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A REVISION OF THE FAMILY PODOCERIDAE (AMPHIPODA: GAMMARIDEA)

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SUMMARY

The podocerid genera *Cyrtophium, Icilius, Laetmatophilus, Leipsuropus,* and *Podocerus* have been investigated to elucidate their generic characters. Four of these genera are very closely related, with only minor differences between them; *Icilius* has proved to be non-corophioidean and is removed from Podoceridae. The family Iciliidae, and a new podocerid genus *Styloxenodice,* to accommodate *Xenodice macrophthalma,* are diagnosed. Four groups of genera are recognised within Podoceridae, and are given subfamilial status: Podocerinae, Xenodicinae, Neoxenodicinae, and Dulichiinae. It is suggested that Podoceridae is derived from a basic corophioidean *Gammaropsis*-type ancestor through an ancestral form that would have been similar to *Styloxenodice.*

INTRODUCTION

The gammaridean amphipod family Podoceridae is diagnosed as a corophioidean having a depressed urosome with the first urosomite more than twice as long as the second. As currently constituted the family contains eleven genera, all of which are marine. The relationships of the six cold water, slender bodied genera (*Dulichia, Dulichiopsis, Dyopedos, Neoxenodice, Paradulichia,* and *Xenodice*) were discussed recently by Laubitz (1977, 1979). At that time it was concluded that there was insufficient information available on the five flat-bodied, warm water genera (*Cyrtophium, Icilius, Laetmatophilus, Leipsuropus,* and *Podocerus*) to include them in the discussion.

I have recently had the opportunity to study specimens of all five of these warm water genera. The result of this investigation made it apparent that the whole family needed to be reassessed, and an attempt needed to be made to determine the relationships between the genera currently placed therein.

OBSERVATIONS

The five depressed-bodied genera *(Cyrtophium, Icilius, Laetmatophilus, Leipsuropus,* and *Podocerus)* classically assigned to the family Podoceridae are superficially very similar. However, study of specimens of these genera produced rather startling results. It quickly became apparent that the genus *Icilius* not only was not a podocerid, but also that it was not even a member of the superfamily Corophioidea. As a result of this discovery it seemed essential to reconsider the characters of all of the genera assigned to Podoceridae and to see whether they could be considered a unique group forming a single family unit, and could be linked together in a logical evolutionary sequence.

The characters of *Icilius* are such that this genus cannot be placed in any of the currently accepted gammaridean families, so that the family Iciliidae (Icilidae of Dana) must be reinstated. Characters that specifically bar the Iciliidae from being included in the Corophioidea are: antenna 1 with short peduncular articles; gnathopods slender, simple, and alike; coxal plate 4 excavate; coxal gill on pereopod 7; uropod 3 well developed, inner ramus much longer than outer; telson entire, not fleshy.

TAXONOMY

Iciliidae Dana 1849, **emend.**

Body strongly depressed, may be posteriorly processiferous, urosomite 1 elongate. Antenna 1 shorter than antenna 2, both with well-developed flagellum, accessory flagellum minute. Buccal mass small. Upper lip notched, lobes symmetrical. Lower lip, inner lobes developed. Mandibular molar and incisor strong, palp slender with segment 2 the longest. Maxilla 1 inner plate setose, outer plate with 11 apical spines. Maxilla 2 inner plate setose. Maxilliped plates and palp strong. Coxal plates small, processiferous, overlapping slightly; 4th slightly excavate, 5–7 anterolobate. Gnathopods 1 and 2 similar, small, simple. Pereopods 5–7 similar, 7 slightly the longest, bases with processiferous posterodistal lobes. Coxal gills simple, on pereopods 2–7; brood plates large, with simple marginal setae, on 2–5. Pleopods with medially broadened peduncles, long rami. Rami of uropods 1 and 2 linear, unequal, apically spinose; uropod 3 inner ramus lanceolate, outer ramus linear, unsegmented, about as long as peduncle. Telson not fleshy, short and entire, pointed ovate to bluntly rounded.

Remarks. The relationship of the family to the superfamilies proposed by Bousfield (1979) is obscured by its adaptive characters. Iciliidae appears to be closest to the family Paramphithoidae on the basis of the acuminate coxae, vestigial accessory flagellum, combination of mouthparts, and simple gnathopods, and must therefore be assigned to the Eusiroidea. The atypical appearance and characters of Iciliidae are presumed to be the result of adaptation to an as yet unknown way of life.

Icilius Dana 1849

Head flat, rostrum small, eyes round and lateral. Accessory flagellum one-segmented. Maxilliped palp 4 falcate. Coxae 1 and 2 small; 3 and 4 larger, posteroventrally acuminate; 5 large and anteroventrally acuminate. Gnathopods 1 and 2 simple, with articles 5 and 6 elongate and setose. Pereopods 3 and 4 strongly grasping; 5-7 without palmar development. Epimeral plates with pointed posteroventral corners. Pleopod peduncle may be very greatly broadened. Urosomite 1 more than twice as long as urosomite 2. Uropods 1 and 2, peduncle depressed, outer ramus shorter than inner; uropod 3 inner ramus longer than outer, lanceolate, and strongly spinose apically.

Type species. *Icilius ovalis* Dana 1852.

Remarks: There are currently four species in this genus; material of *I. australis* Haswell and *I. danae* Stebbing was examined. The extremely depressed body, simple gnathopods, and subchelate pereopods 3 and 4 make this genus easily recognisable. Stebbing (1910) discussed the four species, which he had previously treated as one (1906), remarking that the incomplete state of all collected specimens made a final decision on their status impossible. Current knowledge of this genus is no further advanced than in Stebbing's day.

Podoceridae Leach 1814, emend. Stebbing 1906. **Revised.**

Diagnosis. Corophioidea with urosomite 1 more than twice as long as urosomite 2, and uropod 3 reduced or absent. Body variable, either broadly depressed or slender cylindrical, occasionally processiferous; pereonites and urosomites variously fused; abdomen flexed beneath pereon. Antenna 1 and 2 elongate, setose, flagellum shorter than peduncle, accessory flagellum present or absent. Upper lip bilobed; mandibular molar strong, palp variable; maxilla 1 inner plate strongly setose to absent, outer plate with 9 (rarely 8 or 10) apical spines; maxilla 2 inner plate setose, sometimes with facial setae; maxilliped plates and palp strong. Coxal plates small, usually discontiguous; coxal gills simple, 3-6 pairs; brood plates 3-4 pairs. Gnathopods variable, 2 the larger, subchelate. Pereopods 3 and 4 sometimes glandular. Pleopods with slender peduncle. Urosomite 1 at least more than twice as long as urosomite 2; uropod 1 normal; uropod 2 biramous, vestigial or absent; uropod 3 uniramous, vestigial or absent. Telson fleshy, short, entire.

Podocerinae n. subfam.

Diagnosis. Podoceridae with strongly depressed body, head anterodorsally elongate, coxal plates equal to or longer than pereonites. Antenna 1 shorter than antenna 2; accessory flagellum 1-segmented or absent. Mandibular palp heavy, strongly setose; maxilla 1 inner plate reduced and non-setose, or absent. Pereopods 3-7 essentially similar, non-glandular, without propodal palm; gills on pereopods 2-6. Pleosome not greatly reduced; urosomite 1 shorter than or equal to pleosomites 2+3.

Podocerus Leach 1814.

Pereon depressed, with 5-7 segments; urosome of 3 segments. Accessory flagellum present; maxilla 1 inner plate reduced and non-setose or absent, outer plate with 9 spines; maxilla 2 without facial setae; maxilliped palp 4 blunt; brood plates on pereopods 2-4 or 2-5; uropod 2 biramous, uropod 3 without rami.

Remarks. There are about 30 species currently recognised in this genus, which is badly in need of revision. Specimens of seven species were examined: *P. andamanensis* (Giles), *P. brasiliensis* (Dana), *P. chelonophilus* (Chevreux & Guerne), *P. cristatus* (Thomson), *P. inconspicuus* (Stebbing), *P. septemcarinatus* Schellenberg, and *P. variegatus* Leach. The genus shows variation in the degree of fusion of the posterior pereonites; the brood plate on pereonite 5, when present, is very small.

Laetmatophilus Bruzelius 1859.

Pereon depressed, with 5-7 segments; urosome of 2 segments. Accessory flagellum absent; epistome produced; maxilla 1 inner plate greatly reduced, non-setose, outer plate with 9 spines; maxilla 2 without facial setae; maxilliped palp 4 blunt; gnathopod 2 of female nearly as large as that of male; brood plates on pereopods 2-4; uropod 2 without rami, uropod 3 absent.

Remarks. There are currently seven species in this genus. Specimens of four species were examined: *L. durbanensis* K. Barnard, *L. leptocheir* K. Barnard, *L. purus* Stebbing, and *L. tuberculatus* Bruzelius (includes *L. armatus*). The tendency to fusion of the posterior pereonites appears to be non-specific, some specimens of *L. durbanensis* having pereonites 6 and 7 fused while others did not.

Cyrtophium Dana 1852.

Pereon depressed, with 7 segments; urosome of 3 segments. Accessory flagellum absent; epistome produced; maxilla 1 inner plate absent, outer plate with 9 spines; maxilla 2 without facial setae; maxilliped palp 4 blunt; gnathopod 2 of female nearly as large as that of male; brood plates on pereopods 2-4; uropod 2 biramous, uropod 3 without rami.

Remarks. There are two currently accepted species in this genus; material of *C. minutum* Haswell was examined.

Leipsuropus Stebbing 1899.

Pereon depressed with segments 6 and 7 incompletely fused; urosome of 3 segments. Accessory flagellum absent; epistome produced; maxilla 1 inner plate absent, outer plate with 8 spines; maxilla 2 without facial setae; maxilliped palp 4 blunt; gnathopod 2 of female nearly as large as that of male; brood plates on pereopods 2-4; uropod 2 absent, uropod 3 without rami.

Remarks: This genus had been considered to be of doubtful status (e.g., Barnard, 1969) because of the peculiar conformation of the urosome as described in the literature. However, information received from J.L. Barnard (personal communication) and subsequent study of specimens of the single species in the genus, *L. parasiticus* (Haswell), have supported the absence of any sign of uropod 2, and thus the correctness of the original description.

Xenodicinae n. subfam.

Diagnosis. Podoceridae with cylindrical body, head anterodorsally elongate, coxal plates equal to or shorter than pereonites. Antenna 1 longer than antenna 2; accessory flagellum comparatively long, 4- or 5-segmented. Mandibular palp heavy, strongly setose; maxilla 1 inner plate strongly setose. Pereopods 3-7 essentially similar, increasing in length posteriorly, non-glandular, without propodal palm; gills on pereopods 2-6. Pleosome not reduced; urosomite 1 shorter than pleosomites 2+3.

Xenodice Boeck 1870.

Pereon cylindrical, with 7 segments; urosome of 3 segments. Maxilla 1 outer plate with 9 spines; maxilla 2 without facial setae; maxilliped palp 4 blunt; brood plates on pereopods 2-5; gnathopods 1 and 2 subequal in male and female; uropod 2 biramous, uropod 3 without rami.

Remarks. Specimens of the single species in this genus, *X. frauenfeldti* Boeck, were examined.

Styloxenodice n. gen.

Diagnosis. Xenodicinae with uropod 3 with single, styliform ramus; anterior coxal plates closely contiguous; maxilla 1 outer plate with 10 apical spines; maxilla 2 with facial setae.

Description. Pereon cylindrical, with 7 segments; urosome of 3 segments. Maxilla 1 outer plate with 10 spines; maxilla 2 inner plate with facial setae; maxilliped palp 4 blunt; brood plates on pereopods 2-5; gnathopods 1 and 2 subequal in male and female; uropod 2 biramous, uropod 3 uniramous.

Type species. *Xenodice macrophthalma* Schiecke 1976.

Etymology: The genus name is based on the Greek word 'stylos', which describes the uropod 3 ramus, plus *Xenodice.*

Remarks. The well-developed uropod 3 ramus is the most obvious character distinguishing *Styloxenodice* from *Xenodice;* other characters include the long accessory flagellum, closely contiguous coxae, 10 spines on maxilla 1 outer plate, and facial setae on maxilla 2. I have not seen any specimens of the single species in this genus, and the diagnosis is based on Schiecke's (1976) very complete description of that species.

Neoxenodicinae n. subfam.

Diagnosis. Podoceridae with cylindrical body having greatly elongated anterior pereonites, head anterodorsally elongate, coxal plates equal to or shorter than pereonites. Antenna 1 longer than antenna 2; accessory flagellum 1-segmented. Mandibular palp heavy, strongly setose; maxilla 1 inner plate reduced, non-setose. Pereopods 3-7 dissimilar, non-glandular, without propodal palm; gills on pereopods 2-4. Pleosome reduced; urosomite 1 shorter than pleosomites 2+3.

Neoxenodice Schellenberg 1926.

Pereon cylindrical, with 7 segments; urosome of 3 segments. Maxilla 1 outer plate with 9 spines; maxilla 2 without facial setae; maxilliped palp 4 blunt; brood plates on pereopods 2-4; pereopods 3 and 4 very small; uropod 2 biramous, uropod 3 without rami.

Remarks. The genus comprises two species; specimens of *N. cryophile* Lowry were examined.

Dulichiinae n. subfam.

Diagnosis. Podoceridae with cylindrical body, head triangular to rectangular, coxal plates equal to or shorter than pereonites. Antenna 1 longer than antenna 2; accessory flagellum short, 1- to 5-segmented. Mandibular palp slender, sparsely setose; maxilla 1 inner plate reduced, non-setose. Pereopods 3-7 dissimilar, 3 and 4 glandular, 5-7 with or without propodal palm; gills on pereopods 2–5 or 3-5. Pleosome reduced; urosomite 1 longer than or much longer than pleosomites 2+3.

Remarks. Laubitz (1979) stated that the subfamily is confined to the colder waters of the northern hemisphere. During examination of collections from Australian waters, I came across one specimen of a *Dulichiopsis* species from Bass Strait (841 m) and many specimens of a *Dulichia* species from Western Port, Victoria. The zoogeographical status of Dulichiinae is thus less clear than was previously thought.

Dulichia Kroyer 1845, redefined Laubitz 1977.

Head triangular; pereon cylindrical, with 6 segments; urosome of 2 segments, urosomite 1 longer than pleosome. Accessory flagellum with 3 articles; maxilla 1 outer plate with 9 spines; maxilla 2 inner plate with facial setae; maxilliped palp 4 blunt; gills on pereopods 2-5, brood plates on 2-4; pereopods 5-7 without propodal palm; uropod 2 biramous, uropod 3 absent.

Remarks. There are five species in the genus; for material examined see Laubitz, 1977.

Dulichiopsis Laubitz 1977.

Head rectangular; pereon cylindrical, with 6 segments; urosome of 2 segments, urosomite 1 longer than pleosomites 2+3. Accessory flagellum with 3-4 articles; maxilla 1 outer plate with 9 spines; maxilla 2 inner plate with facial setae; maxilliped palp 4 falcate; gills on pereopods 2-5, brood plates on 2–4; pereopods 5-7 with propodal palm; uropod 2 biramous, uropod 3 absent.

Remarks. There are six species in the genus; for material examined see Laubitz, 1977.

Dyopedos Bate 1857.

Head triangular to rectangular; pereon cylindrical, with 6 segments; urosome of 2 segments, urosomite 1 longer than pleosomites 2+3. Accessory flagellum with 1-4 articles; maxilla 1 outer plate with 9 spines; maxilla 2 without facial setae; maxilliped palp 4 blunt; gills on pereopods 3-5, brood plates on 2-4; pereopods 5-7 without propodal palm; uropod 2 biramous, uropod 3 absent.

Remarks. There are nine species in the genus; for material examined see Laubitz, 1977.

Paradulichia Boeck 1870.

Head rectangular; pereon cylindrical, with 6 segments; urosome of 2 segments, urosomite 1 longer than pleosome. Accessory flagellum with 3-5 articles; maxilla 1 outer plate with 9 spines; maxilla 2 without facial setae; gills on pereopods 2-5, brood plates on 2-4; gnathopods 1 and 2 subequal in male and female; pereopods 5-7 without propodal palm; uropod 2 minute, with 1 or no rami, uropod 3 absent.

Remarks. There is one species in the genus; for material examined see Laubitz, 1977.

Key to the subfamilies and genera of Podoceridae

1. Head triangular or rectangular; mandibular palp slender, sparsely setose; pereopods 3 and 4 glangular; gills on pereonites 2-5 or 3p5; urosomite 1 longer than pleosomites 2+3. **(Dulichiinae)** 4
— Head anterodorsally elongate; mandibular palp heavy, strongly setose; pereopods 3 and 4 not glandular; gills on pereonites 2-4 or 2-6; urosomite 1 no longer than pleosomites 2+3 2
2. Pereon strongly depressed; antenna 1 shorter than antenna 2; pereopods 3-7 similar; gills on pereonites 2-6; maxilla 1 inner plate reduced or absent. **(Podocerinae)** 7
— Pereon cylindrical; antenna 1 longer than antenna 2; pereopods 3-7 of increasing length; if gills present on pereonites 2-6 then maxilla 1 inner plate setose 3
3. Pereopods 3 and 4 greatly reduced in size; anterior pereonites elongate, pleosome reduced; accessory flagellum short, of 1 article; gills on pereonites 2-4; maxilla 1 inner plate reduced ..... **Neoxenodicinae**
— Pereopods 3 and 4 not reduced in size; anterior pereonites not elongate, pleosome well developed; accessory flagellum long, of 4-5 articles; gills on pereonites 2-6; maxilla 1 inner plate well developed and setose **(Xenodicinae)** 10
4. Uropod 1 normal, uropod 2 rudimentary; gnathopods 1 and 2 of equal size in male and female ..... *Paradulichia*
— Uropods 1 and 2 normal; gnathopods 1 and 2 of equal size in female, grossly unequal in male 5
5. Gills on pereonites 3-5; basis of pereopods 3 and 4 greatly expanded; maxilla 2 inner plate without facial setae ..... *Dyopedos*
— Gills on pereonites 2-5; basis of pereopods 3 and 4 not greatly expanded; maxilla 2 inner plate with facial setae 6
6. Eyes large, strongly convex; pereopods 5-7 without propodal palm; maxilliped palp with short stout terminal article ..... *Dulichia*
— Eyes abnormal, poorly developed, or absent; pereopods 5-7 with propodal palm; maxilliped palp with long slender dactyl ..... *Dulichiopsis*
7. Urosome with only two urosomites, uropod 2 without rami ..... *Laetmatophilus*
— Urosome with three urosomites, uropod 2 either biramous or absent 8
8. Uropod 2 absent, uropod 3 present; maxilla 1 outer plate with eight apical spines ..... *Leipsuropus*
— Uropod 2 biramous, uropod 3 present; maxilla 1 outer plate with nine apical spines 9
9. Accessory flagellum 1-segmented ..... *Podocerus*
— Accessory flagellum absent ..... *Cyrtophium*

10. Uropod 3 uniramous; maxilla 1 outer plate with ten apical spines; maxilla 2 inner plate with facial setae ..... *Styloxenodice*

— Uropod 3 without rami; maxilla 1 outer plate with nine apical spines; maxilla 2 inner plate without setae ..... *Xenodice*

DISCUSSION

The four warm-water depressed-bodied podocerid genera (Group 1 in Table 1) appear to be closely similar and are herein designated subfamily Podocerinae. They share the following characters: there is a tendency for the posterior two or three pereonites to become fused; antenna 2 becomes large and heavy, with loss of setation, in mature specimens; pereopods 3 and 4 are non-glandular; the female gnathopod 2 is comparatively large, particularly in *Cyrtophium, Laetmatophilus,* and *Leipsuropus,* where the propodus approximates the male form; also in these three genera, and occasionally in *Podocerus,* the epistome is produced into a point. Within the group the evolutionary trend is toward: exaggerated flattening of the body; loss of urosomites, accessory flagellum, and maxilla 1 inner plate; and development of the female gnathopod 2 with its large propodus and elongated, distally extended article 4. Distribution is temperate-cosmopolitan to southern subtropical.

The slender-bodied podocerid genera were discussed recently by Laubitz (1979), and it was then suggested that *Xenodice macrophthalma* Schiecke might not belong in that genus. Further study of the characters of *Xenodice* indicates that *X. macrophthalma* should indeed be placed in a new genus, *Styloxenodice,* as defined above. This genus is close to *Xenodice* but differs in several basic characters, such as the well-developed uropod 3 ramus and the facial setal row on the inner plate of maxilla 2. Both *Xenodice* and *Styloxenodice,* subfamily Xenodicinae (Group 2 in Table 1), differ from other podocerids in having: a long multisegmented flagellum on antenna 1 and 2, with a long accessory flagellum (i.e. longer than the basal two segments of the primary flagellum); a well-developed, strongly setose inner plate on maxilla 1; slender oostegites; and a comparatively strongly developed pleosome. These genera show the greatest number of primitive characters and the closest resemblance to other corophioids. Currently-known distribution is limited to the northeastern Atlantic and the Mediterranean.

The *Dulichia* group (Table 1, Group 4) of cylindrical-bodied genera (Laubitz, 1979), the Dulichiinae, is characterised by head shape, slender mandibular palp, glandular pereopods, very long urosomite 1, and climbing behaviour. The distributional limits of this group are currently uncertain.

Neoxenodice (Table 1, Group 3) differs from the other podocerids by its greatly elongated anterior pereonites, very small anterior coxal plates, gills on pereonites 2-4, and minute pereopods 3 and 4, and is assigned to the subfamily Neoxenodicinae. The genus is morphologically distinct and geographically isolated from the other cylindrical podocerids, having a subantarctic-antarctic distribution.

Laubitz (1979) concluded that the family Podoceridae contained three, and probably four, groups of genera, based on morphology, behaviour, and distribution. It has been shown above that the family can indeed be divided into four groups of different body types (Figure 1), a division supported by analysis of specific morphological characters (Table 1, Figure 2). These four groups are considered to be sufficiently distinctive that they are herein designated subfamilies.

Apart from their corophioidean characters, and the elongation of urosomite 1 and reduction of uropod 3, the podocerid genera share other characters to a greater or lesser degree. Gnathopod 2 much larger than gnathopod 1 in male (Groups 1, 3, 4) and female (Groups 1, 3); pereopods 3 and 4 reduced in size (Groups 3, 4); pereonite 1 short and oriented toward the head (Groups 1, 4); some pereonites elongated (Groups 3, 4); maxilla 1 inner plate reduced and non-setose, or lost (Groups 1, 3, 4); number of gills (Groups 3, 4) and brood plates (Groups 1, 3, 4) reduced.

The main diagnostic character of the Podoceridae has always been the elongate urosomite 1. The presence of this long urosomite in *Icilius,* which has had to be removed from the family, shows that it is not an exclusive taxonomic character; unfortunately, its functional significance is unknown. Since the long urosomite 1 thus cannot be of major taxonomic significance, one must question whether Podoceridae is not just a heterogeneous collection of subfamilies sharing a convergent character. Xenodicinae, for example, would appear to fit quite well into Aoridae (of Bousfield, 1973) along with *Neohela* and *Unciola;* however, Aoridae as defined has such excluding characters as gnathopod 1 larger than gnathopod 2, mandibular palp tapering, and pereopods 3 and 4 glandular. Similarly, Podocerinae is strongly reminiscent of *Jassa* in Ischyroceridae; but the similar, non-glandular pereopods, non-setose maxilla 1 inner plate, and reduced uropods of Podocerinae militate against a close relationship.

TABLE 1. Morphological characters of the Podoceridae, with the genera arranged by subfamily

4. Dulichiinae; 3. Neoxenodicinae; 2. Xenodicinae; 1. Podocerinae

+ = present; 0 = not developed; – = absent

4				3	2		1				
Dulichiopsis	Dulichia	Dyopedos	Paradulichia	Neoxenodice	Xenodice	Styloxenodice	Podocerus	Laetmatophilus	Cyrtophium	Leipsuropus	
triangular-rectangular				← recessed →							Head shape
← slender →				← expanded →							Md. palp
+	+	+	+	–	–	–	–	–	–	–	Pereopod glands
← U1 at least > P2+3 →				← U1 shorter or equal P2+3 →							Urosome: Pleosome
2-5	2-5	3-5	2-5	2-4	2-6	2-6	2-6	2-6	2-6	2-6	Coxal gills[1]
6	6	6	6	7	7	7	5-7	5-7	7	(6)	No. of pereonites
2	2	2	2	3	3	3	3	2	3	3	No. of urosomites
–	–	–	–	0	0	1	0	–	0	0	Uropod 3 rami
← cylindrical →							← flat →				Body shape
← Antenna 1 > Antenna 2 →							Antenna 1 < Antenna 2				Antennae
0	0	0	0	0	0	0	0-+	+	+	+	Epistome produced
← reduced →				setose			reduced-absent		absent		Mx. 1 inner plate
3-4	3	1-4	3-5	1	long 4-5	long 4-5	1	–	–	–	Acc. flag. segments
2>>1	2>>1	2>>1	2≥1	2>>1	2≥1	2≥1	2>>1	2>>1	2>>1	2>>1	♂ Gn. 2: Gn. 1
2>1	2≥1	2≥1	2≥1	2>>1	2≥1	2≥1	2>1	2>>1	2>>1	2>>1	♀ Gn. 2: Gn. 1
2-4	2-4	2-4	2-4	2-4	2-5	2-5	2-(5)	2-4	2-4	2-4	Brood plates[1]
S-E	S-E	S-E	S-E	S	E-S	E	E	E	E-L	E-L	Coxa size[2]
← strongly dissimilar →					of increasing length		← similar →				Pereopods 3-7
2	2	2	0-1	2	2	2	2	0	2	–	Uropod 2 rami
9	9	9	9	9	9	10	9	9	9	8	Mx. 1 apical spines
+	+	–	–	–	–	+	–	–	–	–	Mx. 2 facial setae
falcate	← blunt →										Mxpd. palp 4
+	0	0	0	0	0	0	0	0	0	0	Pereopod 5-7 palm

1. Pereopods on which coxal gills and brood plates are present.
2. S-shorter than, E-equal to, L-longer than, pereonite.

Despite the differences between the subfamilies, the podocerids do have a number of shared, although not necessarily exclusive, characters other than the urosomite 1. Antenna 1 and 2 are strongly developed; gnathopod 2 is dominant, usually strongly; the coxae are reduced, frequently greatly; and, most significant, uropod 3 (and sometimes uropod 2) is reduced or lost. The structure of the head is hard to interpret, but appears to have been caused by the posteriad deepening of the inferior antennal sinus to create on the one hand the 'recessed' head (defined by Barnard, 1973) of Groups 1, 2, and 3, and

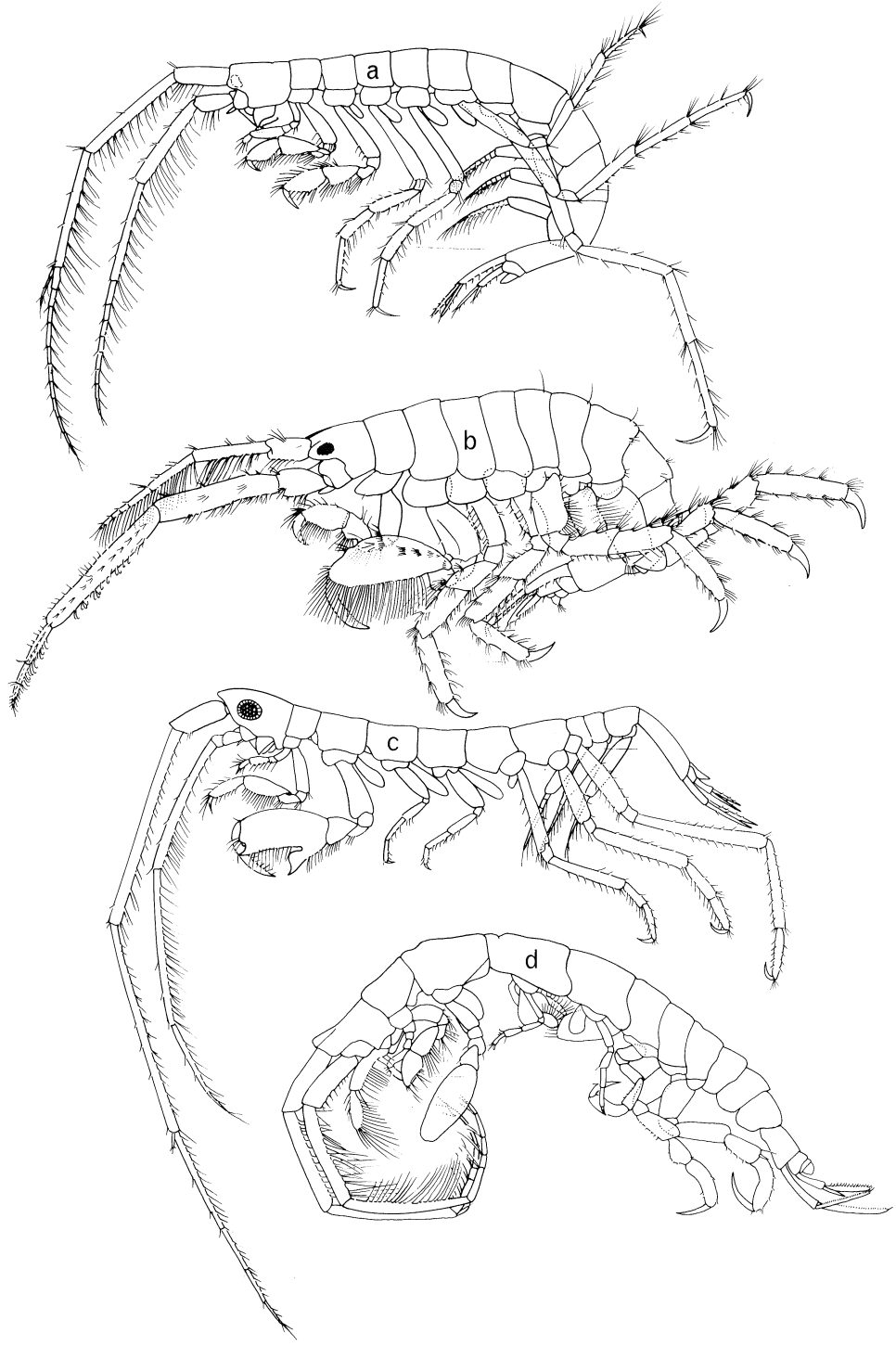

Fig. 1. Gross morphology of the four subfamilies of Podoceridae. **a** Xenodicinae. **b** Podocerinae. **c** Dulichiinae. **d** Neoxenodicinae. (Redrawn from Baranard, Sars)

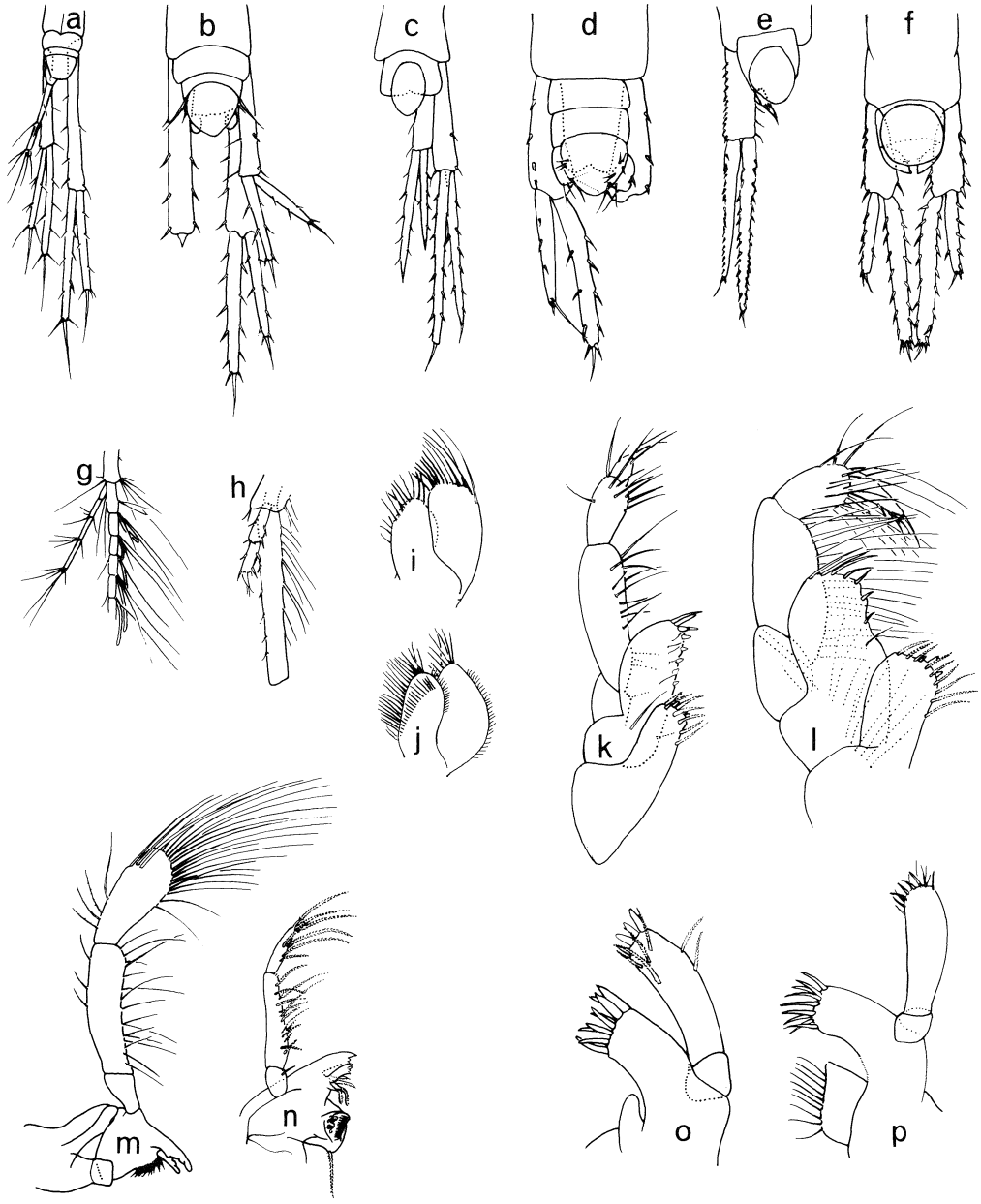

Fig. 2. Posterior urosome of **a** *Styloxenodice,* **b** *Xenodice,* **c** *Dulichia,* **d** *Leipsuropus,* **e** *Paradulichia,* **f** *Laetmatophilus.* Accessory flagellum of **g** *Styloxenodice,* **h** *Dulichia.* Maxilla 2 of **i** *Podocerus,* **j** *Styloxenodice.* Maxilliped of **k** *Neoxenodice,* **l** *Dulichiopsis.* Mandible of **m** *Styloxenodice,* **n** *Dulichia.* Maxilla 1 of **o** *Styloxenodice,* **p** *Neoxenodice.* (Redrawn from Barnard, Laubitz, Lowry, Sars, Schiecke, Stebbing; d original.)

on the other hand the even more exaggerated distinctive head of Group 4. Certainly, the combination of characters exhibited by the podocerids is unique, and although both the Xenodicinae (with long flagella and strong pleosome) and the Neoxenodicinae (with almost caprellidean gross morphology) are atypical, they can be assumed to show the two extremes of degree of evolutionary development within the family.

The highly adaptive characters of most podocerid genera tend to obscure their relationship with and evolution from other corophioids. However, the combined characters of gnathopod 2 dominance, long article 3 on antenna 1, and recessed head all point to a *Gammaropsis* type ancestor (Barnard, 1973). Assuming that the family originated in the temperate Pacific (Laubitz, 1979), distribution (north-eastern Atlantic) and characters (e.g., loss of glandular pereopods) make *Styloxenodice* itself an unlikely ancestral podocerid. One can, however, visualise a *Styloxenodice*-like form, still retaining glandular pereopods, from which all four generic groups could have been derived. While it is possible, perhaps even probable, that Podoceridae is polyphyletic, it would at present be premature to subdivide it at the family level when we have limited knowledge of many aspects of the constituent genera and species. The genera currently accepted within the family are all sufficiently distinctive to be readily recognisable, by their combination of characters, as Podoceridae.

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