

PLEIOTROPY AND *PLEUROMAMMA*, THE LOOKING-GLASS  
COPEPODS (CALANOIDA)

BY

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I N T R O D U C T I O N

Almost fifty years ago Adolph Steuer (1932) published the results of an extensive study of the copepod genus *Pleuromamma*. He documented the interesting distribution of asymmetrical characters in these calanoids and made some suggestions about the phylogeny of the genus based, in part, on asymmetry. Despite the provoking implications of Steuer's work, to my knowledge, no author has contributed to this subject since. In this paper, I discuss the subject of asymmetry in *Pleuromamma*, describe several asymmetrical characters overlooked by Steuer, and suggest pleiotropic control of the distribution of asymmetrical characters in the genus. In addition I outline several ideas about causal factors responsible for the present distribution of asymmetry and examine, briefly, the implications of a pleiotropic process in copepod evolution.

In the following text asymmetrical characters on an individual are described as showing "unique concordance" when their positions relative to one another, on the body, do not vary. All species considered exhibit the population phenomenon of "dimorphic asymmetry". That is, the groups of asymmetrical characters may be found in reversed positions on different animals. Figure 4 illustrates unique concordance of asymmetrical characters and dimorphic asymmetry in *Pleuromamma xiphias*. The attribute of dimorphic asymmetry provides animals of the genus with their common name, looking-glass copepods, after Alice Liddell's mirror (see Gardner, 1960).

A S Y M M E T R Y   A N D   *P L E U R O M A M M A*

A study of the distribution of bilaterally asymmetrical characters in populations which exhibit dimorphic asymmetry can provide insight into the process of morphological change. In comparing interspecific diversity of species-specific homologous structures, an infinite series of intermediate structures may be hypothesized for a finite, but unknown, set of intermediate animals. Thus in comparing the shape of the genital segments of two species of *Pleuromamma* (figs. 1a and b), an infinite series of intermediate



shapes can be envisioned. However, only a finite, but unknown, number of animals ever existed. This is Zeno's legacy to morphologists (for further information about Zeno's paradoxes of plurality see Russell, 1945).

Studies of asymmetry in fundamentally bilaterally symmetrical animals avoid this apparent paradox by initially defining a small, discrete set of outcomes for the character states. A paired structure on an individual may be symmetrical or asymmetrical; in the latter case it may also exhibit dimorphic asymmetry. This set of

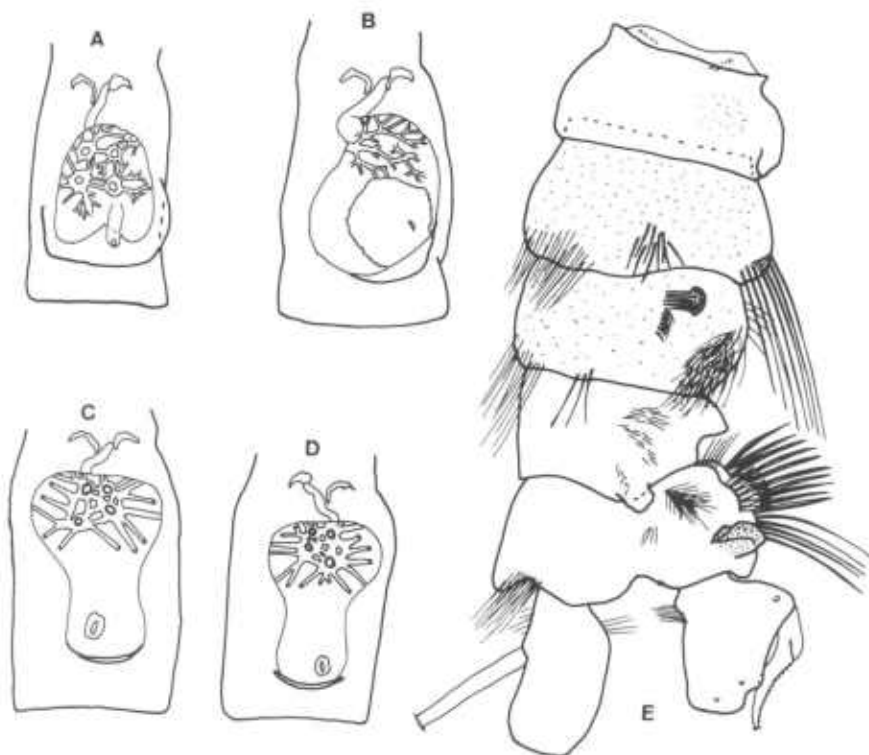


Fig. 1. Female genital segments, ventral, of: A, *Pleuromamma gracilis* (Claus); B, *P. piseki* Farran; C, *P. borealis* (F. Dahl) (with black organ on right side); D, *P. borealis* (with black organ on left side); E, urosome, ventral of *P. xiphias* (Giesbrecht).

outcomes may be ordered in several ways to reflect presumed ancestor/descendant relationships. Groups of animals like the copepod genus *Pleuromamma*, which exhibit dimorphic asymmetry, often without symmetrical alternative character states among the species, provide a binary set of outcomes for the expression of asymmetry.

Calanoid copepods of the genus *Pleuromamma* are fundamentally bilaterally symmetrical animals. Symmetry is exhibited in many external morphological characters, such as the serially arranged paired appendages of the cephalic and thoracic segments. Evidence

TABLE I

Extent of bilateral asymmetry (+) in structural morphology of *Pleuromamma*

	<i>P. xiphias</i> (Giesbrecht, 1889)	<i>P. abdominalis</i> (Lubbock, 1856)	<i>P. indica</i> Wolfenden, 1905	<i>P. scutulata</i> Brodskii, 1950	<i>P. robusta</i> (F. Dahl, 1893)	<i>P. quadrangulata</i> (F. Dahl, 1893)	<i>P. borealis</i> (F. Dahl, 1893)	<i>P. gracilis</i> (Claus, 1863)	<i>P. piseki</i> Farran, 1929
FEMALE									
black organ	+	+	+	+	+	+	+	+	+
genital segment	+	+	+	?	+	+	+	+	+
MALE									
black organ	+	+	+	+	+	+	+	+	+
A1	+	+	+	+	+	+	+	+	+
P5 Re	+	+	+	+	+	+	+	+	+
position genital opening	+	+	+	?	+	+	+	+	+
P1 Bsp <sup>+</sup>	+	+	-	?	-	-	-	-	-
P2 Bsp <sup>+</sup>	+	+	-	?	-	-	-	-	-
P2 Re <sup>+</sup>	+	+	-	?	-	-	-	-	-
P2 Ri <sup>+</sup>	+	+	-	?	-	-	+	+	+
P3 Bsp <sup>+</sup>	+	+	-	?	-	-	+	-	-
P3 Re <sup>+</sup>	+	+	-	?	-	-	-	-	-
P4 Bsp <sup>+</sup>	+	+	-	?	-	-	+	-	-
P4 Re <sup>+</sup>	+	+	-	?	-	-	-	-	-
P4 Ri <sup>+</sup>	+	+	-	?	-	-	-	-	-
Ur <sup>++</sup>	+	+	+	?	+	+	+	+	+

\* Includes changes in structure (generally on margins) or armature of at least one article.

\*\* Includes torsion, structural modification or changes in armature of at least one segment.

of asymmetry, absent in naupliar stages (Björnberg, 1972), appears after metamorphosis. The presence of a black organ on the left or right side of the first pedigerous (second thoracic) segment of the copepodid, is a diagnostic feature of the genus. On immature males of *P. xiphias*, the only species whose immature stages were examined carefully, the right exopod of leg 5 is slightly longer than the left.

Asymmetry is most pronounced in adult (stage VI copepodid) females and males (table I). In addition to the black organ, fema-

les possess an internal tube which appears to originate at the anteriodorsal face of the seminal receptacle and, passing anteriorly in the genital segment, bends toward the left or right. Within the female seminal receptacle are a complex series of interconnecting canals whose pattern is asymmetrical and species-specific. The canals seem to be internal extensions of the wall of the seminal receptacle. The pattern, impossible to reproduce in a line drawing, is depicted for *P. borealis*, *P. piseki*, and *P. gracilis*, in figures 1a, b, and c. The genital opening of these last three species is positioned asymmetrically relative to the midline of the genital segment.

In addition to the black organ, all males exhibit asymmetry in paired antenna 1, leg 5, and position of the genital opening. The urosome of all males examined shows slight asymmetry in the position of setae or complex asymmetry of segmental projections, setae, spines, and (fig. 1e) torsion of the urosome, e.g., *P. xiphias* and *P. abdominalis*. These two species share with *P. gracilis*, *P. piseki*, and *P. borealis* loss of the curved medial attenuation, and its attendant axial spine, on a posterior inner margin of endopod 1 of leg 2. These structures are present on both left and right endopod 2's of adult females, immature males, and immature females. This loss in males occurs on one side or the other, never both, rendering the endopods asymmetrical. Males of *P. xiphias* and *P. abdominalis* alone exhibit striking asymmetry in legs 1-4. This includes modifications in the structure and/or armature of one or more elements of the basipod of leg 1, basipod, exopod, and endopod of leg 2, basipod and exopod of leg 3, and basipod, exopod, and endopod of leg 4.

#### D I S T R I B U T I O N O F A S Y M M E T R Y I N P L E U R O M A M M A

Steuer (1932) recognized that species of *Pleuromamma* could be grouped in several ways utilizing the distribution of asymmetry. In males of *P. quadrangulata*, *P. robusta*, *P. borealis*, and *P. gracilis* female-like antenna 1, black organ, mitten-shaped leg 5 (spermatophore holder), and genital opening show unique concordance; that is, they always occur together on the same side of the body, usually the right. The geniculate antenna 1 and blade-shaped leg 5 (female holder) also show unique concordance; they always occur together on the same side of the body and always on the side opposite the first four characters. They usually occur on the left side. *P. scutullata* and *P. piseki*, erected since Steuer's work, fall into this group. The smooth, inner-edge endopod on leg 2, when present in members of this group (*P. borealis*, *P. gracilis*, and *P. piseki*) and which renders the endopods asymmetrical, is always on the same side as the black organ, usually the right. Populations of these males only infrequently exhibit dimorphic asymmetry. Steuer reported a few specimens of three species with the black organ on the left side (table II) but did not mention the position of any other structures.

TABLE II

Distribution of the Black Organ in species of *Pleuromamma* (adults)

	Present studies		Steuer (1932)	
	female L:R	male L:R	female L:R	male L:R
<i>P. xiphias</i>	392:658	1001:1	1130:1808	1677:3
<i>P. abdominalis</i>	206:528	459:3	1775:1775	1797:1
<i>P. indica</i>	19:24	24:19	2000:1000	1000:500
<i>P. scutullata</i>	0:2	0:0	-	-
<i>P. robusta</i>	0:100	0:28	2:1115	2:791
<i>P. quadrangulata</i>	0:56	0:13	1:516	0:257
<i>P. borealis</i>	1:5004	0:196	0:4738	few:3330
<i>P. gracilis</i>	0:35	0:1	} combined 1:21658	5:7757
<i>P. piseki</i>	0:135	0:8		

In males of *P. abdominalis* and *P. xiphias* all structures discussed so far show the same unique concordance. However, the positions are usually reversed relative to the first group. The female-like antenna 1, black organ, mitten-shaped leg 5, and genital opening always occur together, usually on the left side; the blade-shaped leg 5, geniculate antenna 1, and smooth inner-edge endopod of leg 2, present in both species, are opposite the first four and usually on the right. These males also only rarely exhibit dimorphic asymmetry. Steuer reported individuals of both species with the black organ on the right. Similar male specimens of both species, found in the present study, verified the unique concordance in the position of all asymmetrical characters noted above, as well as, all remaining characters on legs 1-4 and the urosome. In addition on an immature male of *P. xiphias* with the black organ on the right side, the left exopod of leg 5 was slightly longer than the right.

Only males of *P. indica* commonly exhibit dimorphic asymmetry within a population (table II) and in all cases examined the concordance of character position remained unique. The female-like antenna 1, black organ, mitten-shaped leg 5, and genital opening always occurred together on the same side of the body and always on the side opposite the concordant geniculate antenna 1 and blade-shaped leg 5.

Females can be divided into two groups. Populations of *P. quadrangulata*, *P. robusta*, *P. gracilis*, and *P. borealis*, as well as, *P. piseki* and *P. scutullata* rarely exhibit dimorphic asymmetry. In these species the black organ is usually on the right (the same side as the conspecific males) and the anterior tube of the

genital segment turns left. Steuer reported specimens with a left black organ for all species except *P. borealis*. One female of this species was found in the present study with the black organ on the left. The genital segment of this female is shown in fig. 1d and can be compared with the usual female morphology in fig. 1c. The tube turns to the right. The position of the genital opening, shape of the seminal receptacle and its interconnecting canals are all found on the opposite side of the midline relative to the usual female. These asymmetrical characters then also show unique concordance.

Females of *P. abdominalis*, *P. xiphias*, and *P. indica* commonly exhibit dimorphic asymmetry (table II). The position of the tube in the genital segment shows unique concordance with that of the black organ. The former turns to the left when the latter is found on the right side and vice versa. Because the wall of the seminal receptacle in these species is thick and opaque, the interconnecting canals have not been studied. The genital opening of these females is positioned on the midline of the segment.

#### P L E I O T R O P Y   A N D   P L E U R O M A M M A

The idea that an allele at a single locus on a chromosome may influence the manifestation of a large number of characters has significant evolutionary implications. Changes at one locus could then mediate a number of changes in the phenotype. A cursory review of the literature about pleiotropy indicates that analyses of this process center around the singular co-occurrence of two or more morphological, physiological, or biochemical characters. Often these characters are not associated with the same organ system and the reason for the co-occurrence of the characters is seldom understood.

As has been indicated, the distribution of asymmetrical characters of *Pleuromamma* shows unique concordance. Where function can be deduced from studies of another calanoid (Blades & Youngbluth, 1979) characters such as male and female genital segments, male leg 5, and geniculate antenna 1 belong to the reproductive system of the animal.

Two hypotheses might explain the unique concordance. Pleiotropy - the asymmetrical expression of all characters is controlled at single locus. Changes at that locus concurrently alter the side that every character occurs resulting in unique concordance. Linkage - the asymmetrical expression of each character is controlled at its own locus. Unique concordance will result if all individual loci are positioned on the chromosome in such a way that most mechanical processes affecting the chromosome fail to recognize these individual loci, if together all loci are usually treated as a single genetic unit.

Should linkage obtain, rare mechanical chromosomal processes might be expected to recombine the individual loci to produce, for example, males with the geniculate antenna 1 on the same side as the black organ or males with the mitten-shaped (spermatophore-

-bearing) leg 5 on the side opposite the genital opening. Such individuals should be incapable of completing parts of the ritualized reproductive behavior (Blades & Youngbluth, 1979) and therefore would be unable to pass this combination of characters to the next generation.

Thus the study of preserved specimens of *Pleuromamma* cannot prove conclusively a hypothesis of pleiotropy; evidence will always be circumstantial. Pleiotropy can be disproven by accepting the hypothesis of linkage. Conclusive evidence for linkage would be provided by specimens with unusual combinations of asymmetrical characters - specimens which vitiate the unique concordance of characters found to date.

TABLE III

Nine possible cases for the predominant distribution of the Black Organ in *Pleuromamma*

Case	Attributes		Representatives*
1	female-left or right	male-left or right	<i>indica</i>
2	female-left or right	male- <del>right</del> left	<i>abdominalis, xiphias</i>
3	female-left or right	male- <del>left</del> right	none
4	female-left	male-left or right	none
5	female-right	male-left or right	none
6	female-left	male-left	none
7	female-left	male-right	none
8	female-right	male-left	none
9	female-right	male-right	<i>scutullata, robusta, quadrungulata, piseki, borealis, gracilis</i>

\*Based on present understanding of *Pleuromamma* systematics/external structural morphology.

#### THE EXTANT DISTRIBUTION OF ASYMMETRY - CAUSAL FACTORS

In this section the controlling factor for unique concordance of asymmetry (whether pleiotropy or linkage) is assumed not to have changed during the evolutionary history of *Pleuromamma*. Factors selecting for the distribution of asymmetry may change, altering a dynamic equilibrium over time. Since asymmetrical characters in both females and males show unique concordance, the position of the black organ alone will be used to represent all other characters during the discussion of distribution of asymmetry.

Any causal mechanism for the distribution of asymmetry must, among other things, explain the attributes and representatives found in table III. Influences may include strict inheritance, en-



vironmental determination, or a combination of both. Ideas about the first two are presented here.

In strict inheritance genes determining left or right position of the black organ are present in the populations and the various attributes would be obtained by gene recombination during sexual reproduction. In many species one gene is repressed in both sexes (Case 9) or expressed only in females (Case 2). The presence of this gene may be fatal to males or males and females before they reach stage I copepodid.

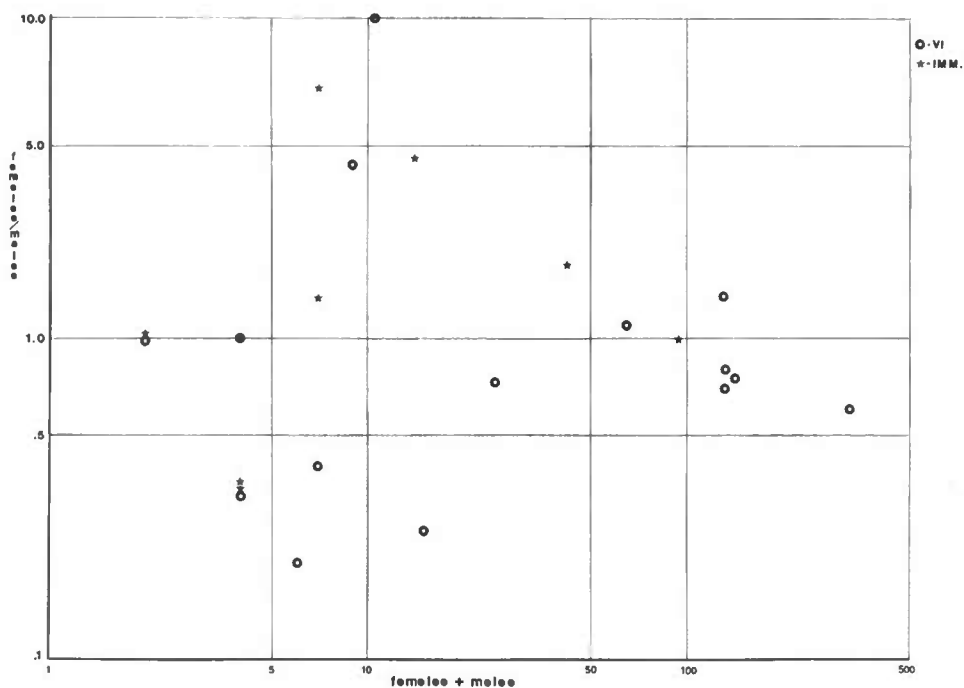


Fig. 2. Total number of males and females vs. ratio of males to females of both adult (VI, dark star) and immature (IMM, light star) *Pleuromamma xiphias* (Giesbrecht) from selected stations.

A preliminary analysis of *P. xiphias* will illustrate some of the complexities of the approach. *P. xiphias* was chosen because specimens are large and easy to recognize with their cephalic crest. Females commonly, but males only infrequently, exhibit dimorphic asymmetry. It is possible in this species that most males with the gene for right side black organ die. Among 177 male immature copepodids examined only one had the organ on the right side; mortality of right side males seems to occur before metamorphosis. If the gene for black organ position is sex-linked and females heterogamic (XY) 25% or 75% of the males would die, depending on whether the right side gene is recessive, or dominant homozygous or heterozygous. If males are heterogamic (Marshall & Orr, 1972, for *Calanus*), 50% of them would fail to survive.

TABLE IV

*Pleuromamma xiphias* (Giesbrecht); number of females (F), males (M), total (T), ratio of males to females (M/F), and ratio of females with left or right black organs (L/R) for both adult (VI) and immature (IMM) specimens from selected stations

	VI					IMM				
	F	M	T	M/F	L/R	F	M	T	M/F	L/R
Albatross IV *	73	59	132	.80	.52					
Oregon II *	55	75	130	1.36	.57					
Bache 10182	81	61	142	.75	.72	3	11	14	3.66	.0
Bache 10192	73	58	131	.79	.70	47	47	94	1.00	.47
Bache 10176	12	3	15	.25	.20					
Bache 10173	2	7	9	3.50	1.00	0	3	3	∞	0
Bache 10166	4	0	4	.0	.0					
Bache 10186	2	2	4	1.00	.0	0	1	1	.0	0
Bache 10163½	0	1	1	∞	0					
John.SI 86	1	10	11	10.00	.0					
John.SI 30	5	1	6	.20	.66					
John.SI 84	1	3	4	.33	∞					
John.SI 60	0	2	2	∞	0					
Alb. 4700	202	122	324	.60	.63	16	27	43	1.70	.14
Alb. 4732	31	34	65	1.10	1.21	1	6	7	6.00	.0
Alb. 4707	14	11	25	.73	.56	0	1	1	∞	0
Alb. 4681	5	2	7	.40	.25	1	1	2	1.00	∞
Alb. 2195	0	4	4	∞	0					
Alb. 5063	2	0	2	.0	.0					
Alb. 4619	2	0	2	.0	.0					
Alb. 5155	1	1	2	1.00	.0	3	4	7	1.33	.50
Alb. 4703	1	0	1	.0	∞					
Alb. 2224	1	0	1	.0	∞					
Alb. 4695	1	0	1	.0	.0					
Alb. 4717	0	1	1	∞	.0					
Alb. 4709	0	1	1	∞	.0					
Alb. 4734						3	1	4	.33	.50
Alb. 4574						3	1	4	.33	2.00

\* Combined series of stations, close temporally and spatially, assumed to sample the same population.

Assuming no mortality for females and no further mortality differences between sexes after metamorphosis, the ratio of male to female copepodids should be instructive. Table IV shows this ratio for both adults and immature copepodids from a series of selected stations. The ratios are variable and might be sample-size dependent. Figure 2 shows each ratio plotted against total number of adult or immature specimens. At sample sizes above 20 specimens the variability of the ratio is reduced; values fall between .60 and 1.70 with five or nine below 1.00. Of the five samples with over 100 specimens, four ratios fall below 1.00. Further indirect support for sample-size dependence of the parameter is seen in a similar reduction in variability for the ratio of left to right females plotted against total number of females (fig. 3).

The above data suggest a reduction of the male/female ratio below 1.00 for large sample sizes, lending some credence to the idea that left male copepodids fail to survive. Attempts at deciding which theoretical ratio obtains cannot be made for the following reason. All asymmetrical characters show unique concordance and, as far as is known, are involved in reproduction. In males of *P. xiphias* a number of asymmetrical characters are found on legs 1-4. If the function of these legs in adult males has shifted from a purely swimming role, assumed for adult females and immature females and males, adult males may be weaker swimmers and more easily collected with nets. Their numbers then will be overestimated relative to adult females.

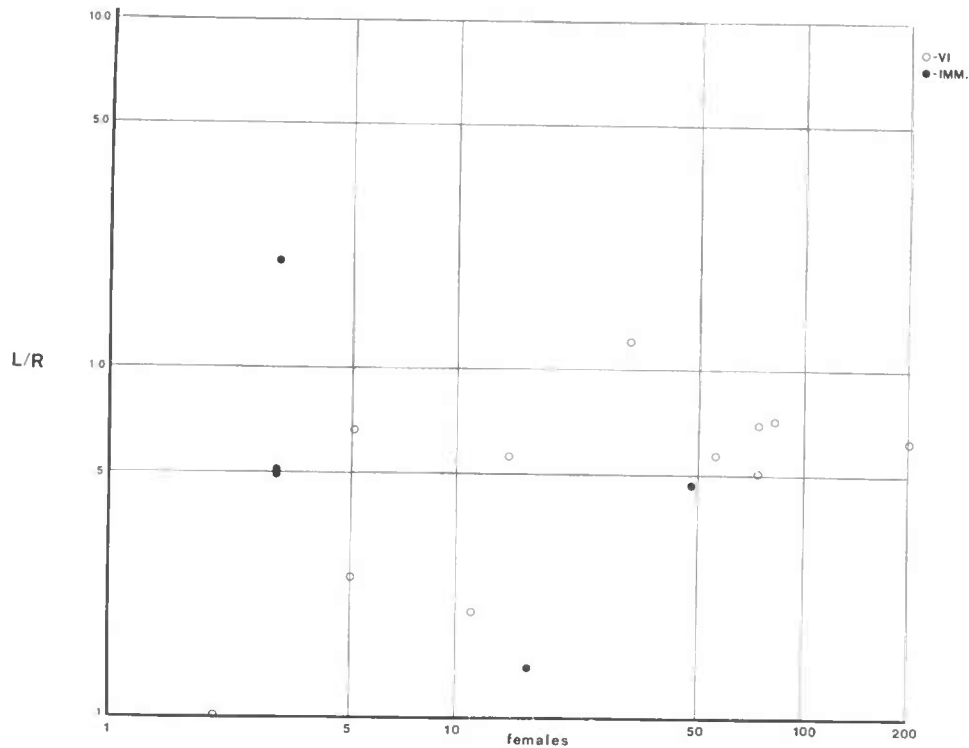


Fig. 3. Number of females vs. ratio of females with left or right black organ (L/R) of both adult (VI, light circle) and immature (IMM, dark circle) *Pleuromamma xiphias* (Giesbrecht) from selected stations.

Such a bias may be avoided by using ratios of immature males to immature females. Like most free-swimming copepods, they show little sexual dimorphism and are most similar to adult females. In this study immature copepodids of *P. xiphias* were rare; the few ratios available to date for immature animals are too variable to provide relevant information. Similar studies of males

without modified legs 1-4 (e.g., those in Case 9) are complicated by the low frequency of dimorphic asymmetry in conspecific females or (Case 1) high frequency of dimorphic asymmetry in the males themselves.

A second approach is to assume that all zygotes have the potential of being left or right sided and the actual position is determined by environmental conditions as, for example, is sex determination in some freshwater turtles (see Bull & Voght, 1979). Steuer implies such a possibility in his discussion of local variation in the ratio of left to right animals. Indirect support for such an explanation through biogeographical studies, presently underway, is complicated by the variety of environmental conditions encountered by *Pleuromamma* spp., some of the most exemplary migrators among the calanoid copepods.

Since a number of asymmetrical characters are involved in reproductive behavior, the question of preferential selection during mating should also be addressed. Even if *P. indica* can be assumed to represent two reproductively isolated populations and thus could be divided by either of two alternate methods, i.e., left females with left males (Case 6) and right females with right males (Case 9) or right females with left males (Case 8) and left females with right males (Case 7), there are still species, *P. xiphias* and *P. abdominalis*, in which a predominantly left male population can select left or right females. Frequency of attached spermatophores may give some indication of selection but such instances are uncommon. No specimens of either species were found in the present study although cases were reported but not analyzed by Steuer.

A second consideration of mating preference would be to what extent morphological asymmetry implies functional or behavioral asymmetry. Because males exhibit more pronounced morphological asymmetry do females select for left or right males based on functional asymmetry during mating behavior? Except for *P. indica* dimorphic asymmetry is infrequent in males of extant species. Because females are only weakly asymmetrical is a male less likely to prefer left or right females if they show correspondingly weak functional asymmetry? Does this explain frequent dimorphic asymmetry in females of three of the nine extant species?

If mate selection occurs in *Pleuromamma*, it would argue for an environmental causal agent for asymmetry or some other source of both left and right genes into the populations exhibiting dimorphic asymmetry. Otherwise even weak selection should produce a noticeable shift in gene frequency in fifty years. As the above questions indicate, data on mate preference for males or females, as well as more general information about the reproductive behavior of the species, would make a significant and much needed contribution to understanding the extant distribution of asymmetry in *Pleuromamma*.

PLEIOTROPY - ITS POTENTIAL  
EVOLUTIONARY SIGNIFICANCE

In this section pleiotropy is assumed to be the controlling factor for the unique concordance of bilaterally asymmetrical characters and is assumed not to have changed during the evolutionary history of *Pleuromamma*.

As far as is known species of *Pleuromamma* share the attribute of male dimorphic asymmetry with only one other calanoid; the amphiscandrian *Clausocalanus furcatus* (Brady, 1883) (see Frost & Fleminger, 1969) shows unique concordance in leg 5 and genital opening. In most heterarthandrian families all males have the geniculate antenna 1 on the right. Families in which the reverse is true include Lucicutiidae, Arietellidae and Heterorhabdidae (see Andronov, 1974). Besides *Pleuromamma* of the Metridiidae, *Euaugaptilus* of the Augaptilidae is the only reported genus with species having the geniculate antenna 1 on the right, *E. hecticus* (Giesbrecht, 1889), and left, all other species. *E. hecticus* is a poorly known species; the position of its genital opening and configuration of its leg 5 has not been reported.

Thus males with left geniculate antenna 1 have evolved at least three times, apparently independently, within the heterarthandrian line: in *Pleuromamma*; in *Euaugaptilus*; and in Lucicutiidae, Heterorhabdidae, and Arietellidae. If pleiotropic control of asymmetric sex characters obtains throughout the Calanoida then "left" males have also evolved at least once in the amphiscandrian family Clausocalanidae (here males lack a geniculate antenna 1).

Steuer placed *P. indica* close to his "stem form" of the genus. Heuristically this is an interesting concept and has a superficial appeal since *P. indica* is the only species which exhibits frequent dimorphic asymmetry in both sexes. However, this is an unusual attribute. Only *P. xiphias* and *P. abdominalis* exhibit frequent dimorphic asymmetry in females and no other species in *Pleuromamma* exhibit this in males. However, based on the more frequent positions of the male geniculate antenna 1, leg 5, and genital opening, males of *P. xiphias* and *P. abdominalis* are more similar to males of other genera in the Metridinidae. Both *Metridia* and *Gaussia* males have right geniculate antenna 1, and left genital opening and spermatophore-bearing leg 5.

An equally superficial phylogeny, utilizing dimorphic asymmetry alone, might assume a metridinid ancestor; evolution of dimorphic asymmetry with selecting factors promoting infrequent expression in both sexes and males still predominantly with a right geniculate antenna 1; relaxation of those factors which might result in frequent expression for females; further relaxation might result in frequent expression for both sexes; introduction of a new set of factors might result in infrequent expression for both sexes and favoring males with a left geniculate antenna 1. Here *xiphias/abdominalis* are the oldest extant species, with *indica* next; all others are younger.

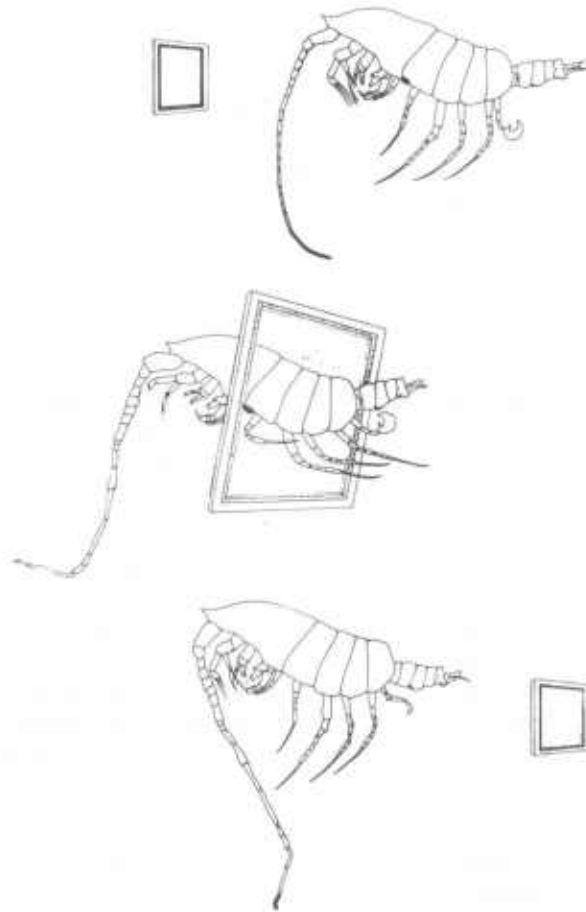


Fig. 4. *Pleuromamma xiphias* (Giesbrecht) fancifully passing through Alice's looking-glass and illustrating the unique concordance of asymmetrical characters and the origin of dimorphic asymmetry.

The genus *Pleuromamma* exhibits unique concordance in the position of a number of characters apparently confined to a single system, the reproductive system. The set of potential outcomes for the expression of these characters, left or right, is a binary one. Infrequent expression of dimorphic asymmetry among males seems to indicate selection for a singular outcome in this sex. Pleiotropy has been suggested as the controlling mechanism for the unique concordance. The potential significance of changes from left to right during evolutionary history on the biology of the animals is unknown. Based on our understanding of the importance of secondary sex characters in speciation of calanoids (Fleminger, 1975), changes in frequency of dimorphic asymmetry in sex characters should have had a significant influence on these populations.

Equally significant was the introduction or origin of dimorphic asymmetry into a homogeneous asymmetric population, if the latter was the ancestral *Pleuromamma*, or the introduction of asymmetry in a symmetrical heterarthrandrian ancestor if an *indica*-like dimorphic asymmetrical animal was ancestral to *Pleuromamma*. In either case there was a major change in the expression of a number of characters assumed to be controlled at a single gene locus. Furthermore consider the case of the origin of left individuals from a homogeneous right population. The potential set of outcomes for any individual in the descendant generation is a binary set: left or right. The introduction occurred, then, in a generation; the same situation holds for the origin of right individuals from a homogeneous left population. In considering the origin of asymmetrical individuals from a homogeneous symmetrical population a similar analysis holds. The potential set of outcomes for an individual in the descendent population is a binary set: symmetrical or asymmetrical. Again the introduction occurred in a generation in all three hypothetical situations. There are no intermediate alternatives to the binary set of outcomes; change is abrupt.

Do the above circumstances, that is immediate change, pleiotropically manifested in a number of characters, have any evolutionary significance beyond the phylogeny of *Pleuromamma*? Any evolutionary model can be thought to consist of processes working on substrates. The classic model of speciation articulated by Mayr (for example see 1963) finds much support in morphological and biogeographical studies of calanoid copepods (Fleminger, 1975; Fleminger & Hulsemann, 1974 and 1977). This model involves slow accumulation of slight genetic changes which eventually bring about reproductive isolation by the accumulation of slight changes in the reproductive behavior of spatially isolated populations of copepods. Here the process is slow and cumulative. The substrate is the reproductive system of the animals. The environment acts only initially, by spatially isolating the populations. Beyond this, the model is mediated through behavioral interaction of sexes within the isolated populations.

In the case for *Pleuromamma* the process of morphological change is abrupt. Changes at a single gene locus may have been magnified by pleiotropy to manifest a more general change in the reproductive system of the phenotype. In this case the substrate is also the reproductive system. But it need not be. Any system of the copepod, feeding, locomotor, etc., would qualify if a single gene controls, through pleiotropy, the expression of a large number of phenotype characters. The second model differs from the first in a number of ways: first, the amount of time needed to manifest change; next the substrate, the first model is confined to the reproductive system, the second to any system in the animal; finally, the role of the environment. In the first model, as noted, the environment plays an initial role in separating populations spatially. In the second its role is more immediate

and demanding and is illustrated by the following example. If a number of aspects of the locomotor system of calanoids, e.g., aspects of the structure of the exopods and endopods of the swimming legs, the extent of the development of their plumed setae, the prosome to urosome ratio, and the position and development of the corresponding musculature, is determined by a single genetic unit and controlled pleiotropically, a change in this unit could manifest a significant change in the phenotype. Theoretically such animals, by changes in their locomotor behavior, could occupy a new niche. If this niche is not defined in the environment or is defined and available but already occupied, the result of such a change is failure.

#### A C K N O W L E D G E M E N T S

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#### A B S T R A C T

Bilaterally asymmetrical characters in the calanoid copepod genus *Pleuronomamma* are described; most are found in the reproductive system. All asymmetrical characters on an animal show unique concordance; their positions on the body are always fixed relative to one another. Together, however, their positions on the left or right side of the body may change from one animal to another; that is populations may exhibit dimorphic asymmetry. All species exhibit dimorphic asymmetry although frequency of expression varies among species and sometimes between sexes. Both pleiotropy and linkage are considered as controlling factors for this unique concordance of asymmetrical characters. Causal factors briefly discussed include strict inheritance and environment. The process of pleiotropy is examined within the broader framework of calanoid evolution.

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## DISCUSSION

*G.A. Boxshall*: Given that the number of crossovers between tightly linked genes is going to be very small, do you think your samples are large enough to show evidence of pleiotropy?

*Answer of lecturer*: Obviously, if pleiotropy occurs, the number of individuals observed is more than enough, especially considering my poor eyesight. If linkage obtains then obviously the number of individuals I have seen is too small by at least one.

ERROR in Fig. 2: the ordinate should read "males/females"; the figure legend is correct.

MORPHOLOGY OF THE ANTENNA AND ITS IMPORTANCE IN  
THE SYSTEMATICS OF THE CYCLOPIDAE

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I N T R O D U C T I O N

In the systematics of Copepoda the general morphology of the mouthparts and the antennulae has been studied fairly intensively, as illustrated by the works of Hartog (1888), Claus (1863), Lang (1946), Fryer (1957) and others. Recently, electron microscopic data of some of those appendages have become available through the publications of Strickler & Bal (1973), Friedman (1980), and Ong (1969).

In Cyclopoida, the number of antennal segments was used for subdivision at the family level, but was considered of no importance at the genus and species level (Kiefer, 1928). The structural details of the antennae were never fully investigated. Data on the general morphology were reported by Gurney (1933) and Sars (1913-1918).

In recent years, the study of sensory and non-sensory cuticular structures became of great interest. This led to an increasing list of various types of structures and patterns, observed in several crustacean groups (Mauchline & Ballantyne, 1975; Mauchline et al., 1977; Mauchline, 1977; Anderson, 1975; Schmalfuss, 1978; Klepal & Kastner, 1980). Pores, located on the integument of the calanoid genus *Eucalanus* were investigated by Fleminger (1973) and mapping of these pores proved to be relevant to systematics and phylogenetics.

The detailed study by Van de Velde (this volume) of the antennae in the genus *Mesocyclops* clearly shows the taxonomic importance of the basipodite ornamentation at the species level. In the present study, the antennae of 45 species and/or subspecies belonging to 14 cyclopid genera and subgenera, were carefully examined and compared.