

DESCRIPTION AND PHYLOGENY OF
ISAACSICALANUS PAUCISETUS, N. GEN., N. SP.,
(COPEPODA: CALANOIDA: SPINOCALANIDAE)
FROM AN EAST PACIFIC HYDROTHERMAL
VENT SITE (21°N)

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Abstract.—A new genus and species of Spinocalanidae is described under the name *Isaacsicalanus paucisetus*. It was collected from the submersible R/V *Alvin* adjacent to the seafloor of the East Pacific Rise off the mouth of the Gulf of California. The copepod was observed swimming in a small swarm, apparently unispecific and all adult females, among concentrations of macrobenthic invertebrates typical of known hydrothermal vent communities. The new copepod's most distinctive morphological features relative to other spinocalanids are the longer urosome, shorter antennule, and fewer setae on oral appendages. Phylogenetic analysis supports the hypotheses that the new genus occupies a highly derived position within the Spinocalanidae and that the family is the most primitive within the superfamily Clausocalanoidea.

Taxonomic reports on the recently discovered bathyal suspension-feeding macrobenthos assemblages immediately adjacent to hydrothermal vents along oceanic spreading centers (Lonsdale 1977) reveal that virtually all the constituent species and their respective genera are new to science. The taxonomically unique qualities of these assemblages suggest that these species have persisted within a hydrothermal vent-dominated habitat for appreciable periods of evolutionary time. Micro-invertebrates have also been represented; Humes and Dojiri (1980) described a new genus and species of thigmotactic siphonostome copepod found on the tentacular crown of tubicolous vestimentiferan worms from vent localities on the Galapagos rift. The present report considers a free-living planktobenthic calanoid copepod that appears to be a member of a hydrothermal vent community on the East Pacific Rise at the mouth of the Gulf of California.

The new form is morphologically most like *Teneriforma* Grice and Hulsemann, 1967; several unique character states in the new form require minor emendation of Damkaer's (1975) description of Spinocalanidae.

Materials and Methods

Thirty-two adult female individuals comprise the specimen series available for this study. They were collected adjacent to the seafloor at the East Pacific Rise several hundred kilometers west of Cabo Corrientes, Mexico; sampling details are presented below as part of the species' description. Initial preservation was by freezing in sea water at -20°C following transfer to the surface. The specimens were stored frozen at -70°C for about 10 weeks in the laboratory before transfer to formalin. They were immersed in glycerol for study. Internal organs are mostly

indistinguishable, presumably a consequence of freezing at relatively high temperatures and precluding observations on the nature and contents of the midgut as well as limiting evaluation of ovarian development.

All measurements were made of specimens immersed in glycercol. Figures were drawn with the aid of a camera lucida. Habitus views were drawn from specimens in which soft tissues were removed by KOH digestion and the cuticle lightly stained with chlorazol black.

List of abbreviations used in text and figures.—A1, antennule; A2, antenna; B1, coxal segment of appendage; B2, basal segment of appendage; Li1, 2 . . . , medial lobe(s) on protopod of cephalic appendage; Md, mandible; Mx1, maxillule; Mx2, maxilla; Mxp, maxilliped; P1, 2, 3 . . . , paired swimming legs 1, 2, 3 . . . ; Re1, 2 . . . , exopod, segment 1, 2 . . . ; Ri1, 2 . . . , endopod, segment 1, 2 . . . ; Sel, 2 . . . , lateral spine on exopod of swimming leg; Si, seta; St, terminal spine on distalmost exopodal segment of swimming leg; ThI, II, III, IV, V pedigers (=thoracic segments, Bowman 1976:187) bearing swimming legs 1, 2, 3 . . . respectively.

Family Spinocalanidae Vervoort, 1951

Diagnosis (emended from Damkaer 1975).—Calanoids with P1 Re trimerous. P1 Re1 with 0 or 1 Se, Re2 with 0 or 1 Se, Re3 with 1 Se, 1 St and 4 Si; Ri with one segment and 3 to 5 Si. Re trimerous in P2–4, Re3 with 3 Se, 5 Si, and one finely serrate St; lateral margin of Re3 not serrate. P2 with bimerous Ri, Ri2 with 2 medial, 2 terminal and 0 or 1 lateral setae. P3–4 with trimerous Ri, Ri2 with 1 medial seta, Ri3 with 2 medial, 2 terminal and 0 to 2 lateral setae. In female, cephalosome and ThI separate, ThIV and V usually separate, ThV distal end sometimes prolonged, apex may be pointed; P5 absent; A1 with segments 8 and 9 fused, 24 and 25 articulating or fused; A2 Re usually equal to or longer than Ri; setation of mouthparts and other details given in Tables 1 and 2.

Isaacsicalanus, new genus

Diagnosis.—Robust spinocalanid; female with elongate urosome about half length of prosome. Short A1 about as long as prosome. Rostrum short, lobate without any semblance of bifurcation. Mx1 with B2 fused to proximal part of Ri and bearing 4 Si; Li 2 with 1 seta, Li3 lacking Si. Distal Si of Mx2 and Mxp unarmed except for very fine setules on proximal side. Mxp B1 with 2 Si. P1 Re1 and 2 lacking Se. P1 Ri with 5 Si and prominent shoulder (lateral swelling produced anterodistad, knob-like) at segment's midlength and bearing spinules concentrated at apex. P2–P4 with Re3 Se3 about twice as long as Sel 1 and 2. A2 Re1 without Si, Re2 and 3 not fused, Re2 with 1 Si. Posterior surfaces of P2–P4 without spines.

Etymology.—The generic term *Isaacsicalanus* is masculine and a combination of the late John D. Isaacs' surname and *-calanus*, the suffix of many calanoid copepod genera. The name is proposed in memory of John D. Isaacs, a pioneering leader in oceanography, to acknowledge his many scientific contributions, the brilliant and the outrageous, and for his unwavering and most generous support of zooplankton research at Scripps Institution of Oceanography (SIO). It is also a personal expression of gratitude for the many kindnesses he showed me during 20 years of collegial association at SIO.

The type-species of the new genus is by original designation, *I. paucisetus*, described below.

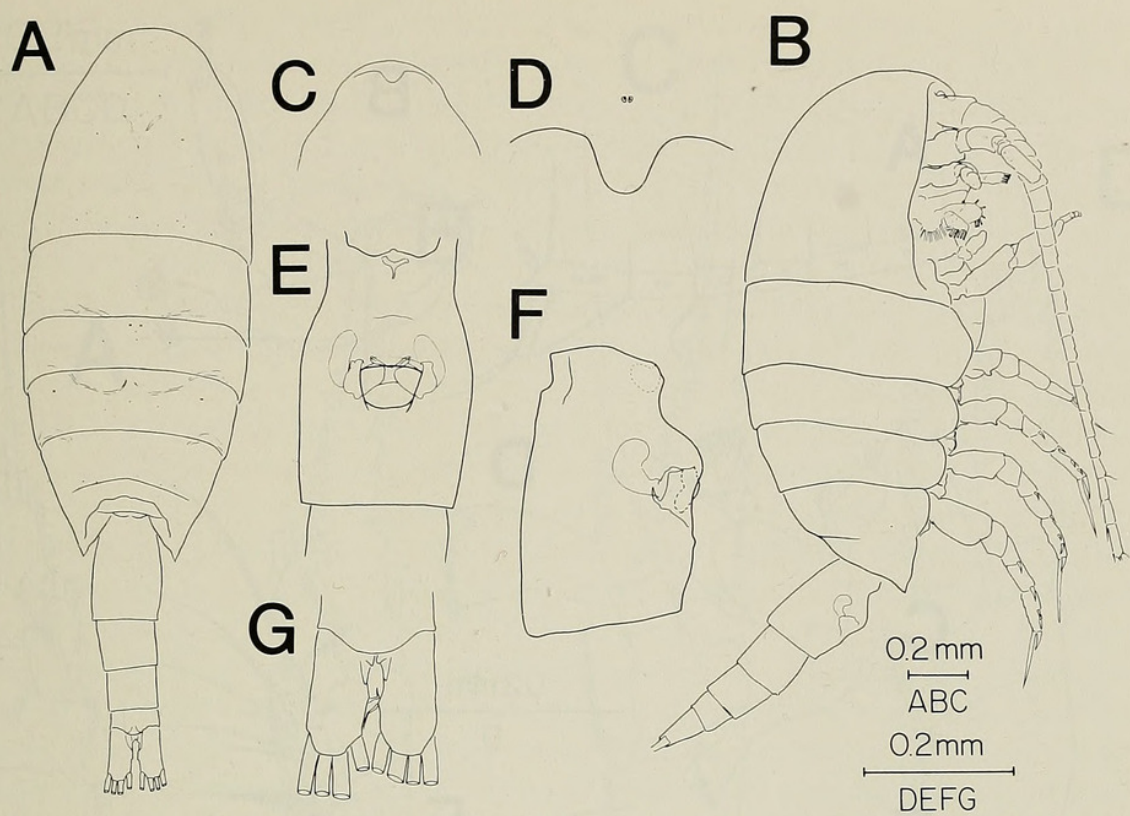


Fig. 1. *Isaacsicalanus paucisetus*. Adult female. A, Habitus, dorsal; B, Habitus, lateral; C, Forehead and rostrum, ventral; D, Rostrum, anterior; E, Genital segment, ventral; F, Genital segment, lateral; G, Furca, dorsal.

Key to Adult Females of Spinocalanid Genera

- 1. P1 Re1 with Se; P2 to P4 with one or two rows of spines on posterior surface of Ri2 2
- P1 Re1 without Se; P2 to P4 lacking row of spines on posterior surface of Ri2 3
- 2. Rostrum produced into 2 strong spiniform processes *Monacilla* Sars, 1905
- Rostrum absent *Spinocalanus* Giesbrecht, 1888
- 3. Rostrum absent. Prosome at least 4 times length of urosome, caudal ramus length not more than 1.5 times width *Mimocalanus* Farran, 1908
- Rostrum present but not bifurcate. Prosome no more than 3 times length of urosome. Caudal ramus length about 2 times width 4
- 4. A1, extended, reaching to anal segment, A2 with endopod longer than exopod, Mxp B1 with 5 Si *Teneriforma* Grice and Hulsemann, 1967
- A1, extended, reaching to ThV, A2 with exopod longer than endopod, Mxp B1 with 2 Si *Isaacsicalanus*, gen. n.

Isaacsicalanus paucisetus, new species

Figs. 1, 2, 3

Measurements.—Adult female total length to distal end of caudal ramus, range 2.44 to 2.56 mm, \bar{x} 2.501 \pm 0.0259 mm (95% C.L., N = 10, s = 0.0368).
Prosome:urosome length ratio, measurements taken along mid-sagittal plane from apex of forehead to hinge between prosome and urosome and from hinge to distal end of right caudal ramus; range 2.03 to 2.19:1, median 2.15:1 (N = 10).

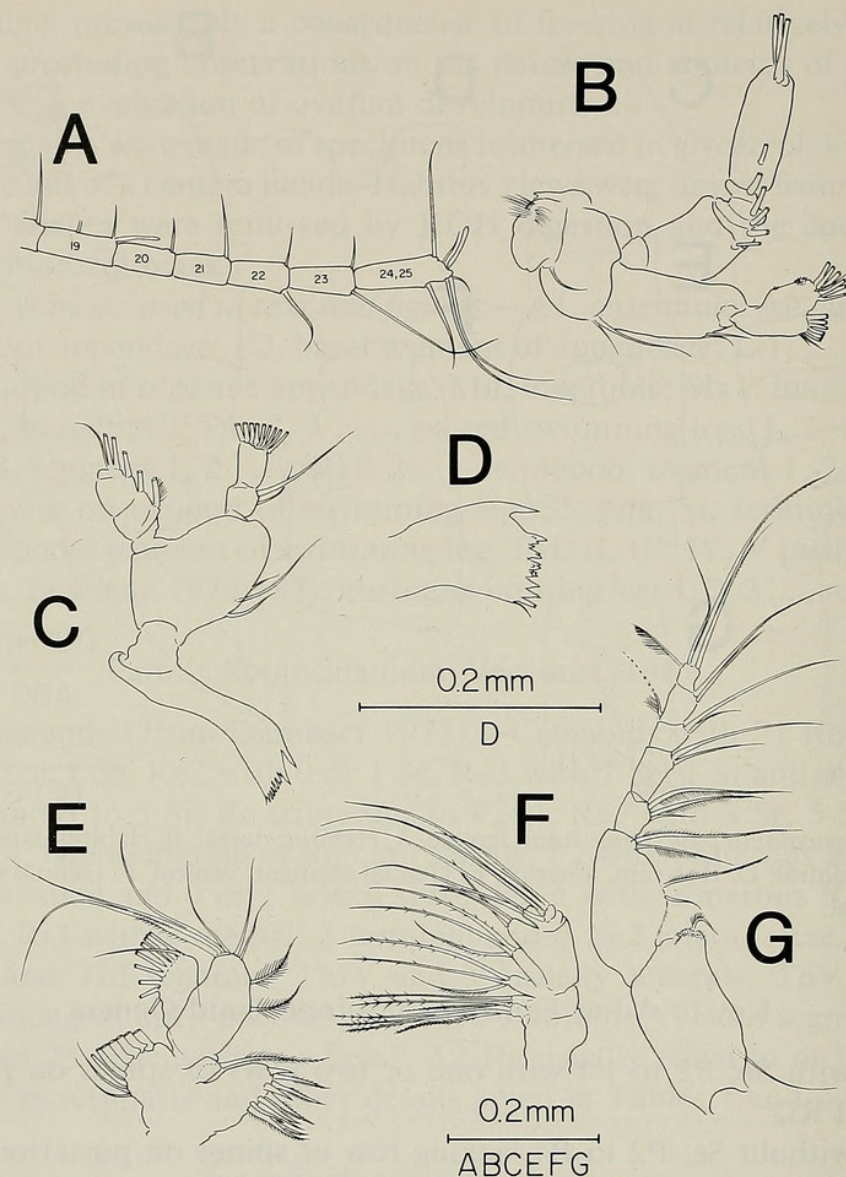


Fig. 2. *Isaacsicalanus paucisetus*. Adult female. A, Right A1 segments 19 to 25, dorsal; B, Right A2, posterior; C, Right Mnd, posterior; D, Right Mnd gnathobase, posterior; E, Right Mx1, posterior; F, Right Mx2, anterior; G, Left Mxp, anterior.

Description and diagnosis of adult female.—Habitus (Figs. 1A, B), forehead broadly rounded, prosome short, about $2.15 \times$ length of urosome; in *Teneriforma naso* (Farran, 1936) prosome is at least $2.5 \times$ length of urosome (measured as above using illustrations in Farran 1936, Grice and Hulsemann 1965 and Wheeler 1970); ThV distal end produced and terminating in a sharp point; A1 short, extended posteriorly not reaching beyond ThV. Caudal ramus about twice as long as wide (Fig. 1G) bearing 4 terminal setae and 1 short medial seta at about midlength of ramus. Cephalosome and ThI separated, ThIV and V incompletely separated, remnant of line of articulation appearing on dorsal side. Rostrum in lateral view short knob-like; in frontal and ventral views (Figs. 1C, D) a short simple lobate process. Genital segment with relatively large seminal receptacles curving anteriorly and swollen distally (Figs. 1E, F).

A1 with 23 articulating segments, segments 8 and 9 and 24 and 25 fused (Fig. 2A). A2 (Fig. 2B) with Re about 1.3 times longer than Ri. Re with total of 9 Si;

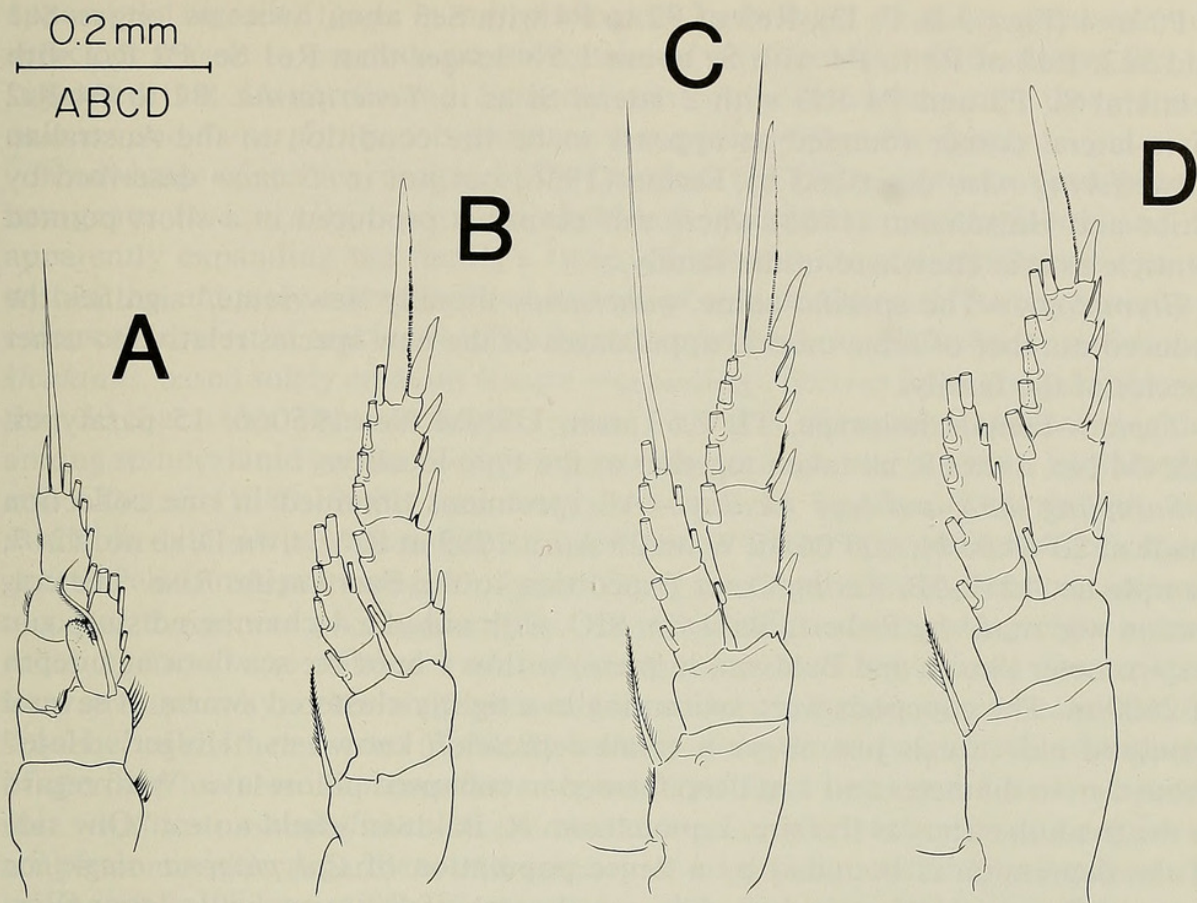


Fig. 3. *Isaacsicalanus paucisetus*. Adult female. A. Right P1, anterior; B, Right P2, posterior; C, Right P3, posterior; D, Right P4, posterior.

Re1 lacking Si, Re2 with 1 Si, remnant of apical segment (Re8) with 3 Si, distinctly separate from preceding segment, Re7, by visible remnant of intersegmental suture; Re7 with 1 Si. Re in *Teneriforma* with total of 11 Si.

Md palp (Fig. 2C) with setation similar to that in *Teneriforma* and *Mimocalanus*. Left and right gnathobase similar, with 8 major teeth of roughly equal size, a small intercalary tooth between the second and third and the third and fourth major teeth and a slender, short Si (Fig. 2D). Ventralmost tooth slender, spiniform, set off from others by deeply cut angular notch; remaining teeth distally bifid; 3 proximalmost teeth bordered by minute denticles.

Mx1 (Fig. 2E) with proximal portion of Ri totally fused to B2 and bearing 4 Si; these parts also fused in *Teneriforma* but combination bearing 10 setae; Ri and B2 not fused elsewhere in family. Li2 with 1 seta, Li3 much smaller than Li2 and lacking Si; elsewhere in family Li1 and 2 bear a total of 6 or more Si.

Mxp (Fig. 2G) with B1 bearing 2 Si, elsewhere in family this segment with 5 or more Si. Si on distalmost segments with minute setules. Ri segments 2 and 3 with 2 Si, Ri4 with 3 Si.

P1 (Fig. 3A) with B2 Si strongly curved as in *Monacilla*; this Si straight in *Teneriforma*. Lateral shoulder of Ri located at about midlength of segment, strongly produced anterodistad in knob-like process with apex bearing numerous spinules; Ri bearing 5 Si as in *Monacilla*. Both Re1 and Re2 lacking Se as in *Teneriforma* described by Farran (1936); Grice and Hulsemann (1965) show P1 Re2 in *Teneriforma* with 1 Se.

P2 to 4 (Figs. 3 B, C, D). Re3 of P2 to P4 with Se3 about twice as long as Se1 and Se2. Re2 of P2 to P4 with Se about $1.5 \times$ longer than Re1 Se. P2 Ri2 with 1 lateral Si; P3 and P4 Ri3 with 2 lateral Si as in *Teneriforma*. P2 to P4 Ri2 disto-lateral corner rounded as appears to be the condition in the Australian *Teneriforma naso* described by Farran (1936) but not in *T. naso* described by Grice and Hulsemann (1965) where this corner is produced in a short pointed denticle as it is elsewhere in the family.

Etymology.—The specific name, *paucisetus*, literally ‘few setae,’ signifies the reduced number of setae on oral appendages of the new species relative to other species of the family.

Types.—Female holotype, TL 2.63 mm, USNM No. 195066; 15 paratypes, USNM No. 195067, all taken together at the type-locality.

Sampling data and type locality.—All specimens obtained in one collection made at 20°49.05'N, 109°06.40'W on 23 April 1982 at R/V *Alvin* Dive no. 1217, Sample no. 1217-3B, during Oasis Expedition to the East Pacific Rise. The collection was made by Roberta Baldwin, SIO, with aid of a 4-chambered slurp gun respirometer (Smith and Baldwin, in press) within 1 m of the sea floor at a depth of 2600 m. The copepods were swimming in a tightly clustered swarm of several thousand individuals just above a small depression known as “Holger’s Hole” about 1 m in diameter and 1 m deep formed in collapsed pillow lava. With regard to the macrobenthos at the site, I quote from R. Baldwin’s field notes: “One side of the depression is bounded by a dense population of *Calypptogena magnifica* Bossard Turner (Vesicomidae) and a small patch of *Riftia pachytila* Jones (Vestimentifera); the bottom, littered with broken lava pieces, is inhabited by the clams and *Munidopsis* sp. (Galatheididae). Water temperatures in the depression range from 5° to 15°C. The collapsed pillow lava site is located in an area known as “clam acres” (2613 m depth) where dense populations live in the mineral-rich waters of the hydrothermal vents off Baja California. The area is located 240 km south of the Baja peninsula and 21° north of the equator on the East Pacific Rise, an area of seafloor spreading where bottom-water temperatures range from 2.2°C over the clam fields to an excess of 350°C in the stalagmite chimneys known as “black smokers.” The collection was incubated *in situ* in the respirometer for about 48 hours before being brought to the surface and frozen. Randomly selected subsamples from the copepod swarm, totalling 32 individuals are all adult females of the new species.

Phylogenetic Relationships among Spinocalanid Genera

The family Spinocalanidae was established to accommodate three genera, *Spinocalanus*, *Monacilla* and *Mimocalanus*, that Vervoort (1951) appropriately removed from the family Pseudocalanidae (=Clausocalanidae Giesbrecht in Bowman and Abele 1982). Knowledge of spinocalanid diversity and distribution accumulated rapidly during the ensuing 20 years in response to widespread oceanic exploration and increased use of opening-closing nets sampling meso- and bathypelagic depths where spinocalanids tend to be most commonly encountered. Damkaer (1975) brought these advances into full focus by virtue of his thorough review of the Spinocalanidae. He recognizes 32 species and 4 genera: 19 species in *Spinocalanus*, 4 in *Monacilla*, 8 in *Mimocalanus* and 1 in *Teneriforma*. Damkaer

apparently regarded gaps in morphological knowledge of many spinocalanids sufficient reason to preclude consideration of phylogenetic relationships, but he suggested that *Monacilla* and *Spinocalanus* comprise a group and that *Mimocalanus* and *Teneriforma* comprise another group within the family.

Knowledge of species recognized by Damkaer (1975) has not advanced, but the new genus *Isaacsicalanus* provides additional infrastructure to the family and, in apparently expanding the family's range of habitats to a planktobenthic niche within the uniquely warm bathyal waters of a hydrothermal vent community, enhances interest in seeking its phylogenetic relationships. Classification of *Isaacsicalanus*, based solely on adult female morphology, derives from analysis of more than 30 characters. These characters reveal a number of apparent synapomorphies among spinocalanid genera. Following procedures discussed at length by Eldredge and Cracraft (1980:19–85) and briefly outlined by Sanders (1981:96–98), the available data set has been used to hypothesize a first approximation of phylogenetic relationships among the spinocalanid genera. In this exploratory attempt to order the genera phylogenetically, character states representing other spinocalanid genera were collated from published accounts of the species. Two criteria were stressed in hypothesizing apomorphies and deciding upon the transformation sequence of character states (Table 1), namely, uniqueness and relative abundance of meristic features. For repetitive segments or their armature I have assumed that within a monophyletic lineage the highest numbers of setae and segments are plesiomorphic, regardless of frequency of occurrence, and that reductions are apomorphic. The most primitive state for each character, found in one or more members of a genus was selected to represent that genus.

For some characters, determining the sequence of character state transformations is readily obvious from the first principles of apomorphy by reduction. Many calanoid morphological features are generally conservative and the plesiomorphic condition widespread. Derived states are immediately recognizable when meristic features are reduced by developmental modifications, e.g., by fusion of adjacent segments, loss of the fifth pair of legs in the females, reduced number of setae on certain appendages, the absence of the rostrum or its failure to bifurcate. The direction of transformation in other characters may not be obvious. Solution requires outgroup comparison, i.e., comparative analysis using as references closely related antecedent and derived taxa in which the character states in question are unmistakably primitive or derived relative to the states under consideration.

Selection of an appropriate outgroup for the Spinocalanidae is not immediately obvious. As is typical of supraspecific calanoid taxa, the present concept of Spinocalanidae is a constellation of mostly plesiomorphic states that distinguishes it from the other 10 families comprising the superfamily Clausocalanoidea (Bowman and Abele 1982). Assuming that convergent reversals have not contributed to the formation of spinocalanids, their ancestry must derive from calanoids with character states as follows:

1. Bifurcate rostrum
2. P2–4 with Re3 bearing 3 Se and 5 Si
3. A1 with 25 articulating segments or with 8 and 9 fused
4. Left and right members of male P5 biramous
5. Trunk segmentation and genital segment morphology: i.e., cephalosome and

Table 1.—Catalogue of characters.

Character code	Character	States recognized and proposed sequence of transformation*	Derived character state no.
*Character state symbols: 0 = primitive condition, derived states coded by integers; → → → hypothesized sequentially derived autapomorphies; ← → hypothesized irregularly derived autapomorphies; ↓ hypothesized autapomorphies reversing sequence.			
SA	P1 Ri	1-segmented with lateral shoulder, 3 to 5 Si	01
SB	P1 Re3	with 4 Si	02
SC	P2-4 Re3	with 3 Se and 5 Si	03
SD	P5	lacking in female, endopod may be present in male but lacking setae	04
SE	A1 segments 8 and 9	partly to totally fused	05
SF	cephalic appendages	show reductions in size and setation in male relative to female	06
A	rostrum	bifurcated—0; absent—07; uniramous—08 hypothesized transformation 07←0→08	07, 08
B	A1 segments 24 and 25	articulated—0; fused—09	09
C	A2 Ri1 setae no.	2—0; 1—10	10
D	A2 Ri2 setae no.	18—0; 16—11; 15—12 0 ↓ ↓ 11 12	11, 12
E	A2 Re1 setae no.	1—0; 0—13	13
F	A2 Re2 setae no.	4—0; 3—14; 1—15; 0—16 0→14→15 ↓ 16	14, 15, 16
G	A2 Re7 setae no.	1—0; 0—17	17
H	Mnd, no. teeth	8—0; 7—18	18
I	Mnd, B2 setae no.	4—0; 3—19	19
J	Mnd, Ri setae no.	14—0; 13—20; 11—21 0→20→21	20, 21
K	Mx1 Re setae no.	12—0; 11—22; 10—23; 9—24 0→22→23 ↓ 24	22, 23, 24
L	Mx1 Ri + B2 setae no.	30—0; 21—25; 20—26; 13—27; 8—28 0→27→28 ↓ 25 ↓ 26	25, 26, 27, 28
M	Mx1 Ri and B2 segments	articulated—0; fused—29	29
N	Mx1 Li3 setae no.	4—0; 2—30; 0—31 0→30→31	30, 31
O	Mx1 Li2 setae no.	6—0; 5—32; 4—33; 1—34 0→33→34 ↓ 32	32, 33, 34

Table 1.—Continued

Char- acter code	Character	States recognized and proposed sequence of transformation*	Derived character state no.
P	Mx1 Li1 setae no.	14—0; 13—35; 12—36; 10—37 0→35→37 ↓ 36	35, 36, 37
Q	Mx2 Li1 setae no.	6—0; 5—38; 3—39 0→38 ↓ 39	38, 39
R	Mx2 Li2 setae no.	3—0; 2—40	40
S	Mx2 Li5 setae no.	4—0; 3—43	43
T	Mx2 Ri setae no.	7—0; 5—41; 4—42 0→42 ↓ 41	41, 42
U	Mxp B1 setae no.	10—0; 9—44; 5—45; 2—46 0→44→45→46	44, 45, 46
V	Mxp B2 setae no.	5—0; 4—47	47
W	Mxp Ri1 setae no.	5—0; 4—48; 3—49; 2—50 0→48→49 ↓ 50	48, 49, 50
X	Mxp Ri2 setae no.	4—0; 3—51; 2—52 0→51→52	51, 52
Y	Mxp Ri3 setae no.	3—0; 2—53	53
Z	Mxp Ri4 setae no.	4—0; 3—54	54
AA	P1 B2Si shape	curved—0; straight—55	55
BB	P1 Re1 spine no.	1—0; 0—56	56
CC	P1 Re2 spine no.	1—0; 0—57	57
DD	P1 Ri setae no.	5—0; 4—58 0 ↓ 58	58
EE	P2—4 spines on post. face of rami	yes—0; no—59	59
FF	P3—4 Ri2 outer distal corner	pointed—0; rounded—60	60
GG	ThV posterior corner	rounded—0; pointed—61	61

ThI not fused, ThIV and ThV not fused; female abdomen with 4 segments and genital segment with large vertically oriented seminal receptacles

6. Appreciable sexual dimorphism modifying appearance of male’s prosome, A1, and setation of cephalic appendages

Spinocalanidae is the only family of the Clausocalanoidea with species exhibiting states 2 and 4 above in combination (*Monacilla* spp. and *Spinocalanus* spp.). Additional plesiomorphic states within the family (e.g., numbers 3 and 5 above, oral appendages with highest number of typical setae within superfamily) mark it as containing the most primitive taxa within the superfamily.

Within the Clausocalanoidea aetideid genera *Aetideopsis* Sars, 1902, *Pseudotharybis* T. Scott, 1909, and, to a somewhat lesser extent, *Bradyidius* Giesbrecht, 1897, came close to agreeing with the five character states characteristic of Spinocalanidae listed above. They are, however, apomorphic to spinocalanids in characters 2 and 5; i.e., relative to spinocalanids they all show a loss of 1 Si on Re3 of P2–P4 and their thoracic segmentation includes partial to total fusion of cephalon and ThI as well as ThIV and ThV or pronounced foreshortening of ThV. Based on all characters analyzed in this study (Table 1) it is conceivable and even likely that these three aetideid genera derive from a *Monacilla*-like ancestor. The search for a closely related outgroup differing from spinocalanids only in a plesiomorphic direction was extended to other superfamilies. Looking beyond the Clausocalanoidea, the family Megacalanidae of the Megacalanoidea (also containing Calanidae, Calocalanidae, Paracalanidae, and Mecynoceridae; Bowman and Abele 1982) appears to be the most promising candidate in that the majority of characters I examined (Table 1) are symplesiomorphic or synapomorphic to spinocalanids and the remainder are plesiomorphic. Two possible anomalous characters, 1., a noncatalogued condition of asymmetry in adult males and, 2., character L, require special consideration, however, before designating the Megacalanidae as the outgroup of choice for determining the direction of transformation sequences (i.e., polarity of morphoclines) in spinocalanids.

Among the males of *Spinocalanus* the orientation of asymmetries found in the A1 and P5, and presumably the position of the genital pore, may appear on the left or the right side of the body depending upon the species (Damkaer 1975:14). To my knowledge asymmetries in megacalanid males do not vary between or within the species. Interspecific reversals in asymmetry, however, are known to occur in *Clausocalanus* (Frost and Fleminger, 1968), *Calocalanus* Giesbrecht, 1888 (Andronov 1973) and the genital opening, typically on the left side in Calanoida, occurs on the right side of the urosome in *Mecynocera* Thompson, 1888 (Andronov 1973). I have infrequently observed intraspecific reversals of asymmetry in the P5 of males of *Eucalanus pileatus* Giesbrecht 1888 inhabiting southeast Asian waters (unpublished). Variation in male asymmetries is a well known feature of the Metridiidae (superfamily Augaptiloidea, a likely source of the Megacalanoidea). Thus, reversal in the asymmetry of spinocalanid males clearly is of no special phylogenetic significance *vis à vis* the Megacalanidae. Reversed asymmetry in males may be an old synapomorphy of the Augaptiloidea, Megacalanoidea, Clausocalanoidea and Eucalanoidea, or in view of its sporadic occurrences merely a number of convergent autapomorphies.

The second exception to the evidence favoring Megacalanidae as the most suitable antecedent outgroup for Spinocalanidae is the number of setae on Mx1 Ri plus B2 (Character L, Table 1). I have not found any species of calanoid to match the total of 30 setae on these segments occurring in *Mimocalanus crassus* (Park 1970:479, Fig. 5). Within Spinocalanidae setal count values range from 21 or, less frequently, 20 setae in *Spinocalanus* (Park 1970: Figs. 27, 47, 73; Damkaer 1975: Figs. 15, 48, 71, 122), 18 to 20 in *Monacilla* (Farran 1908: Pl. 1, Fig. 17; Scott 1909: Pl. II, Fig. 14; Sars 1925: Pl. XI, Fig. 9), 19 to 30 in *Mimocalanus* (Tanaka 1956: Fig. 13d; Vervoort 1957: Fig. 13c; Park 1970: Fig. 5), 13 in *Teneriforma* (Grice and Hulsemann 1965: Fig. 8F), and 8 in *Isaacsicalanus* (Fig. 2E). The Mx1 has not been characterized for a number of described spinocalanids.

Table 2.—Apparent synapomorphies among spinocalanid genera.

Char- acter code	Character	<i>Mona- cilla</i>	<i>Spino- calanus</i>	<i>Mimo- calanus</i>	<i>Teneri- forma</i>	<i>Isaacsi- calanus</i>	Rever- sals
Females							
A	Rostrum	bifur- cated	absent		uniramous		
B	A1 segments 24 and 25		articulated		fused		
C	A2 Ri1 setae no.	1	2	2	2	2	x
D	A2 Ri2 setae no.	15	16	16	15	18	x
E	A2 Re1 setae no.	1	1	0	1	0	x
F	A2 Re2 setae no.	4	3	0	3	1	x
G	A2 Re7 setae no.	1	1	1	0	1	x
H	Mnd no. teeth	8	8	8	7	8	x
I	Mnd B2 setae no.	4	4	3	3	3	
J	Mnd Ri setae no.	14	14	14	13	11	
K	Mx1 Re setae no.	12	11	11	9	10	x
L	Mx1 Ri + B2 setae no.	20	21	30	13	8	x
M	Mx1 Ri and B2 segments		articulated		fused		
N	Mx1 Li3 setae no.	4	4	4	2	0	
O	Mx1 Li2 setae no.	5	6	4	4	1	x
P	Mx1 Li1 setae no.	12	14	13	10	10	x
Q	Mx2 Li1 setae no.	6	6	6	3	5	x
R	Mx2 Li2 setae no.	3	3	3	3	2	
S	Mx2 Li5 setae no.	4	4	3	3	3	
T	Mx2 Ri setae no.	5	7	4	4	4	x
U	Mxp B1 setae no.	10	9	9	5	2	
V	Mxp B2 setae no.	5	5	5	4	4	
W	Mxp Ri1 setae no.	5	4	4	2	3	x
X	Mxp Ri2 setae no.	4	4	4	3	2	
Y	Mxp Ri3 setae no.	3	3	3	2	2	
Z	Mxp Ri4 setae no.	4	4	4	4	3	
			curved		straight		x
AA	P1 B2 seta					curved	
BB	P1 Re1 spine no.	1	1	0	0	0	
CC	P1 Re2 spine no.	1	1	1	1	0	
DD	P1 Ri setae no.	5	5	4	4	5	x
EE	P2–4, spines on post. surfaces of rami		yes		no		
FF	P3–4 Ri2 outer distal corner		pointed		rounded		
GG	Th5 posterior corner		rounded		pointed		
Males							
HH	P5		biramous		uniramous		? ?

Mx1 Ri plus B2 may bear 21 setae in *Clausocalanus* (Frost and Fleminger 1968: Pl. 6, Fig. c) and in metridiids (Giesbrecht 1892: Pl. 32, Fig. 4). Calanids do not appear to exceed 19 setae, whereas megacalanids, also the outgroup of choice for calanids (in prep.), have 17 or fewer setae (Sars 1925: Pl. I, Fig. 11; Pl. III, Fig.

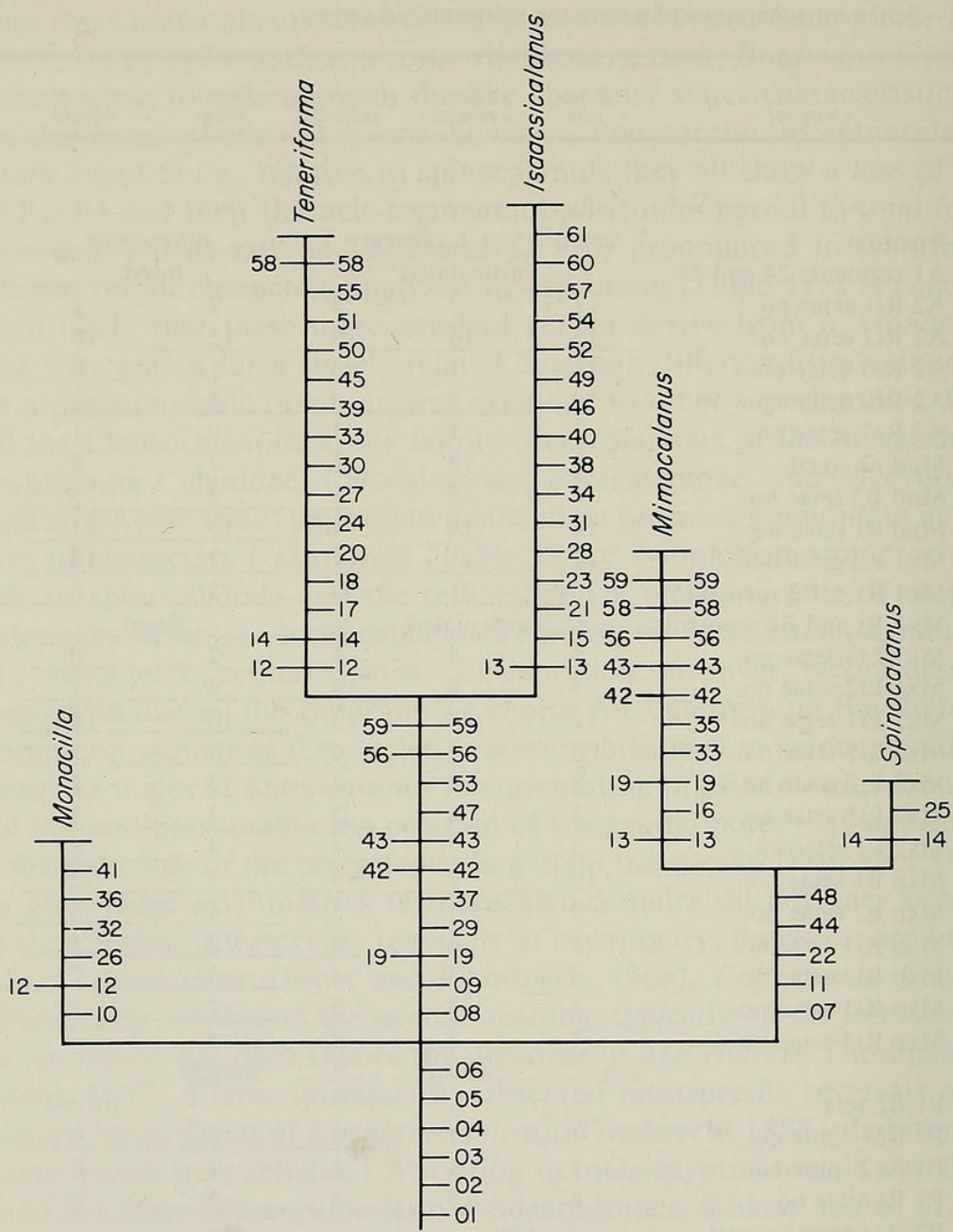


Fig. 4. Dendrogram to summarize distribution of derived character states among spinocalanid genera; derived states defined in Table 1 and discussed in text.

7; Pl. IV, Fig. 7; Bjornberg 1968: Figs. 7, 27, 48, 57, 66). The low number of setae on these segments of Mxl in megacalanids may be an autapomorphy in the known bathypelagic species that appear to be adapted for predation, carrion feeding or large particulate detrital feeding. Considering the incomplete state of knowledge on Mxl setation in the families in question, the 30 setae found on the Mxl Ri plus B2 in *M. crassus* is tentatively regarded to be the plesiomorphic condition for Megacalanoidea and Clausocalanoidea.

In summary, I have hypothesized a megacalanid-like ancestry for the Spinocalanidae and present the direction of character state transformations, i.e., morphoclines, and proposed synapomorphies in Tables 1 and 2, respectively.

As noted above, morphocline direction may be determined from the first prin-

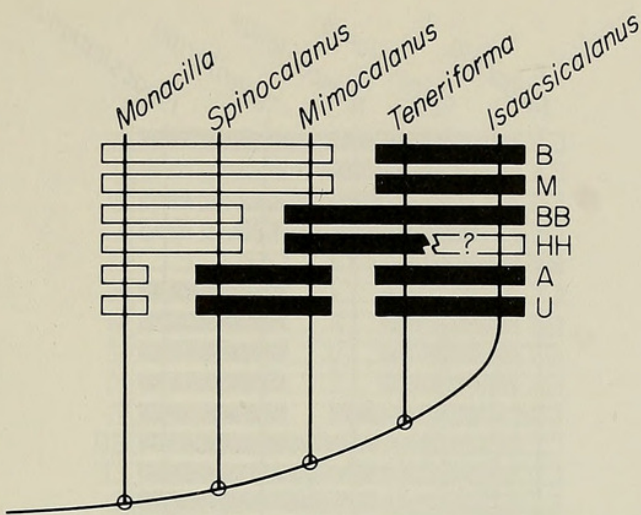


Fig. 5. Cladogram of hypothesized synapomorphies in transformation sequences whose direction is proposed on the basis of first principles of calanoid copepod morphology. Further discussion in text.

ciple of apomorphy by reduction in several instances. For example, the primitive condition of articulating segments of appendages or trunk are replaced autapomorphically by fused combinations of adjacent segments as in the case of Nos. A and M (Table 2). Another assumed plesiomorphy is the bifurcate rostrum produced in a pair of slender processes as found in *Monacilla*. Complete loss of the rostrum (Character No. A) is synautapomorphic in *Spinocalanus* and *Mimocalanus*. Extension of the base of the rostrum into a single nonbifurcate process constitutes a second synautapomorphy in *Teneriforma* and *Isaacsicalanus*.

Results of Phylogenetic Analysis

In the process of classifying *Isaacsicalanus* 33 intrafamilial and six interfamilial character states were determined by microscopic examination of available adult females. States in the other spinocalanid genera were collated from published accounts of the species (Damkaer 1975; Farran 1908, 1936; Giesbrecht 1892; 1971; Grice and Hulsemann 1965, 1967; Park 1970; Scott 1909; Sars 1903, 1925; Vervoort 1951, 1957; Farran and Vervoort 1951; Tanaka 1956; Wheeler 1970). Transformation sequences were proposed, generally on the basis of the first principle of calanoid copepod morphology and confirmed by outgroup comparison with Megacalanidae as described by Sars (1925), Sewell (1947), Bjornberg (1968), and my unpublished observations on *Megacalanus* and *Bathycalanus*. Character states and proposed transformation sequences are presented in Tables 1 and 2. States designated primitive indicate primitiveness of that state in that taxonomic category. This simplifying assumption is necessary due to the general lack of character surveys on calanoid families and genera as well as the logistic difficulties of obtaining specimens for study of seemingly critical species. In Table 1 all characters have been coded by letters, all derived, i.e., autapomorphic, states are coded by integers.

All derived states were used to construct a dendrogram (Fig. 4), following Johnson (1982) that depicts the distribution of derived states among genera of

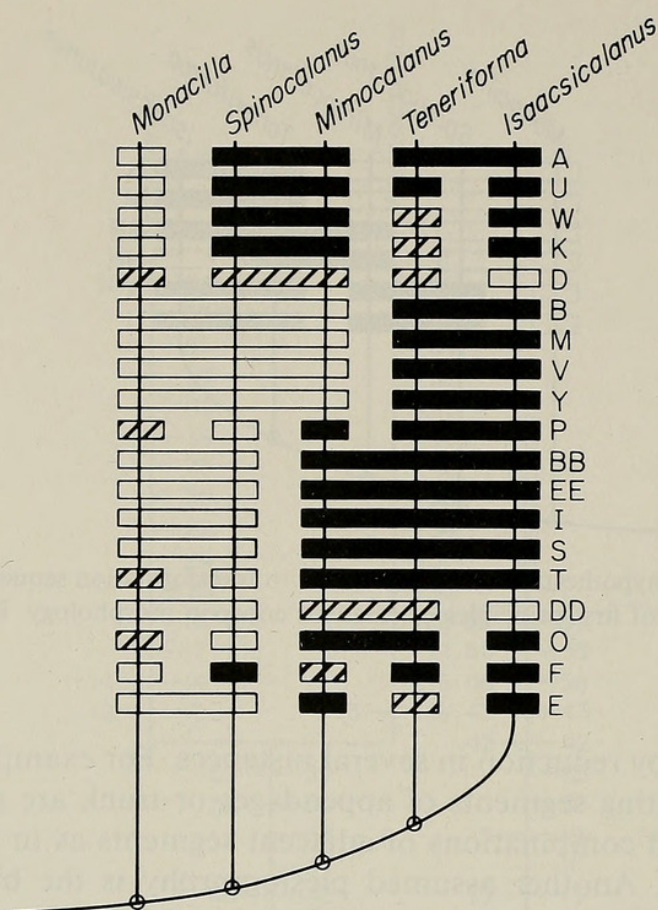


Fig. 6. Cladogram of hypothesized synapomorphies where criterion in meristic states is identical numbers. Transformation sequences determined by outgroup comparison; further discussion in text.

the Spinocalanidae. States 01 to 06 are familial and set Spinocalanidae apart from other families of the Clausocalanoidea. The remaining states provide compelling evidence of the distinctiveness of the five recognized genera and of the apparent synapomorphies that link *Spinocalanus* to *Mimocalanus* and *Teneriforma* to *Isaacsicalanus*. The handful of states appearing in more than one column, marked by the horizontal bar and integers appearing on both sides of the column, provide no indication of phylogenetic relationships suggested by the analyses of proposed synapomorphies presented below.

Potential synapomorphies are presented in Table 2. Initially troubled by the seemingly considerable taxonomic distance between the outgroup Megacalanidae, a primitive member of the Megacalanoidea, and Spinocalanidae, a primitive member of the Clausocalanoidea, I utilized sets of synapomorphies chosen by three different criteria to construct three separate cladograms for comparison.

The first cladogram uses only those proposed synapomorphies (Table 2) whose transformation sequences appear reasonable and unequivocal solely on the basis of first principles of calanoid copepod morphology, i.e., the readily apparent transformation sequences B, M, BB, HH, A and U (Fig. 5). Reductions in the number of setae were arbitrarily omitted from consideration in this analysis, though a number of them (e.g., I, P, S, T, V, Y) satisfy the criteria as well as those characters that were selected. Knowledge of character HH, the presence or absence of endopods on the male's fifth pair of legs, remains incomplete pending discovery

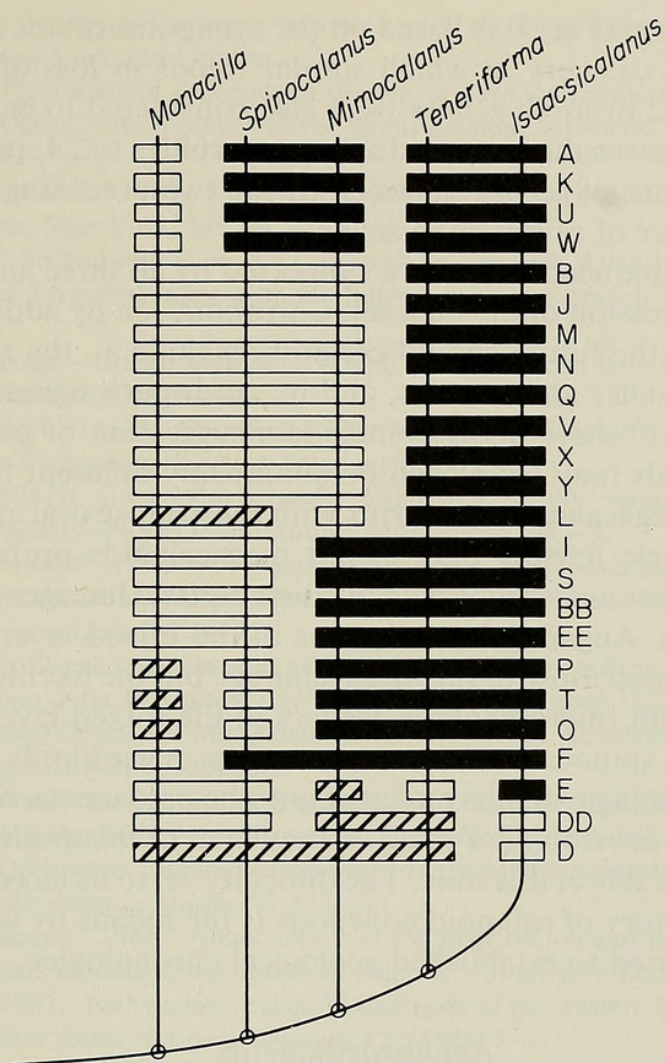


Fig. 7. Cladogram of hypothesized synapomorphies where criterion in meristic states is relaxed to group values with reductions trending similarly. Transformation sequences determined by outgroup comparison; further discussion in text.

of an adult *Isaacsicalanus* male. The six transformation sequences contain no reversals and support the hypothesized phylogenetic relationships shown by this cladogram.

The second cladogram uses transformation sequences in Table 2 that have two or more genera sharing identical derived states; e.g., synapomorphy is proposed when two or more genera share the same number of setae on a given structure other than the value designated primitive. Nineteen such synapomorphies were found, and the resulting hypothesized phylogenetic sequence (Fig. 6) agrees with that of Fig. 5. Nine of the characters show one or more reversals, 8 being readily accountable by assuming autapomorphic losses of one or more setae by the genus showing the reversal. Character D, however, requires autapomorphic losses in 4 genera. Altering the sequences of *Monacilla* and *Spinocalanus*, *Spinocalanus* and *Mimocalanus*, *Mimocalanus* and *Teneriforma*, or *Teneriforma* and *Isaacsicalanus* in each instance increases the number of reversals measurably. Obviously more extensive alterations in the sequence of genera would increase the number of reversals still further.

The third cladogram (Fig. 7) is based on the synapomorphies proposed for Fig. 6 and an additional category in which similar trends in loss of setae in a given character shown by 2 or more genera were also considered to be synapomorphic. This procedure increases the proposed synapomorphies to 24, produces the same hypothesized sequence of genera obtained by the two preceding cladograms, and decreases the number of reversals to seven.

The phylogenetic sequence of genera supported by all three analyses appears to be a reasonable expression of the data set. Corroboration by additional characters to be considered in the future should certainly include a., the sexually modified structures of adult males and females, and b., adult pore signatures.

The implications of these findings include a suggestion of past ages when the mixed-layer calanoids may have been taxonomically different from those dominating at present. Megacalanid-like forms with fully setose oral appendages adapted for smaller-particle feeding than extant megacalanids probably occupied at least some mixed-layer niches now held by more derived lineages of megacalanoids and clausocalanoids. Augaptiloid radiations in the mixed layer may have overlapped with or preceded those of the megacalanids, but the likelihood is a changing sequence of dominant microplankton feeders in the mixed layer over time. Megacalanid survivors, spinocalanids, and most of the augaptiloids are now confined to meso- and bathypelagic depths and appear to be predaceous or detrital feeders.

The prospects of developing a relative sequence of taxonomic changes in the mixed layer are favorable at this time. The difficulty yet to be faced in the continued absence of fossil history of calanoid copepods is the means by which these major changes may be related to established geological chronologies.

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