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# A morphological comparison of the phyllopodous thoracic limbs of a leptostracan (*Nebalia* sp.) and a spinicaudate conchostracan (*Leptestheria* sp.), with comments on the use of Phyllopoda as a taxonomic category

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# A morphological comparison of the phyllopodous thoracic limbs of a leptostracan (*Nebalia* sp.) and a spinicaudate conchostracan (*Leptestheria* sp.), with comments on the use of Phyllopoda as a taxonomic category

**Joel W. Martin and Jennifer C. Christiansen**

**Abstract**: The fourth thoracic appendage of an adult female *Nebalia* sp. (class Malacostraca, order Leptostraca) is compared with that of an adult female *Leptestheria* sp. (class Branchiopoda, order Spinicaudata). Although these limbs are "phyllopodous" (flattened, leaflike) in both orders, they differ markedly in the size and arrangement of endites, type and number of setae, and function. Setal types found on the fourth thoracopod of *Nebalia* sp. are variations of a basic plumose or plumodentate seta, and the diversity of setal types is low. None of the setae is annulate, a distinction in setal formation. In contrast, on the fourth thoracopod of *Leptestheria* sp. there is a wide variety of setal types and stout spines, some of which have been reported from other "conchostracans" (orders Spinicaudata and Laevicaudata) but not from the thoracopods of any leptostracan. Nearly all of the setae are annulate. Thus, the single character (phyllopodous thoracic appendages) supposedly linking leptostracans and branchiopods in some classificatory schemes (e.g., the class Phyllopoda sensu Schram) has clearly arisen independently in these two taxa and in several other crustacean groups, and cannot be used as an indicator of phylogenetic affinity. The rejection of the class Phyllopoda as defined by Schram is supported, as are arguments for retention of leptostracans within the Malacostraca. The use of Phyllopoda as a taxonomic name, regardless of which crustacean groups are considered to compose the taxon, is discouraged in light of the rather convoluted history and inconsistent application of this term.

**Résumé** : Le quatrième appendice thoracique d'une femelle adulte de *Nebalia* sp. (classe Malacostraca, ordre Leptostraca) est comparé à celui d'une femelle adulte de *Leptestheria* sp. (classe Branchiopoda, ordre Spinicaudata). Malgré leur qualificatif de « phyllopodes » (aplatis, en forme de feuille) chez les deux ordres, ces membres sont très distincts par la taille et l'arrangement de leurs endites, par le type et le nombre de leurs soies et par leur fonctionnement. Les soies trouvées sur le quatrième thoracopode de *Nebalia* sp. sont des variations du modèle de base d'une soie plumeuse ou plumodentée et la diversité des soies est faible. Aucune de ces soies n'est annelée, un caractère distinctif dans la formation des soies. Par ailleurs, il existe sur le quatrième thoracopode de *Leptestheria* sp. une grande variété de types de soies et de grosses épines, certains déjà observés chez d'autres « choncostracés » (ordres Spinicaudata et Laevicaudata), mais pas sur les thoracopodes des leptostracés. Presque toutes les soies sont annelées. Donc, la seule caractéristique (appendices thoraciques phyllopodes) supposée relier les leptostracés et les branchiopodes dans certains systèmes de classification (e.g., la classe Phyllopoda sensu Schram) est de toute évidence apparue indépendamment chez les deux taxons et chez plusieurs autres groupes de crustacés, et ne peut donc pas servir d'indice d'affinités phylogénétiques. L'abandon de la classe des Phyllopoda telle que définie par Schram est justifiée, de même que le sont les arguments en faveur du maintien de l'ordre des leptostracés parmi les malacostracés. L'utilisation du Phyllopodes pour désigner un taxon est donc déconseillée, quel que soit le groupe de crustacé dont on parle, puisque le terme ne semble pas avoir été toujours employé de façon cohérente.
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**Fig. 1.** Fourth thoracic appendage of a female of an undescribed species of *Nebalia* from the coast of southern California. (*a*) Entire limb, medial side toward the right, distal at the bottom. (*b*) "Naked" setae of the distolateral part of the exopod (see *a*) at higher magnification. (*c*) Naked (actually minutely serrulate) seta on the lateral border of the exopod. SEM. (*d*) Distal segment of endopod at higher magnification, showing densely setulate setae lacking an annulus. (*e*) Larger diameter plumose setae typical of the medial border of the endopod. (*f*) Thinner, more densely plumose setae arising from a curved row at the base of the protopod. (*g*) Overlapping thin and thick plumose setae from the same area as in *f*. SEM. Scale bars: 1.6 mm for *a*; 0.5 mm for *c*–*f*; 50 μm for *b* and *g*.

## Introduction

As an obvious adaptation for swimming or for generating water currents, flattened, leaflike limbs have arisen in a large number of marine invertebrate taxa. This is particularly true among the Crustacea, a group that is third in species number but undoubtedly foremost in terms of morphological diversity (= disparity; see Fryer 1985; Martin 1992). Natatory, or at least leaflike, appendages are present even in those crustacean taxa whose predominant mode of locomotion is not swimming; for example, the abdomen of reptant decapods nearly always bears leaflike pleopods, which are employed for a variety of purposes depending upon the taxon.

Although limb morphology is often used as a basis for crustacean classification, the great morphological plasticity of crustacean appendages means that there is always some risk in doing so. In the case of the various crustacean taxa sometimes referred to as phyllopods (see the Discussion and also Fryer 1987; Dahl 1987) it is clear that a number of unrelated taxa have independently developed this type of limb. Nevertheless, the idea that some of these phyllopodous groups may be related (based mostly on shared possession of these limbs) is an old and persistent one. According to Dahl (1987), Milne Edwards regarded leptostracans and branchiopods as members of the same taxon as early as 1840; Schram (1986, p. 543) credits an earlier paper by Latreille (1825) for the first use of Phyllopoda as a formal taxonomic name. In the most recent compendium that attempts to cover the entire Crustacea, Schram (1986) revived this grouping, encompassing under the heading Phyllopoda the branchiopods, cephalocarids, and leptostracans. Because Schram's classification appeared in book form, whereas critical reviews of that work appeared in scientific journals (e.g., Abele 1987; Dahl 1987; Fryer 1987), there is the possibility that some subsequent popular or textbook accounts of the Crustacea will perpetuate this concept of the Phyllopoda. For example, in the newest edition of Meglitch's textbook *Invertebrate Zoology* (coauthored by Schram) this usage appears without any mention of doubt or concern about the arrangement (Meglitsch and Schram 1991, p. 476). Thus, the beginning student of crustacean morphology and phylogeny might be led to believe, despite a rather large amount of evidence to the contrary (e.g., Hessler and Newman 1975; Dahl 1987, 1992), that this concept of the Phyllopoda is, in fact, a viable alternative to the traditional placement of leptostracans within the Malacostraca and the treatment of the cephalocarids as a separate crustacean class. In this paper we address what might be regarded as the sole synapomorphy proposed for the recognition of a class Phyllopoda (e.g., Schram 1986), the presence of polyramous and foliaceous limbs. Dahl (1987, 1992) has addressed the question of polyramy (a basic feature of malacostracans and so not a phyllopod synapomorphy; see also Hessler and Newman 1975). He noted also that foliaceous limbs are possessed by a number of other taxa, are not always indicative of filter feeding, and are quite different between leptostracans and branchiopods. We provide additional evidence from studies at an ultrastructural level showing how these limbs differ in derivation, form, and function.

## Materials and methods

Specimens of a large (to 15 mm total length) undescribed species of the leptostracan genus *Nebalia* were sent to us by E. Vetter, Scripps Institution of Oceanography, La Jolla, California. The specimens were collected on 29 February 1992 using an air-powered suction device on a detrital mat at the head of Scripps Canyon, approximately 1000 m north of the Scripps Institution pier, La Jolla, California, 32°52.5′N, 117°15.5′W, at a depth of 19 m. Sediment and debris collected in this manner were washed through a 55-μm sieve. Animals were preserved in 4% formalin in seawater and later transferred to 70% ethyl alcohol.

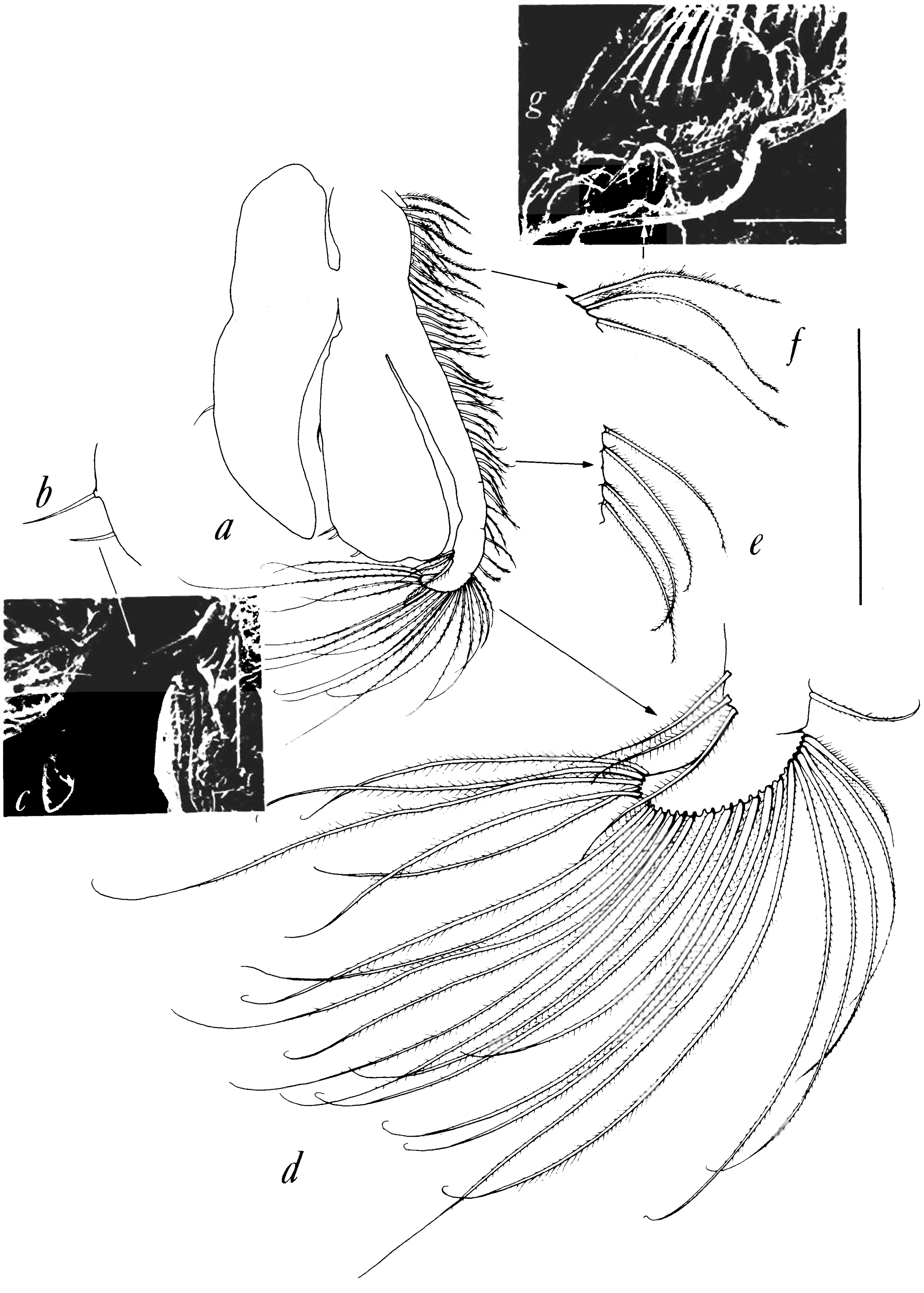
Specimens of the spinicaudatan conchostracan genus *Leptestheria* were taken from a large collection in the Natural History Museum of Los Angeles County. These specimens are readily identifiable as *Leptestheria compleximanus* (Packard) (see Martin and Cash-Clark 1993). The specimens lack data concerning date or place of collection, but are presumably from the southwestern United States, considering the known range of *L. compleximanus*. We used only adult females of both species, and removed and illustrated only the fourth thoracic appendage for both taxa.

Drawings were made with the aid of a Wild M5APO dissecting stereomicroscope and a Nikon Labophot compound microscope, each equipped with a camera lucida. Specimens prepared for scanning electron microscopy (SEM) observation (for photography and to verify our light microscopy observations) were dehydrated in a graduated ethanol series, dried using hexamethyldisilazane (Nation 1983), and mounted with carbon tape prior to sputter-coating with gold and viewing with a Cambridge 360 stereoscan electron microscope.

## Results

### *Nebalia* sp. (Fig. 1)

In *Nebalia* sp. (Fig. 1*a*), the endopod is essentially undivided, or at most weakly incised, along its medial edge, and all of the setation consists of short to long plumose setae. The distinction between the endopod and the protopod is not clear, and neither is the distinction between the "proximal endite" and more distal endites (but see Walossek 1993). Divisions of the endopod are most evident distally, where three segments can be discerned, and subdivisions are more evident in more anterior thoracopods and in some other species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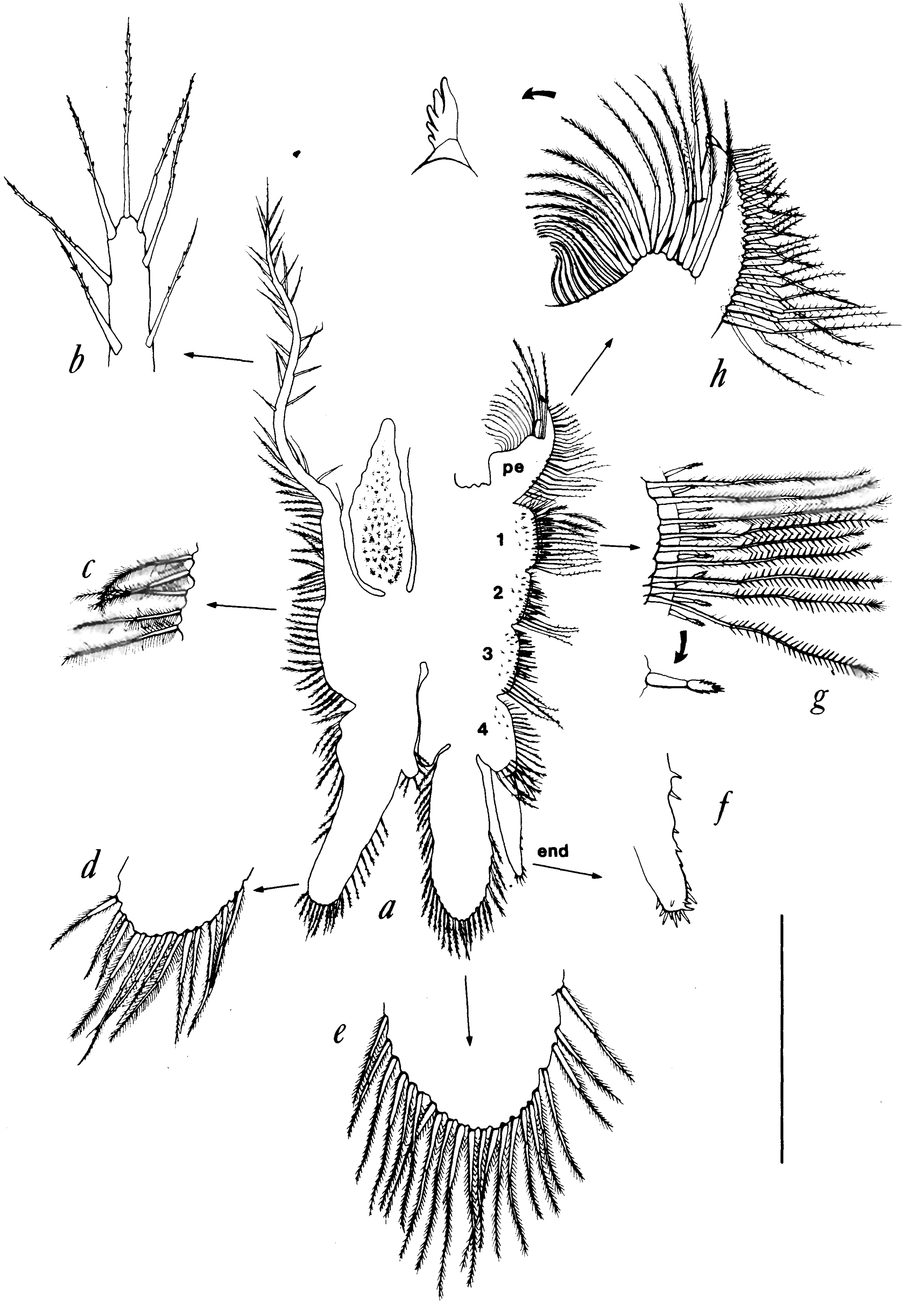
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**Fig. 2.** Fourth thoracic appendage of an ovigerous female *Leptestheria compleximanus* (Branchiopoda, Conchostraca, Spinicaudata). (*a*) Entire limb (orientation is the same as for the limb shown in Fig. 1, (i.e., medial side toward the right, distal end toward the bottom). (*b*) Extremity of dorsal lobe of exopod, showing stout setae with short projections from the shaft (see also Fig. 3*e*). (*c—e*) Plumose annulate setae typical of the lateral border of the exopod, ventral lobe of the exopod, and distal tip of the protopod, respectively. (*f*) Short, stout spines on the endopod. (*g*) Setation of the first endite of the protopod, with three different setal types shown; a stout, serrate, spinelike setal type is shown enlarged (arrow). (*h*) Proximal endite, showing overlapping fields of plumose to pappose setae, and with the distal spinelike tip enlarged at the left (arrow). Numbers 1–4 refer to the endites. *pe*, proximal endite; *end*, endopod. Scale bars: 1.6 mm for *a*; 0.5 mm for *b–h*. Enlargements (arrows) are not drawn to scale.

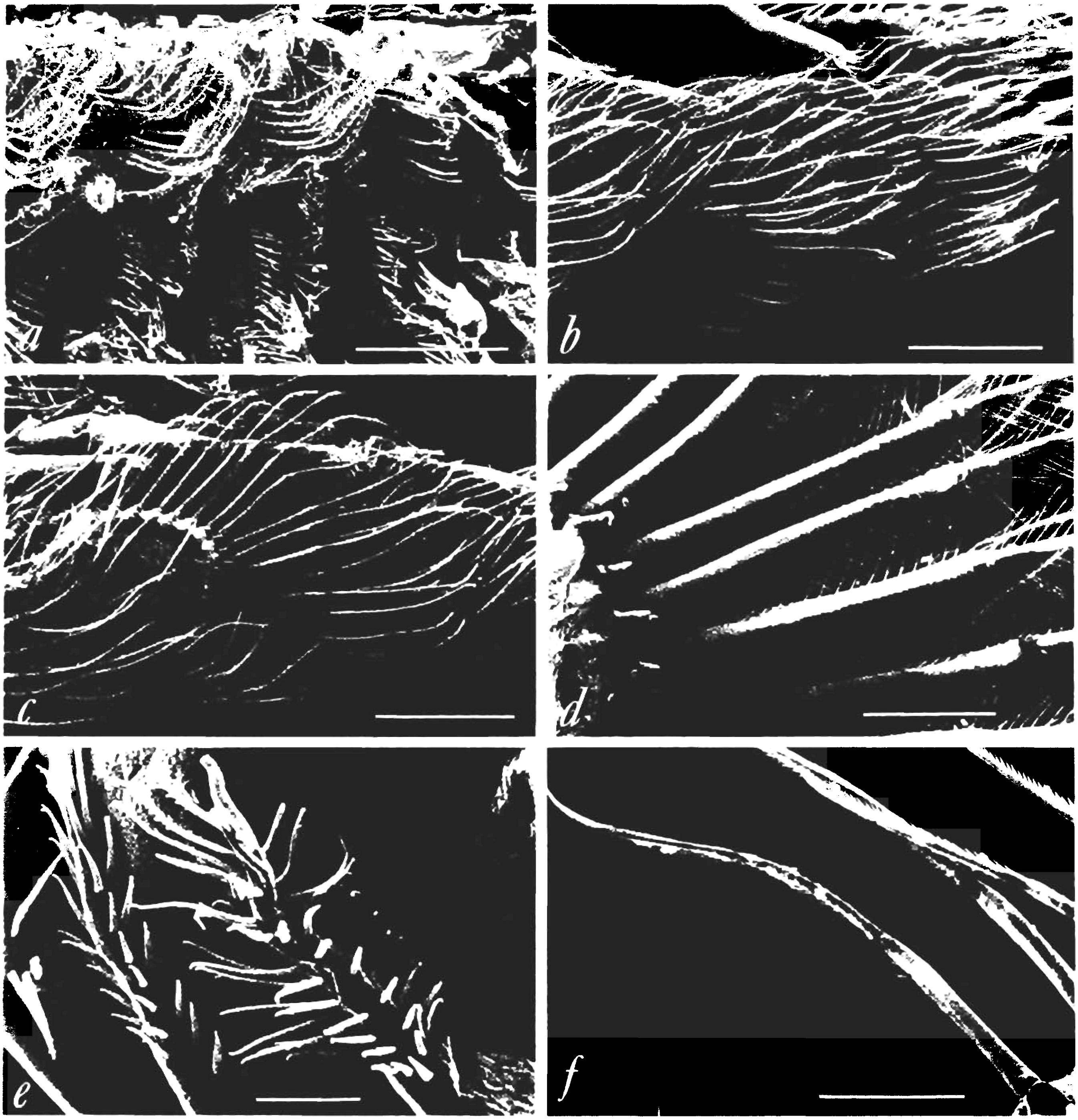
(for example, see Figs. 35–37 in Dahl (1985) for *Nebalia borealis*). There are some subtly different types of plumose setae on the leptostracan limb. Such subtle differences were also noted by Hessler (1984, especially his Figs. 3D and 3F showing the fifth thoracopod) for the thoracic limbs of the deep-sea genus *Dahlella*, where setal diversity appears to be slightly higher than in our species of *Nebalia* In our species, there is a curved row of setae near the base of the appendage that originates on the face of the limb rather than on its edge. These setae are thinner than those found along the medial border of the limb, and the setules are more closely spaced, giving them a feathery appearance (Figs. 1*f*, 1*g*). Thus, these are most similar to what Hessler (1984) termed the anterior filter setae of the coxal lobe. Beneath (behind) this row, the setae are larger in diameter and less densely setulose, perhaps corresponding best to Hessler's (1984) brush setae. As one moves distally along the medial border, the setae become a bit less plumose, with the individual setules oriented at more of an angle from the setal shaft (Fig. 1*e*). Thus, they are more or less "pappose," closest to setal type I.A.2 of Watling (1989), although lacking an annulus. The distal tip of the endopod, more clearly demarcated from the more proximal part of the limb, bears long, densely setulate setae (Fig. 1*d*); as such the specimens are clearly identifiable as sexually mature females, following the functional groupings of Dahl (1985), who referred to these setae as "pinnate." On the outer margin of the exopod and epipod are a few scattered short setae. These appear unarmed under light microscopy but can be seen to bear minute setules under SEM (Figs. 1*b*, 1*c*). There is no evidence of an annulus. Thus, there are basically four types of setae on the limb, all of them being more or less derivable from a basic plumose seta such as Jacques' plumose seta type 4*b* (Jacques 1989, p. 9; "setae with setules; on two opposite generative lines, without ringing" [annulus] and with "spaced setules"), Factor's (1978) type A, or an annulus-lacking form of the type I.A.1 plumose seta of Watling (1989, p. 22) (unfortunately referred to as type I*a* in Watling's Fig. 4).

### *Leptestheria compleximanus* (Figs. 2–4)

The leg of *L. compleximanus* (Fig. 2*a*) bears a large number of very different setal types. The protopod is subdivided into a number of endites, each with an apparently unique array of spines and (or) setae. The overall impression is of a flattened, leaflike limb with long, plumose setae (Figs. 2*a*, 2*c*–2*e*, 3*a*–3*d*). Such setae can be found on the dorsal and ventral lobes of the exopod (Figs. 2*c*, 2*d*) and on the distalmost lobe of the protopod, which actually exceeds the endopod in length (Fig. 2*e*). These setae are similar to what was described above for *Nebalia* sp. but with the distinction that these setae always bear an annulus, from which we infer that they are formed by a different process (see Watling 1989, p. 19; see the Discussion), and as such they would not be considered homologous with setae formed without the same type of epidermal invagination process (according to Watling 1989, p. 20; see Discussion).

The dorsal lobe of the exopod (Figs. 2*b*, 3*e*) bears scattered stout setae with short, blunt setules. These setae lack an annulus and do not appear to correspond closely to any of the more basic crustacean setal types (e.g., those described or listed by Factor 1978; Jacques 1989; Watling 1989; and references therein). The endopod (*end*; Fig. 2) is very reduced, and appears similar to the more proximal endites of the protopod, but is delineated from them by a clear suture. It bears stout, short spines (nonarticulating with limb cuticle) and setae (articulating with a basal socket) at its tip (Fig. 2*f*). The more basal endites of the protopod (endites 1–4) carry an assortment of setal types, including setae most commonly referred to as pappose, cuspidate (Figs. 2*g* (large arrow), 4*a*), and plumose. The basalmost (first) endite bears at least three quite different setal types (Fig. 2*g*). The anterior faces of endites 1–4 bear numerous short, curved spinelike setae (Figs. 2*a*, 4*b*, 4*c*). These setae are always curved in the direction of the endite's setal border and articulate with the face of the limb by way of a socket that is buttressed on its lateral side by a cuticular ridge, probably serving to prevent movement of the seta beyond a certain angle. The proximal endite (Figs. 2*a* (*pe*), 2*h*) is oriented at a different angle from any of the other endites, and may have a different evolutionary origin (see Walossek 1993). It is this endite that is responsible for the mechanical movement of food particles anteriorly along the food groove (e.g., Martin 1989). Both borders of the proximal endite bear long, plumose annulate setae as well as two rows of pappose setae on the medial border, each of which always appears bent at a slight angle to the axis of the shaft (Fig. 2*h*). The tip of this lobe is unique, differing not only from the leptostracan thoracopod but also from all known branchiopods, and bears a single stout, toothed, comblike spine (Fig. 2*h* (arrow), 4*d*, 4*f*). The teeth of this heavy spine are directed upward, into the food groove, and undoubtedly play some role in the manipulation of food particles toward the mouth. We have not been able to locate an identified spine or setal type in the literature that quite matches this, although perhaps it can be thought of as a modification of Factor's (1978) cuspidate type H2 spine. Just posterior to this leg, the complexity of the thoracopod setae and spines becomes even greater. The proximal endite develops rows of stout cuspidate setae and denticulate setae (Fig. 4*e*), and the distal tip becomes even heavier, with teeth outwardly directed to both sides rather than just toward the food groove as shown for leg 4 (Fig. 4*f*).

**Fig. 3.** Selected setal types of the fourth thoracopod of *Leptestheria compleximanus*. SEM. (*a*) Cutaway view of thoracopods, with food groove (and therefore proximal endite) toward the top of the figure. Scale bar = 500 μm. (*b*) Overlapping plumose setae of the protopod and ventral lobe of the exopod of several thoracopods. Note the annulations at the approximate midpoint of each seta (more obvious in *d*). Scale bar = 200 μm (*c* and *d*). Plumose setae at successively higher magnifications. Note the annulations toward the right in *d*. Scale bars: 200 μm in *b*; 50 μm in *d*. (*e*) Stout setae bearing short projections at the tip of the dorsal lobe of the exopod (corresponding to Fig. 2*b*). Scale bar = 10 μm. (*f*) Plumodenticulate setae typical of basal endites (refer to Fig. 2*g*). Scale bar = 50 μm.

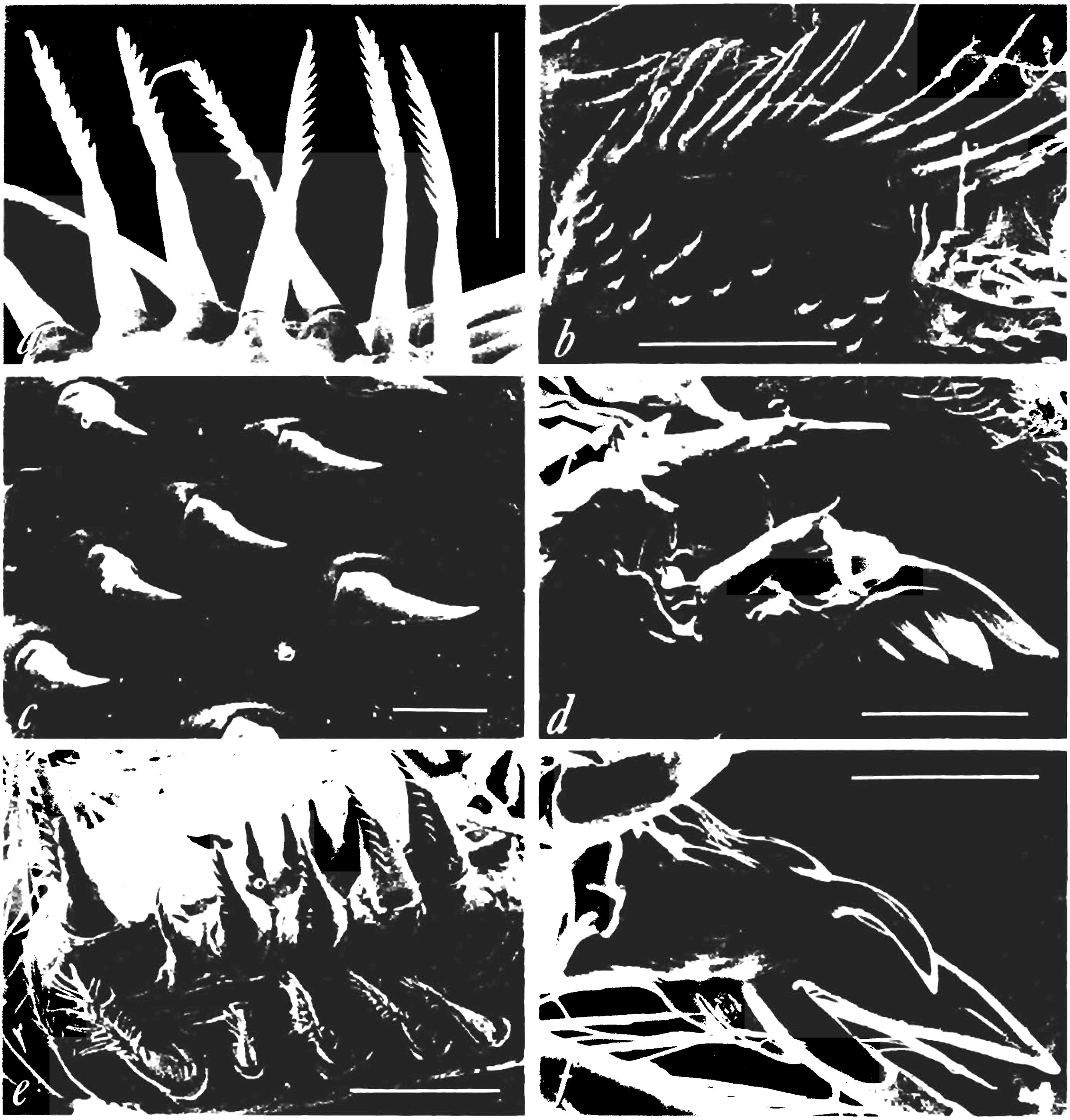


## Discussion

### Form and function of the thoracic limbs

Even at relatively low magnification, the differences between the fourth thoracic limbs of *Nebalia* sp. and *L. compleximanus* are striking. The simpler condition is exhibited by *Nebalia* sp. (Fig. 1*a*), where the endopod is only weakly incised along its medial edge and barely discernible from the protopod, and where all of the setation consists more or less of variations on a central theme of short to long plumose

**Fig. 4.** Additional SEM views of selected setal and spine types of the fourth thoracopod of *Leptestheria compleximanus*. (*a*) stout, serrulate, spinelike setae from protopodal endites (see Fig. 2*g*). Scale bar = 50 μm. (*b*) Outer face of endites 2 and 3, showing stout curved spines. Scale bar = 200 μm. (*c*) Stout spines seen in *b*, at higher magnification. Scale bar = 20 μm. (*d*) Distal tip of proximal endite of limb 4, showing stout comb-like spine at extremity. Scale bar = 20 μm. (*e*) Basal endite from a more posterior thoracopod (11th limb), showing stout spines on the medial border (these are not found on thoracopod 4). Scale bar = 50 μm. (*f*) Distal extremity of the proximal endite of a limb posterior to the fourth thoracopod, showing changes occurring from anterior (*d*) to more posterior (*f*) limbs (compare with fourth limb, at the same magnification, directly above). Scale bar = 20 μm.



setae. In contrast, the leg of *L. compleximanus* (Fig. 2) is grossly different in shape and organization and bears a large number of very different setal types.

Statements concerning the function of a crustacean limb based on morphology alone can be misleading. Although both of the taxa compared in this paper are relatively well known, there is a paucity of basic data on the function of individual limbs and their spines and setae. Clam shrimp, for example (indeed all branchiopods), are often depicted as simple filter-feeding animals. Not only is this untrue for this species (*L. compleximanus*), it is also untrue for clam shrimp in general, many of which appear to employ scraping and scavenging instead of, or in addition to, some filtering of particulate matter from the water (G. Fryer and J. Martin, unpublished data). Additionally, branchiopods, the most morphologically diverse group of the entire Crustacea (see Martin 1992), employ many different modes of feeding. As one example, Fryer (1966) documented that the large anostracan *Branchinecta gigas* is a raptorial predator, despite being closely related to species that clearly live by filtration. Many other feeding modes exist as well (for summaries of the extant orders see Martin 1992). We have observed *L. compleximanus* burrowing and scraping in mud and scavenging dead or dying members of its species. Presumably the relatively heavy setae and spines on its thoracopods reflect these habits. Therefore it is clear that filtration is not the only mode of food acquisition in this species, and may not be an important one, and this multiplicity of functions may be reflected in the relatively greater diversity of setal and spine types. Martin et al. (1986) described a similarly diverse array of spines and setal types in the clam shrimp *Lynceus gracilicornis*, a member of the other order (Laevicaudata) of branchiopods formerly treated with spinicaudates as the Conchostraca (see Fryer 1987; Martin 1992).

*Nebalia* sp., on the other hand, displays greater regionalization, with a recognizable abdomen that bears pleopods. With a clearer division of labor among its appendages, less diversity on any particular limb perhaps is easier to understand. The functional morphology of leptostracans has received slightly more attention than that of the spinicaudate conchostracans, and there seems to be general agreement that the foliaceous limbs of species of *Nebalia* are used to generate food currents (e.g., see Cannon 1927).

According to Watling (1989), whose brief review was based on the work of several earlier authors, crustacean setae can be formed in at least two distinct ways. Invagination of the epidermis results in the formation of an indentation on the setal shaft, called the ring or annulus (Watling 1989, p. 20; see also Aiken 1973; Reaka 1975; Longmuir 1983). Annulate setae are commonly encountered on the limbs of clam shrimp and other branchiopods. Setae lacking such an annulus apparently are formed without the process of epidermal invagination (Watling 1989, p. 20, and above references). Therefore, not only do the types of setae differ between branchiopods and leptostracans, but it is apparent that they are formed by different processes. We are not certain that this implied difference in setal formation is profound or necessarily indicates that annulate and nonannulate setae are nonhomologous. Long setae, regardless of whether they possess an annulus, almost certainly must be formed by some similar manner of epidermal invagination, and so we are reluctant to base any hypotheses of homology or phylogeny on this difference alone. Additionally, it is rather easy to find taxa bearing annulate and nonannulate setae on the same endite. Nevertheless, the differences in setal type and overall limb function noted herein constitute yet another difference between leptostracan and branchiopod "phyllopodous" limbs, and further weaken the already shaky case for combining these groups into one taxon. Along these lines we should also note the considerable number of shared features of leptostracans and malacaostracans, a point made previously on the basis of morphological, embryological, functional, fossil, and ontogenetic evidence (e.g., see Rolfe 1969, 1981; Hessler and Newman 1975; Hessler 1992; Dahl 1987, 1992).

### Use of Phyllopoda as a taxonomic name

The use of "phyllopod" to describe flattened, leaflike limbs has a long history. Although it is not our intent to give an exhaustive account of all historical uses of this term, we believe that it is useful to point out that the term was used as a taxonomic category at least as long ago as 1825 by Latreille to encompass branchiopods as well as leptostracans, according to Schram's classification (1986, p. 543). Fryer (1987) reviewed the more important historical classifications of the Branchiopoda, several of which employ the category Phyllopoda in one sense or another. Thus, Sars (1867) used it to encompass all of the non-cladoceran branchiopods as well as phyllocarids (leptostracans), although later (Sars 1890) he used it to embrace only the Anostraca, Notostraca, and Conchostraca (see Table 1 in Fryer 1987). There are scattered references to "phyllopods" and "phyllopod beds" in the paleontological literature as well. According to Gould (1989, p. 69), Walcott's original description of the Burgess Shale arthropod *Marella* sp. placed it among the phyllopods, although *Marella* sp. is no longer thought to be a crustacean. Preuss (1951) included in the Phyllopoda only the Notostraca and Onychura (the latter being the combined Cladocera and Conchostraca), and excluded the Anostraca. This usage was followed by Flossner (1972). After several years during which the term was more or less abandoned by crustacean systematists, Schram (1986) resurrected the taxon Phyllopoda, but this time it was used to encompass all of the branchiopods and also the Leptostracans, a group whose affinity to the Malacostraca has been rather thoroughly documented (and further supported by the present study). Also included in Schram's Phyllopoda were the Cephalocarida, which to most carcinologists are deserving of separate class status (e.g., see Hessler and Newman 1975; Hessler 1992; and references therein). Most recently, Walossek (1993) has used the term to embrace the non-anostracan branchiopods (as did Preuss 1951; and Flossner 1972), which is perhaps an unfortunate choice in light of the fact that all species of the Anostraca have phyllopodous thoracic limbs, whereas many of the non-anostracans (among the four former cladoceran orders; see Fryer 1987; Martin 1992; Martin and Cash-Clark 1995) do not. Thus, there have been at least six distinct groupings placed at one time or another under the heading Phyllopoda: (1) all crustaceans with leaflike limbs (e.g., Latreile 1825), (2) leptostracans plus all branchiopods except the cladocerans (e.g., Sars 1867), (3) all branchiopods except the cladocerans (e.g., Sars 1890), (4) miscellaneous (and probably unrelated) fossil forms, such as *Marella* sp., plus extant taxa with foliaceous limbs (e.g., Walcott, as cited in Gould 1989), (5) all branchiopods except the Anostraca (e.g., Preuss 1951; Flossner 1972; Walossek 1993), and (6) all branchiopods and leptostracans plus the Cephalocarida (e.g., Schram 1986).

While a history of confusing usage is by itself no reason to abandon a taxonomic name, there are existing names, many with historical precedence, that are more informative, more commonly employed, and therefore more recognizable and less confusing. Although the term was at one time useful, placing together crustaceans that possess superficially similar appendages, it appears to have outlived its usefulness, and should perhaps be included with such other crustacean taxonomic category names that are now of historical interest only (Entomostraca, Schizopoda, Natantia, Eubranchiopoda, Gnathostraca, and others). At the very least, we urge systematists to define carefully any such use of the term to avoid further confusion.

## Acknowledgments

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