MORPHOLOGICAL VARIABILITY OF *PLEUROMAMMA ABDOMINALIS* (COPEPODA, CALANOIDA, METRIDINIDAE) ALONG TWO LATITUDINAL TRANSECTS IN THE EASTERN NORTH PACIFIC OCEAN

BY

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ABSTRACT

Adult females and males of *Pleuromamma abdominalis* were examined from 26 plankton samples taken at stations in the eastern North Pacific Ocean along two latitudinal gradients, 150°W between 21.55°N and 14.00°S, and 119°W between 17.09°N and 20.00°S. The species was found at all stations except three between 17.9°N and 12.6°N along 119°W. Variation within a sample was observed in the ventral attenuations [= spiniform outgrowths] of the first segment of antenna 1 of females, and specimens referable to *P. abdominalis* forma *edentata* could not be distinguished unequivocally from other females. Males with a strongly asymmetrical urosome and re-curved lateral seta on the left caudal ramus, referable to *P. abdominalis* forma *abdominalis*, were found, as were males with a quasi-symmetrical urosome and simple lateral seta on the left caudal ramus, referable to *P. abdominalis* forma *abyssalis*. Specimens of the latter form were not restricted to deep water but were present in samples taken as shallow as 200 m. Males with a slightly asymmetrical urosome, not as pronounced as that of *P. abdominalis* forma *abdominalis*, and with a simple lateral seta on the left caudal ramus, also were found. The degree of asymmetry among this third group of males was variable. There was no discernable pattern in depth or geographical distribution of either female or male morphs. Based on gradations of morphological states traditionally used to diagnose the different forms of *P. abdominalis*, the species appears to be variable, but the nominal forms should not be considered subspecies. Morphological variation among females and males of *P. abdominalis* should continue to be registered; in situations where groups of *P. abdominalis* can be clearly categorized, they should be denoted simply as morphs.

RÉSUMÉ

Des femelles et des mâles adultes de *Pleuromamma abdominalis* ont été examinés dans 26 échantillons de plancton prélevés dans la partie orientale de l’Océan Pacifique Nord, à différentes stations situées le long de deux gradients latitudinaux, 150°W entre 21.55°N et 14.00°S, et 119°W entre 17.09°N et 20.00°S. L’espèce a été trouvée dans toutes les stations sauf trois d’entre elles entre 17.9°N et 12.6°N le long du 119°W. La variation à l’intérieur d’un échantillon a été observée au

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level of ventral prominences [= evaginations pointues] of the first segment of the antennule of females, and the specimens attributed to *P. abdominalis* forma *edentata* n’ont pu être distingués clairement des autres femelles. Les mâles ayant un urosome **fortement** asymétrique et la soie latérale recourbée sur la rame caudale gauche, caractéristiques de *P. abdominalis* forma *abdominalis*, ont été trouvés, de même que des mâles ayant un urosome quasi-symétrique et une soie latérale simple sur la rame caudale gauche, correspondant à *P. abdominalis* forma *abyssalis*. Les spécimens de cette dernière forme n’ont pas été trouvés uniquement en eau profonde, mais étaient aussi présents dans des échantillons prélevés à une profondeur faible de 200 m. Des mâles présentant un urosome légèrement asymétrique, cependant moins que chez *P. abdominalis* forma *abdominalis*, et ayant une soie latérale simple sur la rame caudale gauche, ont aussi été trouvés. Le degré d’asymétrie dans ce troisième groupe de mâles était variable. Il n’y avait pas de schéma évident de distribution en fonction de la profondeur ou de la géographie, des morphotypes chez les mâles comme chez les femelles. À partir des gradations d’états morphologiques traditionnellement utilisés pour la diagnose des différentes formes de *P. abdominalis*, l’espèce apparaît très variable, mais les formes nominales ne devraient pas être considérées comme des sous-espèces. Les variations morphologiques des femelles et des mâles devraient continuer à être enregistrées ; dans les situations où des groupes de *P. abdominalis* peuvent être clairement identifiés, ces derniers devraient être simplement notés comme des morphotypes.

**INTRODUCTION**

The calanoid copepod genus *Pleuromamma* (Metridinidae) is well-circumscribed, characterized by the presence of a “pigment knob” (Blades-Eckelberger & Youngbluth, 1988) on the left side or the right side of the third thoracic somite which bears swimming leg 2. The species are planktonic, free-living, and usually oceanic. There are eleven recognized species in the genus: *Pleuromamma abdominalis* (Lubbock, 1856); *P. gracilis* (Claus, 1873); *P. xiphias* (Giesbrecht, 1889); *P. borealis* (Dahl, 1893); *P. quadrangulata* (Dahl, 1893); *P. robusta* (Dahl, 1893); *P. indica* (Wolfenden, 1905); *P. piseki* (Farran, 1929); *P. antarctica* (Steuer, 1932); *P. scutullata* (Brodsky, 1950); and *P. johnsoni* (Ferrari & Saltzman, 1998). With the exception of *P. johnsoni*, the species have been known for more than fifty years. The species *P. princeps* (Scott, 1894), originally *Pleuromamma princeps*, was removed to the genus *Gaussia* (see Wolfenden, 1911; Tanaka, 1963), and *P. wolfendeni* (Brady, 1918) is an immature copepodid stage V. The name *P. brevicornis* (Björnberg, 1963) is without description or illustrations; the name may have been a typographical error (in Björnberg, 1963, table 17).

Intraspecific variation within species of *Pleuromamma* has presented problems throughout the taxonomic history of the genus. Characters such as the size of attenuations [cf. spiniform outgrowths] on the proximal segments of antenna 1 of both sexes, the shape of the female genital complex, epicuticular extensions of the female anal flap, degree of asymmetry expressed in male urosomites, and morphology of setae on the male caudal ramus, may vary significantly. Studies of variation in these characters among four species have led to proposals of ten forms and
one variety. Among these are three forms of *P. abdominalis* originally described from the Atlantic Ocean, viz., *P. abdominalis* forma *abdominalis* Lubbock, 1856 [henceforth forma *abdominalis*] is known from both female and male specimens; *P. abdominalis* forma *edentata* Steuer, 1932 [henceforth forma *edentata*] is known only from female specimens; and *P. abdominalis* forma *abyssalis* Giesbrecht, 1893 [henceforth forma *abyssalis*] is known only from male specimens.

*Pleuromamma abdominalis* is one of the common species of the genus, and is well studied in the North Atlantic (Roe, 1972; Hunt & Pakhomov, 2003), including the adjacent Mediterranean Sea (Anderson et al., 2004) and the Gulf of Mexico (Bennett & Hopkins, 1989), and specimens have been collected from the surface to 2000 m depth (Steuer, 1932, 1933; Grice & Hulsemann, 1967; Roe, 1972). *P. abdominalis* has been reported from the Indian Ocean (Grice & Hulsemann, 1967) to the edge of the Southern Ocean (Labat et al., 2002). In the North Pacific Ocean, there are both taxonomic (Davis, 1949; Tanaka, 1963) and distribution records (Jimenez-Perez & Lavaniegos, 2004; Sedova, 2006). In the eastern North Pacific Ocean, Davis (1949: 53) attributed most females to *P. abdominalis* forma *edentata*, one of two female morphs, mentioning the absence on antenna 1 of strongly curved attenuations that are diagnostic for forma *edentata* females. However, he did not provide any other morphological details and did not identify the other female morph. Davis (1949: 53) reported that all males were of *P. abdominalis* forma *abdominalis* [reported as forma *typica*]. His specimens were sorted from plankton samples collected at three different locations and in three different years: 37°57′N 123°56′W from 10 m to 25 m on 25 August 1935; 60 miles off Cape Flattery (geographical coordinates not given; Cape Flattery is 48°22′N 124°42′W) from 0 m to 1100 m on 29 May 1937; 55°03′N 155°34′W from 400 m to 600 m on 19 July 1931. The purpose of this paper is to extend observations of morphological variability expressed by *Pleuromamma abdominalis* in the eastern North Pacific Ocean by examining specimens taken in plankton samples from latitudinal transects along 150°W and 119°W.

**MATERIAL AND METHODS**

Specimens were sorted from archived plankton samples collected at 26 stations during two NORPAX cruises undertaken by the R/V “Kana Koeki” in January 1978 and July 1978, and during one EASTROPAC cruise undertaken by the R/V “Argo” late January through early February 1967. Samples were chosen to provide a latitudinal gradient from 21.55°N to 14.00°S at 150°W and from 17.09°N to 20.00°S at 119°W. Locations and depths from which the samples were collected are summarized in table I. Stations 78-7-5, 78-1-1 through 78-1-4, and Cr11-32
through Cr11-48 are located in the general area of the westward flowing North Equatorial Current. Stations 78-1-6 as well as Cr11-60 and Cr11-68 are located in the general area of the Equatorial Counter Current. Stations 78-1-7 through 78-1-16 and Cr11-72 through Cr11-173 are located in the general area of the South Equatorial Current. Samples from stations 78-1-9 and 78-1-10 may have been taken either in the westward flowing South Equatorial Current or the deeper, eastward flowing subsurface Cromwell Current that often overlay one another in that area. Catch per unit effort could not be determined.

Specimens were cleared in 100% lactic acid and stained with Chlorozal Black E dissolved in a 70% ethanol/30% de-ionized water solution. Specimens were sorted and dissected using a dissecting microscope; drawings were made with a compound microscope fitted with a camera lucida. Setules are extensions of the epicuticule of a seta, denticles are extensions of the epicuticule of a limb segment, and spinules are extensions of the epicuticule of a body somite.

*Pleuromamma abdominalis* is one of six mid-sized species (length 3.0 to 4.5 mm) along with *P. robusta*, *P. quadrungulata*, *P. scutullata*, *P. johnsoni*, and *P. antarctica*. *Pleuromamma robusta*, *P. quadrungulata*, and *P. johnsoni* often co-occurred in the plankton samples studied here, and were separated in the following ways. Specimens of *P. abdominalis* have a circular pigment knob on the third thoracic somite; the pigment knob is oval on *P. robusta*, and on *P. johnsoni* it is pointed anteriorly and posteriorly (Ferrari & Saltzman, 1998). Females of *P. abdominalis* also can be separated from females of *P. robusta* by the greatest width of the genital somite complex, which corresponds to the location of the copulatory pore. In ventral view of the complex, *P. abdominalis* is widest at the middle of the complex; in a ventral view of *P. robusta* the genital somite complex is widest toward the anterior end of the complex. Females of *P. johnsoni* have an asymmetrical knob dorsal to the rostral area; this knob is not present on *P. abdominalis*. Females of *P. quadrungulata* have two curved attenuations on the proximal articulating segment of antenna 1 and one curved attenuation each on the second and fourth articulating segments; females of *P. abdominalis* have at most one curved attenuation on the first articulating segment of antenna 1 and at most one curved attenuation on the second segment.

Males of *P. abdominalis* with a circular pigment knob on the left side of the third thoracic somite were separated from males of *P. robusta* and *P. quadrungulata* with the knob on the right side. Males of *P. johnsoni* have the pigment knob on the left or right side but have an asymmetrical knob dorsal to the rostral area; this knob is not present on males of *P. abdominalis*.

Females of forma *abdominalis* from the Atlantic Ocean are distinguished from females of forma *edentata* by the degree of development of the attenuations on the first and second articulating segments of antenna 1 (Steuer, 1932, 1933). These
Tab. 1

Station positions and occurrences of the different morphs of *Pleuromamma abdominalis* (Lubbock) for two NORPAX cruises in 1978 and EASTROPAC cruise 11 in 1967. AUCS, male with a strongly asymmetrical urosome and lateral seta on caudal ramus re-curved [referable to forma *abdominalis*]; AUSS, male with slightly asymmetrical urosome and lateral seta on caudal ramus straight [referable to forma *abyssalis*]; QUSS, male with a quasi-symmetrical urosome and lateral seta on caudal ramus straight; RS, female with 1 large curved attenuation on proximal segment of antenna 1 [referable to forma *abdominalis*]; SS, female without curved attenuation on proximal segment of antenna 1 [referable to forma *edentata*]; depth in meters.

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<th>Longitude</th>
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<th>QUSS</th>
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Attenuations usually arise between the proximal seta and the distal seta + aesthetasc of the classical setal trithek on antenna 1 of female calanoids (Giesbrecht, 1893; Boxshall & Huys, 1998). On females of forma *abdominalis*, the distal attenuation associated with the distal trithek on the proximal segment is very distinctive, long, and curved proximally toward the body of the copepod. The attenuation on the following segment also is long and curved proximally. In forma *edentata*, there
may be up to three short, simple, tooth-like attenuations on the proximal segment of antenna 1 and one short, simple, tooth-like attenuation on the following segment.

Males of forma *abdominalis* from the Atlantic Ocean are distinguished from males of forma *abyssalis* by the degree of the asymmetry of the urosomites and the shape of the lateral spine on the left caudal ramus (Steuer, 1932, 1933; Wilson, 1932; as forma *typica*). In forma *abdominalis*, the second and fourth urosomites, viewed dorsally, have distinct lateral projections on the left side; the third urosomite has a group of long spinules on the right side; left and right pore-bearing extensions of the anal somite are asymmetrical; the lateral seta on the left caudal ramus is distinctly re-curved but the seta on the right is simple; two hook-like attenuations, proximal and distal, are present on the proximal endopodal segment of the left swimming leg 2 but the endopodal segment on the right retains only the proximal attenuation. In forma *abyssalis* there are no distinct lateral projections on male urosomites; pore-bearing extensions of the anal somite are symmetrical; the lateral seta on the left caudal ramus is simple, like that on the right; swimming leg 2 is identical to that of forma *abdominalis*.

**RESULTS**

One thousand, seventy-eight (1078) females and 492 males of *Pleuromamma abdominalis* were sorted from 12 NORPAX and 14 EASTROPAC samples. Females with the pattern of attenuations comparable to forma *abdominalis* (fig. 1A, B) co-occurred with females comparable to forma *edentata* (fig. 1C-I) in 19 of 22 samples where either form was found. In contrast to specimens reported from the Atlantic Ocean, the attenuation on the segment adjacent to the proximal segment is not curved toward the body (Steuer, 1932, text-fig. 27) but points ventrally or disstoventrally. Females of forma *abdominalis* were found in 3 samples (NORPAX 78-7-5, EASTROPAC Cr11-88, EASTROPAC Cr11-167) where females of forma *edentata* were not found and 42 females of forma *edentata* were present in one sample (EASTROPAC Cr11-60) where females of forma *abdominalis* were absent. Females were not recovered from 3 stations (EASTROPAC Cr11-32, EASTROPAC Cr11-40, EASTROPAC Cr11-48).

Females with morphologies that appear intermediate between forma *abdominalis* and forma *edentata* occur at many stations in which 5 or more females were recovered. These morphologies were not categorized, but six specimens (fig. 1A-F) from NORPAX 78-1-9 (1.00°N 150.00°W) and three (fig. 1G-I) from NORPAX 78-1-13 (7.50°S 150.00°W) exemplify the gradations between forma *abdominalis* and forma *edentata*. A large, curved, distal attenuation and a broader, straight, proximal one flank an undeveloped middle attenuation in fig. 1A; in fig. 1B the
distal attenuation is less pronounced and in fig. 1G the distal attenuation is only slightly curved. On six specimens (fig. 1C-F, H, I), the distal attenuation is not curved proximally and on three specimens (fig. 1F, H, I), the distal attenuation is not much more pronounced than the middle or proximal attenuations.
Four-hundred and twenty-one males (86%) corresponding to forma *abdominalis* were present in 19 of 25 samples; specimens of this morph always were present in samples with the other male morphs (table I). Among the six samples without males, females also were absent from three of those samples (EASTROPAC Cr11-32, EASTROPAC Cr11-40, EASTROPAC Cr11-48) taken along 119° between 17.9°N and 12.6°N at about 200 m. However, both males and females of *P. abdominalis* were present in two samples (NORPAX 78-1-1, NORPAX 78-1-2) taken at similar latitudes, 16.48°N and 13.50°N, along 150° and from slightly deeper tows, from 950 m.

The urosome of forma *abdominalis* males (fig. 2A) is strongly asymmetrical. The second and fourth urosomites have a rounded projection on the left side, and the third somite has a group of long spinules on the right side. A group of long spinules is directed posteriorly from both projections. The projection on the second urosomite is much larger and broader, and a longitudinal muscle originating on the adjacent anterior somite inserts within this projection; the projection on the fourth urosomite is narrow, and there is no insertion of a muscle. The left and right pore-bearing extensions of the anal somite are asymmetrically positioned relative to one another; the left extension points posteriorly, the right posterolaterally. The caudal rami are asymmetrical, the left more quadrate in shape than the right; both have denticles medially. The lateral seta on the right caudal ramus is simple. The lateral seta on the left caudal ramus is re-curved, and has a line of papillae near its base as well as the long setules along its entire length. The setules frequently are broken on the specimens here. Terminal setae on the caudal ramus bear setules; the dorsal seta is small. The left proximal endopodal segment of swimming leg 2 has a distal hook-like attenuation and a proximal tooth-like attenuation; that on the right endopod is smooth distally but retains the proximal tooth-like attenuation (fig. 3). The pigment knob is on the left side of the third thoracic somite of all specimens. The left exopod of leg 5 has denticles distally on the distal segment (see Steuer, 1932, text-fig. 32a-b).

Fifty-two males (10%) of *P. abdominalis* with a quasi-symmetrical urosome and a simple, rather than re-curved, seta on the left side of the caudal ramus (fig. 2B) were found in seven widely separated stations (table I) from the North and South Pacific Equatorial Currents, the Equatorial Counter Current, and the Cromwell Current. The specimens, referable to forma *abyssalis* were collected between the surface and 950 m with four of the samples taken from the surface to less than 300 m. Forty specimens were found in a single sample (NORPAX 78-1-16) taken from the surface to 275 m. The left lateral projection on the second and fourth urosomites, distinctive for forma *abdominalis*, is absent on these specimens, although the fourth urosomite has a very slight, quadrate protrusion (fig. 2B). With this protrusion and tufts of denticles on the right side of the third urosomite, the
Fig. 2. *Pleuromamma abdominalis* (Lubbock, 1856), male, dorsal view of urosome. A, specimen attributable to forma *abdominalis*, with strongly asymmetrical urosome and re-curved seta on left caudal ramus, from EASTROPAC 11 st. 114; B, specimen attributable to forma *abyssalis* with quasi-symmetrical urosome, and simple lateral seta on the left caudal ramus, from EASTROPAC 11 st. 60; C, specimen intermediate between forma *abdominalis* and forma *abyssalis* with slightly asymmetrical urosome and simple seta on the left caudal ramus, from EASTROPAC 11 st. 114; D, specimen intermediate between forma *abdominalis* and forma *abyssalis* with slightly asymmetrical urosome, from 78-1-6. Anterior is up, apical setae of caudal ramus with elliptical cutoff; arrowhead to dorsal seta of caudal ramus; setules, denticles, and spinules much less dense than natural; scale line is 0.5 mm.
urosome has a quasi-symmetrical appearance. Pore-bearing extensions of the anal somite appear symmetrical, as do the caudal rami. The lateral seta on the left caudal ramus is not re-curved or curved, so that setation of the caudal ramus also appears symmetrical. The proximal endopodal segment of left and right swimming leg 2 do not differ from those of forma *abdominalis*, and the pigment knob is on the left side of the third thoracic somite of all specimens. The left exopod of leg 5 lacks denticles distally on the distal segment (see Steuer, 1932, text-figs. 43, 44).

Nineteen specimens (4%) of a third male morph were found in three of the samples examined here (table I). These male specimens were restricted to the North and South Equatorial Currents. They co-occurred with males referable to forma *abdominalis* and to forma *abyssalis* in two of the samples (EASTROPAC Cr11-60 and Cr11-114), but the sample with 16 specimens (EASTROPAC Cr11-68) had only one other male, of forma *abdominalis*. The urosome of these males is slightly asymmetrical (fig. 2C, D); the second and fourth urosomites have projections on the left side and are armed with tufts of denticles that are directed posteriorly. However, the projections appear somewhat smaller and less pronounced than those found on forma *abdominalis*. In addition, some variation is observed in the degree of development of these projections (compare fig. 2C with 2D). A longitudinal muscle originating from the adjacent anterior somite inserts on the projection of the second urosomite, but there is no muscle insertion on the projection of the fourth urosomite; a tuft of spinules originates on the right side of the third urosomite, all as in forma *abdominalis*. However, the lateral seta on the left caudal ramus is simple. The left and right pore-bearing extensions of the anal somite are asymmetrical; the left extension points posteriorly, the right posterolaterally. As in the other morphs, the left proximal endopodal segment of swimming leg 2 retains hook-like attenuations; the right endopod has only the proximal attenuation. These specimens also have a pigment knob only on the left side of the third thoracic somite. The left exopod of leg 5 has denticles distally on the distal segment, like in forma *abdominalis*. 
DISCUSSION

Female specimens of *Pleuromamma abdominalis* collected in the Atlantic Ocean expressed variations in attenuations of antenna 1 similar to those reported here, although not from a single sample (see Steuer, 1932, text-figs. 33a, b, 34), and the number of specimens exhibiting each morphology is not given. Based on this variation, Steuer (1932) described *P. abdominalis* forma *abdominalis* (as forma *typica*) and *P. abdominalis* forma *edentata*. There was no discernable pattern in the geographical distribution of these two forms (Steuer, 1933). Wilson (1932) did not mention female forms nor did he refer to any variation in the proximal segment of the antenna 1. The widespread distribution of morphs attributable to forma *typica* and forma *edentata*, their co-occurrences, and the presence of specimens exhibiting morphologies incrementally graduated between the two forms, suggest that these two morphological forms of *P. abdominalis* are examples of a continuous variability within this species. Thus, we do not believe that forma *edentata* should be treated as a subspecies of *P. abdominalis*.

*Pleuromamma abdominalis* has an extensive vertical distribution. Among male specimens, *P. abdominalis* forma *abyssalis* were found at depths ranging from 2000 m to 2500 m in the Atlantic Ocean (Steuer, 1932). Without reference to morphs, Sedova (2006) reported a vertical range of more than 1,000 m in the eastern Okhotsk Sea for the species. In addition, *P. abdominalis* displays an extensive vertical migration in the Florida Current (Moore & O’Berry, 1957); in the Gulf of Mexico it migrated vertically over 700 m (Bennett & Hopkins, 1989) and Roe (1972) found evidence of vertical migration over at least 650 m in the eastern North Atlantic Ocean. Here specimens referable to forma *abyssalis* were collected as shallow as about 200 m. Consequently, the difference in vertical distribution between specimens of forma *abdominalis* and forma *abyssalis* does not appear significant.

The morphology of the second and fourth urosomites and the anal somite can be considered either asymmetrical or quasi-symmetrical. Gradations appear among males with an asymmetrical urosome, from strongly asymmetrical to slightly asymmetrical. However, differences among males with an asymmetrical urosome are less pronounced than the differences between males with a slightly asymmetrical urosome and males with a quasi-symmetrical urosome.

Results here suggest only two kinds of lateral seta may occur on the left caudal ramus. The lateral seta on the right caudal ramus is simple, but the lateral seta on the left caudal ramus may be re-curved or simple. This variation appears to accentuate the asymmetry of the urosome. However, alignment of the different kinds of urosome with the two different kinds of setae remains problematical. Males with an asymmetrical urosome may have either a lateral re-curved seta on
the left caudal ramus or a simple seta. Males with a quasi-symmetrical urosome always have a simple lateral seta on the left caudal ramus.

Given the incremental gradations among specimens with an asymmetrical urosome, a lack of alignment among asymmetrical character states, the lack of latitudinal, hydrographic, or vertical separation of the different male morphs, and an inability to distinguish sets of females to pair with any of the male morphs, we do not believe that forma "edentata" or forma " abyssalis" should be treated as subspecies of *P. abdominalis*. However, we do believe it is important to continue to register the morphological variation among males of *P. abdominalis*. In situations where groups of females or males of *P. abdominalis* can be clearly categorized, they should be denoted simply as morphs.

**REFERENCES**


PLEUROMAMMA ABDOMINALIS, MORPHOLOGICAL VARIABILITY


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