The Amphipod Functional Model and Its Bearing upon Systematics and Phylogeny

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The peculiar habitus of Amphipods with lateral compression, deep coxal plates 1–4, broad bases of pereaeopods 5–7, and enlarged pleura (epimeral plates) of abdominal segments 1–3 is seen as a functional system closely dependent upon the currents produced by the incessant beating of the pleopods. The derivation and position of branchiae and oostegites is discussed. The morphology of more or less aberrant groups, including the suborders Caprellidea and Ingolfiellidea, and its correlations with the mode of life and the basic functional model is analyzed. The possible bearing of the functional model system upon the position of the Amphipoda among the Peracarida is briefly dealt with.


1. Introduction: Aspects of the Amphipod structural plan

Although Amphipod morphology is very well known, little attention has been paid to the functional integration of the structural plan. The aim of the present paper is to look somewhat more closely into the Amphipod functional model system (sensu Dahl 1976) and to discuss some of its implications which appear to be of interest to Amphipod systematics and perhaps also phylogeny.

There are a number of features in which the Amphipod structural plan differs from those of all other Malacostracan groups and which could be regarded as synapomorphies in the Hennigian sense. For the present purpose the following four are of particular interest.

1. The deep coxal plates of the four anterior pairs of pereaeopods, which emphasize the lateral compression of the body.

2. The broad posterior expansion of the basal article of the three posterior pairs of pereaeopods, as a rule increasing in size from P5 to P7. In those cases where the basis is more or less linear, this is obviously a secondary condition.

3. The presence of deep pleural (epimeral) plates on pleon segments 1–3 but not on the following segments.

4. The subdivision of the five anterior pleopods into two groups, the three anterior pairs retaining normal pleopod structure and function while the two posterior ones are modified and in current nomenclature together with the sixth pleopod classified as uropods.

Together the parts mentioned under 1–3 above, viz. coxal plates 1–4, basal plates 5–7, and pleon pleura 1–3 enclose laterally a deep ventral groove, stretching from the base of the maxilliped to the base of the first uropod. This ventral groove and the pleopod current sweeping through it together provide the key to the understanding of the Amphipod functional model.

Below a description will be given of the main features of the pleopod current system in Gammarus pulex de Geer. A Gammarus species was chosen because, as shown by Schellenberg (1942) and, particularly, by Barnard (1969), the genus represents the Amphipod structural plan in its most typical form. The importance of the peculiar arrangement mentioned above to respiration, reproduction, sensory perception, and locomotion will be discussed. The ontogenetic processes involved in the formation of the ventral groove will be described together with implications concerning branchiae and oostegites. Some groups with a morphology deviating from the basic pattern will be analyzed. In the final discussion, the bearing of the functional system on some systematic and evolutionary questions will be examined.

2. Current systems in Gammarus pulex

2.1. Resting position.

When resting, the animals lie on the side or cling to various objects in a curled up position. The cephalon and anterior segments are curving slightly ventrad, the pleon being more distinctly arched, with the posterior part generally directed somewhat anteriad (Fig. 1). Roughly speaking the dorsum of the animal forms a little more than half the circumference of a slightly irregular circle, with the posterior part of the pleon cutting slightly into it.

The antennae are raised, pointing dorsolaterally. From time to time they are rapidly passed over mouth-parts and gnathopods. The antennae are directed forwards and somewhat ventrad and diverging slightly. Most of the time they

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mouthparts are kept immobile but at irregular intervals the maxilliped and maxillulare palp are vibrating. The gnathopods are held in the vertical plane of the body with the basis directed obliquely posteriad-ventrad and the distal part of the appendages bent forwards from the basis-ischial and ischio-meral joints. P3–P4 are curving laterally and somewhat dorsally, the curving being gradual and affecting all joints from the basis-ischial one outwards. In P5–P7 the basis is kept vertical but the distal part of the appendage is bent dorso-laterally from the basis-ischial and ischio-meral joints.

The pleopod current was briefly described by Schellenberg (1942) but is more complicated than apparent from his account. Barnard (1969) also briefly refers to the current in a way showing that he has understood its mechanism. He does not, however, discuss its implications.

The fast and regular beating of the pleopods makes their tips swing in a wide arc, posteriorly reaching to between the bases of the two anterior pairs of uropods and anteriorly into the ventral furrow between the branchiae up to the level of the second gnathopod.

The current systems set in motion by the pleopods were studied by means of carmine and fine detritus suspensions. They affect an area with a radius several times the body length of the specimen and converge upon it from all directions except the ventro-posterior one (Fig. 1).

Particularly strong currents are drawn in from the anterior and antero-ventral directions. The anterior current sweeps over the antennary flagella and the mouth-parts and enters the branchial region between and around the gnathopods. In front of the cephalon it is joined by weaker currents with about half the velocity or less which come from a dorsal direction over and between the spread out antennulary flagella and become faster as they approach the antennary bases.

The anterior current is not sharply delimited from the antero-ventral one which, when it approaches the cox 4–P5 region attains the highest velocity of the whole afferent system. The focal point of the current is the gap between the coxa of P4 and the basis of P5 where it enters the region of the actual pleopod swing and also meets the anterior current.

Owing to this and above all the forceful action of the pleopods, there is much turbulence in the posterior part of the branchial region.

The slow but steady dorsal and posterodorsal currents flow over the sides of the body. In the anterior part they enter the anterior current system and in the middle part they are drawn into the turbulent area of the P4–P5 region, while those flowing over the pleon join the lateral part of the efferent current.

The efferent current has the greatest velocity of all. According to Schellenberg (1942) the pleopod branches and hairs straighten out during the backward beat to form an oar-shaped structure, which increases the effect.

The current sweeps backwards between and below the two anterior pairs of uropods and below the third uropod which forms a very sharp divide between the efferent current and the posterodorsal afferent currents.

The efferent current passes very close to the posterior, fastest part of the antero-ventral afferent current, and in the narrow space between them there is some slight turbulence, but the interference between the two systems is less than one would expect considering their directions.

In the resting position the current systems seem to maintain a perfect equilibrium, which allows a specimen to lie on a smooth glass plate without its position being shifted.

2.2. Swimming position
As soon as a specimen begins to straighten itself from the curled-up resting position, the pleopod beat produces a forward movement, faster the straighter the animal becomes. In the straight swimming position (cf. Schellenberg 1942) the pleopods, which hardly straighten out during the forward beat, do not reach further anteriad than about the level of the fifth pereaeopod. The third and fourth pereaeopods actively help in swimming.

The current systems become simpler when the Amphipod is swimming. In specimens glued back downwards to the floor of a petri dish the currents become, in the straight swimming position, roughly parallel to the long axis of the body. When swimming fast, the specimen continuously enters undisturbed water in front.

3. The branchiae and the respiratory current
The arrangement of the branchiae in a double row flanking the ventral groove ensures a maximum benefit from the pleopod current. In the resting position, when the pleopod flagella beat into the groove between them, the branchiae are in uninterrupted vibration. This may result in better internal circulation and also improved contact with the current. In the straightened out, swimming position, when the anterior swing of the pleopods does not reach the bottom of the ventral groove, the branchiae do not vibrate. On the other hand, the ventral groove becomes more open to the water through which the animal moves so that the surface of the branchiae is continuously being bathed by fresh water. Thus, the peculiar Amphipod device of a deep ventral groove in combination with a strong pleopod current is most effec-
The amphipod functional model

Fig. 2. Scanning electron micrograph showing arrangement of oostegites in female Gammarus angulosus Rathke with egg-filled marsupium.

tive for maintaining a good aeration of the branchiae even if this result is achieved in different ways in the resting and in the swimming positions.

There may exist an adaptive connexion between the beating of the pleopods and the number of branchiae. In Amphipods, there are normally 5 pairs of branchiae, attached to the coxae of the pereaeopods 2–6. As noted above, the forward beat of the pleopods in the resting position reaches approximately to the level of the branchiae of the second pair of gnathopods. This, in combination with the normally greater bulk of the second gnathopod, projected forwards in the resting position, may provide a mechanical explanation for the absence of branchiae from the first gnathopods. At the other end of the series the seventh pereopod pair also lacks branchiae. In the resting position the basal part of this last pereopod pair comes to lie within the action radius not of the flexible first pleopod flagella but of the much stouter and less flexible peduncle. It seems reasonable to presume that a pair of branchiae on the last pereaeopods would impede pleopod action, and that may be a reason, again mechanical, for their absence.

Mechanical difficulties of the kind described above do not exist in forms where the branchial epipodites assume their normal lateral position. In Lophogastrida, such lateral branchiae are present also on the last pereopod.

The position of the Amphipod branchiae on what appears to be the medial side of the coxa has been difficult to understand (cf. Siewing 1956) and to my knowledge no satisfactory explanation has been given. In fact, however, the matter is quite simple. What happens is that during embryonic development, at a stage when articulations begin to form in the anterior pairs of pereaeopods and the branchial rudiments are already large, a broad fold forms laterally on the proximal part of the coxa. This fold grows downwards past the distal part of the coxa, and at the time of hatching it covers also a large part of the basis of pereaeopods 1–4 and of the branchiae of pereaeopods 2–4. This process is one of the essential features in the formation of the Amphipod ventral groove. It can be followed in detail in figs. 22–26 in the account of the embryology of Gammarus pulex given by Weygoldt (1958) and my own observations of embryos of the same species have given identical results. Thus, the morphologically distal part of the coxa projects from the medial central region of the coxal fold as a short process, articulating with the basis and carrying the branchia and, in the female, the oostegite. As shown by adult morphology of a wide range of families this situation is typical of all Amphipoda Gammairidae.

Nothing of this kind happens in the pereaeopods 5–7. There, the coxa is broad but much shorter than in the anterior legs and the attachment of the basis to its distal edge shows that it is not folded.

4. The oostegites and the respiratory current

Oostegites are normally present in 5 pairs in Amphipoda on the same pereaeopods that carry branchiae. Giesbrecht (1913) and Siewing (1936) indicated the possibility that oostegites are really modified epipodites. There seems to be a good deal to say in favour of such an interpretation. Thus, in Gammarus pulex, the mutual position of branchiae and oostegites corresponds very well to that of the two epipodial branchiae of Anaspides (Snodgrass 1952; Siewing 1956).

The Amphipod oostegites do not form a closed marsupium, on the contrary, between the oostegites there are rather large gaps covered only by the fringing setae (cf. Fig. 2 here and figure of G. pulex in Schellenberg 1942).

In the curled-up resting position the tips of the pleopods beat upon the marsupium of the ovigerous female, and the mechanical disturbance caused in this way may help to improve water circulation within the marsupium.

5. Antennal chemoreception and the respiratory current

There is now much definite evidence available in support of the traditional view that both pairs of antennae are important in crustacean chemoreception. Experimental and ultrastructural investigations have shown this to be the case also in Amphipods (Dahl et al. 1970; Dahl 1970, 1973, 1975).

From the description of the current systems given above, it is evident that the currents coming from in front and from above favour antennular and antennar chemoreception in the resting Gammarus pulex (Fig. 1). As mentioned above, the antennulae of the resting G. pulex are directed anterodorsally and rather widely diverging in their distal parts, while the shorter and less flexible antennae are directed antero-ventrally and not diverging to nearly the same extent. This means that the antennular flagella are kept in an area of comparatively slow water movement and mainly exposed to the low-velocity currents drawn in from above. The antennar flagella, on the other hand, are exposed to the swift anterior current. These currents are likely to bring in chemosensory information from distances several times the body length of the specimen. This may explain the rather strong concentration of

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presumably chemosensory setae on the antennal flagellum of
G. pulex. and although it is still an open question whether
the calceoli are directly involved in chemoreception (Dahl
1975) it is a point of interest that in the Gammarus group of
genera the calceoli, when present, are to be found on the
antennal flagellum.

When the animal is swimming, differences in the degree of
exposure to the surrounding water disappear, for the anterior
part of the animal the whole time comes into contact with
water undisturbed by its own pleopod current. The position
of the two pairs of antennae is more or less the same in the
swimming and resting positions. The antennulary flagellum is
much longer than the antennary flagellum and well provided
with chemosensory hairs along the whole of its length. There­
fore, the relative chemosensory importance of the antennulae
probably increases when swimming. It should be noted that
the lobus olfactorius, the main association centre, for the
information coming in from the antennulae, is well developed in
Gammarus (Gräber 1933) but that the same applies to the
tritocerebral centres, which serve the antennae.

Little seems to be known concerning the normal position
and degree of exposure of the antennae in other Amphipods.
Something can, however, be said about the Lysianassidae.
Here the antennulae as a rule are a good deal stouter than the
antennae, and often shorter. Sometimes the flagellum of the
antenna is longer than that of the antennula and in various
genera there exists a varying degree of sexual dimorphism,
the flagellum of the male antenna being longer than that of
the female. There is often a notable concentration of long
sensory hairs on the ventral side of the proximal articles of the
antennulary flagellum.

The current system set up by a resting Lysianassid, e.g.
Tmetonyx cicada (O. Fabricius), although not studied in
detail, seems to be generally comparable to that found in
Gammarus. Both in the resting and the swimming position
many Lysianassids (species of Tmetonyx, Orchestomene and
Eurythenes) keep the antennulae straight and directed for­
wards or slightly depressed, while at least in Eurythenes
where the antennary flagella are rather long, the antennae
curve upwards and outwards (information from unpublished
deep-sea photographs by Dr R. R. Hessler). Thus, with
respect to the mutual position of the two pairs of antennae
the situation is rather the reverse of that found in Gammarus.

It is obvious that the sensory hairs on the ventral side of
the antennulary flagellum are very well placed in relation to
the anterior current created by pleopod beating in the resting
position and that also in the swimming position their situa­
tion is favourable.

6. The significance of deviating structural plans and habits

The general structural plan described above for Gammarus
recurs with comparatively small modifications in most gam­
marid families, and it may not be too bold to presume that
the basic functional pattern is also similar. Some forms which
deviate from the normal morphological pattern are of interest
in this connexion.

Most tube-building families conform in most basic features
to the Gammarus pattern (e.g. Ampeliscidae, Isaeidae). In
the Corophiids, however, the ventral groove tends to disap­
pear, and it may be significant that all the three major
elements contributing to it, viz. the coxae of P 1–P 4, the
bases of P 5–P 7 and the pleura of pleon segments 1–3, are all
materially reduced in size. The pleopods, on the other hand,
are well developed. Presumably the wall of the tube helps to
concentrate the current set up by the pleopods in such a way
that branchiae and marsupium are well aerated in the ab­sence of a ventral groove of the normal shape.

Reductions of a similar type are even more notable in the
Podoceridae (Fig. 4). The behaviour of the genus Dulichia
was studied by Schellenberg (1942) and Enequist (1949) who
found that specimens of D. monacantha Metzger and D. por­
recta (Bate) cling to algae and hydroids by means of their
powerful P 5–P 7. The cephalon and the mesosome are kept
straight in a position resembling that characteristic of Cap­
rellids ("Bereitschaftsstellung", Wetzel 1932) with both pairs
of antennae spread out to catch particles carried by water
currents. Enequist (i.c.) on the basis of aquarium observa­
tions classifies the Dulichia species as detritus feeders. How­
ever, each one of 11 sectioned specimens of D. porrecta
from the Öresund besides small quantities of detritus, dia­
toms, and occasional algal fragments contained remains of
crustaceans, probably at least partly calanoids, which thus
under normal conditions may constitute the main food item,
although Dulichia, like many other amphipods, may be rather
flexible with respect to its choice of food. In any case the
high incidence of what seems to be at least predominantly
planktonic Crustacea indicates a considerable degree of water
movement. In the virtual absence of a ventral groove of the
usual type such water movement may be more or less suffi­
cient for respiration and brood care in the slender-bodied
Dulichia. Considering the morphology and the normal pos­
ture it seems unlikely that the pleopods, although well devel­
oped, are of any greater importance in respiration. On the
other hand, the Dulichia swim well (Enequist i.c.), which
implies that one of the functions of the pleopods is retained.

The Caprellidea (Fig. 5) with a more or less complete
reduction of the pleon are still more definitely adapted for a
mode of life of the type described above for Dulichia. Lacking
pleopods they are entirely dependent on water movement
for respiration and, on the whole, also for feeding. Their
narrow and cylindrical body with exposed branchiae and
marsupium can be regarded as adapted for this mode of life.

The supralittoral and terrestrial species of the family Tali­
tridae provide other interesting aspects of adaptation. Tal­i
trids retain a ventral groove of the normal type. The supra­
littoral forms of genera like Talitrus, Orchestia, and Talor­
chestia have normal pleopods. They are often submerged,
and below water the respiratory current system functions
on the whole along the same lines as in Gammarus. As shown
by Dahl (1946), a species like Orchestia gammarella may
live submerged for weeks and can swim for very long periods.
In air, however, pleopod action is suspended, and in truly
terrestrial forms partial pleopod reduction often sets in.
Although Talitrids live in air where oxygen content is high
and the danger of desiccation great, their branchiae are
I have not had opportunity to study the relevance of the results reported above to the question of Gammarid-Hyperiid relationships. On the other hand they appear to throw some new light on the organization and possibly the derivation of the other two suborders, the Caprellidea and the Ingolfiellidea.

As pointed out above the Caprellidea appear to be adapted to a type of sessile life in which the pleopod current has lost its importance and been replaced by a reliance upon the movements of the surrounding water. The Caprellids cling to objects by means of the two or three posterior pairs of strong peraeopods. All parts behind the mesosome have lost their original functions and become partly or more or less completely reduced (other Caprellids and Cyamids).

Secondarily a new method of swimming by means of alternate bending and stretching of the body has developed (Schellenberg 1942).

It is of particular interest in this connexion that not only the pleopods and the pleura of the three anterior pleon segments have disappeared but also the more anterior specializations connected with the pleopod current, viz. the posterior expansions of the bases of $P_5-P_7$ and the coxal folds of $P_1-P_4$. All that remains of the mesosome is a narrow, elongate, more or less cylindrical body, carrying 4 to 7 pairs of peraeopods, some of them with branchiae, and in the female a short marsupium. This organization has thus been adapted to its mode of life as a result of the loss of a whole
complex of functional systems. The narrow and cylindrical body provides a relationship between surface and volume which should be advantageous from the point of view of respiration.

The definition of the suborder Caprellidea, then, must be based almost exclusively on negative characteristics, on the loss of features present in its presumed ancestor. The only positive characteristic being the fusion of the first free mesosome segment with the cephalon. The functional significance of this fusion is unknown, and under these circumstances its systematic importance is difficult to evaluate.

As early as in 1903 Hansen pointed out that the separation of the Caprellidea from the Gammaridea is not very important from a "strictly scientific point of view, but it is certainly very practical, and may therefore be accepted". Calman (1909), Reibisch (1927), Ruffo (1951), and Barnard (1969) all more or less explicitly agree with Hansen. To the morphological arguments of the authors mentioned can be added the functional ones reported here, which, by giving what appears to be a coherent explanation of the reductive processes, seem to detract further weight from the reasons for maintaining a separation. However, it seems preferable to let a possible revision of the higher systematics of the Amphipoda comprise the whole order. Therefore, it also appears justified at present to maintain the suborder Caprellidea if only for the practical reasons quoted by Hansen, which do indeed seem to carry more weight than the systematic ones.

Concerning the Ingolfiellidea Hansen (1903), while admitting that a new taxon should be established in the first place as an analogy to the Caprellidea, advanced four arguments for its separation from the Gammaridea. These were the presence of separate "eye-lobes", the partly reduced state of the pleopods, and, less important, the shape of the mandibular and gnathopodal setae. Among these Ruffo (1951) regarded only the reduction of the pleopods as significant but added as further diagnostic features the reduction of the coxal and epimeral plates and the subcylindrical shape of the body.

Siewing (1963) after examining the internal anatomy of the small species Ingolfiella ruffoi Siewing and the only large species, I. leleupi Ruffo (Fig. 6), added a number of features which he considered to support the view that the Ingolfiellidea assume an isolated position within the Amphipoda. He mentions the presence of outgrowths from the central nervous system particularly evident in the small species but indicated also in the large one, further the abbreviation of the heart in I. ruffoi as compared with I. leleupi, the elongation of the stomodeal stomach in both species, the position of the germ layer in the gonads, especially in I. ruffoi, and, in agreement with Ruffo, the elongate and slender body shape.

With respect to the relationships between the small, interstitial I. ruffoi and the large I. leleupi, living in pools in a Central African cave, Siewing (1963) finds no objections to the presumption that I. leleupi represents the less advanced evolutionary stage, which may have to be regarded as ancestral.

All the known species of Ingolfiella, the sole genus of the suborder, are either marine interstitial or troglobiontic. They have a large vertical range, from the deep sea to caves 1900 m above sea level. They appear to be represented in all oceans and in inland waters at least in Europe and Africa. Only I. leleupi attains a comparatively large size, up to 14.5 mm. All the other known species are small with a body length of 2.5 mm or less. Spooner (1960) who described a new interstitial species, I. britannica, from the English Channel and had the opportunity of watching it alive, noted that the specimens moved among the sand-grains by means of wriggling movements. Uropod setal combs were used for cleaning the gnathopods.

Concerning the presumed diagnostic features quoted by the various authors I agree with Ruffo that the mandibular and gnathopodal characters mentioned by Hansen cannot be regarded as important. Nor could the compound dactyl of gnathopod 1 and 2 used by Barnard (1969) in his suborder key be given any higher systematic value, despite its usefulness in that particular connexion. A trend in the same direction occurs in various amphipods (Paradalisca, males of certain Aoridae and Corophiidae). Hansen, Ruffo, and Siewing were unanimous in accepting the reduction of the pleopods and the elongation and subcylindrical shape of the body as features of diagnostic importance. Apparently the mainly interstitial Ingolfiella species do not swim (Spooner 1960) and owing to their small size and slender body respiration should offer no great problem. Thus, owing to adaptations to an interstitial habitat the pleopod current is no longer essential. This is perhaps the probable reason for the far-reaching even if not complete reduction of the pleopods. At least in I. leleupi, of which species I have had occasion to study sectioned material, all intrinsic and extrinsic pleopod musculature seems, however, to be completely reduced. Apart from the fact that it lives in subterranean pools, Ruffo even uses the expression "lac". nothing is known about the ecology of I. leleupi. A reduction of pleopods is unusual in species living in larger bodies of subterranean waters (cf. e.g. Niphargus, Crangonyx, Hadzia) as distinct from really interstitial forms. It hardly supports the suggestion by Siewing (1963) that I. leleupi is less advanced, perhaps even ancestral to, the interstitial type of species within the genus.

Considering what has been said above concerning the close correlation between the pleopod current and certain morphological features, it is only logical that in Ingolfiella the coxal and epimeral plates should be reduced and that the posterior expansions of P5–P7 should disappear. The general body shape only follows the normal pattern of adaptation to the interstitial habitat in becoming elongate and subcylindrical (Remane 1940, 1951; Delamare Deboutville 1960).

The outgrowths from the central nervous system observed by Siewing especially in I. ruffoi need not be very important from a systematic point of view. Parallel phenomena can be seen in the Mystacocarida (Dahl 1952) especially in the suboesophageal ganglia. Generally speaking, in small Crustacea, the central nervous system comes to occupy a proportionally very large part of the interior space, a fact which can easily be verified in any small or larval form. It appears as if the CNS is too complicated an apparatus to permit unlimited re-
duction in size. The production of outgrowths, as in *I. ruffoi* and *Derochbotcriius salutaris* Dahl, is one way to make use of available space and need not have any deeper significance. Like Siewing I have studied the situation in *I. leleupi* and I agree that in that larger species, too, there exists a certain tendency to produce outgrowths. But it is not very pronounced and most notable in the suboesophageal region where space seems to be rather limited.

The elongation of the stomodaeal stomach is very striking indeed, but it is not unique. I have found it also in *Orchomene* (Orchomenopsis) *excavata* (Chevreux), an otherwise typical carrion-feeding deep-sea Lysianassid. There it is even more remarkable, for the pylorus lies almost at the posterior end of the mesosome. This is obviously an adaptation to the need of consuming and storing large quantities of meat. The feeding habits of *Ingolfiella* are unknown apart from the fact that I have observed considerable quantities of coarse detritus in the intestine of *I. leleupi*. It does not appear justified to regard an elongate stomodaeal stomach as a diagnostic feature of high validity and certainly not as a criterion at the suborder level.

Concerning the two other features of internal anatomy specially mentioned by Siewing, viz. the length of the heart and the extension of the germ epithelium, these are of undoubted interest in comparing the small *I. ruffoi* with the large *I. leleupi*. Thus for the interrelationships within the genus, *I. leleupi* does not appear justified to regard an elongate stomodaeal stomach as a diagnostic feature of high validity and certainly not as a criterion at the suborder level.

As in the case of the Caprellidea, there seems to remain in the end only one diagnostic morphological feature, the separate "eye-lobe". Its functional significance is unknown, and it contains no dioptric and apparently no nervuous elements. Its location, however, corresponds well with that of the lobate rudiment of the compound eye in *Gammarus* (cf. Weygoldt 1958).

In summing up I agree with Siewing (1963) that the derivation of the Ingolfiellidea has been independent of that of the Caprellidea. On the other hand, the arguments for retaining the Ingolfiellidea as a separate suborder are, in my opinion, no stronger than in the case of the Caprellidea, rather they appear weaker. The Ingolfiellidea are essentially Gammaridean in their basic plan, with the single exception of the existence of an "eye-lobe" in some but not all species (Ruffo 1951). Their presumed diagnostic features are due to the reduction of the pleopods, to other adaptations to their habitat, or to reduction in size.

It is interesting in this connection to note that another genus, sharing the interstitial habits of at least most *Ingolfiella* species, viz. *Bogidiella* (Fig. 7) displays a number of the characteristics of *Ingolfiella* although in less extreme form. In *Bogidiella*, too, we find a tendency towards pleopod reduction. The endopod is either completely lacking or much smaller than the exopod, which has lost the typical multi-articulate flagelliform appearance, and the whole pleopod is very sparsely setose. Those pleopods are certainly not suited to producing the effective current of the typical Gamma-ridean. It is not surprising then that in the *Bogidiella* species coxal and epimeral plates are strikingly small and the bases of P5-P7 hardly expanded. The body is long and slender. It is not difficult to derive an *Ingolfiella*-like form from a *Bogidiella* by means of a few further evolutionary steps in the same direction.

As in the case of the Caprellidea I do not at present recommend any definite action concerning the taxonomic status of the suborder Ingolfiellidea, but I find that the arguments which have presented themselves as a consequence of the present approach should be taken into account in connection with a future more general revision of Amphipod systematics.

### 7.2. The Amphipod model and Peracaridan evolution

It is obvious that the formation of the ventral groove and utilization of the pleopod current are key points in Amphipod organization and mode of life. We have no fossil record to indicate how this characteristically Amphipod model system evolved. There exist no pre-Tertiary Amphipod fossils, and the earliest known forms, from Upper Eocene or Lower Oligocene Baltic amber are of the normal modern type (Hessler 1969; Hurley 1973). Earlier evolution, probably of small marine forms with delicate cuticles seems to have left no traces. The last statement applies in fact to all Peracarida. The only actual indication of the time-scale of their early evolution is provided by a Phreatoicid isopod described by Schram (1970) from the Pennsylvanian of North America. This would seem to suggest a first radiation of the superorder hardly later than the Mid-Paleozoic.

The present-day distribution of the interstitial fauna of marine littoral sands provides some evidence which may indirectly support this view. The interstitial sand fauna which, generally speaking, has great difficulty in spreading over large open seas (Remane 1951; Delamare Deboutteville 1960) contains e.g. Peracarid genera with a very wide, even world-wide distribution. This applies to *Ingolfiella*, *Bogidiella*, and various Isopod genera. Consideration of the interstitial marine fauna as a whole led Delamare Deboutteville (l.c.) to conclude that the colonization of the marine littoral sands by a fauna much resembling the present one "est anterieure à la séparation définitive des grandes masses continentales". Indirect evidence of this kind should always be treated with caution but coupled with the fossil record quoted above it at least tends to place Peracarid origin and radiation earlier than has generally been supposed.

The relationships between Amphipods and other Peracarida remain enigmatic. Both Siewing (1956) and Fryer (1964) placed the Amphipoda as an early branch near the root of the superorder and not far from the Lophogastrida. shown by Siewing (l.c.) to retain many primitive features, especially in their internal anatomy, and therefore of great interest to discussions of Peracarid evolution. Despite the presumed position of the Amphipoda near the root of the Peracarid tree, the systematic position of the Amphipoda within the superorder has, during the last century, been given much less attention than that of most other Peracaridan groups.

The most characteristic general feature of Amphipod morphology is the marked concentration of external func-
tional systems to the ventral side. This concentration is certainly connected with the dependence upon the pleopod current for a variety of functions, as described above.

One probable consequence of the ventral concentration is the loss of the pereapod exopods. It is difficult to see any role for these exopods in the Amphipod functional system. This is so both with respect to the four anterior pereapods where the deep coxal folds normally cover at least most of the basis and where the presence of an exopod would obviously cause mechanical difficulties, and with respect to the three posterior pairs where the elongation and expansion of the bases would create other problems. Above all, exopods seem to be made superfluous by the pleopod current which serves both respiration and locomotion in a very effective way. Nor would exopods be of any use to alimentation in the Amphipod model.

The ventral concentration results in the dorsal and lateral sides forming a vault-shaped structure, the more lateral parts of which become more or less vertical in relation to the long axis of the body. This puts a certain emphasis upon the pleural parts, an emphasis generally more notable in the more posterior than in the anterior segments. It is a fact, very often neglected in drawings of amphipods that at least in many forms (e.g. representatives of the families Gammaridae and Talitridae) the pleura of the four anterior mesosome segments project a short distance past the bases of the coxae. This is interesting because in carapace-bearing forms the pleura of the segments covered by the carapace are always reduced, and it raises the question whether Amphipods and other Peracarida with well-developed anterior pleura really could be derived from carapace-bearing ancestors as generally presumed (cf. Dahl 1976). On the whole, it is difficult to see any function for a carapace in an Amphipod model where respiratory organs are concentrated ventrally and well protected laterally.

It should be noted that Amphipods, despite the ventral concentration, retain the broad Peracarid sternum and the lateral attachment of the pereapods. This meets the need of space for the marsupium and is, moreover, a requirement for the function of the pleopods in the way described above.

Among the Peracarida a ventral concentration of structures and functions has taken place also in the Cumacea but in an entirely different manner leading also to an entirely different result.

The results recorded above may help to give a better understanding of Amphipod structure and function but they do not bring us much nearer an understanding of the relationships between Amphipods and other Peracarida. Despite the ancient features retained by the Lophogastrida it appears improbable that Peracarid ancestors were pelagic forms. The present organization of the Lophogastrida may have been the result of an early adaptation to the oceanic pelagic, permitting the retention of primitive traits (Dahl 1976). It seems more probable that the early Peracarida were benthic or perhaps rather epibenthic and that waves of adaptive radiation may have led to an extension of their range into all kinds of marine and later also into lacustrine and even terrestrial habitats. In the almost complete absence of relevant fossils, only a considerable accumulation of new information concerning the interaction between structure and function in various groups can provide a basis for an improved understanding of the evolution of the Peracarida and the position of the Amphipoda among them.

References