Phylogeny, evolution and biogeography of the marine isopod Subfamily Idoteinae (Crustacea: Isopoda: Idoteidae)

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Abstract. The patterns of spatial distribution attained by the genera of Idoteinae are discussed in light of a cladistic analysis of the suborder Valvifera and the subfamily Idoteinae. A schematic pattern analysis technique is demonstrated and reveals the probability of multiple origins of similar pleonal morphologies among various genera of Idoteinae. Reduction in the maxillipedal palp has occurred numerous times within the Idoteinae, while loss of the biramous uropodal condition has probably occurred twice. A geographic cladogram of temperate Gondwanan shores is proposed. An evolutionary-biogeographic narrative is presented, in which a set of hypotheses is developed to describe the history of the Idoteinae in time and space. The subfamily Idoteinae appears to form two principal lines of descent, both arising in the Triassic or Jurassic. One of these lines remained closely tied to the Southern Hemisphere (primarily Old World) temperate marine shores from which the Idoteinae is derived. The other line invaded the Northern Hemisphere and various New World environments, and more recently (Cenozoic) underwent a radiation in the American tropics. The success of this latter lineage (e.g., *Erichsonella, Eusymmerus, Parasymmerus, Cleantioides*) may be due to certain morphological and life history adaptations not found in New World species of the former line (e.g., *Idotea, Synidotea*). The Valvifera probably originated in the temperate Southern Hemisphere, at least by Permean/Triassic times. Global distribution patterns of some genera can be ascribed most parsimoniously to vicariance processes, and in others to dispersal, ecological phenomena, or a combination of processes. Other factors have apparently also affected modern distributional patterns of idoteine genera, for example, extinctions. Biogeographical data can be used to elucidate viable alternative cladistic hypotheses to those generated solely on parsimonious patterns of synapomorphy. Biogeographic data can also be used, in conjunction with the cladogram, to identify probable ancestral taxa.

INTRODUCTION

Few groups of marine invertebrates have enjoyed analysis by cladistic techniques, despite the current popularity of the method. The only previous attempt to examine the phylogenetic relationships of an isopod taxon by strict cladistic (Hennigian) methodology was that of Williams (1970), who analyzed the relationships of North American epigean species of *Asellus* (Asellota); but, as was common with early attempts at Hennigian analyses, he used a weakly defined method of character state polarity assessment. Despite this, he was still able to construct a very plausible phylogenetic hypothesis, or cladogram, for the 14 species he treated.

One reason for the paucity of cladistic studies on marine invertebrates is the necessity to work with a group whose taxonomic relationships are reasonably well known within the context of the larger hierarchical taxon to which the study group belongs. Without this knowledge, an assessment of character polarity is difficult to obtain, and without polarities, construction of both cladograms and phylogenetic (evolutionary) trees must be based on speculatively generated hypothetical ancestors (expressed or implied). Although several marine invertebrate taxa are well understood systematically (e.g., certain families of molluscs, crabs, barnacles), the great majority are not. Several crustacean isopod groups are also well understood in this regard. The subfamily Idoteinae (suborder Valvifera; family Idoteidae) is one such group.

The present study attempts to answer questions about the evolutionary history of the Idoteinae using cladistic techniques. Specific questions addressed are: What are the

phylogenetic patterns and relationships of the genera of Idoteinae? What are the spatial patterns and relationships of the genera of Idoteinae? What evolutionary history is suggested when these patterns are compared to one another and to the earth's geological and ecological history? Previous studies on these topics include comments on the phylogeny and biogeography of the genus *Idotea* by Menzies (1950*a*); on the genus *Synidotea* by Menzies and Miller (1972); and on the comparative morphology of the valviferan higher taxa in general by Sheppard (1957). A review of the distribution of shallow-water idoteine species in the northeastern Pacific was given by Brusca and Wallerstein (1979*b*), and a discussion of the possible ecological and historical mechanisms regulating distribution and latitudinal trends in morphology and behavior in that taxon is provided by Wallerstein and Brusca (1982).

Methods

The methods used in this study are largely summarized in 3 recently published books (Eldredge and Cracraft 1980, Nelson and Platnick 1981, Wiley 1981). However, even the principal spokesmen of current cladistic theory are not without disagreement on both details of procedure and certain underlying philosophical issues. As Eldredge and Cracraft (1979) point out, "No two cladists agree with each other (or, for that matter, with Willi Hennig) on every point, and this 'school' of systematics is no more a monolith than that of the more traditional 'evolutionary taxonomy'." The overall concept of cladistic or "phylogenetic" analysis has evolved considerably since Hennig (1966), and indications are that it will continue to change for some time to come. For these reasons, and others, I offer the following position statements.

While the present study is cladistic in nature, it is my opinion that such analyses are most useful as investigatory techniques and do not represent the final word on phylogeny. The most powerful (and important) aspect of cladistic methodology is its ability to posit and define monophyletic groups in an unambiguous and testable manner. Synapomorphy patterns, however, do not constitute the sole source of phyletic information on a taxon, but rather must be compared to other kinds of data and analyses when constructing phylogenetic trees, evolutionary scenarios, AND classifications. A cladogram depicts only a sequence of character appearances, which may or may not correspond to speciation events (Hull 1979). There appear to be 4 principal products that can result from phylogenetic analyses: cladograms, phylograms (evolutionary trees), evolutionary scenarios, and classifications. The cladogram should be viewed as a "best guess" in the face of uncertainty (Felsenstein 1973, Harper 1979, Hull 1979, Simberloff et al. 1981, Endler 1982), and information contained in any of these other products of phylogenetic analyses can legitimately be used to improve any other, including the cladogram itself (Hull 1979). In the present study I construct a cladogram, a phylogram, and an evolutionary scenario for the subfamily Idoteinae, and use the latter two products to shed new light on, and make ammendments to, the cladogram.

Nomenclature and general terminology are taken from current literature on valviferan isopods (see above references). Morphological structures discussed in this paper are illustrated in Fig. 1. Analysis of character polarity is based on out-group analysis (see Eldredge and Cracraft 1980, de Jong 1980, and Watrous and Wheeler 1981). I believe that out-group comparisons need not be rigidly constrained by nomenclatural rank or Linnean hierarchical structure, but are applicable at all levels of a cladogram. Though parsimony is a potent methodological tool, it is primarily a method of logical analysis, not a biological law or principle. Application of parsimony should be an initial technique, or one to be used in the absence of other data. To continue to hold to the

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Figure 1. Aspects of the morphology of idoteid isopods discussed in the text. **a**, *Synidotea harfordi*; note multiarticulate flagella on antennae 2 and 0+1 pleonal morphology. **b**, *Cleantioides occidentalis*; note uniarticulate (clavate) flagellae on antennae 2 and 3+1 pleonal morphology. **c**, *Colidotea findleyi*; note multiarticulate flagellae on antennae 2 and 0+1 pleonal morphology. **d**, Mandible of *Eusymmerus antennatus*;
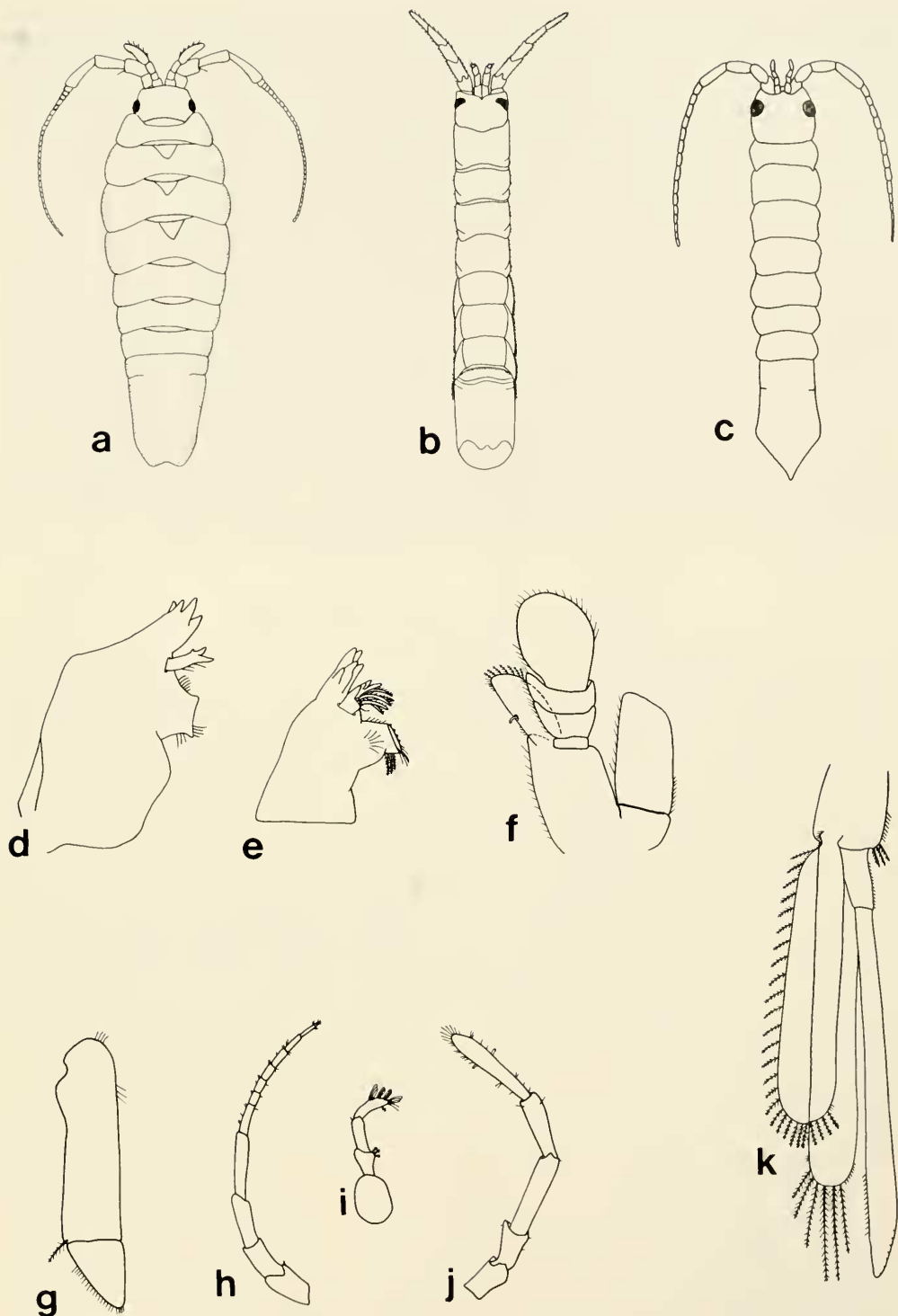
note large 4-toothed incisor, smaller lacinia mobilis, and stout molar process. **e,** Mandible of *Colidotea findleyi*; note 5-toothed incisor, large lacinia mobilis, and stout molar process. **f,** Maxilliped of *Colidotea findleyi*; note 4-articulate palp. **g,** Uniramous uropod of *Colidotea findleyi*. **h,** Antenna 2 of *Colidotea findleyi*; note multiarticulate flagellum. **i,** Antenna 1 of *Colidotea findleyi*; note uniarticulate flagellum. **j,** Antenna 2 of *Erichsonella cortezi*; note uniarticulate (clavate) flagellum. **k,** Pleopod 2 of *Erichsonella cortezi* (male); note appendix masculinum.

"simplest" explanation (i.e., the shortest cladogram) in the face of biological evidence indicating a less parsimonious but more biologically reasonable explanation is both nonscientific and an abuse of the tool. There is little point in creating a falsifiable hypothesis if one does not accept all forms of data that can falsify it. In this regard I agree with Kitts (1981) that phylogenetic patterns (and hence analyses) ARE historical in nature and this involves describing the real world; one could not be writing history if one supposed every relationship between events to have transpired in the "most direct" manner. Whether or not any particular phylogeny is parsimonious is something to be found out in the course of a historical investigation, it is not something to be assumed.

Finally, my technique for the historical biogeographic analysis follows the hypothetico-deductive method, primarily as described by Morse and White (1979). I assume no particular paradigm to be of overriding importance, but rather attempt to interpret the patterns of characters and distributions in the most parsimonious (biological parsimony) fashion possible. McDowall (1978) was, of course, correct in noting that one can never know with certainty whether any given individual component track is the product of vicariance or dispersal. However, that both phenomena exist in nature can hardly be denied, and it has been my task in the present study to decide, where possible, which of these two phenomena (or others) produced the biogeographic patterns seen today in the genera of Idoteinae. Needless to say, I have been severely hampered in this regard by the absence of cladograms for other coastal marine taxa.

Higher Classification of the Order Isopoda and the Suborder Valvifera

Out-group analysis requires acceptance of some higher level classificatory structure before statements regarding the relationships of lower, inclusive taxa can be made. For the purposes of this study, I accept the monophyletic nature (*sensu* Hennig, 1966) of three taxa: the order Tanaidacea, the order Isopoda, and the suborder Valvifera. The monophyletic nature of these distinct taxa are, to my knowledge, unquestioned.

While the nature of the primitive isopod body plan (presented below) is generally agreed upon, the relationships of the 9 isopod suborders are unknown and fraught with speculation (see Schultz 1979 for recent summary comments). Various authors have described the nature of the primitive or ancestral isopod morphotype, which is characterized by the following combination of characters: carapace wanting; pereopods uniramous; respiratory structures (heart and branchial surfaces) primarily abdominal; pereopodal coxae forming marginal plates on pereonites; first and second antennae with multiarticulate flagella; mandible with a multiarticulate palp; appendix masculina present only on second pair of pleopods; uropods biramous (probably attached terminally or subterminally to telson or pleotelson, although some authors suggest a lateral attachment vis-à-vis the cirolanoids); eyes entirely sessile; all pereopods more or less similar; pereon of 7 free somites (thoracomeres 2–8); pleon of 6 free somites and a telson (or possibly 5 free somites and a pleotelson); maxilliped with a large basal endite and reduced endopodal articles (the latter forming the 5-articulate palp); maxilliped with a small, ovate, nonbranchial epipodite (the "endognath"); penes and opening of vas deferens on thoracomere 8; simple foregut; and maxillary glands present in adults.

This generalized ancestral isopod plan was first developed in the early studies of Bate and Westwood (1861–1868), Stebbing (1893), and Calman (1909), and more recently by Schram (1974) and Hessler et al. (1979). The concept of this morphotype is supported by fossil data as well as by comparison with other peracarid and malacostracan taxa. It is also compatible with all three "competing" hypotheses of extant primitive isopod morphotypes (i.e., cirolanoid, phreatoicoid, asellote).

The Valvifera stand apart as perhaps the most distinct of the isopod suborders in several regards. Important features distinguishing the valviferan body plan are (see Fig. 1): (a) coxae of thoracic legs (pereopods) with both dorsal and ventral plates, the latter extending over the sterna; (b) uropods attached laterally on pleotelson, but modified

to form ventral opercular plates covering the pleopods; (c) vas deferens (and penes) opening on abdomen of male, rather than on thorax as in all other isopods, excepting the Oniscoidea (i.e., on pleonite 1 or on the articulation of pleonite 1 and thoracomere 8); (d) flagella of first antennae reduced to one or a few vestigial articles; (e) pleon of 4 or fewer free somites (plus the pleotelson); (f) uropods biramous or uniramous; (g) maxillipedal palp of 3–5 articles; (h) second antennae uniramous, flagellum multiarticulate or uniarticulate; (i) mandible with or without a 3-jointed palp. Attributes (a) and (b) are unique synapomorphies that distinguish the Valvifera from all other isopod taxa; attributes (c) through (f) are valviferan synapomorphies that also appear in one or more other isopod suborders (apparent convergences).

The current classification of the isopod suborder Valvifera is as follows:

Order Isopoda Latreille, 1817
   Suborder Valvifera Sars, 1882
      Family Holognathidae Thomson, 1904
      Family Idoteidae Fabricius, 1798
         Subfamily Idoteinae Dana, 1852
         Subfamily Parachiridoteinae Elkaim and Daguerre de Hureaux, 1976
         Subfamily Glyptonotinae Miers, 1881
         Subfamily Chaetilinae Dana, 1852 (=Macrochiridoteinae Nordenstam, 1933)
         Subfamily Mesidoteinae Racovitza and Sevastos, 1910
      Family Xenarcturidae Sheppard, 1957
      Family Arcturidae G. W. Sars, 1897
      Family Amesopodidae Stebbing, 1905
      Family Pseudidotheidae Ohlin, 1901

The relationships of the 6 valviferan families have long been unclear. The only cogent discussion of the topic was that of Sheppard (1957). The cladogram in Fig. 2 depicts the best arrangement that I have been able to devise for these families, being the most parsimonious, and admitting no convergences, parallelisms or reversals. A convincing higher level classificatory scheme of the 9 isopod suborders does not presently exist, and carcinologists disagree over the relationships among these taxa. For this reason, the Tanaidacea was used as an out-group to construct the cladogram of valviferan families (Fig. 2). Tanaidacea is the peracarid order "traditionally" (Schram 1981) taken to be the most probable sister-group to the Isopoda (also see Siewing 1963 and Fryer 1964). Whether or not it is the actual sister-group of the isopods is unimportant for its use in out-group comparison, however, as it is clearly a closely related taxon within the unified peracarid line. Character polarity assessments based on tanaids were compared to those obtainable by using the Amphipoda, Cumacea and hypothetical ancestral isopod as out-groups and no changes in polarity were required when these other groups were used in place of tanaids.[1] A step-by-step discussion of the cladogram of valviferan families follows, the numbering in the text following that of Fig. 2.

Tanaids are united to the isopods only by possession of their peracarid attributes, the most obvious of these being: (a) pereopodal coxae with thin ventral plates (oostegites) that form a female brood pouch for the developing young; (b) mandibles with lacinia mobili in adult stages of life cycle, and (c) young released from the marsupium in subadult "mancoid" stage. At this level of analysis these attributes are symplesiomorphies; I know of no synapomorphies unique to the tanaids and isopods.

The Isopoda are united by the features listed above for the primitive isopod morphotype. The first 4 of these are synapomorphies, as follow: (1) carapace wanting (vs. present in tanaids); (2) pereopods uniramous (vs. retaining vestiges of exopods); (3) respiratory structures (branchial pleopods and heart) primarily abdominal (vs. thoracic); (4) pereopodal coxae forming marginal plates on pereonites (vs. not forming plates).[2]

The Holognathidae shares in common with its sister-group (the remaining 5 valviferan families) the 4 valviferan synapomorphies listed earlier: (5) pereopodal coxae form ventral (sternal) plates; (6) uropods modified into opercular plates covering pleo-
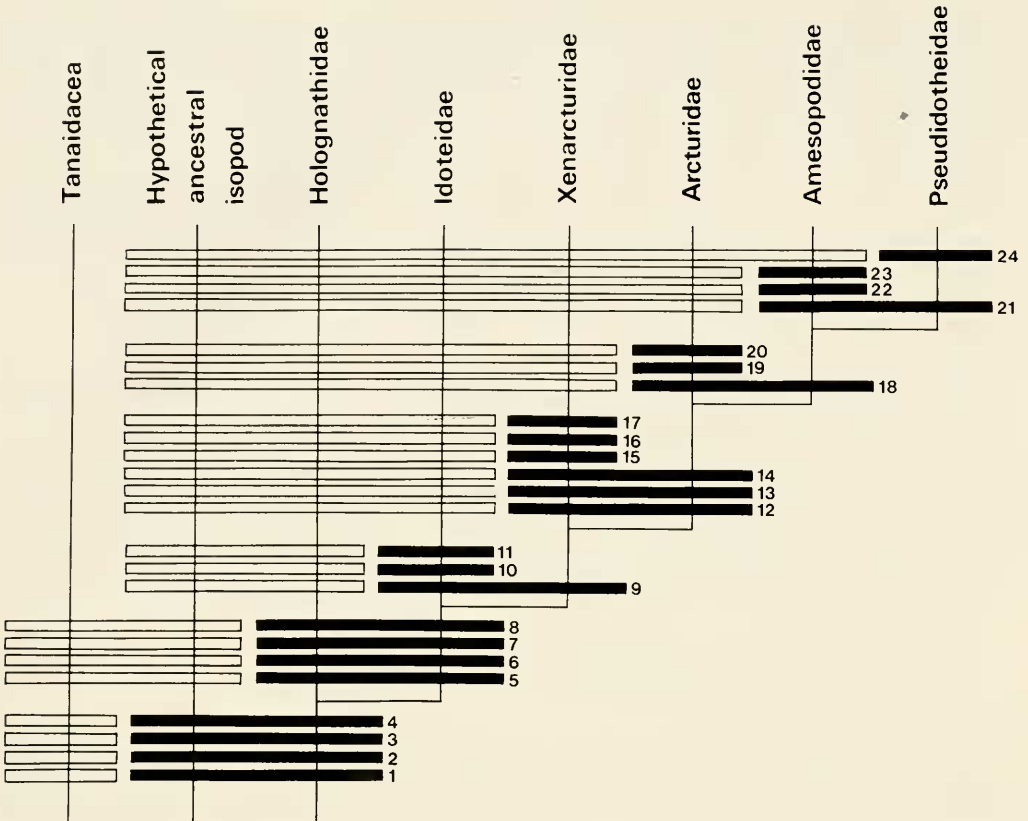
FIGURE 2. Cladogram of families of Valvifera. Closed boxes indicate apomorphies; open boxes plesiomorphies. Numbering of characters corresponds to text discussion.

pods; (7) vas deferens and penes opening on abdomen of male, rather than on thorax; (8) flagella of first antennae reduced to one or a few vestigial articles. The Holognathidae is a monotypic family containing but one species, *H. stewarti* (Filhol). It cannot be distinguished by an autapomorphy of its own, although it stands apart from all other species in the suborder Valvifera by its retention of a palp on the mandible, as well as numerous other primitive attributes (e.g., biramous uropods, 5-articulate maxillipedal palp, pleon of 4 free somites plus the pleotelson). *Holognathus* may be considered a relict taxon within the Valvifera. Nordenstam (1933) long ago recognized the lack of apomorphies in *Holognathus,* suggesting that it might best be incorporated into the Idoteidae. Were this done, however, *Holognathus* would probably have to be ranked as a sixth subfamily, rather than included in the Idoteinae as Nordenstam suggested. The presence of 4 free pleomeres places this genus at a position ancestral to both the Idoteinae and the Glyptonotine-group discussed below (see Fig. 3). The remaining valviferan families are thus united by the loss of the mandibular palp (9). Clearly, were one to place *Holognathus* in the Idoteidae, characters 5–8 would become synapomorphies uniting Idoteidae to all other valviferan families.

The Idoteidae stand apart as the only family in which the uropods may be reduced from the primitive biramous state to a uniramous condition (10), and in which a reduction of the maxillipedal palp takes place (11). The Idoteidae have been characterized by two other "synapomorphic trends": trends towards fusion of the pleonites and towards fusion (or loss) of the flagellar articles on the second antennae. These reductions, however, are convergent to patterns that also occur in other valviferan families and thus have not been used to construct the cladogram (Fig. 2). The Idoteidae
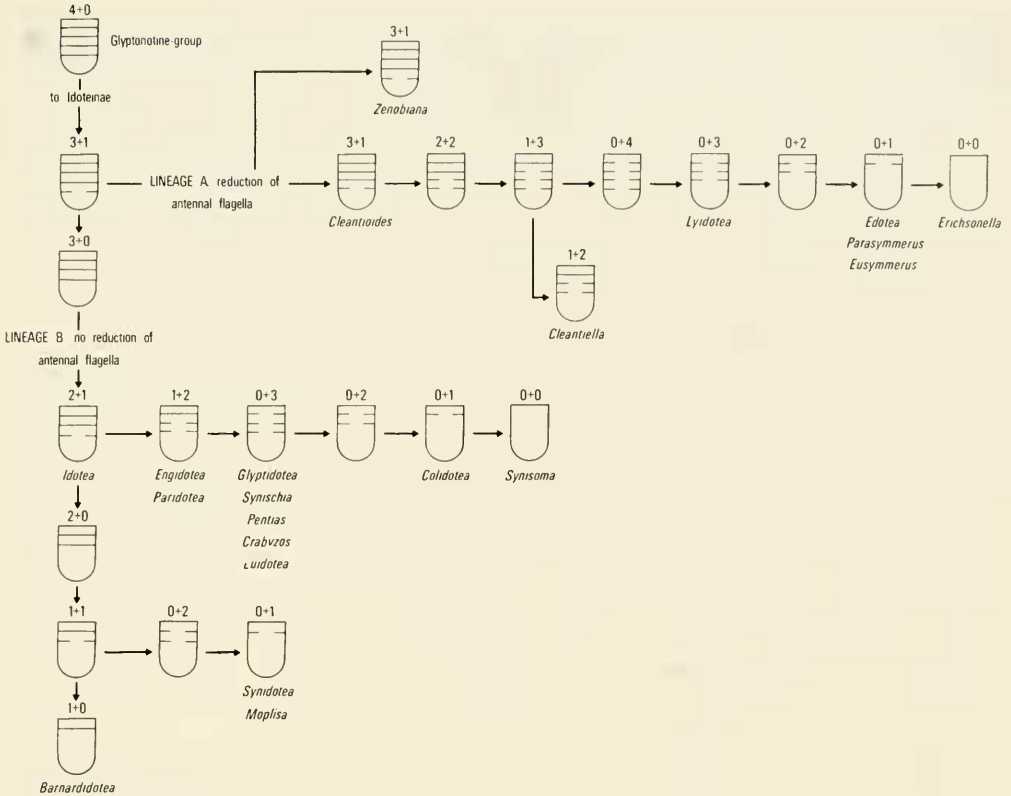
FIGURE 3. Schematic representation of possible phylogenetic pathways for pleonal fusion in the Idoteinae. Pleonal formulas are written above pleonal diagrams and indicate number of free and number of fused pleomeres. Genera assigned to given pleonal morphology are indicated below diagrams. See text for discussion.

stands out most strikingly from the 4 families that comprise its sister-group in the retention of numerous plesiomorphic attributes (e.g., free penes retained in 4 of the 5 subfamilies; free cephalon; one pair of appendix masculina, on the second pleopods). Racovitza and Sevastos (1910) long ago recognized the primitive nature of the Idoteidae, regarding it as an "ancient" family. The Idoteidae was the first valviferan family to be described, subsequent families being distinguished from it by elucidation of new characters acquired outside the Idoteidae. Thus, historically a diagnosis of the Idoteidae has been developed largely upon absence of characters (a phenomenon common among older taxa). The discovery of new distinguishing attributes (apomorphies) for the Holognathidae and Idoteidae is clearly needed and will provide important data for testing the hypotheses contained in the cladogram.

The Xenarcturidae and its sister-group (Arcturidae-Amesopodidae-Pseudidotheidae) are distinguished by the following synapomorphies: (12) first pleopods of males bearing "accessory appendix masculina" (in addition to the true appendix masculina of the second pleopods); (13) cephalon fused medially to pereonite I (second thoracomere); (14) peduncle of first pleopods greatly elongated. The Xenarcturidae is a monotypic taxon distinguished by the following autapomorphies: (15) pereonites I-IV with lateral margins expanded into large plates covering bases of pereopods; (16) second antennae with flagella reduced to single articles; and (17) flagella of second antennae directed towards mouth, rather than away from buccal field.

The Arcturidae and its sister-group (Amesopodidae-Pseudidotheidae) are distinguished by a synapomorphy in the functional grouping of the pereopods (18). Only in these taxa are pereopods I-IV similar and directed forward to form a functional group

distinct from pereopods V–VII. In all other valviferan taxa the pereopodal functional grouping is I–III and IV–VII. Arcturidae is distinguished by two synapomorphies: (19) the unique body shape (cylindrical or tubular, often geniculate), and (20) having pereonite IV generally manifestly enlarged or elongated.

The Amesopodidae and Pseudidotheidae are distinguished by the synapomorphic condition of having pereonites II–IV grossly enlarged (21). Amesopodidae is a monotypic family (*A. richardsonae* Stebbing, 1905) distinguished by the autapomorphies of highly reduced second pereopods (22), and the complete loss of pereopods III and IV (23). Pseudidotheidae contains two genera distinguished by the synapomorphy of fusion of the first two articles of the peduncle of the second antennae (24).

The Family Idoteidae and the Subfamily Idoteinae

The systematic history of the family Idoteidae can be traced through the following works: H. Milne Edwards (1840), Dana (1853), Bate and Westwood (1868), Harger (1880), Miers (1881), Chilton (1890), Ohlin (1901), Richardson (1905a), Stebbing (1905), Collinge (1917), Barnard (1920), Nordenstam (1933), Menzies (1950a), Sheppard (1957), and Menzies and Miller (1972). The American idoteid fauna is well known, largely due to the work of Dana (1853), Harger (1880), Benedict (1897), Richardson (1899a, b, 1900, 1901, 1904, 1905a, b, 1909), Hatch (1947), Menzies and Waidzunas (1948), Menzies (1950a, b), Menzies and Bowman (1956), Menzies and Frankenberg (1966), Menzies and Miller (1972), and Brusca and Wallerstein (1977, 1979a,b). All species of Idoteidae are marine, although two species of the subfamily Mesidoteinae also extend their distributions into fresh water. *Saduria* (=*Mesidotea*) *entomon* has been found in several deep Scandinavian lakes, and *Austridotea lacustris*[3] occurs from the littoral zone to fresh water rivers and lagoons in New Zealand.

The subfamily Idoteinae contains 22 valid genera (Table 1). The great majority are shallow-water and, for the most part, intertidal species. Few species are restricted to depths greater than 30 m. For the past 150 years (since the work of Brandt 1833 and H. Milne Edwards 1840) studies on this group have consistently found that the use of a few clearly defined characters provided a basis for a classification that has been both stable and reliable. Thus most idoteine genera are clearly defined, unambiguous, and easily distinguished from one another. As will soon be seen, however, not all idoteine genera can be defined by unique apomorphies. The few genera that are not clearly differentiated from one another comprise 2 small groups of largely monotypic, Southern Hemisphere genera that are in need of reexamination. Principal characters used to distinguish the idoteine genera are external and easily recognized, as follows.

Uropods. — The uropods of Idoteinae are either biramous or uniramous. The primitive biramous condition, while being clearly distinct from the uniramous condition and hence useful in pattern analysis, is not understood ontogenetically (see Calman 1909, Racovitza and Sevastos 1910, Tait 1917, Nordenstam 1933, and Menzies and Miller 1972). Loss of one uropodal ramus has occurred at least twice among the valviferan families, in the Idoteidae (subfamily Idoteinae) and again in a single species of Arcturidae (*Microarcturus digitalis* Nordenstam 1933). Whether or not these separate losses were by the same "mechanism" is not known.

Pleon. — Isopod taxa are characterized by varying degrees of fusion of the pleomeres and telson. Although trends towards fusion of pleomeres are evident throughout the Isopoda and occur in every suborder, no one has yet attempted to analyze these morphoclines in a systematic fashion (Fig. 3). In the Valvifera, there are always four or fewer free pleomeres, plus the pleotelson. The term "pleotelson" refers to that region of the pleon consisting of the telson and its fused pleomeres. For many years, the pattern of discrete character states manifested by fusion of pleomeres in the idoteine genera has been taken to represent a morphocline that is a sequence of phenotypes presumed to reflect the probable evolutionary pathway of descent. The polarity or direction of this morphocline is clearly shown by out-group analysis to be towards levels of increasing pleomere fusion. Fusion of the pleomeres is often (but by no means always) indicated by the presence of partly free lateral margins, distinguishable by the presence

TABLE 1. Summary of "traditional characters" used to differentiate the genera of Idoteinae (from Menzies and Miller 1972; with corrections). See text for additional characters. *Edotea* includes the synonym *Epelys*, and *Zenobiana* includes the synonym *Cleantis*. *Erichsonella* includes the synonyms *Erichsonia* Dana and *Ronalea* Menzies and Bowman. Pires (pers. comm.) has a manuscript in preparation in which she intends to remove the monotypic genus *Ronalea* from synonymy with *Erichsonella*, based on the alleged presence of a single pair of lateral incisions in *R. pseudoculata* (Boone). I have not examined *R. pseudoculata* myself. Such a change would require a minor revision in the cladogram (Fig. 17b), by adding *Ronalea* as a fork at the tip of the line leading to *Eusymmerus*, making these two genera sister-taxa.

Genus	Flagellum of Antenna 2			Pleonal formula	No. articles in Mxp palp	Uropods	
	Multi-articulate	Clavate	Vestigial			Uniramous	Biramous
Barnardidotea Menzies & Miller	X			1 + 0	3	X	
Crabyzos Bate	X			0 + 3	5	X	
Engidotea Barnard	X			1 + 2	5	X	
Glyptidotea Stebbing	X			0 + 3	5	X	
Moplisa Moreira	X			0 + 1	3	X	
Pentias Richardson	X			0 + 3	5	X	
Paridotea Stebbing	X			1 + 2	5	X	
Synidotea Harger	X			0 + 1	3	X	
Synischia Hale	X			0 + 3	5	X	
Idotea Fabricius	X			2 + 1	4–5	X	
Colidotea Richardson	X			0 + 1	4	X	
Synisoma Collinge	X			0 + 0	4	X	
Zenobianopsis Hale	X			2 + 2 ? / 4 + 1	5	X	
Euidotea Collinge	X			0 + 3	4	X	
Cleantiella Richardson		X		1 + 2	5	X	
Erichsonella Richardson		X		0 + 0	4	X	
Eusymmerus Richardson		X		0 + 1	4	X	
Parasymmerus Brusca & Wallenstein		X		0 + 1	3	X	
Lyidotea Hale		X		0 + 3	3	X	
Zenobiana Risso (as *Zenobia*)		X	X	3 + 1	5		X
Cleantioides Kensley & Kaufman		X		3 + 1	4–5	X	
Edotea Guerin-Meneville			X	0 + 1	3	X	

of lateral incisions (generally referred to as "suture lines"). Presence of free lateral margins on the fused pleomeres is taken to represent incomplete fusion (i.e., medial fusion only) of these somites, and hence a less derived state than absence of the free lateral margins (i.e., complete fusion).

Maxillipeds. — The palp of the idoteid maxilliped is composed of 5 or fewer articles. Out-group analysis indicates the plesiomorphic state (occurring in all families except Idoteidae) is 5 free articles; reduction in the number of articles thus represents a derived condition. It is not known with certainty whether reduction in the number of articles is due to fusion or to actual loss, although Brusca and Wallerstein (1979a) have suggested that both processes may exist among various genera (e.g., loss in *Idotea*, fusion in *Zenobiana*).

Antennae. — In valviferans, the flagellum of the second antenna is either (1) multiarticulate (the primitive condition); (2) reduced to a single clavate article with 1 to 4 minute "vestigial" apical articles; (3) reduced to a single clavate article only; or (4) reduced to just the minute "vestigial" articles. Brusca and Wallerstein (1979a) point out that these two kinds of reduction (clavate vs. vestigial articles) are probably the result of two different processes, the former being a case of fusion of the flagellar articles, the latter being an actual loss or reduction in the number of articles, creating a "vestigial" flagellum. In one genus (*Zenobiana*) both the clavate condition and/or the vestigal condition may both occur, suggesting that the two morphologies are somehow linked, perhaps both developmentally and phylogenetically. The early reduction was apparently a situation in which partial fusion of the flagellar articles produced the clavate mor-

phology while retaining a few vestigial, unfused, apical articles (as seen in some *Zenobiana* species). This condition could have progressed in either of two directions—loss of the vestigial articles to leave just the remaining clavate process (as in *Cleantiella, Erichsonella, Euysmmerus, Parasymmerus, Cleantioides,* and *Lyidotea*), or loss of the clavate process to leave just the remaining vestigial articles (*Edotea* and some species of *Zenobiana*). The relationships between the clavate and vestigial conditions may not be resolvable in a phylogenetic sense, and may represent differing avenues of a flexible developmental program. However, unlike the pleonal and maxillipedal palp characteristics (above) which show varying degrees of reduction, the antennal flagella are either reduced (states 2–4 above) or not reduced.

Coxal plates. Although the coxal plates have been used extensively in valviferan taxonomy, use of these structures has not been consistent. Previous workers have treated these structures in a variety of ways and one worker's description is not always comparable to another's. These problems have been discussed at length by Nordenstam (1933), Sheppard (1957), and Brusca and Wallerstein (1979a). For these reasons, the coxal plates are not considered in the following analysis.

While the genera of the Idoteidae appear to be reasonably well-defined, the 5 nominate subfamilies are not. The subfamily Idoteinae stands apart from the other 4 in numerous features, and appears to represent a monophyletic group. The other subfamilies (Glyptonotinae, Chaetilinae, Parachiridoteinae, and Mesidoteinae) cannot be easily separated from one another, nor be distinguished unambiguously in a cladogram. For this reason, these 4 subfamilies collectively are herein considered an outgroup of the Idoteinae. They may be thought of as representing an unresolved polychotomy on the cladogram in Fig. 4. In the following discussion these 4 subfamilies are treated as one and referred to as the "glyptonotine-group."[4] A second out-group used to construct a cladogram of Idoteinae genera is the Holognathidae (see Fig. 2). Numbers in the following discussion correspond to that on the cladogram in Fig. 4.

The glyptonotine-group is distinguished by the following synapomorphies: (1) cephalon strongly produced laterally, moving eyes to dorsal position; (2) body broadened and dorsoventrally depressed; (3) pereopods I–III subchelate or prehensile. It retains the symplesiomorphy of separate penes. The Idoteinae is distinguished by the following synapomorphies: (4) reduction of the pleon to the 3+1 condition; (5) fusion of the penes into a single structure (Fig. 4).

Paleontological data, limited as they are, corroborate the out-group comparison for the Idoteinae. The oldest known idoteid fossils are referred to the monotypic genus *Proidotea* (*P. haugi* Racovitza and Sevastos, 1910), from mid- to late Oligocene deposits of eastern Europe. This genus clearly falls within the subfamily Mesidoteinae (the glyptonotine-group). The only other fossil data for the Valvifera are Pleistocene to Recent specimens of *Saduria* (=*Mesidotea*)—probably the holarctic *S. sabini* (Krøyer). In both of these genera, the pleon is composed of 4 somites, plus the pleotelson. The maxillipedal palp of *Saduria* is 5-articulate. The uropods of Mesidoteinae are biramous, as in the subfamilies Glyptonotinae, Chaetilinae, and Parachiridoteinae.

The genus *Zenobianopsis* Hale, 1946 is not indicated on the cladogram (Fig. 4). The status of this deep water taxon is uncertain. Only two species have been reported and they differ markedly in morphology. Species of *Zenobianopsis* have a pleon of 4 free somites, plus indications of a fifth (although in *Z. caeca* Hale, 1946, these somites appear somewhat reduced). Other attributes indicate that *Zenobianopsis* is a very primitive member of Idoteidae (Table 1), presumably with its origin at or about the time of separation of the Idoteinae from the glyptonotine-group. The early isolation of these species is further suggested by the fact that both are known only from deep subantarctic waters of the Indian Ocean. *Zenobianopsis* is indicated by a dashed line in the evolutionary tree in Fig. 16; further research may place the two species in separate genera.

Within each of the two principal idoteine lineages depicted in Fig. 4, the trend towards fusion of pleomeres is expressed in a "directed" fashion. That is, the greater the degree of pleomere fusion in a taxon, the farther up the cladogram it appears. Fig.
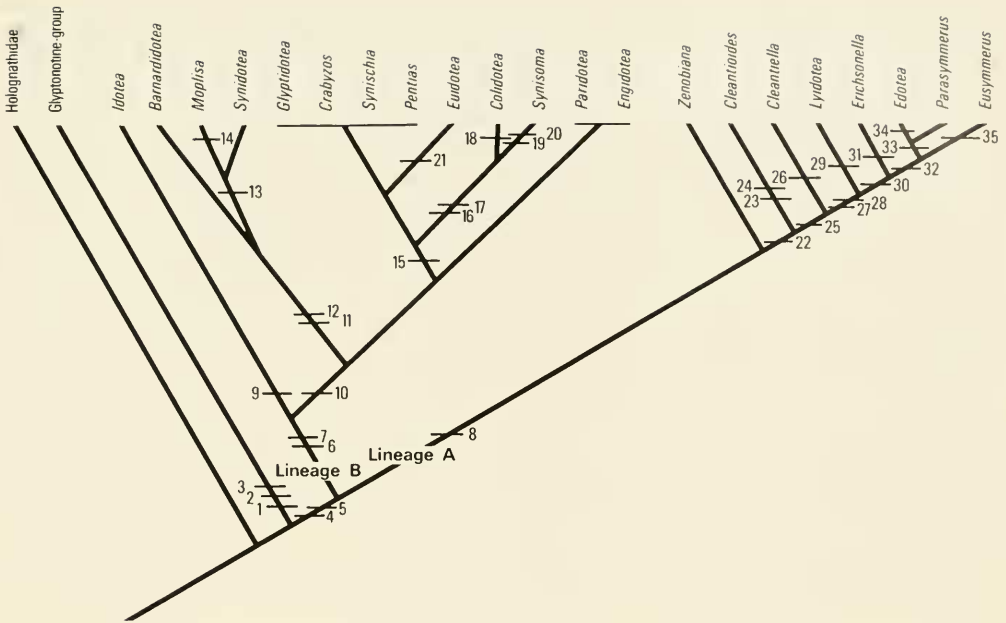
FIGURE 4. Cladogram of Idoteinae genera. Only apomorphies are indicated. Numbering of characters corresponds to discussion in text. For characters uniting Holognathidae to Idoteidae *see* Fig. 2 and text.

3 provides a schematic representation of known pleonal morphologies beginning with the 4-segmented pleon found in the glyptonotine-group. The pleonal formulas are written in two digits, separated by a plus sign. The first digit is the number of complete pleomeres present in the pleon (not counting the pleotelson); the second digit is the number of lateral incisions present, representing remnants of incompletely fused pleomeres.

There are 14 possible combinations or pleonal formulas that species of Idoteinae might possess: 3+1, 3+0, 2+2, 2+1, 2+0, 1+3, 1+2, 1+1, 1+0, 0+4, 0+3, 0+2, 0+1, 0+0. However, there are over 100 possible different steps in which fusion may progress to give rise to these 14 combinations. Each of these 100+ pleonal morphologies is derived in a unique manner and hence each constitutes an "attribute" (*sensu* Platnick, 1979:542). Not every pathway is represented in Fig. 3; only enough steps are shown in order to reach the existing morphologies of the known idoteine genera in a parsimonious fashion. This large "uncertainty" problem, as well as the seeming parallelism of pleonal fusion, can be resolved by careful examination of the schematic pattern analysis in Fig. 3. All known genera of Idoteinae have pleonal formulas that must have arisen from one of two main lines; one line beginning with a 3+1 configuration (indicated on Figs. 3 and 4 as "lineage A"), and the other beginning with a 2+1 configuration (indicated on Figs. 3 and 4 as "lineage B"). Assignment of genera to one or the other of these lineages can be based on the antennal features described above. That is, the 13 genera with multiarticulate second antennal flagella are hypothesized to represent a lineage or series distinct from the 8 genera that have lost the multiarticulate conditions. Any other assignment of these genera requires accepting convergent evolution of these antennal morphologies; parsimony is maintained by presuming these antennal morphologies to have arisen only once. This split clearly places all genera on one or the other of these two main lines of descent involving pleomere fusion, and further suggests that evolution of identical pleonal formulas in these two lines of descent was through different steps, and hence not true convergence at all.

Not all 14 possible patterns are represented by extant species. In fact, only 9 are known at present (4+1, 3+1, 2+1, 2+2, 1+2, 1+0, 0+3, 0+1, 0+0). Other morphologies

presumably existed in the past (in extinct intermediate taxa) or exist at present but await discovery. Fig. 3 predicts the nature (overall morphology) of these yet to be discovered genera, and hence sets the stage for testing the hypotheses contained therein.

Fig. 3 is not a cladogram OR an evolutionary tree. It is merely a graphic arrangement of pleonal morphologies in a sequence of most primitive at the top, with increasingly derived morphologies (increased fusion) expressed following the arrows down and across. As can be seen in Figs. 3 and 4, reduction in pleomere number corroborates the reduction in the antennal flagellum (i.e., there are no conflicts).

Lineage B (Fig. 4) is distinguished by two synapomorphies: (6) pleonal fusion has advanced to the 2+1 morphology, and (7) the uropods have lost the primitive biramous morphology, deriving a uniramous condition. Lineage A is defined by the synapomorphy of (8) antennal flagellum reduction to condition 2 described above (i.e., fusion of most flagellar articles into a clavate process bearing on its apex a few remaining "vestigal" articles).

Within lineage B, the genus *Idotea* is distinguished by the apomorphy of (9) reduction in maxillipedal palp article number; the sister-group to *Idotea* has reduction of pleonal morphology beyond the 2+1/2+0 condition (10). *Barnardidotea, Moplisa*, and *Synidotea* have maxillipedal palp reduction to 3 articles (11), as well as continued fusion of pleomeres to produce a 1+0 pleonal morphology (12). *Barnardidotea* is distinguished from *Moplisa* and *Synidotea* by retention of the 1+0 pleonal formula, while the latter two genera have achieved the 0+1 condition (13). *Moplisa* and *Synidotea* can be distinguished from one another by the loss of the molar process in the former (14).

The *Paridotea-Engidotea* line is distinguished from its sister-group by retention of the symplesiomorphic pleonal condition, 1+2 (vs. the synapomorphic condition, 0+3) (15). These two genera cannot be clearly distinguished from one another on morphological criteria as they are currently understood. The *Colidotea-Synisoma* group is distinguished from its sister-group by two synapomorphies: (16) lacinia mobilis of mandible greatly enlarged (as large or larger than incisor process), and (17) reduction to a 4-jointed maxillipedal palp. *Colidotea* is distinguished by (18) a 0+1 pleonal morphology. *Synisoma* is distinguished by two synapomorphies: (19) pleonal morphology 0+0, and (20) an elongate pleon (⅓ or more total body length). *Euidotea* is distinguished from its sister-group by (21) possession of a 4-jointed maxillipedal palp (vs. 5-jointed in the *Glyptidotea-Pentias-Crabyzos-Synischia* line). The latter 4 genera cannot be distinguished by morphological criteria as they are currently understood and are hereafter referred to as the *Glyptidotea*-group.

Within lineage A, *Zenobiana* can be distinguished only by the symplesiomorphous retention of biramous uropods; whereas its sister-group has achieved the synapomorphic condition of uniramous uropods (22). Some species of *Zenobiana* have lost the minute apical articles on the tip of the second antennae, while others retain these terminal articles. I am in agreement with previous authors that these differences do not warrant the splitting of *Zenobiana* into several genera (e.g., Bate and Westwood 1861–1868, Issel 1913, Collinge 1917, Barnard 1925). I have not taken the presence or absence of the "vestigial" articles into consideration in construction of the cladogram.

Cleantioides, as defined here, contains only two species, *C. occidentalis* (Richardson) and *C. planicauda* (Benedict). This genus is distinguished by 2 synapomorphies: (23) reduction of the fourth pair of pereopods to nonambulatory appendages, and (24) reduction of the maxillipedal palp to 4 articles in one species (*C. occidentalis*). It retains the symplesiomorphic 3+1 pleonal morphology, while its sister-group has achieved the 2+2 or less stage (25).

Cleantiella is distinguished by the apomorphy of pleonal reduction to the 1+2 condition (26). *Lyidotea* and its sister-group bear 2 synapomorphies: (27) the pleon has achieved the 0+3 morphology, and (28) the maxillipedal palp has been reduced to the 3- or 4-articulate condition. *Lyidotea* bears an apomorphic condition in which the last pereonal somite has become fused with pleomere 1 (29); its sister-group is distinguished by the 0+2 or less pleonal morphology (30).

Erichsonella is distinguished by the apomorphy of (31) complete pleonal fusion, resulting in the 0+0 condition, although some species retain a faint transverse furrow presumably representing the fused juncture of pleomere 1 to the remainder of the pleon. *Erichsonella*'s sister-group (*Eusymmerus-Parasymmerus-Edotea*) has achieved the 0+1 morphology (32). *Edotea-Parasymmerus* are defined by the synapomorphy of maxillipedal palp reduction, to the 3-articulate condition (33). *Edotea* is distinguished by its acute subtriangular pleon (34). *Eusymmerus* is distinguished by the unique 3-pointed spine that arises between the lacinia and incisor process on the left mandible (35).

This cladogram (Fig. 4) reduces the number of character convergences to two. Reduction in the number of articles on the maxillipedal palp appears to take place time and again, throughout the various idoteine lines, and no sensible cladogram design can eliminate it. In Fig. 4 it occurs four times in lineage A and three times in lineage B. For this reason, it was given lower priority than all other characters used in the analysis. Maxillipedal palp reduction is common throughout the order Isopoda and represents a kind of convergence or parallelism known as canalized evolutionary potential. This character also expresses both "inside" and "outside" parallelism (*sensu* Brundin 1976, 1981). The second convergence (or parallelism) is loss of the ancestral biramous uropod condition, which takes place in (and characterizes) lineage B, and then again in the *Cleantioides* through *Eusymmerus* line of lineage A (synapomorphy 22).

While the cladogram in Fig. 4 is highly parsimonious, what is clearly needed is the elucidation of additional synapomorphies to further test the contained hypotheses. Six terminal taxa (or groups) cannot be distinguished by unique apomorphies at this time. As Sheppard (1957) and Brusca and Wallerstein (1979*a*) pointed out, a critical examination of the nature of the pereopodal coxae in the various idoteid genera will surely prove enlightening and undoubtedly provide us with a new suite of character states with which to test evolutionary relationships among the genera. The exact nature of the reduction in flagellar articles on the second antennae needs to be investigated (particularly regarding *Zenobiana, Cleantioides,* and *Edotea*), and this too might shed new light on the cladogram. This reduction, as well as reduction in maxillipedal palp articles and free pleomeres, tends to follow Brown's (1965) "Rule of Evolutionary Reduction." Finally, two unresolved polychotomies exist within the Idoteinae that can be resolved only by synonymizing genera or by the elucidation of new characters to differentiate these taxa. It is my belief that a careful study of the coxal plates, lacinia mobili, second antennae, and pleopods 3–5 could resolve all of these problematic areas among the idoteine genera.

Biogeography and Evolution of the Idoteinae Genera

Idoteids, like other isopods, brood their developing young in a marsupium, from which they are hatched as "mancas," which are subjuveniles that resemble miniature adults except for lacking the seventh pair of pereopods. There is no evidence, ecological or morphological, that the manca stage is planktonic, and in those species that have been reared in the laboratory, hatchlings are always benthic crawlers like their parents. The only published records of idoteids in plankton are for the 2 widespread species, *Cleantioides planicauda* and *Idotea metallica,* and the 2 species belonging to the questionable genus *Zenobianopsis.* Both mancas and adults of most species, however, are capable of swimming in short bursts over small distances (e.g., between algal fronds). When idoteids are dislodged from the substratum by waves or surge they sink or swim quickly to the bottom (Jansson and Matthiesen 1971, Salemaa 1979, Sywula 1964, Lee and Gilchrist 1972, Wallerstein and Brusca 1982). Idoteids are clearly a component of the benthic community in marine shallow-water habitats, where their niche is that of a cryptic herbivore and occasional scavenger. This suggests that idoteids, particularly intertidal species, are probably not good dispersers.

Because the following discussion deals with the Idoteinae at the generic level, it must remain fairly general. Even at this level, however, these generalizations describe patterns of geographic distribution that can be correlated with the cladogram (Fig. 4),
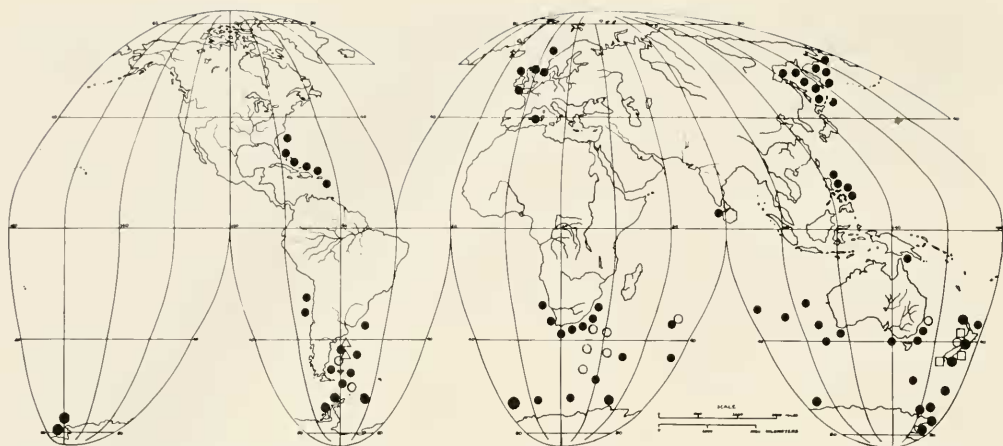
FIGURE 5. Distribution of valviferan families (excluding Idoteidae): Amesopodidae [O], Arcturidae [●], Holognathidae [□], Pseudidotheidae [O], Xenarcturidae [△].

and which can most parsimoniously be ascribed either to vicariance or non-vicariance events. Geological dates of events described in this section have been used to transform the cladogram into the evolutionary tree depicted in Fig. 16. It is not my purpose to present a detailed analysis of each genus here; that must await a species-by-species study of each genus (e.g., see Brusca 1983 for the genus *Colidotea*). The latter will clearly be an enormous undertaking, but one for which the following analysis could provide a starting point.

The Valvifera as a whole show strong correlation to southern temperate latitudes, 3 of the 6 families being restricted to that geographic region, 1 known only from the shores of India, and the other 2 being widespread (Fig. 5). The idoteine genera show a similar geographic trend (Figs. 7–14). Numerous studies have recently appeared that examine the relationships of distributional patterns of terrestrial flora and fauna to the geological history of the Southern Hemisphere (e.g., Keast 1973, Raven and Axelrod 1972, Cracraft 1974, 1980). However, similar studies on marine groups have been few. For these reasons, Gondwanan shores are discussed in some detail. A brief review of the breakup of Gondwana follows, based on Kennett (1977), Smith and Briden (1977), Norton and Sclater (1979), Knox (1979), Durham (1979), Grant-Mackie (1979) and Hallam (1981).

Throughout most of the Permian, the Triassic, and most of the Jurassic periods, Gondwana was unified as a single land mass. The proto-southern continents were all situated at higher latitudes than they are today. Although Permian glaciation probably existed in the highest southern latitudes, that cold era came to a fairly abrupt halt by the Jurassic. By mid-Mesozoic times climates in the Southern Hemisphere had changed markedly, as a long-lasting global warming trend became established. Paleontological evidence suggests that by the middle or late Jurassic the northern shores of Gondwana had already begun acquiring a warm-water Tethyian biota, thus restricting temperate coastal biota to the southernmost latitudes. A common temperate marine fauna probably inhabited the contiguous coastline of Gondwana south of 55°–65°S latitude. This shallow coastal sea washed the shores of southernmost South America, southeast Africa, eastern Antarctica and eastern Australia. The continuous coastal topography, coupled with non-glacial and generally equable climates of the Jurassic, facilitated "warm-water cosmopolitanism" along the shores of northern Gondwana, and "cold-water cosmopolitanism" along the shores of southern Gondwana. These two regions were probably physically isolated from one another until at least the early Tertiary, when separation of Australia from Antarctica instituted a direct high latitude southern connection between the Indian and Pacific oceans. The distribution of modern coastal temperate

faunas in the Southern Hemisphere can thus be hypothesized to be, at least in part, the product of the fragmentation of an early to mid-Mesozoic temperate Gondwanan track.

That part of Gondwana composed of Antarctica, Australia, New Zealand and South America rotated southward during the Mesozoic, although as early as the Late Jurassic these land masses were beginning to separate as Antarctica-Australia-India began uncoupling from Africa and South America. By the Early Cretaceous (about 120 MYA) sea floor spreading had started to form the south Atlantic Ocean. At about the same time, India began to decouple from Antarctica-Australia-Africa. Marine conditions developed between India and Antarctica-Australia by 105 MYA. Africa was clearly separated from Gondwana about 90 MYA. New Zealand split from Antarctica-Australia 70–80 MYA. By the mid-Cretaceous the south Atlantic Ocean was open along its entire length as Africa and South America pulled away from one another. The free ocean connection (the "Vema Gap") between the north and south Atlantic was established by the Late Cretaceous as the transverse Rio Grande-Walvis Ridge sank below the 1 km depth (approximately 78–80 MYA). Australia was last to decouple from Antarctica, about 50–60 MYA. During the Paleocene these land masses were probably separated by a shallow narrow seaway; however, the South Tasman Rise acted as an effective barrier to the development of a circum-Antarctic current until about 30–50 MYA, subsequent to which the southern circum-polar current began to develop. The modern deep-flowing Antarctic Circumpolar Current could not have been established until the opening of the Drake Passage, 22–28 MYA, when deep-sea conditions developed between southern South America and Antarctica (plate boundaries and timing of geotectonic events in this region are still very controversial).

During most of the course of events described above, Antarctica continued a slow drift southwards, reaching a position close to its present location by Late Cretaceous; it has remained nearly stationary throughout the Cenozoic. Thus, deep marine conditions began to develop in the Southern Ocean by the Late Paleocene, although a corridor of scattered highlands and shallow seas persisted between Australia and Antarctica until about the Late Eocene or Early Oligocene.

South America has moved progressively westward since the Late Cretaceous. India collided with Asia about this same time. Coincidental with this southern fragmentation, the highest post-Carboniferous sea levels ever to occur (Campanion Era, about 75 MYA) submerged roughly ⅓ of the present continental area below shallow epicontinental seas. Deep water flows from the Pacific into the Atlantic across Central America commenced about 55 MYA, only to be halted in the Pliocene when the Panama Isthmus emerged.

The shallow-water marine fauna would not have responded to the breakup of Gondwana in the same manner as the terrestrial fauna, because the initial separation of the land masses created intervening shallow seaways that fostered the spread of marine biota before separation of the biotas occurred (for a comparison with the fragmentation of the terrestrial fauna of Gondwana see Cracraft 1974 and Rosen 1978). As South America and Africa moved northward, and Antarctica moved southward, relative to one another, the effect on temperate coastal marine life was most likely to have created two disjunct faunas. One of these faunas, the western coastal fauna, would have inhabited the shores of southern South America, southern Africa, and northwestern Antarctica. The eastern fauna would have been restricted to Australia, eastern Antarctica and southernmost India. New Zealand, at this time, was situated in warm-water latitudes. By the mid-Cretaceous, the Southern Ocean had become extensive enough to break the western fauna into two separate temperate regions: southern South America (and probably the region of the Antarctic Peninsula) and southern Africa. The eastern Gondwana, mid-Cretaceous, temperate coastal region remained unchanged even though New Zealand had split from the warm-water shores of Australia. By the mid- to Late Cretaceous the shallow sea between India and Antarctica had deepened to isolate these regions entirely from one another, India having drifted into the tropical waters of the Indian Ocean. The coastal environment of southern Australia remained
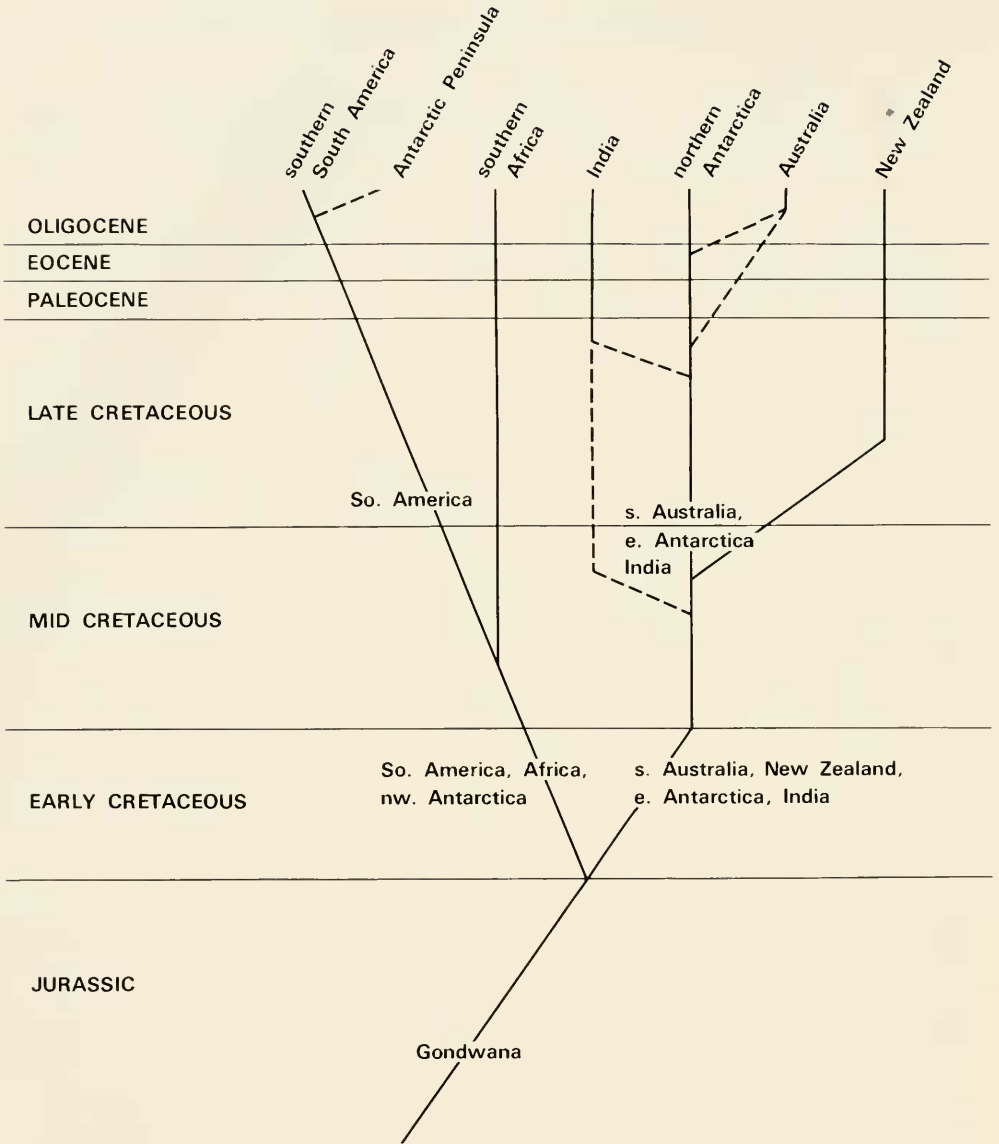
FIGURE 6. Proposed geographic cladogram of temperate, shallow-water, Gondwanan coastal areas. Note the significant differences between this cladogram of shallow continental shores (marine geographic areas) and Rosen's (1978) cladogram of Gondwanan continents (terrestrial geographic areas). *See* text for discussion.

tied to northern Antarctica until the Cretaceous-Tertiary boundary, or perhaps even to the Early Oligocene. These relationships are pictured in Fig. 6.

Because paleoclimates and oceanographic conditions were not the same during the Mesozoic and Cenozoic as they are today, latitudinal distributions of shallow-water marine life would have been under quite different thermal regimes. This ecological component must be taken into account when considering paleobiogeographical reconstructions. A brief review of Mesozoic-Cenozoic climates follows; for more detailed information consult Fleming (1975, 1979), Margolis et al. (1978), Grant-Mackie (1979), Durham (1979), Frakes (1979), Zinsmeister (1982), and references therein.

Overall, middle and late Mesozoic climates were extremely equable, with ocean temperatures exceeding those of the present day by 7°–15°C. Polar ice caps did not
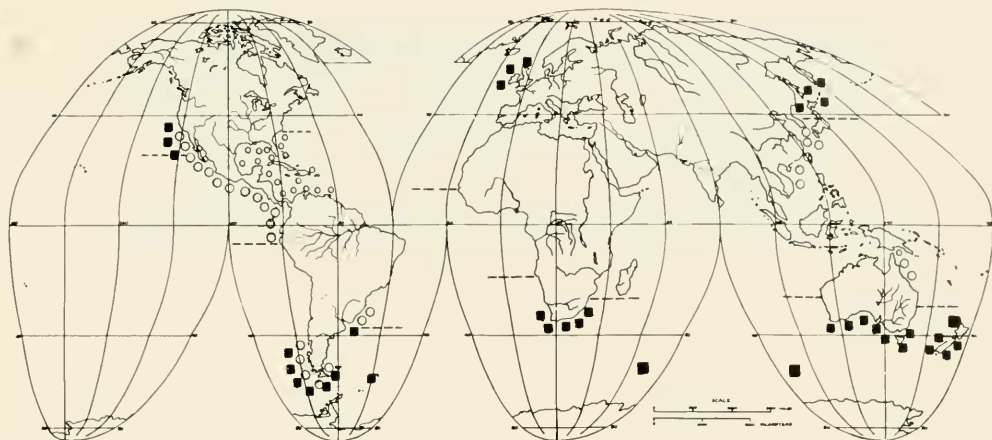
FIGURE 7. Composite distribution map of all idoteine genera, except the 3 cosmopolitan taxa (*Idotea, Synidotea, Zenobiana*). Dashed lines indicate limits of warm-water (tropical/subtropical) regions; open circles = genera of lineage A; closed boxes = genera of lineage B.

exist and both terrestrial and marine biotas exhibited little evidence of latitudinal zonation. Cosmopolitanism was common. Cool sea water existed in the southern oceans only south of about 50°S latitude. Early Cretaceous sea bottom temperatures were approximately 10°–15°C warmer than today; Late Cretaceous sea bottom temperatures were approximately 7°C warmer than today. The Eocene marked the beginning of a global cooling trend that ultimately led to the Cenozoic glaciations and cooling of deep ocean bottom waters to their present thermal regimes (Shackleton and Kennett 1975). As late as the Eocene (38–55 MYA), all but the southernmost Antarctic seas were warm-temperate in nature. The steep thermal drop over the Eocene/Oligocene boundary was probably related to the establishment of the Antarctic Circumpolar Current and subsequent South Polar glaciation. Although land masses occupied both poles by the Early Paleocene, large-scale Antarctic glaciations probably did not begin until the Miocene. The Antarctic Convergence began moving northward in the Oligocene. Cooling trends continued throughout the Cenozoic, apparently marked by several periods of severe chilling.

Fossil reefs, requiring relatively warm surface waters, grew to paleolatitudes of about 40° throughout the Paleogene, as in the Cretaceous. In the northeast Pacific, tropical environments (i.e., surface temperatures ≥20°C) extended to approximately 45°N in the Eocene, and have contracted equatorward steadily since that time. Abundant paleoceanographic and stratigraphic data exist to indicate that New Zealand shores were bathed primarily by warm subtropical waters throughout the Cretaceous and Paleocene (Fleming 1962, 1975, Durham 1979, Knox 1979), although a distinct cooling trend began in the middle to Late Miocene, eventually resulting in present-day temperate coastal conditions. At best, only southernmost New Zealand might have experienced temperate waters from the Eocene to the Miocene. By early Pleistocene subantarctic waters had reached about 40°S latitude on New Zealand shores. The middle Oligocene marked the end of "high latitude subtropical communities," and by the Late Miocene modern water bodies and their associated biological provinces had begun to be established. The Australian Subantarctic water mass had formed by about 15 MYA. For the past 10–15 million years the Southern Ocean temperature, circulation and zonational water masses have remained essentially the same.

If the distributions for all species of Idoteinae are plotted on the globe, nearly every sea and shore is seen to be inhabited by one or more genera. Fig. 7 is a composite distribution map plotting the ranges of all taxa of Idoteinae EXCEPT the 3 cosmopolitan genera—*Idotea, Synidotea,* and *Zenobiana*. These 3 taxa are omitted from the com-

FIGURE 8. Distributions of *Cleantiella* [●], *Lyidotea* [·], and *Cleantioides* [○].

posite distribution map because they provide no particular insights into a global pattern analysis at this level. Distribution maps of the individual genera are given in Figs. 8–14, and are discussed below. It will be seen from these distribution maps and the following discussion that most idoteine genera are endemic to only one or a few coastal regions. The dashed lines on Fig. 7 indicate the limits of the tropical/subtropical regions, based on Ekman (1953), Briggs (1974), and Brusca and Wallerstein (1979b). While some disagreement exists regarding the exact limits of the tropical zones, the latitudes that I have chosen clearly separate the "warm-water" faunal regions of the world's shores from the "cold-water" regions. The only serious arguments with these delimitations might be in whether one regards the Mediterranean Sea as warm-temperate or subtropical. The best comprehensive discussion of Mediterranean zoogeography is probably that of Ekman (1953), who in describing the complex mixtures of northern and southern elements, couldn't comfortably label this sea either warm-temperate or subtropical. The nature of south African faunal designations has also been a matter of some controversy, and was recently reviewed by Brown and Jarman (1978).

Several general patterns are revealed when Fig. 7 is examined. In the New World, endemic idoteine genera are distributed fairly equally in both warm and cold waters. In the Old World, however, there is a marked absence of records from the tropics. Only 3 genera on this map represent Old World tropical taxa: *Cleantiella* and *Cleantioides* both occur on the east Asian coast, while *Lyidotea* is known from a single species in northeastern Australia (see Fig. 8). A second pattern seen is that Old World endemic genera tend to form 3 distinct clusters, as follows: (1) a Southern Hemisphere cold-water group, (2) a European cool- to cold-water group, and (3) a northeast Asian cool- to warm-water group. Only 2 of the genera depicted in Fig. 7 occur in both the Old and New Worlds: the southern temperate *Paridotea* and the northern tropical *Cleantioides*. Because most species and genera of Idoteidae are restricted to temperate or polar seas, the family has long been considered a "cold-water centered taxon" (see Brusca and Wallerstein, 1979b and references therein). It is of particular interest that the Old World and New World tropical regions are inhabited by entirely different genera. The New World tropical genera are *Cleantioides, Erichsonella, Parasymmerus,* and *Eusymmerus*. The Old World tropical genera are *Cleantiella, Lyidotea, Idotea, Synidotea,* and *Zenobiana*. As the latter 3 are largely cosmopolitan taxa, the obvious question is, "Why have species in these genera been unable to invade the tropics in the New World?" Let us now examine the distributions of the individual idoteine genera.

Idotea is nearly a cosmopolitan genus (Fig. 9). It occurs in most waters of the Old World, including the tropics, but in the New World it is notably absent from the warm seas between the Tropics of Cancer and Capricorn in both the Pacific and Atlantic.
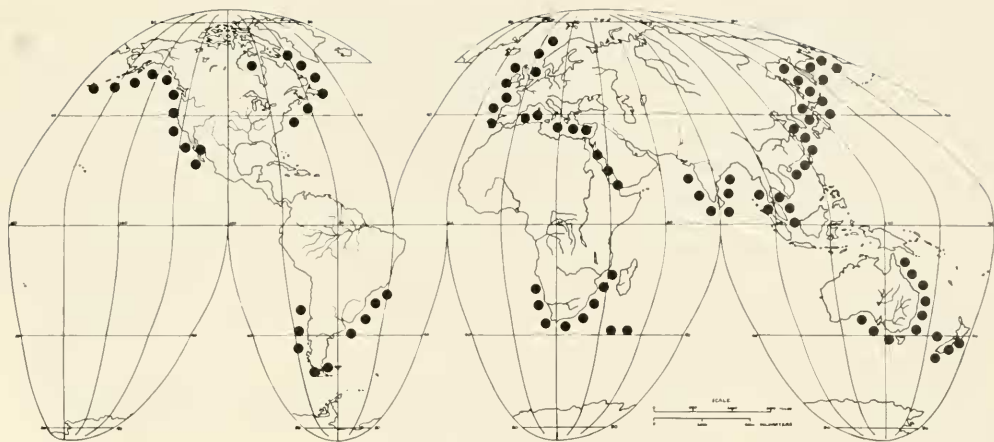
FIGURE 9. Distribution of *Idotea*.

Brusca and Wallerstein (1979*b*) reviewed literature documenting the eurythermal nature of *Idotea* species, and suggested that biological factors (competition or predation), rather than temperature, could be excluding the 2 New World temperate isopod genera, *Idotea* and *Synidotea*, from the Western Hemisphere tropics. Wallerstein and Brusca (1982) subsequently provided experimental and comparative morphological evidence that predation by crustacivorous fishes is possibly restricting species of *Idotea* from the New World tropics. In the latter study they proposed a model that envisioned "faunal waves" of tropical predator species (primarily fishes) moving northward from the equatorial region during warm Pleistocene interglacials, pushing the southern latitudinal range end points of non-adaptable temperate species northward ahead of them, and thus excluding *Idotea* and *Synidotea* from the New World equatorial region (see Addicott 1970 and Zinsmeister 1974 for a discussion of similar north-south faunal displacements in Mollusca). The nearly global distribution of *Idotea*, as well as its position on the cladogram (Fig. 4) relative to other genera in lineage B (see discussion below) suggests that *Idotea* is an old genus (pre-Cretaceous). It should be emphasized that, while the genus *Idotea* is cosmopolitan, the species in this taxon are themselves largely endemic to restricted coastlines. Only one species of *Idotea* is cosmopolitan, *I. metallica*. Its cosmopolitanism has been explained by drift dispersal of the algae on which it lives (Naylor 1972, Poore 1981).

Nine of the 12 remaining genera in lineage B are endemic to the Southern Hemisphere (Table 2) and are probably descendants of a pan-austral, cold-water, Gondwanan, pre-Cretaceous fauna. The concept of a pan-austral terrestrial biota was apparently first recognized by Hooker (1853, 1860) and Huxley (1868). Though largely suppressed by 100 years of "Wallaceian dispersalism," the concept has finally experienced a rebirth owing largely to the work of Pantin et al. (1960) and Brundin (1966, 1970, 1972*a, b*, 1976). For a recent summary of many subsequent papers see N.Z. DSIR (1979). Only recently, however, has serious documentation and discussion of generalized temperate pan-austral marine tracks begun (e.g., Zinsmeister 1976, 1982, Fleming 1975, Knox 1975). The mid-Cretaceous/early Tertiary fauna that inhabited this temperate, shallow-

TABLE 2. Distribution of the 8 Idoteinae Genera of Lineage B Endemic to the Southern Hemisphere.

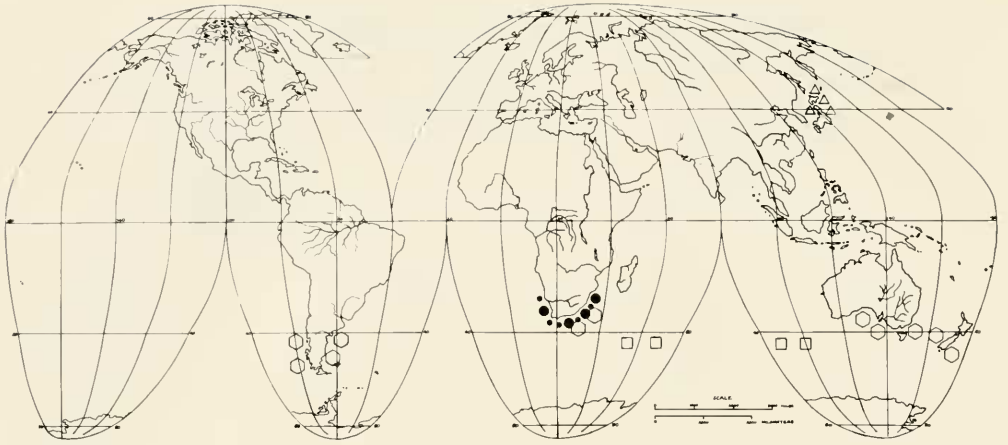| Geographic occurrence	*Moplisa*	*Pari-dotea*	*Eui-dotea*	*Craby-zos*	*Syn-ischia*	*Glypti-dotea*	*Barnardi-dotea*	*Engi-dotea*
Southern South America	+	+						
South Africa		+	+			+	+	+
Southern Australia		+	+	+	+			
New Zealand		+	+	+				

FIGURE 10.   Distributions of *Glyptidotea* and *Barnardidotea* [●], *Engidotea* [•], *Pentias* [△], *Zenobianopsis* [□], and *Paridotea* [○].

water, southern Gondwanan region has been referred to as the Weddellian Province by Zinsmeister (1976).

One of the earliest appearing genera in this post-*Idotea* radiation was *Synidotea*, which like *Idotea* is nearly cosmopolitan but notably absent from the New World tropics (Fig. 11). The same comments that apply to Idotea above are probably applicable to *Synidotea*. The origins of *Synidotea* appear old enough that the Early Cretaceous circum-Arctic seaway probably served as one of several principal dispersal routes, this being reflected in the modern distribution of the genus, which has by far the majority of its species concentrated in the Northern Hemisphere. This hypothesized age of origin, plus the restriction of both *Barnardidotea* and *Moplisa* (*Synidotea*'s sister-group) to the Southern Hemisphere, argues strongly for the origin of *Synidotea* in the southern seas. This contrasts with the opinion of Gurjanova (1935) and Menzies and Miller (1972), who suggested that the place of origin of *Synidotea* was the north Pacific. Menzies and Miller's opinion appears to have been based solely on the fact that most species of *Synidotea* presently occur in this area, which they considered to be its "center of origin." The present analysis, however, does corroborate Menzies and Miller's (op. cit.) dating of the origin of this genus. *Synidotea*'s sister-group, *Moplisa*, consists of a
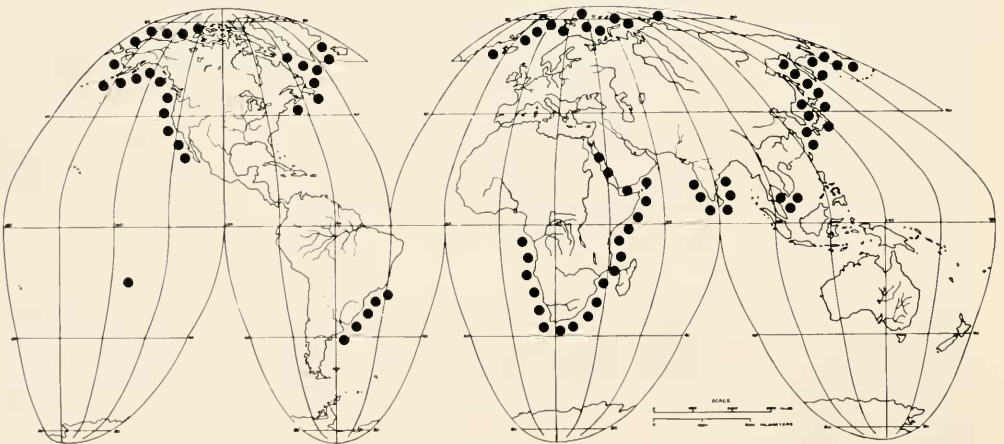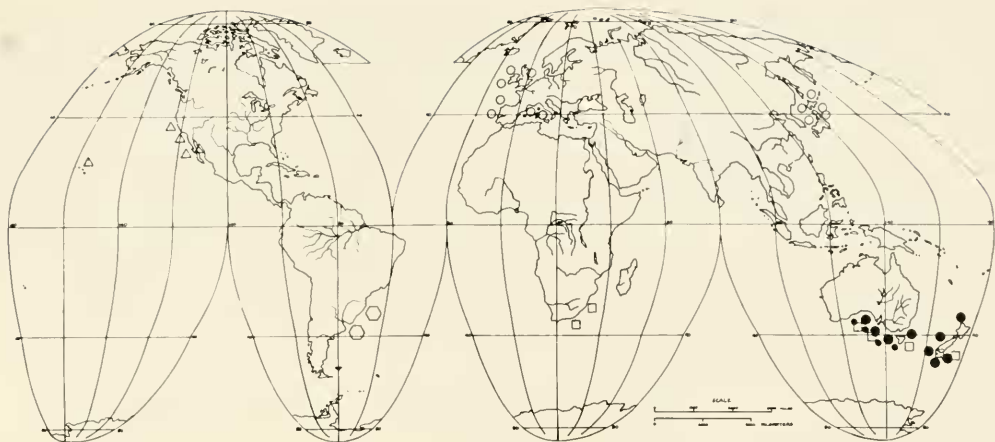

FIGURE 11.   Distribution of *Synidotea*.

FIGURE 12. Distribution of *Crabyzos* [●], *Synischia* [•], *Euidotea* [□], *Synisoma* [O], *Colidotea* [△], and *Moplisa* [O].

single species, *M. sphaeromiformis* (Mane-Garzon, 1946), so far known only from a short stretch of coastline in southern Brazil (Fig. 12). The cosmopolitanism of *Synidotea* (vs. the restricted distribution of the monotypic *Moplisa*), and the absence of an apomorphy to distinguish *Synidotea* from *Moplisa* strongly suggests that *Moplisa* evolved either in sympatry or as a peripheral isolate from a continuing stock of *Synidotea*. These relationships are pictured in the phylogram (Fig. 16) and are consistent with the cladogram.

Although *Glyptidotea*, *Crabyzos*, *Pentias*, and *Synischia* cannot be separated by cladistic analysis (Fig. 3), the biogeographic data provide evidence regarding their origins. *Glyptidotea* is endemic to temperate South Africa (Fig. 10); *Crabyzos* and *Synischia* are endemic to temperate Australasia (Fig. 12). These patterns suggest that these 3 genera arose subsequent to the initial east-west split of Gondwana (i.e., post-Jurassic). The absence of *Glyptidotea* from the South American component of the west Gondwanan track suggests that this genus arose subsequent to the separation of these two land masses (i.e., mid-Cretaceous or later). The closely related genus *Pentias* is today restricted to temperate shores of northern Japan (Fig. 10). The simplest explanation for its occurrence would seem to be fortuitous jump dispersal across the warm
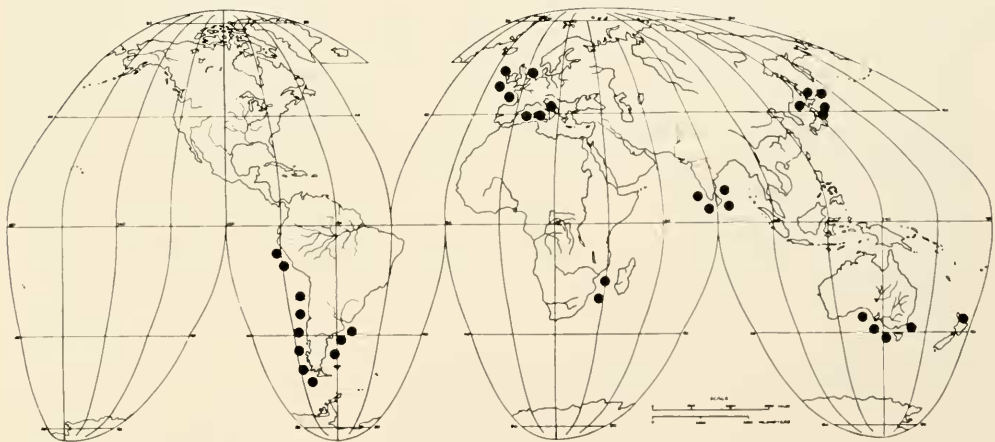

FIGURE 13. Distribution of *Zenobiana*.

FIGURE 14.   Distribution of *Eusymmerus* and *Parasymmerus* [●], *Edotea* [○], and *Erichsonella* [·].

waters of the equatorial region, perhaps during a period of global cooling and tropical compression such as the late Tertiary (although the western Pacific was probably far less affected by marine cooling than other regions on the globe). A second, remote possibility is that it (or its ancestors) reached Japan via China, which may have originally been part of the Gondwanan continent (see Crawford 1974).

None of the above southern taxa occur along the warmer shores of the Indian Ocean. Their distributions suggest that these genera are Cretaceous to post-Cretaceous descendants of the widespread Jurassic-Early Cretaceous temperate Gondwanan track discussed earlier in this section. The ancestor(s) inhabiting this track is indicated in the evolutionary tree by "GonAnc" (Fig. 16).

Because several genera cannot be clearly distinguished from one another by the cladogram, it is difficult to seek congruence between lineage B and the geographic cladogram of Fig. 6. However, a partial correlation (38%) is nonetheless evident (Fig. 15a, b). Table 2 provides a distributional summary of the 8 Idoteinae genera of lineage B that are Southern Hemisphere endemics. Fig. 15 gives reduced taxon-area and geographic cladograms for the groups in question. The cladogram congruence with the *Synidotea-Barnardidotea-Moplisa* line corroborates the hypothesis that the latter two taxa arose subsequent to the splitting of South America from Africa, while *Synidotea* continued to persist unchanged. Correlation also exists for *Synischia*. If one accepts the probable dispersal of *Crabyzos* from Australia to New Zealand, the correlation between these cladograms is raised to 50%. *Paridotea* has retained its circumpolar distribution, corroborating its early (pre-Cretaceous) origin.

The occurrence of *Euidotea* on African, Australian, and New Zealand shores (Fig. 12), and its absence from South American coasts today, argues for either (1) its origin prior to the break-off of Africa and its subsequent extinction in South America, or (2) its origin on African shores after the break-off of that continent and its subsequent spread to Australasia via West Wind Drift. Recall that New Zealand probably did not achieve its present temperate coastal thermal regime until well after the deep water barriers were formed that isolated it from Australia, probably not until the Eocene at the earliest. Thus, introduction of the cold-water genus *Crabyzos* could have been via dispersal from Australia in fairly recent times (mid- to late Tertiary). This same reasoning must apply to the other temperate New Zealand genera, *Paridotea* and *Euidotea*. The fact that none of these three taxa are endemic to New Zealand (all 3 also occur in southern Australia) lends support to this probability.

The sister-groups *Colidotea* and *Synisoma* are restricted to warm-temperate and subtropical waters of the New and Old World respectively (Fig. 12). This restriction, plus the widespread occurrence of *Synisoma* (Europe, Far East), suggests that these
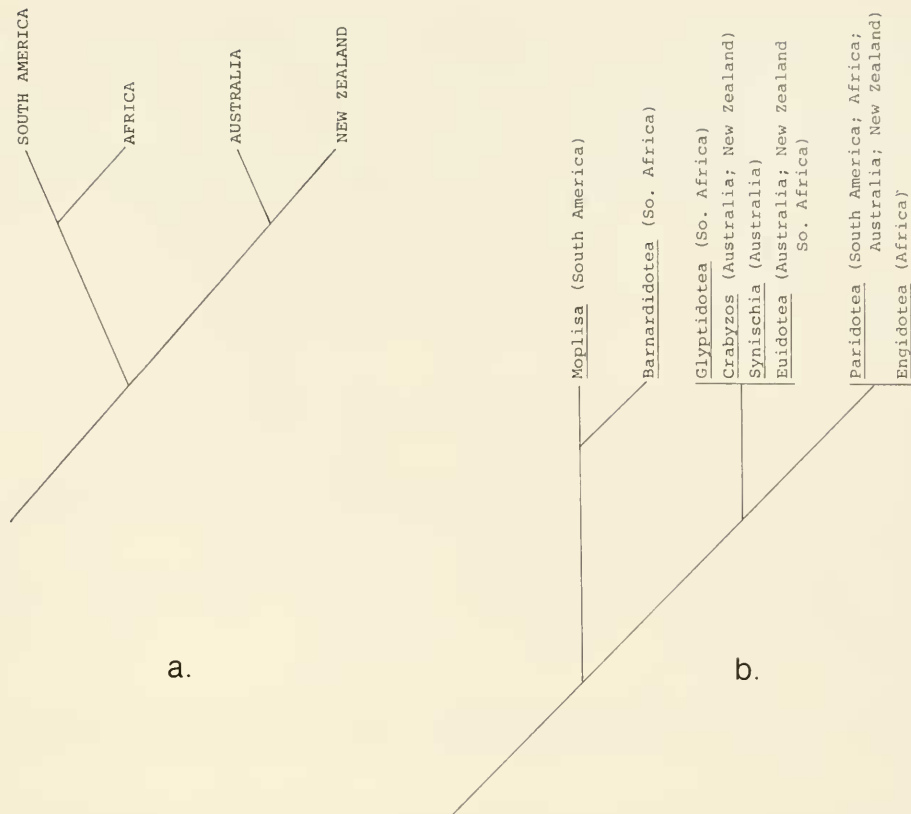
FIGURE 15a. Reduced geographic cladogram of 4 extant temperate shores derived from Gondwana (*see* Fig. 6). 15b. Reduced taxon-area cladogram of Southern Hemisphere endemic idoteine genera (*see* Fig. 3 and Table 2).

taxa are vicariant descendants of a widespread, circumglobal, northern Tethyian track. The absence of either of these genera on eastern American shores is most easily explained by local extinction on that coast. Closure of the Panama seaway in the Pliocene, or simple isolation from the parental stock as the North Atlantic opened up, could have provided the setting for the origin of these two taxa as we know them today. Judging by its extreme disjunct distribution, *Synisoma* has remained unchanged since at least the Paleocene, when the Gibralter gap closed. Thus, it appears that the ancestors of these two taxa were members of the Tethyian fauna, at least marginally, while the extant descendants have been pushed northward to the subtropical and warm-temperate portions of their former range.

In summary, the genera comprising lineage B appear to have remained closely tied to their ancestral (Jurassic) temperate Gondwanan distribution. Historical hypotheses that are consistent with the cladogram suggest that vicariance alone can account for the modern distributional patterns of only a few taxa, most having modern distributions clearly tied to both former vicariant and dispersal/extinction events. These probable extinctions, dispersal events, and biological interactions affecting ranges add to the uncertainty in ascribing geographic origins to the relatively old taxa comprising lineage B.

Turning to lineage A, we see one broadly distributed genus, the primitive *Zenobiana*, which occurs in both temperate and tropical waters of the Old World, but is restricted to temperate South America in the New World (Fig. 13). *Zenobiana* is the only genus of Idoteinae to retain the primitive biarticulate uropods. As was the case with *Idotea, Zenobiana*'s cladistic relationship and widespread distribution initially
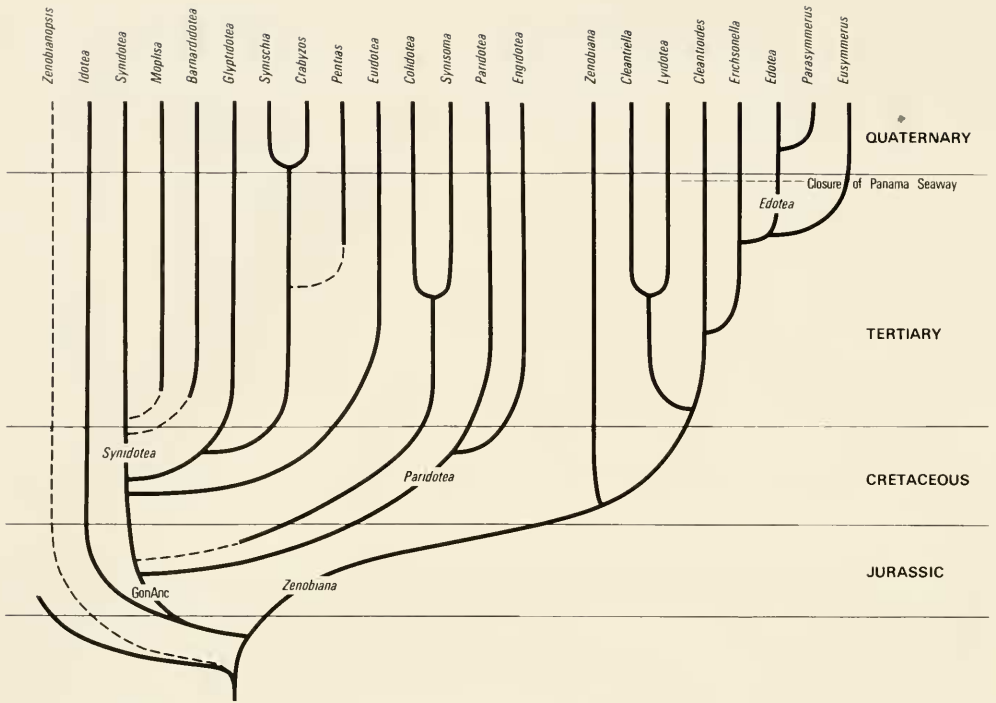
FIGURE 16. Proposed phylogeny of the genera of Idoteinae, based on Fig. 17 and other data. *See* text for discussion.

suggests that *Zenobiana* was pre- to Early Cretaceous in origin (i.e., pre-Gondwanan fragmentation). *Zenobiana* cannot be much older than this as it clearly shows no alliance to the Permo-Triassic Tethyian Sea radiation, owing to its near absence from the tropical Indo-West Pacific region; only one species occurs in Indo-Pacific waters, *Z. natalensis* (Barnard 1925). Thus, *Zenobiana*'s limited invasion of tropical environments apparently took place after the final closure of the Tethyian Sea, in the early to mid-Tertiary. Its alliance to and probable origin on temperate shores is further indicated by its present distributional pattern. All genera that appeared subsequent to the establishment of the globally distributed *Zenobiana* (the 7 remaining genera in lineage A) are warm-water taxa, or at least probably initially evolved as warm-water taxa (i.e., *Edotea*). The absence of identifiable apomorphies to distinguish *Zenobiana* indicates that this genus was both the ancestor to, and persisted after the origin of its sister-group.

Cleantioides consists of only 2 species: *C. occidentalis* is endemic to the tropical eastern Pacific; *C. planicauda* is a widespread tropical species known from both coasts of the Americas and from eastern Asia. *Cleantiella* and *Lyidotea* are western Pacific descendants of a *Cleantioides*-like ancestor. *Cleantiella* is restricted to the warm shores of USSR and China, and most likely arose as a post-Cretaceous northwest Pacific endemic (Fig. 8). *Lyidotea* is restricted to the warm waters of northeastern Australia. The absence of *Cleantiella* and *Lyidotea*, both warm-water taxa, from the equatorial region of the west Pacific is enigmatic and suggests 3 possibilities: (1) dispersal of the ancestor of *Lyidotea* from Asian shores to Australian shores; (2) the former existence of a N–S tropical *Cleantiella*-like track joining these two regions, with subsequent fragmentation into northern and southern tropical isolates with extirpation in the equatorial region; or (3) an artifact of collection records. The paucity of records for species in any other genus of Idoteidae from this region, and the unlikelihood of alternatives 1 and 2 above, suggest the third possibility may be the correct interpretation. According to Poore (in litt.) virtually no collecting has ensued in this region since the Siboga Expedition (ca. 1900).

All remaining genera in lineage A are New World endemics and represent descendants of the post-Cretaceous ancestors of this line. *Edotea* has an anti-tropical distribution, occurring on both North and South American shores (Fig. 14). Brusca and Wallerstein (1979*a*) have discussed this unusual distribution, concluding that *Edotea*, although evolving in the New World tropics as part of the early transisthmian track biota (the "Tertiary Caribbean Province" of Woodring 1954, 1966; the "Panamanian Track" of Croizat et al. 1974), was promptly excluded from this warm-water region by competition with the better adapted tropical genera like *Cleantioides, Eusymmerus, Parasymmerus*, and *Erichsonella*. Modern species of *Edotea* now occur only in temperate latitudes to the north and south of the New World tropics. "Better adapted" includes the possession of such predator avoidance adaptations as small body size, early reproduction, and cryptic morphologies (see Wallerstein and Brusca 1982, for details of these adaptations).

Edotea, Erichsonella (Fig. 14), and *Cleantioides* are all components of the Tertiary Caribbean Province (Woodring 1966) that have retained their amphi-American distributions. Numerous eastern Pacific-western Atlantic analog or geminate species can be identified within these genera. *Eusymmerus* and *Parasymmerus* (Fig. 14) are tropical eastern Pacific endemics. *Parasymmerus* probably evolved subsequent to the Pliocene closure of the Panama seaway. However, if the relationships depicted on the cladogram are correct, *Eusymmerus* probably evolved prior to the closure of the seaway (in order to be the sister-group or ancestor of *Edotea-Parasymmerus*). Its present restriction to the eastern Pacific implies that either (1) it evolved there and never became part of the transisthmian fauna, or (2) it was part of the transisthmian biota but has subsequently become extinct in the western Atlantic. The latter seems far the more probable sequence of events. Woodring (1966) has pointed out that many molluscan genera presently restricted to the tropical eastern Pacific occurred throughout the eastern Pacific-western Atlantic Tertiary Caribbean Province during Miocene times. These geographic data, as well as the cladistic relationships, imply that *Edotea* was both the ancestor to *Parasymmerus* and remained essentially unchanged subsequent to the origin of *Parasymmerus* (Fig. 16). It is unfortunate that fossil material for isopods is rare, for such data could provide excellent corroboration or refutation of the above hypothesis.[5]

The data summarized in the cladogram and biogeographic review clearly imply that there were both Old World and New World warm-water genera derived from an ancestral global "*Zenobiana-Cleantioides* line." The extant Old World fragments of this line are *Cleantiella* and *Lyidotea*; the extant New World fragments are *Erichsonella, Edotea, Parasymmerus*, and *Eusymmerus*.

The relationships in the cladogram suggest that these latter 4 New World endemic taxa were derived as the sister-group of *Lyidotea* (an Old World endemic). This necessitates trans-Pacific (west to east) dispersal of the ancestor of these 4 New World genera. An alternate scenario would have the New World taxa of lineage A descended not from the geographically restricted *Lyidotea* line or its Old World ancestor, but from the widespread ancestral *Zenobiana-Cleantioides* line. This could be accomplished simply by reconstructing a portion of lineage A, as shown in Fig. 17. This new cladogram of lineage A is longer than the original (Fig. 4) in requiring 9 pleonal transformations, versus 8 in the original. The new cladogram requires four transformations (but two convergences) in maxillipedal palp reduction, as in the original. Thus, for lineage A we are faced with a cladogram slightly more parsimonious (one less step) but requiring a major successful trans-Pacific dispersal event to establish the entire New World tropical lineage of idoteine genera, versus a cladogram slightly less parsimonious but requiring only an easily explained vicariant origin of the New World line from a pre-drift cosmopolitan track. This is perhaps a case of strict methodological parsimony versus "biological parsimony." Given the multitude of avenues for pleonal reduction, I see no compelling reason to accept one cladogram over the other. Such problematic relationships can probably be resolved only by the elucidation of new generic-level attributes, and by careful examination of the morphological and biogeographic relationships of the individual species in these genera.

Discussion

The above phylogenetic and biogeographic analysis sheds light on several problems in understanding the evolution of the Idoteinae. First is the problem of discordant character trends. Although trends toward fusion of body somites and appendage articles (pleon, antennae, maxillipedal palp) have been noted for many decades, it was not until Menzies and Miller (1972) summarized and tabulated these data that the discordant trends in these different morphological features were recognized, suggesting probable high levels of homoplasy in the Idoteinae (see Table 1). Generating schematic pattern analyses (Figs. 4 and 17a) reveals that identical pleonal morphologies can be derived in a great many ways. For example, previous workers have assumed the 0+1 pleonal morphology of *Colidotea* to have been derived in the same manner as the 0+1 pleonal morphology of *Eusymmerus, Parasymmerus,* and *Edotea* (i.e., to be homologous), despite the fact that the former has a multiarticulate second antennal flagellum whereas the latter 3 genera have uniarticulate (clavate) second antennal flagella, the latter presumably being a fundamentally significant difference. In fact, the 0+1 pleonal morphology can be derived in any of about a dozen different ways, and in the above case it is clear that the derivation of *Colidotea* was probably quite different from that of the other 3 genera (see Figs. 3, 4, 16 and 17). Use of this schematic approach to pattern analysis in the Idoteinae also facilitates placement of the primitive genus *Zenobiana* in a single lineage apart from *Cleantioides,* even though both taxa have identical pleonal morphologies and have been confused with one another in the past. Further, the schematic analysis provides clear visual descriptions of all potential intermediate stage morphologies for the Idoteinae genera, lending high predictability (hence testability) to hypotheses contained in the above analysis.

That isopods, and peracarids in general, were already diverse and important taxa by the late Paleozoic has been fairly well documented by Schram (1970, 1974). By as early as the Pennsylvanian, the Peracarida had radiated into most if not all its currently recognized orders (except perhaps the Amphipoda). As Schram (1974) stated, ". . . peracarid radiation was probably initiated in Devonian time, when it is generally thought caridoid eumalacostracans were taking origin," ". . . the Peracarida are now known to be among the most ancient of the eumalacostracans," and ". . . the superorder Peracarida was a major element in the late Paleozoic radiation of eumalacostracans and contributed the principal caridoid types of that time." The earliest isopods known from the fossil record are phreatoicids from the middle Pennsylvanian; spelaeogriphacians, tanaids, and mysidaceans first appear in the lower Carboniferous.

The origins of the subfamilies of Idoteidae hypothesized in this study are consistent with Schram's data, and also with dates offered by Schultz (1979), who stated that most isopod families were well-defined before the Triassic.

The present analysis reveals the existence of two principal lines of descent within the Idoteinae (Fig. 16), lines that separated from one another early on (Jurassic or perhaps even Triassic). One of these lines remained closely tied to its origins in the Old World Southern Hemisphere temperate biota, while the other invaded New World environments and undertook a radiation in the New World tropics (producing genera such as *Cleantioides, Erichsonella, Eusymmerus,* and *Parasymmerus*). Brusca and Wallerstein (1979b) hypothesized that idoteids might only recently have invaded the New World tropics, perhaps in close association with a similar invasion of these regions by the brown algae (Phaeophyta), which probably serve as the principal habitat and food resource for most idoteine species. That the late Triassic-Early Jurassic periods might have had a widespread southern temperate Idoteinae distribution of little or no endemism is hardly surprising. As Hallam (1981) points out, Jurassic marine faunas as a whole were decidedly more cosmopolitan than those of the present day. These early origins in temperate waters explain the long-held belief that the Idoteidae and Idoteinae are "cold-water centered taxa." Plate movements became increasingly influential in promoting endemism within the Idoteinae from Late Jurassic through Late Cretaceous, as Pangaea fragmented. The high degree of endemism among Idoteinae genera contrasts

sharply with claims by Taylor and Forester (1979) that cold-water psychrospheric isopod biofacies (generic assemblages) tend to be similar regardless of latitude or depth.

This study has shed some light on the place of origin of both the Idoteinae and the Idoteidae, as well as the Valvifera itself. Distributions of the Idoteidae subfamilies (excluding the Idoteinae) are given in Fig. 18; distributions of the five other valviferan families are given in Fig. 5. As can be seen, two of the five Idoteidae subfamilies are distinctly Gondwanan in distribution (Glyptonotinae and Chaetilinae), one is predomintly Laurasian (Mesidoteinae), one is ubiquitous (Idoteinae), and one is endemic to the shores of Morocco (Parachiridoteinae). Of the six valviferan families, two are cosmopolitan (Idoteidae and Arcturidae), and the remaining four are all Gondwanan, including the most primitive family, the Holognathidae. No valviferan family is distinctly Laurasian in distribution. These data taken together strongly suggest that the Valvifera originated in the temperate Southern Hemisphere at least by early or mid-Pangaean times (Permian/Triassic), if not earlier.

Hurley and Jansen (1977) reviewed the zoogeography of the isopod family Sphaeromatidae on Southern Hemisphere coastlines. Their data on generic and species distributions reflect patterns similar to those seen here in the Idoteinae. Hurley and Jansen found generic affinity between all southern continents, as well as generic endemism on all shores (endemism levels reported are 12 genera [48%] in Australia; 7 genera [41%] in South Africa; 3 genera [20%] in New Zealand; and 1 genus [11%] in Chile). Hurley and Jansen invoked strict dispersalist mechanisms to account for these distributions, however, and stated, "The possibility of invoking continental drift as an agency is hardly necessary in view of the fact that littoral species are involved." What this statement is meant to imply is not clear. Presumably the authors are suggesting that littoral organisms are expected to disperse across ocean barriers with great regularity, thus negating the roles of continental drift and vicariance in establishing endemism. This view seems inconsistent with their data, however, which record high levels of endemism at both generic and species levels on southern continental shores (species endemism on Australian shores was reported as 91%; South African shores, 80%; New Zealand, 89%; Chile, 62%). In any event, Hurley and Jansen (1977) did not present any phylogenetic analyses of the taxa in question, making it impossible to evaluate alternative biogeographic scenarios for the Southern Hemisphere Sphaeromatidae.

The present study reveals several situations wherein ancestral taxa apparently persisted while new (sister) taxa evolved as peripheral isolates (or perhaps in sympatry) in restricted geographic regions. For example, *Synidotea* almost certainly persisted unchanged during the events that produced *Moplisa* and *Barnardidotea*. Similar situations exist for: *Paridotea* and *Engidotea*; *Zenobiana* and its sister-group; and *Edotea* and *Parasymmerus* (see Fig. 16).

This study suggests that both dispersal and vicariant forces probably played important roles in creating modern-day distributional patterns of idoteine genera. Dispersal via the Antarctic Circumpolar Current appears to have played only a minor role, however, as endemism on southern shores is high. The unique (highly endemic) nature of these southern continental shores was established long ago. Even New Zealand, which spans 13 degrees of latitude and sits just 1760 km off Australia, is noted for its high endemicity of coastal species. Examples include 24% endemism for polychaetes (Augener 1924), 50% for crabs (Chilton and Bennet 1929), 64% for echinoderms (Mortensen 1925), and 89% for sphaeromatid isopods (Hurley and Jansen 1977). Because the present analysis was at the generic level rather than the species level, and because several Southern Hemisphere genera cannot be clearly distinguished in a cladogram, resolution of all geographic patterns has not been achieved. What is clearly needed are similar analyses for each of the idoteine genera (e.g., see Brusca 1983). It is of particular interest to note that the major lines of descent within the Idoteinae appeared prior to the mid- to Late Cretaceous global warming trend, no doubt further facilitating the temperate-based distribution of this taxon. The present study adds further evidence to a large body of data demonstrating the concept of the Crustacea being a taxon fraught with convergences. As Schram (1978) deftly pointed out, "The central dominating
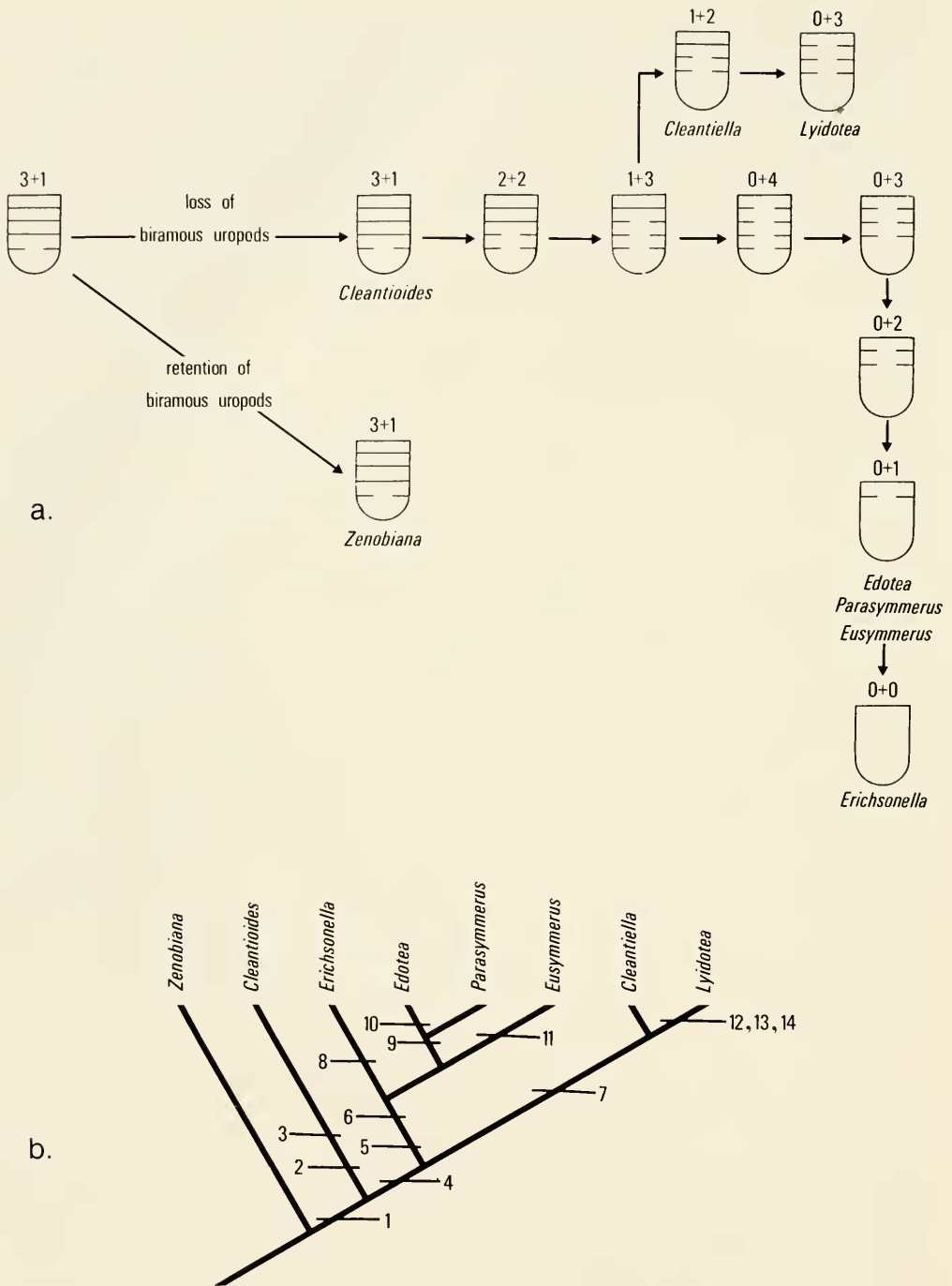
FIGURE 17a. Alternative schematic representation for lineage A, based on biogeographic analysis. 17b. Alternative cladogram for lineage A, based on 17a. Synapomorphies are as follow: (1) uropods uniramous, (2) pereopods IV reduced, (3) maxillipedal palp reduced in some species to 4 articles, (4) pleon 2+2, (5) maxillipedal palp reduced to 4 articles, (6) pleon 0+1, (7) pleon 1+2, (8) pleon 0+0, (9) maxillipedal palp reduced to 3 articles, (10) pleon with unique, acute, subtriangular shape, (11) left mandible with 3-pointed spine arising between lacinia and incisor, (12) pereonite VII fused to pleonite 1, (13) maxillipedal palp reduced to 3-4 articles, (14) pleon 0+3. *See* text for discussion.
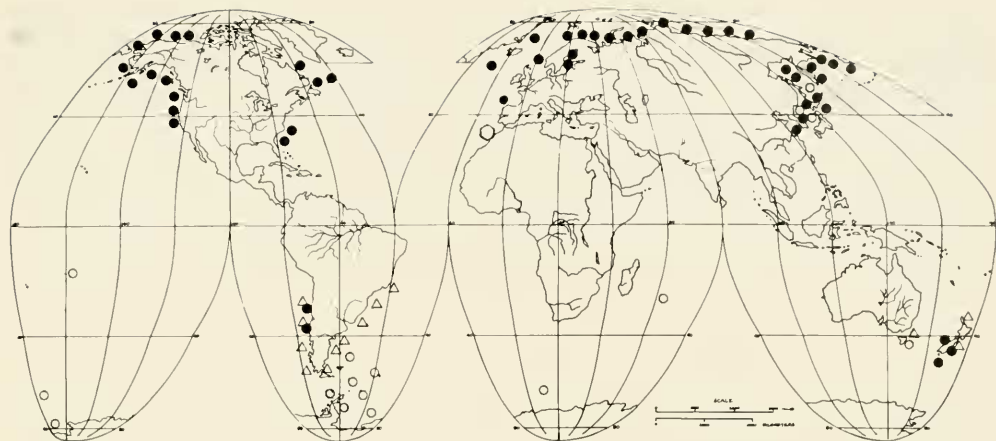
FIGURE 18.   Distribution of the subfamilies of Idoteidae (except Idoteinae): Mesidoteinae [●], Chaetilinae [△], Glyptonotinae [○], Parachiridoteinae [⊙].

theme of arthropod evolution is the multiplicity of convergent development. No phyletic scheme, monophyletic or polyphyletic, can escape this."

Wiley (1981) divided biogeography into three subdisciplines: descriptive, historical, and ecological biogeography. He felt that the goals and interests of the ecological biogeographer lie more with ecology than with systematics, whereas the opposite is true of the historical biogeographer. Finally, he suggested that systematics has little to contribute directly to the field of ecological biogeography. I disagree with Wiley, and feel I have shown here and through a series of studies that there is a logical sequence of basic taxonomy/descriptive biogeography/ecological-historical biogeography, all these studies existing within the realm of systematics (i.e., Brusca and Wallerstein 1977, 1979a, b, Wallerstein and Brusca 1982, Brusca 1983). Hessler and Wilson (in press) provide further evidence of these relationships by their implication of both ecological and historical factors in reviewing the probable causes for differences in distribution of major crustacean taxa. Pregill and Olson (1981) came to similar conclusions with regards to the Caribbean land vertebrates, as did Stock (1981) regarding the Caribbean crustacean stygobionts. While the methods of ecological and historical biogeography may differ, the two endeavors are clearly complementary; to attempt one at the expense of the other is to invite error.

Only a few genera of Idoteinae can be confidently tied to vicariance events associated with the breakup of Pangaea. Only one New World genus (*Parasymmerus*) can be clearly tied to such major geological events. Vicariant relationships seem to be more easily distinguished at the species level (*see* Brusca 1983). It would seem that, at least in idoteid isopods, too much time has passed and too many unknowable events transpired (new taxa have evolved and gone extinct, extant taxa have undergone local extinctions in selected portions of their range, dispersal events, etc.) to confidently extract clear vicariant patterns at the level of supraspecific taxa. Furthermore, those idoteine taxa that do appear to be products of vicariance phenomena can only be tested by comparison to cladograms and distributional data for other intertidal groups. Cracraft (1982) has recently detailed such a procedure. Briefly, allopatric vicariant speciation (type 1a of Bush 1975) implies the appearance of a barrier. In the case of littoral isopods, these barriers would be new stretches of ocean or new land barriers across shallow seaways. Such a barrier would be expected to influence the vicariance patterns of numerous intertidal taxa, and one would thus predict that concordant pairs of sister-taxa would exist on either side of the barrier. In contrast, speciation resulting from a dispersal event to a new area (a founder individual or population; type 1b speciation of Bush 1975) is generally taken to be a random event. Hence, one would predict not

to find concordant vicariance patterns from one clade to another. Absence of such concordance with other intertidal taxa thus would suggest that speciation was initiated not by a vicariance event, but by a dispersal event. Thus, the need for cladograms of other marine invertebrate groups becomes evident, and without such studies one cannot critically assess the hypothesized processes responsible for the patterns present today in the idoteine taxa. Finally, the low levels of congruence between the cladogram of taxa-area and geographic cladogram can also be explained by the simple hypothesis that Gondwanan distributions of ancestral idoteid taxa were NOT widespread, but fragmented and local. This possibility, of course, denies a popular premise of generalized tract theory, that ancestral ranges can be assumed to be the sum of the ranges of the descendants.

FOOTNOTES

[1] There have been several recent attempts to cast doubt on the monophyletic nature of the Peracarida (Watling 1981, Dahl and Hessler 1982, Hessler in press). This is not the place to present detailed analyses and criticisms of each of these studies. However, it should be pointed out that in Watling's "cladistic" analysis only certain selected characters were used, numerous character transformations were illogical and unexplained, character states attributed to various taxa were incorrect, and a clear method of character polarity assessment was not provided. Although the other recent studies (op. cit.) employed a variety of approaches, often in the guise of cladograms, none attempted to analyze character state polarities in a strict logical order or with any clearly expressed methodology. Schram (1981) was concerned with the recognition of basic structural plans within the Eumalacostraca, and his classification is based on a strictly random array of character associations. The phenogram he chose for conversion into a classification is the one he felt "most comfortable with." Hessler's (in press) "cladogram" of the Peracarida (his fig. 5) is entirely unjustified by the data he presents. Among other problems, no attempt was made to achieve parsimony and the "cladogram" actually requires more convergences (at least 24) than its contained character transformations (23). In the case of Watling (1981) and Hessler (in press) it appears as though evolutionary scenarios were conceived first, these then being transformed into dendrograms (incorrectly called cladograms) upon which the appropriate "apomorphies" were overlain. Hessler's dendrogram of the Peracarida is essentially Siewing's (1963 and earlier publications) concept of peracarid relationships. This procedure, of course, ignores parsimony considerations and is the exact reverse of what a phylogenetic (cladistic) analysis is meant to accomplish.

The fact is, there exist many unique synapomorphies that unite the peracarid orders: (1) maxilliped with basis produced into an anteriorly directed, bladelike endite; (2) lacinia mobilis present in adults; (3) oostegites formed on inner pereopodal coxal margin; (4) young brooded in a brood chamber or "marsupium" (the location of the brood chamber varies from a simple oostegial pouch to invaginations of the sterna, modified oviducts, or even to the inner carapace region in the thermosbaenaceans); (5) direct development, with no true postnaupliar larval stages; (6) release of the young as "manca"; (7) whiplike immobile sperm, devoid of fibrils and mitochondria (this character needs further documentation); (8) a large suite of embryological attributes (see below); and (9) a large suite of attributes associated with the functional morphology of the pereopods. These functional and morphological skeletomuscular adaptations are associated with a system unique to the Peracarida, in which the body-coxa articulation has lost the caridoid "gimbal" joint and become either immobilized or capable of only limited abduction/adduction, and the coxa-basis articulation become monocondylic but capable of performing a complete suite of motions. This peracaridan system for ambulation is present in the incipient condition in mysidaceans. Hessler (1982) views these particular peracaridan leg synapomorphies as adaptations necessitated by the development of the marsupium and its attendant oostegites. Although thermosbaenaceans have lost the oostegites, they still retain the infolded monocondylic articulation of the pereopodal coxa and basis (see Hessler 1982, for details).

The loss of the oostegites in the thermosbaenaceans is probably a response necessitated by unique morphological (fusion of pereopodal articles) and functional (locomotory) adaptations of the pereopodal endites in this group. Loss of oostegites and concomitant relocation of the brood chamber is not unique to the thermosbaenaceans among the Peracarida (it occurs in several hyperiid amphipods and isopod higher taxa). This matter has been competently dealt with by Fryer (1964) and need not be repeated here (also see Hessler 1982 and Siewing 1958).

The presence of lacinia-like movable spines in the larvae of a few species of euphausids and shrimps suggests two possibilities: (1) the lacinia of adult peracarids is a paedomorphic attribute (sensu Gould 1977) retained from a nonperacaridean ancestor with lacinia in larval stages only, or (2) these are superficially similar convergent features. The absence of postnaupliar larval stages in the Peracarida, and their direct development to a juvenile hatching stage, argue for their origin not from a eucarid ancestor but from a line separate from the eucarids. Hence, the second hypothesis is the more parsimonious. The structural simplicity of the "lacinia" of eucarid larvae, versus the complexity of the peracarid lacinia supports this contention. Should one choose to consider the movable mandibular spine of certain adult bathynellaceans to be true lacinia (see Siewing 1963, Schminke 1972, and Dahl and Hessler 1982), one is confronted again with two possibilities: (1) the adult lacinia is a feature representing a potential synapomorphy for a bathynellacean-peracarid line, or (2) this character is convergent in these two groups. I would accept either interpretation as a working hypothesis. The latter seems the more likely considering the presence of movable spines in certain eucarid larvae and the apparent plasticity of the spines of the mandibular row. The point is, however, that acceptance of either hypothesis would not affect the monophyletic status of the Peracarida! Frankly,

with regards to the monophyly of the Peracarida, all the fuss over the lacinia seems "much ado about nothing."

The Peracarida retain an "underlying unity in development" (Anderson 1973) distinct in numerous ways from the Eucarida and Syncarida. This unity has been well documented and succinctly summarized by Anderson (1973). Unique attributes of peracaridan development appear in virtually all stages of embryogenesis, and include among other things: the early segregation of primordial germ cells as a definite presumptive area; the teloblastic development of the postnaupliar segments; the vitellophage modifications in the early development of the midgut; the unique embryogeny of the digestive glands; the distinct embryogeny of the ectoderm; and the formation of a second pair of "dorsal organs" (the ectodermal dorsolateral organs).

The "mancoid" stage appears to be little more than the product of alterations in embryogeny and timing in the release of the young. Its absence in mysids and amphipods may be tied to a more rapid embryological development (or to a delayed postembryonic development) in these two taxa (see Steele and Steele 1975), which may also be linked to the presence of ventrally curved embryos and completion of cleavage in the early stages in these groups (i.e., rapid early holoblastic cleavage). Furthermore, although amphipods leave the marsupium with all 7 pairs of pereopods "in place," there is a great deal of variation in the structure and development of this appendage, particularly in the hyperiids. Laval (1980) has even recognized hyperiid "larvae," with distinct hatching stage morphologies. Much of the distinction between Laval's "larvae" and the adults involves the nature of the pereopods, and some hyperiids certainly appear to have "virtual mancoids." The seventh pereopods seem especially plastic in hyperiids and amphipods in general. The rudimentary nature of the seventh pereopods in "juvenile" amphipods of certain species has been known at least since the work of Bate (1861) on *Vibilia*. One could also posit the origin of the mancoid stage subsequent to the origin of the mysids and amphipods during peracaridan cladogenesis. This would remove this attribute from the list of synapomorphies defining the Peracarida, but it would certainly not destroy the monophyletic nature of that taxon; rather, it would simply make the "mancoid stage" a synapomorphy defining a subset within the Peracarida.

An embryological attribute that might suggest alliance among the amphipods, mysids and eucarids is the retention (from the larval stages) of the functional antennal glands in these three taxa. Since all Crustacea have antennal glands during their embryogeny, the retention of these glands into adulthood in these taxa hardly seems surprising and is most likely either a convergence or simply a symplesiomorphy retained from a common ancestor (i.e., a plesimorphy not lost until the appearance of the mysids and amphipods had been achieved during peracaridan cladogenesis).

I believe that a carefully (and correctly) accomplished cladistic analysis of the Peracarida will reveal the amphipods to be the nearest relative if not the sister-group of the isopods. No such analysis has been published to date, although one is in preparation by F. Schram. Watling (1981), Hessler (in press) and others have chosen to ignore or deemphasize the fundamental synapomorphies unique to these two taxa (e.g., sessile compound eyes; pereonites with coxal plates; pereopods entirely uniramous; carapace entirely lost; mandible of the transverse biting type), and rely instead on differences and retained plesiomorphies in their analyses. As indicated in Fig. 2, I do not believe that there are ANY shared derived characters unique to the tanaids-isopods.

[2] Note that were the amphipods taken to be the sister-group to the isopods, attributes 1, 2 and 4 would become synapomorphies uniting these two taxa.

[3] The genus *Austridotea* is in need of further study; it may have to be removed to the Idoteinae.

[4] Poore (in litt.) has suggested that the 4 non-idoteine subfamilies are synonymous and should be combined. At the time of this writing I am in general agreement with Poore, but do not address the matter here.

[5] The single Old World species of *Edotea* (*E. dilatata* Thomson, 1884) has been shown to be the female of *Crabyzos elongatus* (Miers 1876) (see Hurley 1961:292).

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Note added in proof: Kussakin (1982) recently synonymized west Pacific records of *Cleantioides planicauda* (as *Cleantis planicauda*) with his new *Zenobiana rotunda* Kussakin, 1982. This move restricts the genus *Cleantioides* to the tropical Pacific and Atlantic waters of the New World. (Kussakin, O., 1982, Marine and brackish-water Isopoda of cold and temperate waters of the Northern Hemisphere. II. Anthuridae, Microcerberidae, Valvifera, Tyloidea. [in Russian] Opredeliteli po faune SSSR. Akad. nauk SSSR [Acad. Sci. USSR, Zool.], No. 131.