cannot be seen in the figures.

JUVENILE (DZ, WHOI B. Sta. 76).—During the examination of external morphology, the juveniles were observed to vary greatly in the relative development of their pleopodal setae (length and numbers on the endopod). Since this might signify more than merely natural variability among individuals, two animals were sectioned: DZ, with

poorly developed pleopods, and EA, with a higher degree of pleopodal development.

The ovaries in DZ begin at the anterior end of pereonite 4 and continue posteriorly to the level of pereopod VI. Their cross-sectional shape is usually wedge-shaped between ten large swellings (e.g., DE, Figure 89B) present on each side. This is similar to the pear-shape described for *Heterotanais oerstedi* by Bückle Ramírez (1965:746, fig. 27). These swellings are undoubtedly developing eggs, and at times they are as large or larger than the ova of the preparatory female 1 (below).

The ovaries apparently are attached to the pericardial septum by connective tissue ligaments (see CTL, Figure 90A). Clearly distinguishable oviducts were not apparent, but at the level of pereopod 5 there is a dark, thin, flattened, laterally directed extension of each ovary that may represent the oviducal tissue (discussion of oviducts, p. 213).

The gonadal tisssue becomes very narrow in the anterior part of pereonite 7, and at the level of pereopod VII it has turned ventrally on each side to form fine vasa deferentia (VD) which pass medially below the ventral longitudinal muscles (Figure 89c).

JUVENILE (EA, WHOI B. Sta. 76).—The ovaries begin in the anterior part of pereonite 4 and continue rearward as exceedingly thin strands, some- ·times flat, and appearing to be solid. They become slightly wider posteriorly (Ov, Figure 89D), and at the level of pereopod V they expand laterally, forming rudimentary oviducts which pass laterally toward the fifth pereopods. The oviducts are thin, but slightly larger in diameter than the ovary, and contain a few relatively large, dark, oval nuclei.

The gonadal tissue continues posteriorly as a thin strand in pereonite 5 and becomes exceedingly fine in pereonite 6. At the level of pereopod VI it expands enough to be readily noticeable; and it is decidedly round in cross section. At pereopod VII the two strands expand considerably into two poorly developed testes (Te, Figure 89E). These turn ventrally, forming vasa deferentia which are directed medially under the ventral longitudinal muscles. There is no trace of a seminal vesicle. The diameter of the testes and of the efferent ducts are at least twice as great as those of juvenile DZ (cf. C and E of Figure 89).

In cross-sectional view, the sternite of pereonite 7 is concave medially with an expanded area on
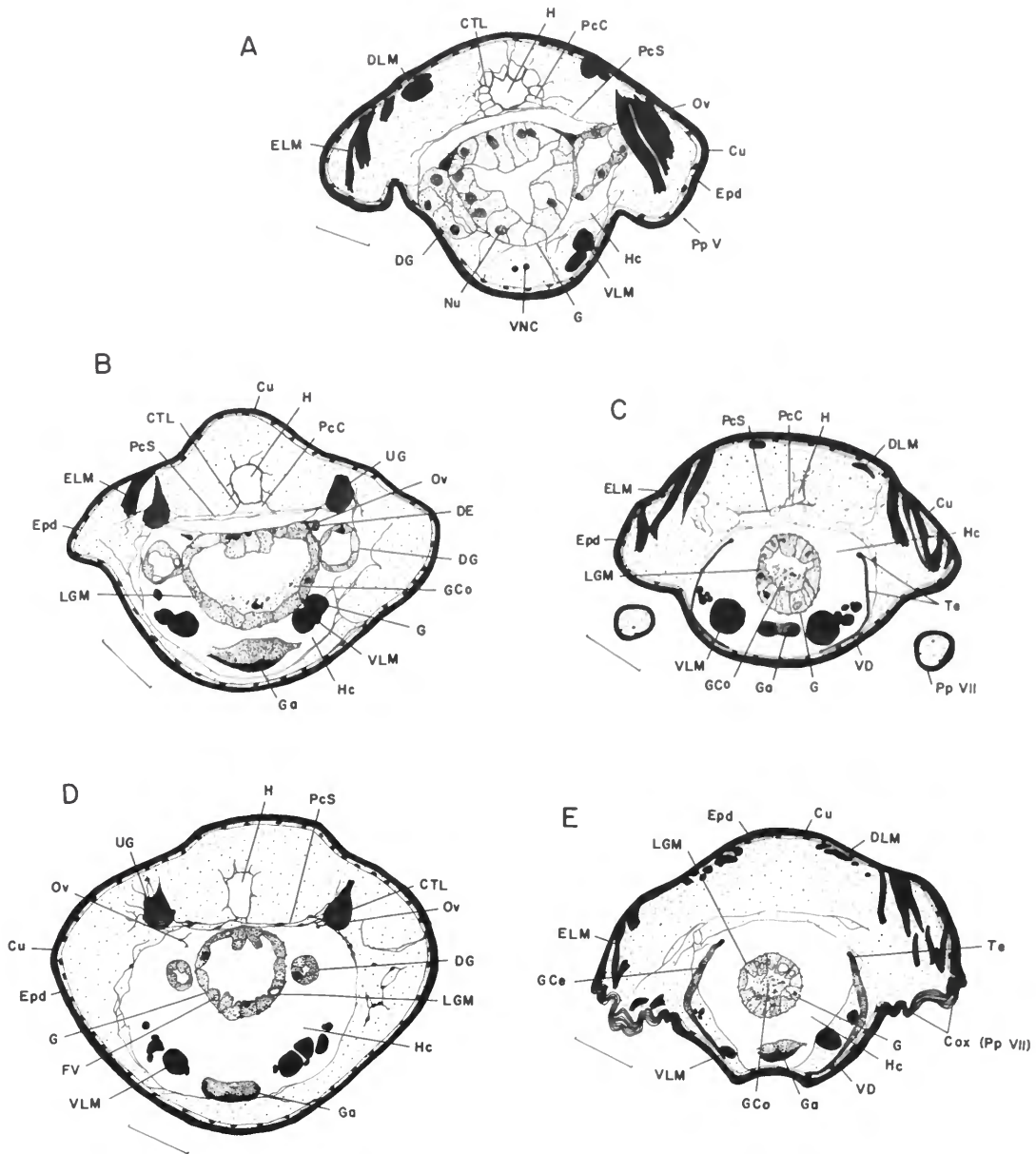
FIGURE 89.—Sexual development in *Neotanais micromopher*. Semidiagrammatic cross-sectional views showing internal structures (all animals are from WHOI Benthic Stations): A, a manca 1 (Sta. 65) at the level of the anterior part of pereonite 5 showing the ovaries; B, a juvenile (DZ, Sta. 76) at the level of the border between pereonites 4 and 5 showing the ovaries (this animal destined to become a female?); C, the same animal in the area of pereopod VII showing testes and vasa deferentia; D, another juvenile (EA, Sta. 76) just anterior to pereopod V showing the ovaries; E, the same animal just behind pereopod VII showing testes and vasa deferentia (this animal destined to become a male?). Each figure represents several sections superimposed in order to show, for example, both testes and vasa deferentia, not normally in the same plane. The scale line represents 0.1 mm.
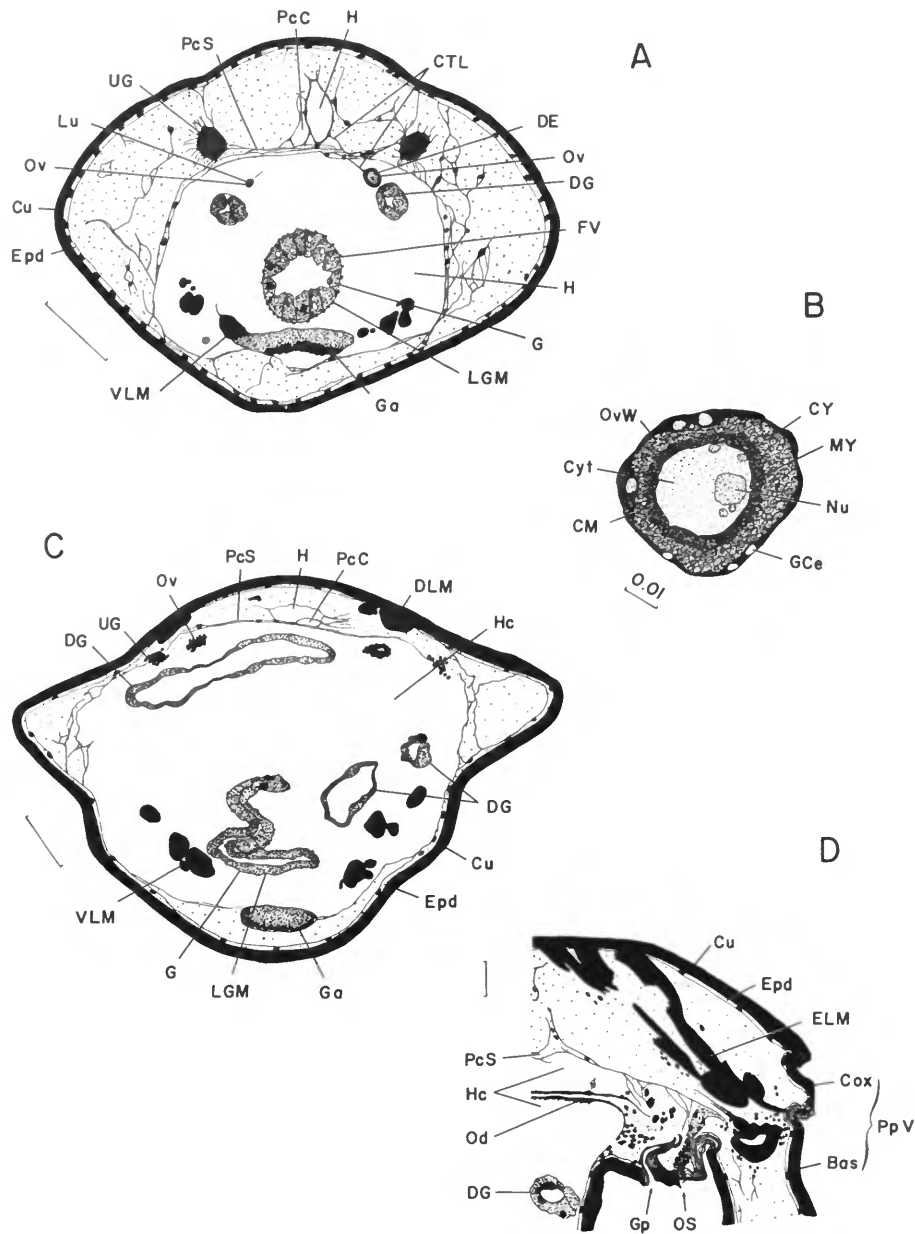
FIGURE 90.—Sexual development in *Neotanais micromopher*. Semidiagrammatic cross-sectional views showing internal structures (all animals from WHOI Benthic Stations): A, a preparatory female 1 (DW, Sta. 76) at the level of midpereonite 5 showing the ovaries; B, section through the ovary of a preparatory female 2 (Sta. HH 3) showing the structure of the developing ovum; C, a copulatory female (Sta. 95) just anterior to pereopod V showing the ovaries; D, an enlargement of the left side of another copulatory female (Sta. 72) at the level of pereopod V showing the oviduct and female gonopore. Each figure represents several sections superimposed to show all structures. Scale line represents 0.1 mm except where noted.
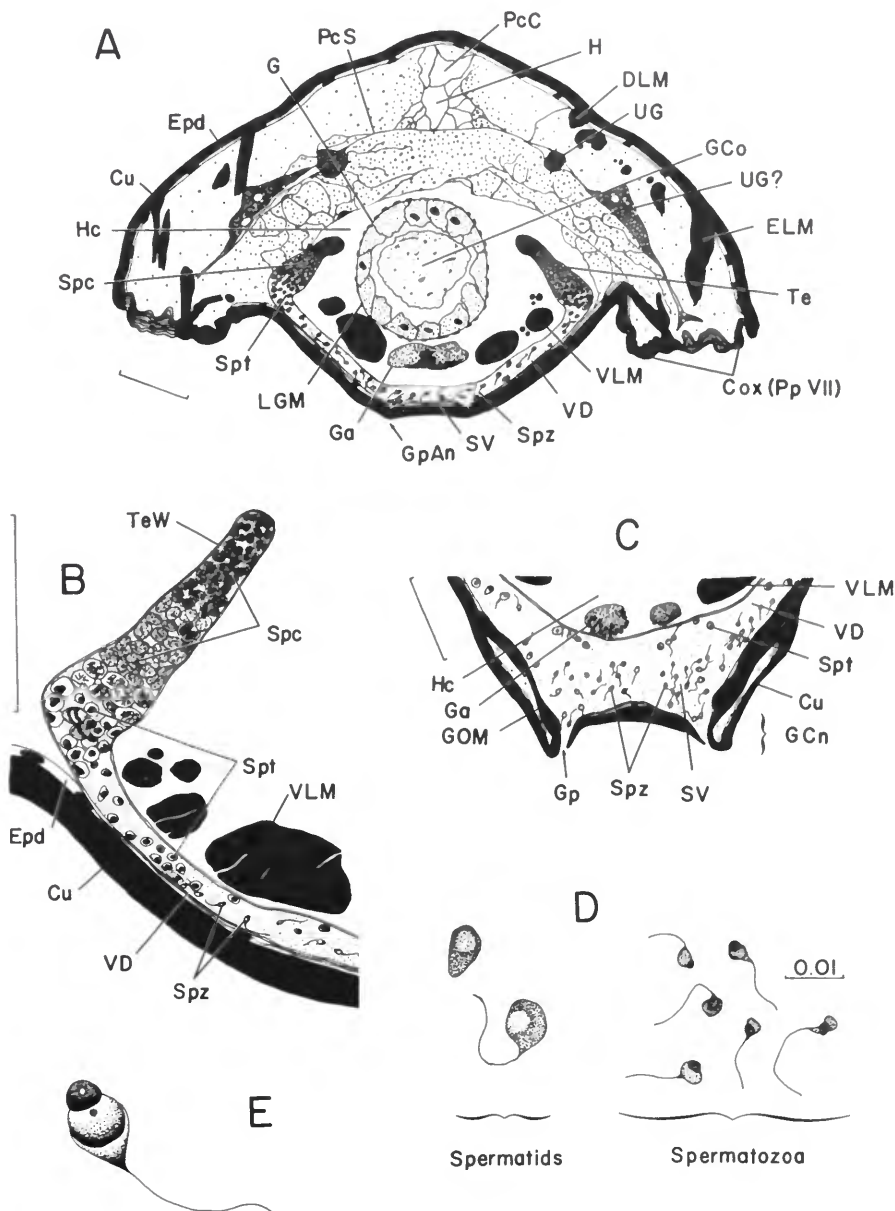
FIGURE 91.—Sexual development in *Neotanais micromopher*. A–C, Semidiagrammatic cross-
sectional views showing internal structures (all animals from WHOI Benthic Stations): A, a
preparatory male (DT, Sta. 76) at the level of pereopod VII showing the major features of the
male reproductive system; B, enlargement of the right testis and vas deferens of the same animal
(slightly different plane) showing the location of various stages of spermatogenesis; C, area of
the seminal vesicle (section through the genital pores) of a secondary copulatory male, chela
type B (Sta. 112). D, Representative spermatids and spermatozoa from the seminal vesicle of the
male in C above. E, Diagrammatic reconstruction of a typical spermatozoan as visualized from
prepared sections. Figures A–C represent several sections superimposed in order to show both
the testes and vasa deferentia, not normally in the same plane. The scale line represents 0.1 mm.

either side of the concavity (Figure 89E), thus resembling the sternite of a preparatory male (Figure 90E) or even of a mature male (Figure 91A). This is decidedly not the case in DZ (Figure 89c) which more closely resembles the preparatory female.

PREPARATORY FEMALE 1 (DW, WHOI B. Sta. 76).—The ovaries begin about the middle of pereonite 4 and are of varying and irregular cross-sectional shape. The lumina are occasionally visible (Lu, Figure 90A) and appear lighter in color than the ovarian wall. There are 11 developing ova (DE, Figure 90A), probably oocytes, swelling the left ovary, and 10 on the right side. Each ovum gives the ovary a more rounded shape at that point. The ova are lighter in color than the surrounding ovarian wall, and each ovum contains a bright spot, presumably the nucleus, with its attendant, centrally located cytoplasm. The ova are small, about one-third to one-half the diameter of those in the preparatory female 2 (Figure 90B).

At the level of pereopod V very thin oviducts arise from the ovaries and extend ventrolaterally along the side of the main body cavity toward the fifth pereopods. The gonadal material continues posteriorly into the seventh pereonite, the testes and vasa deferentia lying in the area of pereopod VII. Both structures are very slender and about as well developed as in juvenile DZ (Te, VD, Figure 89c).

PREPARATORY FEMALE 2 (WHOI B. Sta. HH 3).—The ovaries start at the anterior border of pereonite 4 and are at least twice the diameter of those of the preparatory female 1 (Ov, Figure 90A). They are often cuneate in cross section where they are not swollen by a developing ovum.

An ovum is illustrated in Figure 90B. The ovarian wall (OvW) is considerably darker than the enclosed cell. There appear to be two concentric layers of yolk granules, here termed cortical yolk (CY) and medullary yolk (MY). The former surrounds the latter and consists of slightly larger granules than the latter and is not as darkly stained.

The interior of the egg is considerably brighter than the yolk but is also granular in appearance. It contains one large, darker structure and several, similarly stained, smaller structures. The large structure is probably a nucleus (Nu) surrounded by cytoplasm (Cy) as described by Scholl (1963: 503, fig. 1a) for *Heterotanais oerstedi*. The border of the cytoplasm is not perfectly smooth and may

be imagined sending out processes into the yolk in a manner similar to that described by Scholl (1963: 502). The ovum is irregularly shaped and presumably immature; however, the diameter is roughly estimated as 400 μm. Scholl gives 130 μm as the diameter of a mature ovum of *Heterotanais oerstedi*, and Forsman (1944) states that the egg of the isopod *Jaera albifrons* is 260 to 285 μm across.

This specimen was poorly prepared and all connections of the ovaries to the body wall were destroyed, including the oviducts which must be present in this stage.

The testes pass ventrally to form vasa deferentia at the level of the anterior part of pleopod 1. Both structures are rudimentary and about as well developed as in juvenile DZ (Te, VD, Figure 89c).

PREPARATORY FEMALE 2 (WHOI B. Sta. 65).—The reproductive system in this animal is notable in that the only detectable portion is the ovaries (Ov, Figure 92A). The ovaries are so greatly swollen that they fill the main body cavity, pushing other structures out of the way. They extend from the anterior part of pereonite 3 all the way to the border between pleonites 3 and 4. The usual extent of the ovaries or ovarian material before becoming greatly enlarged by mature ova is indicated by the stippled strip above the appropriate pereonites in Figure 92A (manca 1 through early preparatory female 2).

Yolk granules (YG) fill the ovaries. The boundaries of the ova are not visible; this condition is probably an artifact resulting from processing and sectioning the animal.

COPULATORY FEMALE (WHOI B. Sta. 95).—The ovaries begin about a third of the way into pereonite 4. Their lumina are empty and their walls are strongly convoluted, obviously having shrunken from a previously much-expanded state (Ov, Figure 90c). At pereopod V, prominent lateral oviducts are formed. These are obviously mature, their lumina are clearly visible, and they extend laterally toward the gonopores (see p. 229). All organs lying in the area of the body formerly occupied by the greatly swollen ovaries have been pushed aside, and the thoracic portion of the hemocoel (Hc) is much enlarged. The walls of the gut have been crushed flat and the digestive glands have been dislocated. The posterior ends of the digestive glands are unattached and can be seen to have been moved vertically, horizontally, and even
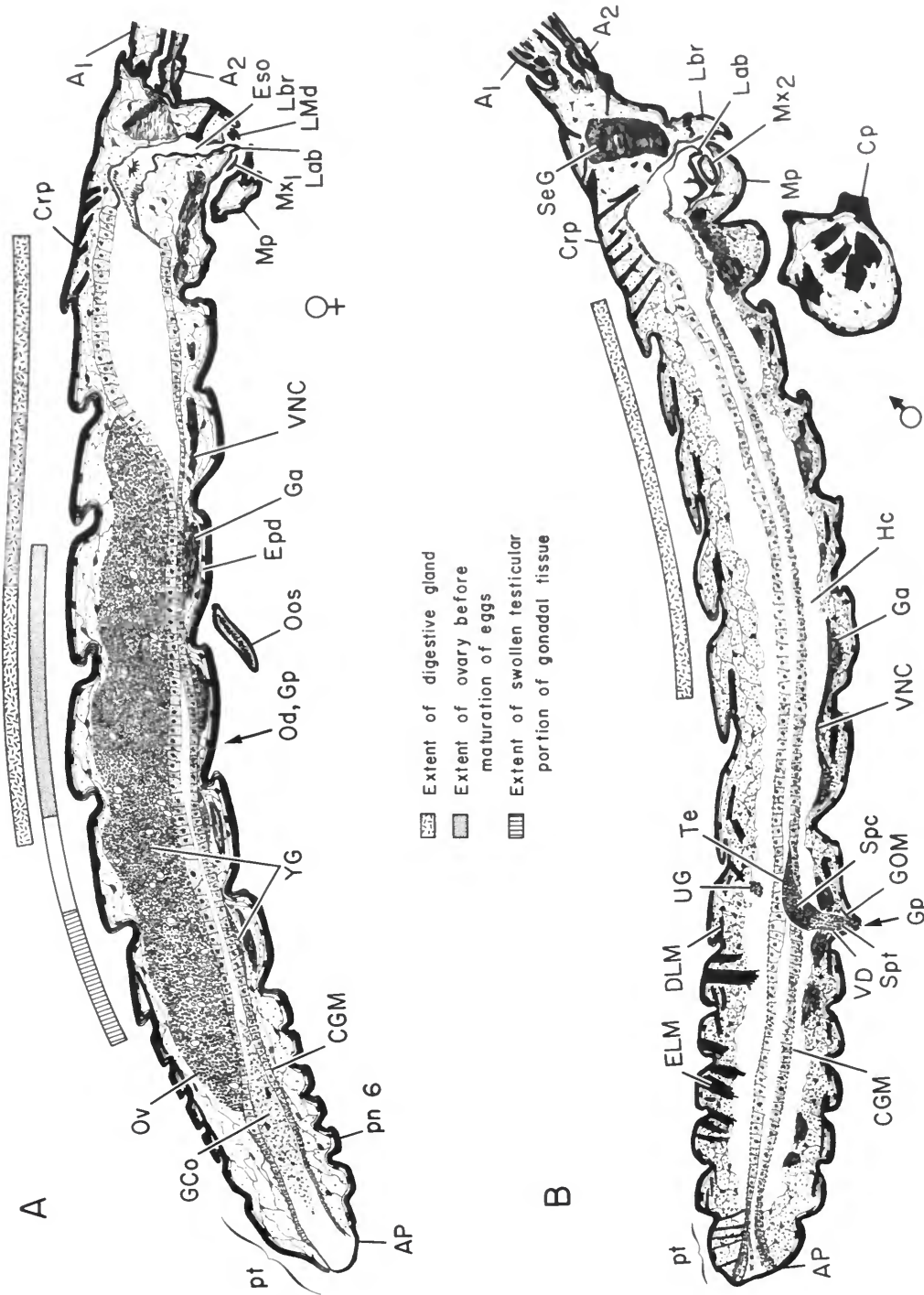
FIGURE 92.—Semidiagrammatic sagittal views of *Neotanais micromopher* showing the structure of the gut and reproductive system: A, a late preparatory female 2 (WHOI Benthic Sta. 75) with ovaries swollen with eggs (outlines of eggs destroyed in sectioning procedure); B, a small primary copulatory male (AU, WHOI Benthic Sta. 64). The figures were constructed by comparing and superimposing several sections. Only the most significant features are shown. Hence, the right testis and vas deferens in B are in three-dimensional perspective on a sagittal view through the gut; the heart and digestive glands are not shown.

turned back on themselves. The darkly stained, unidentified glands (UG) are reduced in size and their constituents are scattered (cf. UG, Figure 90A for the former appearance of these glands). The ovaries terminate at pereopods VI.

The gonadal tissue can barely be followed posteriorly to the testicular area, but the poorly developed testes are unmistakable and have a characteristic, round, cross-sectional shape. In fact, the testes and the vasa deferentia are about as well developed as in juvenile EA (Te, VD, Figure 89E), but this is a considerably greater degree of development than has been observed in previous female instars in which the male reproductive organs were all of about the same degree of development as juvenile DZ (Te, VD, Figure 89C).

The lower portions of the testes and vasa deferentia are located in pleonite 1, the right testis descending in the forward area of the pleonite and the left testis at the level of the first pleopod. The testes contain darkly colored cells, about two abreast at their widest point.

COPULATORY FEMALE (DE, WHOI B. Sta. 76).— The ovary begins about one-third of the way through pereonite 4 and soon takes on the empty, shrunken appearance noted in the previous animal (Ov, Figure 90C). Its diameter, shape, and position within the body vary considerably; it is best developed posteriorly. The characteristic cuneate ovarian shape is visible in certain places, but throughout much of its length the ovary is collapsed and therefore flat in cross section. The ovaries disappear in the midsection of pereonite 5, and no connection with the posterior testes is apparent.

Part of the way through pereonite 5 the ovaries become greatly flattened, their lumina appearing slitlike; the ovaries merge with the oviducts which extend laterally to the area of the gonopores (see discussion, below, under female from Sta. 72).

The thoracic position of the hemocoel is expanded, the thorax is more or less devoid of tissue, and the internal organs are pushed aside. The dark, unidentified glandular masses (UG, Figure 90A,C) are not visible.

The testes are first recognizable as tiny strands at the anterior part of pereonite 7. They soon broaden considerably and form vasa deferentia which can be traced only for about one-half of the distance to the sternite in pereonite 7. The testes

do not protrude rearward into pleonite 1; and they contain large, dark cells similar to those of the previous female. There are about four of these cells abreast in the testes at their widest point; thus, although they are considerably more developed than in the previous female, they are far less so than in the preparatory male (Te, Figure 91A). There is no trace of the male gonopores.

COPULATORY FEMALE (WHOI B. Sta. 72).—The ovaries begin as very tiny threads in the midsection of pereonite 4. These soon expand into large, generally empty structures with greatly convoluted walls as in the other copulatory females (Ov, Figure 90C). Occasionally debris is noticeable in the ovarian lumina. The ovaries become flattened laterally at the level of pereopod V, forming a pair of thin oviducts (Od) that lead ventrolaterally toward the female gonopores (Gp, Figure 90D). The ovaries terminate about halfway into pereonite 6.

There are two breaks in the medial coxal region of each of the fifth pereopods. One of the openings (Gp, Figure 90D) is formed from an invagination of the decalcified cuticular surface of the coxa. Among the sectioned animals, they are found only next to the sternite in the coxal area of the fifth pereopods and only in the three copulatory females. In this female they have diameters of about 80 μm each and are about 120 μm and 140 μm wide, respectively, at their mouths. These openings are the female gonopores (discussion, p. 229), and they connect with the oviducts internally and dorsally in an uncertain manner.

The second, more lateral, opening (OS), is present not only on the fifth pereopods but also on several of the anterior oostegite-bearing legs. These openings often have strands of tissue protruding from them and an internal strand of dark nuclei and connective tissue leading dorsolaterally. These openings are the oostegite scars (cf. OS, Figure 94I); they mark the sites of the former attachment of the marsupial plates. That portion of a scar which is actually open to the interior extends inward for a distance of only about 10 μm.

The thoracic portion of the hemocoel is enlarged as in the previous animal, the organs contained therein are shoved aside, and the dark unidentified glands are reduced in size and their components scattered (cf. Figure 90C).

The gonadal tisssue continues rearward from the ovaries (midpereonite 6) as very fine strands. These

expand slightly at the level of pereopod VI, becoming increasingly larger and filled with large, dark nuclei. The testes are thin-walled, and at their widest part contain about two cells next to each other. These cells resemble the younger spermatocytes found in the preparatory male (Spc, Figure 91B). In this animal the testes are a little better developed (diameter) than in the female from Sta. 95, but they are only about one-half as well developed as female DE from Sta. 76. The testes are more easily recognizable here than in the animal from Sta. 95, but the vasa deferentia are of about the same size and seem to be filled to the same degree with dark nuclei. The vasa drop ventrally at the articulation between pereonite 7 and pleonite 1.

PREPARATORY MALE (DT, WHOI B. Sta. 76).— The only trace of ovarian tissue is an extremely fine thread about one cell thick extending from pereopod III to pereopod V and detectable only after the most careful examination. The male gonadal tissue, on the other hand, is extremely well developed. The fine strand of ovarian tissue continues to the posterior part of pereonite 6 where it expands greatly into a testis filled with cells that clearly are undergoing gametogenesis (Te, Figure 91A,B). The vasa deferentia pass ventrally and join at the midline as a modest seminal vesicle (SV). The walls of all parts of the male system are very thin, and those of the seminal vesicle apparently are composed of simple squamous epithelium. The height and length of this relatively ill-defined organ approximate those of the vasa deferentia.

The seventh pereonite is slightly flattened or even concave midventrally. Incipient male gonopores (GpAn), visible externally as translucent dots, easily are observed to penetrate almost to the outside of the cuticle. Incompletely developed lateral muscles (not shown in Figure 91A,B) lie under the lower part of the vasa deferentia and seminal vesicle. They probably control the gonopores in the adult males (see Figure 91c).

Spermatogenesis: Figure 90B is an expansion of the testis and vas deferens illustrating the locations of various steps in spermatogenesis already underway. The horizontal portion of the testis, as well as the upper area in the descending part, is filled with dark nuclei of cells with apparently little cytoplasm, possibly primary spermatocytes. As these mature in the area below, they increase in size and

the chromatin material becomes more dispersed within the nuclei.

Just below, lying in a narrow band, are still larger cells of limited number in which the chromatin material is condensed into six or eight distinctly linear strands, probably the chromosomes. This is probably the division leading to the formation of the spermatids.

The spermatids (Spt) are first found at the testis/vas deferens junction, and they are round or oval cells with small, dark, and often eccentric nuclei. Progressing ventrally along the vasa deferentia, the spermatids become smaller and have less and less cytoplasm. In the lower vasa deferentia and seminal vesicle there are still a few scattered spermatids, but these are mixed with flagellate spermatozoa (see p. 230).

COPULATORY MALES—All copulatory males examined (one very small primary male, AU, WHOI B. Sta. 64; one large primary male, HA, WHOI B. Sta. 76; and a secondary male, WHOI B. Sta. 112) are similar enough to be described together.

No trace of ovarian tissue could be found in either of the primary males. In the secondary male a pair of shrunken ovaries extends from the anterior part of pereonite 4 to the end of pereonite 5 (cf. Figure 90c). The ovarian lumina, usually visible, are empty, with the occasional exception of clear cells with easily visible nuclei. The body cavity is empty in this part of the animal and is identical in appearance to that of the copulatory females. The body cavities of both primary males were similar to the body cavity of the preparatory male.

The testes begin as very fine threads at the anterior part of pereonite 6 and do not expand until one-third of the way into pereonite 7. The lumina of the testes are filled with dark spermatocytes similar to those of the preparatory male (Spc, Figure 91B) and are approximately the same size as in the latter instar (Te, Figure 91A). The vasa deferentia are slightly more expanded and the seminal vesicle markedly so. However, the latter is not bulbous and apparently is nothing more than an expanded area of the vasa deferentia where they meet at the midline (SV, Figure 92c). That it does not extend a significant distance either anteriorly or posteriorly is demonstrated in Figure 92B, in marked contrast to its location in *Heterotanais*

oerstedi as described by Blanc (1884, pl. 12: fig. 49) and Bückle Ramírez (1965: figs. 37–39).

The seminal vesicle opens to the exterior through the two midventral genital cones (GCn, Figures 91c, 92B), the opening (Gp) to each of which is closed by a cuticular flap. This flap is controlled by a muscle (GOM) inserting on the flap and passing dorsolaterally under the vas deferens and ventral longitudinal muscle to its origin on the upper sternal wall.

Spermatogenesis: In contrast to the preparatory male, the zone of division has shifted dorsally in the mature males. In the large primary and secondary individuals it reaches high into the bulbous testis itself (Te, Figure 92B). It is somewhat lower in the small primary male than in the other two specimens examined.

Bückle Ramírez (1965) had difficulty finding a clearly recognizable growth zone in the testes of *Heterotanais oerstedi*. However, when observed, it was found in the forward part of the testes, and, as in *Neotanais*, it occupied only a small portion of the gonad.

Spermatozoa (Spz. Figure 91c) are found in increasingly large numbers, mostly in the seminal vesicle (SV) and adjoining areas of the vasa deferentia. There is some mixing of mature spermatids among the spermatozoa similar to the preparatory male. Some of the former cells are apparently flagellate (Figure 91D), and in many of them the nuclei are located eccentrically.

Surprisingly, none of the seminal vesicles of the males is filled with sperm. It is possible that they have recently copulated, or if metabolic rates are generally low in the deep sea (Jannasch et al., 1971), it may take considerable time to build up a supply of spermatozoa to replenish those which have been expended. However, the simplest explanation is that many gametes have been lost during sectioning. A description of the spermatozoa is given on page 230.

Summary of Gonadal Structure and Function in Neotanais micromopher

The following summary is based on the histological observations just described. The gonadal tissue, composed of two longitudinal tubes, is partitioned into an anterior ovarian portion, which makes up two discrete ovaries, and a posterior testicular portion. Unless swollen with eggs, the former usually extends from the anterior part of pereonite 4 to about the same area of the sixth pereonite (stippled strip, Figure 92A), and often it is roughly wedge-shaped or triangular in cross section. Each ovary gives off a lateral oviduct at the level of pereopod V just anterior to the posterior end of the female gonad. The oviducts pass ventrally to the female gonopores on the coxae of these limbs. The postovarian gonadal tissue generally forms very slender strands for the duration of pereonite 6. At the border of pereonites 6 and 7 the strands take on a distinctly round cross-sectional shape and expand into the testes, which usually extend for only the length of pereonite 7 before dropping ventrally. Above the sternite the testes turn medially, becoming narrower, and each forms a vas deferens which passes medially under the ventral longitudinal muscles. In the preparatory and copulatory males the vasa meet medially to form a seminal vesicle. The latter communicates to the outside via two gonopores in copulatory males.

It is clear that in most of the stages of postmarsupial development both testes and ovaries are present in both males and females. Clear ovarian structure could not be demonstrated in the manca 1. But there is no question that the intermittent strand of cells lying in the position later occupied by the ovaries and traversing the same path through the thorax does in fact represent the ovaries. Testicular material could not be found in the manca 1. Because the presumptive ovarian and primordial germ cells grow posteriorly from the head region (Scholl, 1963), it is not surprising to find that the posterior areas of the gonad may not be as well developed as the anterior portions in this first postmarsupial instar.

Bückle Ramírez (1965:742) has found that the structure of the gonads (ovaries) in the "manca stage II" (=manca 1) of *Heterotanais oerstedi* had changed little from the preceding, embryonic, stage, being composed of primordial germ cells and small mesodermal cells which later form the gonadal tissue. In a few individuals, the gonads already occupied the adult position, extending forward to the anterior end of pereonite 2. These observations agree with those made on *Neotanais micromopher*. Roubault (1937:150) states that the gonads only begin to differentiate after the first molt in *Leptochelia dubia* also.

Although manca 2 does not display significant development of the ovaries beyond manca 1, the male genital organs have begun to develop. Testes and vasa deferentia are present, and these have the distinctive structure which characterizes them later.

The apparent differential development of the ovaries and testes in the juvenile stages (Ov, Te, Figure 89c,E) indicates that the two sexes have begun to diverge during this instar. These juveniles are equivalent to Bückle Ramírez' (1965) "Neutrum I," so-called because he was unable to determine its sex histologically. However, Claus (1888: 196) was able to distinguish the sexes in *Apseudes latreillii* (=*A. acutifrons*)—which did not yet have external sexual characters—because their gonadal shape could be observed through the translucent cuticle. Presumably these animals were in a stage comparable to the juveniles of *Neotanais*.

In the juvenile DZ, which may become a female, the enlarged ovaries contain developing ova whose number is similar to that of the ova in the preparatory females. However, the testes and male ducts in this animal are not appreciably developed beyond those of the manca 2 (Te, VD, Figure 89c).

On the other hand, the incipient male juvenile EA has rudimentary ovaries which lack any trace of developing eggs (Ov, Figure 89D). The male structures show increased development and include some darkly staining nuclei ventrally. The sternite of pereonite 7 may already be starting to assume the male form (Figure 89E). The presence in this stage of oviducts that are better developed than in juvenile DZ is puzzling.

The first type of juvenile probably will precede a preparatory female 1 whereas the other juvenile probably will develop into a male stage, possibly a preparatory male (see discussion of the external morphological analysis, p. 188).

Preparatory females show increasing development of the ovaries and their enclosed ova (Ov, Figure 90A,B). Development of the ova during these stages seems to be the standard pattern. Bückle Ramírez (1965:746, 747, figs. 28, 29) observed this in *Heterotanais oerstedi*, as did Shiino (1937:60) in *Apseudes nipponicus*. During the second preparatory stage large amounts of yolk are added to the eggs (cf. YG, Figures 90B, 92A) to the point where they completely fill the ovaries. The ovaries, in turn, fill and greatly enlarge the

thoracic portion of the hemocoel (Ov, Figure 92A), which dislocates the organs normally found therein.

This is a common situation not only within the Tanaidacea but also among other peracaridans. Kinne (1954:106) found that in the isopod *Sphaeroma hookeri* the maternal organs are squeezed aside and the gut is, without exception, empty. Bückle Ramírez (1965, fig. 29) illustrates the same situation for *Heterotanais oerstedi* and notes (1965:748) that the fully expanded ovary extends from the level of the maxilliped to the last pereonite (cf. Figure 92A). Under these conditions, he found that, because of their diameter, the eggs alternated with each other of necessity and the ovaries often were of unequal length.

Oviducts were present in the juveniles and in the preparatory females 1. They are surely present in preparatory females 2, but were probably destroyed in one preparation and obscured by yolk in the other. The presence of oviducts in these stages contrasts with the findings of other investigators (Bückle Ramírez, 1965:749; Claus, 1888: 198).

After the eggs are shed, the ovaries contract both in diameter and in length, and their formerly distended walls are thrown into convolutions (Ov, Figure 90C). Bückle Ramírez (1965:750, figs. 32–35) observed that the ovaries are greatly reduced after the shedding of the eggs and generally cannot be found in *Heterotanais oerstedi*. Roubault (1937:150) was unable to find them in females beyond the brooding stage in *Leptochelia dubia*.

This cycle of egg development, together with the presence of oostegite anlagen, presumably is repeated in the intermediate female stage (s), again leading to the extrusion of eggs during a second copulatory female stage.

The testes and vasa deferentia in preparatory females 1 are no better developed than in the "incipient female" juvenile (Te, VD, Figure 89c), a situation essentially the same as in the second manca stage. The male organs apparently are obliterated when the ovaries become greatly distended with yolk (late preparatory female 2), but they appear again and are considerably more highly developed in copulatory females, an indication that they do in fact persist through the preparatory female 2. It is unlikely that the male

organs are destroyed and then regenerate in preparation for the following instar.

Only a faint trace of ovarian tissue remains in the preparatory male. However, the male structures are almost completely developed, the seminal vesicle and the gonopore anlagen are present for the first time, and spermatozoa are present, at least by the end of this instar.

Copulatory males that have fully developed external secondary sexual characters and internal reproductive structures are of two types: gonochoristic primary males that have no trace of ovarian tissue and secondary males that have well-developed but shrunken ovaries identical with those of copulatory females. This provides unequivocal evidence that the latter males are protogynous hermaphrodites.

In his study of simultaneous hermaphroditism in *Apseudes hermaphroditicus* (=*A. spectabilis*), Lang (1953:350) speculates that gonochoristic species also may have both types of gonads in both sexes and that one may still find vestiges of the glands of the opposite sex in adults. This condition has been established for *Neotanais micromopher*, and it is probably true for other potentially protogynous forms. In fact, it is almost certainly a necessity. The rudimentary gonad is available for activation, possibly through environmental stimuli, and the other system, no longer necessary, can be reduced, as occurs in preparatory males in *Neotanais*.

Comparison of Gonadal Structure and Location among the Tanaidacea

Claus (1888:197) described the ovaries in the monokonophoran *Apseudes latreillii* (=*A. acutifrons*) as lying over the digestive glands throughout the midtrunk area in developing animals, a position similar to that in *Neotanais*. However, when the animal has rudimentary oostegites the ovary is swollen with eggs and stretches from the abdomen to the head as in *Neotanais* (Figure 92A). Two alternating rows of carinated eggs lie wedged next to each other. The swollen, pear-shaped testes lie in a similar position over the gut but they do not extend beyond the fourth thoracic segment (pereonite 3). Vasa deferentia extend posteriorly to the genital cones on the seventh pereonite. Claus states that there are muscles on

the outer testicular wall causing them to contract, and that the lower walls of the vasa are contractile. These muscles were not observed in *Neotanais*.

Lang (1953a) made a study of the gonads of *Apseudes spectabilis* in which he found simultaneous hermaphroditism. All specimens, including those with oostegites and ova, had a male genital cone. The ovaries lie in all of the free pereonites, germinal later outward, and each is invested with a thin layer of epithelium. The testes are separated from the ovaries and lie in the anterior part of the third pereonite similar to *A. acutifrons*. Each is composed of two saclike lobes with the germinal layer outward. The vasa deferentia soon unite, and the common duct runs to pereonite 7 and forms a seminal vesicle. The latter opens, apparently singly, on the genital cone.

Lang was unable to study gonadal histology due to poor fixation but he states (1953a:350) that the gametes seem to mature simultaneously and he raises the possibility of self-fertilization.

Roubault (1937:148) described the gonads in a species of *Leptochelia*, probably *L. dubia*. He states that the ovaries extend for at least four or five segments in "young" animals, but his figure 2 shows them extending from the anterior area of pereonite 4 almost to the end of pereonite 6. He says that they extend for six or seven segments in the adult female, but the figure shows them reaching from midpereonite 3 to midpereonite 5, about the same distribution as in *Neotanais*. They lie in the same position relative to the gut and digestive glands as well.

Roubault states that the testes form small cellular masses in the fifth (but his figures indicate fourth) pereonite and are prolonged posteriorly as sperm ducts full of spermatozoa. In older males the testes are considerably reduced, and only the genital ducts remain recognizable. The latter are packed with spermatozoa. Bückle Ramírez (1965:752) found that the testes were shrunken and empty in some individuals of *Heterotanais oerstedi* and that sperm were found only in the seminal vesicle.

In *Leptochelia dubia*, the area of the vas deferens containing spermatozoa extends from midpereonite 4 through pereonite 7 (Roubault, 1937, fig. 3), considerably farther than in *Neotanais*, although the male ducts (or testes?) appear to have a similar structure in both forms. In younger males

there is a cellular mass, somewhat anteriorly, that enters pereonite 3. Roubault claims that the sperm ducts join posteriorly to empty to the exterior through a common opening, a remarkable arrangement for a member of the Dikonophora.

For *Tanais* (=*Heterotanais*) *oerstedi,* also a member of the Paratanaidae, Blanc (1884:247, pl. 12: fig. 53) states that the ovaries, when full of ova, extend from pereonite 2 to pereonite 6, somewhat less than for *Neotanais.* But he also maintains that only four or five ova are developing in each ovary in contrast to the 10 to 12 observed for *Neotanais micromopher.* The testes (Blanc, 1884:246) extend from the anterior part of pereonite 5 to the posterior part of pereonite 7, a greater distance than in *Neotanais.* In pereonite 7 the testes move downward, as in *Neotanais,* maintaining the same diameter throughout (Blanc, 1884, pl. 12: fig. 49). However, Claus (1888:201) states that Blanc described the sperm ducts as testes. In contrast to *Neotanais,* the seminal vesicle formed from the sperm ducts is globose. Claus says that a groove passes along each genital cone from the seminal vesicle to the gonopore. Unfortunately, it is not clear from either Blanc's or Bückle Ramírez' work whether the testes are present in the females.

The only study of the gonads in the family Tanaidae has been that of Lang (1958:538), in which the author claims that "transitional females," which will become secondary males, have ovotestes. The anterior ovarian portion extends from the anterior part of pereonite 2 to the end of the fourth pereonite. The testicular portion runs through the rest of the pereon, opening ventrally through vasa deferentia into a seminal vesicle. Lang was not able to examine fully the gonadal structure because of poor preservation.

With the exception of *Leptochelia,* the pattern of gonadal structure described here for *Neotanais* is similar throughout the known Dikonophora. A consistent pattern of gonadal distribution may appear in the two tanaidacean suborders, with the testes located in the anterior thorax in the Monokonophora and in the posterior thorax and the abdomen in the Dikonophora. A close study of gonadal maturation may show a more or less consistent pattern of postmarsupial development among the dikonophoran families as well. The Monokonophora apparently exhibit appreciable differences in postmarsupial development. How-

ever, much remains to be done before a generalized pattern can be described. Monokonophoran development is not well understood and has never been investigated in certain families.

NOMENCLATURE AND IDENTIFICATION OF THE DEVELOPMENTAL STAGES

The terminology used here follows the precedent set by Zimmer (1926) and by Forsman (1938, 1944) for the Cumacea and Isopoda. Other, earlier authors (e.g., G. O. Sars, H. J. Hansen) have used the terms immature, subadult, young, and juvenile imprecisely, often without definition. The system of Zimmer and of Forsman is adopted here because their terms are more restricted in meaning and often have the additional advantage of being descriptive of the instar to which they apply.

Wolff (1962), following Bocquet (1953), used a series of numbers to designate the stages of development in his deep-sea asellote isopods because he felt that it was still too early to correlate effectively the poorly understood development of isopods with that of the Cumacea. Hessler (1970), working with the same group, used Zimmer's nomenclature effectively for his own animals and for those of Wolff's as well.

Lang (1953b:417) applied this system to the Tanaidacea (*Heterotanais antarcticus*) for the first time. Later, although he utilized certain parts of this scheme in describing the postmarsupial development of *Heterotanais oerstedi,* Bückle Ramírez (1965) introduced a number of new terms into the sequence.

It is not surprising that the postmarsupial development of the Tanaidacea shares certain elements with that of the Cumacea and Isopoda, making possible the utilization of a common terminology. Siewing (1951, 1953, 1963) has demonstrated many similarities among these taxa, and it seems clear that they form an evolutionary unit.

The characters given below for the identification of the developmental stages are very general. For a detailed account of the characteristics of each of the stages in *Neotanais micromopher,* refer to the developmental study (p. 187); for *Herpotanais,* see page 200. The terms used by Zimmer (1926) and by Forsman (1938, 1944) are placed in parentheses following their English equivalents as they are employed herein.

MANCA STAGES (Mancastadien).—The term "manca," introduced by Zimmer (1926) for the cumacean *Diastylis glabra,* referred to a young stage which is free-living and missing the last pair of pereopods. It was named after *D. manca* G. O. Sars, in which the holotype, supposedly neotenous, lacks the last pair of pereopods. Manca stages are the youngest postembryonic instars, referred to as "larvae" by some authors.

Among the Tanaidacea, the last pair of pereopods and the pleopods are often missing in the first manca stage, and they are not present in *Neotanais.* The last pair of pereopods and the pleopods are usually present, although rudimentary, in the second manca stage, and this is true for *Neotanais.* Although exopods are present on the fifth and sixth (manca 1) or on the fifth through the seventh (manca 2) pereopods in *Kalliapseudes* (Lang, 1956:222), these are never present in any other tanaidacean taxon studied so far.

JUVENILE (Jugendstadium).—These animals lack oostegites, oostegite scars, and male or female gonopores or their anlagen. Except for the mancas, they are often the smallest animals. In *Neotanais micromopher* juveniles have poorly developed pleopods.

PREPARATORY FEMALES 1 AND 2 (Vorbereitungsstadium).—These stages, of which there are two in *Neotanais,* are characterized by the presence of rudimentary oostegites on pereopods II–V. The sheaths in which the brood plates are encased are very small in the preparatory female 1 and often are difficult to observe (see Figure 94A–D). Pleopods usually are better developed than in the juvenile, especially in *Neotanais micromopher.* Usually, male gonopore anlagen are not present.

In many forms, such as the cumacean *Diastylis rathkei* (Forsman, 1938) and the tanaidaceans *Apseudes* (Hansen, 1913:7; Lang, 1953b:419) and certain species of *Typhlotanais, Leptognathia,* and *Paranarthrura* (Hansen, 1913:7), the hyposphenians, ventrally directed pereonal spines, gradually become reduced in the region of the marsupium in preparation for the eggs. The degree of reduction sometimes can be used in identifying certain developmental stages. Hyposphenians are never present in the Neotanaidae. In many tanaidacean groups the ventral surfaces of the oostegite-bearing segments become flattened in the copulatory females (Hansen, 1913:7), but this was never observed among the Neotanaidae.

Pleopods are better developed than in the juvenile, especially in *Neotanais micromopher.* Male gonopore anlagen are not usually present .

COPULATORY FEMALES (Weibchen im Brutkleid). —The English term "brooding" female has been used by Hessler (1970). I prefer the terminology used for the adult males (q.v.). These animals have fully developed marsupia at some time during the instar. Immediately after entering a copulatory state in *Neotanais,* the oostegites may remain in their sheaths, not yet having unfolded. The sheaths are swollen and bulblike and cannot be confused with those of preparatory females.

The oostegites are shed sometime after the young leave the mother. Thereafter, copulatory females superficially resemble juveniles and preparatory males, but they can be recognized by the presence of oostegite and female gonopore scars (Figure 84). Male gonopore anlagen may or may not be present (see p. 196).

The first copulatory female stage ("Erstes Brutkleidstadium") immediately follows the preparatory female 2 in *Neotanais* and results from the "maturation molt" ("Reifungshautung" of Forsman). The female probably is now fertile and will shed her eggs following the opening of the gonopores. All stages subsequent to the maturation molt are considered to be adult. Depending upon the taxon, there may be more than one copulatory female instar (see "Postmarsupial Development within the Neotanaidae," p. 187). The first stage is known here as copulatory female 1, the second as copulatory female 2.

INTERMEDIATE FEMALE (Zwischenstadium).— These animals are superficially identical to the preparatory females because they bear rudimentary oostegites. However, they are considerably older, by at least two molts, than the preparatory females and can be distinguished by a comparison of body lengths, degree of pleopodal development (in *Neotanais micromopher*), and length of uropodal endopods. It is unknown whether male gonopore anlagen are ever present. In contrast with some less calcified forms such as *Heterotanais oerstedi* (Bückle Ramírez, 1965), the eggs cannot be seen within the body.

Intermediate females are found between successive copulatory female stages and should probably be designated by arabic numerals similar to those

used for the preparatory females; viz., intermediate female 1 (=I♀1), 2, etc. Because of the limited number of specimens available, it is unknown whether one or two intermediate stages occur between copulatory females in *Neotanais*.

In two papers Forsman (1938, 1944) refers to the intermediate females as the "Zweites Vorbereitungstadium." In the case of *Neotanais* this would be preparatory female 3. This terminology is confusing because there is more than one preparatory female leading to the first copulatory female.

PREPARATORY MALE.—This stage follows the juvenile in *Neotanais* and immediately precedes the primary copulatory male. Zimmer (1926) and Forsman (1938, 1944) do not mention this stage. Bückle Ramírez (1965) refers to it as the "Neutrum II" in *Heterotanais oerstedi*.

It has been difficult to recognize the subadult males in certain tanaidacean taxa because they resemble the females and younger stages; many authors do not even mention them. Hansen (1913:7) enumerates methods for recognizing these young males.

The recognition of preparatory males in *Neotanais* is simple. Oostegites and oostegite scars are absent, pleopods are about as well developed as in copulatory or intermediate females, and male gonopore anlagen are almost always clearly evident. Otherwise, this stage is identical externally to adult female stages and to juveniles. The male gonopore anlagen usually are more easily visible than in other stages where they may be present only in some individuals.

COPULATORY MALES (Mannchen in Hochzeitskleid).—The English terminology was first used by Hessler (1970). These males are the terminal instars in the life history of neotanaids. Except for the complications of protogeny, they are equivalent in their development to the "Mannchen in Hochzeitskleid" of other authors.

Primary copulatory males originate through the male maturation molt from preparatory males and probably from certain juveniles. Secondary copulatory males result from a terminal ecdysis in which a protogynous copulatory female changes its sex.

The copulatory males are easily identified by male secondary sexual characteristics (see "Sexual Dimorphism" under "Intraspecific Variation") which immediately differentiate them from all other stages. The two types of males are identical except for body length (overlapping distributions) and the shapes of their chelae, the latter being species specific.

THE BROOD POUCH EMBRYO

Of all of the copulatory females found in the collections examined, none had eggs or embryos in its marsupium, in contrast to practically all other tanaidacean groups represented in the samples. The eggs or embryos probably were washed out during the collection and processing of the samples. In fact, only two embryos were present (WHOI B. Sta. 131) among over 1000 neotanaids examined. Although the embryos are too poorly formed to make a clear species identification (Figure 93A,B), their lengths, 2.0 and 2.2 mm, and the lengths of their chelipedal dactyli may indicate that they belong to *Neotanais affinis* (both *N. affinis* and *N. sandersi* were collected at Sta. 131). The two embryos are 3.5 and 4.2 times longer than wide.

Little information is available in the literature on the embryos of the Tanaidacea. Bückle Ramírez (1965:740) describes intramarsupial animals as Stage I (="manca stage I"). This stage is anameric and gradually develops into Stage II, a "manca stage II" (my manca 1), without molting. Kjennerud (1950) described four marsupial stages for the isopod *Idotea neglecta*, and the same stages have been observed by Forsman (1944) in *Jaera albifrons* and by Jensen (1955) in *Sphaeroma hookeri*.

The embryos of *Neotanais* correspond to some point in development between Bückle Ramírez' Stages I and II. They share the partial development of the appendages and the presence of segmentation with Kjennerud's Stage II but they do not lie within an embryonic membrane. One embryo still retains its dorsal curvature (Figure 93B); the other is largely straightened. Dorsally curved embryos, present among the cumaceans and isopods, have also been described for *Heterotanais oerstedi* (Scholl, 1963), *Tanais dubius* (=*Leptochelia dubia*) (Müller, 1864b), *Apseudes latreillii* (=*A. acutifrons*) (Claus, 1888), and *Tanais vittatus* (=*T. cavolinii*) (Dohrn, 1870).

The neotanaid embryo bears on its carapace two prominent "dorsal organs." The only known refer-

ence to the dorsal organ among the Tanaidacea is that of Calman (1909:194). Calman (1909) also mentions the presence of this or similar organs in the Mysidacea (p. 180), Isopoda (p. 213), Amphi-

poda (p. 237), and, possibly, Syncarida (p. 164) and Branchiopoda (p. 43). A similar structure is found in certain decapods (Glaessner, 1969:R407).

The dorsal organ assumes various forms in dif-
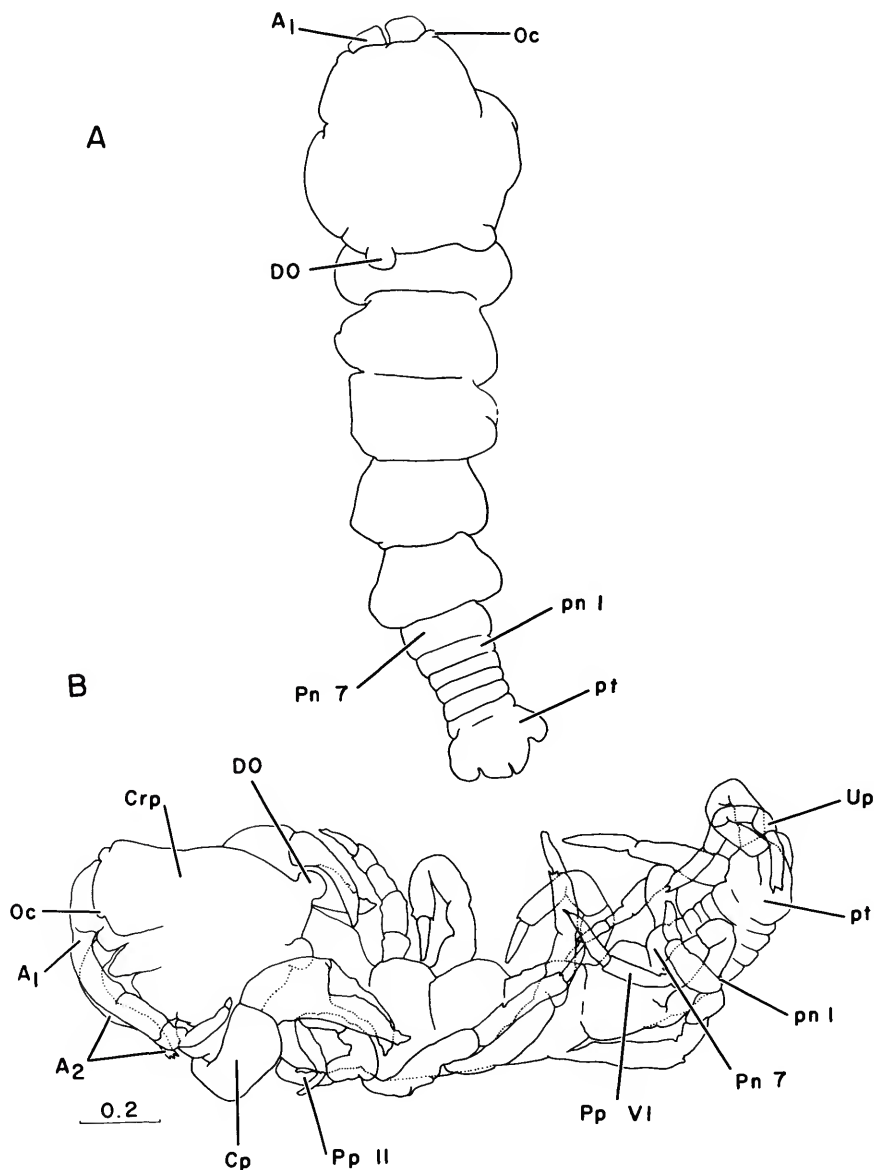
FIGURE 93.—Brood pouch embryo of *Neotanais*: A, dorsal view, B, left oblique lateral view. Both figures are drawn to the same scale. This speciman is one of two individuals collected at WHOI Benthic Station 131. It is not identifiable to species. *Neotanais affinis* and *N. sandersi* were collected at Sta. 131.

ferent taxa and is often glandular, but its specific function is unknown (Moore and McCormick, 1969:R95) although it may have to do with the first ecdysis (Kumé and Dan, 1968).

MISCELLANEOUS MORPHOLOGICAL OBSERVATIONS

Oostegites and Marsupium

Apart from occasional observations such as those of Bückle Ramírez (1965), the oostegites and marsupium have not received much attention by workers dealing with the Tanaidacea. The only detailed study of marsupia was that of Moers-Messmer in 1936. That differences among oostegites are of significance within the Tanaidacea is illustrated by Lang's (1949, 1967) use of these differences in revising the familial hierarchy of the order.

Until now, there has been no description of the marsupium or detailed study of the oostegites in the Neotanaidae, although oostegite anlagen have been illustrated for *Neotanais serratispinosus* (= *N. americanus*) and *N. hastiger* by Norman and Stebbing (1886, pls. 23, 24), for *N. serratispinosus* (=*N. hadalis?*) by Kudinova-Pasternak (1965a, fig. 1), and for *Herpotanais kirkegaardi* by Wolff (1956a, fig. 43).

NUMBER AND LOCATION OF OOSTEGITES AND MARSUPIAL SHAPE.—The number and location of the oostegites vary among the Peracarida and within the Tanaidacea as well. Forsman (1938) reports oostegites on the first three pereopods (thoracopods IV–VI) and on the last maxilliped (thoracopod III) in the cumacean *Diastylis rathkei*. Kjennerud (1950) found five pairs—on the first five pereopods (thoracopods II–VI)—in *Idotea neglecta* and Charniaux-Cotton (1960) reports the same number on the terrestrial isopod *Armadillium vulgare*. Wolff (1962) consistently found four pairs—on pereopods I–IV (thoracopods II–V)—in the deep-sea asellote isopods. Kinne (1954) reports only three pairs—on thoracopods II–IV—in *Sphaeroma hookeri*. Among the amphipods, Sexton (1924) found four pairs—on pereopods II–V (thoracopods III–VI)—in *Gammarus chevreauxi*.

Among the monokonophoran Tanaidacea, Claus (1888:199) states that in *Apseudes latreillii* (=*A. acutifrons*) there are five pairs of oostegites, borne on pereopods I–V (thoracopods II–VI), with the

first pair very small and not contributing to the marsupium. K. H. Barnard (1935:316) found five pairs of rudimentary oostegites on preparatory(?) females of *A. chilkensis* but stated that the chelipedal oostegites "seem to disappear" in copulatory females. Only the plates from pereopods II–V form a pouch, and these display various degrees of fusion with each other. Moers-Messmer (1936:19) found a similar situation in *A. spinosus*, but he states that, in this species, all oostegites become fused into a single marsupium. Shiino (1937:58) reports the same number of oostegites for *A. nipponicus*, and Menzies (1953:457) claims that five pairs are to be found in *Parapseudes pedispinus* (=*P. latifrons*). However, in his statements and figures, Lang apparently consistently maintains that there are four pairs of oostegites present among the Monokonophora (e.g., Lang, 1956b:472, 473; 1968).

Recently I have confirmed (Gardiner, 1973a) the presence of chelipedal oostegites in species of *Apseudes, Carpoapseudes, Leiopus,* and *Cirratodactylus.* In the case of *Cirratodactylus,* at least, this pair of plates does not participate in the formation of the marsupium. Other species clearly lack chelipedal brood plates: *Sphyrapus* sp., *Kalliapseudes* sp., and *Synapseudes* sp. (Gardiner, 1973a); *Cyclopoapseudes diceneon, Metapseudes aucklandiae,* and *Synapseudes idios* (Gardiner, 1973c); and *Calozodion wadei* (Gardiner, 1973b).

The Paratanaidae, as presently conceived (Lang, 1967), have either two or four pairs of brood plates. In *Pseudotanais,* in which there is only a single pair located on the coxae of the fifth pereopod (thoracopod VI), they overlap at their edges to form a single marsupium. In other paratanaid genera which he investigated (*Tanaissus, Leptochelia, Nototanais, Leptognathia*), Moers-Messmer found that the brood plates are not fused and that they form a loose tube, between the thin plates, through which water can circulate.

All genera of the Tanaidae (sensu Lang, 1967) have only a single pair of oostegites borne at the base of the fifth pereopod. Moers-Messmer (1936) investigated formation of the marsupium in "*Tanais.*" But each of the species examined has now been referred to another genus, *Pseudotanais* or *Zeuxo.* Lang (1960:78) examined the marsupium in *Anatanais* (=*Zeuxo*), *Pancolus,* and *Tanais.* He found that these genera all produce

two brood pouches from their single pair of oostegites, each plate forming a separate pouch; however, in all species investigated, a single pouch is sometimes formed. Lang prefers to distinguish between the "real marsupium" of *Cryptocope* and *Pseudotanais* and the "ovisacs" of *Pancolus, Tanais,* and *Zeuxo* (Lang, 1960:77). In *Neotanais* there are four pairs of oostegites, borne posteromedially on the coxae of pereopods II–V (thoracopods III–VI) (Figure 94A–O). The oostegites first appear during the preparatory female 1 stage as imperfectly developed rudiments enclosed in cuticular sheaths (Figure 94A–D). These rudiments, often exceedingly small and easily overlooked, are transparent, rounded, similar to the coxal outline, and hidden by the legs; undoubtedly investigators have overlooked them at times.

Following a molt, the rudiments are considerably larger (Figures 92A, 94E,F). (A detailed discussion of rudimentary oostegites is presented on pages 191–193.) After a second ecdysis (the maturation molt) and the formation of the copulatory female instar, they probably are fully developed but enclosed in spherical cuticular sheaths. At some time after the molt the sheaths break open and the oostegites unfold, similar to the wings of an insect, and the sheaths are lost (Figure 94G). Moers-Messmer (1936) maintains that oostegites probably expand by means of blood pressure.

The eight plates are large, delicate, transparent, and almost equilateral at times. They form a loosely fitting tubular marsupium similar to that of certain of the Paratanaidae as described by Blanc (1884), Moers-Messmer (1936), and Bückle Ramírez (1965).

IRREGULAR DISTRIBUTION.—Wolff (1962:219) comments that, out of a total of 23 specimens, he found fully developed oostegites only on pereopod II (thoracopod III) in five specimens of *Munneurycope murrayi* and *Eurycope inermis.* He found oostegites only on pereopods I and IV (thoracopods II and V) in two other specimens of *M. murrayi,* but he was unable to explain this.

The most likely explanation for Wolff's observations might be that the thin, leaflike plates were lost during collection, processing, or handling in the laboratory. But the consistent pattern of "losses," leaving only the first pair or the first and last pairs, is puzzling. Of the 24 specimens of *Neotanais* spp. with mature oostegites which were ex-

amined, only six, or one-fourth, had all eight oostegites present; no pair of oostegites was present more frequently than the others.

Kudinova-Pasternak (1965a) reports two occurrences similar to those of Wolff: the presence of a single pair of oostegites on pereopod II in *Neotanais serratispinosus* (=*N. hadalis?*) from the Bougainville Trench, and a similar pair on pereopod II in a specimen of *Leptognathia caudata* (but the species description lists all five specimens of the latter species as being "without oostegites"). The oostegites reported by Kudinova-Pasternak on *N. hadalis* are rudimentary (Kudinova-Pasternak, personal communication). Kudinova-Pasternak (1970:345, 348) also found a specimen of *N. tuberculatus* from the Kurile-Kamchatka Trench with a single pair of oostegites (rudimentary?) on pereopod II (*Vitjaz* Sta. 5634—see p. 90).

I have found one juvenile *Neotanais micromopher* with a single, tiny rudimentary oostegite (0.06 × 0.04 mm—cf. Figure 82) on the left pereopod IV. Also observed were a juvenile of *N. armiger* bearing a similar oostegite on the left pereopod V (*Anton Bruun* Sta. 111) and two copulatory males of the same species from the same station bearing similar plates on pereopods II–V. These probably all resulted from aberrant development. On the other hand, it is surprising that two copulatory males of the same species from the same station show the same "aberration."

The sizes of oostegites have been discussed in the developmental analysis above (p. 192). Jancke (1926) reports that the first oostegite in *Heterotanais oerstedi* is the smallest, the second is twice as large as the first, the third is about a third larger still, and the last two are twice as large as the third. Moers-Messmer (1936) states that the first pair of oostegites is smaller than the rest in the paratanaids *Tanaissus, Leptochelia, Nototanais,* and *Leptognathia.* He found that the first pair, borne on the chelipeds, was very small in *Apseudes spinosus* (but see p. 224). In *Neotanais* the oostegites are all similar in size.

ORDER OF APPEARANCE.—In *Neotanais* all oostegites originate simultaneously with the third molt and the formation of the preparatory female 1; apparently other tanaidaceans are similar. This contrasts with the pattern of serial oostegite growth reported by Kinne (1954) for *Sphaeroma hookeri.* In this isopod small oostegite anlagen are first visi-

A

Oos

0.2

B

Oos

0.2

G

0.2

C

0.2

D

E

0.2

F

I

Pp V

OS

GpAn

Cox

0.2

J

Oos

Pp V

Gp

Cox

0.2

H

0.2

L

M

N

O

♂

P

0.2

Q

K
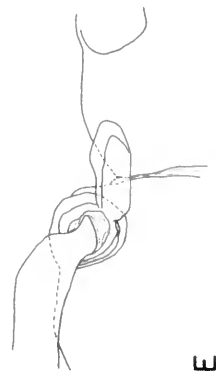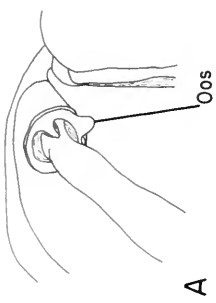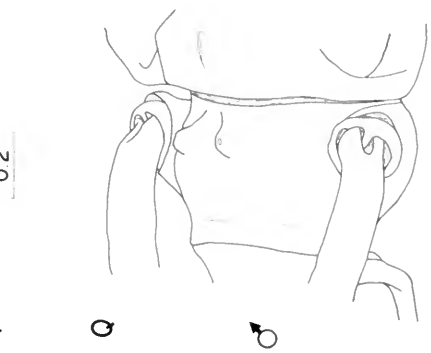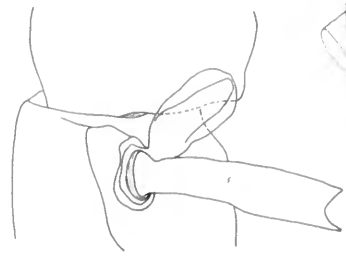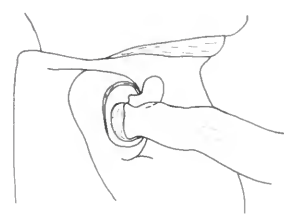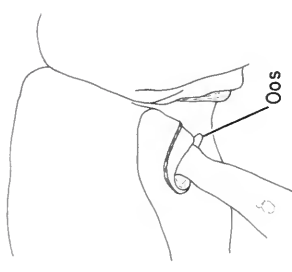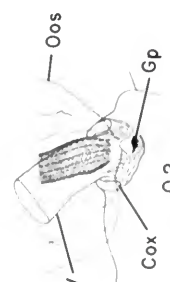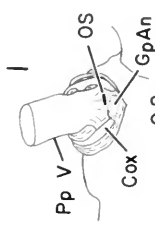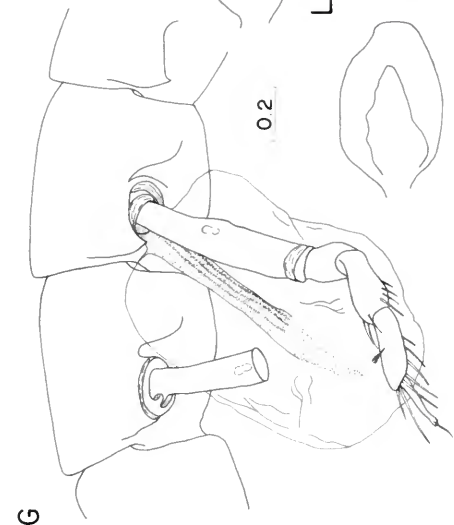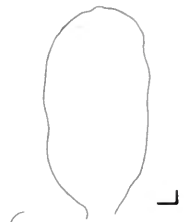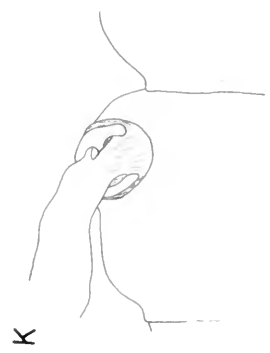
ble on the fourth segment, and only later on the third and second.

INTERMOLT GROWTH.—Bückle Ramírez (1965) found that, in *Heterotanais oerstedi*, preparatory females ready to molt and enter the stage with mature oostegites (copulatory females) had large sheaths around their rudimentary oostegites. However, when they had entered the preparatory instar, the oostegites had not been externally visible and could be detected only by sectioning because they were very small and lay closely pressed to the thoracic sternites. In other words, the oostegite sheaths in *Heterotanais* increase in size during the instar in order to reach their final dimensions before another molt.

When oostegite-sheath length is plotted against body length, there is a more or less random distribution of points in the resultant scatter diagram if growth occurs between molts. Some animals that have just molted will have very small oostegites although they may be near the upper end of the body-size distribution for this stage. Other animals, although they are very small, may have relatively large oostegites because they are ready to undergo another ecdysis to become copulatory females. In other words, there will be little association of low

FIGURE 94.—Development of oostegites and genital pores in three species of *Neotanais* (all animals are *Neotanais micromopher* from WHOI Benthic Stations except where noted): A, B, ventral and lateral views, respectively, of a left pereopod of a preparatory female 1 with extremely small rudimentary oostegites (GG, Sta. 76); C, D, same views of a preparatory female 1 with oostegites of a more nearly average size (FE, Sta. 76); E, F, same views of a preparatory female 2 with large rudimentary oostegites (GE, Sta. 76); G, lateral view of the right pereopod V of a copulatory female with mature oostegites (Sta. 95); H, ventral view of the coxal area of the left pereopod V of a preparatory male—oostegites have never been present; I, same area of a copulatory female of *N. giganteus* (Sta. 72) showing unopened gonopore and oostegite scar (oostegite has been detached) in a decalcified area of the coxa; J, same area of a copulatory female of *N. pfaffi* (*Galathea* Sta. 716) showing opened gonopore at the base of the oostegite; K, same area in another copulatory female (DE, Sta. 76) with the oostegite scar not visible but a large decalcified area obvious in the coxa at the site of the gonopore, now apparently closed; L-O, variation in oostegite shape in preparatory females 2 (Sta. 76); P, ventral surface of pereonite 7 in a preparatory male (DV, Sta. 76) showing small decalcified areas representing the anlagen of the male genital pores; Q, same area in oblique lateral view in a copulatory male (HI, Sta. 76) showing the raised male genital cones with the genital pores at their tips.

values of oostegite-sheath length with low body-length values or high values of one variable with those of the other; the correlation coefficient (r) will be relatively close to zero.

Among the smaller animals at WHOI Stas. 64 and 76 (Figure 83), values of r are high (0.852 and 0.815, respectively), implying lack of oostegite growth in *Neotanais micromopher* during this instar. Among the larger animals r is smaller, although still relatively high (0.758 and 0.584). The value of r for the preparatory females 2 is significantly different ($P=0.05$) from that of the preparatory females 1 at Sta. 76 but not at Sta. 64 (Moroney, 1956). Therefore, the oostegites probably do not grow during the preparatory female 2 instar either, although the evidence is not quite as strong as for the first stage.

The high degree of calcification observed in neotanaids may account for the necessity of two instars during oostegite development and/or the lack of growth in oostegites within a developmental stage, in contrast to the single preparatory stage in *Heterotanais*. Moreover, an additional ecdysis during egg development may provide for thoracic swelling in heavily calcified forms (see Figure 92).

VENTILATION OF THE BROOD CHAMBER.—The form of the marsupium is similar in *Neotanais* and *Heterotanais*, and the method of ventilating the brood chamber probably is similar in the two genera. Ventilation has been described for *Heterotanais oerstedi* by Jancke (1924) and by Bückle Ramírez (1965). The latter observed a stream of water regularly alternating in and out of the opening between the first and second pairs of oostegites. The oostegites opened and closed to provide ventilation and to move the eggs back and forth. During copulation they remained completely open. The oostegites probably are under muscular control, perhaps of muscles similar to certain of the extrinsic limb muscles illustrated in Figure 90D but oriented somewhat differently.

A similar method of ventilation has been described by Jancke (1926) for *Idotea neglecta*. Jancke notes the participation of the legs in this movement and that of the pleopods in current flow.

LOSS FOLLOWING BROOD CARE.—In most samples the proportion of copulatory females of *Neotanais* retaining their oostegites is very small compared to those having only oostegite scars, if indi-

viduals with oostegites are even present. The percentage of the time during this instar when the oostegites are present may be relatively short compared to the entire intermolt period; at some time after the young leave the brood pouch the plates may be shed. At any one time there would be more individuals that have shed their plates than those that would have retained them.

It is possible, however, that the brood plates are lost during the collection and processing of the sample. They are easily detached with forceps in the laboratory, although this may result from increased brittleness following preservation. If the plates are torn off during collection, shreds of oostegal material probably would remain attached to the animals, as is often true when only certain plates are missing. But traces of the oostegite are hardly ever present, only the scar. Also, the number of copulatory females without any oostegites (all species at all stations) far outnumbers those with several intact plates. Therefore, it would be expected that, of those specimens retaining oostegites, most would have only a few (perhaps one to three) remaining if they are being torn off during the grinding and washing involved in collection. Of those animals examined that had one or more mature oostegites, only five individuals had three or less remaining, whereas 19 had four or more, and 12 were missing only one or two or had all oostegites present. This suggests that the plates are shed at some time after a brood is raised rather than being torn off.

Hansen (1913:7) evidently did not understand that the oostegites could be lost, and upon finding females without marsupia which were larger than those with brood plates he postulated a reduction in body length accompanying the development of the eggs and marsupium.

OOSTEGITE SCARS.—References to oostegite scars in the literature dealing with the Tanaidacea are few. Yet, as demonstrated in the developmental study, these scars can be very helpful in the proper identification of certain instars. Shiino (1937:59) was the first to mention the scars as well as to interpret their meaning correctly. When examining *Apseudes nipponicus* he found a "black-coloured stripe" on the coxa of each oostegite-bearing leg in the position where the oostegites had been attached. Wolff (1956a:198) was unable to find similar stripes in females of *Apseudes* (=*Leiopus*)

galatheae; possibly they were present but translucent as in *Neotanais*.

In *Neotanais* the oostegite scars (Figure 94I) are colorless and often very difficult to see. Whether or not the scars themselves can be seen, the posteromedial area of the coxae of pereopods II–V are slightly distorted in copulatory females, making recognition possible. This area is completely decalcified on the fifth pereopod owing to the presence of a functional female gonopore (Figure 94I,J).

CONDITION BETWEEN BROODS.—In the terrestrial isopod *Armadillium vulgare* the oostegites are lost between two successive broods and they reappear just before the eggs are laid (Charniaux-Cotton, 1960). In the case of *Limnoria tripunctata* (Menzies, 1954) and in the Desmosomatidae (Hessler, personal communication) the oostegites are reduced to a rudimentary pregravid state during the molt following release of the young. According to Lang (1953b), the mysids and amphipods retain their oostegites between broods. Charniaux-Cotton (1960) states that in the gammaridean amphipods the marginal hairs of the oostegites become temporarily enlarged for carrying the eggs and larvae.

The pattern of oostegal development between broods in *Neotanais is not clear* (p. 197). If intermediate females are present between brooding stages, they probably form oostegites anew before each brood.

The pattern for other tanaids, where known, appears to be relatively uniform. *Heterotanais antarcticus* (Lang, 1953b) and *H. oerstedi* (Bückle Ramírez, 1965) exhibit a similar alternation of rudiments and mature oostegites between broods. Lang (1953b) states that development is the same in *Leptognathia antarctica* Vanhöffen, *Acanthotanais oculatus* (Vanhöffen), *Nototanais werthi* Vanhöffen, and in several species of *Leptochelia*. Apparently no information is available for the Monokonophora.

Brood Sacs

Kinne (1954:103) and Menzies (1954:375) describe internal brood sacs in the gnathiid and sphaeromid isopods. These are used in brooding the eggs either in conjunction with the marsupium or not. No structures of this sort were found in *Neotanais* nor have they been reported for other tanaidaceans.

Seminal Receptacles

No evidence of seminal receptacles has been found in *Neotanais* such as that cited by Claus (1888:199) for the isopods *Porcellio, Oniscus,* and *Typhloniscus.* Forsman (1944) states that these are enlarged parts of the oviduct in *Jaera albifrons.* Claus failed to find them in *Apseudes* and they have not been reported for the Tanaidacea since his report.

The Female Gonopores

Although a careful external search was made for the female gonopores in *Neotanais micromopher,* they were not detected until the animal was sectioned. The difficulty in discovering them was due to their small size and slit-like shape in which they resemble many wrinkles, cracks, and fissures in the coxal area; problems with variations in the degree of calcification and hence of color and transparency; and the absence of the gonopores in several stages.

LOCATION.—Very few references to the location of the gonopores are available for the Tanaidacea. Müller (1864b:3) states that in *Tanais dubius* (=*Leptochelia dubia*) the opening is unpaired and lies at the posterior edge of the sixth pereonite. Blanc (1884:247) claimed to have found slits in the integument which were very close to each other and near the posterior edge of the sixth pereonite in *Tanais* (=*Heterotanais*) *oerstedi* (see Blanc, 1884, pl. 12: fig. 53). But Claus (1888:200) reexamined *Leptochelia* and was unable to verify Müller's findings, and he commented that Blanc's figure is not convincing. Claus (1888:60) found the openings in *Apseudes latreillii* (=*A. acutifrons*) under the last brood plate on either side and noted that the edges of the slit were swollen.

The female gonopores of other peracaridan groups have been discovered as follows. Cumacea: *Diastylis rathkei,* base of oostegite between oostegite and sternite on pereopod III (=thoracopod VI), Forsman (1938:37). Isopoda: *Jaera albifrons,* ventrolateral position on pereonite 5 (=thoracomere 6), Forsman (1944:22); *Ligia,* small longitudinal slit just at base of last oostegite, on pereopod V (=thoracopod VI), Hewitt (1907:93); *Rhyscotus,* base of pereopod V (=thoracopod VI), Jack-

son (1928:545); *Sphaeroma hookeri,* figured as anteroposteriorly directed slit on sternite medial to base of pereopod V (=thoracopod VI), Kinne (1954:103).

EXTERNAL STRUCTURE.—Many copulatory females were available of *Neotanais micromopher,* the species on which the analysis of development was carried out. But because of the relatively small size of this species and the variable quality of the material, it was not possible to determine the nature of the gonopores in detail. However, an examination of better specimens of larger species was fruitful. A specimen of *N. giganteus* with incompletely expanded oostegites—several of which remained in their cuticular sacs—had no trace of the gonopores. This animal probably had just finished the maturation molt and had become a copulatory female. Another specimen with fully expanded oostegites had distinct swellings at the sites of the future gonopores (GpAn, Figure 94I).

A specimen of *Neotanais pfaffi* had a very clear slit medial to the base of the oostegite on pereopod V (Gp, Figure 94J). This animal had fully expanded oostegites, a very wide medial decalcified area on the coxae of its fifth pereopods, and empty ovaries (viscera visible through the decalcified cuticle). The opening was probed and was observed to lead into the body via a short, tubular depression. The small flap of cuticular tissue lying lateral to the opening presumably is its lateral lip.

INTERNAL STRUCTURE.—Each gonopore (Figure 90D) lies in the coxa between the oostegite scar and the sternite. It appears as an invagination of the decalcified area of the coxa, and cuticular material leads upward for some distance into the body of the animal. Forsman (1938) noted that the distal part of the oviduct in the cumacean *Diastylis rathkei* is apparently chitinized. In the illustrated female of *Neotanais micromopher* the diameter of the cuticular invagination is about 80 μm whereas that of the oviduct is 60 to 70 μm, a close correspondence. The gonopore is considerably wider (120 to 140 μm) and slitlike at its mouth.

SUMMARY OF GONOPORE DEVELOPMENT.—The female does not have gonopores prior to the maturation molt. Immediately following this molt they still are not open, and the oostegites remain in their cases. However, by that time, the most medial portion of the coxae of the fifth pereopods has become decalcified. Sometime after the unfolding

of the oostegites, the decalcified area becomes swollen, probably due to the pressure from the ova within; eventually it spilts, extruding the ova into the marsupium.

The diameter of the gonopore under its mouth is only about 80 μm in *Neotanais micromopher*, whereas that of the only incompletely developed ovum in a preparatory female 2 is roughtly 400 μm. The oviducts and gonopores may expand considerably in order for the eggs to pass into the marsupium. Forsman (1944) noted that the eggs were deformed when passing through the gonopores in the isopod *Jaera*, and he could see yolk granules streaming into that part of the egg already outside. Marked deformation of the eggs also has been observed in the cephalocarid *Hutchinsoniella* (Hessler, personal communication). The function of coxal decalcification in the copulatory females of heavily calcified forms such as *Neotanais* may be an adaptation to ease passage of the ova.

The presence of the gonopores only in copulatory females accords well with the observations of others. The absence of gonopores prior to this stage has been noted by Claus (1888:198) for the isopods *Porcellio* and *Glyptonotus*. Citing a study by Bullar and P. Mayr on the isopod *Cymothoa*, Claus (p. 188) states that the oviduct and gonopores are found only in females with marsupia. Forsman (1944) noted the absence of gonopores in the cumacean *Diastylis rathkei* not only prior to the copulatory stage but also in intermediate females.

Among the Tanaidacea, Claus (1888:199) found the gonopores only in stages with a marsupium in *Apseudes latreillii* (=*A. acutifrons*). Lang (1953a: 350) did not observe them in his collection of *Apseudes hermaphroditicus* (=*A. spectabilis*) and stated that they probably were absent in all but copulatory females. Bückle Ramírez (1965:749) was unable to find the oviducts in females of *Heterotanais oerstedi* with rudimentary oostegites, and presumably the gonopores were absent as well.

The presence of the gonopores apparently is not unrelated to the development of the oviducts. Oviducal tissue was observed as early in development as the juvenile stage in *Neotanais micromopher*, but, in the specimens examined, it was not well developed until the copulatory female. Unfortunately, transverse sections of late preparatory 2 and intermediate females were not made to check

the extent of its development. Forsman (1938) observed that in the early part of the preparatory female stage of *Diastylis* the oviducts were only a thin strand of cells. These could be traced to their openings in the epidermis. The oviducts were well formed in the preparatory stage but still did not penetrate the cuticle; they also were present in the intermediate female stage.

Structure of the Spermatozoa

Flagellate spermatozoa were found in all three adult males examined as well as in the preparatory male. The length of the flagellum varies from about two to over five (but usually three or four) times as great as the head region (Figure 91D,E). Total length varies between about 110 and 220 μm, the mean being about 150 μm.

The structure of the spermatozoa has not been completely revealed because of the staining techniques used, but the presence of a flagellum is certain. The head is composed of a large, relatively clear spheroid and a smaller, more deeply stained, rounded cap. A large, strongly refractive spot apparently lies within the clear portion near its junction with the cap (Figure 91E). Because of the staining techniques employed and the natural twisting of the flagellum, it is not clear whether the tail attaches to the head at the dark structure or on the larger light side, although the latter appears most probable. A cuplike structure joins the tail to the head (Figure 91E).

The spermatozoa of *Neotanais micromopher* are clearly isolated, at least in the preparations examined, and they are not in any way aggregated into "sperm colonies." Bundles of sperm have been found in a number of isopodan taxa: *Porcellio* and *Oniscus* (Siebold, 1836), *Oniscus* (Nichols, 1902), and *Asellus* (Sugiyama, 1933). There are no previous reports of sperm colonies for tanaidacean groups.

Many workers (e.g., Retzius, 1909) have observed that the spermatozoa of crustaceans are markedly different from those of most animals and that they exhibit a great diversity of form. Within the Malacostraca, a clear distinction has been demonstrated between the spermatozoa of the Peracarida and other Eumalacostraca. For instance, the spermatozoa are without flagella among the stomatopods (Nichols, 1902) and are "spherical

vesicular bodies" in *Squilla oratoria* (Komai, 1920). They are dark, rounded, irregular bodies in the decapod *Eupagurus* (Jackson, 1913).

Studies with the Peracarida have shown that the spermatozoa are almost exclusively flagellate; for example, in the amphipods *Gammarus pulex* (Siebold, 1836), *Orchestia gamarella* and *Meinertia oestroides* (Berreur-Bonnenfant, 1967), and *Stegocephalus inflatus* (Steele, 1967). Among isopods that have been examined are *Oniscus murarius* and *Porcellio scaber* (Siebold, 1836), *Oniscus asellus* (Nichols, 1902), *Jaera albifrons* (Forsman, 1944), and *Asellus nipponicus* (Sugiyama, 1933). According to Kumé and Dan (1968), tailed spermatozoa also have been reported from the Mysidacea. These authors suggest an association between complex spermatozoan structure and fertilization within a brood chamber, spherical spermatozoa being found among those crustaceans in which the spermatozoa are placed directly in the oviducts.

Reports on the nature of tanaidacean spermatozoa are few. Lang (1953:349) reports flagellate sperm in *Apseudes hermaphroditicus* (=*A. spectabilis*) among the Monokonophora. However, the records available for members of the Dikonophora do not include any instance of flagellate sperm. Blanc (1884:247, pl. 12: fig. 52) reports a rounded cytoplasm containing a lunate nucleus in *Tanais* (=*Heterotanais*) *oerstedi,* as does Bückle Ramírez (1965:752, figs. 38, 39). Roubault (1937, fig. 3c) states that the sperm of *Leptochelia dubia* are globular with two short expansions of the chromatin resembling the horns of a cow.

It is surprising that all three observations of dikonophoran sperm fail to demonstrate the presence of flagella, whereas these structures are found in the Monokonophora and are so widely distributed among the other Peracarida. The presence of flagella in the Neotanaidae, another dikonophoran group, further accentuates the problem.

The flagella of *Neotanais micromopher* are extremely fine and difficult to see and were detected only after prolonged and careful observation. The nuclei in the spermatids often are eccentrically placed (Figure 91D). In the amphipods *Orchestia* and *Meinertia* (Berreur-Bonnenfant, 1967:527) and the isopod *Asellus* (Sugiyama, 1933, pl. 1e: fig. 34), certain stages in the development of the spermatids are shown with a dark, strikingly crescent-shaped chromatin mass in a clear, globular cytoplasm. Bückle Ramírez' (1965, figs. 38, 39) figures of *Heterotanais* spermatids show a similar structure.

Additional studies of tanaidacean spermatozoa should clarify the situation. It will be of considerable phylogenetic interest to determine if non-flagellated sperm are widely distributed among the Dikonophora or if they are restricted to the Neotanaidae, the most primitive of the dikonophoran families.

Blanchard, Lewin, and Philpott (1961) have suggested that studies of fine flagellar structure may shed light on the relationships among crustacean groups. These authors found that in the groups with actively motile flagella (subclasses Branchiura and Cirripedia) the flagella contained longitudinal fibrils similar to those widely distributed among other animal groups. Among the Peracarida, where motility apparently is either absent or weak, they examined the flagella of the isopods *Cyathura, Idotea,* and *Oniscus* and found that they are composed of a series of discs. It should be profitable to examine the flagella of the Tanaidacea and Cumacea for fine structural details.

Comparisons of sperm length may not be particularly meaningful. The approximate length cited above for the sperm of *Neotanais micromopher* is 110 to 220 μm with a mean of 150 μm. Blanc (1884:247) and Bückle Ramírez (1965:752) both give 20 μm as the diameter of *Heterotanais oerstedi* sperm (without flagellum). The flagellate sperm of the isopod *Jaera albifrons* has a length of 130 μm (Forsman, 1944:15).

Spinning Glands

Blanc (1884:200) first described spinning glands among the Tanaidacea from *Tanais* (=*Heterotanais*) *oerstedi,* and he pointed out that they had been described for a number of amphipods and isopods. Depending upon the taxon, they are located in the thorax, the thoracic legs, or even in the abdomen. Blanc found three pairs of glands in *Heterotanais oerstedi,* in pereonites 2–4. They have been described in detail more recently by Siewing (1953) who also found them in *Tanaissus lilljeborgi*. Lauterbach (1970) describes them from at least pereonite II in *Tanais cavolinii.*

The secretions of these glands drain down through pereopods II–IV and exit at the tips of

the dactyli. Bückle Ramírez (1965) refers to these legs as the "spinning" legs; the secretions emitted from them are used in constructing the animal's tube. Goodhart (1939) found that the tube-building amphipod *Leptocheirus* was unable to build its tube without these legs.

No trace was found of spinning glands in histological sections of *Neotanais micromopher*. This is not surprising and substantiates the notion that the neotanaids do not build tubes (see "Tube-Building and Burrowing" under "Ecology" below).

Male Alimentary Modifications

The reduction of the mouthparts and the permanent closure of the anal opening in neotanaid males has been discussed earlier (p. 179). Similar observations have been made on many tanaids, and early workers were aware of these changes (e.g., Müller, 1864a; Norman and Stebbing, 1886). Norman and Stebbing attributed the reduction of mouthparts to an accomodation to the massive development of the male chelipeds.

Apparently much of the oral musculature remains in *Neotanais,* including what is probably the mandibular musculature, even though the mandibles are reduced and fused to the carapace. Maintenance of nonfunctional musculature or of the male mouthparts themselves may be due to genetic pleiotropy (Mayr, 1963). Although the muscles are no longer functional, they may be controlled by the same genes as other, functional structures. Thus, selective pressure is exerted for the retention of these gene complexes.

Although Müller (1864a) and others have noted that the gut is empty in certain male tanaids, no one, insofar as known, has discussed the structure of the gut in copulatory males. A detailed description is not presented here. Suffice it to say that, for *Neotanais micromopher,* the spines and setae found in the guts of all other stages are completely absent in the copulatory males (see Figure 92A,B). This modification is correlated with the reduction or absence of mouthparts and the permanent closure of the anal opening. Presumably the gut is similar in the Paratanaidae, where the male mouthparts also are reduced.

The guts of the copulatory males were completely empty. Bückle Ramírez (1965) also observed this in *Heterotanais oerstedi,* and he noticed

in addition that the males never fed after the maturation molt. He states that females with mature eggs in their ovaries no longer eat, and that the contents of the gut are limited to the anterior and posterior regions. A similar observation was made for *Neotanais* (Figure 92A). The gut probably is flattened by the expanded ovaries, and passage of material through it is difficult.

In order to live and to carry out their reproductive functions, the males must have a source of energy. That this source can be substantial is indicated by Bückle Ramírez' (1965) observation that captive male specimens of *Heterotanais oerstedi* can live up to 75 days in the laboratory. Just how much energy is used by deep-sea males is, of course, unknown; rates of metabolism may be relatively low among the deep-sea fauna (Jannasch et al., 1971). But the males probably swim in search of females and so far there is little indication that the reproductive biology of deep-sea tanaidaceans is very different from that of shallow-water forms.

Pleonal Fusion

Various degrees of pleonal fusion are observed among the Tanaidacea. Among the Dikonophora, all pleonites and the pleotelson are fused in the "female" of *Anarthrura* (Sars, 1896), with no remaining indication of their former boundaries. All pleonites and the seventh pereonite are similarly fused in *Agathotanais,* but superficial remnants of the articulations between the somites remain (Hansen, 1913).

There is no known reference in the literature to pleonal fusion among the Neotanaidae, and fusion is the exception rather than the rule in this family. However, in *Neotanais giganteus, N. micromopher,* and *N. dinotomer* there is clear and consistent fusion of the pleotelson with the fifth pleonite in all individuals examined, representing all developmental stages (Figures 5A,B,D–I, 14C–E, 15A).

A small area of what appears to be the arthrodial membrane frequently appears middorsally in the groove separating the last pleonite and the pleotelson, especially in *Neotanais giganteus* (Figure 48E); however, practically all remnants of the groove itself are obliterated ventrally in the same species (Figure 48F,G).

The fourth and fifth pleonites also are frequently involved in fusion in *Neotanais dinotomer*.

The functional significance of pleonal fusion in *Neotanais* is unknown.

Morphological and Developmental Abnormalities

A number of abnormalities were noted during the examination of the material for this study. A pereopod was rudimentary and without setae in several animals. In one specimen, two of the ten pleopods were rudimentary and naked. The incisive mandibular spines were occasionally bifid, and the short, terminal propodal or subterminal, carpal spines of the pereopods were doubled in one or two cases. In one animal, two pleonites were partly fused dorsally.

Aberrations involving an entire appendage probably are the result of injury and regeneration, although genetic causes cannot be ruled out.

Another class of anomalies involves the presence of unusual sexual structures. Several juveniles and copulatory males (see p. 225) had one or more tiny oostegites on the coxae of certain legs. Kudinova-Pasternak (1965a:76 and personal communication) describes an animal bearing large rudimentary oostegites only on the second pair of pereopods. Wolff describes an individual of *Neotanais serratispinosus hadalis* (=*N. hadalis*) that displayed both mature male and female characters (Wolff, 1956a:216).

A specimen (6.9 mm) of *Neotanais micromopher* (*Eastward* Sta. 6228) whose body length is about twice that of a manca 1 bears very tiny oostegites and clearly visible male gonopore anlagen. In addition, the pleopods are well developed, having eight terminal endopodal setae and a setal length/endopodal length ratio of about 0.6 to 0.7, equivalent to that of a preparatory female 2 or even a preparatory male.

Ecology

Almost all authors who have dealt with the Neotanaidae have included depth records and some information on the locations at which their animals were collected. However, Wolff (1956a) was the first to attempt a description of the distribution, size relationships, and origin of the Neotanaidae as a whole. Since Wolff's work,

Kudinova-Pasternak (1965a) has offered a few comments on the distribution of the group, but, for the most part, the ecology of the family has been neglected.

The availability of a much larger collection of material than ever before permits a more nearly accurate view of the distribution, species diversity, and reproductive periodicity of the genus *Neotanais*. However, the available material is still far less than adequate for a full description of the environmental relationships of the group.

The present study is part of a continuing effort to understand the ecology of the deep-sea fauna. Several of the topics below will be dealt with again in more detail after additional deep-sea tanaidacean taxa have been studied.

FOOD AND FEEDING

Because of their small size, neotanaids are difficult to observe from a submersible research vehicle, and because of difficulties in collecting it has been impossible to study them alive in the laboratory. Therefore, morphological analysis and the examination of gut contents were utilized in an attempt to understand their feeding habits.

With the exception of the nonfeeding adult males, the mouthparts of neotanaids are, for the most part, similar to those of most other tanaidacean taxa; there is no structural indication that their mode of feeding is markedly different from that of other tanaidacean groups other than the highly modified kalliapseudids. The second maxilla is similar to that of *Apseudes talpa* for which Dennell (1937) has described a filtering role, the medial area bearing a row of filter setae. Dennell suggests that the filter-feeding habit in *Apseudes* is not the primary means of obtaining food; and this is undoubtedly true for the neotanaids as well. For the most part, they probably feed on organic detritus lying on the sediment, or on small animals that they encounter. The chelipeds or mouthparts themselves probably are used in securing the food.

The contents of the guts of several sectioned individuals representing most developmental stages were examined. They were consistently composed of formless material, presumably organic detritus, and occasional fragments recognizable as having had a biological origin. If prey organisms comprised a significant portion of their diet, hard re-

mains (setae, spicules, tests) might be expected to be recognizable in most cases. Gut contents were similar in all of the stages examined except for the copulatory males, in which the gut was empty, and the manca 1, in which the gut contained what I interpret as yolk, similar to the first manca of *Heterotanais oerstedi* (Bückle Ramírez, 1965:740).

Tube-Building and Burrowing

Many dikonophorans construct tubes of cement emitted from their pereopods; however, neotanaids do not build tubes. Over 1000 representatives of the Neotanaidae were examined, and in no case was there evidence of a tube, nor were cement glands found during histological examination of the thorax.

Neotanaids probably are epifaunal, spending their lives on the surface of the deep ocean oozes. Whether they are able to burrow is unknown. Certain monokonophorans are specialized for a fossorial habit; the second pereopod is spatulate and bears heavy propodal spines. Modifications of this sort are unknown in *Neotanais* and *Herpotanais*. However, *Venusticrus glandurus* has the propodi of the third and fourth pereopods modified in a fashion analagous to that of the apseudids (see Figure 72c and p. 166), and it is possible that this species is fossorial in habit.

Regardless of the absence of pereopods specialized for digging, neotanaids probably can burrow when necessary. Bückle Ramírez (1965:724) found that individuals of *Heterotanais oerstedi*, a species without specialized fossorial limbs, were able to dig into the sediment on pilings within a minute after settling on it. The males dug in more quickly than the females because of their greatly developed chelae, which they employed for this task.

Salvat (1967) found that the fossorial, shallow-water monokonophoran *Apseudes talpa* does not occur in greatest densities near the surface of the sediment but from three to nine centimeters beneath the surface. Densities at three to six centimeters are eight times greater than from zero to three centimeters. Monokonophorans are present only in relatively limited numbers in deep-sea samples obtained by Woods Hole investigators; neotanaids are much more abundant. Perhaps the depth to which the former burrow in the deep-sea

oozes is responsible for their infrequent occurrence in samples collected with devices that do not penetrate the substrate deeply. The presence of larger numbers of neotanaids may be additional evidence that they are not fossorial, or at least that they burrow to a lesser degree than do the monokonophorans.

Symbionts

Stalked epicaridean protozoans, possibly ciliates, were frequently observed. They usually appeared on appendages rather than on the general body surface, most frequently on the antennae, pereopods, pleopods, and uropods.

Large, round worms, possibly nematodes, were observed in the interior of certain translucent specimens. The worms often were twice as long as the host, doubling back on themselves, and almost completely filling the interior of the thorax and abdomen.

Species Diversity

All of the species of neotanaids collected at a particular station are listed in Table 1. Table 11 summarizes the numbers of species collected in each sample.

It is readily apparent from Table 11 that most samples (almost 80 percent) contain only a single neotanaid species. In view of the difficulties involved in capturing deep-sea benthonts and in retaining them in the dredge once caught, most samples would be expected to contain relatively few individuals of a species. The number of species represented in a sample is directly related to sample size (Sanders, 1968) and therefore will be low in small samples. However, the appreciable number of stations (37 or 22.2 percent of the total) at which more than one neotanaid species was collected is noteworthy. Surely representatives of more than a single species are present at many other localities, and their failure to appear in the samples is artifactual. Neotanaids are epifaunal organisms and generally are present in the samples much less frequently than paratanaids, which often are tube builders, probably living more sedentary lives and being more closely associated with the bottom than the neotanaids.

Representatives of three species were collected

TABLE 11.—*Relative efficiency of sampling gear in collecting neotanaid species as indicated by percentage of samples containing more than one species*

Gear	Species collected per sample					Total samples	Percentage of samples containing more than one species
	1	2	3	4	5		
Anchor dredge	18*	7*					
	11†					36	18.9
Epibenthic sled	17*	5*	6*	1*			
	6†	4†	1†	1†	1†	42	45.2
Herring otter trawl	6	2				8	25.0
Beam trawl	4	2				6	33.3
Small biology (Menzies) trawl	27	4	1			32	15.6
Other	41	2				43	0.5
Totals	130	26	8	2	1	167	
Percentage, each station	77.8	15.6	4.8	1.2	0.6		

* Collected by WHOI personnel.
† Collected by investigators other than WHOI personnel.

at almost 5 percent of the stations. Four species were found in two samples and five species in one sample. This apparently high species diversity is of interest because very closely related organisms usually are not found in the same habitat or, if they are, their habits are sufficiently different so that they do not compete severely for available resources. Species that fill the same ecological niche usually cannot coexist in a habitat (Hardin, 1960). Much of the deep-sea floor has long been thought to be uniform, with extremely stable environmental conditions and the same sediment type extending for great distances. However, it is unclear how closely similar organisms can coexist under such environmental conditions and what are the boundaries of their niches. The marked similarity of feeding structures among the deep-sea Tanaidacea has already been mentioned, and there is no indication that various species have different sources of food.

A possible explanation of high species diversity is that the deep-sea benthic environment does vary to a greater or lesser extent over relatively short distances with the result that neotanaid species, adapted to various environmental conditions, are unevenly distributed. Dredges passing through these different "microhabitats" collect several species. But this explanation is unappealing. The anchor dredge fills very quickly upon contact with the bottom (within one or two meters) and, when full, rejects further sediment (Sanders, Hes-

ler, and Hampson, 1965). Yet, about 20 percent of the samples collected with this device contained more than one species. It is unlikely that animals from any but a very restricted area are collected by the dredge. Those from other areas adhering to its surface or lodging in the mouth would soon be washed away while the dredge is being raised to the surface.

The apparently high species diversity of the Neotanaidae is consistent with the studies of Hartman (1965) and of Sanders and Hessler (Hessler and Sanders, 1967; Sanders and Hessler, 1969; Hessler, 1970) with other taxa. My preliminary examination of other tanaidaceans collected at WHOI benthic stations has shown that frequently six and, at times, as many as ten genera are present at a station.

The discovery of high tanaidacean diversity in the deep sea bears out the statement of H. J. Hansen (1913:4), who made a similar inference from the much less adequate samples collected by the *Ingolf*:

From [the *Ingolf* collections] we may safely draw the conclusion, that the deep sea . . . in the North Atlantic has a much richer fauna of Tanaidacea than any large northern or tropical part of the Atlantic along the coasts and with depths from 0 to 100 fathoms. And as it seems very improbable that the deep sea near South Greenland is proportionately richer than the deep sea of the subtropical Atlantic, the Indian Ocean or the Pacific, we may infer that hundreds of unknown species of Tanaidacea inhabit the deep areas of the Oceans, and that the fauna from about 300 and down

to at least 2000 fathoms is much richer than the fauna living in depths between 0 and 300 fathoms.

Hansen raised the number of species of tanaids known for that area of the world from nine to 72—or to almost half the number of species known for the whole world at that time. The number of known species of neotanaids has been substantially increased in this work, and there is every reason to anticipate similar results from investigations on other tanaidacean families. I will return to the species diversity of the deep-sea Tanaidacea in detail in a later publication.

EFFICIENCY OF THE SAMPLING GEAR.—The number of species represented in a sample reflects the overall collecting efficiency of a dredge or trawl because of the relationship between the number of species captured and the size of a sample (see above).

Table 11 presents the diversity of neotanaid species obtained by all devices that captured more than a single species in a sample. The equipment used by the *Ingolf* and *Travailleur* cannot be evaluated adequately because of the small number of their samples containing neotanaids. Of the other gear, devices which collect over limited distances, such as the anchor dredge, cannot be expected to be as useful in capturing large numbers of species as those that collect across an appreciable area. Of

SPECIES	STATIONS		INDIVIDUALS		DEPTH RANGE	
N. sandersi	20	14	50	36	2193	3000
N. hastiger	12	3	31	7	2500	3261
N. affinis	23	12	51	24	3215	3467
N. giganteus	13	5	56	49	1368	2301
N. micromopher	32	13	319	274	1032	2461
N. americanus	41	20	193	166	2438	2670
V. glandurus	2	2	2	2	270	
C. mirabunda	2	1	2	1	2690	
N. dinotomer	6	6	40	40	700	

1000	2000	3000	4000	5000	2000	1000

CONTINENTAL SLOPE   CONTINENTAL RISE   ABYSSAL PLAIN   BERMUDA

FIGURE 95.—Vertical distribution of neotanaid species found on the Gay Head–Bermuda Transect. All depths are in meters. The numbers of stations and individuals are, consecutively, total number and number from the Gay Head–Bermuda Transect area (eastern North American continental margin from about the Carolinas to Nova Scotia). Depth ranges are, consecutively, those from the transect and the total range if greater than that of the transect area. The extension of the range of *Neotanais sandersi* is based on specimens of uncertain identification (Pacific). The very shallow Antarctic representatives of *N. americanus* are not included. Solid lines represent known range from the transect; broken lines, additional range elsewhere in the transect area; dotted lines, other records falling outside of the range known for the transect area.

the latter, the epibenthic sled (Hessler and Sanders, 1967) is by far the most efficient, collecting more than one species in almost 50 percent of all samples. The only other trawl for which a significant number of samples is available is the "small biology trawl" (Menzies, 1962). This device collected more than one species in only about 15 percent of its samples.

FAUNAL DENSITY

The epibenthic sled is not a quantitative device and cannot yield samples suitable for estimates of faunal density (Hessler and Sanders, 1967). However, the anchor dredge is thought to be quantitative in its action (Sanders, Hessler, and Hampson, 1965). Of a total of 46 anchor dredge hauls at a depth of 2000 m or more, the depths at which the Neotanaidae are most abundant, 16, or 28.8 percent, captured neotanaids. This is 51.6 percent of the 31 samples containing tanaidaceans. These data imply that neotanaids are relatively rare on the deep-sea floor or that they are unevenly distributed (the assumption is made that they do not burrow deeply enough to escape the dredge). However, one cannot rule out the possibility that the animals, well equipped for swimming, sense the approaching dredge and dart out of its path.

Estimates of densities based on the 22 anchor dredge samples with neotanaids from the Gay Head–Bermuda Transect are 0.75 to 46.7 animals/m² ($\bar{x}$ = 7.12 ± 4.6 animals/m², s = 10.4, C = 1.45). Although Sanders, Hessler, and Hampson (1965) demonstrated significant variations in density with depth for the total benthic fauna, any depth-related trend in density is not apparent for the Neotanaidae because of low numbers of individuals and great variation at each depth. The considerable variations observed in density probably are due to local differences in sediment characters or food supply or in aggregating behavior of the animals.

DISTRIBUTION

Geographic Distribution

Our understanding of the distribution of neotanaid species has been very limited because of the paucity of available samples. At the time Wolff

wrote his paper on hadal tanaids, the family was known from only 22 scattered locations (Wolff, 1956a:232). The systematic confusion among species further complicated the situation, and most distributional inferences based on the Neotanaidae are very much in error. For example, the material known as Neotanais serratispinosus available to Wolff has been shown to include four species (see "Remarks" under N. micromopher).

Neotanaids have now been collected at 167 stations throughout the world. One area, the Gay Head–Bermuda Transect, has been intensively sampled (46 samples containing neotanaids). Whereas only 12 species of neotanaids were known to Wolff, the family is now represented by 28 species; therefore, it is now possible to make a much more realistic evaluation of distributional patterns within the family.

Many species, however, are still known from only a single station or from several stations in the same area. Others (Neotanais americanus and N. sandersi) have had assigned to them widely separated individuals of which some may later be found to be distinct. Determination of the actual distribution of these species is not possible at this time. Nevertheless, there is enough data to demonstrate that some neotanaids are distributed over remarkable distances (Figures 99–102; Table 12).

The genus Neotanais is cosmopolitan in the sense that it occurs in all three major oceans (Madsen, 1961). Herpotanais, Carololangia, and Venusticrus are known from only one or two samples each, and where two samples are available they come from stations located relatively close to each other.

Several species (Neotanais micromopher, N. americanus, N. sandersi, N. hadalis, N. affinis, N. giganteus, and N. hastiger) are found on both sides of either the North or South Atlantic or on one side in the North Atlantic and the other in the South Atlantic. No species is known from both the eastern and western Pacific.

Neotanais americanus, N. hadalis, N. affinis, and N. giganteus (Figures 97–99, 102) have been collected from both the North and South Atlantic. Neotanius hastiger (Figure 100) is known from the Davis Strait to the coast of Guinea (West Africa), N. hadalis (Figure 99) from the coast of Portugal and the Argentine Basin, and N. giganteus (Figure 99) from southeast of Cape Cod,

Massachusetts, to the coast of Gabon (west-central Africa). *Neotanais americanus* and *N. affinis* (Figures 97, 98) are known from Davis Strait to the Weddell Sea, and one specimen, the holotype of the latter, has been collected in the Indian Ocean off South Africa.

In the Pacific, *Neotanais armiger*, *N. pfaffi*, and *N. calcarulus* (Figures 97, 99, 100) have all been collected on the eastern slope of both the North and South Pacific. *Neotanais pfaffi* is known to range from Central America to lower Peru and *N. armiger* and *N. calcarulus* from the Oregon Slope to midway along the Chilean coast.

The only species indisputably known from more than one ocean are *Neotanais armiger*, from all along the Eastern Pacific Slope and in the Florida–Gulf of Mexico region (Figure 99); *N. hadalis*, which occurs in the Kermedec Trench northeast of New Zealand, the Argentine Basin, and the eastern Atlantic west of Portugal (Figure 102); and *N. giganteus*, which has been collected from localities west of New Zealand, off the coasts of Guinea and Gabon, and as far north as Davis Strait (Figure 99).

Sixteen species of neotaniads have been collected from the Atlantic Ocean and 17 from the
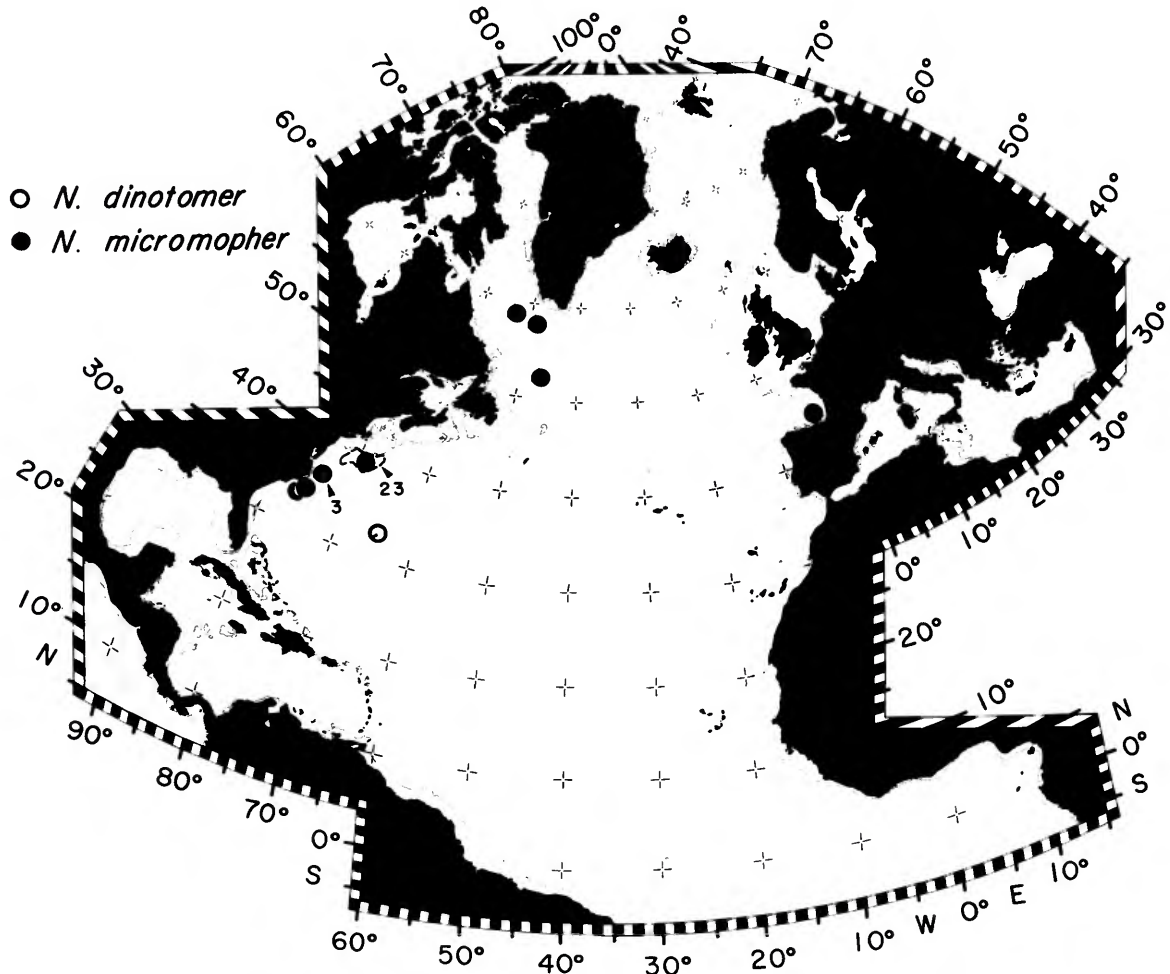
FIGURE 96.—Known distribution of *Neotanais dinotomer* and *N. micromopher*.

Pacific, but only four are definitely found in both oceans. Of the four species known from the Indian Ocean, one also occurs in the Atlantic. No species is known to be cosmopolitan, but this is almost certainly an artifact of sampling.

These patterns of distribution are by no means definitive; many more species will be discovered, and the known ranges of all will be expanded. Therefore, detailed zoogeographic generalization is, for the present, inappropriate. Nevertheless, the

available data demonstrate clearly that many species of neotanaids have extremely wide geographic ranges. Such ranges have been demonstrated for a number of other abyssal benthonic taxa (Madsen, 1961).

A pattern of very wide distribution is not universal among the deep-sea peracaridan Crustacea. The widest distributions that Hessler (1970) cites for species of the asellote isopod family Desmosomatidae are between the Arctic Ocean and the

FIGURE 97.—Known distribution of *Neotanais americanus*, *N. laevispinosus*, and *N. pfaffi*.

North Atlantic and equatorial Atlantic or Mediterranean Sea. Only seven of 69 known desmosomatid species have ranges of this breadth. No species is known to be shared among the three major oceans. Barnard (1961, 1962) has found marked regional abyssal endemism among the gammaridean amphipods.

Thus, the distributional patterns of neotanaid species contrast sharply with these other peracaridan groups. The findings of Barnard and Hessler are in accord with expectations for benthonic organisms that lack pelagic larval stages and that apparently swim for only short distances later in life.

Horizontal water currents above the sediments probably play an important role in the geographic distribution of neotanaids and in the maintenance of their genetic continuity over long distances. Although there is no pelagic larval stage, the older animals are almost certainly able to swim effec-

tively, albeit over short distances. They probably enter the water column and, frequently moving passively with the current, become displayed laterally. Once the deep current systems of the ocean become known, their correlation with many patterns of benthic distribution may be observed.

Wolff (1956a:234, 237) noted that the Neotanaidae apparently were missing from the high polar regions; however, specimens of *Neotanais affinis*, *N. americanus*, and *N. antarcticus* are now known from Antarctic waters. Whether neotanaids will be collected in the Arctic Ocean remains to be seen.

It is almost certain that at least some species are not ubiquitous. The Gay Head–Bermuda Transect has been sampled well enough so that most Pacific species (e.g., *Neotanais armiger*, *N. robustus*, *N. calcarulus* or European species (*N. peculiaris*, *N. laevispinosus*) should have been collected if they were present.

TABLE 12.—*Geographic distribution of the Neotanaidae*

Species	Atlantic Ocean North West	Atlantic Ocean North East	Atlantic Ocean South West	Atlantic Ocean South East	Pacific Ocean North West	Pacific Ocean North East	Pacific Ocean South West	Pacific Ocean South East	Indian Ocean
Neotanais micromopher	X	X							
N. dinotomer	X								
N. americanus	X	X	X					X?	
N. sandersi	X	X						X?	
N. laevispinosus		X							
N. mesostenoceps				X					
N. hadalis		X	X				X		
N. robustus							X		
N. antarcticus									X
N. bulbodens								X	
N. affinis	X	X	X						X
N. vemae					X				
N. peculiaris		X							
N. pfaffi						X		X	
N. giganteus	X	X					X		
N. pfaffioides									X
N. armiger	X					X		X	
N. hastiger	X	X		X		X			
N. tricarinatus			X						
N. calcarulus						X		X	
N. barfoedi							X		
N. bacescui									X
N. hessleri							X		
N. insolitus	X								
N. wolffi					X				
Herpotanais kirkegaardi							X		
Carololangia mirabunda	X								
Venusticrus glandurus	X								

Vertical Distribution

The Neotanaidae is characteristically a deep-sea family; no neotanaid has been found at depths of less than 200 m. In 1956, Wolff (1956a:232) wrote:

... it is an exceedingly pronounced deep-sea and cold water family, no doubt one of the most abysso-hadal families or larger taxons of marine invertebrates to be found: except for [a single] specimen it has been recorded only from depths

exceeding 2000 m and at temperatures below 3.3°C. The average of the total of 22 depth records is 3600 m.

Since Wolff made his study, the deep-sea benthos has been more intensively sampled than ever before, and numerous depth records have been added to those that were available to him (Table 13; Figure 95). However, of the 167 stations from which the family has now been collected, the mean depth is 3110 m, still about the same.
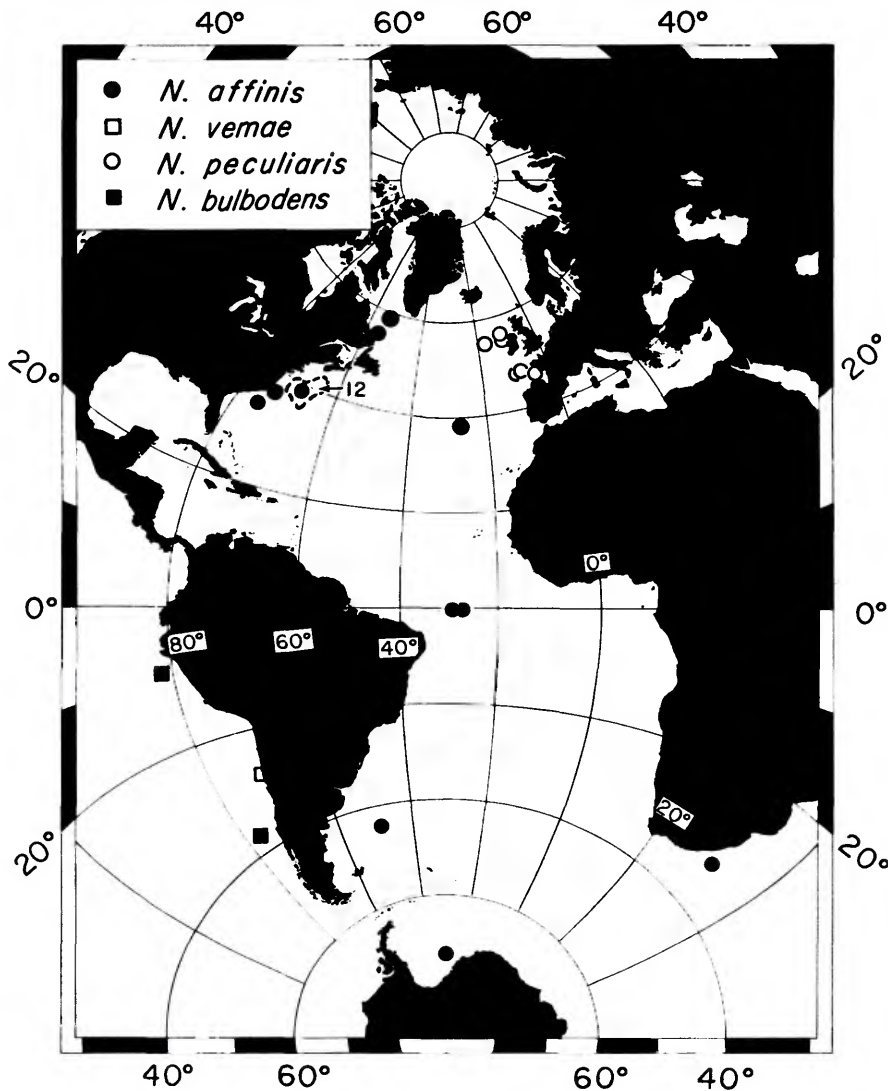
FIGURE 98.—Known distribution of *Neotanais affinis*, *N. bulbodens*, *N. peculiaris*, and *N. vemae*.

Although the Neotanaidae is still indisputably a deepwater taxon, a number of records have been obtained from relatively shallow locations. Whereas in 1956 the holotype of *Neotanais laevispinosus* (677 m) was the only record at a depth of less than 2000 m, *N. tricarinatus* has now been collected at 770 to 805 m and 587 m off Recife, Brazil; *N. armiger* from 1550 to 1740 m, 938 m, and 598 m in the Florida–Gulf of Mexico area; *N. sandersi* at depths as little as 824 m on the Gay Head–Bermuda Transect; and *N. americanus* at 1447 m, 570 m, and 513 m in Antarctica.

The shallowest records, however, are those of *Neotanais antarcticus* from Antarctic waters: 390 to 410 m, 397 m, and 223 m. These polar records are particularly interesting because the distributions of many deepwater forms have been shown

to be elevated at high latitudes (Ekman, 1953:175, 308); species that are found in relatively deep water elsewhere may occur at limited depths in high latitudes, The shallowest records for *N. americanus* elsewhere are 2670 m south of Grand Canary Island and 2802 m on the Gay Head–Bermuda Transect.

Whether *Neotanais antarcticus* demonstrates "polar emergence" cannot be determined at present because of our limited knowledge of the distribution of this species. However, if *N. americanus* occurred at depths of less than 2800 m on the Gay Head–Bermuda Transect, there is a strong probability that it would have been collected, considering the number of samples taken at lesser depths. In this case, the only doubt raised is whether the Antarctic specimens, which exhibit certain mor-
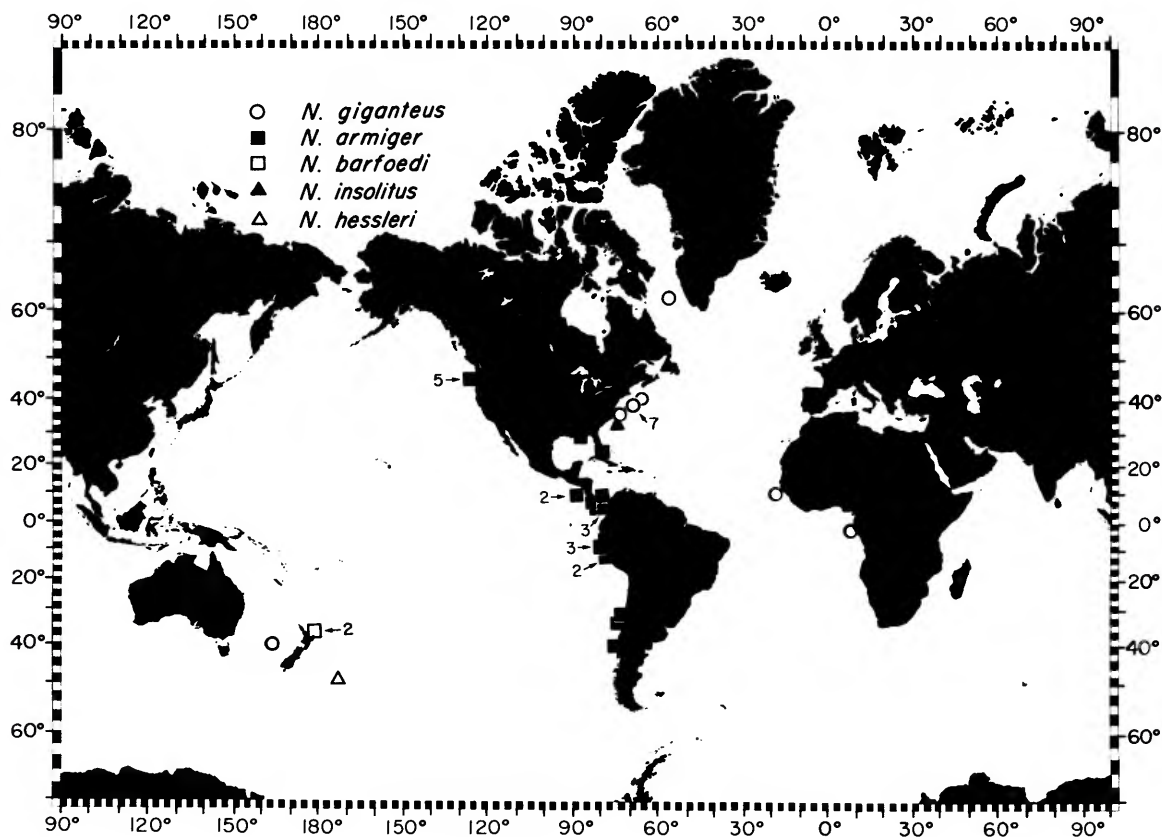
FIGURE 99.—Known distribution of *Neotanais armiger*, *N. barfoedi*, *N. giganteus*, *N. hessleri*, and *N. insolitus*.

phological differences from the North Atlantic populations of *N. americanus,* are conspecific with them.

It is not certain that *Neotanais tricarinatus* and *N. armiger* do not occur at even shallower depths in low latitudes; the Continental Slope of both Brazil and the Gulf of Mexico have been poorly sampled. The U.S. Geological Survey has conducted an intensive survey of the Continental Shelf and Slope of the eastern United States. About 1400 samples were taken over the Continental Shelf and 600 on the Slope and Blake Plateau, a total area of 662,000 km^2 (Emery, 1966). I have examined all tanaidaceans collected by this program. No neotanaids were collected at depths of less than about 2300 m except for a single station at 1865 m (*N. affinis*) and the specimen of *N. ar-*

miger from 598 m.

The known depth range for the family is 223 m (*Neotanais antarcticus*) to 8300 m (*N. hadalis*). If the deep sea is arbitrarily divided into bathyal (200 to 2000 m), abyssal (2000 to 6000 m), and hadal (below 6000 m) zones (Hedgpeth, 1957), 10 species of neotanaids are known to occur in the bathyal, 24 in the abyssal, and four in the hadal zone. Two species, *N. dinotomer* and *N. tricarinatus,* are known from the bathyal zone alone; seven species are found in both the bathyal and abyssal zones, and 15 are found only in the abyssal region. *Neotanais hadalis* is both abyssal and hadal in distribution, *N. wolffi* and *Herpotanais kirkegaardi* are known only from the hadal zone, and *Neotanais armiger* ranges all the way from the bathyal to the hadal zones.
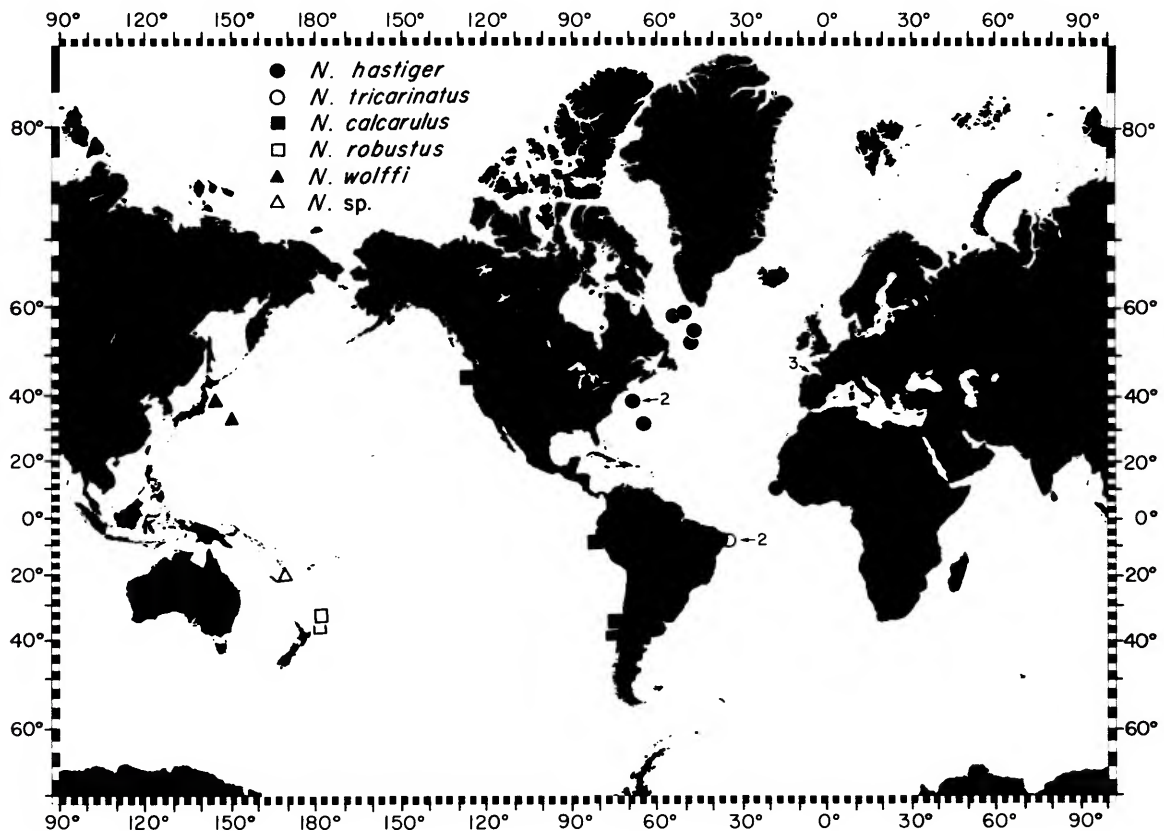
FIGURE 100.—Known distribution of *Neotanais calcarulus, N. hastiger, N. robustus, N. tricarinatus, N. wolffi,* and *Neotanais* sp. of Kudinova-Pasternak (1966).

In a comparison of supposedly archaic forms, Wolff (1956a:235) noted that the Neotanaidae were, with one exception (*Neotanais laevispinosus*), an exclusively abyssal family, in contrast with the bathyal distribution of "most of the living fossils of the deep-sea." However, bathyal distributions are now known for *N. sandersi, N. hastiger, N. affinis, N. dinotomer, N. antarcticus, N. peculiaris, N. armiger, N. tricarinatus,* and *Carololangia mirabunda.*

Sampling in areas other than the Gay Head–Bermuda Transect has been so erratic that almost all inferences drawn from these data regarding depth ranges are meaningless. For this reason, I do not believe we can yet speak dogmatically of species being restricted to, for example, the hadal zone (see Wolff, 1956a:235). The two species known exclusively from depths below 6000 m, *Neotanais wolffi* and *Herpotanais kirkegaardi,* have been collected from two stations and one station, respectively.

Figure 95 shows ranges in depths for species known to occur on the Transect. *Neotanais sandersi, N. hastiger,* and *N. affinis* have ranges of about 3000 to 3500 m, although the range of *N. sandersi* is extended from about 2200 m (GHTB) by two specimens of uncertain identity from the Pacific.

Neotanais giganteus, N. americanus, and *Carololangia mirabunda* have known ranges of about 2300 to 2700 m. (*Carololangia mirabunda* is known from only two stations.)

Neotanais micromopher is known from 31 stations in the western North Atlantic but ranges over a depth of only 1852 m, relatively little more than its range on the Gay Head–Bermuda Transect. Because of its frequency of occurrence in samples, its known range may indicate that its depth distribution in this area is comparatively restricted; however, inclusion of the single European specimen increases its depth range to 2461 m.

The known depth ranges for *Neotanais hadalis* and *N. armiger* are about 3600 m and 5500 m, respectively. The taxonomic situation in *N. armiger* (q.v.) is confused, and there is reason to think that more than one species may be represented among the collections, although it has been impossible to distinguish them.

Hessler (1970) found a depth range of over 2500 m for only two of his 39 species of desmosomatid isopods on the Gay Head–Bermuda Transect; most ranges were much more restricted. In contrast, of the nine species of neotanaids known from the Transect, three have a range of 2500 m or more on the Transect, and the range of *Neotan-*

TABLE 13.—*Vertical distribution (in meters) of species of neotanaids not found on the Gay Head–Bermuda Transect*

Species	Depth			No. stations	No. specimens
	Minimum	Maximum	Mean		
Neotanais laevispinosus	677	2379	1702	3	4
N. mesostenoceps	—	2934	—	1	1
N. hadalis	4707	8300	3593	6	11
N. robustus	4410	4570	160	2	11
N. antarcticus	223	410	187	3	3
N. bulbodens	4116	4423	307	2	6
N. vemae	—	5657	—	1	1
N. peculiaris	1680	2523	843	6	14
N. pfaffi	2599	3950	1351	5	50
N. pfaffioides	—	2780	—	1	1
N. armiger	598	6134	5536	20	102
N. tricarinatus	587	805	218	2	35
N. calcarulus	2838	4423	393	4	8
N. barfoedi	2470	2640	170	2	2
N. basescui	—	4040	—	1	1
N. hessleri	—	5340	—	1	1
N. insolitus	—	4460	—	1	1
N. wolffi	6126	6207	81	2	4
Herpotanais kirkegaardi	6960	7000	40	1	41

ais americanus is 2438 m. At present, it is not possible to say whether there is a real difference between these families with respect to depth tolerance. Of Hessler's 39 species, only six were known from five or more stations, whereas six of nine neotanaid species occurred that often in the collections. In other words, the artifactual dependency of known vertical range on sample frequency among the desmosomatids cannot be ruled out.

The fact that not all species of neotanaids are found all along the Transect and that vertical zonation occurs is illustrated by two very numerous species, *Neotanais americanus* and *N. sandersi*. The latter range from 824 to 2864 m (14 samples), and it is immediately replaced by *N. americanus* (20 samples), which ranges downward from 2802 m. Although these species have been collected at many other stations, the additions to the lower and
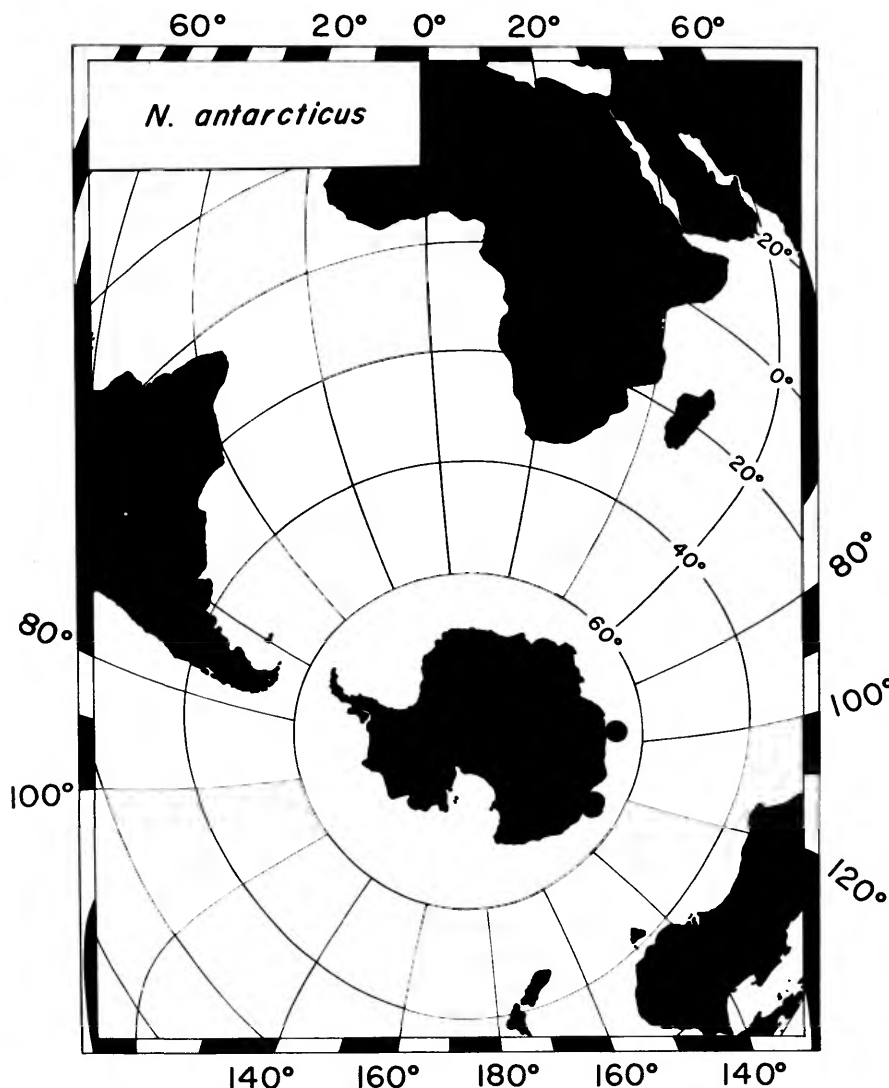
FIGURE 101.—Known distribution of *Neotanais antarcticus*.

upper limits of these ranges, respectively, from other localities in the Gay Head–Bermuda Transect area are trivial.

Insular Faunas

Species can only become distributed over great distances and still maintain their specific status if some mechanism is present to insure an adequate rate of gene flow among their populations. Even though certain neotanaid species (e.g., *Neotanais americanus, N. armiger,* and *N. giganteus*) are known to be very sidely distributed geographically, they display relatively minimal morphologic differences throughout their ranges. Other species, such as *N. hastiger,* demonstrate relatively greater variation (see intraspecific variation under the

various species). These apparent differences in degree of variation among species probably are due both to variable rates of gene flow among their populations—possibly ultimately related to current systems—and to differences in the inherent morphologic lability of the species.

Differences in vertical distribution among species and in different areas probably are related to a species' range of physiological tolerance to environmental stresses. Species may be able to extend their ranges upward or downward in certain areas to a greater or lesser extent as their tolerance to the environment changes.

The shallow marine faunas of oceanic islands are known to differ from those of the nearest continents, various numbers of species being endemic (e.g., see Barnard, 1970). It is of interest to com-
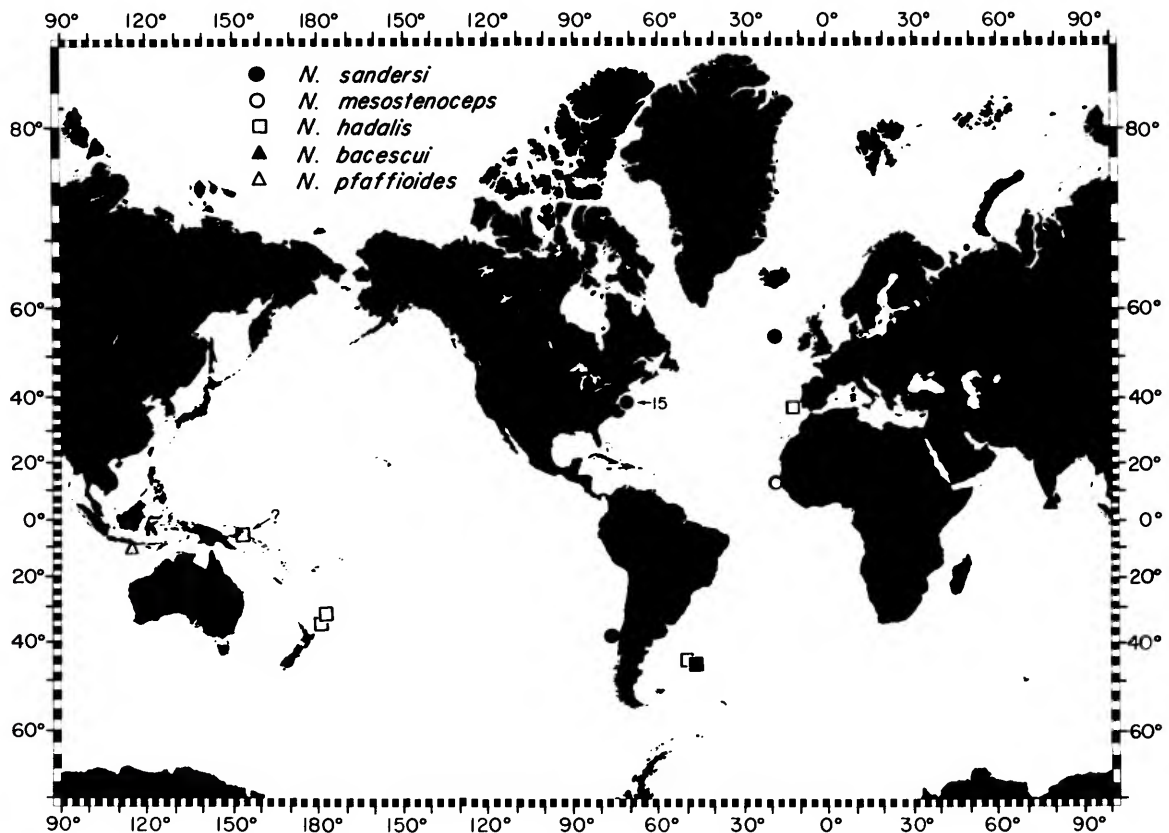
FIGURE 102.—Known distribution of *Neotanais bacescui, N. hadalis, N. mesostenoceps, N. pfaffioides,* and *N. sandersi.*

pare the known neotanaid fauna of Bermuda with that of the North American portion of the Gay Head–Bermuda Transect in order to determine whether a similar endemism is present among the deep-sea benthos. Unfortunately, unusual sampling difficulty experienced on the Bermuda Slope has greatly limited the number of available epifaunal specimens.

A single specimen of *Carololangia mirabunda* was collected on the Bermuda Slope at 2000 m. This individual was small and in poor condition and could not be thoroughly compared with the North American holotype. A few differences between the two individuals are noted for this species in the section on "Systematics" (see also Figure 76D,E).

Two specimens of *Neotanais hastiger* were col-

lected at 2500 m on the Bermuda Slope. They differ from individuals collected on the North American Slope in the number and size of the anterolateral setae of the carapace (Figure 56A,B, E); the size and shape of pleonal hairs (Figure 56A,F,H); the presence or absence of short, propodal spines on pereopod VII; the shapes of the anterior propodal setae of pereopods II–IV (Figure 59G,H); and the dentition of the chelae (Figure 58F,G). This is a remarkable series of differences for a geographic displacement of only several hundred kilometers, and is particularly interesting because animals from the Greenland area agree with those from the Continental Slope in the North American Basin but are separated from them by a much greater distance.
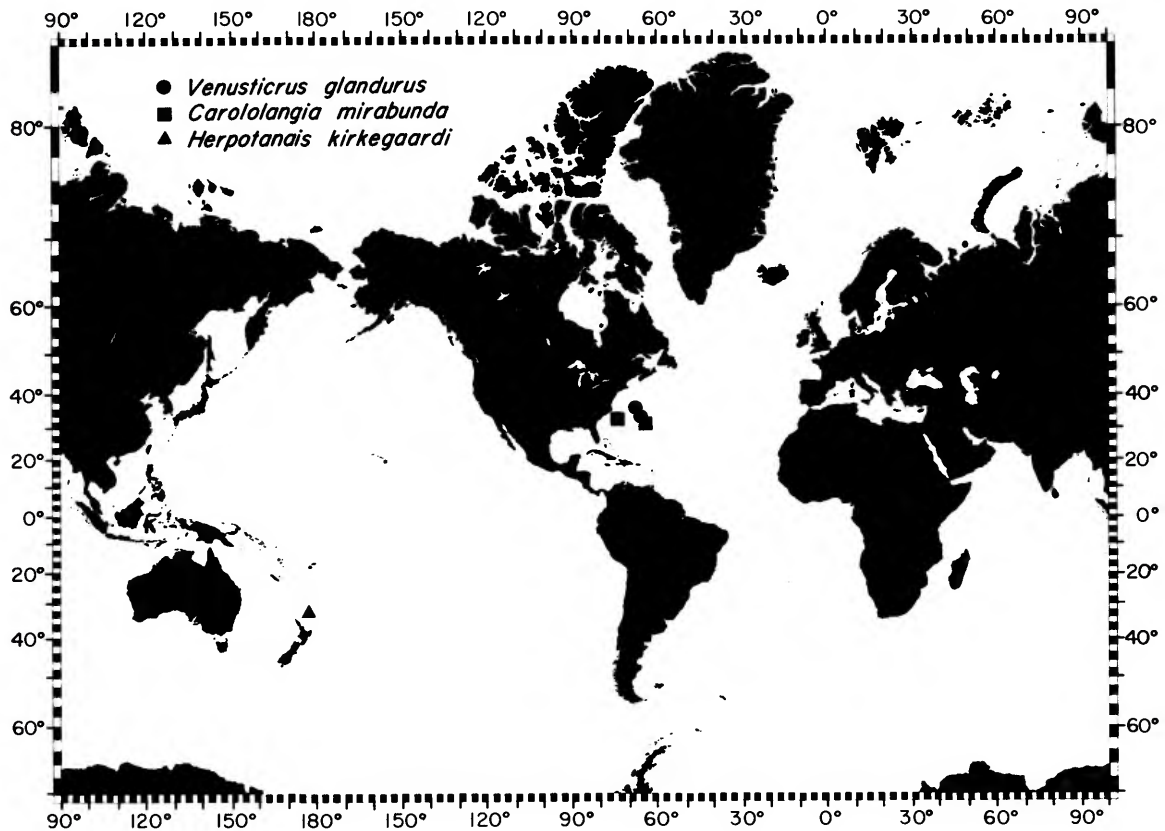
FIGURE 103.—Known distribution of *Herpotanais kirkegaardi, Carololangia mirabunda,* and *Venusticrus glandurus.*

Neotanais dinotomer is known from the Bermuda Slope alone (1000 to 1700 m) although it is closely related to *N. micromopher*, found on the Continental Slope. Whether *N. dinotomer* will be found elsewhere remains to be seen.

Although the available data are insufficient to demonstrate a clear pattern of faunal differences between Bermuda and the North American Continental Slope, they are at least consistent with such a hypothesis. I will return to this topic after examining other deepwater tanaidacean taxa from the Gay Head–Bermuda Transect.

TABLE 14.—*Neotanaid body sizes (in millimeters) and depths (in meters), with sizes based on actual or estimated maximum body lengths of adults*

Size group (largest Cop ♂)	Species	Worldwide depth range	Number of species at following depth ranges:							Largest individual		No. stations	No. individuals
			200–1000	1000–2000	2000–3000	3000–4000	4000–5000	5000–6000	>6000	Size	Stage		
Group 1 (<7.0)	*Neotanais tricarinatus*	587–805								4.6	Cop ♂	2	35
	N. dinometer	1000–1700								6.6	Cop ♂	6	40
			2	1	0	0	0	0	0				
			66.6%	33.3%									
Group 2 (7.5–9.5)	*N. micromopher*	2268–4729								8.6	Cop ♂	32	319
	N. americanus	513–5340								9.0	Cop ♂	40	192
	N. sandersi	824–3017								9.3	Cop ♂	20	50
	N. laevispinosus	677–2379								7.5	P ♀2	3	4
	N. antarcticus	233–410								8.5	Cop ♀	3	3
	N. bulbodens	4116–4423								7.8	Cop ♂	2	6
	N. vemae	5657								7.0	P ♀1	1	1
	N. peculiaris	1680–2523								9.2	Cop ♂	6	14
	N. bacescui	4040								7.2	P ♀1	1	1
	N. insolitus	4460								5.6	Juv	1	1
			4	4	5	3	5	2	0				
			17.4%	17.4%	21.7%	13.0%	21.7%	8.7%					
Group 3 (10.5–13.0)	*N. mesostenoceps*	2934								10.8	Cop ♂	1	1
	N. affinis	1835–5532								12.2	Juv?	23	51
	N. armiger	598–6134								11.4	Cop ♂	20	102
	N. hastiger	2500–3834								9.6	Cop ♀	12	31
	N. calcarulus	2838–4423								12.0	Cop ♀	4	8
	N. hessleri	5340								3.8	M1	1	1
	Venusticrus glandurus	4680–4950								8.9	P ♀1	2	2
	Carololangia mirabunda	2000–4690								11.8	P ♂	2	2
			1	3	6	5	5	3	1				
			4.2%	12.5%	25.0%	20.8%	20.8%	12.5%	4.2%				
Group 4 (>15.0)	*N. hadalis*	4707–8300								20.0	P ♂	6	11
	N. robustus	4410–4570								22.1	Cop ♂	2	11
	N. pfaffi	2599–3950								22.1	Cop ♀	5	50
	N. giganteus	2478–3861								22.3	P ♀2?	13	56
	N. pfaffioides	2780								22.0	Cop ♀	1	1
	N. barfoedi	2470–2640								17.3	P ♂	2	2
	N. wolffi	6126–6207								15.6	" ♀ "	2	4
	Herpotanais kirkegaardi	6960–7000								24.5	P ♀2?	1	41
			0	0	4	2	2	1	3				
					33.3%	16.7%	16.7%	8.3%	25.0%				

Deep-sea and Antarctic "Gigantism"

Wolff has suggested that the deep-sea isopods (Wolff, 1956b, 1962) and the "apseudid" Tanaidacea (Wolff, 1956a) often display increased body length with depth. He (Wolff, 1956a:234) did not comment on the vertical distribution of neotanaid species because his material was too limited.

Many more species and depth records are now available for the Neotanaidae. Their maximum body lengths and the depths at which they have been found are presented in Table 14. If a copulatory male was not available, an estimate of maximum body size was made by comparing the largest available specimen with other, well-known species. The species are grouped in four size categories, and the frequencies of occurrence of the species in each group at various depths are compared.

Several interesting features are apparent. The smallest species, *Neotanais tricarinatus* and *N. dinotomer*, are found in relatively shallow water and are not known below 2000 m. In group 2, 34.8 percent of the total "occurrences" are above 2000 m; a few occurrences, 8.7 percent, are between 5000 m and 6000 m; and no species is found below 6000 m.

In group 3, occurrences above 2000 m have dropped to 16.7 percent, a few more species lie between 5000 m and 6000 m, and one is found below 6000 m.

In group 4, no species is represented above 2000 m, whereas 33.3 percent of occurrences are below 5000 m, 25 percent of these being below 6000 m.

Caution must be exercised when interpreting these data; the number of species is limited, and many of these are known from only a small number of individuals at a few localities. The shallow records for *Neotanais americanus* and *N. antarcticus* (group 2) may be biased due to the phenomenon of polar emergence. The shallow depth listed for *N. armiger* (group 3) may be prejudiced by the taxonomic difficulties involving that species. The shallowest records for *N. armiger* (Florida–Gulf of Mexico) are of animals markedly smaller than those from many other areas (but they are not the smallest).

Because of depth ranges commonly from 2500 to 3500 m, a majority of species should occur in midrange; in addition to species whose depth optima lie there, the ranges of species whose optima are above and below this level will often overlap the midrange area.

The collecting methods of the *Galathea* Expedition were such that the loss of smaller animals was greater than, for instance, that resulting from the methods used at Woods Hole (Sanders, Hessler, and Hampson, 1965; Hessler and Sanders, 1967). Lang (1968) remarks that the *Galathea* collections were not as rich in small specimens as the *Vema* samples which he had examined.

Table 14 indicates the species collected by the *Galathea*, those collected exclusively by the *Galathea*, and those collected in part or entirely by the Sanders-Hessler-Hampson techniques. It is readily apparent that more of the larger species were collected by the former expedition, whereas the reverse is true for the Woods Hole group. The *Galathea* may have lost more of the smaller animals. On the other hand, the *Galathea* often dredged deeper areas than, for instance, the Gay Head–Bermuda Transect (maximum depth, 5200 to 5400 m). If very large species were present on the Transect, the epibenthic sled probably would have collected them.

A trend is possibly indicated by the data in Table 14: the smallest species are known only from very shallow water, and some of the largest species are known from very deep water. Nevertheless, a definitive statement on the relationship between size and depth among the Neotanaidae must await the collection of additional material.

The claim of increased size or "overgrowth" in Antarctic waters (Wolff, 1956b, 1962) is not borne out by the presently available data for the Neotanaidae. The only species known to occur in the Antarctic, south of 60° latitude, are *Neotanais affinis*, *N. americanus*, and *N. antarcticus*, of which two fall in size group 2 and one in group 3. Wolff also found small species of isopods (Wolff, 1962) and "apseudids" (Wolff, 1956a) living in the Antarctic.

Period of Reproduction

Few data are available in the literature concerning seasonal effects on reproductive patterns among the deep-sea fauna. The usual difficulties encountered in obtaining samples of more than a few individuals has made analysis of populations

difficult. Moreover, most deep-sea dredging has been carried out during the warm summer months when work is least arduous. Consequently, relatively few late autumn, winter, or early spring samples are available.

The deep sea, at least the abyssal zone, has been thought to be an aseasonal environment. "Certainly at depths below 2,000 metres, the seasons, so far as they are marked by changes of temperature and light, cease to exist" (Marshall, 1954). It is possible that reproduction will occur more or less continuously throughout the year in an asea-

TABLE 15.—*Seasonal occurrences (summer, June–August; autumn, September–November; winter, December–February; spring, March–May) of young stages, copulatory males, and females with marsupia in certain species of* Neotanais

Species	Season	Date	Depth (meters)	Brood pouch embryo	M1	M2	Cop ♀ with marsupium	Cop ♂	Station (and approximate area*)
N. micromopher	Summer	09 Aug.	2900				1	1	WHOI 112
		20 Aug.	2886		2	7		7	WHOI 64
		20 Aug.	2891		1				WHOI 65
		20 Aug.	2802		4	2		3	WHOI 66
		24 Aug.	2864			2	2	1	WHOI 72
	Autmun	01 Sept.	3316		1	2	1		*Albatross* 2570 (near GHBT)
		28 Oct.	4729		1				*Noratlante* 111 (Bay of Biscay)
		07 Nov.	3057		1				*Eastward* 6228 (SE of Cape Hatteras)
	Winter	17 Dec.	3753			1	1		WHOI 95
	Spring	21 May	2900		3				WHOI HH 3
N. sandersi	Summer	21 Aug.	2496			2			WHOI 62
	Autumn	09 Sept.	2021			1			WHOI G 9
	Winter	16 Dec.	1254		1				WHOI 128
	Spring	04 May	2022		1				WHOI 103
		24 May	2000		1				WHOI G 7
N. affinis	Autumn	06 Sept.	2158				1		WHOI G 7
		09 Sept.	2021			1			WHOI G 9
	Winter	18 Dec.	2178		1				WHOI 131
	Spring	04 May	2022		1				WHOI 103
		24 May	2000		1				WHOI G 7
N. americanus	Summer	20 Aug.	2891		1	2			WHOI 63
		20 Aug.	2886		1			7	WHOI 64
		20 Aug.	2891		7				WHOI 65
		20 Aug.	2802		6	3	1	3	WHOI 66
	Autumn	01 Sept.	3316				1		*Albatross* 2570 (Near GHBT)
		07 Nov.	3057				1		*Eastward* 6228 (SE of Cape Hatteras)
	Spring	21 May	2900		1	1		1	WHOI HH 3
Neotanais sp.	Winter	18 Dec.	2178	2†					WHOI 131
N. peculiaris	Autumn	01 Nov.	1913			1		1	*Noratlante* 126 (W of France)
N. armiger	Autumn	10 Nov.	938					1	*Vema* 15–21 (Caribbean Sea)
	Winter	24 Jan.	2800				1		OSU AD33 (W of Oregon)
	Spring	26 Mar.	2840				1		OSU AD155 (W of Oregon)
		29 Mar.	2400		1		1		OSU AD163 (W of Oregon)
		29 Mar.	2400				1		OSU AD164 (W of Oregon)
		06 May	3570				2		*Galathea* 716 (W of Costa Rica)
		13 May	3270–3670				3		*Galathea* 726 (Gulf of Panama)

* See Table 1 for more detail. All WHOI stations at Gay Head–Bermuda Transect (GHBT).

† Not identifiable as to species, but possibly *N. affinis,* also found at WHOI Sta. 131.

TABLE 16.—*Basic data for stages of* Neotanais micromopher, *new species, from WHOI Benthic Station 64* (statistics are in italics; see Figure 2A–G for methods of measurement)

Stage	Animal	Body length (mm)	Length of pleopodal endopod (mm)	Oostegite Width (mm)	Oostegite Length (mm)	No. articles in Up endopod L	No. articles in Up endopod R	Male GpAn*	Oosteg. scars*
M1	CL	2.6				4	4	0	0
	CM	Broken				4	4	0	0
M2	CA	3.8				6	–	0	0
	CB	3.7				6	6	0	0
	CC	3.8				6	6	0	0
	CD	3.7				6	6	0	0
	CE	3.6				6	5	0	0
	CF	3.6				6	6	0	0
	CG	3.4				6	6	0	0
	N	*7*							
	x̄	*3.65±0.13*							
	s	*0.14*							
	C	*0.038*							
Juv.	BD	4.7	.19			7	7	0	0
	BE	4.5	.18			7	7	0	0
	BG	4.8	.18			6	6	0	0
	BI	4.6	.22			7	7	0	0
	BK	4.4	.17			6	6	0	0
	BL	4.3	.20			7	6	0	0
	BM	4.3	.17			6	6	0	0
	BN	4.4	.16			6	6	0	0
	BP	4.7	.16			6	6	0	0
	BR	4.7	.18			7	7	0	0
	BS	4.7	.22			7	7	0	0
	BW	4.7	.18			7	6	0	0
	BX	4.1	.17			7	6	0	0
	N	*13*							
	x̄	*4.53±0.13*							
	s	*0.21*							
	C	*0.047*							
P♀1	E	5.8	.27	.08	.13	7	7	0	0
	K	6.2	.29	.10	.12	8	8	0	0
	N	6.1	.30	.10	.14	7	7	0	0
	Q	4.9	.21	.06	.08	7	7	0	0
	R	5.6	.25	.08	.10	8	8	0	0
	W	5.1	.23	.07	.10	7	7	0	0
	Z	5.1	.19	.07	.09	7	6	0	0
	BF	5.2	.19	.07	.11	7	7	0	0
	BH	4.9	.17	.03	.05	–	7	0	0
	BJ	5.0	.22	.06	.07	7	7	0	0
	BO	4.9	.19	.06	.08	7	7	0	0
	BQ	4.9	.21	.05	.05	7	7	0	0
	BT	5.2	.23	.05	.07	7	7	0	0
	BU	5.0	.20	.07	.08	7	7	0	0
	BV	5.8	.28	.08	.12	7	8	0	0
	N	*15*							
	x̄	*5.31±0.26*	*.229±.023*	*.069±.010*	*.093±.015*				
	s	*0.46*	*.041*	*.018*	*.028*				
	C	*0.087*	*.178*	*.269*	*.298*				

TABLE 16.— (Continued)

Stage	Animal	Body length (mm)	Length of pleopodal endopod (mm)	Oostegite Width (mm)	Oostegite Length (mm)	No. articles in Up endopod L	No. articles in Up endopod R	Male GpAn*	Oosteg. scars*
P ♀ 2	B	6.4	.30	.19	.38	8	8	0	0
	D	6.1	.29	.18	.35	8	8	0	0
	F	6.9	.30	.17	.39	7	8	0	0
	G	6.4	.28	.16	.36	6	6	0	0
	H	.67	.28	.16	.35	7	7	0	0
	I	6.6	.28	.18	.34	8	8	0	0
	J	6.3	.28	.19	.31	7	7	0	0
	L	6.4	.28	.19	.34	8	8	0	0
	M	6.0	.25	.17	.31	7	7	0	0
	O	5.9	.30	.18	.30	7	8	0	0
	P	6.4	.31	.18	.35	8	8	0	0
	S	6.1	.27	.18	.29	7	7	0	0
	T	5.9	.23	.16	.26	7	7	0	0
	U	6.5	.29	.17	.35	8	8	0	0
	V	6.3	.28	.18	.36	7	8	0	0
	X	6.5	.27	.18	.35	7	7	0	0
	Y	6.4	.29	.18	.32	7	–	0	0
	N	17							
	$\bar{x}$	6.34±0.14	.281±.010	.176±.005	.336±.017				
	s	.27	.019	.010	.033				
	C	.043	.069	.057	.099				
Cop ♀	AB	7.9	.53			8	8	0	+
	AC	7.3	.44			8	9	0	+
	AI	6.9	.43			8	8	0	+
	AJ	7.1	.46			8	8	0	+
	BA	7.0	.46			8	8	0	+
	N	5							
	$\bar{x}$	7.24±0.49	.464±.049						
	s	.40	.039						
	C	.055	.084						
Int. ♀	Type	7.6	.48	.13	.25	9	9	0	0
	C	7.5	.39	.21	.41	9	–	0	0
P ♂	AA	6.2	.39			8	8	+	0
	AD	6.3	.44			8	8	+	0
	AE	6.7	.46			8	8	+	0
	AF	6.7	.42			7	7	+	0
	AG	6.2	.40			8	8	+	0
	AH	5.7	.39			7	–	+	0
	AI	5.0	.29			8	8	+	0
	N	7							
	$\bar{x}$	6.11±0.53	.399±.050						
	s	.60	.055						
	C	.098	.137						
Cop ♂	AP †	8.1	.65			9	9		0
	AQ ‡	7.6	.63			9	9		0
	AR †	8.1	.65			–	9		0
	AS †	8.0	.65			9	9		0
	AT †	7.2	.60			9	9		0
	AU ‡	5.2	.41			7	7		0
	AV ‡	5.6	.43			6	7		0

* 0, absent; +, present.   † Chela type B.

‡ Chela type A. Animal AQ had certain chela type B characters on the right chela.

TABLE 17.—*Basic data for stages of* Neotanais micromopher, *new species, from* WHOI Benthic Station 76 (statistics are in italics; see Figure 2A–G for methods of measurement)

Stage	Animal	Body length (mm)	Length of pleopodal endopod (mm)	Oostegite Width (mm)	Oostegite Length (mm)	No. articles in Up endopod L	No. articles in Up endopod R	Male GpAn*	Oosteg. scars*
Juv.	DF	4.1	.16			7	6	0	0
	DK	4.3	.18			7	7	0	0
	DL	4.3	.19			6	6	0	0
	DN	4.8	.21			7	7	0	0
	DO	4.6	.22			7	–	0	0
	DS	4.2	.17			6	6	0	0
	DX	4.5	.19			7	7	0	0
	DY	4.3	.18			7	7	0	0
	DZ	4.2	.17			7	7	0	0
	EA	4.4	.22			7	7	0	0
	EK	4.7	.18			6	6	0	0
	EQ	4.4	.18			–	6	0	0
	EU	4.4	.17			7	7	0	0
	EX	4.7	.18			–	7	0	0
	EY	4.2	.19			–	6	0	0
	N	*15*							
	x̄	*4.41±0.12*							
	s	*.21*							
	C	*.048*							
P♀1	DA	5.0	.18	.05	.06	–	–	0	0
	DI	4.3	.20	.05	.05	7	7	0	0
	DR	4.6	.16	.05	.06	7	–	0	0
	DW	4.6	.19	.05	.08	7	7	0	0
	EF	4.5	.16	.07	.08	7	7	0	0
	EG	5.3	.25	.08	.09	8	8	0	0
	EJ	4.6	.15	.05	.06	–	7	0	0
	EN	4.6	.19	.06	.08	–	–	0	0
	EO	4.5	.19	.05	.08	–	7	0	0
	ER	4.6	.18	.04	.06	–	–	0	0
	EW	4.5	.18	.05	.05	7	7	0	0
	EZ	4.5	.20	.05	.07	7	7	0	0
	FB	5.3	.24	.08	.09	7	8	0	0
	FE	5.6	.25	.06	.10	7	–	0	0
	FF	5.3	.26	.07	.11	8	8	0	0
	FI	5.4	.26	.09	.12	–	7	0	0
	FS	5.3	.25	.08	.10	8	8	0	0
	GG	4.3	.19	.04	.04	7	7	0	0
	N	*18*							
	x̄	*4.82±0.21*	*.204±.018*	*.059±.008*	*.077±.011*				
	s	*.43*	*.037*	*.015*	*.022*				
	C	*.088*	*.180*	*.255*	*.290*				
P♀2	DQ	5.9	.28	.18	.34	–	–	0	0
	EB	5.8	.29	.17	.32	6	6	0	0
	EE	6.0	.26	.17	.34	7	7	0	0
	FA	5.7	.28	.18	.30	7	7	0	0
	FC	6.3	.29	.20	.32	8	8	0	0
	FD	5.9	.27	.17	.29	7	8	0	0
	FG	5.6	.27	.18	.29	–	–	0	0
	FH	6.0	.29	.18	.33	7	8	0	0

TABLE 17.— (Continued)

| Stage | Animal | Body length (mm) | Length of pleopodal endopod (mm) | Oostegite | | No. articles in Up endopod | | Male GpAn• | Oosteg. scars• |
				Width (mm)	Length (mm)	L	R		
	FJ	5.7	.26	.19	.31	8	8	0	0
	FK	5.8	.27	.19	.28	–	–	0	0
	FL	6.0	.29	.17	.33	–	–	0	0
	FM	5.9	.27	.17	.33	7	–	0	0
	FN	6.6	.32	.19	.37	8	8	0	0
	FO	6.0	.29	.19	.29	–	8	0	0
	FP	5.9	.27	.17	.31	–	7	0	0
	FQ	6.1	.30	.18	.34	8	8	0	0
	FR	6.1	.29	.19	.30	8	8	0	0
	FT	5.9	.30	.17	.33	7	7	0	0
	FU	6.1	.30	.18	.33	8	8	0	0
	FV	5.6	.26	.16	.29	7	7	0	0
	FW	6.4	.30	.19	.31	8	8	0	0
	FX	6.0	.28	.18	.33	8	8	0	0
	FY	5.7	.26	.17	.29	8	8	0	0
	FZ	6.0	.27	.16	.28	–	8	0	0
	GA	6.0	.29	.17	.29	7	7	0	0
	GB	5.6	.29	.17	.31	–	7	0	0
	GC	5.8	.29	.18	.31	7	7	0	0
	GD	5.6	.30	.16	.30	7	7	0	0
	GE	6.3	.31	.18	.36	7	7	0	0
	GF	5.8	.28	.17	.28	–	8	0	0
	GH	6.1	.28	.17	.32	8	–	0	0
	N	31							
	$\bar{x}$	5.94±0.089	.284±.006	.177±.004	.314±.009				
	s	.24	.015	.010	.023				
	C	.041	.054	.057	.075				
Cop ♀	DC	7.1	.49			–	–	0	+
	DD	6.5	.43			–	–	0	+
	DE	6.7	.46			8	8	0	+
	DG	6.4	.45			9	9	0	+
	DH	6.2	.41			–	–	0	+
	DJ	6.3	.43			–	7	0	+
	DM	6.9	.44			8	8	0	+
	DP	6.6	.43			8	8	0	+
	ED	6.3	.40			8	8	0	+
	EL	7.2	.51			–	–	0	+
	EP	6.7	.43			–	8	0	+
	N	11							
	$\bar{x}$	6.63±0.22	.444±.022						
	s	.33	.033						
	C	.050	.074						
P ♂	DB	6.0	.36			3	8	+	0
	DT	5.8	.42			8	8	+	0
	DU	6.0	.42			8	8	+	0
	DV	6.4	.40			–	8	+	0
	EH	4.9	.35			7	7	+	0
	EI	5.7	.40			8	8	+	0
	EM	5.9	.38			–	8	+	0
	ES	5.3	.40			–	8	+	0

TABLE 17.— (Continued)

Stage	Animal	Body length (mm)	Length of pleopodal endopod (mm)	Oostegite Width (mm)	Oostegite Length (mm)	No. articles in Up endopod L	R	Male GpAn*	Oosteg. scars*
	ET	5.6	.41			–	–	+	0
	EV	5.2	.39			8	8	+	0
	N	10							
	x̄	5.67±0.32	.393±.017						
	s	.44	.024						
	C	.078	.060						
Cop ♂ ♂ (pooled)	HA †	6.4	.60			9	9		0
	HB †	6.1	.53			9	9		0
	HC †	5.9	.49			8+	8+		0
	HD †	6.6	.53			8	8		0
	HE †	5.0	.42			7	7		0
	HF ‡	7.2	.65			–	8+		0
	HG ‡	6.4	.58			9	9		0
	HH §	7.0	.60			9	–		0
	HI §	7.0	.59			8	9		0
	HJ §	8.0	.69			9	–		0

* 0, absent; +, present.
† Chela type A.
‡ Chelae missing.
§ Chela type B.

sonal biotope. Therefore, Schoener's (1968) evidence of apparent seasonal reproduction in certain deep-sea ophiuroids is particularly interesting. George and Menzies (1967, 1968) have proposed distinctly seasonal reproduction for certain deep-sea isopods. Unfortunately, the limited data available to them do not permit definitive conclusions. Insofar as is known, there is little additional data in the literature dealing with time of reproduction among the deep-sea fauna.

Information on the reproductive behavior of the Tanaidacea is also very limited. Bückle Ramírez (1965) has reported a markedly cyclic pattern of seasonal reproduction for the shallow-water paratanaid Heterotanais oerstedi. Similar seasonal changes have been noted for other shoal-water paratanaids.

Bückle Ramírez found only females, juveniles, and preparatory males present throughout the year in a population in the North Sea–Baltic Sea Canal near Kiel. Copulatory males were present only between the end of May and the latter part of September. By the end of June, these males

made up 70 percent of the population. They are secondary males and originate from copulatory females that have overwintered. Young are produced in early July, and some mancas remain in the population until late October. The mancas all die before winter; and only the females, juveniles, and preparatory males are able to overwinter.

Salvat (1967) found a different reproductive pattern for the monokonophoran Apseudes latreillii. Both adult males and "juveniles" (includes mancas) were present all year long in a population from Arcachon. The latter were especially abundant in November (72 percent of the population), December (61 percent), January (42 percent), and February (46 percent). Brooding females were collected throughout the period March to December; breeding was suspended for only two months.

It is impossible to say how much of the difference between the findings of Bückle Ramírez and Salvat is due to inherent biological differences between Heterotanais and Apseudes (or the Dikonophora and Monokonophora) and how much is due to environmental variation alone. Bǎcescu

(1961:160) reports finding ovigerous females of *Apseudes latreillii mediterraneus* collected on the coast of Israel on 14 December. The coldest water temperatures in winter recorded by Salvat for Arcachon were 7° to 8° C. Kiel is about 970 km (600 miles) north of Arcachon, and the water there is considerably colder in winter. Bückle Ramírez was able to raise copulatory males of

Heterotanais oerstedi throughout the year by keeping the animals at warm temperatures. Comparative winter observations of northern populations of *Apseudes* and southern populations of *Heterotanais* would be of great interest.

In order to make a comparison of the reproductive patterns of the deep-sea Tanaidacea with shallow-water forms for the first time, all collec-

TABLE 18.—*Basic data for stages of* Neotanais micromopher, *new species, from miscellaneous stations* (statistics are in italics; see Figure 2A–G for methods of measurement)

Stage	Station	Animal	Body length (mm)	Length of pleopodal endopod (mm)	No. articles in Up endopod Left	Right	Male GpAn[•]	Oosteg. scars[•]
M1	WHOI 66	GL	2.7		4	4	0	0
		GM	2.6		4	4	0	0
		GN	2.9		4	4	0	0
		GO	2.8		4	4	0	0
		N	*4*					
		$\bar{x}$	*2.75±0.21*					
		s	*.13*					
		C	*.047*					
	WHOI 65	—	2.9		4	4	0	0
M2	WHOI 66	GI	3.7		6	6	0	0
		GK	3.4		6	6	0	0
	WHOI 85	—	3.7 †		–	–	0	0
	WHOI HH 3	—	3.3 †		6	–	0	0
Juv.	*Ingolf* 22	—	4.3		6	5	0	0
P♀2	WHOI 65	—	6.9 †		8	8	0	0
	WHOI HH 3	—	6.3 †		8	8	0	0
Int. ♀	*Challenger* 45	—	6.7		–	–	0	0
Cop ♀	WHOI 72	—	7.6 †	.49	9	9	+	–
	WHOI 95	—	6.1 †	.41	8	7	0	–
Cop ♂ ♂ (pooled)	WHOI 66	—	7.1 ‡		8	8		0
		—	8.1 ‡		9	9		0
		—	7.6 ‡		9	9		0
	WHOI 72	—	6.1 §		9	9		0
	WHOI 112	—	6.9 ‡		9	9		0
		—	7.5 §		8	8		0
	CMS 2072	—	6.7 §		7	8		0
		—	6.6 §		9	9		0
	CMS 2118	—	7.3 ‡		9	9		0
	CMS 2125	—	7.3 §		9	9		0
	CMS 2144	—	8.3 ‡		8+	–		0
	CMS 2145	—	6.9 #		9	9		0
	CMS 2154	—	7.0 §		9	9		0

[•] 0, absent; +, present.
† Specimen sectioned for analysis of gonadal development.
‡ Chela type B.
§ Chela type A.
# Chelae missing.

tions containing neotanaids from periods other than the summer (Northern Hemisphere) were examined for possible indications of the reproductive pattern. Although the data are limited for any one species, one can make a number of interesting observations.

The results of the examination are summarized in Table 15. Most of the data are based on geographically restricted samples from the area of the Gay Head–Bermuda Transect. All records of animals clearly identifiable as mancas 1 and collected in autumn, winter, and spring months are included, as are copulatory females that bore marsupia. In addition, three copulatory males and two brood-pouch embryos—the latter the only ones known for the Neotanaidae—are included. In all of these species, where mancas, females with marsupia, or copulatory males were collected in the summer, these records also are included by way of comparison. In the case of *Heterotanais oerstedi* (Bückle Ramírez, 1965), which resembles the neotanaids in many respects, these are the stages absent in the winter. Neotanaid preparatory females, copulatory females without marsupia, and preparatory males are found throughout the year in the deep sea.

Also listed in Table 15 are miscellaneous records of females with marsupia and copulatory males collected in seasons other than the summer in the Northern Hemisphere (*Neotanais peculiaris* and *N. armiger*).

The data for *Neotanais micromopher* include mancas from the summer, early September, October (European), November, mid-December, and May. Copulatory females with marsupia were collected in August and early September as well as in mid-December. Mancas of *N. americanus* were collected only in May and August, but copulatory females with marsupia were obtained in August, early September, and November.

Mancas were collected in August, September, mid-December, and through May for *Neotanais sandersi*. Mancas of *N. affinis* were found in early September, mid-December, and early and late May, but only a single female with marsupium was available from early September.

The two brood-pouch embryos, possibly belonging to *Neotanais affinis*, also collected at WHOI B. Sta. 131 (as was *N. sandersi*), were obtained in mid-December.

TABLE 19.—*Typical patterns of pereopodal setation in* Neotanais micromopher, *new species*

Stage	WHOI benthic station	No. animals	Pp	Number of setae			
				Propodus		Carpus	
				Ant. row	Post. row	Ant. row	Post. row
M1	66	4	II	0	2	2	2
			III	0	2	1	2
			IV	0	2	1	2
			V	2	3	1	2
			VI	2	3	1	2
M2	64	2	II	1	2	3	2
	66	2	III	2	3	2	3
			IV	2	3	2	3
			V	3	3	2	2
			VI	3	3	2	2
			VII	0	0	0	0
Juv.	76	4	II	2	3	4	2
			III	4	4	2	4
			IV	4	4	2	4
			V	4	4	3	4
			VI	4	4	3-4	3
			VII	2	3	1	2
P♀2	76	4	II	3	3	3-4	3
			III	5	5	3-4	4-5
			IV	5	5	3	4
			V	5	4-5	3-4	4
			VI	5	5	4	4
			VII	3-4	4-5	2-3	2
Cop ♀	76	5	II	4-5	4-5	5	4
			III	5-6	5-7	2-3	5
			IV	5-6	5-7	2	5
			V	5	5	4-6	4-5
			VI	4-6	5-6	3-5	4-5
			VII	5	5-6	3-4	4-5
P♂	76	5	II	2-3	2-4	4	2-3
			III	5	5	2-3	1-4
			IV	4-5	5	2-3	3-4
			V	4	4	3-4	3-4
			VI	4-5	5	3-4	3-4
			VII	3-4	3-5	3	2
Cop ♂	64	1	II	4	4-5	4-5	3-4
(1°, 3*;	76	5	III	6-7	7-8	3	5
2°, 2)			IV	6	7-9	3	5
			V	6	6	5-6	4-5
			VI	6	6	4-5	4-5
			VII	5-6	7	3-4	3-4

NOTE: See Figures 12 and 13. For explanation of method for obtaining counts, see page 176.

* Small primary male HE was not used in averaging because of its much smaller size and number of setae. Large primary and secondary males were similar enough to each other in number of setae that they are pooled here for comparison with other stages.

TABLE 20.—*Variation in uropodal length (number of articles) in Neotanais micromopher, new species*

Stage	WHOI benthic station	N*	Length of Up (no. of articles)	f †	f × 100 / N (approx.)	No. articles most frequently occurring in Up	Gain in articles since previous stage
M1	66	4	4,4	4	100	4,4	—
M2	64	7	6,6	7	100	6,6	2
	66	2	6,6	2	100	6,6	2
Juv.	64	13	6,6	5	38.5	6,6; 7,7	0 or 1
			6,7	3	23.1		
			7,7	5	38.5		
	76	15	6,6	5	33.3	7,7	0 or 1
			6,7	1	6.7		
			7,7	9	60.0		
P♀1	64	15	7,7	12	80.0	7,7	0 or 1
			7,8	1	6.7		
			8,8	2	13.3		
	76	15	7,7	11	73.4	7,7	0 or 1
			7,8	1	6.7		
			8,8	3	20.0		
P♀2	64	17	6,6	1	5.9	7,7; 8,8	0 or 1
			7,7	7	41.2		
			7,8	3	17.7		
			8,8	6	35.3		
	76	27	6,6	1	3.7	7,7; 8,8	0 or 1
			7,7	11	40.8		
			7,8	2	4.4		
			8,8	13	48.1		
Cop ♀	64	5	8,8	4	75.0	8,8	0 or 1
			8,9	1	25.0		
	76	7	7,7	1	14.3	8,8	0 or 1
			8,8	5	71.5		
			9,9	1	14.3		
Int. ♀	64	2	9,9	2	100.0	9,9	0 or 1
P♂	64	7	7,7	3	42.9	8,8	0 to 2
			8,8	4	57.1		
	76	9	7,7	1	11.1		
			8,8	8	89.0		
Small 1° Cop ♂	64	2	6,7	1	50.0	7,7	0 or 1
			7,7	1	50.0		
	76	1	7,7	1	100.0		
Large Cop ♂ ♂ (1°, 2° pooled)	64	4	9,9	4	100.0	9,9	0 or 1
	76	6	8,8	2	33.3		
			8,9	1	16.7		
			9,9	3	50.0		

* Number of individuals analyzed from each station. Only those animals with at least one intact uropod are included, in which case it is assumed that the missing or incomplete appendage had the same number of articles. Where an individual had an unequal number of articles in the two uropods, where one was unsually high, the other was counted. When inequality was due to an obvious fusion of two articles on one side, the higher count was used.

† Frequency of occurrence of the given number of articles.

In summary, mancas are found throughout the year in *Neotanais micromopher, N. sandersi,* and *N. affinis.* Copulatory females bearing marsupia and probably brooding or just recently having raised a brood are known to exist in summer and winter in *N. micromopher* and from August through November in *N. americanus.*

Although the climatic conditions at the surface off the Oregon coast are not as severe as in the area of the Gay Head–Bermuda Transect, there is no reason to suppose that the deep-sea fauna off the coast of Oregon is subject to altogether different seasonal influences. Females of *Neotanais armiger* with marsupia have been collected in January and late March in that area.

Because of low temperatures and high pressure, rates of metabolism may be low in the deep sea (Jannasch et al., 1971). Animals may reproduce infrequently, require relatively long periods of time for development, and live for a long time. If this is true, all or most developmental stages might be represented in samples at all seasons of the year. However, at present there are apparently no data supporting unusually low metabolic rates among the deep-sea metazoan fauna.

On the assumption that rates of metabolism and development are much the same among deep-sea tanaidaceans as in shallow water, several conclusions may be drawn from these data. At least *Neotanais micromopher, N. sandersi,* and *N. affinis* reproduce throughout the year with the continuous production of young animals. Although it is possible that the mancas may be passing through a quiescent, nongrowing period reminiscent of shoal-water "overwintering," this is unlikely in view of deep-sea environmental uniformity. The presence of brood-pouch embryos and of females with brood pouches in some species betokens active reproduction.

Thus, at least some species of *Neotanais* reproduce in late autumn and winter as well as in the summer months, and it is improbable that the species are greatly different in their reproduction. This is the sort of pattern expected in the deep sea, and it stands in contrast to that of Schoener's ophiuroids.

The reproductive period of *Neotanais* is markedly different from that of *Heterotanais* in the area of Kiel: (a) reproduction occurs in the fall and winter in *Neotanais,* and (b) very young stages

and possibly copulatory males are found throughout the year in some species.

Other tanaidaceans in the deep-sea winter samples examined had brood pouches, some containing eggs or embryos. A more detailed resolution of reproductive patterns among the deep-sea Tanaidacea must await the examination of more material and gonadal analysis of the adults which will be the subjects of a later study.

Summary and Conclusions

1. Twenty-eight species of neotanaids are now known, 25 of which belong to the genus *Neotanais* and one each to the genera *Herpotanais, Carololangia,* and *Venusticrus.* Twelve new species are described, including representatives of the two new genera, *Carololangia* and *Venusticrus,* and nine species are completely redescribed.

2. The morphological conservatism displayed by the family Neotanaidae necessitates lengthy, detailed descriptions and copious illustrations.

3. One pair of "sibling" species, *Neotanais americanus* and *N. sandersi,* has been differentiated.

4. Intraspecific morphologic variation within *Neotanais.*

   a. Appreciable but regular and predictable among developmental stages other than copulatory (adult) males.

   b. Enormous between all other stages and the strongly dimorphic copulatory males; however, all stages share a number of important characteristics and, with care, they can be recognized and linked together by using the species descriptions and diagnoses presented in this study.

   c. Relatively low, when detectable, among geographically separated populations, and expressing itself in various characters and to a greater or lesser degree in different populations and in different species.

   d. Minimal and usually undetectable among vertically separated populations.

5. The postmarsupial development of *Neotanais* is much like that of other peracaridan taxa with the additional complication of protogyny in which the genus resembles the shallow-water genus *Heterotanais* (Paratanidae).

a. Two successive manca stages lead to juveniles which become preparatory males or females.

b. Following an ecdysis, the single preparatory male stage leads to the sexually mature, gonochoristic primary copulatory male.

c. Two successive preparatory female stages, each bearing rudimentary oostegites, lead to the sexually mature copulatory female stage following another ecdysis.

d. Copulatory females also can molt and become sexually functional, protogynous, secondary copulatory males.

e. Copulatory males are the nonfeeding, terminal stages in their particular developmental lines: their mouthparts, when present, are reduced; they lack triturating devices in the gut; the gut is empty; and the anal aperture is fused closed.

6. Postmarsupial development is much the same in the neotanaid genus *Herpotanais*.

7. The gonads, or their rudiments, of both sexes are connected to each other and both are present in almost all developmental stages except primary copulatory males (ovaries) in *Neotanais*.

a. The ovaries are located between the anterior part of pereonite 4 and the posterior end of pereonite 5 except when expanded with ova; then they are greatly swollen and fill the body cavity of the female.

b. The testes lie mostly in the seventh pereonite.

8. Spermatogenesis begins in the preparatory male stage and continues in the copulatory male, producing flagellate sperm.

9. The four pairs of oostegites (on pereopods II–V) do not grow within an instar, all are about the same size when mature, form a loosely fitting marsupium in the copulatory female, and probably are shed at some time following release of the young from the marsupium. The remaining oostegite scars are important in the recognition of copulatory females that have lost their oostegites.

10. The female gonopores are located posteromedially on the coxae of the fifth pereopods

(thoracopod VI) and are an important means of recognizing copulatory females.

11. There are two different phyletic lines represented within the family Neotanaidae: one includes *Neotanais* and *Herpotanais*, the other *Carololangia* and *Venusticrus*.

12. Neotanaids apparently feed on organic detritus, probably removed directly from the deep-sea oozes on which they live.

13. *Neotanais* and *Herpotanais* do not build tubes and are almost certainly epifaunal, their legs being adapted for walking. The life habits of *Carololangia* and *Venusticrus*, the newly described genera, are uncertain; their pereopods are markedly specialized for different functions than those of *Neotanais* and *Herpotanais*.

14. Neotanaids were found in 28.8 percent of all anchor dredge samples taken below 2000 m and in 51.6 percent of those samples (31) containing tanaidaceans. They occur in densities of 0.95 to 46.7 animals/m² ($\bar{x} = 7.12 + 4.6$ animals/m²) in 22 anchor dredge samples taken along the Gay Head–Bermuda Transect. Limited numbers of individuals did not permit evaluation of variation in density with depth.

15. Up to five species of *Neotanais* have been collected in a single sample, indicating high species diversity among the deep-sea Tanaidacea, in marked contrast to that in many shallow-water environments. No separation of niches among species is apparent, contrary to what would be expected from the competitive exclusion principle.

16. The epibenthic sled was, by far, the most efficient device employed in the capture of neotanaids.

17. The Neotanaidae contains a number of species that are distributed over ranges of several thousand kilometers, and other species will certainly be shown to be as widely distributed. However, neotanaids are not ubiquitous.

18. The Neotanaidae is a deep-sea family, but it is now known from a number of locations in relatively shallow water (as little as 223 m) in both the Antarctic (possibly demonstrating polar emergence) and the tropical and subtropical regions.

19. Known depth ranges vary within the family

and are largely dependent on the number of times a species has been collected. Nevertheless, some ranges are very large, 3500 m or even possibly 5500 m in one case. *Neotanais micromopher*, very well known from the Gay Head–Bermuda Transect, demonstrates a range of only 1852 m in the Transect area.

20. Two of the three species of neotanaids collected on the Bermuda Slope display morphological differences from populations on the North American Slope; in *Neotanais hastiger* these differences are marked. *Neotanais dinotomer*, known from Bermuda alone, is very close to *N. micromopher* from the North American Slope.

21. The smallest neotanaids are known from the shallowest waters and the largest ones from the greatest depths. However, because of limited data and the possible biasing effects

of different sampling procedures, the presence of deep-water "gigantism," or overgrowth, is not certain.

22. The hypothesis of Antarctic "gigantism" is not supported by the Neotanaidae.

23. Manca stages of *Neotanais micromopher*, *N. sandersi*, and *N. affinis* are found throughout the year on the Gay Head–Bermuda Transect; copulatory females with marsupia of *N. micromopher* have been found in both summer and winter in the same area; and brood-pouch embryos of an unidentified species are known from mid-December. These data indicate that some species of *Neotanais* are reproducing in midwinter, some apparently reproduce all year, and their pattern of reproductive activity differs markedly from that of certain temperate, shallow-water forms in which reproduction is limited to the warmer months.

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