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The road to the Janiroidea: Comparative morphology and evolution of the asellote isopod crustaceans

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Received on 18. November 1986

Abstract

This paper presents a new phylogenetic estimate of isopod crustaceans of the suborder Asellota with the aim of clarifying the evolution of the superfamily Janiroidea, a large and diverse group inhabiting all aqueous habitats. The phylogenetic analysis is based on a morphological evaluation of characters used in past classifications, as well as several new characters. The evolutionary polarity of the characters was determined by outgroup analysis. The characters employed were from the pleopods, the copulatory organs, the first walking legs, and the cephalon. The resulting character data set was analyzed with numerical phylogenetic computer programs to find one most parsimonious cladogram, which is translated into a classification using the sequencing convention. The new phylogenetic estimate is significantly more parsimonious than previous trees from the literature, and several of its monophyletic groups have robust confidence limits. The superfamily Stenetrioidea belongs to the clade including the Janiroidea, not with the Aselloidea as previously suggested. The sister group of the Janiroidea is the family Pseudojaniridae, which is elevated to superfamily rank. The clade including the families Gnathostenetroididae and Protojaniridae is not the sister group of the Janiroidea, and is derived earlier in janiroidean evolution than the Stenetrioidea. Within the Janiroidea, the family Janiridae is not the most primitive taxon as previously believed. The clade including the families Munnidae and Pleurocopidae contains the earliest derived janiroideans. The data also indicate that the unusual sexual morphology of the Janiroidea did not appear suddenly but developed as a series of independent steps within the Asellota.

Key words: Morphology – Evolution – Janiroidea – Asellota – Isopoda – Numerical phylogenetics – Copulatory organs

Introduction

For most of this century, isopod biologists interested in the order Asellota have been comfortable with the concept of the relative primitiveness of the superfamily Aselloidea, and the evolutionary gradation of morphotypes represented by the Stenetrioidea (Hansen 1905) and the genus *Protojanira* (Barnard 1927) to the major marine group, the

U. S. Copyright Clearance Center Code Statement: 0044-3808/87/2504-0257/$ 02.50/0
Z. zool. Syst. Evolut.-forsch. 25 (1987) 257–280

ISSN 0044-3808

Janiroidea. This picture has been augmented by the addition of new intermediate forms to the asellotan pantheon: the correctly (but awkwardly) named Gnathostenetroidoidea (AMAR 1957; FRESI et al. 1980; SKET 1982), and the newest family Pseudojaniridae Wilson, 1986a. Several attacks on this comfortable arrangement have been made: a failed attempt (SCHULTZ 1978, 1979; SKET 1979; WILSON 1980a), and a more reasoned approach to the revision of the systematic structure of the Asellota (WÄGELE 1983). This latter work persuasively inserted the Microcerberidae into the Asellota, undoubtedly a surprise to those that believed these tiny phreatobiotes to be members of the Anthuridea (e.g., PENNAK 1958; SCHULTZ 1969), or at least related to anthurids (e.g. LANG 1960; SCHULTZ 1979; KUSSAKIN 1979). WÄGELE (1983) also argued that the Stenetrioidea are more closely related to the Aselloidea than evolutionary clade including the superfamilies Gnathostenetroidoidea, Protojaniroidea, and the Janiroidea, a direct contradiction to previous thinking.

This paper offers new view of asellotan phylogeny, with the focus on understanding the ancestral form of the isopod superfamily Janiroidea. In numbers of species and broadness of distribution, the janiroideans are the most successful group of the Asellota. This success is largely due to an important evolutionary radiation in the deep sea of many janiroidean taxa (WOLFF 1962; HESSLER et al. 1979), resulting in great numbers of species which contribute a significant proportion of the deep-sea benthic biota (WILSON, in press). Many questions relating to their evolution and biogeography remain unanswered or even unevaluated because basic systematic relationships have not been known for the higher taxonomic levels. Few relatively explicit phylogenies of the Janiroidea at the family level have been published (KUSSAKIN 1973, 1979; FRESI et al. 1980), and most other knowledge is based on taxonomic conjecture.

Current literature offers two different, unrelated sister groups for the Janiroidea: the Protojaniridae (SKET 1982, 1985; WÄGELE 1983), and the stenetrioid-like Pseudojaniridae WILSON (1986a). The protojanirids have been considered good sister group candidates, because their pleopods bear characters seemingly homologous to those of the janiroideans. HANSEN (1905) demonstrated that the pleopods characters help form a natural arrangement of the asellotan families. His results have been amplified by other workers (AMAR 1957; FRESI and SCHIECKE 1968; FRESI et al. 1980; WÄGELE 1983; SKET 1985). The primary characters that imply close relationships between the Janiroidea and the Protojaniridae are the opercular female pleopods, one free anterior pleonite, and a copulatory stylet on the endopod of the male pleopod II. The homologies of some of these feature have not been adequately demonstrated, and are examined below. This paper demonstrates that the Pseudojaniridae is a better sister group for the Janiroidea. Traditional characters among the families are compared and several new features are discussed that have been overlooked until now, such as the female copulatory organ, described by WILSON (1986b). The results of these character studies are the source for a new estimate of the asellotan phylogeny, presented as a well-corroborated cladogram and a classification.

Materials and methods

Specimens and study techniques

Several mature specimens of the protojanirid *Enckella lucei major* Sket came from its type locality, Istripura cave in Sri Lanka. Specimens of the other genera discussed in this paper were taken from an isopod research collection at Scripps Institution of Oceanography. Examples of *Munna*, *Paramunna*, *Notasellus* and *Santia* were collected at Palmer Station, Palmer Penninsula of Antarctica (RICHARDSON 1976). *Asellus* was collected near Lund, Sweden. The remaining specimens were collected in various localities in the deep Atlantic Ocean by vessels of the Woods Hole Oceanographic Institution. Precise localities for these specimens are available on request from the author.

Preserved specimens were immersed in ethylene glycol on depression slides for studies of external morphology. The illustrations in this paper were inked from pencil drawings made using a Wild M20 microscope fitted with a camera lucida drawing tube.

Superfamily classification and taxa used

The classification used here is that of Bowman and Abele (1982) with the following corrections and emendations. The superfamily Protallocoxoidea Schultz (1978, 1979) is not valid and should not be included in further classifications of the Asellota (Sket 1979; Wilson 1980a). Wägele (1983) represented the families Gnathostenetroididae and Protojaniridae as belonging to separate superfamilies, as discussed by Sket (1982). The taxon Protojaniroidea is used here only for the sake of comparison with other groups and is rejected in the final classification. The classification of the families Microcerberidae and the Atlantasellidae (Sket, 1979) as Aselloidea (Wägele 1983) is provisionally accepted, although some characters justifying this assignment may be plesiomorphies (Wilson 1986a; see discussion of pleopod III below), some are apomorphies not necessarily derived from an aselloidean condition, and others are reduction characters of lesser phylogenetic value. These families are not evaluated for the analysis; the less modified Stenasellidae and Asellidae represent the Aselloidea in this paper. Therefore, the operational taxonomic units (OTUs) at superfamilial taxa used are Aselloidea, Stenetrioidea, Gnathostenetroidoidea, Protojaniroidea, *incertae sedis* (Pseudojaniridae Wilson, 1986a), and Janiroidea.

Within the Janiroidea, three family-level OTUs are recognized: 1. Munnidae and Pleurocopidae (see Wilson 1980b), 2. Paramunnidae (= Pleurgoniidae: Bowman and Abele 1982; Hooker 1985) and Abyssianiridae (Wilson 1980b), and 3. the remaining families, represented here by the family Janiridae. This division of the Janiroidea is made because the Munnidae and Pleurocopidae have a cuticular organ positioned differently than in the remainder of the janiroideans (Wilson 1986b), and the form of the first pereopod is shown to separate the Paramunnidae and the Abyssianiridae from the remainder of the Janiroidea. These characters are evaluated below.

Phylogenetic techniques

Outgroups and character analysis

Knowledge of the evolutionary sequence of primitive to derived in a taxonomic group's characters is a primary requirement of phylogenetic analysis (Hennig 1966). This study uses outgroup analysis because of its effectiveness on morphological characters (Watrous and Wheeler 1981; Maddison et al. 1984). To verify the polarity of characters within the Asellota, its sister group should be determined. Although no detailed phylogeny of the Isopoda has been published, opinions as to general relationships do exist. For example, Kussakin (1973, p. 21) wrote "Asellota probably originated from the ancient Phreatoicidea". Van Lieshout (1983) allied the newest suborder, Calabozoidea, most closely to the Asellota, although this taxon is specialized, and has several reduced features. The Calabozoidea were not compared with the Phreatoicidea, leaving Van Lieshout's analysis incomplete. The Asellota appears to be the most derived taxon in Wagner analyses of the order Isopoda, although its exact placement depends on the polarities of some characters (R. Brusca, personal communication). A phylogenetic analysis of the order Isopoda exceeds the scope of this work, so polarity arguments will rely on the common or prevalent form of a character over all the suborders of the Isopoda. This is possible because most characters discussed below, such as the form of the first pereopod or the male pleopods, recur in all suborders.

Because the intent of this work is to discover relationships between taxa, characters that are found in two or more taxa of the Asellota are emphasized, and, in general, autapomorphies are not included in the analyses. This, however, does not mean that monophyletic groups at the terminal branches are not supported by apomorphies: they simply were not used in the current data to avoid inflating the consistency values. The monophyly of the Aselloidea as currently defined, however, may not be supported by a known apomorphy because of the heterogeneity of the included taxa. This problem will be returned to in the discussion.

Numerical phylogenetics

The phylogenetic analyses were run on an IBM PC/XT microcomputer for which several useful programs were available. The analysis package used initially was the microcomputer-based system PHYLIP, version 2.8 (FELSENSTEIN 1985). From this package, the program MIX, which runs both Wagner (KLUGE and FARRIS 1969) and Camin-Sokal (CAMIN and SOKAL 1965) parsimony methods, was used most frequently. Recently PHYLIP has been criticized for the failure of the program WAGNER, the predecessor of MIX, to find the most parsimonious trees (LUCKOW and PIMENTEL 1985). This failure is due to the single run nature of their analysis, and can be corrected by 10 or more MIX runs on shuffled data (FELSENSTEIN, PHYLIP documentation). For the small data set used here, PENNY was a more effective PHYLIP program; it implements the branch and bound algorithm of HENDY and PENNY (1982). Another program, PAUP version 2.4.1 (SWOFFORD 1985) was employed to verify that the most parsimonious trees were found. PAUP has powerful analysis and output options, and can analyze multistate characters in an "unordered" mode, used here on the pereopod character 15. In several analyses, taxa polymorphic for particular characters were duplicated, and both new OTUs were scored with different character states; this procedure helped verify the monophyly of the polymorphic taxa. Because polymorphisms occurred in only a few taxa, the number of extra OTUs generated were minimal (one in the case of character 15, 3 in the case of character 16). In all cases, both PAUP and PHYLIP PENNY agreed on the same most parsimonious tree, so no technical comparison of the programs is presented.

Phylogenetic significance

Because a single most parsimonious tree is found for the Asellota, its significance should be discussed, both for its intrinsic qualities and in comparison with other trees. A nagging problem for phylogenetic studies, however, is a lack of knowledge of the significance on the monophyletic groups found in a particular analysis. With perfectly Hennigian data (no incompatible characters), only a single character is necessary to define a monophyletic group. If this character is interpreted differently with a new point of view or knowledge, the resulting form of the phylogeny may be greatly changed. This problem arises because we have no independent statistical estimates of the variance associated with the phylogeny; parsimony and consistency values are merely indexes that measure the likelihood of a phylogeny. Therefore, methods for assessing our confidence in a monophyletic group in a phylogeny would be highly useful. A new technique introduced by FELSENSTEIN (1985) uses a bootstrap method (EFRON and GONG 1983; DIACONIS and EFRON 1983) for an estimate of confidence limits on a monophyletic group. The PHYLIP program BOOT (FELSENSTEIN 1985) provided confidence limits for monophyletic groups in this study. The bootstrap method, implemented for phylogenies, randomly resamples *with replacement* among the characters in a data set to derive a new data set from the original data. This procedure may randomly eliminate, use without change, or multiply the characters in the data set. In the program BOOT, this is done by manipulating character weights, rather than creating new data sets. A phylogeny is calculated on the new data and monophyletic groups generated by the randomized data are noted. This process is reiterated many times (500 times per run in the current instance), and frequencies of the monophyletic groups are derived from the multiple runs. This frequency is reported as a percentile, and is a nonparametric estimate of the confidence limits around each monophyletic group (FELSENSTEIN 1985). Percentiles are reported in this paper as independent estimates, so if the joint probabilities of two or more monophyletic groups are desired, it is necessary to multiply the percentiles. This will result in lower confidence limits for the joint existence of the monophyletic groups, although the groups cannot be contradictory if each has a percentile above 50 % (FELSENSTEIN 1985).

A limitation of the program BOOT is that it evaluates only fully bifurcating trees. Consequently, one must interpret identical *and* adjacent confidence values on the resulting consensus tree as either being independent estimates or the same estimate. This is done by examining the original data set to see whether any apomorphies occur on the branch separating the two nodes indicated in the bootstrap analysis; if there is at least one apomorphy, the bootstrap confidence limits must be independent, and if there are none, the percentiles may be indicating a 0-length branch and a polychotomy in the phylogenetic estimate. This problem, however, did not occur in the original data set for the Asellota.

The most parsimonious tree for the Asellota was compared with cladistic hypotheses from the literature by means of the derived parsimony values and consistency indices. Both PAUP and PHYLIP MIX allow specification of predefined trees and calculation of summary parsimony values and consistency indices for these phylogenies. Such values were obtained for the trees of KUSSAKIN (1973), FRESI et al. (1980), and WÄGELE (1983), and compared with those of the unrestrained Wagner tree for the Asellota.

Character analysis of the asellotan superfamilies

This section evaluates a variety of characters that have been used in the literature as well as several new characters. The results of this analysis are displayed in Table 1 and the distribution of the character states among the major taxa of the Asellota are shown in Table 2.

The cuticular organ

A survey of the asellote cuticular organ (WILSON 1986b) shows that this complex structure is not a defining synapomorphy of taxa within the Janiroidea (e. g. VEUILLE 1978b), because it occurs in other superfamilies, i. e., the Aselloidea and the Stenetrioidea. Therefore, the question of how the cuticular organ developed is set to a higher systematic level, a problem that will not be addressed here. Evolutionary polarity for cuticular organ transformation is not estimated because the distribution of the cuticular organ outside the Asellota and the sister group for the Asellota are unkown. The condition seen in *Asellus* (WILSON 1986b) is preferred as the plesiomorphic state of the cuticular organ, because the dorsal cuticular organ of the Janiroidea has not been reported in isopods outside of the Asellota. The position of the cuticular organ's opening (character 1) is considered to have two states: directly associated with the opening of the oviduct (state 0), and on the anterodorsal surface of the fifth pereonite (state 1). Other features, such as whether or not the spermatheca has a cuticular sheath, are not used because the morphology of the organ is unknown for many asellote taxa.

Male pleopods I

The male pleopod I (Figs. 1–3) throughout the Asellota is similar: paired uniramous, and typically small limbs. At the level of the Isopoda, this is an apomorphy because most of the suborders have biramous first pleopods. In the Calabozoidea, the pleopods I are essentially uniramous, with a rudimentary endopod (VAN LIESHOUT 1983). The least modified state of the pleopod I in the Asellota is a uniramous, two-segmented limb, as exemplified by *Asellus* (Fig. 1A). The first pleopods of *Asellus* take no part in sperm transmission, as the penes are brought into direct contact with the endopod of the second pleopod for this purpose (MAERCKS 1931). They are small compared to pleopods III-V, but they generally cover the second pleopods. Although both sides of the paired pleopods are not fused (character 2, state 0), they may be connected by coupling hooks on the basal segment. A modification of this form is the fusion of the basal segments (state 1), so that both members of the pair are forced to act together, thus eliminating the need for coupling

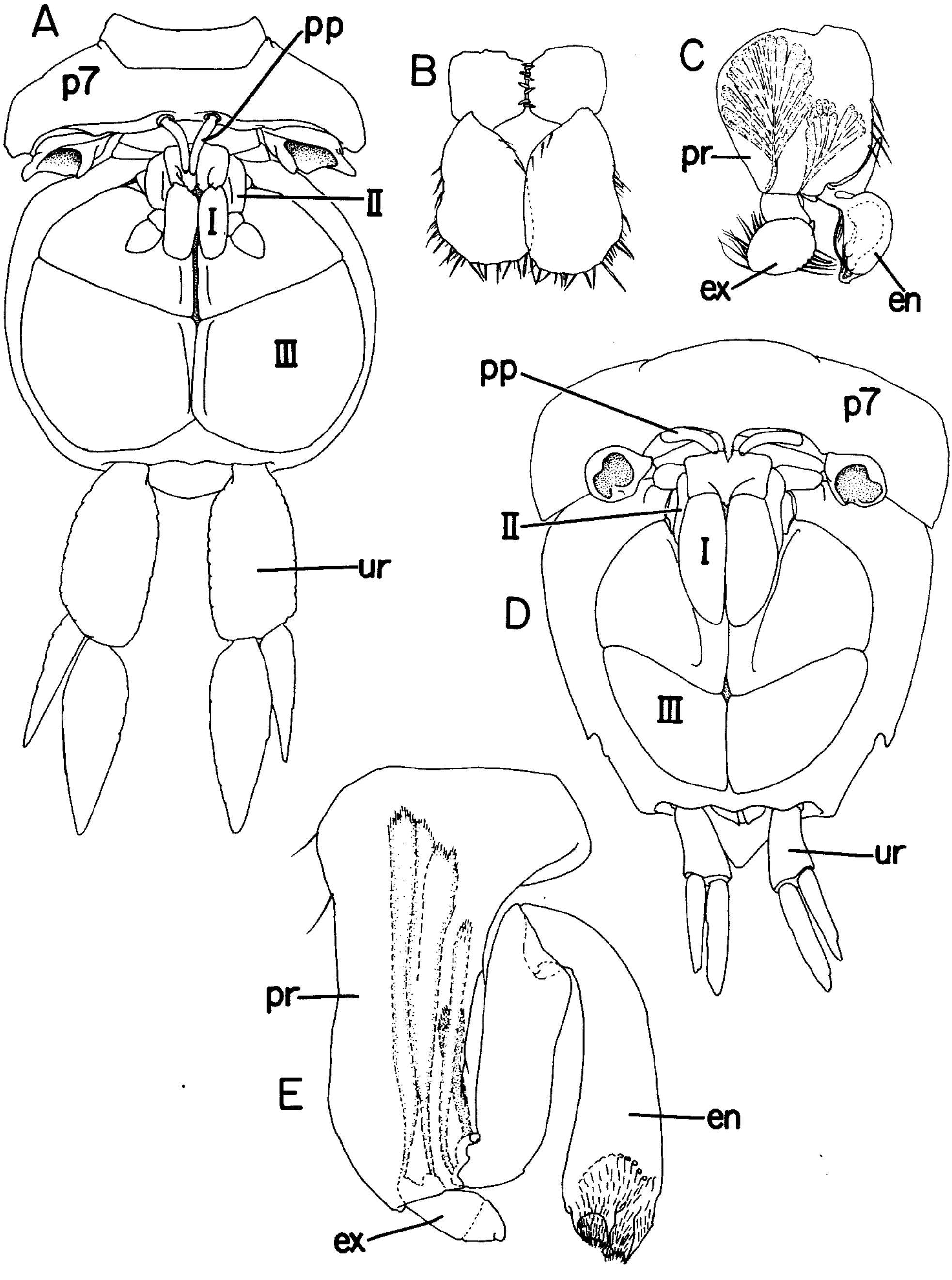

Fig. 1. Male copulatory organs in two Asellota. A–C: *Asellus aquaticus* (Linneus). A = drawn from specimen in collection; B–C = after MAERCKS (1931). A: ventral view of pereonite 7 and pleotelson of male. B: enlargement of pleopods I. C: enlargement of right pleopod II, extrinsic musculature of exopod shown. D–E: *Stenetrium dagama* Barnard. D: ventral view of pereonite 7 and pleotelson of male. E: enlargement of pleopod II, extrinsic musculature of both rami shown. (I = pleopod I, II = pleopod II, III = pleopod III, pp = penile papilla, pr = protopod (basal segment), en = endopod of pleopod II, ex = exopod of pleopod II, ur = uropod, p7 = pereonite 7)

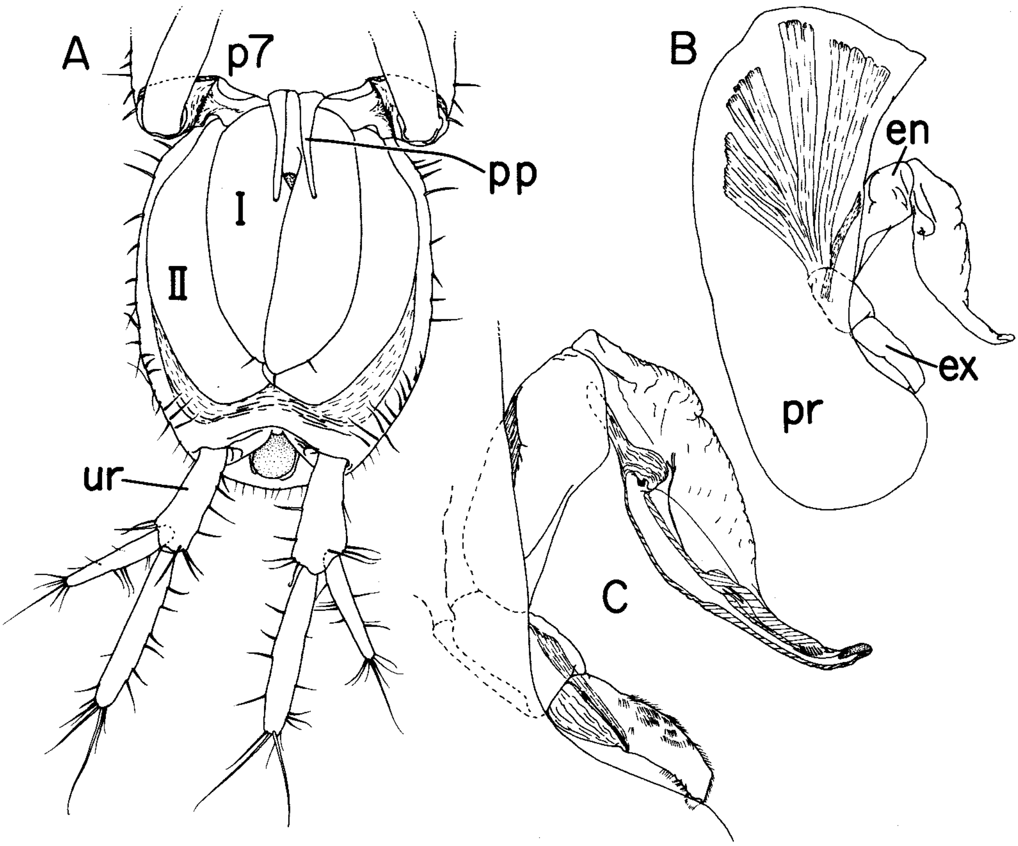

Fig. 2. Male copulatory structures in *Enckella lucei major* Sket. A: Ventral view of pleotelson and pereonite 7. B: Pleopod II, ventral view, extrinsic musculature of exopod shown. C: Enlargement of exopod and endopod, pleopod II, showing intrinsic musculature in exopod and internal cuticular structures (hatched) in distal article of endopod. (I = pleopod I, II = pleopod II, pp = penile papilla, pr = protopod (basal segment), en = endopod of pleopod II, ex = exopod of pleopod II, ur = uropod, p7 = pereonite 7)

hooks. Fused basal segments are found in the remainder of the Asellota: *Stenetrium* (Fig. 1 D), the gnathostenetroidids, the protojanirids (*Enckella*, Fig. 2 A), *Pseudojanira* (Wilson 1986 a), and the Janiroidea (Fig. 3 A, C), although the size of the segment varies considerably.

A defining apomorphy of the Janiroidea is medial fusion of male first pleopods and a cuticular tube for sperm conduction on the line of fusion (Veuille 1978 a; Fig. 3 A, C; character 3, state 1). In Asellota that have this character complex, the proximal end of the tube is a funnel into which the penes fit, and its distal end opens on the dorsal side of the fused pleopods above the distal segment of the second pleopodal endopod. All other Asellota have unfused distal rami of the first pleopods (state 0). This latter state is plesiomorphic because all other suborders of isopods have separate first pleopods. The form of the penile papillae correlates with presence of the sperm tube and is not considered a separate character: only janiroideans have short, conical, and adjacent papillae, whereas the remainder of the Asellota have elongate, tubular, separate papillae (see Figs. 1 A, D; 2 A; 3 A, C). The latter taxa are probably like *Asellus* (Maercks 1931) in bringing the papillae in direct contact with the second pleopod's endopod for sperm transfer (as suggested for the Protojaniridae by Sket 1985).

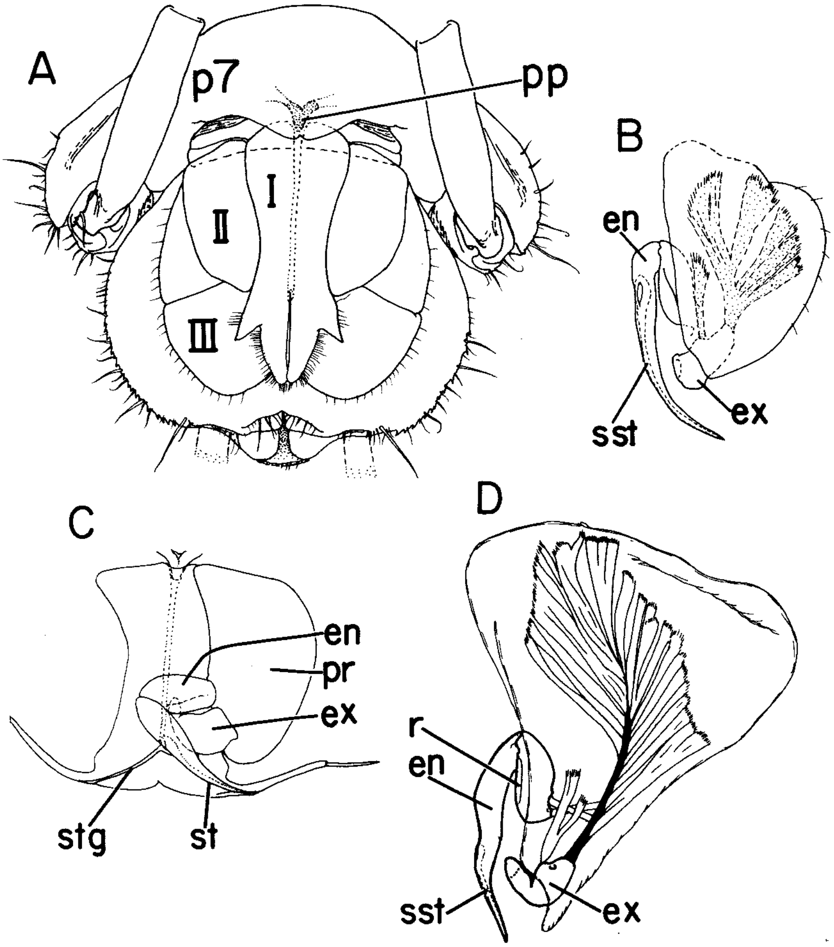

Fig. 3. Male copulatory structures in several Janiroidea. A: *Notasellus sarsi* Pfeffer, ventral view of pleotelson and pereonite 7; dashed line crossing pleopods I and II is posterior margin of pleonite 2. B: pleopod II of *Notasellus sarsi*, ventral view, showing extrinsic musculature of exopod. C: pleopods I and II of *Jaera italica* Kesselyak, dorsal view, showing position during copulation (after Veuille 1978a). D: pleopod II of *Eurycope diadela* Wilson (a highly modified deep-sea janiroidean), showing extrinsic musculature of the exopod; basal podomere shown as being transparent to emphasize the internal musculature and articulations of the rami. (p 7 = pereonite 7, pp = penile papillae, I = pleopod I, II = pleopod II, III = pleopod III, en = endopod, st = stylet, sst = sperm tube in stylet, ex = exopod, pr = protopod (basal segment), r = ridge on proximal segment of endopod)

The presence or absence of stylet-guiding grooves on the male pleopod I provides character 4. These structures (state 1) are found on the dorsal surface of the broad tips of first pleopods in *Pseudojanira* (Wilson 1986a) and in the Janiroidea (Fig. 3C). The stylets on the endopods of the second pleopod fit into these grooves, directing the motion of the stylets during copulation (Veuille 1978a). The guides and function of the stylet are intimately related to one another, implying that those taxa having elongate, pointed endopods on pleopods II but lacking the grooves (Stenasellidae, Magniez 1974; Protojaniridae, Fig. 2A) must mate in ways different from the Janiroidea and *Pseudojanira*. The dorsal side of the first pleopods also has a pair of cuticular tabs which help lock them in position between the two second pleopods, effectively forming an operculum with both pairs of limbs. This character may be linked to the presence of the stylet guides, and is not considered independent of other characters. Lack of the stylet guides (state 0) is plesiomorphic because nothing similar occurs in any nonasellotan.

The Gnathostenetroidoidea and the Protojaniroidea have male first pleopods that are different from other Asellota: they are large, broad, and lamellar (character 5, state 1). Other asellotes have male first pleopods that are either small or narrow, and all are generally thicker (state 0). The large lamellar first pleopods are assigned the apomorphic state although the true ancestral state is unknown.

Male pleopods II

Ancestral form

The primitive condition for the male asellote pleopod II (Fig. 1C, E; 2C, D; 3B–D) is well established (WÄGELE 1983), although the phylogenetic significance of some details has gone unnoticed. Within the Asellota, the basal segment is somewhat enlarged and muscular, and both rami have two segments each. The endopod is geniculate, and is distally elaborated either with a groove or pocket for transferring the sperm. The exopod and the endopod have structures that allow them to couple and act in concert during the copulatory act (e. g. *Asellus*, MAERCKS 1931; *Jaera*, VEUILLE 1978a); the exact form of the coupling mechanism varies among the asellotan taxa. The interlocking of the endopod and exopod is homologous in all asellotan taxa because they all have elongated and enlarged exopodal musculature for the copulatory function. The entire limb generally is as small as or smaller than the first pleopod.

None of the taxa examined had all these features unmodified, although this configuration is exhibited by the Stenasellidae (e. g. MAGNIEZ 1974) of the Aselloidea. Non-asellotan taxa also have copulatory male pleopods II but the asellotan form does not occur in any of them, especially the structures for the linking of the exopod to the endopod. The typical non-asellotan male pleopod II is a biramous structure with a small rectangular basal segment with lamellar rami (see KUSSAKIN 1979: his Fig. 16). In the outgroups, the endopod generally bears a narrow, cylindrical, and blunt appendix masculina, although this structure may be more elaborate distally. Whether the unknown sister group of the Asellota has exopods with one or two segments remains uncertain because some suborders (including the Calabozoidea) have an unsegmented lamellar exopod, and others, like the Phreatoicidea or the Anthuridea (which has a primitive pleonite and telson configuration), have two segments in the exopod.

Exopod

Character 6 of the male second pleopod is whether the exopod has two segments (state 0) or is fused into 1 segment (state 1). As just said, it is not certain which is the plesiomorphic state, although a two-segmented exopod (Fig. 1C) is favored because it is found in the least modified asellotes and in the somewhat similar Phreatoicidea. This ramus is short and uniarticulate in *Stenetrium* (Fig. 1E), *Pseudojanira* (WILSON 1986a), and in the Janiroidea (Fig. 3B–D). In *Pseudojanira*, and in the Janiroidea, the exopod forms a blunt hook that links with a groove in the proximal article of the endopod, making the exopod character 7 to be the presence (1) or absence (0) of the hook. Because none of the non-asellotan taxa has a short, hook-shaped exopod, the lack of this form is plesiomorphic.

Endopod

The endopod displays divergent trends among the Asellota. In *Asellus*, both articles of the endopod are fused, although this ramus retains its geniculate form (Fig. 1C); in the

Stenasellidae and the other superfamilies, the endopod remains biarticulate thus limiting the usefulness of the endopodal fusion for phylogenetic analysis. A more useful character is the presence (character 8, state 1) or absence (state 0) of a stylet-like endopod. Non-asellotan taxa lack any of the endopodal specializations seen in the Asellota, so it is difficult to establish the plesiomorphic state on these grounds alone. Some ontogenetic evidence, however, is provided by the development of the stylet in juvenile male janiroideans (Hessler 1970; Wilson 1981), when it resembles the endopod of non-asellotes. At the first molt where the endopod of male pleopod II is expressed, the distal part of this ramus is an undeveloped, club-shaped process, sometimes with a ventral groove on its distal end. After the maturation molt, the stylet is sharp distally and has an internal sperm tube that is open at its tip. The ontogeny of the male stylet in the Janiroideans suggests that the plesiomorphic state is the club-shaped process and the hypodermic needle-like stylet of the Janiroidea is the apomorphic state. The distal article of the endopod is elongate and pointed both in the Janiroidea (Fig. 3 B–D) and in *Pseudojanira* (Wislon 1986 a), different from the club-shaped limbs in *Asellus* and *Stenetrium* (Fig. 1 C, E).

A stylet-like endopod is also seen in the Protojaniridae (Sket 1982; Wägele 1983; Fig. 2 B, C) and in the Stenasellidae (Magniez 1974, especially his Fig. 3). The suspected homologies in the latter group are easiest to dismiss: the stenasellids vary considerably in the form of the male pleopod II endopod, and although one species may resemble the janiroidean condition, closely related species or genera may be completely different. The evolutionary plasticity of this feature in the stenasellids makes it suspect for comparison with other groups external to the Aselloidea. In addition, the structure of the limb is that of coiled folds of cuticle, very different from the solid cuticular tube seen in the Janiroidea. The stylet of the Protojaniroidea is also not homologous with that of the Janiroidea because its structure is different (Fig. 2 B, C). The sperm tube is on the lateral side of the stylet, not on the medial side as it is in all Janiroideans. In this regard, *Asellus*, which has a lateroproximal opening for the elongate penes to deposit sperm (Maercks 1931), is similar. The structure of the protojanirid cuticular tube inside the endopod is also more complex, appearing as though it is made of folds or layers of cuticle, rather than a simple internal tube. Finally, janiroideans that have a short male stylet do not have the abrupt distal bend seen in protojanirid *Enckella*. Except for the lack of a closed sperm tube, the male endopod of *Pseudojanira* is identical to that of the Janiroidea. Therefore, the apomorphic state for character 8 is scored only for the Pseudojaniridae and the Janiroidea. Character 9 (state 1) is the protojanirid form of the stylet, with its plesiomorphic state the same as character 8.

Endopodal sperm tube

Character 10 can be derived from the form of the sperm transmitting surface of the distal segment of the endopod. Most lower asellotes have either a pocket or a groove on this part of pleopod II (state 0). For example, in *Pseudojanira*, the stylet has an elongate groove on the ventral surface (Wilson 1986 a), and the Aselloidea have variously formed pockets (Fig. 1 C). As discussed above, the sperm tubes of the Protojaniroidea (character 11, state 1) and the stenasellids (not scored) are not homologous to the janiroidean condition and is convergent. In the Janiroidea, the groove has become closed into a tube that opens on the bulbous proximal part of the segment and on the distal tip only (Fig. 3 B–D). The presence or absence of this stylet sperm tube is useful in distinguishing the Janiroidea from all the other Asellota. The sperm tube is the apomorphic state because sperm tubes have not been reported from the endopod of the male pleopods II of any non-asellotan taxon.

Stylet guide

Pseudojanira has a unique structure on the tip of the male pleopod II sympod (WILSON 1986a): a broad, triangular processes with a setose groove on the distomedial margin. In the preserved male, the stylet of the endopod rested in the groove of the sympod tip. This odd structure is a defining synapomorphy of this taxon (character 12, state 1), not found in any other Asellota (state 0).

Female pleopod II

In the Aselloidea, the second pleopods are separate, round, uniramous, and lamellar (character 13, state 0). In other Asellota, the left and right sides of the female second pleopods are fused into a single shield-like structure (state 1), which may or may not be opercular. Although the aselloid second pleopods are not biramous, they are most similar to the condition seen in most non-asellotans in that the two sides are not fused together. Therefore, separate pleopods are the plesiomorphic state and fused pleopods are the apomorphic state.

First pereopod

The pereopod I (the second thoracic appendage) proves to be valuable for differentiating major taxa in the Asellota (Fig. 4). In most Isopoda, this limb is a grasping appendage with the opposing surfaces between the propodus and dactylus, with free articulation allowing a large arc of movement (character 14, state 0). The propodus is usually enlarged and muscular. The carpus is short, broad, and nearly triangular, and does not take part in the grasping function (character 15, state 0). The propodus and dactylus typically have stout setae of various types, apparently to aid in the grasping function. Because this type of first pereopod occurs in all non-asellotan taxa, it is the plesiomorphic state for the Asellota. This plesiomorphic state is found in *Asellus, Stenetrium* and *Pseudojanira*, and all other non-janiroidean taxa. Of the Janiroidea, only the Munnidae, Pleurocopidae, Paramunnidae, and Abyssianiridae have a pereopod similar to the plesiomorphic state, although it is modified in that the carpus is longer, more robust, and has elongate stout setae which may participate in grasping (character 13, state 1). The propodus is somewhat reduced in these latter taxa, but still retains a free articulation with the dactylus (character 14, state 0). The higher Janiroidea have a pereopod I which closely resembles the more posterior pereopods: the dactylus is short and stout, and the flexure between the dactylus and the propodus is restricted so that they do not oppose one another (character 14, state 1). In addition, the propodus and the carpus are elongate, and the carpus and propodus fully oppose one another (character 15, state 2). The transformation series for characters 14 and 15 seems counterintuitive, because one would expect the first pereopod of an isopod to resemble the more posterior walking limbs in its most plesiomorphic state. Similarities with all non-asellotans indicate that a first pereopod with grasping between the dactylus and propodus is the plesiomorphic state, and the walking leg form of the higher Janiroidea, with grasping between the propodus and the dactylus, is the most derived state at the level of the suborder Asellota. Some taxa, notably the desmosomatid *Torwolia*, revert to grasping with the dactylus and the propodus, but in all cases the carpus is elongate, indicating its previous walking leg-like condition.

The Protojaniridae, which are best recognized by their pleopod forms, have genera with both the primitive type of first pereopod (*Protojaniroides, Enckella*) and the higher janiroidean type of first pereopod (*Protojanira*) (GRINDLEY 1963; FRESI et al. 1980). The possible homology of the latter form cannot be rejected because GRINDLEY (1963: his Fig. 1) clearly shows a janiroidean style first pereopod on *Protojanira leleupi.* It may differ in its retention of the free articulation of the propodus-dactylus joint; detailed comparisons of the janiroidean and protojaniroidean first pereopods will be required to confirm their

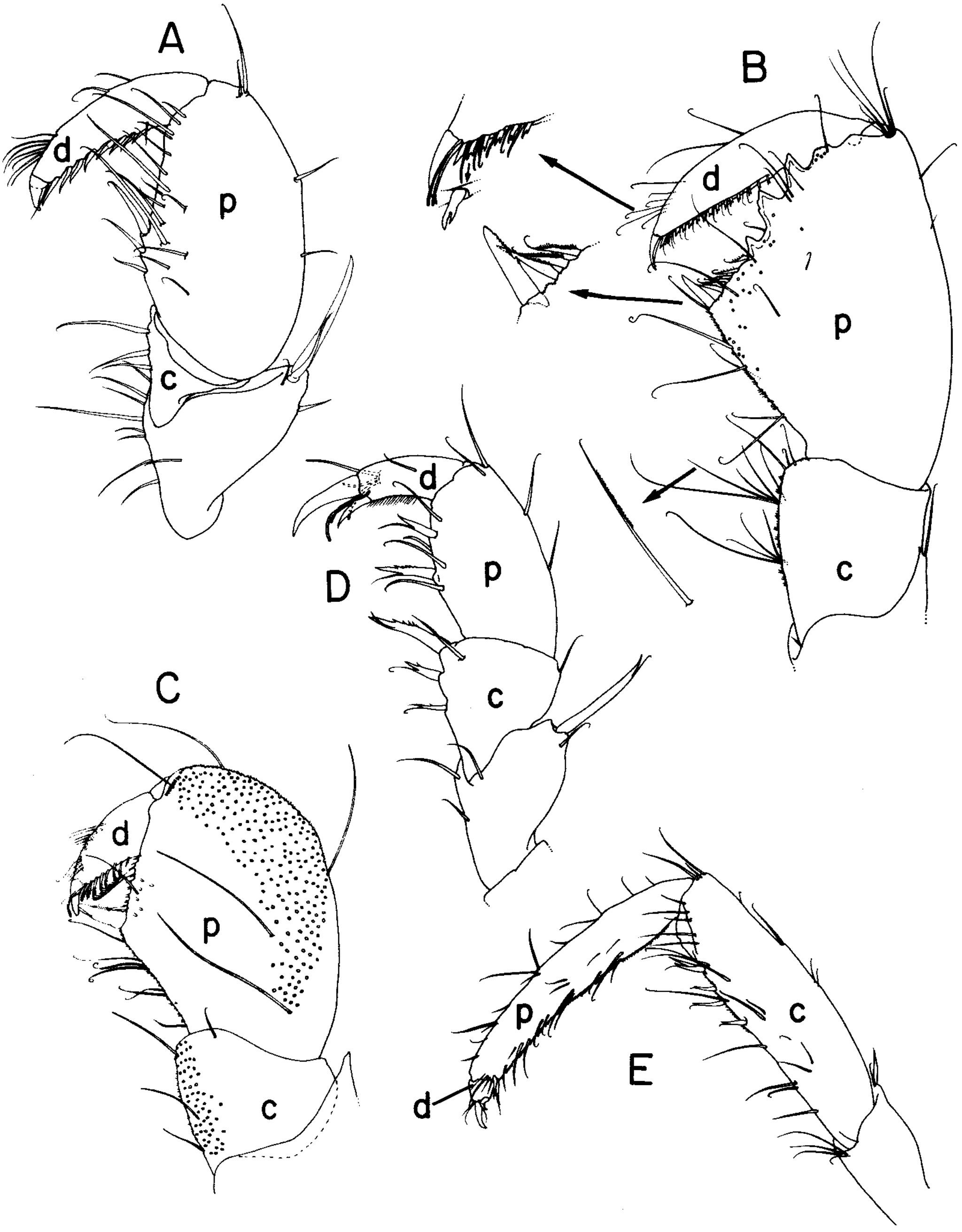

Fig. 4. A comparison of the first pereopods of various Asellota. A: *Asellus aquaticus* (Linneus). B: *Stenetrium dagama* Barnard, with enlargements of the setae on the oppositional margins of the dactylus and propodus. C: *Pseudojanira stenetrioides* Barnard (after WILSON 1986a), all setae not shown, setal insertions shown by "u" or "o" shaped marks. D: *Santia mawsoni* Hale. E: *Notasellus sarsi* Pfeffer, illustrating basic form of first pereopod for most Janiroidea. (d = dactylus, p = propodus, c = carpus)

true homologies. Nevertheless, the Protojaniroidea must be scored with both types of limbs in the phylogenetic analysis. For state 1 of character 15, however, they must receive an unknown character classification because the intermediate form has not been reported for the Protojaniridae.

Cephalic rostrum

Many janiroidean taxa have a cuticular projection on the cephalic frons between the antennulae which is sometimes prominent and sometimes not. This projection is separate and distinct from the tergal cuticle of the cephalon. A homologous, prominent structure occurs in *Stenetrium* and in *Pseudojanira*. A similar rostrum does not appear in the Asselloidea or in the primitive members of other isopodan suborders, although taxa in these latter groups may have a rostrum-like projection of the cephalic tergum. The frontal rostrum of the Janiroidea is scored as an apomorphy shared with the Stenetrioidea and the Pseudojaniridae (character 16, state 1).

Pedunculate eyes

Most isopods have eyes that are protrude only slightly from the dorsal surface of the cephalon (character 17, state 0). Species in the munnid-pleurocopid clade, however, have pedunculate eyes (state 1), a defining apomorphy. Many genera in the family Paramunnidae also have pedunculate eyes which was the original cause for their classification in the Munnidae. A variety of other derived characters (WILSON 1980b) show that the Paramunnidae were derived separately from the Munnidae, indicating that the stalked eyes are a convergence. This is corroborated by the structure of the eyes themselves: where eyes occur in the Paramunnidae, they are made of only a few ocelli; and in the Munnidae and the Pleurocopidae, the eyes are generally well developed with many ocelli. The large eyes of the janirid genus *Notasellus* are on the lateral edge of the cephalon, perhaps indicating that the ancestral Janiroidean may have had the precursor condition to the pedunculate eyes.

Covered anus

The anus of most non-janiroidean Asellota is not covered by the pleopods and it is external to the pleopodal cavity (character 18, state 0). The paramunnid-abyssianirid clade has (among other characters) a unique form of the pleopods (state 1), in which the distal tip of the opercular pleopods (pleopod II in the female and pleopod I in the male) is pointed and covers the anus, thus including it into the pleopodal cavity (WILSON 1980b). The relationship of the anus to the pleopods shows a great variety outside of the Asellota, so the plesiomorphic condition is not clear from evidence external to the phylogenetic analysis presented here.

Characters not used

Even though the characters below are not used in the analysis, it is necessary to discuss them because others have considered them important factors in the phylogeny of the Asellota.

Pleopod III and opercular pleopods

WÄGELE (1983) presents arguments that the primitive third pleopods of the Asellota are biramous structures each with two rami (endopod and exopod) of similar size, but not covering the more posterior pleopods IV and V. On this basis, he divides the Asellota into a "janiroid line" in which pleopods I and II are opercular, and a "aselloid line" in which pleopods III are opercular. His janiroid line includes the superfamilies Janiroidea, Protojaniroidea and Gnathostenetroidoidea, and his aselloid line has the Stenetrioidea as an

Table 1

Results of the character analysis

The following is a list of the character states, their transformations, and polarities derived above. The distribution of the character states among the taxa are shown in Table 2

Character	Character states
1	Cuticular organ opening ventral, adjacent to opening of oviduct (0), or cuticular organ opening dorsal, separate from opening of oviduct (1). Ancestral state not known.
2	Male pleopods I basal segments separate medially (not fused) (0), or male pleopods I basal segments joined (fused) medially (1).
3	Male pleopods I distal segments separate medially (not fused) without medial sperm tube (0), or male pleopods I distal segments joined medially (fused) with medial sperm tube (1).
4	Male pleopods I distal tips without dorsolateral stylet guides (0), or male pleopods I distal tips with dorsolateral stylet guides (1).
5	Male pleopods I small or narrow, thick (0), or male pleopods I large and lamellar (1). Ancestral state not known.
6	Male pleopod II exopod of 2 articles (0), or male pleopod II exopod of 1 article (1). Ancestral state not known.
7	Male pleopod II exopod lobe-like, unelaborated (0), or male pleopod II shaped like blunt hook, shape corresponding to groove on proximal article of endopod (1).
8	Male pleopod II endopod thick distally, not stylet-like (0), or male pleopod II stylet shaped, janiroidean form (1).
9	Male pleopod II endopod thick distally, not stylet-like (0), or male pleopod II stylet shaped, protojanirid form (1).
10	Male pleopod II endopod distal segment with open groove or pocket (0), or male pleopod II endopod distal segment with tube opening only on distal tip and more proximally, janiroidean form (1).
11	Male pleopod II endopod distal segment with open groove or pocket (0), or male pleopod II endopod distal segment with tube opening only on distal tip and more proximally, protojanirid form (1).
12	Male pleopod II sympod distal tip not expanded (0), or male pleopod II sympod distal tip expanded, with distomedial groove (1).
13	Female pleopods II separate and unfused medially (0), or female pleopods II fused medially so that they form single shield-like limb (1).
14	Pereopod I dactylus long; dactylus and propodus with free articulation and can oppose one another to participate in grasping (0), or pereopod I dactylus short; dactylus and propodus with restricted articulation and cannot oppose one another to participate in grasping (1).
15	Pereopod I carpus short and triangular; carpus and propodus with restricted articulation and *cannot* oppose one another to participate in grasping (0), or pereopod I carpus trapezoidal, articulation between carpus and propodus only partially restricted, can oppose one another by means of strong spine-like setae or spines on carpus (1), or long and not triangular; carpus and propodus with free articulation and *can* oppose one another to participate in grasping (2).
16	No rostral projection on cephalic frons (0), or cephalic frons with rostrum (1).
17	Eyes sessile on cephalon (0), or eyes on short thick stalks (1).
18	Anus exposed and separate from the pleopodal chamber (0), or anus inside pleopodal cavity and covered by distally pointed opercular pleopods (1). Ancestral state not known.

offshoot unrelated to the ancestral janiroideans. The ancestor of the Asellota may not have had opercular third pleopods *at the outgroup node*, because all the potential sister groups have large, biramous, lamellar, and nearly similar pleopods. On the other hand, the *immediate ancestor* of the Asellota may have had opercular pleopods III owing to their appearance in most of the superfamilies. As WÄGELE (1983) observed, *most* Janiroidea have a reduced, non-opercular third pleopod. However, males of some taxa such as *Notasellus* (Fig. 3 A) and *Jaera* have third pleopods that are nearly identical to those of *Stenetrium* and *Pseudojanira*. The third pleopod of the Munnidae and the Pleurocopidae is also similar, although it is covered by the first and second pleopods. The pleopod is reduced in females of *Notasellus* and *Jaera*, and in all other Janiroidea in a variety of forms (WILSON, in press). The presence of both types of third pleopod within the Janiroidea establishes that opercular third pleopods were present in their ancestor. Therefore, the basis for separating the Asellota into an aselloid line and a janiroid line is unfounded.

Use of the opercular function as a character could potentially lead to confusion in developing a stable phylogenetic estimate of the Asellota. Because the character is one of function rather than of morphology, convergence may be likely among the various groups. For example, WÄGELE (1983) considers that pleopods I in the males of Janiroidea and Gnathostenetroidoidea are similar because they are opercular, even though the physical structure of these pleopods are quite different. To avoid these problems, opercular pleopods characters are not used here, and only the physical form of the pleopods is used.

Number of free pleonites

FRESI et al. (1980) and SKET (1985), follow WOLFF (1962) by regarding the number of free pleonites as weak indicators of affinity. WÄGELE (1983) and HENRY et al. (1986) follow the older practice of using a single free pleonite to characterize the Janiroidea, and two free pleonites for the remainder of the Asellota. Some Janiridae (e. g. Fig. 3 A), however, have two free pleonites identical in form to that seen in the Pseudojaniridae (WILSON 1986 a), and the Stenetriidae (Fig. 1 D). Moreover, the Protojaniridae have only one free pleonite (Fig. 2 A). The interpretation of free pleonites is clearly more complex than has been recognized. Until the pleotelson and pleonites of all major asellote families are carefully illustrated, especially on the ventral side, this character cannot be used with any certainty.

Results of the phylogenetic analysis

New cladogram

One most parsimonious cladogram for the Asellota results from the numerical analyses of the data set in Table 2. The tree (Fig. 8) is stable in its configuration, regardless of whether Camin-Sokal, Wagner parsimony, or the compatibility methods are being used, primarily due to few conflicting characters. The consistency index of this tree is 0.905 (21 character steps with a theoretical minimum of 19). The cladogram length of 21 steps is calculated by assigning apomorphic condition of the rostrum character in all three clades of the Janiroidea, recognizing that it is lost independently in some but not all taxa of each. If these independent reversals were included, the tree length would be 24 steps (consistency index 0.79).

Two characters (14 and 15, the form of the first pereopod) must be derived twice in the cladogram. The cladogram's distribution of character 15 shows that the protojanirids change directly from the primitive form (state 0) to the most derived form (state 2). If the two forms of the pereopod are represented by two different taxa, these taxa still form the same clade. The transformation of the first pereopod in the pseudojanirid-janiroidean

Table 2

Taxon-character matrix for the Asellota

The character numbers correspond to those listed in text

Taxon	Characters																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Ancestral states	?	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0	0	?
Aselloidea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gnathostenetroidoidea	?	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0
Higher Janiroidea	1	1	1	1	0	1	1	1	0	1	0	0	1	1	2	B	0	0
Munnidae and Pleurocopidae	0	1	1	1	0	1	1	1	0	1	0	0	1	0	1	B	1	0
Paramunnidae and Abyssianiridae	1	1	1	1	0	1	1	1	0	1	0	0	1	0	1	B	0	1
Protojaniroidea	?	1	0	0	1	0	0	0	1	0	1	0	1	0	*	0	0	0
Pseudojaniridae	0	1	0	1	0	1	1	1	0	0	0	1	1	0	0	1	0	0
Stenetridoidea	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0

Non-numeric states: ?, the state of the character is unknown or uncertain; B, both states of the character occurs within the taxon; *, states 0 and 2 occur within the taxon. The taxa are arranged alphabetically only, and no anagenic sequence is implied

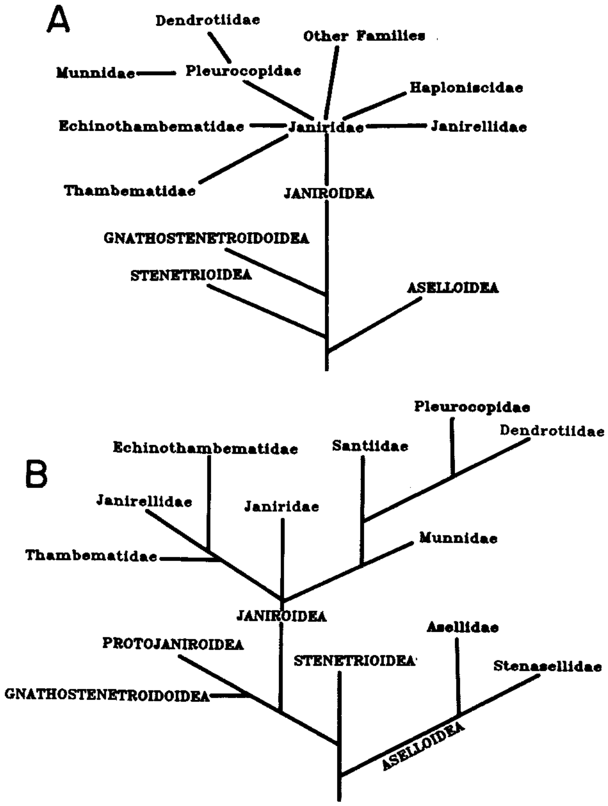

Fig. 5. Previous phylogenetic relationships proposed for the Asellota. A: Tree of Kussakin (1973). B: Tree of Fresi et al. (1980)

clade is linear with the intermediate state represented. Whether this interpretation of the first pereopods is correct must await a careful reappraisal of the Protojaniridae and the form of their first pereopod. The male pleopods of *Protojanira* (e.g. Grindley 1963) and *Enckella* (Fig. 2), however, are nearly identical, indicating that these taxa belong in the same group.

The bootstrap confidence limits around monophyletic clades in this data set (500 iterations) shows that the most robust (defined as its frequency of appearance) clade is that including all taxa of the

Janiroidea (0.996–1.0, 2 separate runs). The next best corroborated clade is the Janiroidea + Pseudojaniridae (0.94–0.998). The last clade and the Stenetrioidea are in the 0.812–0.85 confidence percentile, and all non-aselloids have a percentile of 0.782–0.882. The clade of the higher Janiroidea + Paramunnidae + Abyssianiridae appears only 0.654–0.604 of the time, and the least corroborated monophyletic group is the Protojaniroidea + Gnathostenetroidoidea (0.602–0.568), which is defined by only a single apomorphy. Only the first two monophyletic groups mentioned are sufficiently well corroborated (at or near the 95 % confidence level, see FELSENSTEIN 1985). Changes in single character states of the remainder of the clades are more likely to change the form of the tree. The bootstrap analysis indicates that more characters are needed for a higher degree of global (sensu MADDISON et al. 1984) certainty for some of the monophyletic groups shown in figure 8.

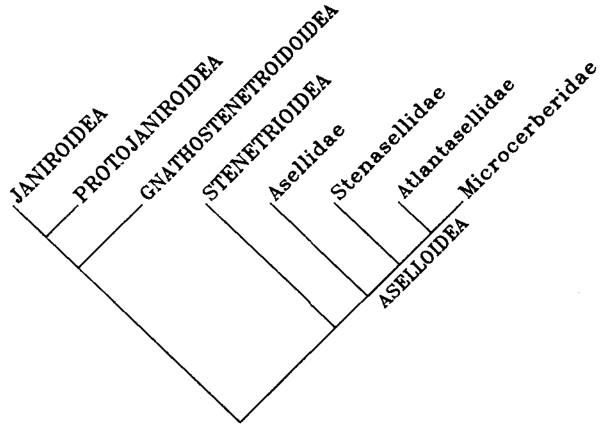

Fig. 6. The proposed phylogeny for the Asellota of WÄGELE (1983)

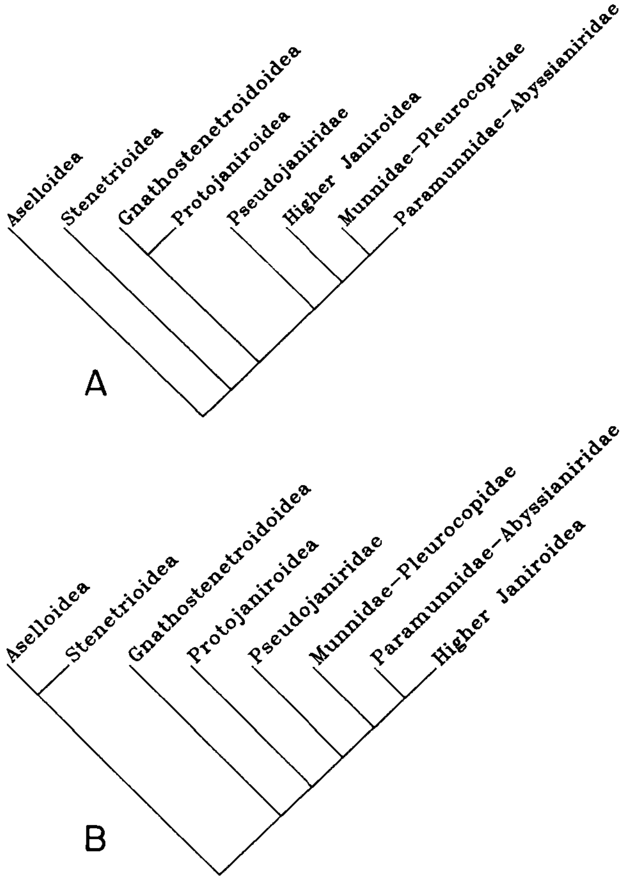

Fig. 7. Equivalent cladograms of the trees in the literature. A: tree for KUSSAKIN (1973) and FRESI et al. (1980). B: tree for WÄGELE (1983)

Comparison with other trees

Many implied phylogenies of the Asellota have been presented as classifications, but three works (KUSSAKIN 1973; FRESI et al. 1980; WÄGELE 1983) display the relationships asellotan subtaxa in explicit branching diagrams. The tree of SCHULTZ (1979) is not considered because of its construction was based on an invalid taxon. KUSSAKIN (1973) and FRESI et al. (1980) present the majority opinion on the evolution of the Janiroidea based on previous classifications and their own work (Fig. 5). Their conception places the Stenetrioidea near the Aselloidea but on the line leading to the Janiroidea. These authors place the Gnathostenetroidoidea (and the Protojaniridae) between the Stenetrioidea and the Janiroidea. WÄGELE (1983), on the other hand, proposes that the Stenetrioidea belongs on the aselloid line, which includes the Aselloidea, and has a descent separate from the ancestral janiroidean (Fig. 6). His phylogenetic concept, based primarily on the opercular third pleopod being an apomorphy of the aselloid line, is not born out in the new cladogram.

These trees from the literature were converted into equivalent cladograms for comparison with the parsimonious tree generated by the data (Fig. 7). Because these previous works did not separate the Janiroidea into the same taxa used here, the additional OTUs were placed in their most parsimonious positions. For example, the Pseudojaniridae were placed before the Janiroidea in all cases. The trees of KUSSAKIN (1973) and FRESI et al. (1980) produce the same cladogram (tree K) using the present OTUs. The tree K has a length of 24 steps, with a consistency index of 0.792, which is substantially less parsimonious than the new cladogram. The cladogram of WÄGELE (tree W) is even worse, having a length of 26 steps, and a consistency of 0.731.

The characters used in this investigation are subject to other interpretations, which could result in longer tree lengths under the current data set. As one allows longer tree lengths, however, the number of possible tree topologies increases rapidly. There are 4 trees possible with a length of 22 steps, each of which is nearly identical to the best tree (Fig. 8). On the other hand, tree K (24 steps) and tree W (26 steps) have 68 and 492 contending topologies (and different character interpretations), respectively. If either of these latter trees is favored, additional characters must be added to the analysis to offset the low parsimony values generated by the current character set.

Discussion

A new phylogeny

At the superfamilial level, the proposed phylogeny suggested by the cladogram (Fig. 8) resembles those presented by KUSSAKIN (1973) and FRESI et al. (1980), but the Protojaniridae and the Gnathostenetroididae are derived before the Stenetrioidea, because they lack the following apomophies: frontal rostrum, and endopod of the male second pleopod with a single segment. This phylogeny conflicts with the superfamily concept of WÄGELE (1983), who commented that "connections" between the aselloid line, which contained the Stenetrioidea, and the janiroid line "are impossible". Nevertheless, placing the Stenetrioidea in the "janiroid line" and away from a close relationship with the Aselloidea removes some of the potential homoplasies created by his proposed phylogeny. The female second pleopods of *Stenetrium* are fused into a single sympod, as in *Pseudojanira* and the Janiroidea, an apomorphy not found in the Aselloidea. The reduction of the male pleopod II exopod to a single segment is derived only once instead of twice as in WÄGELE's scheme. The unique family Pseudojaniridae is the sister group of the Janiroidea primarily due to the male pleopod apomorphies shared with this superfamily. Two branching nodes separate it from the higher Janiroidea and the Janiridae in which it has been previously classified (BARNARD 1925; KENSLEY 1977), forcing a new classification for the Pseudojaniridae Wilson, 1986a.

A reorganization of the presumed evolutionary relationships within the Janiroidea also is necessary. The clade including the Pleurocopidae and the Munnidae is a sister group to all other Janiroidean families; additionally, the superfamiliy is further subdivided by an early derivation of the ancestor of the Paramunnidae and the Abyssianiridae. The Dendrotiidae and the closely related Haplomunnidae are full-fleged members of the higher Janiroidea, and are not derived from a *Pleurocope*-like or a *Santia*-like ancestor as suggested by Fresi et al. (1980) and Kussakin (1973), respectively (see Fig. 5). In these previous schemes, the Janiridae is the central taxon in the evolution of all other janiroid families. This family has been considered to represent the archtypical janiroidean (e. g. Hessler et al. 1979) because many of its features are those found in other superfamilies, giving it the appearance of the presumed ancestor of the group. Such characters are a flattened body with broad tergites; presence of an antennal scale; large biramous uropods; long, unmodified walking legs; and other typically isopodan characters. These characters, however, are plesiomorphies at the level of the Asellota, and can be found in the pleurocopid genus *Santia*, in the Paramunnidae, and other non-janiroid taxa, such as *Asellus*. Therefore, they cannot be used to establish relationship. The janirids have dorsal cuticular organs and leg-like first pereopods, while the ancestor of the superfamily may have had a first pereopod more like that seen in the genus *Santia*, a transitional form between the grasping leg and the walking leg. The ancestral janiroidean did have the highly modified male pleopods but the female was fertilized ventrally, as in the lower Asellota. The Janiridae also have apomorphies at the level of the superfamily, such as enlarged third accessory claws on the pereopods, that are not found in most other Janiroidea. Several distinct phyletic lines, such as that leading to the munnids and paramunnids, had diverged from the basal stock of the Janiroidea before a recognizable janirid had evolved. In spite of its possible overall resemblance, the ancestral janiroidean can no longer be identified as a member of the Janiridae, because this family bears features derived after other taxa of the superfamily arose.

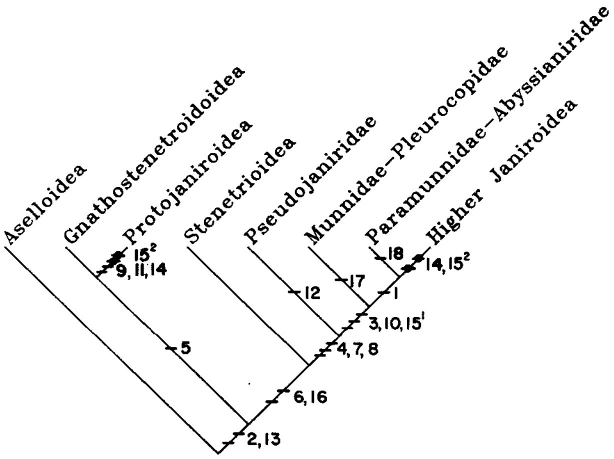

Fig. 8. A new proposal for the phylogeny of the Asellota. Numbers marked on cladogram are apomorphies listed in Table 1. Character 15 is a three state character; the two derived states are represented by 15^1 and 15^2. Approximate positions of the apomorphies are marked by small horizontal bars; apomorphies derived more than once are also marked by a dot

The classification of the Asellota

The classification of the Asellota should match the best estimate of the phylogeny of its taxa. Asellotan phylogeny, however, will undoubtedly need refinement as more information is collected on the Gnathostenetroididae and the Protojaniridae, and on the details of the female reproductive system in these and other families. Furthermore, the systematic position of the Atlantasellidae and the Microcerberidae must be re-evaluated *vis-a-vis* the family Calabozoidae van Lieshout. These three taxa have similarities that may be apomorphic at the ordinal level, thereby casting suspicion on the monophyly of the Asellota *sensu* Wägele (1983). In particular, they differ from all other Asellota in that the exopod of the male second pleopod is small, degenerate, and probably is not used during copulation, at

Table 3

A revised classification of the Asellota, modified from Bowman and Abele (1982)

New categories are not created for the distinct clades of Munnidae + Pleurocopidae, and Paramunnidae + Abyssianiridae

- Order Isopoda Latreille, 1817
  - Suborder Asellota Latreille, 1803
    - Superfamily Aselloidea Rafinesque, 1815 *sedis mutabilis*
      - Family Stenasellidae Dudich, 1924 *sedis mutabilis*
      - Asellidae Rafinesque, 1815 *sedis mutabilis*
      - Atlantasellidae Sket, 1979 *sedis mutabilis*
      - Microcerberidae Karaman, 1933 *sedis mutabilis*
    - Superfamily Gnathostenetroidoidea Kussakin, 1967 *sedis mutabilis*
      - Family Gnathostenetroididae Kussakin, 1967
      - Protojaniridae Fresi, Idato & Scipione, 1980
    - Superfamily Stenetrioidea Hansen, 1905 *sedis mutabilis*
      - Family Stenetriidae Hansen, 1905
    - Superfamily Pseudojaniroidea new superfamily
      - Family Pseudojaniridae Wilson, 1986 a
    - Superfamily Janiroidea Sars, 1899
      - Family Pleurocopidae Fresi & Schiecke, 1972
      - Munnidae Sars, 1899
      - Abyssianiridae Menzies, 1956
      - Paramunnidae Vanhöffen, 1914
      - Remaining families all *sedis mutabilis*
        - Acanthaspidiidae Menzies, 1962
        - Dendrotiidae Vanhöffen, 1914
        - Desmosomatidae Sars, 1899
        - Echinothambematidae Menzies, 1956
        - Haplomunnidae Wilson, 1976
        - Haploniscidae Hansen, 1916
        - Ischnomesidae Hansen, 1916
        - Janiridae Sars, 1899
        - Joeropsididae Nordenstam, 1933
        - Janirellidae Menzies, 1956
        - Macrostylidae Hansen, 1916
        - Mesosignidae Schultz, 1969
        - Microparasellidae Karaman, 1933
        - Mictosomatidae Wolff, 1965
        - Munnopsidae Sars, 1869
        - Nannoniscidae Hansen, 1916
        - Thambematidae Stebbing, 1913

least in the Atlantasellidae and the Microcerberidae. The general habitus of the Atlantasellidae is also similar to that of the Calabozoidae. Furthermore, the definition of the Aselloidea proper will have to be addressed as well. The analysis uses no defining apomorphies for the Aselloidea, in part because of the diversity of taxa it currently subsumes. The cladogram also has no defining apomorphies for the Gnathostenetroidoidea and the Stenetrioidea because autapomorphies for these taxa were not included in the analysis. In fact, each is quite distinctive, especially in their endopods of the male second pleopods, so the monophyly of these taxa is not contested here.

These problems prevent a complete systematic revision on the basis of the cladogram in Figure 8, although a new classification is presented in Table 3. This classification will be revised as information is accumulated on new characters and on the recently discovered taxa. For instance, most Asellota vary in their pleopod morphology, leading to the conclusion that there was considerable evolutionary experimentation in sperm transfer in their ancestors. The pleopods are stable morphologically only in the Janiroidea throughout many species, genera and families. The pleopods are useful for the classification of the

Asellota, but future phylogenetic arrangements of these taxa must be based on additional characters, including some of the characters used here. This agrees with the position taken by WÄGELE (1983, p. 257).

The classification must make changes to previous classifications for the purposes of consistency. A variety of ways to generate a classification from the cladogram exist, but the sequencing convention (WILEY 1981) is the most useful because it requires the fewest changes in current systems. To avoid creating an additional hierarchical rank between the subordinal and superfamilial levels, the Protojaniroidea Wägele is rejected and the Protojaniridae are returned to the Gnathostenetroidoidea. This is in agreement with the classification of HENRY et al. (1986). The form of the male first pleopod defines the Gnathostenetroidoidea adequately, and additional characters may be found as the group is better studied. The Pseudojaniridae are raised to the rank of superfamily, although this may be objectionable because the group is so poorly known (only two specimens have been collected). New categories are not created for the clade Munnidae + Pleurocopidae, or the clade Paramunnidae + Abyssianiridae, because the entire systematic structure of the Janiroidea needs revision (WILSON, in press). If these categories are needed, the "section" category in place of the "superfamily" category could be used, and new superfamilies could be assigned within the Janiroidea. Such a procedure already has some precedence in the Oniscidea (see BOWMAN and ABELE 1982). Alternatively, clades within the Janiroidea, such as the "munnopsoids" (families Munnopsidae, Eurycopidae, and Ilyarachnidae; see WILSON and THISTLE 1985) could be assigned to single families, and the included taxa placed in subfamilies. This latter procedure is somewhat more conservative, and is the one chosen by WILSON (in press). The authorship of various taxa in the Asellota has been subject to some confusion in a variety of the publications cited in this paper. Table 3 follows BOWMAN and ABELE (1982) who show the earliest authorship for most taxa. Some taxa have been eliminated (e.g. WILSON 1980a; WILSON 1982; SVAVARSSON 1984), so the overall classification is shorter than the previous version. Because the evolutionary sequence of the "lower Asellota" described by the new phylogeny is still controversial (WÄGELE in litt.), these are left as *sedis mutabilis* in the classification. Only the best corroborated clades can be accepted without reservation: the Janiroidea, and the clade including Janiroidea + Pseudojaniridae.

Evolution of the sexual characters

The character and phylogenetic analyses of the Asellota clarifies the possibility of coevolution of the female cuticular organ with male copulatory organ. The broad distribution of the cuticular organ in all Asellota indicates that it must predate the stylet form of the male pleopod II endopod. On the other hand, the stylet evolved to the hypodermic needle-like organ diagnostic of Janiroidea, as seen in the Pleurocopidae and the Munnidae, before the opening of the cuticular organ became separate from the oopore. Because the male and female systems undergo major changes at different hierarchical levels, they must have evolved independently from one another, thus corroborating their use as separate characters in the phylogenetic analysis.

The male copulatory system is highly stereotyped within the Janiroidea, and is its chief defining apomorphy. This pleopodal system, however, does not appear suddenly with all its components in place. Parts of the system are found in non-janiroidean taxa, indicating that it evolved gradually with some of the specializations appearing independently of others. In the face of the enormous diversity of the Janiroidea, especially in the deep sea, one is left wondering whether their highly directed and stereotyped system for delivering sperm to the females has been a major factor in the evolutionary radiation of these isopods.

Acknowledgements

This paper has gone through a series of revisions stretching over several years. I received comments on the first version of the manuscript from RICHARD C. BRUSCA, who suggested (among other things) that numerical methods should be tried to lend credence to the cladogram presented in Figure 8. Reassuringly, the tree topology has not changed since then, although the data set has been tinkered with as new information has come in. Later versions of the manuscript have been reviewed by ROBERT R. HESSLER, WILLIAM A. NEWMAN, RICHARD C. ROSENBLATT, WILLIAM R. RIEDEL, and DAN L. LINDSLEY. N. P. KRISTENSEN and anonymous reviewers offered useful suggestions for the improvement of final manuscript. A German translation of the English abstract and comments on the final manuscript were kindly provided by J.-W. WÄGELE. PHYLIP, a numerical phylogenetics package with a variety of separate programs, was generously provided by JOSEPH FELSENSTEIN without charge. PAUP was created by DAVID SWOFFORD and marketed by him for a reasonable price; it proved to be useful and powerful for some kinds of analyses. BORIS SKET generously sent several specimens of *Enckella* for study. ROBERT R. HESSLER permitted access to a large collection of asellota isopods housed in his laboratory, and provided advice and encouragement throughout this research. This research has been partially supported by the Systematic Biology division of the U.S. National Science Foundation, under grant numbers DEB 82-15942 and BSR 86-4573. I am grateful to these people and institutions for their part in this paper.

Zusammenfassung

Der Weg zu den Janiroidea: Vergleichende Morphologie und Evolution der Asellota (Crustacea, Isopoda)

Die Evolution der Isopoden der Unterordnung Asellota ist der Gegenstand einer Vielzahl von phylogenetischen Diskussionen gewesen. Die vorliegende Untersuchung stellt eine neue phylogenetische Einschätzung mit dem Ziel vor, die Evolution der Überfamilie Janiroidea, einer umfangreichen und formenreichen Gruppe aller aquatischen Lebensräume, aufzuklären. Die phylogenetische Analyse fußt auf der morphologischen Bewertung von Merkmalen, die in früheren Systemen verwendet wurden, und dazu von mehreren neuen Merkmalen. Die Lesrichtung der Reihen wurde über den Außengruppen-Vergleich bestimmt. Die verwendeten Merkmale gehören zu den Pleopoden, den Kopulationsorganen, den ersten Pereopoden und dem Cephalothorax. Der erhaltene Datensatz wurde mit numerisch-phylogenetischen Computerprogrammen analysiert, um die sparsamste Kladogramm-Hypothese zu finden, die in eine Klassifikation übersetzt wurde. Die Annahmen für das neue phylogenetische System sind wesentlich sparsamer als in den Stammbäumen der bisherigen Literatur, und mehrere der monophyletischen Gruppen haben einen robusten Vertrauensbereich.

Die Überfamilie Stenetrioidea gehört zusammen mit den Janiroidea zu einem Taxon, nicht jedoch wie bisher angenommen, mit den Aselloidea. Die Schwestergruppe zu den Janiroidea ist die Familie Pseudojaniridae, die in den Status einer Überfamilie gelangt. Das Taxon mit den Familien Gnathostenetroididae und Protojaniridae ist nicht die Schwestergruppe zu den Janiroidea, sondern ist früher als die Stenetrioidea in der Evolution der Janiroidea entstanden. Innerhalb der Janiroidea ist nicht, wie bisher angenommen, die Familie Janiridae das urtümlichste Taxon: Die Gruppe mit den Familien Munnidae und Pleurocopidae enthält die zuerst entstandenen Janiroidea.

Die Daten zeigen auch, daß der ungewöhnliche Sexualdimorphismus der Janiroidea nicht plötzlich, sondern in einer Serie unabhängiger Schritte innerhalb der Asellota entstanden ist.

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