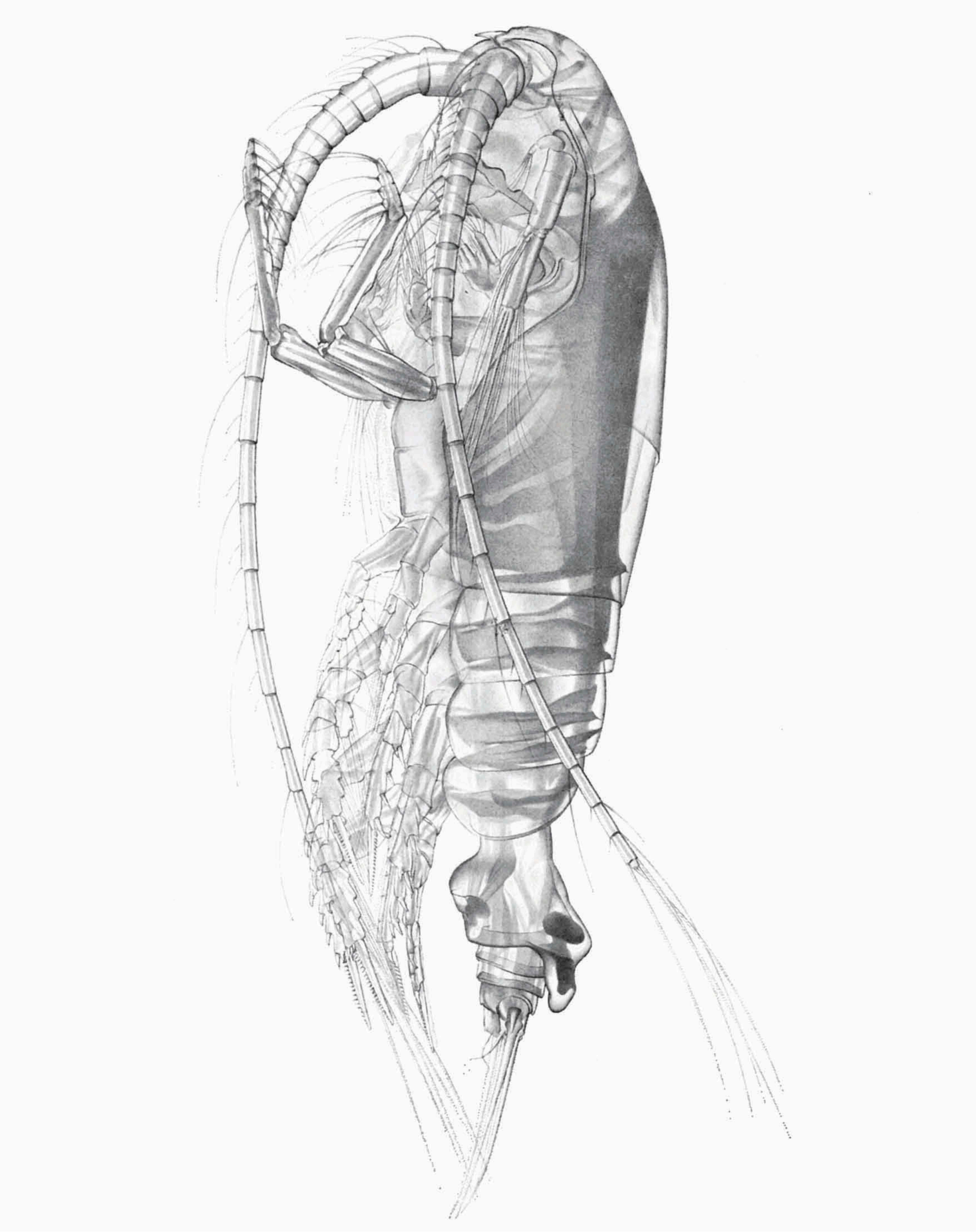

Euchirella messinensis (Claus, 1863), habit of ♀ from "Dana" Exped. sta. 4119ˣ, in left ventro-lateral view. Drawn in pencil and washed ink by H. Heijn.

A TAXONOMIC REVIEW OF THE GENUS *EUCHIRELLA* GIESBRECHT, 1888 (COPEPODA, CALANOIDA).

II. THE TYPE-SPECIES, *EUCHIRELLA MESSINENSIS* (CLAUS, 1863). A. THE FEMALE OF F. TYPICA

by

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With frontispiece, 17 text-figures, and 23 plates

CONTENTS

SUMMARY

The present paper comprises Part II-A of a revision of *Euchirella* Giesbrecht, 1888. The female from the type area is described in extenso, providing many new details on copepod external anatomy, the significance of which is discussed. Reference is made to Part I (Von Vaupel Klein, in press a) for a general introduction and for an outline of this series of publications.

INTRODUCTION

Since Claus' (1863) original description, *Euchirella messinensis* has been described from the Mediterranean, from various localities in the Atlantic Ocean, and from the Caribbean area (e.g., Giesbrecht, 1892; With, 1915; Sars, 1924-25; Wilson, 1932; Rose, 1933; Vervoort, 1952, 1963; Owre & Foyo, 1967; Park, 1976). The single female reported by Esterly (1905) represents the only documented Pacific record of the species.

Though descriptions of authors are suitable for identification purposes, many details are usually omitted or described in such general terms as to be applicable to at least more than one species of *Euchirella*. Besides, due to the current, superficial state of knowledge of calanoid morphology (see Discussion), several structures have been interpreted incorrectly. All this results in none of the available descriptions being sufficiently detailed to be of use in a study on phylogenetic relationships within the genus. The present author, then, is of the opinion that calanoid taxonomy should by now be lifted above the basic inventory stage. Three tools are indispensable for such a purpose: the first is a general, world-wide repertory of the Calanoida (or, even better, Copepoda) described so far; it has been provided by Razouls (1981) for marine and brackish water pelagic copepods, while B. Dussart c.s. (Les Eyzies, France), are preparing a similar compilation of freshwater species. Secondly, a complete bibliography is urgently needed: W. Vervoort (Leiden, The Netherlands) is preparing it. The third is a uniform type of description, founded on a thorough knowledge of calanoid morphology: I hope the present paper may be of use in achieving this tool.

The paper at hand comprises a detailed description of the female of *Euchirella messinensis* from the type area. Part II-B (Von Vaupel Klein, in prep.) will deal with a description of the male; with technical data: diagnoses, full synonymy, measurements, etymology, vertical distribution, etc.; and with zoogeography, including the Atlantic as well as the Indo-Pacific regions. The last topic deserves special attention, since in dealing with *E. messinensis* s.s. the status of the closely related form described as *E. indica* by Vervoort (1949) should be satisfactorily established at the same time. Contradictory opinions exist as to the specific or (infra-)subspecific status of f. *indica* as is evident from previous records by, e.g., A. Scott (1909), Brodskii (1950), and Wilson (1950), and from subsequent records by Tanaka (1957), Grice & Hulsemann (1967), Tanaka & Omori (1969a, b), and Bradford & Jillett (1980). At this (infra-)specific level descriptions of authors are likewise unsuited to supply a taxonomic solution. In Part II-B, however, *E. indica* will be shown to represent the Indo-Pacific form of *E. messinensis* and will be appointed a subspecific status (Von Vaupel Klein, in prep.).

Reference is made to the General Part (Von Vaupel Klein, in press a) for an outline of the series of papers covering this taxonomic review of *Euchirella*.

Acknowledgements. — The frontispiece of the present paper has been skilfully drawn by Mr. H. Heijn, staff-artist of the Afdeling Systematische Dierkunde (Department of Systematic Zoology) of Leiden University. This study has been supported in part by the Netherlands Organization for the Advancement of Pure Research (Z.W.O.), grant no. 87-31.

MATERIAL AND METHODS

Locality data, preservation and preparation techniques, measurements, abbreviations, etc., are all dealt with in the General Part (Von Vaupel Klein, in press a).

DESCRIPTIVE PART

Euchirella messinensis messinensis (Claus, 1863) s.s.

(figs. 1-16; pls. 1-23)

Restricted synonymy. —
Undina messinensis Claus, 1863: 187-188, pl. 31 figs. 8-17.
Euchirella messinensis, Giesbrecht, 1892: 233, 234, 239, 244, 245, 743, 744, pl. 15 figs. 1, 2, 12, 14-17, 21, 24, pl. 36 figs. 14, 15, 18, 24, 25; Giesbrecht & Schmeil, 1898: 35; Esterly, 1905: 151-152, fig. 18; With, 1915: 122-124, pl. 4 fig. 2, pl. 8 fig. 1, text-fig. 31; Sars, 1924-25: 65-67, pl. 19 figs. 6-13; Wilson, 1932: 56-57, fig. 36; Rose, 1933: 103-104, fig. 76; Massuti & Margalef, 1950: 162, fig. 475; Vervoort, 1952: 3, 4, fig. 1; Furnestin & Giron, 1963: 139, pl. 1 fig. 4, pl. 2 figs. 1-4; Giron, 1963: 362, 365, figs. 3-4; Vervoort, 1963: 134, 136-138; Mazza, 1965: 296-307, figs. 11-19; Mazza, 1966: 1032-1036, figs. 3-5; Owre & Foyo, 1967: 47, figs. 267, 268, 273-275; Tanaka & Omori, 1969a: 51, fig. 6a-e; Von Vaupel Klein, 1972: 506, fig. 4b-c, tabs. 1, 2; Park, 1976: 113-114, fig. 5.

Material examined (type area only). — (Extreme values of total length (in mm) and nos. of females with attached spermatophores (*s*) are given between brackets.) "Dana" Exped. sta. 4119^{v}: 1 ♀; sta. 4119^{x}: 22 ♀♀ (4.60-5.00); sta. 4119^{xii}: 13 ♀♀ (4.60-5.00); sta. 4119^{xx}: 16 ♀♀ (5.00) (1 *s*).

Description of the female. — The following description is based on 52 ♀♀ from "Dana" Exped. sta. 4119 in the Mediterranean, close to the type locality.

Body robust and strongly built, with a well-chitinized integument. Total length ranging from 4.60 to 5.00 mm; greatest width and height of the body 1.35-1.60 and 1.40-1.60 mm, respectively, both occurring approximately at the line of fusion between cephalon and thoracic somite 1. The proportional lengths of cephalothorax and urosome are 79 + 21 = 100, so the length of Ur is contained 3.76 times in that of CTh. The greatest length of the furcal bristles is 1.00 mm.

The cephalothorax (fig. 1a, b) is subcylindrical, oblong-ellipsoid in dorsal view. In lateral aspect the back is almost straight, curving smoothly downward from opposite the oral opening to the frontal part of the head. Anteriorly, the fused C-Th1 complex shows slightly tapering sides which are produced into some shallow curves, while posteriorly the cephalothorax is gradually tapering from Th2 onward. With the exception of the rostral and caudal tips, the cross-section is roughly circular, the largest portion of the circumferential integument being composed of a large, arched tergite connected by a pair of small pleurites to the essentially flat sternite (fig. 2a); dorsal and lateral sclerites are largely fused to form a pleuro-tergite, acting as a single unit.

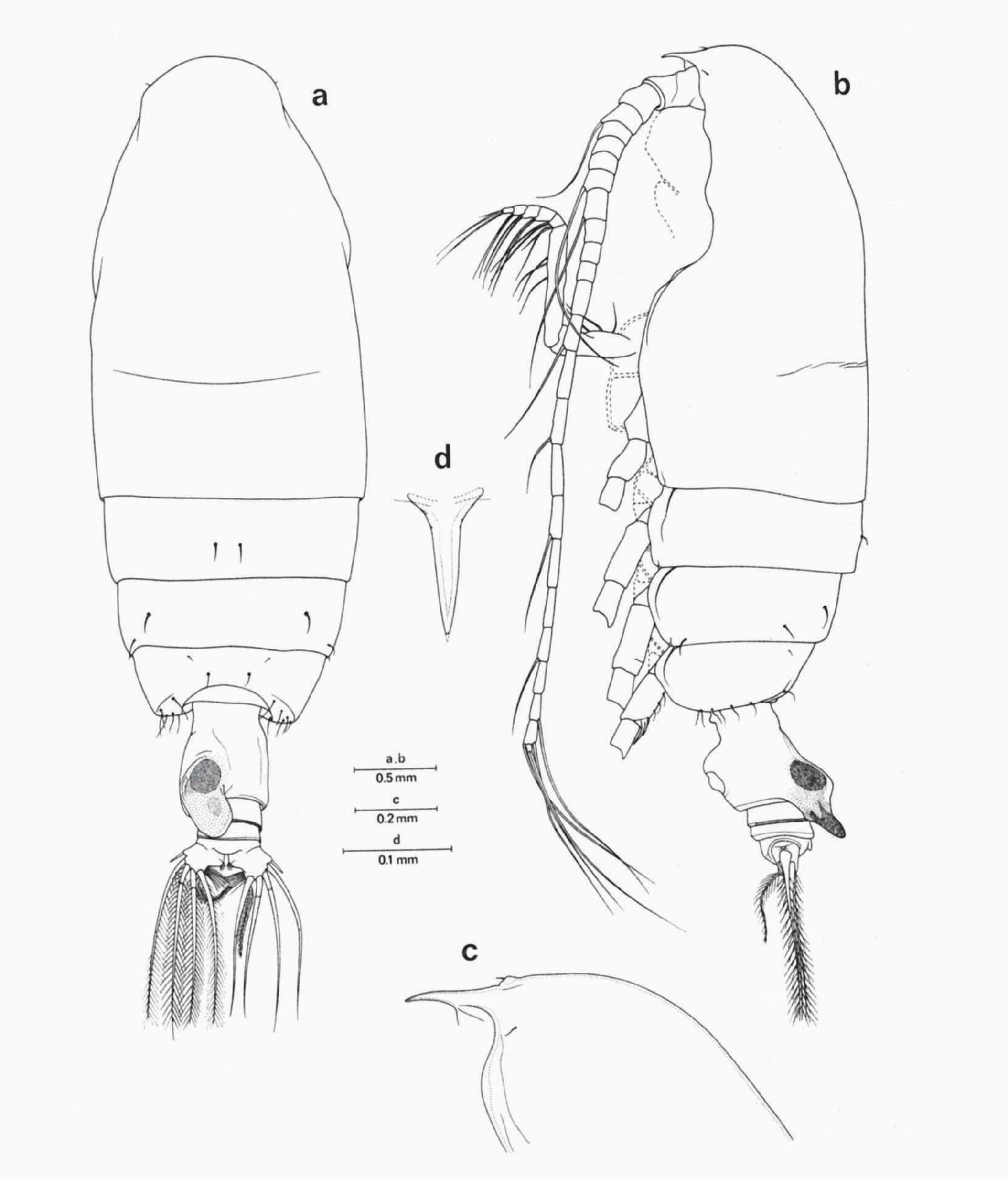

Fig. 1. *Euchirella messinensis* (Claus, 1863), ♀♀ from "Dana" Exped. sta. 4119^x. a, whole specimen in dorsal view; b, lateral view from the left; c, frontal region of head with rostrum, left lateral view; d, rostrum in anterior view.

The head proper (fig. 1c) is smoothly rounded in dorsal as well as in lateral view, no trace of a crest being present; the lateral aspect shows a slightly vaulted frontal part, smoothly merging into the rostrum. This rostrum (fig. 1c, d; pl. 1a) is a heavily chitinized, entire structure, comparatively large and stout, and acutely pointed. It is directed almost straight downward, only its tip showing a faint curve to caudad. The fusion of cephalon and first thoracic somite is almost complete, the line of fusion being faintly visible in dorsal and practically invisible to obsolescent in lateral view; in the latter aspect, it may usually be observed from the dorsal outline downward to approximately two-thirds of the height of the CTh (fig. 1a, b; pl. 1f). The ventral margin of the C-Th1 complex shows some smooth curves in its anterior half and becomes broadly rounded posteriorly (fig. 1b).

The second and third somites of the thorax are free and of subequal length; their ventral margins are broadly rounded. The fourth and the strongly reduced fifth somite are entirely coalesced, a faint line of fusion being discernable just anteriad to the attachment of the urosome (fig. 4a; pl. 9d). The postero-lateral corners of this combined somite are broadly rounded in lateral view and squarish in dorsal aspect, with bluntly rounded-off apices (figs. 1a, b; 4a-c). The pleuro-tergites of Th2, Th3, and Th4+5 sequentially decrease in size thus being able to telescope into the preceding somite's sclerite ring by their anterior edge. The external circumference of this edge is produced into a sturdy ridge, which is slightly weaker middorsally and interrupted at two-fifths of its height (fig. 2b). Ventrally, the ridge curves posteriad, thus marking the anterior part of the former suture between tergite and pleurite; halfway the somite it becomes progressively shallower, to merge eventually into the integument (fig. 2b). The posterior edge of the tergite is not thickened but a ridge is also present along the free caudal and ventral edges of the pleurite, which overhangs the adjacent sternite. The pleural ridge ends rather abruptly anteriorly and the antero-ventral part of the pleurite merges into the sternal sclerites (fig. 2b). It is assumed that the suture between pleurite and sternite is situated mediad to the overhanging pleural ridge but the exact location and nature of this boundary could not be established as yet. The dorsal integument of Th4+5 is steeply depressed, anteriad to the articulation with the urosome. At this site an internal ridge is present which forms the caudalmost insertion of the longitudinal trunk musculature. The ridge is visible in dorsal aspect through the hyaline cuticle of Th4+5 (fig. 4a).

The sternal integument may be considered primarily as one flat plate composed of the (partly) fused sternites of all cephalothoracic somites, bearing large perforations where the appendages are inserted. The sub-

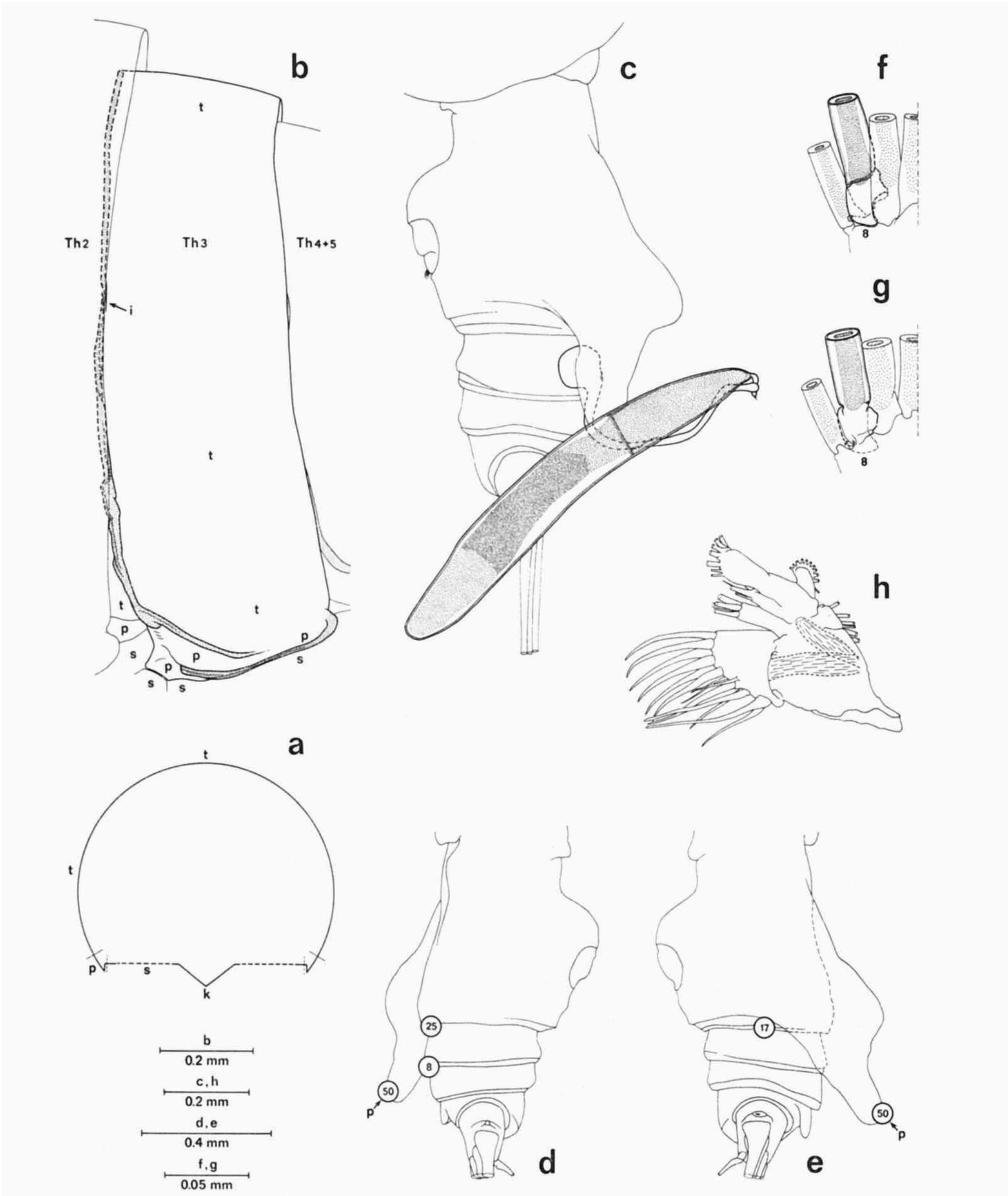

Fig. 2. *Euchirella messinensis* (Claus, 1863), ♀♀ from "Dana" Exped. sta. 4119^{x} and 4119^{xx}. a, schematic transverse section of cephalothorax; b, left lateral view of Th3 showing tracks of chitinous ridges (dotted areas); c, left lateral view of female urosome with attached spermatophore; d-e, urosome in right c.q. left lateral view, showing sites of attachment of spermatophores with the relative incidences in % (N = 12 = 100%); f-g, details of the insertion of the penultimate (8th) seta of the mandibular endopodite, with its supporting pedestal: f, of left mandible, anterior view; g, of right one in posterior aspect; h, semi-schematic drawing of right maxillule in anterior view, showing tracks of large striated muscle for movements of the first inner lobe (arthrite) of Ba1, and for Ba2, respectively. Legends: t = tergum, p = pleuron, s = sternum, k = sternal keel, i = interruption in chitinous ridge.

anterior region is dominated by the oral field (see below), while the posterior part, from the maxillipedal somite onward, is equipped with a series of mid-ventrally protruding keels. The shape of these sternal keels has been indicated by broken lines in fig. 1b. The relative lengths of the somites of the cephalothorax are as follows:

C + Th1		Th2		Th3		Th4+5	
69	+	12	+	10	+	9	= 100

The frontal organ (fig. 1c; pl. 1b, c) consists of a pair of semi-tubular outgrowths, smoothly arising from the extreme anterior integument of the head. Their distal ends are shallowly concave and have a short hair, 30 μm long, in their centre. A small, rounded elevation provided with an elongate pore is situated mid-ventrally to the tubercles. The cuticle of the body is equipped with a diffuse network of integumental organs including slit-shaped glandular pores, hair-, peg-, and pit-sensilla, and circular pores, present either at bilaterally symmetrical sites or along the midline. In a few cases a pit- or peg-sensillum is found in close company with a slit-shaped glandular pore, but this was not observed to be a general rule (17%, with N = 12). The hair-sensilla found on the cephalothorax (table IV) apparently are of two kinds. Judged by their relatively constant shape, the sensilla on C, Th2, and Th3, as well as the dorsal ones on Th4+5, are rather stiff structures with well-chitinized walls. The six to ten caudo-lateral pairs on Th4+5 appear to be more delicate: these do not show one characteristic shape but may be found bent in various directions. The number of the latter sensilla may vary, even on the left and right side of the same specimen; usually nine are found but occasionally six to eight, or even ten hair-sensilla are present. Though these sensilla may easily be damaged, the observed variation in number could only in part be attributed to loss. The arrangement of integumental organs on the dorsal and lateral sclerites of the cephalothorax has been mapped and coded, and is presented in table IV and fig. 13a, b. The sternites have not been studied in detail in the present programme but a few incidental observations have been made, viz., of a pair of slit-shaped glandular pores adjacent to the bases of the antennae, as well as of another such pair situated mediad to the maxillae (fig. 13b).

The oral field (fig. 3; pls. 2-6) is delimited by a large, semi-dome-shaped upper lip and a small, bifid lower lip. The upper lip arises smoothly from the sternal integument; its bulbously rounded antero-medial portion attenuates postero-laterally to form a sturdy, transverse ridge which extends over the

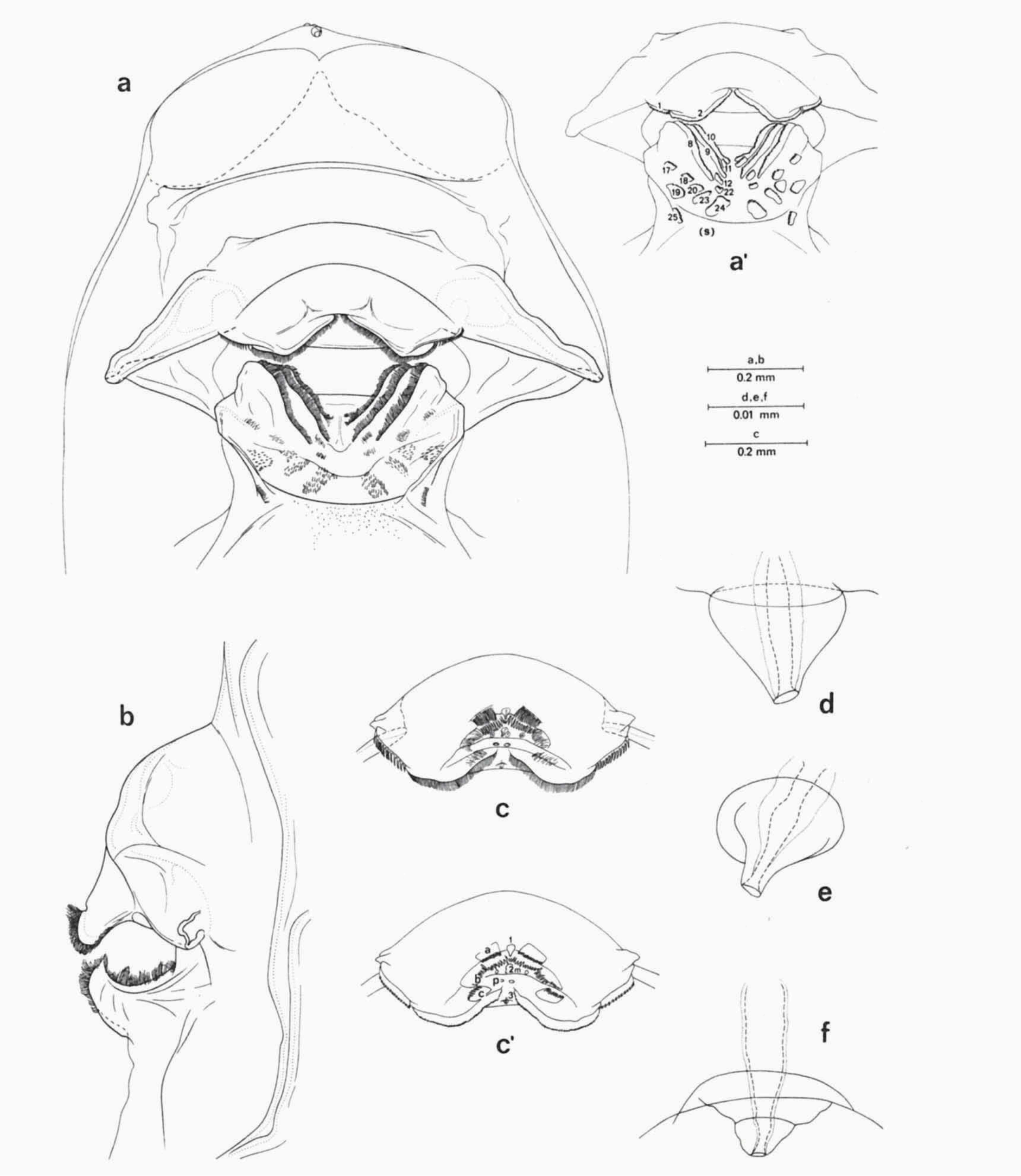

Fig. 3. *Euchirella messinensis* (Claus, 1863), ♀♀ from "Dana" Exped. sta. 4119^x. a, ventral aspect of the oral field, with outline of cephalic region indicated; a', scheme of the same, providing the chaetotaxic code (see also table I); b, left lateral aspect of the oral field; c, central part of the upper lip in ventral view, showing integumental structures of the ventral wall of the oral cavity proper, as visible through the transparent cuticle; c', map of same, presenting chaetotaxic code (cf. table I; patch d not shown), positions of papillae (p) and rows of urn-shaped pores (1-3); d-f, urn-shaped pores 1, 2m, and 3, respectively, as observed under the same conditions as in c.

TABLE I

Chaetotaxy of the oral field of the *Euchirella messinensis* female; see also pls. 2-6 and fig. 3

Code	Situation	Arrangement	Hair/spinule type	Hair/spinule length (μm)
1	upper lip laterad	single row	spinule-like; sharp, curved, slightly flattened, slender	15-20
2	upper lip, mediad	dense, multiple row	hairs; flattened	25-30
3	oral cavity, deepest position	sparsely beset field	spinules; small but acute	3-5
4	oral cavity, intermediate position	single row	spinules; long, slender, smoothly curved, with acute tips	25-30
5	oral cavity, uppermost position	irregular row(s)	spinules; medium sized, slender	10-20
6	oral cavity, posteriad	short, single row	spinules, as in (4), but shorter	10-12
7	lobe of lower lip, antero-mediad	short, single row of about 7 spinules	spinules; very heavy, flattened, smoothly curved, acute	35-50
8, 9, 10	lobe of lower lip, mediad; order from apicalmost (8) to basalmost (10)	three single, long and curved, cascading rows	hairs; slender	25-30
11	lobe of lower lip, adjacent to (10)	short, irregular row	as in (8, 9, 10)	20-25
12	lobe of lower lip, postero-medial position; shifted relative to (8) and (9)	short, irregular row	as in (8, 9, 10)	20
13, 14, 15, 16	lobe of lower lip, antero-medial face; order from apicalmost (13) to basalmost (15) eventually approaching to the "roof" of the oral cavity (16)	four distinct, very densely packed patches	spinules; short, stout, leaf-shaped	5-20

TABLE I (continued)

Code	Situation	Arrangement	Hair/spinule type	Hair/spinule length (μm)
17, 18	lobe of lower lip, postero-laterad; order from distad (17) to proximad (18)	two curved combs, each composed of multiple rows	spinules; curved, slender; of varying size	5-15
19	lobe of lower lip, postero-laterad	patch	spinules; short, acute	2-8
20	lobe of lower lip, postero-mediad	patch	spinules; as in (19), but smaller	1.5-3.5
21	lobe of lower lip, basalmost	long-drawn patch	spinules; minute	c. 1
22	lower lip, sagittal stretch	small patch	spinules; medium-sized, slender	10-12
23	lower lip, near base of lobe	long-drawn patch	spinules; increasing in size from laterad to mediad, curved	4-12
24	lower lip, postero-sagittal position	patch	spinules; as in (23)	4-10
25	lower lip, the very postero-lateral positon	irregular row	spinules; medium-sized, slender	15-22
s	All rows and patches denoted as "s" are regarded as structures of the sternal integument, i.e., not forming part of the oral field. They are composed of a few distinct types of thin hairs. Their composition and arrangement, however, will not be dealt with in detail, here.			
a	ventral wall of oral cavity; outermost position; laterad to midline;	short, contiguous row	fine, hair-like spinules	10-12
b	ditto; intermediate position; all along transverse transect of labrum	long, semicircular row, with irregularities	stout, hair-like spinules	10-12
c	ditto; innermost and lateral position	dense, oval patch	slender, hair-like spinules	10-12
d	ditto; median position between rows 2 and 3 of urn-shaped pores	dense, semicircular patch	short and thick, hair-like spinules of varying size	5-8

entire width of the body. The postero-central part is distinctly set-off from the remainder of the lip and roughly of a semi-circular shape. The free caudal edge of this part is weakly bilobed and fringed with various rows of hairs. Close to the midline, the labrum bears a pair of short, rounded papillae (c. 5 × 8 μm ∅), the exact nature of which could not be established as yet (fig. 3c; pl. 5b). The lower lip, closed-in between the wide proximal parts of the mandibular gnathobases, consists of a largely flattened, semi-circular part of the sternites which bears a pair of blunt, turret-shaped protrusions. The labium and the oral atrium are profusely beset with rows and patches of hairs of different types.

The chaetotaxy of the oral field is characterized, coded, and mapped in table I, fig. 3a, and pls. 2-4, 5a. The groups of hairs c.q. spinules found on the internal face of the labrum have been indicated and coded in fig. 3c and pl. 6. This wall is also equipped with three rows of urn-shaped, apparently glandular, pores (fig. 3c-f; pls. 5c-e, 6). Since no survey of the sternal integumental organs has been made, no coding-system has been worked-out either and these pores have thus been assigned a provisional code. Rows 1 and 3 are composed of a single median pore each (1m and 3m), while row 2 counts three positions: left and right lateral, and medial (2l, 2r, 2m). Normally, all sites are occupied by a single pore but in a few specimens two distinct but contiguous pores were observed in the 2m position (fig. 3c).

Between upper and lower lip there is room for the slender distal parts of the mandibular gnathobases to reach each other in the mid-sagittal plane where the masticatory edges perform their grinding function: the largest, monocuspidate teeth ventralmost, the setiform teeth entering into the oral atrium. To accomodate the mandibles, the adjoining faces of upper and lower lip are strongly arched in lateral aspect (fig. 3b; pl. 2c). The posterior limitation of the oral field is marked by the smoothly rounded sternal surface which runs from between the bases of the maxillules to caudad. These sternites show various scattered patches of integumental hairs.

The urosome (fig. 4a-c; pls. 7, 8a-d) is composed of four free somites and the furcal rami. The fused complex Ur1+2 articulates freely with the cephalothorax. In all somites the dorsal, lateral, and ventral sclerites have coalesced to form a smooth ring. As a whole, the urosome is short, i.e., rostro-caudally compressed. The relative lengths of its components are:

1+2		3		4		5		furca		
52	+	13	+	12	+	8	+	15	=	100

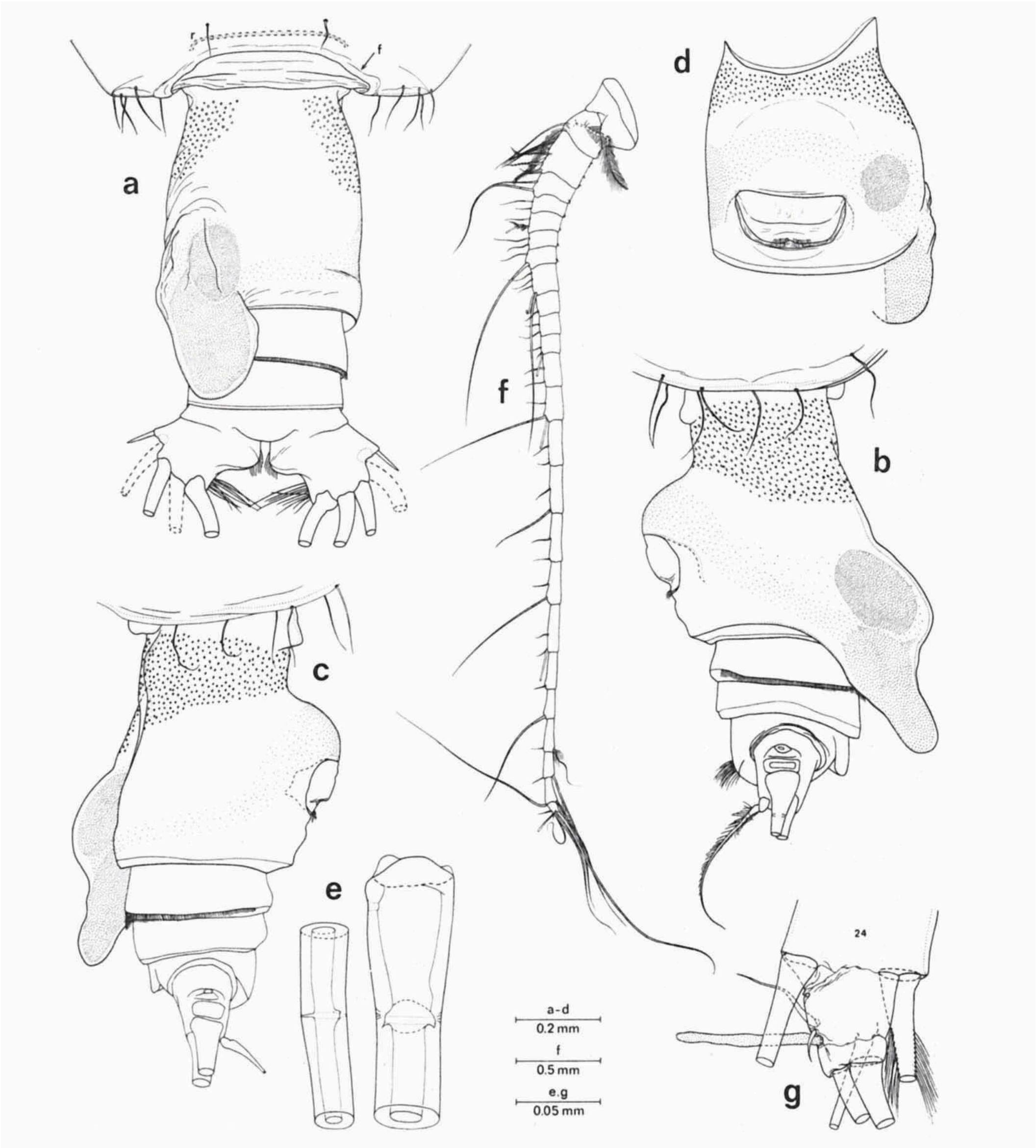

Fig. 4. *Euchirella messinensis* (Claus, 1863), ♀♀ from "Dana" Exped. sta. 4119^{x}. a, posterior part of cephalothorax and urosome in dorsal view; b, do., left lateral view; c, genital somite, right lateral view with outline of rest of urosome indicated; d, genital somite with vulva in ventral view; e, details of breaking planes in large articulating setae of right furcal ramus, in dorsal view: left, medialmost seta with breaking plane halfway its length, right, second seta from laterad, with proximal breaking plane; f, left antennule in lateral view, to show relative lengths of large articulating setae; g, detail of segments 25+26 of left antennule. Legends: r = internal ridge where trunk muscles insert; f = vestigial line of fusion of Th4 and Th5; in figs. a-d, small circles indicate warty areas, while dotted regions indicate internally stored sperm masses.

The genital somite (fig. 4a-d) is strongly asymmetrical, showing a large swelling on its left side. This swelling is produced into a robust dorso-lateral outgrowth, the basal part of which is directed dorso-caudally, followed by a more posteriorly pointing terminal portion; a rather abrupt bend in the outgrowth's dorsal outline marks the site where both parts meet. In dorsal aspect (pl. 8b) the asymmetrical structure appears as a slightly curved, caudo-medially directed hump which covers a large portion of Ur3 and 4, and which reaches most commonly to or even beyond the caudal edge of the latter somite. Place and shape of the outgrowth are highly characteristic for this species. From observations on specimens with filled seminal receptacles, i.e., nearly all adult females, it is clear that both left and right receptacles are situated in the outgrowth, viz., the left receptacle in the anterior elevation, and the originally right receptacle in the posterior part. Both receptacles differ in shape but are of approximately the same size. In fig. 4a-d the distribution of stored sperm in the lumina of the female's reproductive apparatus has been indicated (see also Discussion). The anterior part of the genital somite, rostrad to the genital prominence, shows an almost completely annular field of tiny warts, interrupted only mid-dorsally (fig. 4a-d). The warts are 2-5 μm in diameter, 0-10 μm apart; their shape is roughly circular to ovoid (pl. 10e-f), and their margins are drawn-out into many small points, which gives each wart a stellate outlook. The non-transformed stretch of the caudal edge of the somite is produced into a shallow ridge, not bearing any fringe hairs. The ratio greatest length/greatest width of the somite, excluding its outgrowth, was measured as 1.10.

The ventral outline of the genital somite is broadly rounded. The genital field (fig. 4b-d; pl. 9a, b) is situated on the longer, smoothly sloping face of the genital prominence, posteriad to its apex and bordered caudally by a small, transverse swelling. The vulva is trapezoidal, with the longer parallel side anteriorly. It is covered entirely by the genital operculum, which hinges anteriorly while its remaining sides are free. The surface of the operculum is produced into several ridges and wrinkles; its most prominent structures are: (1) a slightly elevated anterior part with irregular, longitudinal ridges; (2) a strong, transverse ridge halfway its length extending over its medial part, followed by (3) a deep, transverse sulcus; next, (4) a smoothly curved elevation delimits the posterior part of the operculum; this elevation is equipped with (5) a pair of elongate, transverse brushes of short bristles (pl. 9c). The structures (1) to (4) all become shallower laterally, merging via some wrinkles into the essentially flat shape of the operculum. The posterior edge, moreover, is indented medially to leave (6) a small opening. The caudal slit between operculum and sternite gives access to the underlying vulval cavity; here, the fertilization tube of the spermatophore (pl. 9b) may enter to reach the underlying pores. The site of attachment of the spermatophore was studied in 12 specimens. Sites occupied are shown in fig. 2c-e, with the relative incidences indicated. Apparently, position "p" is the preferred site of attachment, occupied in 50% of the cases. The morphology of the spermatophore is dealt with in the description of the male (Von Vaupel Klein, in prep.).

Urosomal somites 3 and 4 are subcylindrical and short, of subequal length. Their caudal edge is produced into a shallow ridge which in Ur3 is fringed with flattened, densely set hairs (c. 30 μm long) dorsally as well as on the sides, its extreme ventral part being smooth; the ridge on somite 4 is completely devoid of fringe hairs; see also fig. 4a, b and pl. 9e. The anal somite (fig. 4a, b) is short and compressed; it bears a broadly rounded anal operculum (pl. 10a, c), which appears slightly vaulted in lateral aspect. The anal opening itself is more or less of an inverted triangular shape (pl. 10c). The posterior part of this somite is bifid, being produced beyond the anal region to bear the furcal rami. This results in a sharply indented ventro-caudal margin (pl. 10a, b); the ventro-medial faces of the bifid part both bear a brush of thin hairs (fig. 4a, b).

The furcal rami (fig. 4a, b; pl. 10d) are fused to the anal somite by the dorso-medial quarter of their circumference (pl. 10a, c); the remaining sector is free. The internal face of each ramus is equipped with a brush of long, stout hairs. There are four large, articulating plumose setae pro ramus; setules are absent only on the proximo-lateral margin of the outermost seta. The plumosity is long and very dense; it has been indicated only schematically in fig. 1a. Modified sites within these setae, referred to as breaking planes, have been indicated in the same figure; these planes are situated proximally in the two intermediate setae, and at approximately one-third the length of the lateral and medial ones (fig. 4e). At the site of such a breaking plane an internal annular sulcus is present in the chitin wall, thus creating a local weakening. The second setae from laterad reach slightly beyond the others, which are subequal in length. A fifth, outermost seta is present laterally, shaped like a short spine. The restricted development of this seta is characteristic at the generic level. Moreover, each ramus is equipped with a short and slender, densely plumose ventro-medial seta (figs. 1a-b, 4b) which projects in a more ventral direction; it reaches about 0.60 the length of the large setae, and it is smoothly curved. Asymmetrical development of setae on the left and right rami was not observed.

Integumental organs of the urosome include slit-shaped glandular pores, tubular pores (pl. 10d), hair-sensilla, and peg-sensilla, which are all mapped

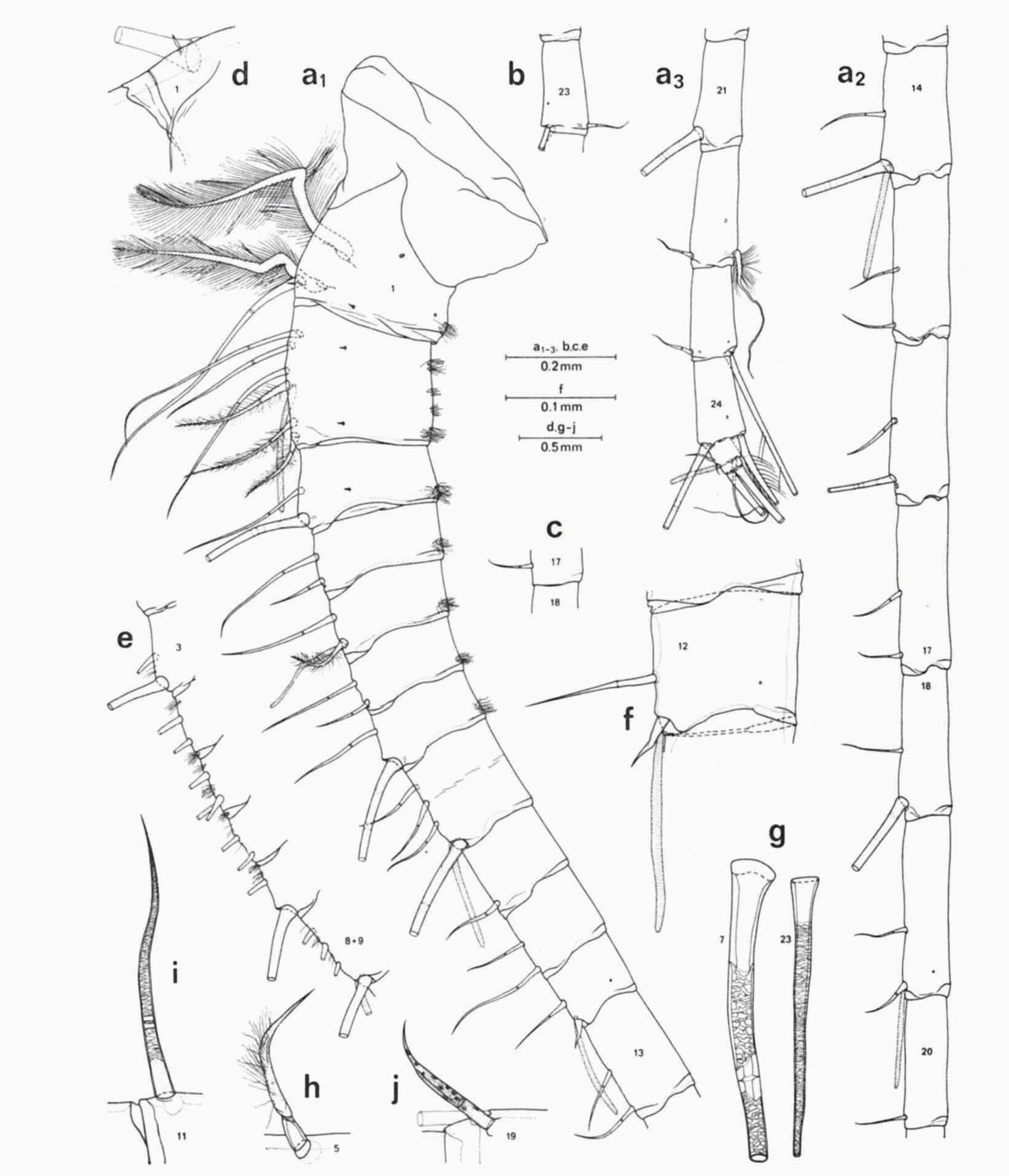

Fig. 5. *Euchirella messinensis* (Claus, 1863), ♀♀ from "Dana" Exped. sta. 4119ˣ. a_{1-3}, left antennule in lateral view, showing shapes of individual segments, arrangement of setae and aesthetascs, as well as the more obvious integumental organs, with segment numbers indicated; b, segment 23 of right antennule, lateral view, showing normal arrangement of integumental organs; c, detail of hinge joint 17/18 of right antennule, medial view; d, antero-distal corner of segment 1 of left antennule, with peg-sensillum;

and coded in fig. 13c-f and table IV. Next, a large pore of irregular shape has been found dorso-caudally on the genital somite of one specimen (pl. 8e).

The antennulae (figs. 4f, $5a_{1-3}$) are comparatively short: when fully stretched backwards they extend beyond the cephalothorax but hardly ever reach the regular posterior edge of the genital somite. They comprise 24 free segments, the nos. 8 and 9 as well as 25 and 26, respectively, being wholly coalesced, though in both cases remnants of the former sutures are discernable (figs. 4g, $5a_1$; pl. 12d, f). In complex segment 2, traces of sutures between the three original components can be detected only by S.E.M. (pl. 12c). The fusion of segments 24 and 25 is intimate but not quite complete. The relative lengths of the segments of the antennula are:

1	2	3	4	5	6	7	8+9	10	11	12	13	14
74 +	49 +	27 +	21 +	24 +	23 +	24 +	39 +	27 +	29 +	28 +	46 +	48 +

15	16	17	18	19	20	21	22	23	24	25+26	
65 +	60 +	67 +	60 +	68 +	52 +	43 +	44 +	36 +	33 +	13	= 1000

The shape of the various segments can best be understood from fig. $5a_{1-3}$. The lateral parts of the intersegmental hinge joints exhibit a complex outline in segments 2 to 18, while the medial edges are less elaborate (fig. $5a_2$, c; pl. 12e). Joint 18/19 and those distad from there on are not that complicated and neither is joint 1/2.

Large, articulating setae are present on segments 3, 7, 8+9, 14, 16, 18, and 21, in each case one only, inserted distally along the frontal edge; on 22 and 23, one only, distally on the caudal edge; on segment 24, two distal setae, one on the frontal and one on the caudal edge; and on segment 25+26, two terminal setae. The lengths of the setae, relative to the length of the antennula (= 1000) are as follows: seta on segment 3 (200), seta on 7 (256), on 8+9 (229), 14 (200), 16 (99), 18 (179), 21 (152), 22 (77), 23 (203), 24 (anterior, 256; posterior, 205), 25+26 (anterior, 211; posterior, 320). So, the posterior seta on segment 25+26 is by far the largest of the antennule. All these setae, but for the one on segment 22, are long

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e, anterior margin of segments 3 through 8+9 of left antennule, showing anteriorly placed brushes of wrinkled hairs; f, detail of segment 12 of left antennule, with short, spiniform seta; g, details of proximal parts of large articulating setae of segments 7 (left) and 23 (right), respectively showing presence and absence of a breaking plane; h, detail of distal small seta of segment 5; i, detail of normal small seta, i.e., the distal one of segment 11 (type I); j, detail of distal small seta on segment 19 (type II).

and slender, with finely drawn-out tips and comparatively heavy chitin walls; their bases are swollen at the articulation with the respective segments (pl. 11a-c). The seta on 22 shows these characteristics in its proximal one-fifth only, its distal part being very slender and delicate (fig. $5a_3$; pl. 11h). This seta as well as the caudal one on segment 24, are plumose proximally; the seta on 23 may also have a few scattered hairs; all remaining large setae are smooth. Breaking planes are found in all frontally situated large setae, viz., at 0.10-0.15 the length of the seta. Such planes comprise a short modified stretch where the chitin wall is thickened, while halfway this thickening a narrow annular region is present where the wall is very thin (figs. 4f, 5a, g; pl. 11a, b). Setae placed caudally or terminally lack a comparable structure (fig. 5g; pl. 11e).

The remaining setal armature of the antennule is as follows. On segment 1 there are three setae, situated medially on its antero-distal corner; one of these is a normal, small seta (see below), the others are of a different structure, having thin, delicate walls, and being densely plumose with coarse setules (fig. $5a_1$). Segment 2 bears six small setae along its anterior margin in three groups of two; the three proximal setae are smooth, the distal ones sparsely plumose (fig. $5a_1$). Small setae are also present along the frontal edges of most other segments, as summarized in table II. Most of these are referable to either one of two distinct types: type I (fig. 5i) is comparatively long and slender, rounded in cross-section, with a distinctly visible wall, and with a breaking region comparable to that of the large setae; the internal organization of type I setae, in preserved condition, shows like a coarse and irregularly transverse striation. Type II setae (fig. 5j) are shorter and broader, with thinner walls, and showing longitudinal ridges indicating a flattened cross-section; their breaking planes are narrow, annular regions only, and their internal structure looks like an evenly granulated matrix. Most small setae are of type I; type II setae are present on segment 2, the three plumose setae; segment 4, the distal seta; the 2nd one from proximad on 8+9; the seta on segment 10; and the distal one on 19. Aberrant small setae are present on segments nos. 5, 12, and 25+26: the distal seta on segment 5 (fig. 5h) is sparsely plumose and does not show an evenly tapering shape; it has an irregular constriction in its proximal part. The distal small seta on segment 12 (fig. 5f) is a short, cone-shaped structure, showing a slight torsion halfway its length; its tip is acute. The distal seta on former segment 25 is inserted subterminally near the caudo-medial edge of the segment. Though its relative length is 104/1000, its structure indicates that it should be considered an extremely long type II small seta.

Breaking planes (fig. 5i, j; pl. 11d) are present in most small setae; they

TABLE II

Structure of the antennula of the *Euchirella messinensis* female

Segment	Large setae	Small setae	Aesthetascs	Brushes of wrinkled hairs
1		1 + 2pd		1c
2		3+3p	1	3-6c
3	1f	1		f+1c
4		2		f+1c
5		1+1p	1	f+1c
6		2		f+1c
7	1f	1		f+1c
8+9	1f	3	1	f
10		1		
11		2		
12		1+1s	1	
13		2		
14	1f	1	1	
15		2		
16	1f	1		
17		2		
18	1f	1		
19		2	1	
20		1		
21	1f			
22	1c(p)	1		
23	1c	1		
24	1f+1c(p)			
25+26	2t	1+1lo	1	

Legends.—f = frontal, c = caudal, t = terminal, (p) = plumose to some extent, p = plumose, s = spiniform, d = delicate, lo = long; (no indication) = normal.

are absent only in both plumose setae on segment 1, in the distal setae on 5 and 12 and in both small setae on 25+26. With the exception of the plumose ones mentioned, all small setae are smooth.

A single aesthetasc is present on each of the segments 2, 5, 8+9, 12, 14, 19, and 25+26; it is situated at the base of the fourth seta from proximad in segment 2, at the base of the frontal small seta on 25+26, and at the base of the distalmost seta in the other segments (e.g., pl. 12g). The arrangement of setae and aesthetascs of the antennule is summarized in table II and figs. 4f, 5a.

Integumental organs and structures of the antennula include slit-shaped

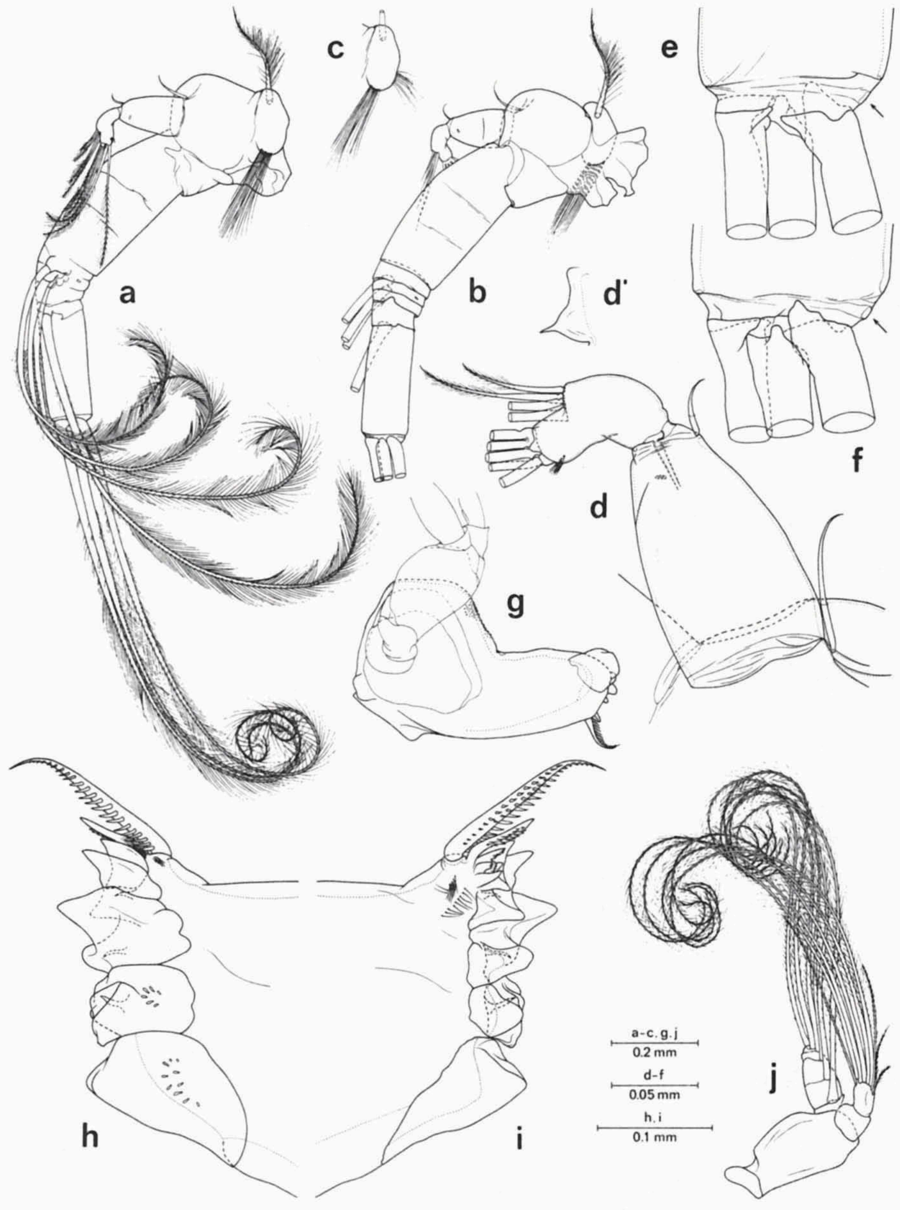

Fig. 6. *Euchirella messinensis* (Claus, 1863), ♀♀ from "Dana" Exped. sta. 4119x. a, right antenna, medial view; b, left antenna, lateral view; c, medial lobe of Ba1 of right antenna of another specimen, showing second brush of hairs; d, endopodite of right antenna, medial view; d', do., detail of lobular outgrowth on terminal lobe; e-f, distal

glandular pores, peg- and pit-sensilla, hair-sensilla, circular pores, and wrinkled hairs. On segments 1 to 8+9, minute brushes of wrinkled hairs are present, viz., one each on segments 1 and 3-7, disto-caudally, and on segment 2, three to six brushes along its caudal margin; disperse brushes are found on the anterior margins of segments 3 through 8+9; (fig. 5a$_1$, e; pl. 12b). The arrangement of integumental organs has been summarized in fig. 14a-b and table V; see also pl. 12a, c.

The antennae (fig. 6a, b) are composed of a short basipodite, a well-developed exopodite, and a markedly reduced endopodite. The strong reduction of the internal ramus is characteristic for the genus. The two basipodal segments are largely fused, the former suture still being distinct anteriorly but faint to obsolescent posteriorly. The first segment is equipped with a single, strongly plumose seta and it is produced into a large, rounded outgrowth medially. This lobe bears a dense brush of long, thin hairs posteriorly, while in some specimens a second brush of shorter hairs is present more proximally (fig. 6c). The second basipodal segment is swollen; it bears one small, naked seta only, inserted near the basis of the endopodite, and with a breaking plane at 0.40 of its length. The part of Ba2 which surrounds the insertion of the exopodite is distinguished from the remainder of the segment by a deep sulcus, particularly marked laterally (fig. 6a, b; pl. 12j).

The endopodite measures c. 0.24 the length of the exopodite. It consists of two distinct segments which exhibit hardly any fusion. The proximal segment is the larger; it bears one small, naked subapical seta with a breaking plane. The second segment is composed of the completely coalesced segments Ri2 and 3; it is produced into a proximal and a terminal lobe; the proximal one is equipped with an apical row of four slender, finely plumose setae which increase gradually in length to distad. The terminal lobe bears an apical row of five setae, also increasing sequentially in length to distad. These setae are slender and delicate, with finely drawn-out tips, smoothly curved, and plumose; four are arranged in a single row, the fifth seta is inserted mediad to the fourth. The medial edge of the terminal lobe is produced into an acutely pointed, lobular outgrowth in front of the row of setae (fig. 6d, d'). A subapical row of some 6-9 short spinules is present on the posterior margin (fig. 6d). The number of setae on the lobes of

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part of Re7 with insertion of the three large setae of right (e) and left (f) antenna, in medial, respectively lateral view, arrows indicate distal ring of sclerotized integument; g, corpus of left mandible in ventral view, with outline of proximal part of palp indicated; h-i, masticatory edge of right mandible in posterior (h) and anterior (i) view; j, palp of right mandible in postero-medial view, showing relative lengths of setae. Scale d' = scale d × 4.

Ri2+3, i.e., 4+5, is generally considered species-specific in *Euchirella*; however, an aberrant specimen was found in sample 4119^{x}, bearing 6+6 setae on the lobes of the right A2Ri2+3 (left A2 not dissected).

The exopodite consists of six largely free segments, the nos. 1 and 2 being coalesced to form a long, cylindrical structure. The site of fusion is indicated by a blunt angle in the anterior outline of the combined segment, as well as by some faint, transverse grooves (pl. 12i); the anterior angle is not produced into a lobular outgrowth; the segment bears no setae. The following four segments are short, annular structures (pl. 12h), the nos. 3 to 5 about equal in length, segment 6 slightly longer; each segment bears one large, smoothly curved plumose seta rostro-medially. The terminal, seventh segment is long and cylindrical; it bears three strong, gently curved plumose setae apically, the two outer setae inserted rather medially, the middle one more to the lateral side. In the thin membrane surrounding these setae a small, incompletely annular sclerite is present (fig. 6e, f). There is no appendicular seta halfway this segment. The relative lengths of the segments of the Re, in lateral aspect, are:

$$\frac{1+2 \quad 3 \quad 4 \quad 5 \quad 6 \quad 7}{50 + 4 + 3 + 3 + 6 + 34} = 100$$

Though largely free, hinge-joints Ba2/Re1+2, Re1+2/3, Re3/4, Re4/5, Re5/6, and Re6/7 are only distinct laterally, whereas their medial sectors are represented by faint sutures only (fig. 6a, b), indicating some degree of fusion between the successive segments. Apart from the two small setae mentioned, no breaking planes are found in the setae of the antenna. Two slit-shaped glandular pores are the only integumental organs present (fig. 14c, table V).

The gnathobasis of the mandible (fig. 6g) is a heavily chitinized structure. There is a wide proximal portion, narrowing abruptly halfway the corpus to continue as a subcylindrical distal part. Two fields of short spinules are present on the steep sloping medial face (fig. 6g; pl. 13b-e); the anterior surface of the corpus is smooth.

The masticatory edge (fig. 6h, i; pl. 13a) is composed of five groups of teeth. There is a multicuspidate molariform complex proximally, in the apical part of which one spinulose setiform tooth and one smaller, serrate setiform tooth are included (pl. 13f, g). The spinulose tooth is equipped with an extensive row of long spinules anteriorly, and two shorter rows of smaller spinules, posteriorly. The smaller setiform tooth has multiple rows of serrations in its middle portion. The remainder of the multicuspidate complex consists of four to six digitiform projections, some of which are smooth, others finely serrated. The complex is limited ventrally by a slender, bicuspidate ridge. The base of the complex bears three groups of slender spinules: a row of c. 10 and a group of c. 10-20, posteriorly, and one small group of about 6 spinules on the anterior face (fig. 6h, i; pl. 13h, i). Next, there are two smaller and one larger bicuspidate molariform complexes, each of which has a setiform protrusion in its central part; these protrusions, however, have not been observed in all specimens. An extremely heavy, monocuspidate molariform tooth terminates the toothed edge distally. Asymmetry in development of the left and right mandibles has not been observed.

The palp (figs. 6j, 7a, b) is weakly developed and shows a moderately swollen basal segment fitting by a constricted proximal part to the ventral face of the gnathobasis' corpus; this segment is devoid of setae. The two segments of the endopodite are small; the proximal one bears an extremely small, spiniform protrusion which represents the remnants of a single seta (fig. 7a, b). The distal segment is equipped with an apical row of nine slender setae: three delicate and finely plumose, consecutively increasing in length, followed by five long, stronger, curved, and densely plumose setae, while the ninth seta is again shorter and also more slender. The penultimate seta, i.e., no. 8, is inserted differently: its base does not articulate directly with the segment but is supported by a well-delimited pedestal-like structure (fig. 2f, g; pl. 14a). The originally six-segmented exopodite (pl. 14b) exhibits incomplete fusion of all segments, to varying degrees: joints Re 1/2 and Re4/5 are the least fused, Re2/3 and Re5/6 have almost completely coalesced, while Re3/4 shows an intermediate degree of fusion. In all joints, however, the intersegmental sutures are most clear-cut anteriorly and less distinct to obsolescent posteriorly. The external ramus bears six long and slender, gently curved plumose setae, one on every segment. No breaking planes were observed in the setae of the mandible. A single slit-shaped glandular pore has been found on this appendage (figs. 7a, 14h; table V); a small granular area is present on the anterior face of Ri2 (fig. 7a).

The first basal complex of the maxillula (fig. 8a, b) is produced into one outer and two inner lobes. The first inner lobe has developed into an arthrite, capable of some mobility relative to the corpus, as evidenced by a distinct anterior suture and the course of large striated muscles (fig. 2h). The second inner lobe plus the outer lobe together form a unit which is distinctly marked posteriorly but largely fused with the corpus along the anterior part of their boundary.

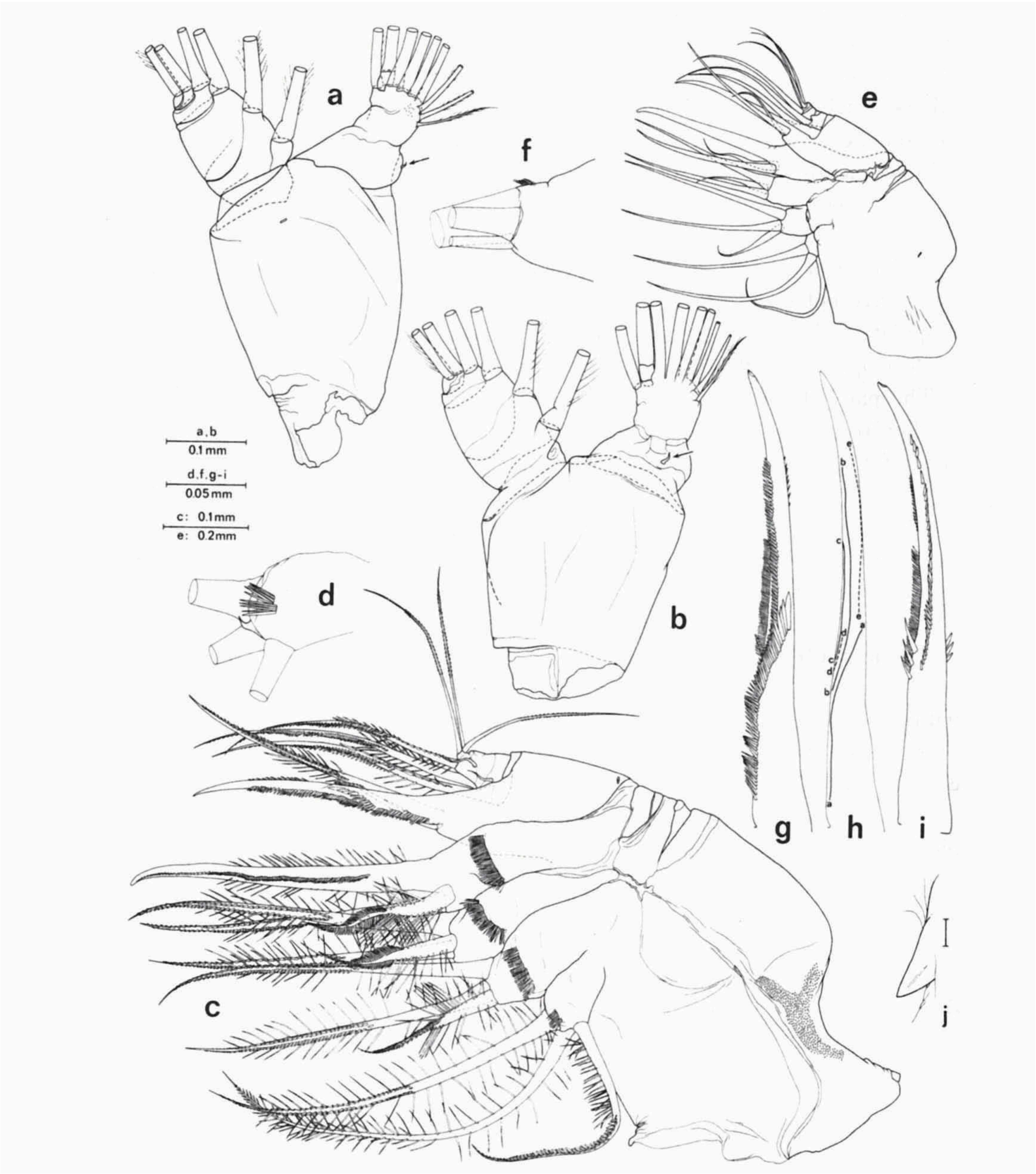

Fig. 7. *Euchirella messinensis* (Claus, 1863), ♀♀ from "Dana" Exped. sta. 4119^x. a-b, left and right palpus mandibularis, anterior respectively posterior view, arrow indicates vestigial seta on Ri1; c, left maxilla in postero-medial view; d, do., detail of first endite showing apical hook-shaped outgrowth; e, right maxilla in antero-lateral

The moderately heavy first inner lobe bears a total of nine setae along its internal margin: the two proximal ones are comparatively long and slender, with blunt tips, and sparsely spinulose; there are long and slender spinules which are distributed irregularly, as well as short and broad, blade-like spinules arranged serially in various longitudinal rows; the four apical spinules in such a row are much larger than the rest. All spinules are widely spaced and inserted all around the circumference of the seta. These two setae have a breaking plane at 0.40 their length, approximately at the boundary between the smooth proximal and the spinulose distal part. The remaining seven setae are stout, with broad bases, and taper to more acute tips. They alternate along the anterior and posterior sides of the edge, starting with a posteriorly inserted distalmost seta, followed by an anterior penultimate one and so on, resulting in four setae posteriorly and three anteriorly. All seven setae are bipectinate distally whereas the anterior ones are also sparsely spinulose in their medial parts. Double pectinations are confined to the anterior face of the seta. The long, stout spinules of the anterior setae concentrate posteriorly in a close brush at the basis of the spinulose part, while this type of spinulosity continues distally along the inner and outer edges (fig. 8a, b; pl. 14c); anteriorly such spinules are also present on a more proximal stretch. Next, a small, bipectinate seta is inserted submarginally on the anterior face of this lobe. Three submarginal setae are present posteriorly; these are both bipectinate and spinulose; the proximal seta is stout, with a broad base, the other two are more slender (fig. 8a, b; pls. 15, 16).

The first inner lobe is also equipped with distinct patches of hairs and spinules, viz., seven on its anterior face and eight posteriorly. Arrangement, composition, and a numerical denomination for each of them are shown in fig. 14d, e and pls. 15-16; see also fig. 8. The chaetotaxy is as follows, with dimensions (length × Ø at base) of the spinules indicated.

Anterior face:

a1: large but disperse patch, composed of very short spinules proximally and long, slender ones distally; 2-12 × 0.5-1 μm; pl. 14g, h;

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view, ornamentation of setae omitted; f, do., detail of spinules at the base of the primary seta on endite 5; g-i, detail of the primary seta of the fifth endite to show arrangement of the five rows of denticles: g, this seta of the left maxilla, postero-medial view; h, do., schematic drawing showing denomination of individual pectines; i, the same seta of the right maxilla in antero-lateral view; j, ventral view of sternal thorn, caudad to insertion of left maxilla (scale equals 0.01 mm).

a2: compact, rounded brush of sharp spinules, which may be directed almost perpendicular to the lobe's axis; 2-10 × 0.5-1 μm; pl. 14g;

a3: dense brush of stout, sharp spinules; 15-20 × 1-1.5 μm; pl. 14f;

a4: dense, elongate brush of slender spinules; 6-10 × 1 μm; pl. 14f;

a5: almost transverse row of very short spinules, delimiting a proximal patch of thin hairs; spinules 2 × <0.5 μm; hairs 10-15 × <0.5 μm; pl. 14e;

a6: small patch of minute spinules, which may eventually be absent; 2-3 × <0.5 μm;

a7: also reduced, i.e., either composed of very small spinules, or absent; 2-3 × <0.5 μm.

Posterior face:

p1: small patch of slender spinules; 3-18 × 0.5-1.5 μm; pl. 17a;

p2: extensive brush of slender, hair-like spinules; 20-30 × 1.5 μm; pl. 17b;

p3: composed of delicate, slender spinules; may be reduced to some degree; 15-35 × c. 1 μm; pl. 17c;

p4: rather diffuse brush of slender spinules; 12-30 × 1.5 μm; pl. 17d;

p5: dense brush of stout spinules; 3-10 × 0.5-1 μm; pl. 17e;

p6: small brush of spinules, which may be absent altogether; 2-3 × 0.5 μm; pl. 17e;

p7: composed of minute spinules, but more often completely absent; 2-4 × <0.5 μm;

p8: elongate brush of sharp spinules; c. 15 × 0.5 μm; pl. 17f.

The spinules generally are directed more or less parallel to the lobe's longitudinal axis, except for *a2*.

The second inner lobe is slender and markedly shorter than the 1st inner one (fig. 8a, b), though it slightly overreaches the endite of Ba2. This lobe bears a close group of four apical setae which are moderately long and apparently rigid. Three setae are bipectinate distally and sparsely spinulose along most of their length; the pectinations are concentrated on the anterior edges. The fourth, proximalmost seta is slightly shorter and it is spinulose only; the spinules are of two types: rather long and thin, widely spaced spinules all along the spinulose part and short, serially arranged spinules confined to the distal half of the seta; the latter spinules terminally approach a pectinate condition. Two setae, including the spinulose one, are inserted on the anterior side of the apical margin, the other two on its posterior side. The anterior setae are equally developed, whereas both posterior setae, likewise equal inter se, are a trifle stouter than the other pair. A small patch of short, slender spinules is present proximally on the anterior face of this lobe in some specimens. The outer lobe of Ba1 shows a squarish outline and is hardly protruding (fig. 8a, b). It is equipped with eight slender, delicate setae in a submarginal row posteriad to its outer edge. The setae vary in size and in plumosity: taken from proximad, nos. 3, 4, and 6-8 are about equally long, nos. 1 and 2 are slightly shorter, and no. 5 is markedly reduced in length and in thickness; next, nos. 1, 2, 6, and 8 are strongly but coarsely plumose while setae 3-7 are minutely and very sparsely plumose, being in fact almost naked. The reduction of the 5th seta is characteristic for the genus.

The second basal segment (fig. 8a, b) is long and slender, exhibiting a length/width ratio of 3.6. It is only moderately well delimited against Ba1 anteriorly but a distinct suture is present on the posterior side. The course of muscles indicates this segment to be mobile relative to basal complex 1 (fig. 2h). Ba2 bears three apical setae, one long and slender, finely bipectinate and partly spinulose, and two small and delicate, plumose setae. On the segment's posterior face just proximad to the setae, an extensive field of thin hairs is present, the outer limit of which is sharply marked by a single, dense row of hairs; some irregular patches of very fine hairs partly cover the remaining posterior surface. The small and only partly free endite of Ba2 does not reach as far as the 2nd inner lobe of Ba1. It bears three delicate setae apically, finely but densely plumose; one of these is as long as the setae of the 2nd inner lobe, the others are about one-third and one-fourth the length of the large seta, respectively. The terminal part of the endite is produced into a blunt tooth (fig. 8c, d), which bears a large tubular pore on the posterior side of its apex. Two extensive brushes of long, thin hairs are present anteriorly on the endite, one elongate, the other shorter.

The minute endopodite is faintly delimited against Ba2, suggesting some degree of fusion (fig. 8a, b; pl. 14d). Due to the extreme reduction of this ramus and by the apparent fusion of its segments, it is not possible to distinguish the composition of the Ri properly; its present functional status, however, is that of a single, partly free segment. The endopodite bears four long and slender setae, bipectinate distally and sparsely spinulose proximally; they decrease slightly in size to distad. The exopodite (fig. 8a, b), apparently well-articulating with Ba2, bears a row of eleven slender, smoothly curved setae, all strongly but coarsely plumose and inserted along the semicircular margin of the Re. The distalmost seta is the shortest and inserted more anteriorly; it is followed by three setae of increasing length, then six slightly longer ones of subequal length, while the proximalmost seta is again shorter. On the anterior face of the segment a shallow submarginal ridge follows the

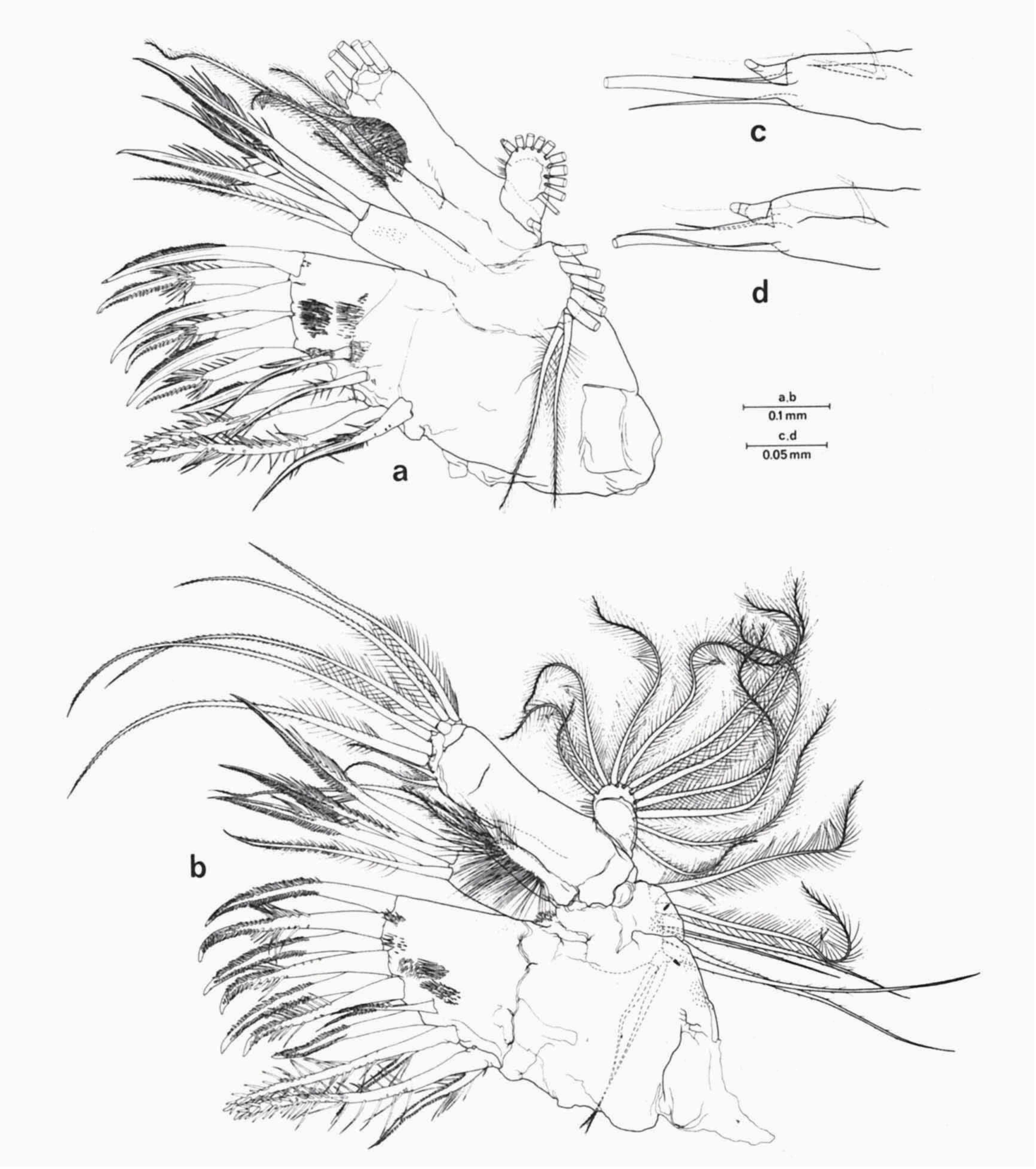

Fig. 8. *Euchirella messinensis* (Claus, 1863), ♀ from "Dana" Exped. sta. 4119^{x}. a, left maxillula, posterior view; b, right maxillula, anterior view; c, detail of the terminal part of the endite of basal segment 2 of left maxillula, showing three setae and the blunt tooth, with hairs and plumosity omitted; d, do., of right maxillula.

TABLE III

Pectinate and spinulose portions of the setae of the maxilla of the *Euchirella messinensis* female, in % of their total lengths

		(bi-)pectinate part	spinulose part
E1[*]	curved seta	distal 60%	proximal 40%
	distal heavy seta	distal 60%	proximal 80%
	proximal heavy seta	—	proximal 95% [1]
E2, 3	2 heavy setae	distal 60%	proximal 75%
	short seta	distal 60%	proximal 50%
E4	very heavy seta	distal 80% [2]	proximal 60%
	heavy seta	distal 60%	proximal 60%
	short seta	distal 60%	proximal 50%
E5	very heavy seta	....	..............[3]
	heavy seta	distal 60%	proximal 60%
	short, slender seta	distal 50%	—
Ri1, 2, 3	large seta	distal 60%	proximal 50%
Ri2, 3	small seta	— (smooth)	—
Ri4	3 slender setae	distal 60%	—

[1] Quadruple rows from 0.50 to 0.90 of the seta's length, taken from proximad.

[2] Pectination single; in the other setae the pectinations are double.

[3] Row *a* from 0.10 to 0.45; *b* from 0.30 to 0.80; *c*, 0.35-0.60; *d*, 0.33-0.40; *e*. 0.45-0.85.

[*] E = endite.

distal outline; it is interrupted about halfway by a small tubular pore. A few slender spinules are present on the antero-medial edge of this ramus.

But for the two spinulose setae of the first inner lobe, none of the setae of the maxillule is equipped with a breaking plane, be it that presence or absence of such plane could not satisfactorily be established in the large terminal seta of Ba2 and in the largest seta of the endite. Next to the tubular pores mentioned, three other integumental organs have been found, all slit-shaped glandular pores; their situation is shown in fig. 14d, e and table V. Granular areas have been indicated on the corpus, the 1st outer lobe, and on the 2nd inner lobe of Ba1 in fig. 8a, b.

The maxillae (fig. 7c, e) consist of a basal complex bearing four endites, a second basal segment produced into a single endite, and a small endopodite. Possibly, Ba1 and Ba2 are fused to some degree. The lateral outline of Ba1 is strongly arched proximally; adjacent to this margin, the posterior integument is covered with small, rounded warts (fig. 7c; pl. 18f).

The basalmost endite is small, the second to fourth are about equally developed, and the fifth is slightly shorter. All endites bear three apical setae: endite 1 (E1), two apparently stiff, moderately heavy setae, and a slightly shorter, more slender seta which is characteristically curved. Both the curved, and the distal heavy seta are bipectinate distally and sparsely spinulose proximally with two rows of widely spaced spinules (table III); the proximal heavy seta is spinulose only, but here four rows of spinules are present. On E2 and E3, there are two heavy setae as in E1 and one short, smoothly curved seta, about half the length of the large ones; this seta has a broad base and tapers quickly to a slender tip; all three setae are bipectinate and spinulose. The two heavy setae of E1-3 are not completely similar, as the distal one in each case tends to be somewhat stronger than the proximal one. E4 bears an extremely heavy seta which is confluent with the endite basally and slightly curved at its blunt apex; it is combined monopectinate and spinulose (pl. 18d). Next, there are one heavy and one short seta, both of the same structure as described above for E2-3. The fifth endite, finally, bears one very heavy seta, resembling the one on E4 but not completely continuous with the endite. This seta is multipectinate with five rows of denticles (fig. 7g-i; pl. 18e), viz., two regular rows (b and e), a shorter row of fine denticles (c), and two rows of stout structures, distally approaching the shape of broad, blade-like spinules (rows a and d). E5 also carries one heavy, bipectinate and spinulose seta, and a short seta, longer and more slender than those on E2-4, which is bipectinate only. The pectinate and spinulose parts of all setae are given in table III. Paired rows of serially arranged, contiguous denticles, characterizing a bipectinate condition, are invariably inserted on the posterior side; such pectination starts proximally with one or two unpaired denticles (pl. 17g).

The first endite also bears an acute, hook-shaped outgrowth, originating from the extreme apical integument and situated between the bases of the setae (fig. 7d; pl. 18b). On the postero-medial faces of endites 1 to 4 a dense, largely single row of long and sharp spinules is found: subapically in endite 1 and situated about halfway on endites 2 to 4 (fig. 7c; pl. 18a). The numbers of spinules are: E1, 9-12; E2, 30-35; E3, 30-35; E4, 30-40. E5 bears a small subterminal row of a few short spinules (fig. 7f).

The small endopodite apparently is composed of four free segments, nos. 1-3 short, annular structures, the fourth being minute and globular. Segments 1-3 are equipped medially with one bipectinate and spinulose seta each, while 2 and 3 also bear a small, smooth seta posteriorly; the terminal segment bears three slender, smoothly curved setae which are finely bipectinate only; see also table III and pl. 18c. Two slit-shaped glandular pores have been located on the maxilla, as apparent from fig. 13f and table V. Though no detailed study of the sternites has been made, it may be mentioned here that a thorn-shaped outgrowth was found to be present near the insertion of the maxilla (fig. 7j).

The maxillipeds (fig. 9a, c) are strongly developed. They are curved in the way characteristic for most Aetideidae: while the first basal segment has kept its original position, the segments distad of hinge-joint Ba1/2 have rotated to mediad whereby their originally anterior margin is now taking a postero-medial position if the maxilliped is completely stretched. These appendages are usually depicted in this position, hence the reversed terminology of the distal parts with respect to anterior and posterior as compared to most other calanoids. However, in situ the maxillipeds are held in a curved and also twisted position, with the secondary posterior margins facing antero-ventrally (fig. 1b; frontispiece). The relative lengths of the segments of the maxilliped are:

Ba1		Ba2		Ri1		Ri2		Ri3		Ri4		Ri5		
33	+	45	+	4	+	6	+	5	+	5	+	2	=	100

The first basal segment is laterally flattened and roughly rectangular (l/w = 2.2). It bears seven setae, arranged in four groups of 1, 2, 3, and 3, respectively. The proximal group consists of a single small, smooth seta inserted medially. The other setae are situated along the anterior margin: a small, smooth seta and a seta of moderate length proximally, the latter multipectinate in its distal half; an intermediate group of three setae, one short and smooth, one longer, distally multipectinate, and one coarsely bipectinate seta of intermediate length. Finally, there is a distal group composed of one small, smooth seta and two thin-walled setae of slightly unequal length, both minutely bipectinate and the shorter also finely plumose proximally. There is an extensive patch of short and sharp, slightly curved spinules on the antero-distal corner of Ba1 (fig. 9d; pl. 19a, b); the spinules decrease in size to the periphery of the patch.

The second segment of the basipodite is long and slender (l/w = 5.5); its anterior outline presents several smooth curves. This segment bears five setae along its (secondary) posterior margin: one smaller, distally bipectinate seta about halfway its length; one shorter and one longer seta at two-thirds, the shorter bipectinate only, the longer bipectinate distally and densely spinulose in its proximal half; and, extremely distally, one short, blunt and

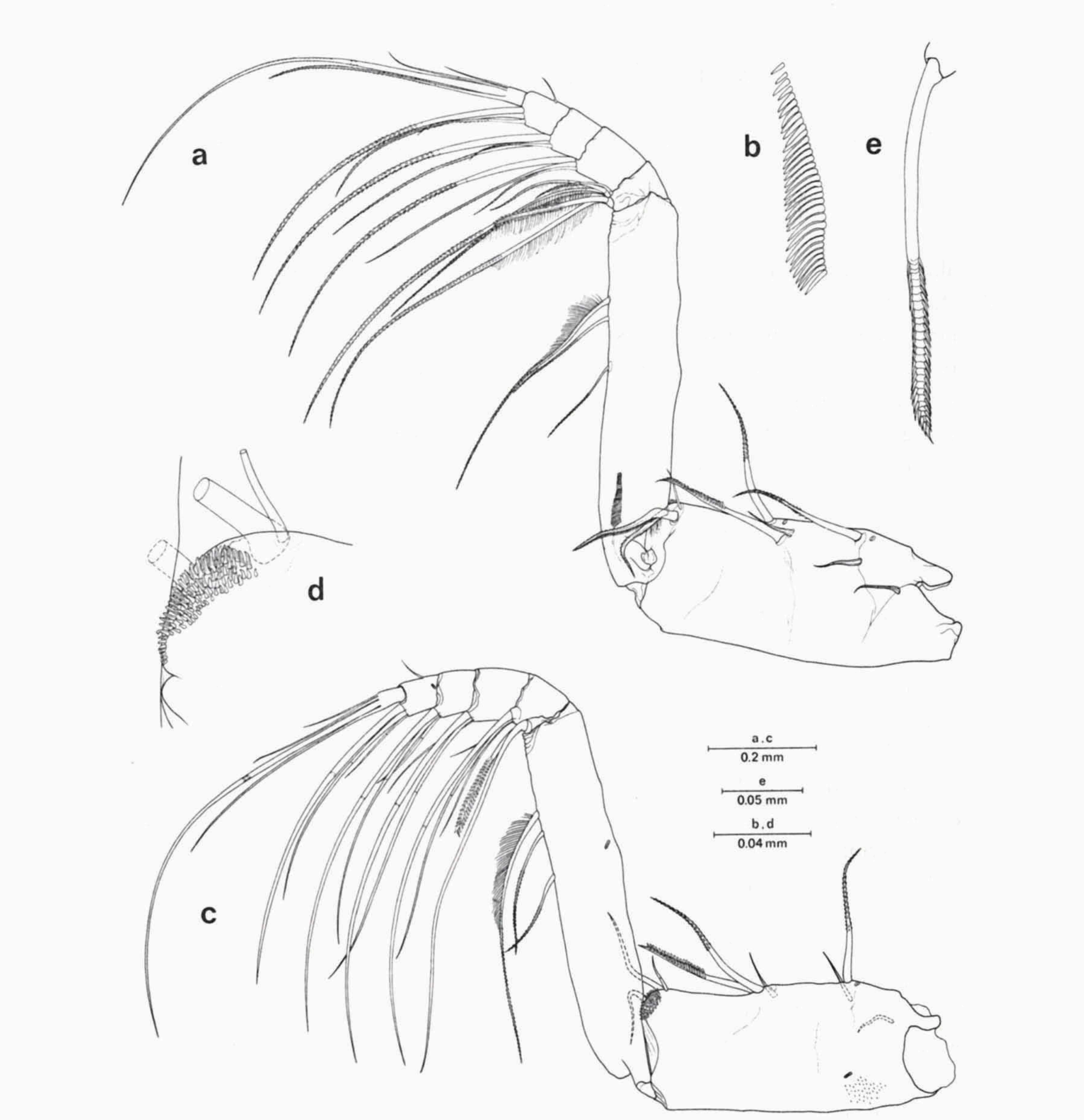

Fig. 9. *Euchirella messinensis* (Claus, 1863), ♀♀ from "Dana" Exped. sta. 4119ˣ. a, right maxilliped in medial view; b, do., detail of comb of spinules on Ba2; c, left maxilliped in lateral view, ornamentation of setae partly omitted; d, do., detail of antero-distal corner of Ba1, showing field of short spinules; e, detail of the shorter distal seta of Ba2 of the left maxilliped, in outer view.

one long, slender seta: the shorter coarsely bipectinate (fig. 9a, c, e), the long one multipectinate and, moreover, spinulose proximally. The larger seta occupies the lateral position, the short one is inserted medially. Proximo-medially on Ba2 a longitudinal comb is present which consists of a single row of 29-35 densely set spinules; these gradually decrease in length to distad and are of a straight, slender shape (fig. 9a, b; pl. 19c, d).

The endopodite is composed of five segments, nos. 1-4 short, annular structures and no. 5 minute (pl. 19e). Segments 1 to 4 each bear a group of setae in their postero-distal corner, every seta distinctly delimited at its base, while the setae on segment 5 are situated apically and are confluent with the segment. These groups are composed of 4, 3, 3, 3, and 3 setae; in each case, there is one long and strong, smoothly curved seta, finely multipectinate in its distal two-thirds, as well as one shorter seta, approximately two-thirds the length of the larger and bipectinate only; on segment 1, these two setae are also spinulose proximally. Next, Ri1 bears two short setae of unequal length: the larger finely bipectinate distally and spinulose proximally, the shorter minutely bipectinate only. Segments 2-5 each bear one short seta, minutely bipectinate in Ri2-4, and apparently smooth in 5. In addition, Ri4 and 5 are equipped with one small, naked seta on the anterior margin, viz., halfway on segment 4 and subterminally on 5. The arrangement of the setae on Ri1-4 is such, that the longest seta is positioned laterally, the others decreasing sequentially in length to mediad. On Ri5, the shortest of the apical setae occupies the anterior position, then the longest seta in the middle, while the second in length is inserted posteriorly.

A breaking plane was observed at about one-third of the length of all setae of the endopodite, with the exception only of the small anterior seta of Ri4. Five slit-shaped glandular pores are present on the maxilliped; the arrangement is given in fig. 14g and table V; a small granular area is shown on Ba2 in fig. 9c.

The left and right first basipodal segments of all four pairs of swimming legs are firmly connected by intercoxal plates. The relative length of the legs, excluding and including (between brackets) the terminal spine of the exopodite, is as follows (standard = P3 + terminal spine = 100):

P1	P2	P3	P4
49 (72)	67 (90)	74 (100)	69 (92)

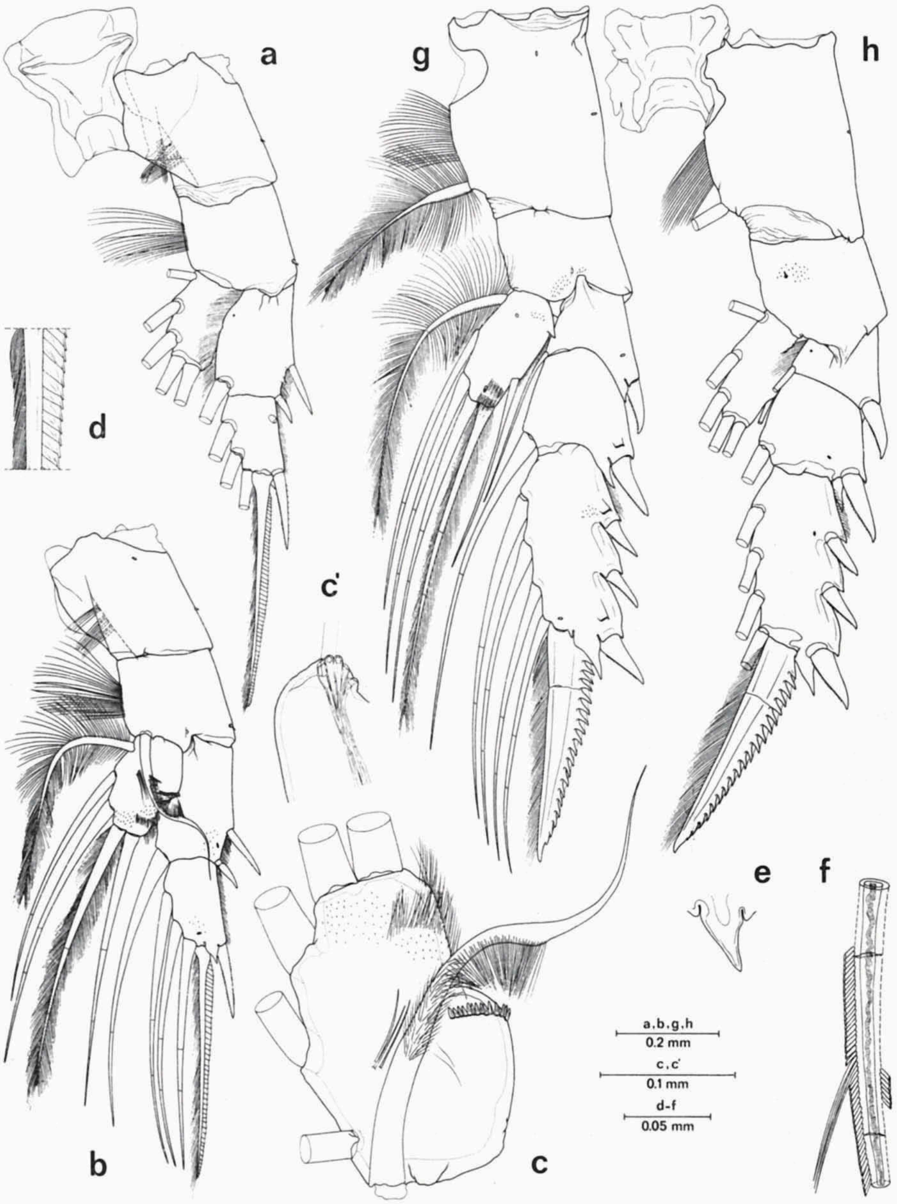

Fig. 10. *Euchirella messinensis* (Claus, 1863), ♀♀ from "Dana" Exped. sta. 4119x. a, right 1st swimming leg with intercoxal plate in posterior view; b, left 1st leg, anterior view; c, detail of the endopodite and the specialized curved seta of Ba2 of the right leg, anterior view; c', do., detail of tubercle, in posterior view, showing complex of five tubular pores and internal tissue strand; d, detail of terminal seta of Re3; e, detail of terminal spiniform outgrowth of Re3; f, detail of one of the terminal setae of the Ri, showing two modified sites and the serially arranged, contiguous setules; g, left second swimming leg in anterior view; h, right 2nd leg with intercoxal plate, posterior aspect.

The exopodites/endopodites are composed of the following numbers of free segments: 1st leg, 2/1; 2nd leg, 3/1; 3rd and 4th legs, 3/3. Fifth legs are absent. The proportional lengths of the segments are:

	Ba1	2	Re1	2	3		terminal spine	Ri1	2	3	ratio Re/Ri
P1	33	+ 23	+ — 23 —		+ 21	= 100	49	—— 21 ——			2.10
P2	31	+ 17	+ 11	+ 13	+ 28	= 100	37	—— 20 ——			2.60
P3	29	+ 15	+ 9	+ 14	+ 33	= 100	38	5	+ 7	+ 12	2.33
P4	26	+ 15	+ 11	+ 16	+ 32	= 100	35	4	+ 9	+ 12	2.36

The setae of the swimming legs are of two main types. Type A setae are found disto-medially on Ba1 of P2-P4, while the proximo-medial setae of P1-P4Ri are of this type as well. Setae of type A are gently curved, relatively thick proximally, and narrowing abruptly at about one third their length to a slender distal part. The plumosity is dense, contiguous, and long; on the thick basal part the setules are coarser whereas finer setules are found terminally. Type B setae are rather straight, apparently more rigid structures, densely but finely plumose with relatively short setules. The remaining setae of the Ri and all setae of the Re are essentially of this type; some of these, however, may be only feebly developed. Specialized setae, viz., on P1Ba2, on P1Re3, and the terminal spines of P2-4Re3, are treated separately below. The setae and spines of the legs often show one or more modified sites along their length (fig. 10f), probably referable to articulations. In type A setae such a site is either absent or present at 1/3rd their length. Type B setae have one or two such sites, at 1/2 and/or 2/3rds, but in reduced setae no such site was observed. The S-curved seta on P1Ba2 has no modified site, whereas the terminal seta on P1Re3 and the terminal spines on P2-4Re3 show such a structure at 1/3rd their length.

The shape of the various segments appears from figures 10-12; details of the armature are described below. With the exception of a specialized organ on P1Ri, the integumental organs are treated separately, following the description of the fourth legs.

The details of the first legs (fig. 10a-f) are as follows. First basipodal segment: one medial brush of long, coarse hairs. Ba2: one medial brush of very long, coarse hairs; and the specialized, doubly curved, plumose seta (fig. 10c) (cf. Von Vaupel Klein, 1972) inserted at the articulation with the endopodite, anteriorly in the segment's disto-medial corner. First and second exopodal segments completely fused; with two short and smooth lateral spines, the longer at 2/3rds, the shorter apically; the margin between these spines finely hairy; two separate rows of long, coarse hairs are present, viz., one each on both the proximal and distal sections of the biconvex inner margin; there is one type B seta disto-medially. Re3: whole lateral margin beset with short, fine hairs (pl. 19f-h); one outer apical spine, minutely pectinate along its inner and outer margin, and flanked by a short and acute, subtriangular outgrowth of the segment (fig. 10e); medial margin with three type B setae; one long, terminal seta, finely plumose along its inner margin and equipped with a serrate edge laterally, which is composed of about 80 serially contiguous, trapezoid denticles (fig. 10d), gradually decreasing in size to distad. Endopodite comprising a single free segment (fig. 10c, c′; pl. 20a) (see also Von Vaupel Klein, 1972); rostro-lateral tubercle well developed, bearing c. 16-23 medium-sized, smooth, slightly curved spinules placed in a single, partly alternating row (pl. 20d, e); 3-5 slender central hairs are present (pl. 20c), with lengths ranging from 0.14 to 0.24 times the length of the segment; the undivided distal hairbrush consists of moderately coarse hairs (pl. 20b), is slender and curved, and hardly reaches the fringe of coarser hairs on the disto-lateral margin; proximally, the medial margin bears one type A seta; there are also two medial, one subterminal, and one terminal type B setae. A specialized integumental organ is found on the postero-medial face of the tubercle, where a complex of four to five tubular (glandular?) pores is found (fig. 10c′; pl. 20f). Internally, a tissue strand runs from these pores to proximad, to be traced as far as the proximal half of Ba2.

The second swimming legs (figs. 10g-h, 11a-d) show the following details. Ba1, one medial brush of coarse hairs and one type A seta near its disto-medial corner. Ba2, smooth and unarmed; posteriorly, the disto-lateral margin is produced into a bluntly pointed outgrowth, near the articulation with Re1 (fig. 11d); this structure probably is a modified spinular organ (see below). Re1, with one short disto-lateral spine (cf. fig. 11c), medially pectinate, and flanked by a small, subtriangular outgrowth rostro-medially, while the lateral outline of the segment is drawn into a small point proximad to the spine; medial margin with a fringe of coarse hairs; one weakly developed, finely plumose seta in the inner apical corner. Re2, lateral outline pointed distally; one terminal outer spine (pl. 21a), minutely pectinate (pl. 21b), and accompanied by a short, subtriangular rostro-medial outgrowth (pl. 21a); one type B seta in the medio-apical corner. Re3, three short, minutely pectinate lateral spines, at 1/3rd, 2/3rds, and apically; the marginal sections of the integument proximad to each spine acutely protruding; the apical short spine flanked by an elongate outgrowth, shorter than the spine and situated on its rostro-

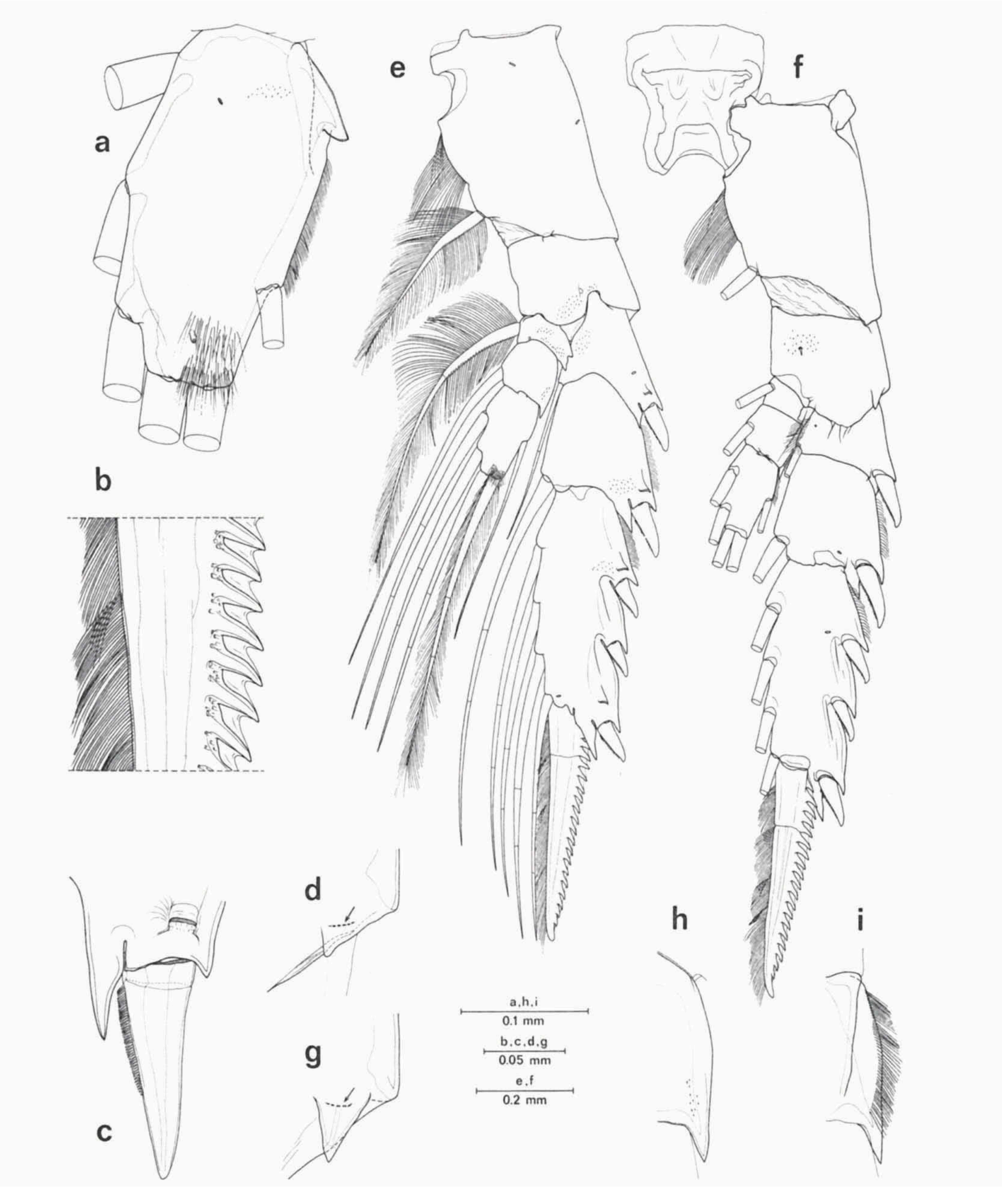

Fig. 11. *Euchirella messinensis* (Claus, 1863), ♀♀ from "Dana" Exped. sta. 4119ˣ. a, endopodite of left 2nd leg, anterior view; b, detail of the terminal spine of P2Re3; c, detail of the short disto-lateral spine of Re2 of the 2nd leg in anterior view, with its adjacent large closing-flap pore; d, right P2Ba2, posterior face, detail of the disto-lateral pointed outgrowth with underlying (?) pore structure (arrow); e, left 3rd swimming leg in anterior view; f, right 3rd leg with intercoxal plate, posterior aspect; g, right P3Ba2, posterior aspect, detail of the disto-lateral outgrowth with (?) pore (arrow); h-i, lateral margin of P3Ri2: h, of left leg, anterior view; i, of right leg, posterior view.

medial side; the outer margin proximad to the basalmost spine is finely hairy. There are three type B setae evenly distributed along the medial margin, as well as one apical such seta. The strong terminal spine (figs. 10g-h, 11b) is densely but finely plumose along most of its medial margin, only the apex being smooth; the lateral margin is produced into a deeply serrate edge with 18-20 sharp denticles, starting with two smaller ones proximally, followed by a number of large denticles while the distal ones gradually decrease in size. Ri (fig. 11a) comprising a single free segment, its lateral margin proximally produced into a short but acute point (pl. 21c). There are a proximal type A and two type B setae along the medial margin, as well as two type B setae terminally. The lateral margin bears a single, feebly developed seta; the section between this seta and the acute proximal outgrowth is fringed with fine hairs. A brush of fine hairs is also present distally, on the segment's anterior face (pl. 21d).

The third swimming legs (figs. 11e-i, 12a-b) do not differ from the second pair in the basipodal segments and in the exopodite, with the exception of the outgrowth on the disto-lateral margin of the posterior face of Ba2, which is larger and more acutely pointed than in P2 (fig. 11g), and the lateral margin of Re2, which is fringed with fine hairs (smooth in P2). The endopod is three-segmented, with the details of the segments as follows. Ri1 (fig. 12a, b), lateral margin produced into sharp, double points (pl. 21f), the distal one of which is the longer and has an acute tip, the shorter, proximal point has its apex rounded; one type A seta medially. Ri2, lateral margin finely hairy along the posterior side of its edge; disto-lateral tip drawn-out into a sharp and slender point (fig. 11h-i; pl. 21g); one type B seta medially. Ri3, frontal face with a terminal patch of fine, short hairs; two type B setae medially and two such setae terminally; the lateral margin bears one feebly developed type B seta; margin proximad to this seta finely hairy.

The details of the fourth legs (fig. 12c-h; pl. 22) are the same as for the third pair, but for Ba1. This segment bears two stout, heavily chitinized spines on the posterior side of its medial margin, which have long and finely drawn-out tips (pl. 22a, b). The spines are situated close to the insertion of the medial seta; they originate from a common base and the medial spine is stronger developed than its lateral companion. Ba1 does not bear a medial brush of hairs in P4. Number and shape of the spines on P4Ba1 are generally considered species-specific in *Euchirella*, and are frequently used as diagnostic characters in identifying the females. However, some variation is found in this character in *E. messinensis*. Various females have three instead of two spines on either the left or the right leg (fig. 12i), while the opposite leg is normal; specimens with three spines on both legs have not been met with, yet.

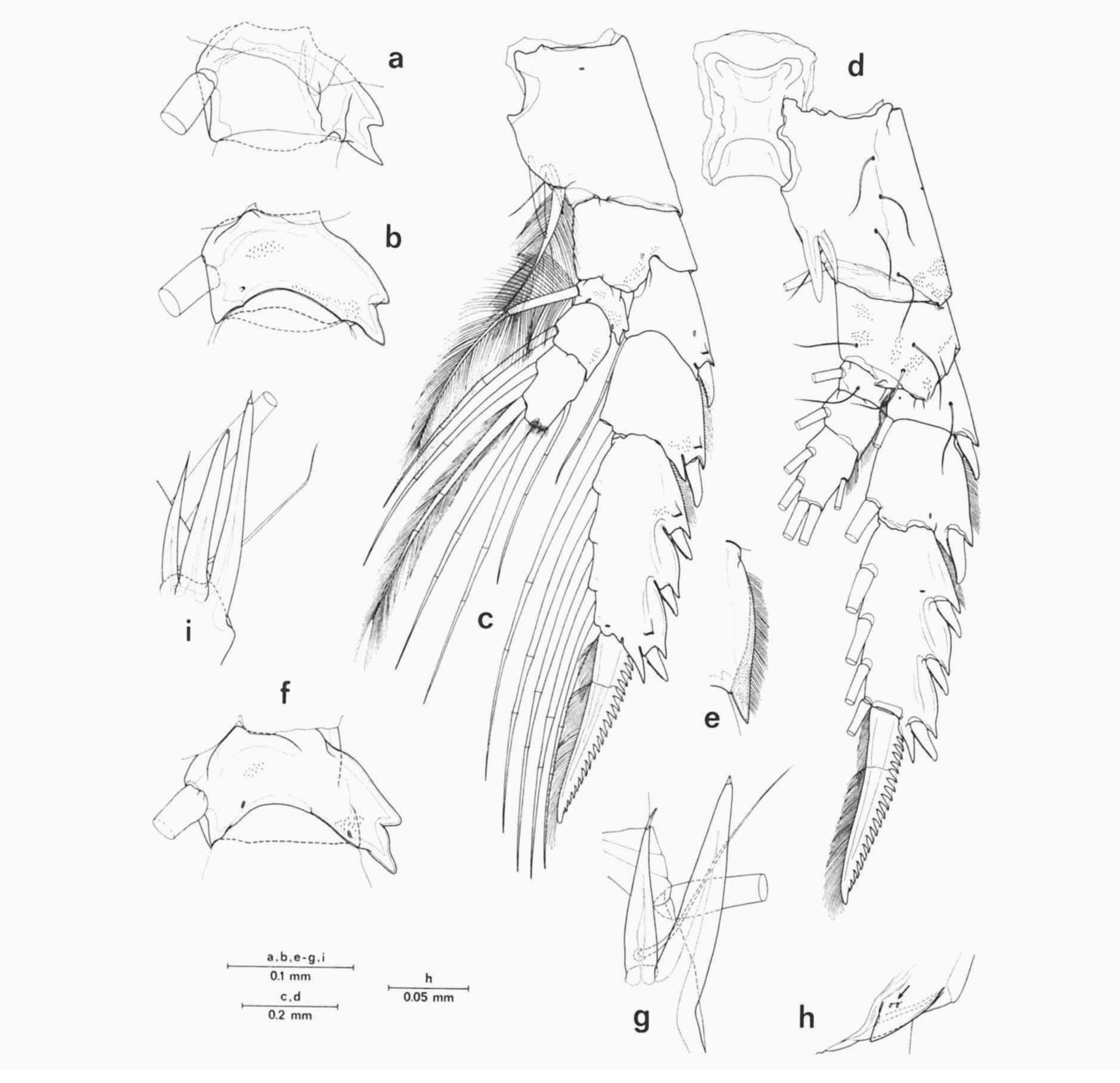

Fig. 12. *Euchirella messinensis* (Claus, 1863), ♀♀ from "Dana" Exped. sta. 4119x. a-b, P3Ri1: a, of right leg, in posterior view; b, of left leg, anterior aspect; c, left 4th swimming leg in anterior view; d, right 4th leg, posterior aspect; e, P4Ri2, left leg, detail of lateral margin in anterior view; f, P4Ri1 of left leg, anterior view; g, detail of the two postero-medial spines of P4Ba1; h, right P4Ba2, posterior face, detail of disto-lateral pointed outgrowth, arrow indicates presumed underlying pore-structure; i, situation on P4Ba1 in an aberrant specimen, where three instead of two spines are present.

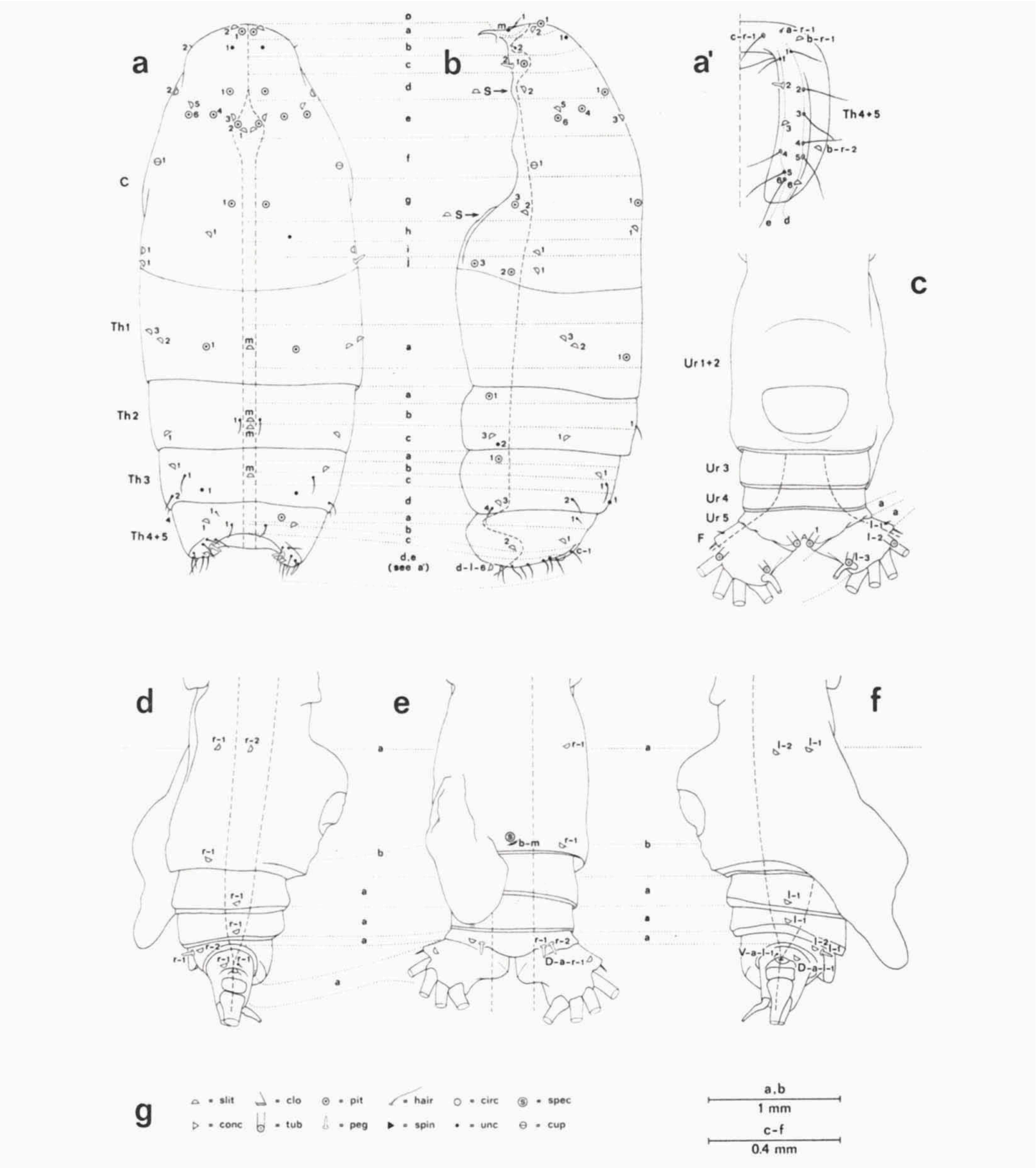

Fig. 13. *Euchirella messinensis* (Claus, 1863), ♀. a-f, distribution and coding of sites of integumental organs of the body; a, cephalothorax, dorsally; a′, enlarged detail of the right portion of Th4+5 in posterior view; b, cephalothorax, left laterally; c-f, urosome, respectively, ventrally, right laterally, dorsally, and left-laterally; g, explanation of symbol-code (adapted from Fleminger, 1973, and enlarged). For explanation of site-codes and abbreviations, see table IV. Broken lines in figures a, b, c-f, indicate parts which are not visible in the other aspects shown.

TABLE IV

Coding of sites and types of integumental organs of the body in the *Euchirella messinensis* female

Full code						
(1)	(2)	(3)	(4)	(5)	(6)	
Body region	Integumental area	Row	Position	Individual number	Type of organ, remarks	
C	- PT	- o	- m		((chemo-)sensory) pore	Frontal organ (see Discussion).
C	- PT	- o	- l,r	- 1	sensory hair	
C	- PT	- a	- l,r	- 1	pit	Associated pairs.
C	- PT	- a	- l,r	- 2	slit	
C	- PT	- b	- l,r	- 1	unc	
C	- PT	- b	- l,r	- 2	hair	
C	- PT	- c	- l,r	- 1	pit	
C	- PT	- c	- l,r	- 2	peg	
C	- PT	- d	- l,r	- 1	pit	
C	- PT	- d	- l,r	- 2	slit	
C	- PT	- e	- l,r	- 1	slit	Associated triplets.
C	- PT	- e	- l,r	- 2	pit	
C	- PT	- e	- l,r	- 3	slit	
C	- PT	- e	- l,r	- 4	pit	
C	- PT	- e	- l,r	- 5	slit	Associated pairs.
C	- PT	- e	- l,r	- 6	pit	
C	- PT	- f	- l,r	- 1	cup	
C	- PT	- g	- l,r	- 1	pit	
C	- PT	- g	- l,r	- 2	slit	Associated pairs.
C	- PT	- g	- l,r	- 3	pit	
C	- PT	- h	- l,r	- 1	Probably slit, but may also be peg	
C	- PT	- i	- l,r	- 1	slit	Associated pairs; either site i-1 or j-1 may be occupied by peg instead of slit.
C	- PT	- j	- l,r	- 1	slit	
C	- PT	- j	- l,r	- 2	pit	
C	- PT	- j	- l,r	- 3	pit	
C	- S	- ..	- l,r	- ..	slit, at base of antenna	
C	- S	- ..	- l,r	- ..	slit, mediad to insertion of maxilla	
Th1	- PT	- a	- m		slit	
Th1	- PT	- a	- l,r	- 1	pit	
Th1	- PT	- a	- l,r	- 2	slit	
Th1	- PT	- a	- l,r	- 3	slit	

TABLE IV (continued)

Full code					
(1)	(2)	(3)	(4)	(5)	(6)
Body region	Integumental area	Row	Position	Individual number	Type of organ, remarks
Th2	- PT	- a	- l,r	- 1	pit
Th2	- PT	- b	- m		slit
Th2	- PT	- b	- l,r	- 1	hair
Th2	- PT	- c	- m		slit
Th2	- PT	- c	- l,r	- 1	slit
Th2	- PT	- c	- l,r	- 2	unc
Th2	- PT	- c	- l,r	- 3	slit
Th3	- PT	- a	- l,r	- 1	pit
Th3	- PT	- b	- l,r	- 1	slit
Th3	- PT	- c	- m		slit
Th3	- PT	- c	- l,r	- 1	hair
Th3	- PT	- d	- l,r	- 1	unc
Th3	- PT	- d	- l,r	- 2	hair
Th3	- PT	- d	- l,r	- 3	slit
Th3	- PT	- d	- l,r	- 4	hair
Th4+5	- PT	- a	- l,r	- 1	Normally hair, but pit may be present instead — Associated pairs.
Th4+5	- PT	- b	- l,r	- 1	slit
Th4+5	- PT	- b	- l,r	- 2	slit
Th4+5	- PT	- c	- l,r	- 1	hair
Th4+5	- PT	- d	- l,r	- 1	At most five hairs; one or more may, however, be absent, *or* one of the hairs may be double.
	do.			- 2	
	do.			- 3	
	do.			- 4	
	do.			- 5	
Th4+5	- PT	- d	- l,r	- 6	slit
Th4+5	- PT	- e	- l,r	- 1	At most four hairs; one or more may, however, be absent.
	do.			- 4	
	do.			- 5	
	do.			- 6	
Th4+5	- PT	- e	- l,r	- 2	peg
Th4+5	- PT	- e	- l,r	- 3	slit
Ur1+2	- PT	- a	- l,r	- 1	slit
Ur1+2	- PT	- a	- l,r	- 2	slit

TABLE IV (continued)

Full code (1) Body region	(2) Integumental area	(3) Row	(4) Position	(5) Individual number	(6) Type of organ, remarks	
Ur1+2	PT	b	m		spec, a specialized, irregular pore structure	
Ur1+2	PT	b	r	1	slit, only present on the right	
Ur3	PT	a	l,r	1	slit	
Ur4	PT	a	l,r	1	slit	
Ur5	PT	a	l,r	1	Normally slit, may, however, be replaced by peg.	Associated pairs.
Ur5	PT	a	l,r	2	peg	
Ur5	S	a	l,r	1	tub	
F	D	a	l,r	1	slit	
F	V	a	l,r	1	hair	
F	V	a	l,r	2	tub	
F	V	a	l,r	3	tub	

Legends.—

(1) Body regions are: C = cephalon; Th1, 2, 3, 4+5 = thoracic somites 1, 2 . . . etc.; Ur1+2, 3, 4, 5 = urosomal somites 1+2 (= genital somite), 3 . . . etc.; F = furca.

(2) Integumental areas within the body regions are: PT = pleuro-tergal; S = sternal. The sternites of the cephalothorax have not been studied systematically, so no specific codes can be applied to sternal sites as yet. For the furcal rami the denominations D = dorsal and V = ventral are used instead of PT or S.

(3) Transverse rows are indicated by a, b, c . . . etc. in an anterior to posterior order.

(4) Positions within rows are divided into three stretches: m = medial (midline only), l = left, r = right.

(5) Individual sites within the left c.q. right stretches of a row are numbered in a dorsal to ventral order.

(6) Abbreviations for integumental organs are used as follows:
slit = regular slit-shaped glandular pore;
conc = (partly) concealed or irregular slit-shaped glandular pore;
clo = large, closing-flap glandular pore;
tub = tubular glandular pore;
pit = pit-sensillum;
peg = peg-sensillum;
hair = hair-sensillum;
spin = spine-sensillum and/or spinular pore;
circ = circular pore, small type;
cup = cup type circular pore;
unc = perforation site of uncertain nature;
spec = specialized structure.

The integumental organs of the swimming legs include almost the complete array of pores and sensilla, excluding only the pit-sensillum. These organs are mapped, coded, and characterized in fig. 15 and table VI. Granular areas are present on P1Re1+2, 3, Ri (fig. 10b); P2Ba2, Re3, Ri (fig. 10g, h); P3Ba2, Re1, 2, 3, Ri1, 2 (fig. 11e, f); and P4Ba1, 2, Re2, 3, Ri1, 2 (fig. 12c, d). See also pls. 21e, f, h, 22f, g.

Various kinds of integumental organs and integumental structures have been found. As a separate paper has been devoted to the regular integumental organs (Von Vaupel Klein, in press b), only a couple of specialized organs will be described below. The integumental structures, involving mere modifications of the cuticle's outermost layer, will be treated in extenso. The thickness of the integument ranges between 5 and 15 μm. The regular integumental organs include both the regular and the partly concealed slit-shaped glandular pore, the large closing-flap pore, the tubular pore, both the small and the cup type circular pore, the pit-, peg- and hair-sensilla, and the spinular organ. The special types of integumental organs include:

1. Spinular organ of the 2nd to 4th legs (figs. 11d, g, 12h; pl. 22c). — Acutely pointed outgrowth in the distal postero-lateral corner of Ba2. The concealed sector of its attachment forms a semicircular ridge and/or slit (pl. 22c). Internal, duct-like structures are usually observed. Whether or not a true canal is present in the protruding part could not satisfactorily be established. Dimensions: protruding part 15-20 μm in length, width at base c. 15-20 μm.

2. Urn-shaped (glandular) pores in the ventral wall of the oral cavity (fig. 3c-f; pls. 5c-e, 6). — Urn- or onion-shaped, protruding structures, with central canal ending in apical, circular pore. Dimensions: diameter at base 12-15 μm, height 8-10 μm, canal 1-2 μm Ø.

3. Large, irregular pore on the genital somite (pl. 8e). — Irregular, elongate depression, the exact nature of which is uncertain. Length c. 25 μm.

4. Complex tubular pore system on P1Ri; see the description of P1, above.

5. Structure of uncertain nature (pl. 23f). — A supposedly integumental organ was found on site P3/4-Ri3-af-1. Its structure could not satisfactorily be ascertained by compound microscope, while the S.E.M. image (pl. 23f) appears not to be conclusive either. The organ looks like a shallow, elongate depression, proximally bordered by a ridge. A ridge- or suture-like structure seems to be present along the longitudinal axis of the depression. Dimensions: 2.5 × 1 μm.

The distribution of integumental organs over the body and the appendages has been summarized in figs. 13-15 and tables IV-VI. Both the sites and the types of organs have been given a code. The inventory is complete with

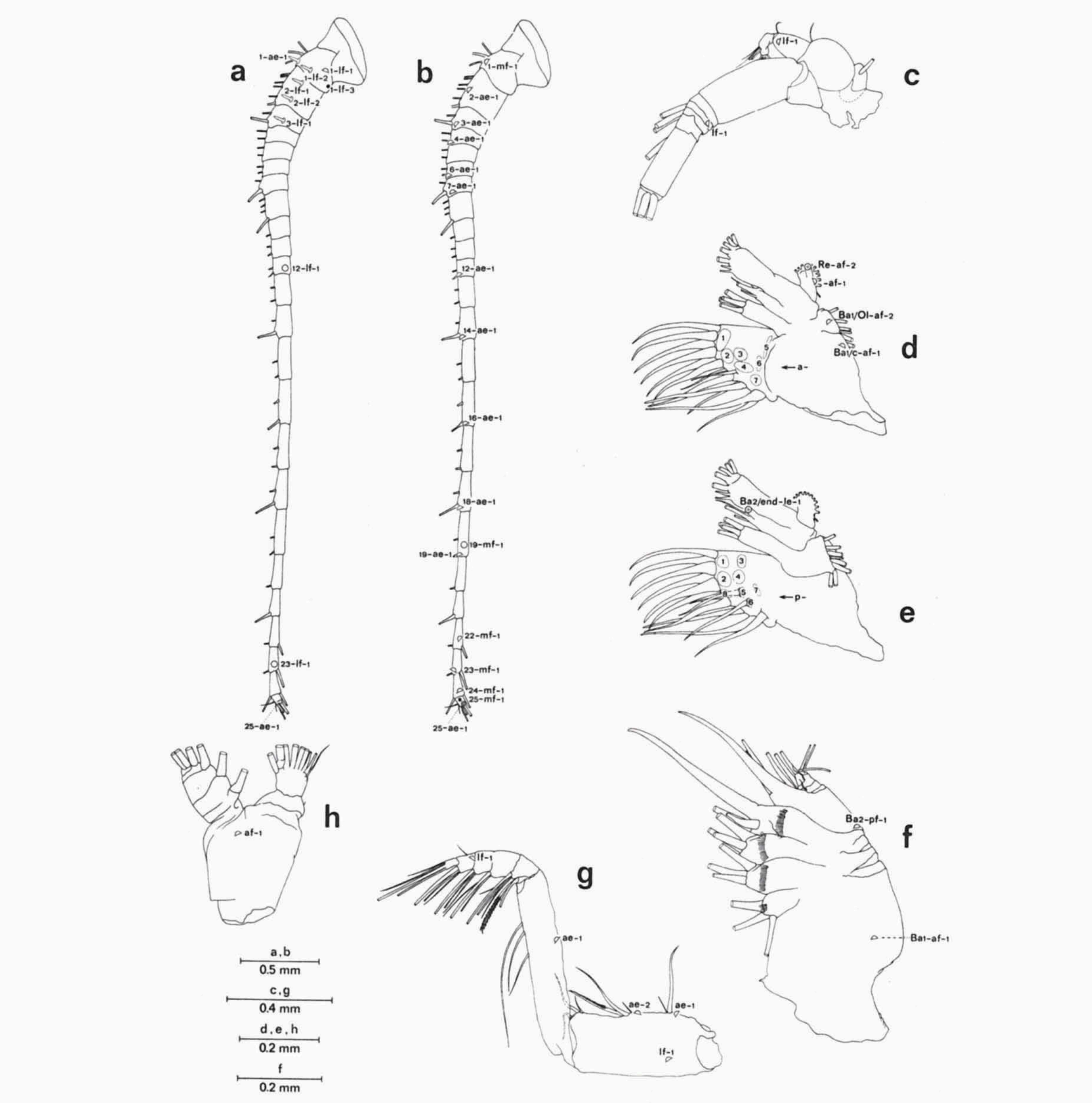

Fig. 14. *Euchirella messinensis* (Claus, 1863), ♀. a-f, distribution and coding of sites of integumental organs of the 'cephalic' appendages. a, b, antennules: a, left one in lateral view; b, right one, medial view; c, left antenna in lateral view; d, e, maxillulae, also showing chaetotaxy of 1st inner lobe (see text): d, right appendage, antero-lateral face; e, left one in postero-medial aspect; f, left maxilla, postero-medial view; g, left maxilliped, lateral aspect; h, left mandibular palp, anterior view. For explanation of site- and symbol-code, see fig. 13 and tables IV and V.

TABLE V

Coding of sites and types of integumental organs of the appendages (excluding the swimming legs) in the *Euchirella messinensis* female

Full code				
(1)	(2)	(3)	(4)	(5)
Appendage	Segment/Region	Aspect	Individual number	Type of organ, remarks
*) A1	- 1	- lf	- 1	slit
A1	- 1	- lf	- 2	peg, but pit may be present instead
A1	- 1	- lf	- 3	unc (probably some kind of sensillum)
A1	- 1	- ae	- 1	peg
A1	- 1	- mf	- 1	slit
A1	- 2	- lf	- 1	peg, but pit may be present instead
A1	- 2	- lf	- 2	peg, but pit may be present instead
A1	- 2	- ae	- 1	slit, at base of aesthetasc
A1	- 3	- lf	- 1	peg, but pit may be present instead
A1	- 3	- ae	- 1	slit **)
A1	- 4	- ae	- 1	slit
A1	- 6	- ae	- 1	slit
A1	- 7	- ae	- 1	slit **)
A1	- 12	- lf	- 1	circ
A1	- 12	- ae	- 1	slit, at base of aesthetasc
A1	- 14	- ae	- 1	slit, at base of aesthetasc
A1	- 16	- ae	- 1	slit
A1	- 18	- ae	- 1	slit
A1	- 19	- ae	- 1	slit, at base of aesthetasc
A1	- 19	- mf	- 1	circ
A1	- 22	- mf	- 1	slit
A1	- 23	- lf	- 1	circ
A1	- 23	- mf	- 1	slit
A1	- 24	- mf	- 1	slit
A1	- 25	- ae	- 1	hair
A1	- 25	- mf	- 1	unc (probably pit or peg)
A2	- Re4	- lf	- 1	slit
A2	- Ri1	- lf	- 1	slit
Md	- Ba2	- af	- 1	slit
Mxl	- Ba1/c	- af	- 1	slit
Mxl	- Ba1/ol	- af	- 2	slit
Mxl	- Ba2/end	- le	- 1	tub, situated terminally on blunt tooth
Mxl	- Re	- af	- 1	slit
Mxl	- Re	- af	- 2	tub

TABLE V (continued)

Full code				
(1)	(2)	(3)	(4)	(5)
Appendage	Segment/Region	Aspect	Individual number	Type of organ, remarks
Max	- Ba1	- af	- 1	slit
Max	- Ba2	- pf	- 1	slit
Mxp	- Ba1	- lf	- 1	slit
Mxp	- Ba1	- ae	- 1	slit
Mxp	- Ba1	- ae	- 2	slit
Mxp	- Ba2	- ae	- 1	slit
Mxp	- Ri4	- lf	- 1	slit

Legends.—(See also legends to table IV.)

(1) Appendages are characterized by their usual abbreviations.

(2) Segments are likewise numbered c.q. denominated as usual. Regions are indicated if necessary: c = corpus; ol = outer lobe; end = endite.

(3) Aspects of segments are denoted, dependent upon the way the segment is flattened, i.e., either laterally or rostro-caudally. Either: ae = anterior edge; lf = lateral face; mf = medial face; pe = posterior edge; or: af = anterior face; le = lateral edge; me = medial edge; pf = posterior face.

(4) Individual numbers are assigned to the organs of each of the four aspects of a segment separately, in a proximal to distal, *and* lateral to medial or posterior to anterior order (see also Discussion).

*) On A1, all organs designated as in the "ae" position are situated directly mediad to the anterior row of setae.

**) Sites A1-3-ae-1 and A1-7-ae-1 are placed rather medially but this is due entirely to the strong development of the large seta, at the base of which the organ is situated.

the exception of the sternites of the CTh, of which only incidental records exist. Various body parts of some ten specimens have been inspected for integumental organs. All sites indicated were found occupied in every specimen, with the exception only of the large pore Ur1+2-b-m, which was observed in one female only. Variability in the type of organ present at a given site has been indicated in tables IV-VI.

Integumental structures (cf. Von Vaupel Klein, in press b) are of five distinct types:

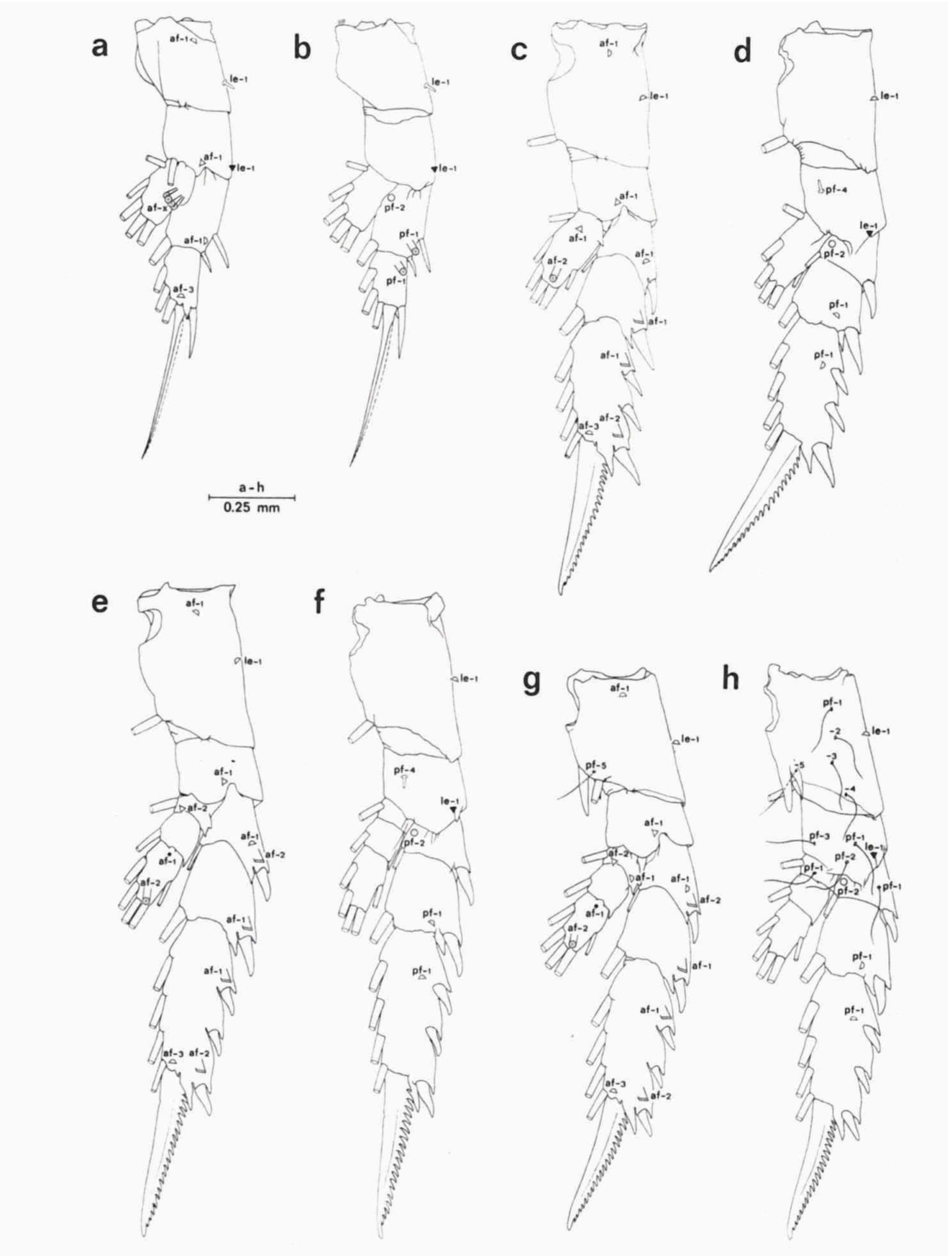

Fig. 15. *Euchirella messinensis* (Claus, 1863), ♀. a-h, distribution and coding of sites of integumental organs of the swimming legs. a, b, left and right 1st leg, anterior respectively posterior view; c, d, left and right 2nd leg, anteriorly c.q. posteriorly; e, f, left and right 3rd leg, anterior c.q. posterior view; g, h, left and right 4th leg, anterior and posterior aspect. For explanation of site- and symbol-code, see fig. 13 and tables IV to VI.

1. Wrinkled hairs (pls. 3, 12b, 23a). — Wrinkled, hair-like structures, with or without a basal swelling; bases not delimited from the surrounding integument. Arranged in small groups. Dimensions: 8-15 μm long, 0.5 μm Ø.

2. Straight integumental hairs (pls. 3, 23b, c). — Slender, pointed structures with bases confluent with the integument. Arranged in patches. Size: length 8-25 μm, diameter at base c. 0.5 μm.

3. Granular areas (pls. 21e, 22f, g, 23d, e). — Small patches of minute, suboval grains, which protrude from the integument and which show a distinctly marked circumference. Dimensions of grains: 0.2-0.5 × 0.5-2 μm.

4. Stellate warts (fig. 4a-d; pl. 10e, f). — Small, rounded elevations of the cuticular outer layer, with a stellate circumference. Diameter 2-5 μm.

5. Globular warts (fig. 7c; pl. 18f). — Small, globular structures, largely elevated above the surrounding integument. Diameter c. 0.5-1 μm.

Integumental structures apparently are confined to discrete body regions. Wrinkled hairs are present on the antennules (fig. 5a, e) and on the sternites of the cephalothorax (pl. 3). Straight hairs have been observed on the sternites of the CTh only (pl. 3). Granular areas have been mentioned in the descriptions of the appendages and are indicated in the respective figures; however, these areas may hardly be observed by light-microscopy, and an exhaustive inventory by S.E.M. has not yet been made. Stellate warts are present on the genital somite only and globular warts have been observed exclusively on the maxilla.

Other organs in close relation to the integument include setae, spines, setules, spinules, aesthetascs, hairs, and various kinds of outgrowths. These are all well-known structures in calanoid morphology but, as their possible origins will be discussed, a brief characterization of each type has to be presented.

1. Outgrowths of somites and segments (e.g., rostrum; sternal keels Th1-Th4+5; thorns on sternite at insertion of maxilla; anal operculum; lobular outgrowth on A2Ri2+3; molariform teeth of MdBa1; setiform teeth of MdBa1; hook-shaped outgrowth on E1 of MaxBa1; (?) heavy seta on E4 of MaxBa1; (?) heavy seta on E5, MaxBa2; pointed outgrowth next to terminal seta/spine of P1-P4Re3; similar outgrowths flanking lateral spines of P2-P4Re1, 2; disto-medial double spine on P4Ba1; lateral point on P2Ri1+2; lateral points on P3-4Ri1; disto-lateral point on P3-4Ri2). — Structures that are completely continuous with the somite or segment they originate from, by both integument and internal lumen; consequently non-mobile; of varying shapes and dimensions.

2. Articulating setae (e.g., on the furca and on one or more segments of each of the appendages; including the terminal seta of P1Re3). — Elongate,

tapering structures with generally swollen bases; more or less flexible; inserted via an articulating joint in distinct interruptions of the surrounding integument; chitin walls not related in thickness to the integumental lining of the supporting structure (i.e., ramus or segment); internal lumen not directly continuous with that of supporting structure but connected via narrowed opening; lumen filled with diffuse tissue and/or tissue-fibres, and body-fluid. One or more modified sites are present along the length of natatory setae (P1-4); a breaking plane is present in the proximal half of many of the other setae. Setae are either smooth or plumose, spinulose, pectinate, serrate (with denticles), or equipped with a combined armature, either in single or multiple rows, or diffuse. Dimensions variable: length 40-1300 μm; Ø at base 2-50 μm.

3. Articulating terminal spines of P2-P4Re3. — Despite their different appearance and apparent rigidity, these spines are comparable with natatory setae in all aspects of insertion, internal lumen, and the presence of a modified site. The armature consists of a dense plumosity along the medial edge, the lateral edge is serrate. Dimensions: width × length up to 60 × 450 μm.

4. Articulating spines (e.g., the short lateral spines on the various segments of P1-P4Re). — Short, bluntly pointed structures with broad bases; directly comparable in structure and type of insertion to articulating setae but apparently more rigid and of a constant shape; traces of a modified site are present at c. 0.30 of a spine's length; either smooth or pectinate. Sizes (Ø at base × length) vary from 30 × 80 to 40 × 140 μm.

Nos. 5-8 comprise secondary structures on setae and spines:

5. Setules (e.g., on all plumose setae; on the terminal spines of P2-P4). — Long and slender, articulating outgrowths of the integument; inserted at discrete, concave sites; bases widest, evenly tapering to fine tips; cross-section flattened; apparently very flexible; no internal lumen. Placed in one or two single rows, in the latter case on opposite edges of the seta; serially arranged, either spaced or contiguous. Dimensions (Ø at base × length) in μm: on natatory setae, 2 × 80 (coarse plumosity) or 0.5 × 45 to 1 × 80 (finely plumose); on other setae, 0.5 × 40 to 1.5 × 125.

6. Spinules on setae or spines (e.g., on spinulose setiform tooth of Md; on many of the setae of Mxl, Max, and Mxp; on the lateral spines of P2-P4Re1-3). — Stout, tapering structures, often acutely pointed; cross-section either flattened or rounded; other characteristics the same as for setules but apparently more rigid. Arranged either scattered or serially, spaced or contiguous, in the latter case forming a pectination. Pectinations may be single, double, or multiple, but are generally concentrated on one side of a seta or spine. In a bipectinate condition, the rows proximally converge to end in

TABLE VI

Presence or absence of integumental organs on the swimming legs in the *Euchirella messinensis* female

Site		P1	P2	P3	P4	
P*x* - Ba1	- af - 1	slit	slit	slit	slit	
P*x* - Ba1	- le - 1	peg	slit	slit	slit	
P4 - Ba1	- pf - 1				hair	
P4 - Ba1	- pf - 2				hair	
P4 - Ba1	- pf - 3				hair	
P4 - Ba1	- pf - 4				hair	
P4 - Ba1	- pf - 5				hair	
P*x* - Ba2	- af - 1	conc	conc	conc	conc	
P*x* - Ba2	- le - 1	spin	spin	spin	spin	
P4 - Ba2	- pf - 1				hair	
P4 - Ba2	- pf - 2				hair	
P4 - Ba2	- pf - 3				hair	
P*x* - Ba2	- pf - 4		peg	peg		
P1 - Re1+2	- af - 1	slit	—	—	—	
P1 - Re1+2	- pf - 1	tub	—	—	—	
P1 - Re1+2	- pf - 2	circ	—	—	—	*)
P*x* - Re1	- af - 1	—	slit	slit	slit	
P*x* - Re1	- af - 2	—		clo	clo	
P4 - Re1	- pf - 1	—			hair	
P*x* - Re1	- pf - 2	—	circ	circ	circ	*)
P*x* - Re2	- af - 1	—	clo	clo	clo	
P*x* - Re2	- pf - 1	—	slit	slit	slit	
P*x* - Re3	- af - 1		clo	clo	clo	
P*x* - Re3	- af - 2		clo	clo	clo	
P*x* - Re3	- af - 3	slit	slit	slit	slit	
P*x* - Re3	- pf - 1	tub	slit	slit	slit	
P1 - Ri1+2+3	- af - x	complex of 4-5 tub's	—	—	—	
P2 - Ri1+2+3	- af - 1	—	conc	—	—	**)
P*x* - Ri1	- af - 2	—	—	conc	conc	
P*x* - Ri1	- af - 1	—	—		slit	
P2 - Ri1+2+3	- af - 2	—	tub	—	—	**)
P*x* - Ri3	- af - 2	—	—	tub	tub	
P*x* - Ri3	- af - 1	—	—	unc	unc	

Legends. —

Coding and legends the same as in table V; see also legends of table IV; moreover: (open) = not present; — = not comparable.

*) and **) These represent comparable sites for the various legs, despite different coding, which results from differences in segmentation of the legs.

one or two single, median spinules. Dimensions (Ø at base × length): scattered spinules 3 × 10 to 2 × 45 μm; in pectinations up to 4 × 20 μm for the largest proximal spinules, distally decreasing to 0.5 × 3 μm and less.

7. Serrations on setae or spines (e.g., on serrate setiform tooth of Md; on terminal spines of P2-P4Re3). — Comparatively shallow, acutely pointed emergents of the cuticle, apparently rigid; no independent lumen, though the internal limits of the integument of seta or spine more or less follow the externally present protrusions. Arranged in single or multiple rows, rather densely packed; often diminishing in size from proximad to distad. Dimensions: width at base × length, 2 × 5 to 20 × 30 μm.

8. Denticles on outer edge of terminal seta P1Re3. — Short and flattened, rigid emergents of the cuticle; shape trapezoidal; no lumen. Placed in a single, contiguous row. Size (length × height) up to 5 × 15 μm, decreasing distally.

9. Hairs delimited at base (e.g., on Ur5; on furca; on A2Ba1; on MxlBa2 and its endite; ? on heavy seta of MaxBa1, E4; on P1-P3Ba1; on P1Ba2; on P1Re1+2 mediad and laterad; on P2-P4Re1; on P3-P4Re2; on P1-P4Re3; on P1Ri; on P2Ri; on P3-P4Ri1-2). — Long and slender, tapering, flexible structures; cross-section flattened or rounded; distinctly delimited at the base, which is often widened; inserted directly on somite or segment at discrete, concave sites, which often protrude as shallow pedestals; no visible lumen. Arranged in loose or dense brushes, or serially in single or multiple rows, either spaced or contiguous. Dimensions: Ø distad to base 0.5-3 μm; length 10-225 μm.

10. Hairs in fringe on Ur3. — More flattened and more acute, relative to the hairs under (9); detached hairs have not been observed, so type of insertion uncertain; other structural details apparently not essentially different from other primary hairs. Placed in a densely contiguous row. Width × length c. 1 × 30 μm.

11. Spinules with pedestals (e.g., ? on A2Ri2+3; ? on MxlRe; on MaxBa1, E1-4; ? on MaxBa2, E5; on MxpBa1-2; on P1Ri). — Short and stout, cone-shaped structures, apparently rigid and of a constant shape; cross-section rounded, sometimes flattened; either acutely or bluntly pointed; bases often widened; inserted directly on somite or segment, on protruding pedestals which are equipped with a discrete, concave insertion-site; no visible lumen. In case of the structures on A2Ri2+3, MxlRe, and MaxBa2, the presence of pedestals could not be determined with certainty. Arranged in dense patches or in single or multiple rows, often contiguous. Dimensions in μm (Ø at base × length): on A2Ri2+3, 0.5 × 10; on MxlRe, 0.5 ×

12; on MaxBa1, 1.5 × 15; on MaxBa2, 0.5 × 10; on MxpBa1, 1.5-2 × 2-8; on MxpBa2, 1.5 × 6-15; on P1Ri, 1.5-2 × 4-6.

12. Hairs/spinules without pedestal (e.g., brushes on genital operculum; all patches in the oral region; on MdBa1; on 1st and 2nd inner lobe of MxlBa1). — Short or elongate, tapering structures; often acutely pointed; more or less flexible; bases smoothly merging into the surrounding integument, never discretely marked; apparently no lumen. Arranged in loose or dense patches or in rows. Dimensions variable; see the specific descriptions.

13. Aesthetascs (on various segments of A1). — Relatively large, fusiform organs with rounded apices; covered by thin, membranaceous integument; type of insertion comparable to setae and spines; definite internal lumen filled with cellular material, among which many nerve-fibres (cf. Ghiradella, Case & Cronshaw, 1968a, b, c). Dimensions: 0 × length, c. 10 × 200 μm.

DISCUSSION

Descriptions of Calanoid Morphology

More than 200 years have passed since the first species of calanoid copepod was described by Gunnerus (1770) as *Monoculus finmarchicus*. Yet, calanoid taxonomy has not progressed beyond the initial inventory stage, descriptions of authors being adequate only to place new species in a certain genus and to distinguish them roughly from their congeners. There have been two notable exceptions to this general rule: W. Giesbrecht and W. Vervoort, who both included as many morphological details when describing a species as they apparently were able to discern. However, the scrutiny of these authors has not been followed, let alone enhanced and the present-day result is, that previously published descriptions are largely unsuitable for tracing phylogenetic relationships within the Calanoida.

The above recognition seems the more peculiar when compared to various other branches of micro-crustacean taxonomy, as, e.g., in the Ostracoda, the Conchostraca, and, more or less, in the Cladocera and various groups of the Amphipoda. Taxonomists working in those taxa have since long reached a high level of precision, and at the same time have achieved a remarkable uniformity in their descriptions. What could possibly be the reasons for copepodologists to lag so far behind? Of course, such reasons must be severalfold and in my opinion the most important ones include the following:

1. Unlike many other groups of micro-Crustacea, the Calanoida are hardly known from the fossil record. Therefore, taxonomists have never suffered from a lack of systematic characters, as do palaeontologists as a

result of the nature of their material. Moreover, the Calanoida represent a relatively small group of some 2000 species, so there generally was no need to characterize a species by anything else than its more obvious characteristics.

2. Apparently, their own geographic position or the availability of some large plankton collection at hand have restricted authors in their ambition of recruiting materials from abroad. The indirect importance of pelagic copepods for commercial fisheries, for the study of food chains, etc., will also have dictated more than once the presentation of a concise identification manual, of use to biologists of other disciplines and covering a restricted area only. As a result, most authors have confined themselves to working on particular collections or areas, thus producing extensive, annotated lists of localities rather than works with an actually taxonomic approach: the true revisions produced up till now are only a few.

3. The methods of study used in copepodology may also have promoted superficial descriptions to be drawn up: proper dissection of specimens has not always been performed and, if it was, the habit of staining will have resulted frequently in many fine details becoming obscured. Besides, examination of in toto specimens with the dissecting microscope only is inadequate to reveal all details present. On the other hand, appendages should be studied employing parallel observations of slide preparations by compound microscope and of parts in situ under the stereo-microscope; this, in fact, was already pointed out by Hansen (1893), but seems to have been hardly ever followed.

As a matter of fact, the above litany needs not be conceived as being confined to the Calanoida. In dealing with parasitic forms, Kabata (1979: i, 44) also stated that, until recently, our knowledge of copepod morphology was "deplorable". So, what the author hopes to accomplish is, that future calanoid research will yield extensive and standardized descriptions, resulting more often in a phylogenetic approach of the taxonomy of the Calanoida. This does not mean to advocate, however, that a lengthy description as presented herein should be drawn up for every species. On the contrary, descriptions should preferably be much conciser, provided that these can refer to a thorough knowledge of the type-species of the genus concerned.

Calanoid Biology and Internal Anatomy

The existing literature on the biology of Calanoida is considerable, but data are largely scattered. More or less exhaustive accounts have been presented for only two species, viz., *Calanus finmarchicus* (Gunnerus, 1770) and *Pseudocalanus elongatus* (Boeck, 1864) by, respectively, Marshall & Orr (1955) and Corkett & McLaren (1978). Because of the multidisciplinary approach to a single species, these studies are of great significance for a proper understanding of calanoid biology. Remaining records deal with differing aspects of the biology of a variety of species and, together with the above monographs, constitute what is known about 'general calanoid biology'. Such knowledge has been summarized in various textbooks (e.g., Rose, 1933; Brodskii, 1950) while recent reviews are given by Dussart (1967, 1969) and Owre & Foyo (1967). Data on Aetideidae were briefly summarized by Bradford & Jillett (1980). A review of specific data on the biology of *Euchirella* spp. will be included in Part II-B of the present study (Von Vaupel Klein, in prep.).

Detailed reports on internal anatomy are available for *Calanus finmarchicus* (cf. Lowe, 1935) and *Epilabidocera amphitrites* McMurrich, 1916 (cf. Park, 1966). Moreover, the classical account of Claus (1863), though in places out of date, presents information on general anatomy of free-living copepods. Hartog (1888) already presented a detailed report on the internal anatomy of *Cyclops*, whereas exhaustive accounts for harpacticoids have been given by Lang (1948a) and Fahrenbach (1962). Together, these papers provide an adequate reference framework for general considerations about the internal organization of Calanoida, and will accordingly be referred to in the proper context.

CODING SYSTEMS

Throughout the descriptions, various structures have been described by code-numbers, -letters, or -symbols. Apart from the old-established abbreviations for body tagmata and appendages, coding is applied to: (a) the chaetotaxy of the oral field; (b) the chaetotaxy of the first inner lobe of the maxillule; (c) the spinulation on the primary seta of the maxilla's fifth endite; (d) the sites of integumental organs on the body as well as (e) on the appendages; and (f) characterization of the integumental organs. Basic requirements for any coding system are, that (1) it should be as simple as possible or, if complex codes are inevitable, it should at least be easy to be read; (2) its construction should be sufficiently versatile to comprise new elements without affecting the stability of the already present codes. With the exception only of integumental perforation sites of the body (Fleminger, 1973), none of the structures mentioned has ever been assigned a code. Thus, the systems presently designed could be based on the conditions in *Euchirella* only. This obviously stresses the need for a versatile character, since new elements are likely to require accomodation in the various systems. It is also clear that the coding systems can only be provisional, because those to be adopted as definite should eventually be based on a survey throughout the Calanoida or, preferably, all of the Copepoda. The codes introduced under (a), (b), and (c) conform to the criterion of simplicity, whereas those under (d) and (e) are admittedly complicated but may easily be read; the symbol-code (f) is both simple and accessible. Criteria of versatility-stability will be discussed for all systems separately.

The existing 'system' of descriptive names designed by With (1915) for the oral field chaetotaxy was left, because it does not meet requirements of simplicity and versatility and also because it is far from being complete: only the more obvious elements were included by With. The versatility of the present number-code is gained by the possibility of adding a second coding unit in cases of insertions or asymmetries, thus avoiding re-numbering. The original figure the new codes are derived from, should be characterized by a zero for a second unit (e.g., a new element between 12 and 13 is coded 12.1, 12 becomes 12.0, and 13 remains unchanged). The codes for the patches of hairs and spinules on the maxillule's 1st inner lobe may be replenished in the same sense. Here, anterior and posterior faces are numbered separately, so addition of an element on either one side does not affect the codes on the other. The code for the spinulation of the maxillary seta (c) is extremely simple and does not require further explanation.

The integumental organs are characterized by complex site-codes and by symbols as well. The system adopted is primarily based on Fleminger's (1973) design which is considered convenient and adequate, be it that two modifications proved to be necessary. The first involves subdivision of the cephalic region into transverse stretches corresponding with the various appendages: in the species of *Eucalanus* with their elongate bodies, these divisions may be clearly distinguishable but in the rostro-caudally compressed body of *Euchirella* they are not. Hence the cephalic region has not been subdivided in Fleminger's sense. Secondly, the distinction Fleminger (1973) made between tergal and pleural sites cannot be maintained. Not only is the boundary he draws arbitrary and vague, it is also incorrect, as the pleurites have been shown in the present description to represent a much smaller portion of the dorso-lateral integument than Fleminger apparently assumed. In this context it is relevant to mention a forthcoming study of J. R. Mauchline (see Mauchline, 1977) which will deal with perforation signatures of the body in over 230 species of calanoid copepods. The construction of a more generally applicable coding-system may be expected, once these data will become available.

The coding system for integumental perforation sites of the appendages has been grafted on the same principles as that used for the body. The consecutive tagging of sites on a given aspect of a segment, as briefly explained in the caption of table V, simply forms a linear proximal-to-distal order in the case of edges. As regards segmental faces, the sequence as stated should be interpreted as a clock-wise spiral when observing a left-hand appendage in either anterior or lateral view, whichever is appropriate. As in the case of the body integument, it would have been preferred to take more species into consideration when designing the code. The only noteworthy account of integumental organs of the appendages, however, is the paper by With (1915), who tentatively composed (his pp. 4-5) a pattern of the "original numbers of pores" present on the calanoid swimming legs. Yet, as With mentions primarily the large slit-shaped pores and only incidentally any other organs, his report does not yield many data of interest in a comparative study. Versatility and stability of the codes of integumental perforations involve similar constructions as outlined for oral field chaetotaxy, above.

A final remark should be made about the abbreviations used for body parts and appendages. This system was designed by Giesbrecht (1892), based on Latin terms (not, as Fleminger (1967) supposed, by Giesbrecht & Schmeil, 1898) and has since been used throughout copepod literature, with various slight modifications. It constitutes a permanently applicable system of codes, and its continued use in morphological descriptions deserves to be acknowledged as promoting universal stability in terminology.

Morphological Terminology

The terminology used in descriptions of calanoid morphology is manifold, due to the lack of one coherent set of terms for all of the Copepoda. The 'system' most widely in use today is based on the classical 19th century terminology (e.g., Claus, 1863; Giesbrecht, 1892; Giesbrecht & Schmeil, 1898), with some modifications originating from comparative studies on segmentation of appendages and on characterization of body tagmata (e.g., Hansen, 1893, 1925, 1930; Sars, 1901-03; Borradaile, 1926; Gurney, 1931; Heegaard, 1945, 1947a, b). The propositions of these investigators have been followed to a varying degree by subsequent workers, but no single system has proven convincing enough to be adopted completely. The definite set of terms should obviously reflect true homologies and thus be founded on copepod phylogeny, eventually in relation to the other Crustacea. This includes determining the composition of body and appendages in the Ancestral

Copepod. Though conclusive results should await at least some substantial progress in copepod macrosystematics, a few remarks may be made from the anatomy of *E. messinensis* which may aid in interpreting structures in other Calanoida. Since such remarks are of relevance only in the proper context, they will be presented below under the specific headings.

As I have pointed out before (Von Vaupel Klein, 1980), the introduction of a single, coherent set of changes in terminology should be preferred to an endless stream of small emendations. Therefore, I am not venturing to change any term in the present paper. Instead, I am applying those terms which, in my opinion, are most commonly used and which cannot be misinterpreted. Yet, I am well aware that also this provisional choice may be disputed, as even in the principal works on Calanoida discordances exist with regard to the use of morphological terms (cf., e.g., Giesbrecht, 1892; Sars, 1901-03, 1924-25; A. Scott, 1909; Wolfenden, 1911; Sewell, 1929, 1931, 1947; Gurney, 1931; Wilson, 1932; Rose, 1933; Brodskii, 1950; Tanaka, 1956-65; Vervoort, 1957, 1963, 1965; Owre & Foyo, 1967; Dussart, 1967, 1969). Some authors have tried to perceive true homologies and thus consistently use equivalent terms for supposedly comparable structures (e.g., Hansen, 1893, 1925, 1930; Borradaile, 1926; Heegaard, 1945, 1947a, b). Others have merely made an inventory of the status quo and thus have named structures in a purely descriptive way (e.g., Giesbrecht, 1892; Rose, 1933; Lang, 1948a; Brodskii, 1950). Reviews and evaluations of terms used throughout copepod literature have been given by Gurney (1931), Lang (1948a), Gooding (1957, 1960), Illg (1958), Fleminger (1967), and Dussart (1967-69), but none of these authors has been able to present a better solution to universality in terminology than his personal view as to which terms might presumably be correct in a homological sense, and which would be the most practical. Therefore, various other workers in this field have come and are still coming with their own ideas as well, and the various terminologies advanced during the last decade, of which those by Ferrari & Bowman (1980) and McLaughlin (1980) are only two of the most recent examples, all constitute sincere attempts at bringing order and uniformity to descriptive nomenclature. However, equally well all suffer from a lack of support, in the absence of a sufficiently detailed and sufficiently comprehensive knowledge of copepod, c.q. crustacean, comparative morphology. Current terminology, therefore, may be characterized after Gurney (1931: 36) as "a compromise between custom, convenience and homology".

Nomenclature of Body Tagmata

In the classical 19th-century terminology (e.g., Claus, 1863; Brady, 1878, 1883; Giesbrecht, 1892) the two principal tagmata of the calanoid body were variously denoted as 'cephalothorax' and 'abdomen', 'anterior body' and 'posterior body' or equivalent terms. The use of the former pair of names bears evidence of the underlying idea that the arthropod body is primarily divisible into cephalon, thorax, and abdomen, which is unquestionably of entomological origin; the latter pair expresses cautiousness as regards the validity of such homologizations.

Sars (1901), in seeking homology with malacostracan tagmosis, assumed the development of the mesosome (= thorax minus maxillipedal somite(s)) to be suppressed in copepods and thus introduced the terms 'cephalosome' (= cephalon + Mxp-somite), 'metasome', and 'urosome', the last two representing a subdivision of the primary abdominal tagma. However, Sars' ideas have not been accepted (e.g., Gurney, 1931), and this may explain why his terminology has been largely neglected, initially. It was only after Wilson (1932) resurrected the terms of Sars, that these have been more widely acknowledged, even to the present day, because they are convenient to express views upon rearrangement of somites from the supposedly original crustacean tagmata into the present functional regions of the copepod body. Gooding (1957) introduced 'prosome' for cephalosome + metasome, whereby distinction of the two divisions anteriad and posteriad to the major articulation of the body became possible also in the new terminology. Most twentieth-century investigators agree, or simply conform, to the idea that the functional head region is derived from the cephalon plus the first thoracic (= maxillipedal) somite, and that the original Th7 together with the former abdomen constitute the urosome, the intermediate region comprising the remaining thoracic somites.

Disregarding general considerations on the composition of the anterior end of the arthropod body (see below), the original cephalon is thought to consist of six primary somites, viz., including those successively bearing the eye-stalks (though not developed in Copepoda), the A1, A2, Md, Mxl, and Mx2. Yet, with the exception of Lang (1948a) and Illg (1958), all authors also include the maxillipedal somite in the anterior body region, which is described as 'cephalosome', 'cephalic region', 'head', or by an equivalent term (e.g., Pesta, 1928; Gurney, 1931; Rose, 1933; Brodskii, 1950; Gooding, 1957; Dussart, 1967; Fleminger, 1967; Owre & Foyo, 1967; Kabata, 1979; Fleminger & Bowman, 1980). This concept has also been employed by Wilson (1932) and Vervoort (e.g., 1957, 1963, 1965) although they denote the head as 'a single segment' or as the 'cephalic somite', which should, however, be appreciated merely in an exclusively descriptive sense. The only hypothesis seriously in discordance with the above is that of Heegaard (1945). Based on the postulate that the 'lateral cuticle spine' (= post-antennary process) be referable to a true appendage instead of a cuticular spine, this author assumed that originally a pair of 'first maxillae' was present in front of the maxillules, and that consequently the primary cephalon be terminated by the present maxillulary somite. Though in his earlier work Z. Kabata conformed to this Heegaardian view, he recently (Kabata, 1979) changed his mind.

Recognition of the somite of the maxillipeds as a thoracic element has apparently been founded primarily on considerations of homology between copepods, malacostracan crustaceans, and other arthropods (e.g., Hansen, 1893): if a head composed of six fused somites is accepted, it automatically follows that the next somite in line belongs to the original thorax. This postulate seems to have been supported by the reconstruction of the triassic fossil *Euthycarcinus kessleri* Handlirsch, 1914, in which the somite in question was tentatively described as separate from the head and bearing biramous appendages. The description (Handlirsch, 1914) and its discussion (Pesta, 1915) were extensively reviewed by Gurney (1931), who qualified this part of it as "pure guesswork" (p. 35) but all the same conformed to the consequent morphological implications. The connection of the proximal segments of the maxillipeds in some copepods by an intercoxal plate, directly comparable to those of the natatory legs, has likewise been regarded a strong argument in favour of a thoracic origin of the Mxp-somite (cf., e.g., Lang, 1946, 1948a). Apparently, authors have not been very much impressed by the similarity in structure of maxilla and maxilliped in at least some Calanoida, which admittedly may be caused by functional convergence. The recent discussion upon the possibly polyphyletic origin of the Arthropoda (cf., e.g., Manton, 1977; Gupta, (ed.), 1979) appears not to have influenced views upon this aspect of copepod tagmosis, either (see also below).

The classical use of the term 'cephalothorax' has never been consistent throughout literature. Either it refers to the anterior complex of the body, comprising the head and one or more thoracic somites, or it describes the complete 'anterior body', while some authors (e.g., Claus, 1863) employed the term in both meanings. Wilson (1932) explicitly restricted the use of 'cephalothorax' to denote a fused complex of 'head' (including the Mxp-somite) plus one (or more) succeeding thoracic somites. However, Wilson's action has hardly contributed to a more consistent use of the term until Gooding (1957) re-established it in its Wilsonian sense (though not referring to Wilson). Both Lang (1948a) and Illg (1958) also redefined 'cephalothorax' as a fused complex of cephalon plus one or more thoracic somites. However, as a consequence of their respective definitions of the head, the authors cited arrive at different conclusions as to the shortest tagma that possibly may be qualified as a cephalothorax: in Lang's and Illg's sense, it may include cephalon + Mxp-somite only whereas by the Wilsonian definition the somite bearing the first pair of swimming legs has to be involved in the complex as well. The former terminology, to my knowledge, has not been followed but that founded by Wilson (1932) has been adopted, upon its revival by Gooding (1957), by, e.g., Dussart (1967, 1969), Fleminger (1967; though not explicitly), and Kabata (1979). Owre & Foyo (1967) quite confusingly consider 'cephalosome' to be equivalent to 'cephalothorax' sensu Gooding.

The remaining section of the anterior body consists of the thoracic somites situated between the maxillipedal somite and the major articulation of the body. Despite recognition of the incorporation of thoracic elements in both cephalon and urosome, the intermediately remaining part is quite often denoted as 'thorax' (e.g., Pesta, 1928; Gurney, 1931; Brodskii, 1950; Owre & Foyo, 1967). Others have adopted Sars' (1901) term 'metasome' (e.g., Gooding, 1957; Fleminger, 1967), while equivalent use of both terms has been indicated by Rose (1933), Lang (1948a, b) and Dussart (1967-69). Seriously confusing are the respective concepts of 'metasome' as adopted by Wilson (e.g., 1932, 1950) and Owre & Foyo (1967). The former has applied this term to the entire anterior body, apparently based on an erroneous interpretation of Sars' (1901) definition, as pointed out by Gooding (1957). Owre & Foyo (1967) on the contrary, consider the metasome as only comprising the free thoracic somites, i.e., those not fused into a cephalothorax sensu stricto, and not incorporated in the urosome.

The presumably thoracic nature of the first somite contained in the calanoid urosome is deduced from (a) reference, in a homological sense, of the somite bearing the gonopores to the 6th and 8th thoracic somites of female and male Malacostraca, respectively, and (b) from the presence of a vestigial sixth pair of legs in some podoplean copepods. It is generally agreed that this former seventh thoracic somite, though commonly denoted as Th6, comprises the genital somite of male calanoids while Th6 plus the original 1st abdominal somite together form the composite metamere constituting the female genital complex. Though a few authors ignore the latter consideration by labelling the female Gnsom merely as 'Abd 1' (e.g., Rose, 1933; Brodskii, 1950) it may hardly be assumed that their terminology has more than simple, descriptive significance. Two views, however, represent a major discordance to the above scheme: the first is that of Gurney (1931, fig. 2) who considered the female genital complex to be composed of two thoracic somites, i.e., Th6 + Th7 [as: Th7 and Th8]. Next, Owre & Foyo (1967) have an aberrant point of view, viz., that the genital somite in male and female alike comprises only the single somite Th6. The erroneous thoughts of Giesbrecht (1899) about the non-homologous nature of the fifth pedigerous metamere in gymnoplean and podoplean copepods, including, respectively, the disappearance of Th6 and Th5, have long been abandoned, as has been outlined in extenso by Gurney (1931) and Lang (1948a).

So far, we have dealt with the situation of the major caesurae between the primary tagmata of the body and their possible reference to the present functional tagmosis of the Calanoida. Two other penetrating questions concern the composition of both the anterior and the very posterior end of the body.

First, the discussion about the composition of the head region of the arthropods, including crustaceans, has not at all been settled, as evidenced by the repercussions of various hypotheses, summarized by, e.g., Smith (1923), Fahlander (1938), Vandel (1949), Borradaile et al. (1963), Sharov (1966), Kaestner (1967), Barnes (1968), and Storer et al. (1971). In particular the position of the presomital acron, whether or not bearing the eye-stalks or possibly homologous structures, and whether or not including the antennulary 'somite', is still obscure. Likewise, the proper reference of the labrum, either to a sternal structure, or to a pair of fused 'appendages', either corresponding to a part of the acron or to an 'intercalary' somite, is as yet uncertain. Once properly established, the correct situation will have to be expressed in the terminology denoting the body regions and in the consecutive numbering of somites. This obviously is not a specifically copepodan problem, but relates instead to all of the Arthropoda. Apart from the handbooks mentioned, reference of copepod morphology to cephalization in crustaceans and in arthropods in general has been made by, e.g., Hansen (1893, 1925, 1930), Heegaard (1945, 1947a, b), and Dahl (1956a, b, 1963).

The complex formed by anal somite, anal operculum, and furca, has also been variously interpreted. After Giesbrecht (1892), the anal somite is usually considered to be the last true somite, bearing a pair of caudal rami, whether or not homologous with 'true' appendages, and a lobular outgrowth constituting the anal operculum. However, some authors do not consider the anal somite (or 'perianal ring') a true somite (e.g., Illg, 1958) while others, on the contrary, even regard the furca to be a completely cleft true somite (e.g., Claus, 1863), the classical views having been reviewed by Lang (1948a). The latest contribution to elucidate the composition of the terminal region is that by Bowman (1971), who considers the anal metamere as the last true somite, bearing a reduced, non-articulated 'telson' in the form of the anal operculum, whence the furcal rami should be considered equivalent to the malacostracan pair of 'uropods'. Recently also Kabata (1979) has adopted this theory of Bowman.

In these respects, the recent discussion on the possibly polyphyletic origin of the Arthropoda (cf., e.g., Manton, 1977; Gupta, (ed.), 1979), is of interest, as it appears to preclude a solution of these aspects of copepod tagmosis by comparison with other arthropod groups. As Manton (e.g., 1977) has shown, the embryological development of crustaceans indicates that the primary head region at best may be conceived as comprising the anterior end of the body up to and including the mandibles, because of the lack of distinctness between these somites, dorsally. However, at the same time she stipulates that (1) the adult configuration of appendages relative to the oral opening is irrelevant for their characterization, as all corresponding somites, including the pre-antennulary somite, are ontogenetically postoral in origin; and (2) that the posterior limit, between head and trunk regions, is in fact not clearly demarcated, indicating the absence of a fundamental distinction of body regions between acron and telson, other than the individual somital boundaries. Next to Manton (1977), others have also seriously questioned the fundamental difference between thoracic and abdominal somites (e.g., Dahl, 1963; Tiemann, in press). This would consequently imply a mere linear enumeration of all sixteen to eighteen originally present somites, whether or not including distinctions for, e.g., head, genital, or anal region. The presence of vestiges of a seventh and eighth pair of legs in some Harpacticoida (e.g., Lang, 1948a) has obviously contributed to such a concept. Moreover, the absence of a subdivision in the long 'trunk' of the presumably primitive crustacean order Remipedia (cf. Yager, 1981) also pleads in favour of the secondary nature of the tagmosis of the other Crustacea, including copepods.

Notwithstanding the above considerations, the use of 'cephalothorax' sensu lato has persisted to the present day (e.g., Farran, 1929; Sewell, 1929, 1931, 1947; Brodskii, 1950; Vervoort, 1957, 1963, 1965) and seems to be more widely in use than Gooding's (1957) 'prosome', which has been adopted by, e.g., Fleminger (cf. 1967) and Ferrari & Bowman (1980). Though Brodskii (1950: 16) defines 'cephalothorax' in the sense of Wilson (1932), he invariably uses it to denote the complete anterior body in his descriptions. As regards the terms describing the limbless posterior body, 'abdomen' has been used by, e.g., Pesta (1928), Farran (1929), Sewell (1929, 1931, 1947), Gurney (1931), Brodskii (1950), and Vervoort (e.g., 1957, 1963, 1965), while 'urosome' has found wider acceptance, in particular recently (e.g., Wilson, 1932; Gooding, 1957; Illg, 1958; Fleminger, 1967; Owre & Foyo, 1967; Ferrari & Bowman, 1980). Unfortunately, reference of abdomen and urosome to each other as equivalent terms has also been made (Rose, 1933; Lang, 1948a; Dussart, 1967-69) but as this is confusing, it should be avoided. Owre & Foyo (1967) consider 'abdomen' in a restricted sense, i.e., excluding the genital somite (= genital complex in the female). The same stand has been taken by Kabata (1979), following from this author's concept that the female genital tagma is "at least partially thoracic [in] nature" (p. 2). Although an aberrant view as such is to be respected, the uncritical use of the term 'abdomen' only for those somites posteriad to the genital complex adds even more to confusion and should thus be considered undesirable.

A consequence of considering the maxillipedal somite as the first true thoracic one would be to number it Th1 as well. However, this is hardly ever practised, and most authors just start numbering the metamere bearing the first pair of legs as Th1 and so forth. To avoid this obvious ambiguity, a minority of investigators prefers Gooding's (1957) term 'pedigerous somite' (Pg), allowing these somites to be numbered in a non-committal way 'Pg1' to 'Pg5', concurrently with the 1st to 5th pairs of natatory legs (e.g., Fleminger, 1967; Ferrari & Bowman, 1980).

So, in all, none of the above 'systems' seems to be completely satisfactory because descriptive terms either do not reflect homology, are ambiguous, or have been confused too often. This is why the classical use of 'cephalothorax' (i.e., sensu lato) has been retained by the present author, along with the concept of a 'cephalon' including the maxillipedal somite, and the enumeration of the pedigerous somites as Th1 to Th5. The term 'urosome', however, has been adopted to indicate the composite nature of the posterior body region as the abdomen plus (at least) one former thoracic somite. Unfortunately, the anatomy of *E. messinensis* does not appear to provide clues to any of the above questions that are still in dispute at present. Thus, only some functional considerations regarding the composition of the body will be given below.

THE CEPHALOTHORAX

Fusion and Reduction of Somites

The extent to which somites are capable of functioning as separate units may be considered an inverse measure for the degree to which they are fused. Criteria to determine this condition are the course and insertion of muscles and the intimateness of connections between sclerites.

In the case of the boundary between cephalon and thoracic somite 1, accounts of authors vary as to the extent of fusion of the dorso-lateral sclerites accomplished in *Euchirella* spp., due to the varying degree of visibility of the pleuro-tergal suture by light microscopy. As observed on the present material, this criterion is not reliable: while any optical technique involving the examination of in toto specimens failed to reveal more than only the dorsal stretch of the suture, the S.E.M. demonstrated its presence all along the pleuro-tergal boundary. The exact nature of the coalescence can only be established by studying preparations of longitudinal sectionings. However, observations in situ show that the fused track is relatively weak compared to the surrounding, continuous integument. Damages involving tearing of the pleuro-tergites regularly coincide with the line of fusion, and separating the cephalic and 1st thoracic pleuro-tergites proved to be relatively easy. Yet, movements of the first thoracic somite relative to the cephalic complex are not likely to be possible any more. The anterior ridge, as present on free somites, is completely absent, while the trunk musculature is continuous all along C-Th1. Besides, this character appears not to be constant in *E. messinensis*, since in specimens from the Western Atlantic no trace of the suture could be discovered (cf. Von Vaupel Klein, in prep.). Therefore, I doubt variation in the presence of this suture to be characteristic at the specific level, in which quality it is often presented in the course of descriptions.

Thoracic somites 4 and 5 are invariably characterized by authors as being 'completely coalesced'. However, from the absence of a fifth pair of legs and the disappearance of corresponding musculature, some reduction may also be expected. In *E. messinensis*, the pleuro-tergal remnants of somite 5 are reduced to the extreme posterior rim of the combined somite. The degree of fusion between somites 4 and 5 indeed is high: though the line of fusion is discernable, there is no indication that this would be a site of easy detachment as in the case of C-Th1. The musculature of Th4+5 does not show any sign of previous independence of the somites and no trace of an anterior ridge on Th5 is found any more. A comparative study of the integumental organs of Th4+5 in *Euchirella* and in *Pseudochirella*, where Th5 is less reduced and still separate, will have to establish if the presence of Th5 may be deduced from the perforation pattern as well.

The remaining articulations of the cephalothorax evidence some degree of fusion between adjoining somites. All sternites are fused to form one long, sternal plate but visible sutures still exist between the functional pedigerous somites. Though the nature of these sutures has not been studied in detail, it is suggested that they are at least in part responsible for the flexibility of the sternal complex, necessary to allow the in- and out-telescoping movements of the pleuro-tergites of CTh1, Th2, Th3, and Th4+5, between which completely free joints exist.

Sclerites of the Body

It is proposed herein to distinguish a large tergal and a pair of small pleural parts constituting the dorso-lateral sclerites of the cephalothorax. This seems to make more sense than designating any other portion of the lateral integument as the pleurite: there is only one distinct boundary between dorsal and lateral elements, viz., the ventral continuation of the chitinous ridge. For the remaining part, the integument is completely continuous with the exception only of an interruption in the anterior ridge (see fig. 2b); this may, however, be related to muscle attachment rather than indicate a former boundary. Lang (1948a) likewise referred to the refolded ventro-lateral integumental flaps ("Hautduplikaturen") that form the 'epimeral plates' of authors, as "pleura" in harpacticoids. Gooding (1957), in dealing with semi-parasitic copepods, also tentatively applies the term "?pleurite" to these structures. The reference Fleminger (1973) makes to the "pleural" areas in the calanoids *Eucalanus* spp. should, in my opinion, rather be assessed in terms of descriptive topography, i.e., indicating 'lateral sclerites' in general.

I have found no other relevant data in literature as regards the pleuro-tergal boundary in copepods, nor does any of the principal works on Calanoida (see p. 60) provide information on the composition of the body integument as considered by its transverse section. Besides, in terms of general crustacean anatomy, accounts referring to the lateral sclerites are not in agreement. Barnes (1968) and Storer et al. (1971) assume the sclerite ring to be composed of tergite, sternite, and a pair of pleurites, just like in other arthropods; McLaughlin (1980: 2) states that the crustacean exoskeleton is "...usually differentiated into dorsal tergite and ventral sternite...". Evidently, no thorough study upon the true nature of the lateral integument of the Crustacea has been made as yet.

This implies that it may even be questioned whether pleurites are present at all. In my opinion, however, copepod anatomy should be considered in terms of general arthropod morphology, i.e., including a pair of pleurites per somite, until the contrary has been proven unequivocally. Then, if the presence of pleurites is presumed, there are two possibilities for their situation: one, as presently suggested, being a small pleurite in the cephalothoracic somites, which forms the ventro-lateral rim of the integumental ring. The other possibility would be that the sternites are considered to be reduced to the midventral track, eventually comprising hardly more than the sternal keels, while the pleurite would in fact reach from the pleuro-tergal boundary (see above) to mediad, beyond the insertions of the appendages. One argument in favour of the last hypothesis would be that in the general arthropodan scheme (cf., e.g., Barnes, 1968), the appendages primarily insert on the pleurites. However, as a shift in position of the insertions, relative to the skeletal elements of the trunk, is frequently found as an answer to functional demands (cf. Manton, 1977), this criterion cannot be decisive by itself. The final solution of this problem thus obviously is a matter for further research.

The sternal keels may, apart from providing rigidity to the individual sternites, be functional in swimming as well. This aspect will be dealt with in discussing the swimming movements of the legs, below.

The Frontal Organ

The term 'frontal organ' has been used for different structures in the Crustacea, even within the Copepoda (cf. Lang, 1948a; Dahl, 1953, 1963; Elofsson, 1963, 1966, 1971). Here, it is being used in the classical, copepodological sense to denote the paired 'frontal sensilla' plus the 'frontal pore' (Park, 1966). The apparently sensory hairs (Dahl, 1953; Elofsson, 1971) are no hair-sensilla as defined elsewhere (Von Vaupel Klein, in press b), because they are devoid of a basal disc as evident from the narrow, slit-shaped hole left by a detached hair (pl. 23g). Whether or not the hairs are of purely integumental nature could not be ascertained but if so, they would undoubtedly form another kind of 'hair-sensillum' than the single type recognized at present.

The exact nature of the frontal pore has not yet been established. Results of Park (1966) revealed that it is internally connected with neural as well as glandular tissues in the calanoid *Epilabidocera amphitrites* McMurrich, 1916. According to Elofsson (1971) these single or multiple pore structures are rather variable throughout the Copepoda but he assumed all of them to contain at least a (chemo-)sensory component.

The Frontal Tubercles

The paired tubercles which support the hairs of the frontal organ are outgrowths of the cephalon and therefore not 'integumental'. As Kabata (1979: 16) states "it is generally agreed that the first somite bears no appendage in copepods". However, a counterpart of the compound eye and its stalk has never been described in copepods, and I suggest the paired frontal tubercles are a likely candidate for acquiring this status. Compound eyes occur throughout the Crustacea, whether sessile or stalked, the latter condition applying to the majority of the Malacostraca (see Dahl, 1963, for a review). The primary light-sensitive organ of copepods is the nauplius eye, while the accessory lenses found in a few genera are simple and apparently of secondary origin (e.g., Claus, 1863; Lang, 1948a). Though no consensus has yet been reached, homology of the eye-stalks with the appendages of an embryonic first (pre-antennulary) somite c.q. a presomital acron, has been proposed more than once (e.g., Smith, 1923; Vandel, 1949; Borradaile et al., 1963; Kaestner, 1967; Barnes, 1968; Storer et al., 1971). The extreme anterior position of the tubercles of copepods would certainly match with such a 'somite' and the innervation of the frontal sensilla by a primary stem of the optic nerve (Elofsson, 1971) would also plead in favour of this hypothesis. Finally, both eye-stalks and frontal organ contain glandular tissues: the endocrine activity of the sinus gland, often situated in the eye-stalk, is well-known (e.g., Lockwood, 1968), whereas the innervation of the frontal pore, also by a branch of the optic nerve (Elofsson, 1971), was found by Park (1966) to be intimately associated with glandular tissue, thus suggesting some neurosecretory activity. Carlisle & Pitman (1961) already established the presence of endocrine activity in neurosecretory fibres connected with the frontal organ of *Calanus* and *Euchaeta*. The apparent similarity of the glandular components, however, has yet to be assessed in terms of homology. The recent discovery of a pair of "pre-antennular processes" in the Remipedia (Yager, 1981) also adds to the probability of the plesiomorphous nature of the presence of 'appendages' corresponding to a pre-antennular 'somite' in crustaceans.

The Oral Field

The chaetotaxy of the oral field has never been studied in detail, with the sole exception of With (1915), who described some oral characters in various calanoids. Most structures found at present could be related to With's figures of *Euchirella* spp. but since his account of the groups of hairs and spinules is not complete, a detailed comparison is not relevant. With (1915: 4-5) already noticed that the fine structures on labrum and labium are of taxonomic importance but that descriptions in literature were either lacking or inaccurate. This statement, regrettably, is still appropriate today. Therefore, the present account can only be an initial inventory of the structures of the oral field.

The functions of the emergents probably include retaining food particles in the oral area, as the hairs and spinules are invariably directed towards the oral opening. There is no evidence for assuming an additional sensory function, yet. The paired papillae on the upper lip could not be characterized in detail, but the absence of ducts indicates the connection with any secretory function to be improbable. It is suggested that a sensory function of some kind be the most likely for these organs. The urn-shaped pores found in the internal wall of the labrum will be discussed in the section on Integumental Organs, below.

Labrum and Labral Papillae

Theories about the origin of the arthropodan labrum are still controversial (Smith, 1923; Vandel, 1949; Kaestner, 1967). It is either regarded as an outgrowth of the sternal sclerites or as a fused pair of embryonic appendages, whether true appendages of a somite, or appendage-like protrusions of (a part of) the presomital acron. It is evident that this question may be solved only in the course of a reassessment of the complete crustacean c.q. arthropodan tagmosis.

The same holds more or less for the labral papillae. As far as I know, no other data are available on the papillae, whence a discussion upon these necessarily is speculative. Yet, I think it worthwhile that they be taken into account in a comparative study regarding other possibly preoral appendages, such as the premandibular 'postantennary process' of some (semi-)parasitic copepods (e.g., Heegaard, 1945; Kabata, 1979), and the 'pre-antennular appendages' recently described from the new order Remipedia (cf. Yager, 1981). To homologize such appendages inter se as well as with 'true' appendages is tempting, but sound conclusions have yet to be reached. Anyway, the position of the papillae in front of the mandibles in combination with their paired nature suggests, that such a relationship cannot be completely precluded.

The Labium

There appears to be no doubt that the lower lip or labium constitutes a purely sternal formation. The structure has been regarded as such throughout literature (e.g., Claus, 1863; Hansen, 1893; Gurney, 1931; Illg, 1958; Kabata, 1979; McLaughlin, 1980). Though superficially the paired 'paragnaths' of a largely cleft labium might be suggestive of a possible relation with former appendages, this apparently is entirely secondary in nature. In fact, Lang (1948a) clearly demonstrated the development of the bifid condition to be variable even at the specific level, whereby such condition evidently is not of fundamental significance. While in some copepods the paragnaths may be distinctly constricted basally, in *E. messinensis* they are completely continuous with the surrounding sternal integument.

THE UROSOME

Genital Somite and Reproduction

Morphological considerations at the organismal level

Reproductive biology primarily affects the genital somite but also the very posterior part of the thoracic region; all structures involved will be dealt with under the above heading.

Reproduction starts with the male locating the female, probably by chemical communication via pheromones (Katona, 1973; Griffiths & Frost, 1976). The way in which the female releases the pheromone into the sea water is not known, but as suggested by Von Vaupel Klein (in press b) the tubular pores in the hairbrushes on sites P2-Ri1+2+3-af-2 and P3/4-Ri3-af-2 might play a role in this process. The male detects the diffused compounds via the aesthetascs on its A1 (Griffiths & Frost, 1976).

The sequence of mating events is quite well understood for various Heterarthandria (cf. Wolf, 1905; Gauld, 1957; Jacobs, 1961; Roff, 1972; Katona, 1975; Blades, 1977; Blades & Youngbluth, 1979); though accounts on copulation in amphascandrian calanoids are still wanting, a roughly analogous pattern may be expected. In the absence of a prehensile antennule, the male will have to seize the female [? with his maxillipeds and next grasp her] genital somite with his right-hand fifth leg. The field of stellate warts as found in *E. messinensis* may either provide a mechanical orientation for the male informing him that the right fifth leg is properly positioned, or serve as a local roughening of the female's exoskeleton to create a better holdfast, or may be both.

Next, the spermatophore is placed by the terminal pincer of left leg 5. The site on the tip of the genital somite's asymmetrical outgrowth apparently is the preferred spot, be it that 50% of the spermatophores are attached at one of the other three sites that have been found occupied. Variability in site of attachment has been considered extensively by Katona (1975), Blades (1977), Hopkins & Machin (1977), and Ferrari (1978, 1980), especially concerning sites away from the vulva proper. However, these authors never found more than one 'alternative' site, whereas another, 'regular' site was always situated on or close to the genital area. It is noteworthy that spermatophores were never found attached directly to the genital field in *E. messinensis*, and that three distinct alternative sites are involved.

From the attached spermatophore a fertilization tubule (Ferrari, 1978) (pl. 9b) grows to the vulval cavity, underlying the genital operculum. Here, the seminal pore(s) and/or gonopore(s) are situated. Despite the fact that once a major division of copepods was based on the presence of either one or two genital pores (cf. Monoporodelphya and Diporodelphya of Canu, 1892), recent accounts of authors vary as to the separate (Brodskii, 1950) or common (McLaughlin, 1980) nature of the orifice of the pair of oviducts in calanoids. Lowe (1935) found a single pore in *Calanus*, while a paired nature of the gonopores has been described by Gruber (1879) and Steuer (1923) for *Acartia*, by Park (1966) for *Epilabidocera*, and by Geptner (1968) for the Euchaetidae. Likewise, accounts of authors are not in conformity as to the common or separate nature of the pores of the primary genital system and those of the seminal storage system (e.g., Brodskii, 1950; Marshall & Orr, 1955; Illg, 1958; Dussart, 1967). The inconclusiveness of these generalizing accounts obviously is due to the fact that no generalizations are possible. In *Acartia*, the paired seminal pores open separately into the vulval cavity, but an internal canal connects the spermathecae to the terminal stretch of the corresponding, paired, oviducts as described by Steuer (1923). In *Calanus*, the paired spermathecal ducts open separately into the extremely short, fused stretch of the oviducts, close to the single, median gonopore (Lowe, 1935). Park (1966) described a similar situation in *Epilabidocera*, with non-fusing oviducts. In the Euchaetidae, the oviducts enter the enlongate receptacula anteriorly and there is only one pair of pores, which are thus combined seminal/gonopores (Geptner, 1968). The account of Frost & Fleminger (1968) is not conclusive as to the common or separate nature of seminal pores and oviducal pores in *Clausocalanus*, though the pores are tentatively described as separate structures. In view of this variable situation in the Calanoida, and taking into account that in harpacticoids there may be two separate pairs of distantly situated pores (cf. Fahrenbach, 1962), a general statement about the conditions in calanoids cannot be made. Therefore, as data on Aetideidae are not available, at least to my knowledge, the actual situation of the pores in *E. messinensis* remains as yet uncertain. Anyway, once the proper contact has been established, the spermatophore pushes (cf. Heberer, 1932; Fahrenbach, 1962; Park, 1966; Blades, 1977; Ferrari, 1978) the immobile spermatozoa into the receptacula seminis, which are both situated in the asymmetrical outgrowth (fig. 16). This outgrowth is formed during the maturation moult; its formation will be outlined below.

In the female copepodid V, the immature genital somite is small and symmetrical (cf. Mazza, 1965); apparently the 'Anlagen' for the seminal receptacles are still in symmetrical positions. Upon casting the C-V exuvium, the genital somite grows rapidly and attains its adult size and shape. In this process, the right receptacle has to move from a right lateral position via a latero-dorsal path around the centrally positioned digestive tract to left postero-dorsad. At the same time the left receptacle moves mainly to dorsad

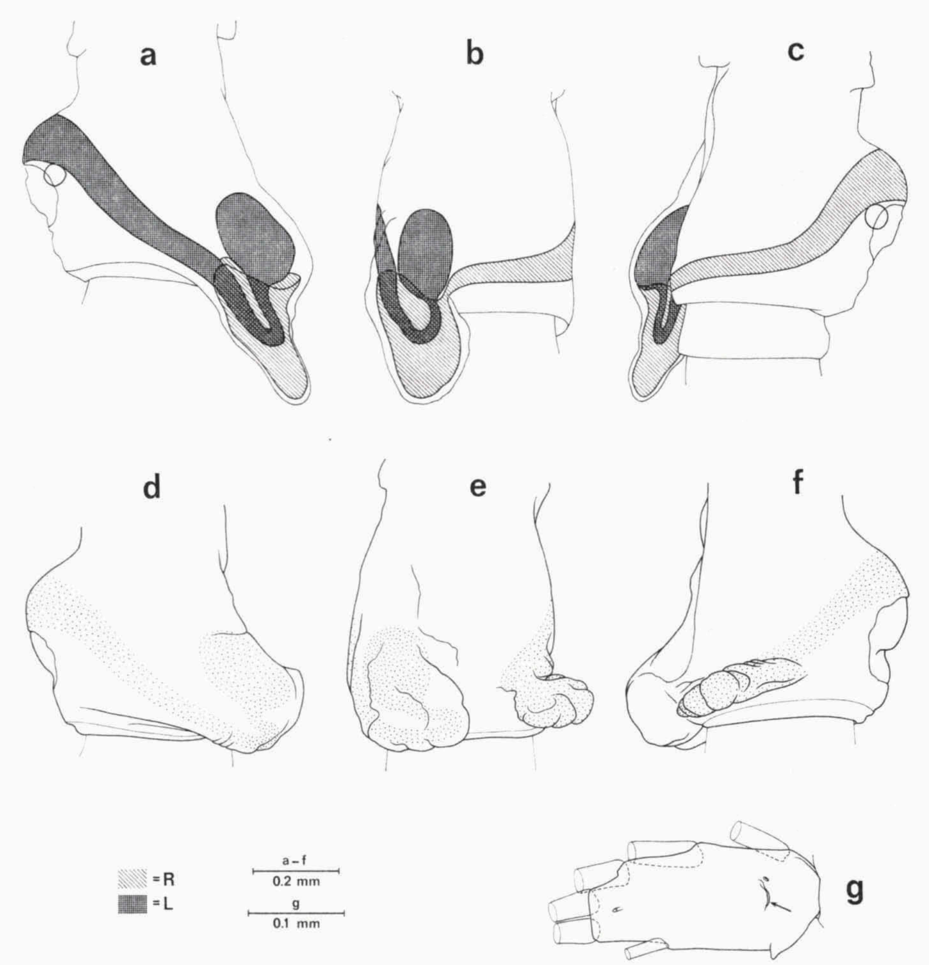

Fig. 16. *Euchirella messinensis* (Claus, 1863). a-c, semi-schematic drawings of genital somite of female, showing internal lumina of seminal receptacles in, respectively, left lateral, dorsal, and right lateral view; d-f, genital somite of aberrant female from "Bache" sta. 10176, note structures on the left being normal, including the recurved seminal duct, while the right receptacle has apparently got stuck, resulting in a separate swelling for its accomodation; g, ♀ from "Dana" Exped. sta. 4119^{x}, left P2Ri in anterior aspect, note remnants of suture Ri1/2 (arrow). (R = right seminal duct plus receptacle; L = ditto, left; open circle represents sperm-plug.)

to reach its left postero-dorsal place. At a certain stage both moving receptacles, each enclosed in a proliferating lining of soft integument, come into contact, whereupon the right receptacle encloses the left one and the left receptacle turns to anteriad, to yield the situation as in fig. 16a-c. The integument then hardens and the arrangement of the receptacles is fixed. The course of the process described may be deduced from a few aberrant specimens found in material from the Western Atlantic (fig. 16d-f). In these, the right seminal receptacle is situated in a separate elevation, about mid-dorsally on the posterior edge of the somite, while the left receptacle takes its normal position. This evidences (1) that the left receptacle can reach its regular position independent of the 'collision' with the right one, and (2), that the right receptacle did not reach its proper position in time, i.e., before the exoskeleton became too hard to allow the receptacle to move. So, the process of migration of the receptacles appears to be dependent upon the presence of a soft cuticle, during a restricted period in the moult to the adult stage.

The eggs may be fertilized in the terminal stretch of the oviducts when passing through (Dussart, 1967; Geptner, 1968) or along (Steuer, 1923; Lowe, 1935; Brodskii, 1950; Park, 1966) the seminal storage system, in the latter case via small connecting canals, or else when passing the genital atrium where the orifice(s) of the seminal duct(s) and the gonopore(s) are in close proximity (i.e., if not combined; cf. Illg, 1958). The sperm-plugs which remain after fertilization and which obstruct the pores (Lee, 1972; Ferrari, 1980) will have to be removed but data on this process are apparently not available. To allow the eggs free passage, the genital operculum will have to be opened during shedding. Though the pressure of the egg-mass might just push the operculum out of the way, the structure of the musculature in the antero-ventral part of the genital somite suggests that the opening event is at least in part an active process (cf. also Park, 1966). The eggs are carried in a paired (or bifid) egg-sac (Sars, 1924-25; Brodskii, 1950), possibly produced by a secretion of accessory glands, situated in the Gnsom (cf., e.g., Geptner, 1968). Females carrying egg-sacs were not met with in the present material but in various specimens remnants of the ruptured membrane were observed, attached to the genital area.

Reproduction apparently affects some thoracic structures as well. These probably include: (1) the postero-lateral rows of integumental organs, mainly hair-sensilla, on Th4+5; (2) the hair-sensilla on the posterior faces of the fourth legs; and (3) the spines on P4Ba1. The hair-sensilla under (1) and (2) present a highly concentrated group, compared to the rest of the body. They may be functional in detecting the presence of the male, the spermatophore, or the egg-sac, as already suggested by Wolf (1905). It is noteworthy that no hair-sensillum is found on any of the other legs, nor on the anterior face of P4.

Spines on P4Ba1 are well developed in all species of *Euchirella* and in various other aetideid genera as well. Comparable structures are lacking in calanoid families in which the females are equipped with fifth legs and also in Aetideidae where a fifth pair of legs is still present, i.e., some species of the genus *Bradyidius* (cf. Bradford, 1969). Such arrangements of spines might perform some function in positioning or handling the egg-sac during and/or after shedding. On the other hand, they might also be instrumental in removing the empty spermatophore after sperm discharge; a function of this kind has been suggested by Ferrari (1980) in *Pseudochirella*, on the analogy of the use female *Labidocera aestiva* Wheeler, 1901, make of their P5 (cf. Blades & Youngbluth, 1979). Thus, irrespective of what process might have caused the disappearance of the fifth legs in female aetideids, the spines on P4Ba1 may be considered a secondary sexual character. In view of this, I agree with Fleminger (1975), Lawson (1977), and Blades & Youngbluth (1979), that the small, modified fifth legs found in the females of most Calanoida, had better be described as 'specialized' rather than 'reduced', which latter characterization is frequently used in literature. Ferrari (1980) observed the groups of spines to be asymmetrically developed on the left and right P4Ba1 of *Pseudochirella squalida* Grice & Hulsemann, 1967; such asymmetry has, however, not been found in *Euchirella messinensis*.

Functional considerations at the population level

Various authors have emphasized the significance of the species-specific combination of male fifth legs, spermatophore coupler, and female genital somite, which, together with the highly ritualistic behaviour of the male during mating, may act as a premating reproductive isolating mechanism (premating RIM; Bush, 1975), thus functioning in insuring the genetical integrity of the species (e.g., Steuer, 1923; Fleminger, 1967, 1975; Lee, 1972; Fleminger & Hulsemann, 1974; Lawson, 1977; Blades & Youngbluth, 1979). The role of isolating mechanisms of this kind, also termed prezygotic, in speciation processes has been repeatedly reviewed in literature (e.g., Mayr, 1963; Mettler & Gregg, 1969; Bush, 1975; White, 1978; Templeton, 1981). Apart from mechanisms working at the distributional or the (sub)cellular level, several are apparently operating at the level of the individual. In copepods, such premating RIM's may be functioning in various stages of the mating sequence. In the pre-copulatory phase (phases defined after Blades, 1977) the male (1) has to locate and recognize the female while next (2) the proper clasp of his chelate leg 5 around her genital somite has to be attained. During copulation itself, the male (3) has to attach the spermatophore properly, and finally, in the post-copulatory phase (4) the spermatophore must transfer the sperm to the seminal receptacles of the female.

The structure of the male fifth legs as well as of the female genital complex are remarkably species-specific throughout the genus *Euchirella*, including *E. messinensis*. The site of spermatophore attachment proved to be variable in the present species, as four distinct sites have been found occupied; yet, each site represents a small, discretely limited area of integument. The spermatophore coupler is a simple, globular, apparently aspecific structure which is, however, capable of forming an effective fertilization tubule of considerable length. This combination of conditions in *Euchirella* will be assessed in terms of a correct course of the mating event and the possibility for interspecific isolating mechanisms to occur.

Premating RIM's may be effective in each successive step of the mating sequence. To act as such, a given part of the process has to be species-specific, i.e., there has to be a high probability that it may properly be performed by conspecific mates, while at the same time chances of successful performance by partners belonging to different species have to be kept as low as possible.

These goals may be reached in step (1) by the specificity of the pheromone. Chemical communication in copepods has already been presumed by Parker (1902), and more specifically later on by Fleminger (1967, 1975) and Strickler (1975b). The role of sex pheromones in mate-seeking has been sufficiently demonstrated by Katona (1973) and Griffiths & Frost (1976). Though chemical composition has not been investigated in copepods, data from groups throughout the animal kingdom, in particular insects, indicate that most pheromones constitute exactly measured blends of organic compounds that are often highly specific (e.g., Shorey, 1976). Such specificity, however, may either pertain to the family-, the generic, or the specific level, depending, inter alia, on the group of organisms involved and on their distributional and phylogenetic relationships (cf. Wilson, 1968). The complex swimming pattern known as 'mate-seeking behaviour' has been described for the males of a variety of calanoids (e.g., Parker, 1902; Jacobs, 1961; Roff, 1972; Katona, 1973, 1975; Griffiths & Frost, 1976). Katona (1973) demonstrated that such behaviour is largely directional, rather than random, and at least in part involves trail-following. Detailed studies by Katona (1973, 1975) and Griffiths & Frost (1976) have shown that mate-seeking is strongly elicited by conspecific females at relatively long range (up to 20 mm). It may also be evoked by female conditioned water, by isolated pieces of females or even by inanimate objects that have been coated with juices of crushed females. The same authors all reported some degree of attractiveness of other males and of specimens of either sex of other species, but only in in vivo situations; male conditioned water, e.g., elicited no seeking response. Successful copulations, however, are reported almost exclusively from conspecific male-to-female encounters. This is consistent with Jacob's (1961) observation that males occasionally attacked each other but that copulation posture was never achieved. Likewise, Katona (1975) reported vigorous struggling of attacked males in male-to-male encounters, which invariably resulted in shaking off the assaulting 'mate'. The same author observed that a single female, having been isolated in the presence of 16 males, was carrying 31 spermatophores. Finally, various reports exist on non-selective sexual behaviour of males under laboratory conditions in the absence of females (e.g., reviewed by Katona, 1975), involving attempted mating up to and including actual spermatophore attachment to other males, immature females, other copepods, or even non-copepod crustaceans. Together these results indicate that a water-borne pheromone, diffused by the female, forms an important and largely species-specific cue also in calanoid reproduction, by triggering male mate-seeking behaviour and by enabling the male to locate his partner. The limited attractiveness of males or of specimens of other species should possibly be interpreted as responses to turbulence rather than to chemical stimuli. The sexual behaviour of the male, once elicited, evidently is highly ritualistic in the sense that he will be urged to complete the full sequence, eventually resulting, in the absence of conspecific females, in spermatophore attachment to alien objects. However, erroneous approaches appear to be largely prevented by the presence of close-range selective thresholds of chemical or mechanical nature operating upon physical contact and/or by defense reactions of improper mates, and thus may hardly ever be expected to occur under natural circumstances. As to this part (1) of the pairing process, no data on *Euchirella* are available but it may be assumed that also in the species of this genus pheromones play a similar role in mate-seeking and mate-selection behaviour.

In stage (2) of mating, the mechanical compatibility of the secondary sexual structures of either sex is at issue. The highly species-specific nature of male fifth legs and female genital region in many calanoids is well known. Details of functioning of such structures as key-and-lock mechanisms have been investigated by Lee (1972), Katona (1975), Fleminger (1967, 1975), Blades (1977), Ferrari (1978), and Blades & Youngbluth (1979). Lee (1972) noticed that even small aberrations in shape would seriously interfere with the possibility of a correct fit. As pointed out by Ferrari (1978), the spermatophore will be placed exactly in the desired position as a result of purely mechanical conditions alone, once the correct configuration of male and female has been attained. Proper matching of male P5 and female genital somite, therefore, appears to be a crucial step in the mating sequence. It obviously follows that the clasp has to be firm and that the male will have to be informed that his fifth leg is correctly positioned. For these purposes, specific configurations of epicuticular structures in the female genital region may function as mechanical aids to the male (Lee, 1972; Blades, 1977; Ferrari, 1978; Blades & Youngbluth, 1979). The additional possibility of short range chemical cues has been postulated (Katona, 1973, 1975; Griffiths & Frost, 1976) but has not been confirmed. In *E. messinensis*, the field of stellate warts in the anterior half of the genital somite as well as the shape of the somite as a whole, thus bear evidence of a direct relationship to the course of the mating event. As shape and surface structure are characteristic at the species level and directly influence the efficiency of reproduction, their functioning as an interspecific reproductive barrier seems highly probable. The pattern of integumental organs in the genital region does not appear to be especially adapted to provide chemical information to the male, and consequently no support for such a hypothesis can be presented from the anatomy of this species.

In some families, the male is already carrying a spermatophore in one of his fifth legs before the initiation of mate-seeking behaviour (Hopkins & Machin, 1977; Ferrari, 1978). In others, the spermatophore is extruded immediately prior to copulation (cf. Roff, 1972; Blades, 1977; Blades & Youngbluth, 1979). In the last case, tactile information about the right fit of the clasp may influence the male to actually produce the spermatophore. As far as I know, no accounts exist on spermatophore extrusion in *Euchirella*, or any other genera of the subfamily Euchirellinae. However, the structural similarity of the male P5 as compared to the presumably closely related Euchaetidae, suggests that, just like in *Euchaeta* (cf. Hopkins & Machin, 1977; Ferrari, 1978), males produce spermatophores independently of the presence of a mate, and next swim around, holding the neck or the coupler in the grip of the terminal pincer of their free leg 5.

The primary function of the coupler, of course, is to firmly cement the spermatophore to the female urosome (cf., e.g., Blades, 1977). Evidently, a proper position relative to the seminal pore(s), is a primary prerequisite for the ultimate goal of mating, the effective transfer of sperm to the female spermathecae. As shown above, proper placement, step (3) in the pairing process, may be promoted by a correct fit of the male clasp. It may be further insured by a specific shape of the spermatophore coupler in some families of calanoids (cf. Fleminger, 1967, 1975; Lee, 1972; Blades, 1977; Blades & Youngbluth, 1979). Couplers of this kind are large and elaborate structures which exactly mirror the shape of the female somite. Once such coupling device has been attached, the orifice of the spermatophore and the seminal pore(s), whether or not located in the genital field, are automatically in close proximity. Such conditions have been reported from *Centropages* (cf. Lee, 1972; Blades, 1977) and *Labidocera* (cf. Fleminger, 1967, 1975; Blades & Youngbluth, 1979). To accomodate a closely fitting coupler the female genital somite obviously must be clean, which has to be ascertained by the male prior to transfer. Such inspection behaviour may be performed by the free fifth leg and has been described by Blades & Youngbluth (1979) as 'stroking'. To present a clean genital somite in successive matings, it is of importance that the female is able to remove a discharged spermatophore. This may be accomplished mechanically by a female fifth pair of legs [or a substitute structure on P4, see above] and/or chemically by dissolving the adhesive substance of the coupler with a secretion from cutaneous glands (see Blades & Youngbluth, 1979). In species that produce small, aspecific couplers, the seminal pores are situated in the vulval cavity and the coupler thus has to be attached in the immediate vicinity of the genital field. As a key-and-lock fitting structure of interacting male and female organs is not always obvious, it might be assumed that in some families a certain degree of precision in placement itself remains necessary. Apparently, however, the degree to which this is effectively performed is variable among calanoids. Marshall & Orr (1955) report a large proportion of single spermatophore placements, exactly on the genital orifice in *Calanus*. Incidences of 'misplacement' of 20 to 54% were observed by Hopkins & Machin (1977) and Ferrari (1978) in *Euchaeta*. Fleminger (1967) reported alternative placement to be 'sporadical' in *Labidocera*. Interestingly, such misplacements invariably involved only one, discrete alternative site. Various observations have certified that the actual act of attachment is accomplished very quickly (less than 1 second; Gauld, 1957; Fleminger, 1967; Roff, 1972; Katona, 1975; Blades, 1977) which probably reduces the possibility for this action to be performed with great precision. It must be presumed, therefore, that precision in placement is dependent rather on a proper clasp than on attachment itself. As pointed out by Ferrari (1978), misplacements may be caused by inadequate mechanical possibilities resulting from an improper clasp or from an already present spermatophore. The rigid structures involved in the clasp configuration will only make small allowances for improper fits, but those possible will be discrete, whence misplacements are likely to be confined to distinct sites equally well as are proper placements.

The presence of multiple spermatophores has been reported from a variety of species with simple, aspecific couplers (cf. Wolf, 1905; Lucks, 1937; Marshall & Orr, 1955; Roff, 1972; Katona, 1975; Hopkins & Machin, 1977; Ferrari, 1978; Hammer, 1978). Though concurrent fertilization by more than one spermatophore is improbable, there may be some advantages in multiple placements (as discussed by Katona, 1975) but there also is an obvious energetical waste in the form of ineffective sperm. Disregarding considerations like these, it is evident that more or less proper placement of spermatophores with small couplers is not seriously hampered by one or more already present spermatophores. However, also in species which have specific coupling devices multiple placements may occur (Fleminger, 1967, 1975; Blades, 1977). Apparently, inhibition from stimuli informing the male that the female Gnsom is not clean (cf. Blades & Youngbluth, 1979) may be overshadowed by the relative measure of excitement urging him to complete his ritual sequence. To some extent, the degree of versatility of the clasp may be indicated by the positions of multiple spermatophores. In a rigid configuration, couplers will be placed one upon another, as observed in the Pontellidae (cf. Fleminger, 1967), the Temoridae (cf. Katona, 1975) and the Acartiidae (cf. Hammer, 1978). The attachment of couplers scattered over a wider area may evidence less restricted mechanics in the fit of the clasp, as has been reported from species of Calanidae (cf. Marshall & Orr, 1955) and Temoridae (cf. Lucks, 1937). In contrast to large, specific couplers, small, simple couplers may remain cemented to the female, only the spermatophore itself being deciduous (e.g., Candaciidae, cf. Lawson, 1977). General considerations upon retention of an attached spermatophore until egg-laying (cf., e.g., Johnson, 1948; Wilson & Parrish, 1971) have been tentatively outlined by Fleminger (1975) in particular with regard to population genetic mechanisms.

So, in all, the emphasis that has been laid on high precision in the actual act of placement (Fleminger, 1967, 1975; Lee, 1972) appears to be unjustified. Instead, precision should be assumed to be effected rather by the proper fit of the male clasp (Blades, 1977; Blades & Youngbluth, 1979). In *Euchirella messinensis*, the occurrence of four discrete alternative sites evidences the absence of high precision, which obviously is thus not required. As Ferrari (1978: 519) has pointed out, relative imprecision in a given subset of a sequence of specific events, may well relate to relaxation in the necessity of accuracy, once a speciation process has been completed in which that particular subset acted as a premating RIM. Though the application of this postulate in the case of *Euchirella* has yet to be assessed in the course of the revision of the genus, it is noteworthy that Ferrari (1980) reported no alternative placements in *Pseudochirella squalida* Grice & Hulsemann, 1967, a member of the presumed plesiomorphous sister-group of *Euchirella*. It may thus tentatively be assumed, that the emphasis of premating RIM's has shifted in *Euchirella* to steps (1) and (2) of the mating sequence. The relative imprecision of step (3) may be directly related to the possibility created for relaxation by the conditions in the post-copulatory phase as discussed below, in step (4).

The condition under (4), the actual transport of sperm cells to the spermathecae, presents a specific problem in the copepod mating event, caused by the transfer of sperm via a spermatophore, and the immobility of the spermatozoa. Such combination requires a mechanism that directly and infallably carries the sperm cells into the female system. The aflagellate, non-mobile condition characteristic of copepodan male germ cells (Heberer, 1932; Park, 1966; Brown, 1970; Raymont et al., 1974), implies the necessity of an external force as well as proper guidance for them to reach the right place. Discharge of the spermatophore is accomplished by swelling of the modified "Q"-spermatozoa, whereby the fertile cells are pushed out by mechanical (hydrostatic) pressure (Heberer, 1932; Fahrenbach, 1962; Park, 1966; Blades, 1977; Ferrari, 1978). The directional problem, i.e., to travel from the primary orifice situated in the spermatophore coupler to the female receptacles, affects both steps (3) and (4). The demands of these steps are highly interdependent and proper performance of the procedure may apparently be accomplished in various ways. If the orifice of the spermatophore is situated in the immediate vicinity of the female seminal pore(s), only simple requirements are set to the process of sperm transfer. Mere sealing of the area of pores may suffice to produce a short duct which channels the spermatozoa to the seminal vesicles. This is accomplished by hardening of part of the discharged seminal fluid upon contact with the sea water; such sol to gel phase shift has been reported by Blades (1977) and appears to be in accordance with observations by Ferrari (1978). Conditions involving a close proximity of both discharging and recipient pores occur in case of attachment by specific couplers, like in the Pontellidae (cf. Fleminger, 1967, 1975; Blades & Youngbluth, 1979) and the Centropagidae (cf. Lee, 1972; Blades, 1977). The same situation may apply to aspecific couplers when placed on or adjacent to the seminal pore(s). Presumably, it is this apparent prerequisite of short pore distance that has led authors to emphasize the need for high precision in spermatophore attachment though Blades (1977) pointed out that the sealing mechanism can cope very well with misplacements and thus reduces the need for accuracy substantially. However, in the absence of other means of sperm transport, capable of covering longer stretches, the energetical waste resulting from incompetence of misplaced spermatophores would be considerable. Apparently, misplacements have been amply accounted for by the ability of the spermatophore to form a fertilization tubule, connecting the coupler to the female seminal pores. Marshall &

Orr (1955) already noticed that misplaced spermatophores in *Calanus finmarchicus* had an "exceptionally long neck". Hopkins & Machin (1977) described fertilization tubes from material of *Euchaeta norvegica* (Boeck, 1872) and the detailed morphology and formation have subsequently been explained by Ferrari (1978). This author also confirmed the effective discharge of the spermatophore by means of such tube. Apparently, formation of the tubule involves the same solidification process of outflowing seminal fluid as reported for the short-distance sealing in *Centropages* (cf. Blades, 1977; Ferrari, 1978). A functional fertilization tube obviously solves the directional problem in long distance travel of spermatozoa, but the same problem now pertains to the formation of the tube. The reports by Hopkins & Machin (1977) and Ferrari (1978) indicate that these tubes are following a rather distinct trail and are apparently directed straight on to the female pores. Ferrari (1978) suggested that mechanical stimuli presented by the configuration of structures in the female genital region would control the path of growth of the tube in statu nascendi. This seems to be the only likely explanation, since a spermatophore is not an organism, and thus is unable to coordinate a directional growth mechanism, no matter what stimuli would be presented. As the tube apparently is of an acellular nature, not even chemical attraction at the cellular level may be assumed. An observation reported by Marshall & Orr (1955) adds to the probability of Ferrari's (1978) suggestion: in an immature stage V *Calanus*, the erroneously attached spermatophore had formed a tubule, coiled several times around the abdomen. In the absence of the mature configuration of the genital somite, the tubule obviously never could reach a pore, but the simple mechanical conditions merely involving the presence of the body may have caused the forming tube to follow its surface. As a matter of fact, the sol to gel phase shift under the influence of sea water may account for such mechanism: the differences in flowing speed present on the micro-scale gradient just adjacent to the body surface may cause the quicker hardening and thus faster growth along the outer sector of the proliferating opening of the tube, whereby the shape of the body surface is followed automatically. The control system in a normal situation may thus be interpreted in analogous terms. In *Euchirella*, spermatophore couplers are also able to form a fertilization tubule (personal observation) so attachment at sites away from the genital field does not interfere with actual sperm transfer.

In conclusion, the functions of the various steps in the mating sequence of *Euchirella messinensis* may be summed up as follows. The specific action of a sex pheromone may be inferred by analogy with other Calanoida; the species-specific shape of male and female copulatory organs is involved in tactile recognition and acts as a key-and-lock mechanism to a certain limit; the reduced degree in precision of this mechanism, apparently possible by relaxation in the necessity of accuracy, results in four alternative sites of spermatophore attachment; sperm transfer is secured by the potentiality of the small, globular coupler to bridge the distance to the vulva by a fertilization tubule. Together, these conditions indicate that in *Euchirella* one or more premating RIM's are operating at the precopulatory level, primarily involving location and recognition of a conspecific partner. Such presumption would best account for the observed specificity in secondary sexual structures, combined with the variable situation of the spermatophore coupler.

The energetic expense involved in reproduction is high (e.g., Steele, 1974) and it is evident that the sooner an erroneous mating sequence is interrupted by an isolating mechanism, the more efficient this mechanism will be. The efficiency of reproduction is the only operational tool of directional selection (e.g., Mettler & Gregg, 1969), whereby reduction in reproductional energy expense acting via an early intervenience in the formation of hybrid combinations may be strongly favoured. Such conditions account for a shift in isolating mechanisms from postmating to premating (cf. Mayr, 1963; Mettler & Gregg, 1969); they may likewise promote a shift in emphasis of premating RIM's towards the initial steps in the sequence. An early stage RIM, especially involving mate-selection by long distance sensing via pheromones, may thus be assessed as an advanced character state (cf. De Jong, 1980).

However, it should be considered just as well that the more closely related species are, the longer will be the common part in their mating sequences. The point at which a premating RIM will impact is also dependent upon the prevailing zoogeographical conditions (cf. Fleminger, 1967, 1975; Lawson, 1977) i.e., involving either sympatry or allopatry and, in case of the former condition, the degree to which character displacement may influence the respective stages of mating (cf. Brown & Wilson, 1956). In case of aspecific couplers, the accent of isolation may lie in precopulation, whereas copulation and postcopulation processes are acting only to insure subsequent fertilization. Only the presence of highly specific couplers may witness an operational premating mechanism in the copulatory phase, and this seems to be largely restricted to conditions of sympatry (Fleminger, 1967, 1975; Lawson, 1977).

The Genital Operculum

In *Euchirella messinensis* the genital operculum is an unpaired, median structure which hinges by its full anterior edge, and which can, at least to some degree, be actively moved. Though the morphology of the genital area is rather variable in calanoids (cf., e.g., Geptner, 1968, 1971), structures of this kind are not uncommon.

Only a few authors have, to my knowledge, commented on the possible origin of the genital operculum. For instance, Frost & Fleminger (1968) give a detailed description of the genital plate in *Clausocalanus* but do not consider its anatomical status. The external appearance of the operculum suggests it to comprise a deep, proliferated sternal fold, and Geptner (1968: 685 [547]) states that it represents "... genetically a flap of integument from the anterior wall of the [genital] prominence, ...". Considering general crustacean morphology (cf. McLaughlin, 1980), this possibility does not seem improbable as the thelycum found in female penaeid shrimps demonstrates that the sternites of one or more successive somites are capable of modifying into a structure that functions in the reproductive process. On the other hand, the male petasma, as present in various orders (i.e., Stomatopoda, Stygocaridacea, Decapoda: Dendrobranchiata), evidences that also one or more pairs of appendages may partially fuse to form a secondary sexual structure. The structural relationship of the genital operculum in harpacticoid copepods to such a petasma has recently been suggested by Por (in press). Moreover, Lang (1948a) specifically pointed out that from the morphology of the vestigial sixth pair of legs in male and female Harpacticoida, it is evident that the genital operculum corresponds, in a homological sense, to a pair of former P6. This view has also been put forward by Hartog (1888), Claus (1893b), and Corkett & McLaren (1978). Therefore, little doubt may be entertained, in my opinion, that the operculum in copepods originates from a modified and fused pair of sixth thoracic appendages.

The Vulva

The vulva or genital antrum presents several structures that may vary and consequently may prove valuable as taxonomic characters at a certain level. It is worth noticing that With (1915: 4-5) already stipulated the systematic importance of its morphology. However, as in the case of the oral region, that author at the same time recognized the relative poverty of existing accounts, whence comparative studies were out of the question, then. Today, the structures of the vulva have been studied systematically in only a few genera, but it is clear that at least in *Paraeuchaeta* they may be used as taxonomic characters at the specific level (Geptner, 1968). So far, the internal morphology of the genital antrum of *E. messinensis* has not been examined and consequently the description presented above had to be restricted to external structures, mainly concerning the genital operculum.

The Anal Operculum

The crustacean telson is defined as the unsegmented terminal body region that remains once the formation of somites has been completed. According to some authors (cf., e.g., Illg, 1958) any terminal body ring that bears the anus should by this condition alone be considered a telson or a 'perianal ring', not homologous to a true somite. However, both Sharov (1966) and Bowman (1971) have stipulated that a telson, if present in a recognizable form in the adult, may be either fused to the last true somite, or articulated, but it never carries any appendages. Thus, the anal operculum of copepods would represent a reduced, fused type of telson. Though Bowman's (1971) views have not yet won general acceptance, the only serious criticism to his theory was given by Schminke (1976). While Schminke pointed out some inconsistencies in Bowman's argumentation, viz., demonstrated the impossibility of the existence of a completely cleft telson, he did not falsify Bowman's main point. Therefore, Schminke's paper only enhances the probability value of the views of Bowman. In my opinion, the terminology of Bowman applies quite well to the anatomy of the Calanoida.

The Furcal Rami

Classical views on the copepod furca include its qualification as a pair of 'limbs', at least not directly homologous, however, to 'true' appendages (e.g., Hartog, 1888), or else to a completely divided, last (?true) somite (e.g., Claus, 1863). The various opinions have been comprehensively summarized by Lang (1948a). However, according to the already mentioned views of Bowman (1971) it is inconsistent to variously denote the appendages of the caudalmost somite of crustaceans as 'cerci', 'cercopods', 'furcal rami', or 'uropods'. As a telson, if present, never bears appendages (see above under Anal Operculum), there is no basis left for differentiating between the paired terminal structures in the various orders. Consequently, I agree with Bowman that the furca of copepods in fact is homologous with a pair of uropods. Kabata (1979) recently followed Bowman (1971) in denoting the caudal rami as 'uropods' as well.

THE APPENDAGES

Body Parts or Appendages?

Prior to discussing the appendages, four structures of the body should be mentioned for which the homology with appendages is either rather obvious, or at least cannot properly be falsified at present. These include

(1) the frontal tubercles plus central hairs; (2) the labrum plus labral papillae; (3) the genital operculum; and (4) the furcal rami. However, as these structures are most commonly considered as trunk formations, they have been dealt with already under the specific headings, above.

Nomenclature and Comparative Segmentation of the Appendages

Differences in the terminology applied to copepod appendages have been reviewed by, e.g., Gurney (1931), Lang (1948a), and Kabata (1979). A general consensus exists about the terms 'mandible', 'first', 'second', 'third', and 'fourth pair of swimming legs', while no essential difference is involved when 'antennula' and 'antenna' are called 'first' and 'second antenna' instead. However, the three appendages posteriad to the mandible have frequently been named and renamed, whence the following terms may be met with (Mxl = maxillula, Max = maxilla, Mxp = maxilliped):

	(a)	(b)	(c)	(d)	(e)
(1)	Mxl	1st Max	Max	(2nd) Max	1st Mxp
(2)	Max	2nd Max	1st Mxp	1st Mxp	2nd Mxp
(3)	Mxp	Mxp	2nd Mxp	2nd Mxp	3rd Mxp

The terminology under (c) originates from an erroneous concept of Claus (e.g., 1863), who considered the appendages under (2) and (3) as separate rami of the same limb. Though Giesbrecht (1892) and Hansen (1893) pointed out that this is wrong, and he himself (Claus, 1895) rectified his error, these terms have persisted in literature because they were taken over initially by various others, among whom G. O. Sars (e.g., 1901-03, 1924-25). Both Wilson (1932) and Lang (1948a) have extensively reviewed this case already. The terms under (d) refer to the hypothesis of Heegaard (e.g., 1947a), viz., that the 1st maxilla has disappeared in most copepods but is retained in certain parasitic forms as the 'lateral cuticle spine' or 'post-antennary process'. Though Kabata initially adopted this concept as well, he has recently (Kabata, 1979) reconsidered his views. It should be noted in this respect, that a similar terminology has for some years been applied by A. Scott and C. B. Wilson, as reviewed by Kabata (1979). Lang (1946, 1948a) strongly opposed to this, mainly Heegaardian, view. The nomenclature under (e) was sometimes, not consistently, applied by Lubbock (e.g., 1856) but has been hardly ever followed since. However, the names stated under (a) and (b) are regularly met with in literature, up to the present day. Those under (b) suggest a comparable nature of appendages (1) and (2), (a) being non-committal in this respect. Both terminologies infer a thoracic nature of appendage (3). It seems, however, to make no sense relating (1) to (2), as these appendages are always very much unlike throughout the Copepoda. Limbs (2) and (3) are structurally comparable in some Calanoida but, as Kabata (1979: 16) states: "Similarities in appearance are inacceptable as evidence", thereby obviously referring to convergence resulting from functional adaptations. So, in all, the terms under (a) seem least suggestive, merely indicating three successive pairs of distinct mouthparts, with reference of the posteriormost appendage to be of thoracic origin according to the commonly made distinction between cephalic (cf. Mxl, Max) and thoracic (cf. Mxp) somites.

From the anatomy of *E. messinensis* neither of the above hypotheses can be given further support. There is no similarity apparent between the three appendages: maxillula, maxilla, and maxilliped are much unlike, while the maxillipeds do not exhibit their possibly thoracic origin, as an intercoxal plate is absent. In fact, the terms under (a) are most appropriate, although they do not show a possibly comparable origin of either pair of successive appendages; this terminology also is the least confusing.

It is generally acknowledged that the primitive crustacean appendage must have been a biramous leg, consisting of an exopodite and an endopodite united by a protopodite. Consequently, all appendages should be treated as being once originated from this basic concept. To start proximally, the composition of the primitive protopodite, 'basipodite' in copepod terminology, as containing either three or two segments is still controversial, mainly due to the respective studies of Hansen (1893, 1925, 1930) and Heegaard (1945, 1947a, b). Borradaile (1926) already disputed the views of Hansen, and Lang (1948a) sufficiently demonstrated the irrelevance of Hansen's 'proof'. However, this author (Lang, 1948a) also established that a three-segmented composition of the sympodite of some appendages is quite distinct in various copepods. Both the theories of Hansen and Heegaard are founded on scattered, incidental records of, in places, ill documented data. To a lesser degree, this applies to Lang's work as well. McLaughlin (1980) indicates the presence of a third segment in the crustacean protopodite to be "rare". So, the original composition of the sympodite evidently is one of those questions that may only be solved in the course of a comprehensive survey of general crustacean comparative anatomy. Unfortunately, from the anatomy of *E. messinensis* no indication in favour of either hypothesis may be given, as in this species never more than two functional segments are found.

The homology of the internal and external rami of maxillule, maxilla, and maxilliped on the one hand, and those of antenna, mandible, and swim-

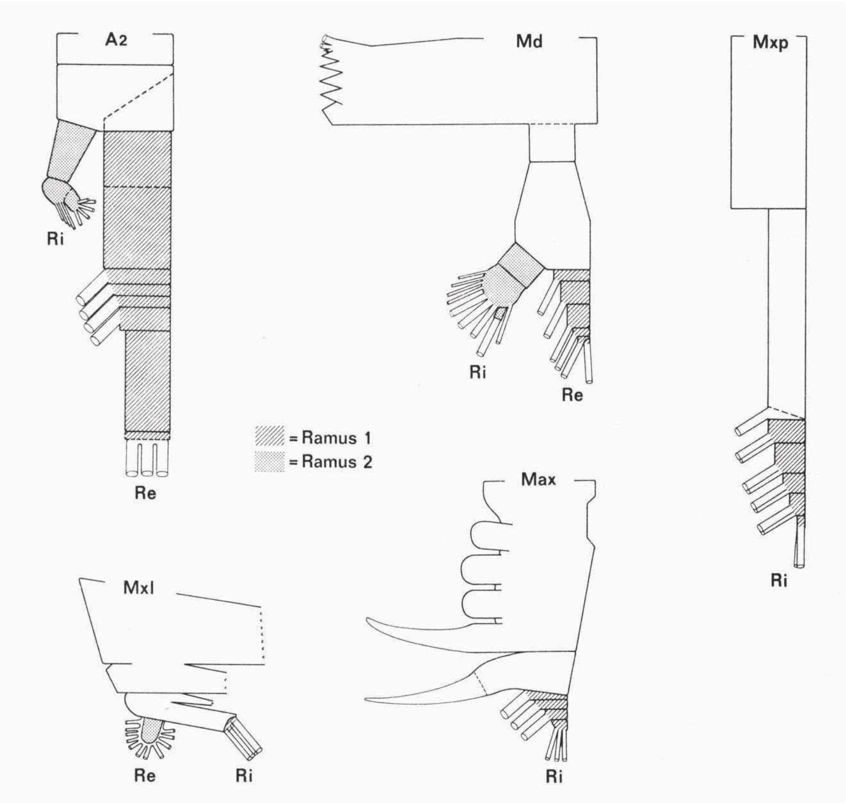

Fig. 17. Comparative schematic drawings of the rami of various appendages of *Euchirella messinensis* (Claus, 1863), as indicated. See also text.

ming legs on the other, has not been satisfactorily solved, too. The repetitive use of the terms 'exopodite' and 'endopodite' suggests that the corresponding rami are serially homologous in all appendages. However, the names as commonly used should be interpreted merely as topographic terms. When comparing the structural details of the rami in *E. messinensis* and taking into account the considerably rotated positions of the mouthparts, it is clear that morphological homology is not reflected by topography alone. In fig. 17, structural similarity has been indicated by numbering corresponding rami as 'ramus 1' and 'ramus 2', respectively, and this indication does not match the exopodite/endopodite distinction. Yet, in my opinion, homologies are reflected better when relating the rami by the numbers 1 and 2, respectively. Ramus 1 is composed of more than three segments: 7 (originally up to 10) in the antenna, 5 (6) in the mandible, 4 (or 5) in the maxilla, and 5 (or 6) in the maxilliped, which numbers may all be reduced as a result of fusion.

Each of the non-terminal segments bears one primary seta, at least originally, and the terminal segment is equipped with one to three primary setae. These setae are all strong and gently curved. The structure as described is not evident in the maxillule, which fact is attributed to the extreme reduction of its ramus 1. Yet, the similarity in development of the setae might give some indication that the tag 'ramus 1' is properly used. In ramus 2, there are less than three free segments: one in the maxillule, two in antenna and mandible; in the last two appendages this apparently results from fusion of segments in an originally three-segmented condition. This ramus is equipped with many smaller, delicate setae, which may be strongly curved: 9 (reduced from 12) in the antenna, 9 in the mandible, and 11 in the maxillule. Ramus 2 is not present in a recognizable form in maxilla and maxilliped. One argument in favour of the above hypothesis might have been provided by the possibility of a twisted position of other appendages as well. However, only Chappuis (1929) has reported a rotation over 180° of the A2 in harpacticoids, assuming an inverse situation of Re and Ri in the adult. As this suggestion has been strongly opposed by Gurney (1931) and Lang (1948a) and has hardly been followed since, Chappuis' observation does not seem to furnish any support, at present. As pointed out by Dussart (1967-69), Lang (1948a: 53-54; fig. 24) concluded that in case of reduction in the rami of mandible or maxillula, the Re is the first to disappear in the Md, whereas the reverse is true for the Mxl. Such observations would agree more conceivably with the presently suggested homology of the rami, as in both cases ramus 1 would be involved. This has, however, not to be assessed in terms of 'evidence', because reduction patterns of rami are not consistent as exemplified by, e.g., the variable development of Re and Ri of the A2 in various families of Calanoida. Referring ramus 1 of maxilla and maxilliped to an exopodite would correspond in part with the conclusions of Heegaard (1947a), though that author also included the segment commonly denoted as Ba2 in his 'exopodite'. Finally, quite similar brushes of small hairs c.q. spinules are found on A2Ri2+3, MxlRe, and MaxBa2(E5), but as their homologous nature has not been established these structures cannot be used as an argument in favour of the homology of ramus 2 (or its vestiges) in the various appendages, at present.

This discussion about the true homology of the rami should not be restricted to the Copepoda, as is evident from Sanders' (1957, 1963) work on Cephalocarida. Here, too, multisegmented conditions have been described in either the Re (A2, Md) or Ri (Mx1, Mx2, and remaining trunk appendages), and again adult topography has apparently been confused with anatomical (ontogenetic) homology. Though Sanders (1963) refers to an unpublished study of Hessler on muscle patterns, this reference is too vague to justify its use as 'proof' as such.

The segmentation of the individual appendages of *E. messinensis* will be discussed in detail, below.

The Antennule

In discussing general tagmosis, the difficulties in explaining the composition of the preoral part of the cephalon have already been indicated. Despite the comparative study of Fahlander (1938) on antennules/antennae throughout the Arthropoda, there is still no consensus about the presence or absence of homologies in these appendages (cf., e.g., Sharov, 1966; Manton, 1977). As far as the copepod antennula is concerned, this uncertain situation has led some authors to question the serial homology of this aberrant, uniramous appendage with the biramous limbs of succeeding somites, which eventually has resulted in considering the A1 as a formatio sui generis (e.g., Corkett & McLaren, 1978). This evidently obviates the need to keep searching for the now vanished branch. Others, like Lang (1948a), do not venture to formulate a definite opinion but refer to the antennule in purely descriptive terms. However, the biramous nature of the antennula in malacostracans and, as recently discovered, also in the supposedly primitive order Remipedia (cf. Yager, 1981), clearly indicates the originally two-branched structure of this appendage as well. Since accounts on the bi- c.q. uniramous condition of the cephalocaridan A1 are not in accordance (e.g., Sanders, 1957, 1963; McLaughlin, 1980), it is uncertain whether or not evidence in this case may also be derived from that order.

Anyway, according to its present functional status, the copepod antennule is a uniramous appendage, comprising a simple, linear arrangement of segments. No sound basis has yet been found for distinguishing one or more proximal segments as of basipodal origin. Yet, in calanoids, and also in *E. messinensis*, the first segment differs in structure from the subcylindrical nos. 2 to 24, segment 1 being composed of a bulbous distal part protruding from a collar-shaped proximal portion. Next, the setal armature of this segment is distinct from that of the other segments, and, in fact, reminiscent of the distal (4th) group of setae on Ba1 of the maxilliped. Reference of segment 1 to the complete basipodite, taking into account this setal arrangement, would match with Heegaard's (1947a) view that the first segment of the maxilliped also comprises a fused complex of the two original Ba segments. The problem of subdividing the antennule in a basal part and a single well-developed ramus would be solved by the discovery of vestiges of a second ramus. Various authors (see review by Lang, 1948a) have tentatively referred an exceptionally long aesthetasc-like structure found in some non-Calanoida to a former second ramus but there seems to be no further support to such theory (Heegaard, 1947a; Lang, 1948a). As reduced rami are often referred to a single seta of some special appearance, the distal setae on segments 5 and 12 are of interest. Both are of unique structure and are situated terminally on their respective segment. There appears to be no other indication, however, that a caesura be laid at either of the joints 1/2, 5/6 or 12/13.

The total number of segments is generally stated to be 25, some of which are fused. The coalescence of segments 8 and 9, and 24 plus 25, as established in *E. messinensis*, is not uncommon in various calanoid families. To date, a larger original number of segments is never mentioned, despite Gurney's (1931: 40-42) presumption that the antennule originally contained 27 to 31 segments. It will be shown below that in *E. messinensis* the antennule comprises at least 28 distinct segments.

First, it is clear that segment 2 is a composite, resulting from fusion of three successive segments. This has already been indicated by Giesbrecht (1899) and Gurney (1931), and is founded on Giesbrecht's 'Trithek'-theory, and on previous observations of Lubbock (1853): each antennular segment would originally have been characterized by a configuration of two setae plus one aesthetasc. In *E. messinensis* the length of this segment is about twice that of neighbouring segment 3; the 2nd segment bears three groups of two setae each; and its posterior margin is equipped with three or more tufts of wrinkled hairs. Next, the single aesthetasc is inserted at the base of the fourth seta from proximad, whereas in simple segments such organ is invariably situated near the insertion of the distalmost seta. Finally, S.E.M.-study has revealed the presence of distinct remnants of the former intersegmental sutures (pl. 12c). The status of segment 2 as a triple segment is thus quite well established.

The minute terminal segment, no. 25 of authors, may on comparable grounds be considered as comprising two former segments. A vestigial suture may be observed by light microscope and by S.E.M. alike; the segment bears four setae, two on the proximal part and two terminally, on the distal part; and the single aesthetasc is inserted proximad to the line of fusion. Thus, it is obvious that the complex should be regarded as being composed of segments 25+26. The number 26 may be used without affecting the serial numbers of the other segments, which is not possible when re-numbering segment 2 as 2+3+4. It is preferable in this case to await a possible solution of the basipodite problem of the antennule before venturing to rename its segments. The dual nature of segment 25 has, to my knowledge, not been suggested before.

The anatomy of the present species presents no support to Gurney's (1931) suggestion that segment 1 might be a composite of two original segments as well, though its setal formula (2+1) certainly is in discordance with the 'Trithek' of Giesbrecht (1899). The wrinkled hairs on the proximal segments will be discussed under Structures of the Integument, below.

The Antenna

From the structure of the antenna the following information may be derived regarding its original segmentation. There is no indication that the basipodite would be composed of more than two segments. The bilobed condition of Ri2+3 is distinct, but there is no trace of a former suture dividing the segment in two. In Ba2 a portion surrounding the insertion of the exopodite is distinctly marked, which would suggest the presence of a former "zero-eth" segment of the Re. Lang (1948a) likewise indicated an originally eight-segmented condition of the A2Re, the former first segment being fused with Ba2. The vestigial suture between Re1 and 2 is still recognizable; there is no indication that segment 7 originates from the fusion of two former segments (cf. the appendicular seta in *Pseudochirella*). The very small but free sclerite at the base of the terminal setae on Re7 may represent the remnants of a former 8th segment. So, if segments 0 and 8 prove to be real, *E. messinensis* evidences the original presence of at least 9 segments in the A2Re.

Two other structures have been found on the antenna, which I have never met with in literature, viz., the outgrowth in front of the row of setae, and the subterminal row of spinules, both situated on the terminal lobe of Ri2+3.

Variation as regards the number of setae on the lobes of Ri2+3 has been mentioned: in one specimen 6+6 were found on one of the antennae, instead of the regular 4+5. The latter configuration is also found in species considered closely allied to *E. messinensis*, while the 6+6 arrangement represents the normal situation in various other species of *Euchirella*. It is concluded that the 6+6 combination in *E. messinensis* should be regarded an atavistic trait.

The Mandible

According to Heegaard (1947a) the gnathobasis (cf. Ba1) is connected by a secondary annular sclerite to basal segment 2. Others (e.g., Hansen,

1893) consider this sclerite a third basipodal segment. However, as both Gurney (1931) and Lang (1948a) have pointed out, such a structure is nowhere evident except in the family Calanidae. These authors consider the 'suture' Hansen (1893) claimed to have observed merely as a fold, enhancing the mobility of the palp. In *E. messinensis,* the narrowed basalmost part of the palp is small and a suture is only evident distally, at the attachment of Ba2. So, the annular part apparently represents a terminal portion of Ba1, not involved in forming the masticatory lobe but serving the attachment of the distal segments.

As regards the exopodite, literature records state this ramus to be composed of five segments, four of which bear a single seta, while the terminal segment bears two. However, Lang (1948a) already indicated that the MdRe be originally composed of six segments. Upon close examination of the terminal part by light microscope as well as by S.E.M. (pl. 14b), I am convinced that the sixth seta is inserted on a separate segment, bringing the total number of segments to six. The spiniform outgrowth on Ri1 probably represents a vestigial seta; in various other species of aetideids (cf. Von Vaupel Klein, papers in prep.) a normal seta is present at this position. The pedestal which supports the eighth seta on Ri2 is distinctly marked against the segment (e.g., pl. 14a). In my opinion, it most probably represents the remnants of a third endopodal segment.

The spiniform outgrowths in the bicuspidate teeth were observed by light microscopy in all relevant slide-preparations but these observations could not be confirmed by S.E.M. studies in this species. Yet, I feel justified in deciding that in many specimens these structures must be present, as I observed these in *Euchirella paulinae* (cf. Von Vaupel Klein, 1980), where parallel observations by light microscope and S.E.M. unequivocally established their presence. Thus, I can only conclude that the present results have to be attributed to individual variation.

The fields of spinules on the gnathobasis will be dealt with in discussing the Integumental Structures, below.

The Maxillula

The composition of this highly modified limb has been variously interpreted (e.g., Giesbrecht, 1892; Sars, 1924-25; Hansen, 1925, 1930; Borradaile, 1926) as reviewed by Gurney (1931) and Lang (1948a). As the Mxl is also very heterogeneous in form among the Calanoida, most discussions pertain to the original number of segments in the basipodite (either two or three) and to the reference of the various endites and exites to either one of the basipodal segments. In *E. messinensis*, the structure of the maxillule presents no indication that the basipodite would originally comprise more than two segments. The first inner lobe clearly is developed as an arthrite, i.e., a mobile endite. The connection of the outer lobe with former Ba2 is rather distinct. Composition as well as actual limitation of the minute endopodite are not discrete. The large seta of Ba2, immediately adjacent to the Ri, is of exactly the same structure as those of the endopodite. Though this may well have a functional cause, it is suggested that this seta might eventually also prove to be a fifth endopodal seta. The present suggestion that a reverse terminology be applied as to the Re and Ri of this appendage, appears to be supported by the situation in various other calanoids (e.g., *Calanus finmarchicus* (Gunnerus, 1770), see Giesbrecht, 1892, pl. 7 fig. 13) in which the composition of the "Ri" is distinctly comparable to a ramus 1.

The chaetotaxy of the 1st inner lobe of Ba1 is variable within the genus, and presents several characters of use in a reconstruction of phylogenetic relationships at the (infra-)generic level (cf. Von Vaupel Klein, in prep.).

The Maxilla

The interpretation of the composition of this mouthpart has also been the origin of much dispute already (e.g., Hansen, 1893; Borradaile, 1926; Gurney, 1931; Heegaard, 1945, 1947a; Lang, 1946, 1948a). Most authors regard the basipodite as composed of three original segments, but which segments are presumed to be involved is dependent upon views of authors where to lay the caesura between the Ba and the single ramus that is still present in a recognizable form. Following Giesbrecht (e.g., 1892), the segment bearing endites 1 to 4 has been denoted either as "segment 1 + 2" or, purely descriptive, as "segment 1" (e.g., Rose, 1933; Brodskii, 1950; Owre & Foyo, 1967), and consequently the segment bearing E5 has been designated as Ba3 c.q. Ba2. However, in the interpretation of others, segment Ba1 is only small, the complex on which E1-4 are found should be named "Ba2+3", while E5 be a formation of the first endopodal segment (Ri1). The latter concept has been advocated by Hansen (1893, 1925) and Gurney (1931), but appears not to have been accepted subsequently. These different views apparently originate in part from the controversial interpretation of an external seta in some calanoids, referred to the former Re, as being inserted on either segment "2" or "3" of the basal complex (cf. also Gurney, 1931, and Lang, 1948a). In the interpretation of Heegaard (e.g., 1947a) the developed ramus also comprises the segment bearing E5, but this author called it exopodite instead of endopodite whereas the former Ri would be referable to endite 4, on the first basal complex. Heegaard consequently disagrees with reference of the above-mentioned external seta to a former Re. In the present species, the maxilla is strongly shortened and its segmentation provides no clues as regards its original composition. A single remark may be made about the segment interpreted as Ri1, which forms a very compressed structure. In this respect, there is some similarity with the situation at the Ba2/Ri1 boundary in the maxilliped. There, too, a compressed structure is found which is, however, generally interpreted as the terminal part of MxpBa2 (see below).

The hook-shaped outgrowth on E1 of Ba1 was found previously also in *Euchirella paulinae* (cf. Von Vaupel Klein, 1980). The warted area on Ba1 will be discussed under Structures of the Integument.

The situation of the orifice of the maxillary gland, the excretory organ in the adult, has been reported from various species to be on the basal complex (e.g., Lowe, 1935; Lang, 1948a; Park, 1966). Consequently, the large pore Max-Ba1-af-1 seems the most likely pore to be referable to this gland, as has already been suggested in reviewing the integumental organs (Von Vaupel Klein, in press b).

The Maxilliped

The structure of this appendage is not really indicative of the former presence of a second ramus. According to Heegaard (1947a) the 4th group of setae on Ba1 represents the original Ri but this can neither be supported nor denied by the conditions in this species. The terminal group of two setae on Ba2, however, is situated on an irregular, compressed part of the segment, which has been considered the original first endopodal segment by Gurney (1931; see also Marshall & Orr, 1955). In *E. messinensis*, this particular part is distinctly set off against the corpus of Ba2 by a (complex of) ridge(s), not by a suture, however. Its distal border is only imperfectly separated from Ri1, whereas the articulation of this last segment with Ba2 is clearly demarcated anteriorly. Therefore, the possibility that group II on Ba2 corresponds with a former segment Ri0 seems unlikely. From the situation in this species, it would seem that the group might more probably be referable to a ramus 2, if related to a formerly free segment at all.

The peculiar seta situated terminally on Ba2 (cf. fig. 9a, e) appears to be similar in structure to the setae Friedman & Strickler (1975) described in *Gladioferens pectinatus* (Brady, 1899), and for which they assumed a chemo-sensory function. However, the internal structure of this seta has not been examined, whence a function of this kind cannot be ascertained, yet.

The medial comb of spinules on Ba2 has been described and figured quite regularly though few authors state the number of spinules present; the terminal spinules on Ba1 have been paid less attention. However, both structures are distinct and two possible functions may be attributable to them. The first would be to increase friction when a prey is being seized and/or held by the maxillipeds but this does not seem to be the most likely explanation. In the living animal, viz., the parts distad to joint Ba1/2 are held in an inwardly twisted position, i.e., rotated over some 90° relative to the unnatural, flattened position shown in fig. 9. Thus, it is apparent that in situ both the patch and the row of spinules are in direct contact. This suggests a second and more probable function for these structures, viz., that together they form a pair of adhesive pads, fixing the relative positions of Ba1 and 2 without (or: with less) continuous muscular contraction being necessary. Similar structures, termed 'Haftorgan' have been described from a variety of Lepidoptera (cf. Kuijten, 1974) where they are functional either in coupling the anterior and posterior wings, or in fixing the resting position of the wings. Recently, a comparable structure has also been described from euphausiids (Nicol & Nicol, in press).

The Natatory Legs

The primitive calanoid swimming leg is composed of three-segmented rami as, e.g., in the Calanidae. So, the two-, one-, and one-segmented conditions of P1Re, P1Ri, and P2Ri in *Euchirella* result from either fusion or reduction. It is evident that P1Re1+2 was formed by mere fusion: the terminal spine of Re1 is still present along the combined segment's outer edge while the biconvex medial outline clearly indicates the former segmental boundary. As regards the endopodites of P1 and P2, it is far less easy to decide to which degree fusion or reduction have been involved in achieving the one-segmented condition. Comparison with the endopods of P3 and P4 learns, that the setal armature of both P1 and P2Ri may be explained by reduction of Ri2: the A-seta referable to Ri1 is present and the remaining setae correspond to Ri3. In P2Ri, the integumental organs are referable to both Ri1 and Ri3, whence the incorporation of the latter two in the combined segment is probable; the absence of such organs on Ri2 makes it impossible to trace its presence in this way. The integumental organs of P1Ri are not comparable to P2-4. In some specimens the proximal part of P2Ri is still demarcated by an incomplete suture (fig. 16g), but this does not prove anything else than that a composite segment is concerned. In all, both endopods of P1 and P2 evidence the incorporation of Ri1 and Ri3, whereas Ri2 cannot be traced any more and is to be regarded as, at least partly, reduced.

The ancestral composition of the rami has been discussed by Chappuis (1929), Gurney (1931), and Lang (1948a). As indicated by the first two authors, each segment would primarily have borne an internal seta and an external spine, whereby the arrangement of setae and spines on Re3 would evidence its formation from four former segments, bringing the total number of segments in the Re and Ri to six. Lang (1948a) subsequently pointed out that in some copepods a second seta is present on Re2, so that an original number of seven segments might be presumed. On the other hand, Lang questions if each seta or spine really should be regarded to represent a formerly free segment (Lang, 1948a: 62). The arrangement of 4 setae, 3 spines, and one terminal spine on the exopodite of *E. messinensis*, then, conforms to the theory of Chappuis (1929) and Gurney (1931) but cannot support Lang's (1948a) view, although it does not falsify the presumption of this author, either. The armature on the Ri (P3-4) in this species is not really indicative of four former segments as it is not clear whether the inner terminal seta should be regarded as originating from the "inner" or "outer" ancestral arrangement.

Swimming Movements of the Legs

The swimming behaviour of planktonic copepods has been reviewed by Gauld (1966) and Katona (1975). It includes gliding movements, discontinuous leaps, and mate-seeking behaviour (see also Barrington, 1967 and Manton, 1977). Lowndes (1935) has extensively dealt with gliding swimming movements caused by the filtering action of the mouthparts and by the propulsive power of the antennae. The hop-and-sink pattern, comprising a series of discontinuous, short bursts, has been analyzed by Strickler (e.g., 1970, 1975a) which author also pointed out the role of urosome movements in the whole of the hydrodynamics of the swimming action.

The natatory legs of copepods are really functional in swimming, as demonstrated by, e.g., Storch (1929), Strickler (1975a), and Kerfoot et al. (1980). The rostro-caudally flattened shape of the segments obviously is related to this function and the large setae with their fine, densely contiguous plumosity, evidently serve as natatory setae. Hartog (1888) and, in particular, Claus (1893a), presented an extensive description of the sternal keels ("Bauchwirbel") and of the intercoxal coupler plates, interpreting their function in terms of providing rigidity to the sternum and allowing the formation of a sturdy hinge-joint for the swimming legs. In a more recent study Perryman (1961) accurately described the joint between left and right Ba1 plus coupler on the one hand, and sternal keels on the other, including also internal structures. This author pointed out the importance of the complete configuration for achieving a wide angle of swing, necessary for the powerful, rapid jump type of locomotion (see also Manton, 1977). Storch (1929) has shown that the legs move in a 4-3-2-1 metachronal rhythm when a swimming powerstroke is performed. The morphology of the muscles that allow the legs' movements has been examined in detail by Lowe (1935), Lang (1948a), Perryman (1961), Fahrenbach (1962), and Park (1966), in their studies on internal anatomy of various free-living copepods.

However, two anatomical aspects of swimming have not exhaustively been dealt with up till now. These include the point of cessation of the propulsive stroke and the hydrodynamics of the recovery stroke. As to the cessation of both back- and forward strokes, anatomical details show that the rigidly linked legs of a pair are restricted in their movement by the configuration of (1) the intercoxal plate, (2) the midventral sternal keel of their own somite, in front, as well as (3) the keel of the succeeding somite, behind. Consequently, the muscles will move the legs back and forth till the point they collide to either the anteriorly or the posteriorly present keel. In the fourth legs, there is no posterior sternal keel, so the legs of this pair are capable of reaching further backward, till eventually a position parallel to the body axis is attained and the complex of left and right Ba1 plus intercoxal plate is stopped by the sternal integument proper. Apparently, the articulating membrane connecting the first basipodal segments to the sternite does not limit the swimming movement in itself. Though both Claus (1893a) and Perryman (1961) have extensively dealt with the Ba1-coupler-sternal-keel-complex, quite surprisingly neither one of them did refer to this functional aspect of the configuration.

The hydrodynamic requirements of the recovery stroke may be served by a curved position of the legs when moving forward, as opposed to the stretched position when performing the powerstroke. In this case, one would expect many, if not all, hinge-joints between the various segments, as well as the joints between segments and setae (including the terminal seta (P1) or spine (P2-4)), to be constructed as one-way joints, viz., providing stiffness in performance and suppleness in return. Two kinds of structures may be present to achieve that a joint's posterior movements are possible, while anterior movements are blocked: the posterior integument of successive segments may be partly fused, or anterior apophyses may be present on one or both sides of a joint. The former condition applies to joints Ba2/Ri in P2 and Ba2/Ri1 in P4; the latter condition is found in Ba1/2 of P1-4, in

Ba2/Ri of P1, and Ri2/3 of P3-4; and both structures are present in Ba2/Re of P1-4. In the absence of one-way joints, the required rigidity-flexibility variation between segments may be accomplished by muscular action as well. The necessity for movements of the complete natatory setae and the terminal spines by muscular action in the shift from forward to backward stroke and vice versa has already been pointed out by Strickler (1975a). Moreover, all setae and terminal spines apparently are restricted in their forward movements, as their articulations are invariably situated to the posterior side of the segments' edges.

With regard to the setae themselves, it is suggested that their 'modified sites' represent joints, allowing the seta to bend when the return stroke is in progress. Comparison of the positions in which the various setae of *E. messinensis* may be found shows, that all are generally smoothly curved or eventually curled, indicating that exogenous forces are distributed evenly via the apparently smooth gradient of strength within a seta. This includes also the breaking region, which, apparently, is being affected only by forces exceeding a certain threshold and/or by pulling forces. In the natatory type-B setae, on the contrary, faint curves may only be observed in the constituting parts, whereas slightly angled connections between the sections are present at the modified sites. Though type-A setae are smoothly curved, here also the sections proximad and distad to the sole modified site may show an angled connection. These observations indicate that forces exerted on natatory setae do not always provoke an evenly progressing reaction along a seta's length, which evidences that at least a discontinuous gradient of strength is possible. From the above, it is likely that the modified sites actually are joints, allowing relatively rigid sections of the seta to interarticulate. The stiffness, necessary when propulsive power has to be exerted, might be gained if these joints, too, would be one-way joints; however, their structure does not indicate such condition to be present. So, if the joints are not direction-limited, the required rigidity may be provided by muscular action. If a muscle inserts basally in the seta (or in the segment) on one side, and apically on the other, contraction will cause the seta to straighten, whereas upon relaxation the seta will be allowed to bend in any direction. Within natatory setae (cf. fig. 10f) a fibriform tissue-strand is always present; whether or not muscle-fibres c.q. tonofibrils are contained in it has, however, yet to be determined.

What applies to the segments and setae will, mutatis mutandis, hold for the setules on the setae as well. These, too, may be expected to present one-way jointed insertions and/or one-way suppleness. The purely integumental nature of the setules (cf. Raymont et al., 1974; Friedman & Strickler, 1975) defies the possibility of a muscular component to be involved, here.

STRUCTURES OF THE INTEGUMENT

These include integumental organs and integumental structures as defined by Von Vaupel Klein (in press b), to which paper is also referred for a discussion upon the regular integumental organs and for a review of the scanty literature dealing with such minute structures in Crustacea.

The observation of integumental organs, as performed by various authors (e.g., Fleminger, 1973; Pulsifer, 1975; Mauchline, 1977; Ferrari & Bowman, 1980), includes both light microscopy and scanning electron microscopy. Preparative procedures frequently involve digestion of tissues by KOH, and staining of the resulting clean integument. However, digestion often results in loss of integumental organs, leaving only empty perforations to be mapped, whereas staining may obscure the minute structures which are to be observed. In my experience, normal in toto preparations may be made by routine procedures (cf. Von Vaupel Klein, in press a). These yield quite satisfactory objects for observation, in the case of S.E.M. techniques just as well as in light microscopy, albeit that it has to be recommended to use the compound microscope with differential interference contrast equipment. The above holds also for integumental structures, with the exception only of granular areas; these structures may only be recognized with certainty in S.E.M. observations.

Two ways of mapping the perforation sites of the body are possible. Fleminger (1973) used schematic habit figures, and this method has also been employed in the present study. Mauchline's (1977) maps show the integument of the various segments spread out flatly, allowing all sites to be drawn rather easily into a single figure per species. For comparative purposes Mauchline's method seems to be the more convenient, because quick checks are easy. However, the design of Fleminger gives the in situ positions of the organs, which is preferable when functional considerations are being made. Therefore, both methods have their merits but Fleminger's is the more adequate for general purposes, whereas use of the 'flat maps' of Mauchline should be confined to comparative studies only.

Integumental Organs

The spinular organ of Ba2 on swimming legs 2-4 is supposed to represent a modified form of the 'spine-sensillum and/or spinular pore' as found on P1Ba2 (see Von Vaupel Klein, in press b). Presumably, the disc with its continuous spiniform outgrowth has been completely fused to the remainder of the segmental integument, while it has apparently shifted from an exclusively lateral position to postero-laterad. The morphology of the hidden part of the attachment of the spiniform outgrowth (the edge of a semicircular slit?) is identical in this structure in the 2nd-4th legs and in the spinular organ of leg 1 (cf. pl. 22c and Von Vaupel Klein, in press b, pl. 10). Next, the situation of the organ on Ba2 of legs 2-4 closely approximates the site occupied on Ba2 of the first legs.

The urn-shaped pores found in the ventral wall of the oral cavity very probably represent the external orifices of underlying glands. The only glands described so far from the labrum of copepods are the labral glands (cf., e.g., Richard, 1892; Lowe, 1935; Lang, 1948a; Fahrenbach, 1962; Park, 1966; Ong, 1969). The proper origin of such glands, if present also in *E. messinensis*, has, however, yet to be established, more in particular as regards a possible derivation from an essentially integumental gland. Richard (1892) observed a varying number of unicellular glands opening via a single common, median pore in various genera of freshwater copepods. Lowe (1935) and Park (1966) found eight syncytial glands in *Calanus finmarchicus* and in *Epilabidocera amphitrites*, respectively, each gland with its own orifice on the inner wall of the labrum. Lang (1948a) described ten unicellular glands from the upper lip of a harpacticoid, eight of which discharge into a common salivary reservoir, which opens via an elevated pore structure ("Zipfel") in the central part of the labrum. Fahrenbach (1962) also reports labral glands from a harpacticoid, while Ong (1969) found such glands in *Gladioferens pectinatus* (Brady, 1899). In particular Richard (1892) made reference of the similarity in structure of labral glands and unicellular cuticular glands, but subsequent reports are not conclusive as to this point. The internal structure of the urn-shaped pores has not yet been elucidated either. For the two reasons mentioned, the proper integumental status of the urn-shaped pores could not be assessed as yet. The presence of these large, protruding pores may well be related to raptorial feeding habits of *Euchirella*, as aetideids are known to be mixed feeders (cf., e.g., Anraku & Omori, 1963; Gauld, 1966; Arashkevich, 1969; and papers reviewed by Bradford & Jillett, 1980). Cahoon (1982) observed sudden secretions of large amounts of mucus by females of *Euchirella venusta* Giesbrecht, 1888, for immobilizing prey. It seems that only the urn-shaped pores together form a complex of structures capable of performing such function in the oral area.

As regards the large, irregular pore on the genital somite, this structure seems very distinct but in a single specimen only. Although it has been included in the present description, the possibility that it might eventually turn out to be an artifact cannot be ruled out altogether.

The complex tubular pore system on P1Ri can only be approached in descriptive terms at the moment. Though the structure of this complex looks very similar to a multiple, tubular glandular pore, its true function can be determined only after the nature of the internal tissue-strand has been established: whether composed of glandular ducts, or glandular in itself, or neural. As has been suggested before (Von Vaupel Klein, 1972) the structures on P1Ri together with the associated curved seta of P1Ba2 might well form a grooming-apparatus of some kind, whereby a glandular function of the pore-system would be the most likely. However, the possibility that some chemo-sensory function is being served here cannot be completely ignored. In this case the specifically arranged plumosity on the curved seta could serve to bring probes to the openings of the pore-system, comparable to the function of the bifid tongue of a snake.

The structure found basally on Ri3 of P3-4, characterized as being of uncertain nature, could not be described more specifically, unfortunately. However, it might perhaps be tentatively referred to the "slit with closing valves" Mauchline (1977) described as occurring in several species of the family Heterorhabdidae.

The possibly integumental nature of the components of the frontal organ, i.e., the pair of 'frontal sensilla' and the 'frontal pore', has been dealt with in the discussion on the cephalothorax, above.

In addition to my review of integumental organs in copepods (cf. Von Vaupel Klein, in press b) observations cited by Lang (1948a: 126) may be mentioned here, which include indications that cuticular glands in certain harpacticoids may be functional in escape and encapsulating reactions. Blades & Youngbluth (1979) reported the presence of extensive fields of another kind of integumental organs, "pitpores", on the urosome of female *Labidocera aestiva,* which according to the authors may be instrumental in producing a solvent to loosen the cement of the spermatophore coupler. Blades & Youngbluth also observed associated "peg and pore" arrangements, possibly involved in a "trigger-and-discharge" mechanism on the genital somite of the same species. The dense fields of cuticular pores Giesbrecht (1899) described from the cephalothorax of asterocherid copepods, viz., "Rohrenporen" ('tube-pores') and "Trichterporen" ('funnel-pores') could not be referred to any of the pores observed in *E. messinensis.* Finally, Tyson & Sullivan (1980) described a kind of peg-sensillum or sensory seta from the frontal knobs of male brine shrimp, *Artemia,* but these do not appear to be referable to integumental organs described from *E. messinensis,* either.

The distribution of integumental organs may be considered from two distinct aspects. First, the distribution over body and appendages of the *E. messinensis* f. typica female should be examined as such. As noticed by

Fleminger (1973) and Mauchline (1977), integumental organs are frequently serially homologous on various somites. Though this phenomenon should preferably be studied in the course of a survey throughout the Calanoida, some observations of restricted conclusiveness may be made from the present data.

Perforation sites on cephalothorax and urosome (fig. 13) are either bilaterally symmetrical or present in the midline. The bilateral symmetry is only absent on Ur1+2, where a major asymmetry in the shape of the body occurs. A probably homologous series of perforations is formed by the middorsal sites (m) on Th1, 2, and 3. Next, three other presumably repetitive series may be recognized. These include a dorsal, a dorso-lateral, and a ventro-lateral series, respectively comprising the sites as indicated in table VII. Based solely on the situation in a single species, these series necessarily are speculative, though some stretches seem to be quite convincing. However, from Fleminger's (1973) study on *Eucalanus* it is evident that perforation patterns may vary considerably within a genus. A reasonably clear picture of an underlying pattern can, therefore, be established only when at least a complete genus is taken into consideration: as Fleminger found, no more than c. 60% of the sites possible for the genus are ever occupied in any of its species. So, the incidental presence or absence of a few sites in a certain species always provides an incomplete picture and thus may easily give a false idea of serial homologies, if no other species are taken into account.

Next, functional aspects of sensing and lubrication, as surmised for various organs (Von Vaupel Klein, in press b), obviously are closely related to, e.g., body form and swimming performance. Requirements of these kinds may also affect distribution of integumental organs and thus obscure the, presumably primitive, repetitive nature of the organs on succeeding somites. Finally, the hairs in the postero-lateral rows on Th4+5 should not be taken into account in a serial comparison, as these appear to constitute a specialization, directly related to the adaptation of that body region to various functions in the reproductive process.

Though not yet operational by lack of comparative data, the phenomenon of serial homology of (integumental) organs is of special interest. Recognition of a regular repetition in the pattern found on succeeding somites might eventually provide new clues to the metameric composition of the copepod body. As outlined above, many questions about the original number of somites composing the ancestral copepod are as yet unsolved.

In this respect, the peculiar semi-circular configuration of the six sites C-PT-e-l,r-1,2,3, just dorsad to the oral opening, immediately draws atten-

TABLE VII

Tentative serial homologies of integumental perforation sites of the body in the *Euchirella messinensis* female (indication "PT" omitted, for brevity)

dorsal series	dorso-lateral series	ventro-lateral series
C - a - 1	C - a - 2	
C - b - 1		C - b - 2
	C - c - 1	C - c - 2
C - d - 1		C - d - 2
C - e - [1, 2, 3]	C - e - 4	C - e - 5 *and/or* - 6
		C - f - 1
C - g - 1	C - g - 2	C - g - 3
C - h - 1		
	C - i - 1	
	C - j - 1	C - j - 2 *and/or* - 3
Th1 - b - 1	Th1 - b 2, 3	
		Th2 - a - 1
Th2 - b - 1		
	Th2 - c - 1	Th2 - c - 2 *and/or* - 3
		Th3 - a - 1
Th3 - b - 1 *and/or*		
- c - 1 *and/or*	Th3 - c - 2	
- d - 1		Th3 - d - 3 *and/or* - 4
Th4+5 - a - 1		
	Th4+5 - b - 1	Th4+5 - b - 2
Th4+5 - c - 1		
		Th4+5 - d - 6
	Th4+5 - e - 2	
Ur1+2 - a - 1	Ur1+2 - a - 2	
Ur1+2 - b - 1		
	Ur3 - a - 1	
	Ur4 - a - 1	
Ur5 - a - 1	Ur5 - a - 2	
1) F - D - a - 1	F - V - a - 1	

1) Only if the furca is considered an element of the trunk instead of an appendage.

tion. As similar concentrations are found at approximately the same location in various *Eucalanus* species (cf. Fleminger, 1973), this group might refer to a couple of contracted somites. Of course, the configuration might just as well have some functional cause and originate, e.g., from the multiplicity of an originally single site.

Serial homology in the integumental organs of the successive appendages is only obvious in the four pairs of natatory legs (fig. 15, table VI). In fact, virtually all organs show serial homology, provided that the addition of organs from rostrad to caudad (i.e., from P1 to P4) is not considered to be in contradiction with the principle of serial homology. As reduction (e.g., number of segments) primarily affects legs 1 and 2, a similar situation may be expected as regards the integumental organs. The only organ lost in a caudally progressing series is the peg-sensillum Ba2-pf-4, present in P2 and 3, but absent in P4. Specialized organs, i.c., the tubular pore system on P1Ri, and the hair-sensilla on the caudal face of P4, obviously do not show serial homology.

As regards the remaining appendages, these apparently are too specialized, i.e., too highly modified relative to the primitive, biramous leg, to be directly comparable. As also the question of the homology of the rami has not yet been solved, no conclusions about possible homologies of perforation sites can be drawn in the case of the antennule up to and including the maxilliped. The A1, however, shows another phenomenon of interest, viz., a certain regularity in repetitive occurrence of integumental organs on succeeding segments of the appendage itself. Obvious examples are the peg-sensilla on segments 1 to 3, and the slit-shaped pores, often occurring with aesthetascs and/or with large setae. Though relationships of this kind may well have a functional cause, they should at least be taken into account in studies which try to explain the segmental composition of the antennule on the basis of the ancestral, biramous leg.

The second aspect of distribution of integumental organs pertains to a comparison with other Calanoida, but unfortunately this does not appear to be fruitful at this stage of knowledge. The only other systematic approaches involving calanoids are the reports by Fleminger (1973) and Mauchline (1977). Fleminger (1973) mapped and characterized the integumental organs of the pleuro-tergal sclerites of the cephalothorax and those of the urosome in the calanoid genus *Eucalanus*. Mauchline (1977) merely mapped perforation patterns in a variety of crustaceans, including calanoids, on the dorsal and lateral integument of the body. Comparison of the present data with the above accounts reveals that several perforation sites are similar among various calanoid copepods and that the nature of a number of integumental organs at similar sites is the same for *Eucalanus* spp. as it is for *Euchirella messinensis*. However, the purely incidental character of the available data does not provide a basis for a sound and detailed intergeneric comparison. Such comparison should at least await the forthcoming study of Mauchline (in prep.; see Mauchline, 1977), which will deal with perforation signatures in over 230 calanoids. Preferably, even, Mauchline's data should also be specified to include the nature of the organ present at each site. In all, a comparative approach to perforation patterns is as yet inopportune.

Substitutions of Organs at Fixed Sites

Within the material studied, no sites were ever found unoccupied, indicating that the presence of some integumental organ at any given, predesigned site, is tied to rather rigid genetic rules. On the other hand, in a few instances sites were found occupied by an organ different from the type normally present. This phenomenon has been observed in site Th4+5-PT-a-r-1, where in one specimen the usual hair-sensillum was found substituted by a pit-sensillum, and in site Ur5-PT-a-r-1, where the usual slit-shaped glandular pore was replaced by a peg-sensillum. In both these cases, one of the organs of an associated pair was concerned, viz., the hair-sensillum of a hair-slit pair, respectively the slit-shaped pore of a peg-slit pair.

Though various kinds of aberrations may be found in copepods, facts like these are worth noticing because they cannot infrequently shed light upon (1) relative apo- and plesiomorphies when the aberrant situation involves the recurrence of an atavistic character state or (2) the ontogenetic relationship of organs, as very probably pertains to the above mentioned substitutions.

From the fact, viz., that in an associated pair one of the components is replaced by an organ different from that regularly present at its site, two suppositions may be made. The first is, that apparently the site of an integumental organ is primarily determined genetically, but that the expression of the pertinent genetic information may not too difficultly be modified by either somatic mutation or by exogenous influence to yield a different type of organ. On the other hand, the 'normal' pattern of organs is far too regular to suppose that no information about the type of organ would be present at all. Secondly, in associated pairs (as characterized arbitrarily, by merely taking into account the small distance between two organs), there apparently is some ontogenetic link between the two components of a pair: as suggested by the peg-peg substitution of a peg-slit, such a pair may well have a common origin, indicating very probably an ultimate functional relationship in the operational stage. Such interrelated functions could be, e.g., the sensor (i.e., the peg) either triggering the secretory function of its companion (the slit) or monitoring the result. Which of the last two functions of the peg-sensillum is the more probable, entirely depends on the peg's true nature: either mechanosensory, e.g., water-current sensing, which would imply triggering the secretion [of lubricant ?] via the slit, or chemosensory, which would be instrumental in monitoring the extrusion of the secretion (see Von Vaupel Klein, in press b).

The 100% presence of perforations at given sites, as found in the present material, seems rather striking, but very probably is an artifact resulting from the small series (N = 10). Fleminger (1973) who examined larger series of his *Eucalanus* spp., found variable percentages of occurrence, frequently between 80 and 100%, but also less.

Integumental Structures

Structures like those presently described occur throughout the Arthropoda; they constitute modifications of the epicuticle in the sense that the normally smooth surface has become sculptured (cf. Richards, 1951). Integumental structures (cf. Von Vaupel Klein, in press b) differ widely in shape and apparently serve a variety of functions, but they have in common that all eventually represent acellular processes (Richards, 1951). As far as crustaceans are concerned, cuticular formations frequently involve roughened areas composed of individual structures variously termed 'humps', 'pimples', 'protuberances', 'terraces', 'teeth' and 'spinules', which provide increased friction for grasping, clinging, or producing sound (e.g., Fujino, 1975; Caruso & Costa, 1976; Meyer-Rochow & Penrose, 1976; Schmalfuss, 1978a). 'Scales', or 'plaques' have been described to reduce undesired adhesiveness of the body surface to, e.g., wet leaves (Holdich & Lincoln, 1974; Schmalfuss, 1978b; Klepal & Kastner, 1980), while 'feathery cuticular hairs' may serve to retain a film of water (Gruner, 1966; Meyer-Rochow, 1980) or to prevent settlement of alien organisms on the body (Meyer-Rochow, 1980). Next, many authors mention the presence of simple or branched cuticular hairs of various kinds. I have never met with a detailed account on structures of this kind in calanoid copepods, but the unspecified terms 'hairs' and 'spinules' are likely to include, inter alia, several types of integumental structures. Within the genus *Euchirella*, a 'pitted area' is known to be present on the genital somite of *E. truncata* Esterly, 1905 (cf., e.g., Park, 1975), probably referable to a field of shallow, integumental pits.

Thus, as regards the integumental structures of *E. messinensis* I have found no records of any of those in descriptions of Calanoida apart from the, often implicit, reference of authors to 'straight integumental hairs'. As only in toto preparations have been examined, no statements are possible about either fine structure or way of formation of any of the structures found. External appearance, arrangement, and location might provide clues to their functions but, in my opinion, fail to do so for either the straight or the wrinkled integumental hairs, or the granular areas. The globular warts on the maxilla might constitute an area of increased friction, just as many other structures found on the mouthparts; the possible functions of the stellate warts on the genital somite have been discussed under Reproduction, above.

The shape of the wrinkled hairs on the antennule is, at first glance, reminiscent of the filamentous bacteria described by Shelton (1974) and Shelton et al. (1975) from shrimp aesthetascs. However, considering difference in size (∅ 0.5 vs. 2-3 μm, length 8-15 vs. up to 240 μm), difference in structure, viz., wrinkled filaments of constant thickness vs. curved filaments with regularly spaced annular constrictions, and, above all, the regular arrangement of the tufts of wrinkled hairs, I am convinced that these indeed constitute a formation of the copepod body and not an alien organism, although admittedly only sectioned preparations may provide final proof in this matter.

Integumental structures should apparently be considered morphological answers to locally specific, physical requirements. They may be classified, for practical purposes, according to (a) external appearance or (b) the way in which they are formed by the integumental epithelium. However, the direct relationship to local functional demands defies homologization of structures that are not completely identical and, in fact, makes it even hazardous to relate apparently comparable structures on different body parts unless serial homology may be assumed. Classification by ontogenetic criteria of growth and differentiation does not seem to be appropriate either, as the number of fundamentally different pathways (Richards, 1951) obviously is limited when employing a single cell-layer, and the possibilities actually available may be further restricted by the ultimately required shape: the ontogenetic pattern needs not be a primary characteristic of the resulting structure. Therefore, it seems realistic to consider each distinct type of integumental structure a formatio sui generis, until the contrary has been unequivocally established. This means that integumental structures can be regarded homologous only as far as their common origin from the epidermis is concerned and that they should rather be characterized as individual expressions of the vast and pluriform potentialities of the integumental tissues. This aspect of morphogenetic versatility is already evident from the infinite variety of cuticular formations (e.g., Richards, 1951). It is also stressed by the possibility for the integument to solve one problem, e.g., undesired adhesiveness, in different ways, viz., either via micro-sculpture like scales, or by adapting macro-morphology in the form of tubercles and ridges (cf. Schmalfuss, 1975, 1977, 1978b), which latter structures are classified as outgrowths or processes, not purely integumental in composition.

On the other hand, there are certain cases that evidence different integumental structures to have evolved from each other. The intergrading of structures in transformational series may be considered such evidence, provided that either (1) the series can be taken from a clinal variation in a continuous patch on a single animal or (2) the series can be related to the phylogenetic tree of a group of closely related species and can be composed of structures occurring at the same site of the body. Another aspect of the evolution of integumental structures involves the pattern formed by the individual emergents. Evolutionary trends in arrangement, tentatively read in the direction from chaos to order, have been pointed out recently by Klepal & Kastner (1980).

As far as homologization of integumental structures of Calanoida with non-Copepoda is concerned, the results of Price & Holdich (1980), and of previous work reviewed by them, indicate that the formation of the epicuticle may differ fundamentally among arthropods and even among crustaceans, whence speculation upon the homology of structures in distantly related taxa seems to be rendered quite impossible.

Intergrading of integumental structures with integumental organs has been reported from isopods, viz., in the formation of the characteristic 'tricorns' (= sensilla squamiformia) from a modified scale plus a 'sensory pit' (cf. Holdich & Lincoln, 1974; Schmalfuss, 1978b; Klepal & Kastner, 1980). Data like these simply invite hypothesizing about the possible origin of other, more complex formations from simple integumental structures. Though sheer speculation, such evolutionary relationships are not too hard to visualize: the simple cuticular hairs or 'microtrichs', and cuticular spinules, composed of solid cuticle, all start ontogenetically with a core of one or more living cells. A mere increase in size might very well result in retention of a cellular lumen and thus give rise to 'processes' or primary 'hairs c.q. spinules not delimited at their base'. On the other hand, a cuticular hair developing a basal articulation (or: proximal breaking-plane) is structurally identical to a secondary setule on a plumose seta or spine. Thus, though evidence is still scanty, evolutionary pathways like the above cannot be completely precluded.

OTHER EXTERNAL ORGANS

Setae and spines and their secondary structures, as well as outgrowths and aesthetascs, are much larger than the Structures of the Integument dealt with in the previous chapter. Consequently they may have a substantial influence on the gross morphology of the somite or segment they originate from. As some of these organs are apparently similar in structure, the total may be classified into a limited number of categories of differing origin. Below, possible homologies will tentatively be outlined; the preliminary conclusions reached should be appreciated at the level of a working hypothesis. Various authors have roughly defined setae, spines, and aesthetascs before (e.g., Gurney, 1931; Owre & Foyo, 1967; Arashkevich, 1969) but such characterizations appear to be useful only for general, descriptive purposes. The definitions by Klepal & Kastner (1980) are considerably more detailed, but lack any specific indication of dimensions. The study of Fish (1975) on the isopod *Eurydice pulchra* Leach, 1815, gives a detailed classification of the setae of that species but, as it is based solely on light microscopic observations, it is not always possible to integrate Fish' results satisfactorily into modern concepts of setal anatomy, in which S.E.M. and T.E.M. techniques have been used.

Outgrowths or processes all have in common that their internal lumen is continuous with the lumen of the somite or segment they originate from, while their integumental lining is not delimited against the surrounding cuticle. They should apparently be considered non-homologous structures, with the exception only of serial homologues, as they each involve a local modification in shape of a somite or segment, which presumably has a directly functional cause. For most structures mentioned in the description, these general remarks are the only that can be made. However, five kinds of outgrowths need to be treated separately:

Both the molariform and the setiform teeth of the mandible all have an internal lumen which is continuous with that of the segment, though due to their extremely heavy wall the molariform teeth practically have no lumen left. With the exception of the serrate setiform tooth, all teeth are distinctly delimited at their base. As far as this may be judged from their overall morphology, all these structures either represent original outgrowths of the segment proper, or they might be regarded strongly modified masticatory setae, like those of the maxillule's 1st inner lobe. The latter possibility, however, seems to apply to the spinulose setiform tooth only.

The heavy seta on the 4th endite of Ba1 of the maxilla is completely continuous with the endite. There are three possibilities to explain its origin: (1) an original outgrowth not homologous with a seta or spine; (2) a formerly articulating seta, now fused to the endite; and (3) one or more fused segments of the former endopodite. When assessing the status of this 'seta' it should be considered that its armature differs from that of the other setae in that it bears only a single pectination along its proximal edge instead of a double one; next, it is finely and contiguously spinulose along its distal edge, as opposed to the coarser and more widely spaced spinulosity of the other, comparable setae of endites 1 to 3. However, the possibility under (2), a former articulating seta, still is the most probable, fitting the commonly accepted view of the morphology of the maxilla, i.e., that endites 1 to 4 are original, comparable outgrowths of basal complex 1, whether the latter be composed of one or of two original segments. The possibility under (3) would match the views of Heegaard (1947a), which have never been properly confirmed, but neither have been properly falsified (cf. Lang, 1946, 1948a; see also Von Vaupel Klein, 1980).

The heavy seta on endite 5 of the maxilla, though largely continuous with its endite, is more directly comparable to the heavy setae on endites 2-3 than to the one on endite 4. Its base is still delimited, albeit vaguely, and its spinulation, though extended, still shows the typical pattern or a 'normal' seta. This seta should rather be considered a now fused, but formerly articulating organ.

The anal operculum either represents an original outgrowth of urosomal somite 5, or it should be regarded as a modified and now fused telson as pointed out by Bowman (1971), the latter possibility being the most probable.

All articulating setae and articulating spines, of the furca as well as of the appendages, and including the terminal seta/spines of the swimming legs, should apparently be regarded as homologous inter se. They represent distinct, relatively independent organs which are remarkably uniform in structure, despite the differences observed in the descriptions, which may relate to their different functions. As regards articulating spines, these show an articulated type of insertion but their actual movability is uncertain. The serial homology of the terminal seta of P1Re on the one hand and the terminal spines of P2-P4Re on the other is questionable, in view of the differences between P1Re3 and P2-P4Re3 in general, i.e., the differing numbers of medial setae (3 vs. 4) and of lateral spines (1 vs. 3).

The sites referred to as 'breaking planes' actually appear to be places where setae are most easily broken from a purely mechanical point of view. At the site of a breaking plane there is an annular region where the thickness of the chitin wall is strongly reduced, thus forming a predetermined site for the seta to break off (figs. 4e, 5g, i; pl. 11a, b, d). Setae that have been proximally broken are often observed to have the remaining stub reaching exactly to this site (pl. 11c). That breaking-off is not only caused by collecting or handling is evident from setae that show an obviously regenerated distal portion, shorter and more slender than the originally present parts, and originating from stubs that are limited distally by the breaking site (pl. 11g). The presence of breaking planes apparently enhances the copepod's chances of survival in case some predator grasps the distal ends of one or more setae. Whether breaking is accomplished by exogenous forces only, or that some sort of autotomy is involved, is not clear. Breaking plane structures have been described from the two intermediate caudal setae already by Schmeil (1892), Claus (1893b), and Gurney (1931), and their observations were confirmed by Lang (1948a). In these setae, the break apparently does not involve the complete cuticular lining, but only its inner portion, whereby a detached seta leaves only a slender stub behind (cf. Claus, 1893b; Lang, 1948a). To my knowledge, no reference has yet been made to breaking planes in any other setae.

Setae may be functioning as mechano-receptors (Strickler & Bal, 1973) or chemo-receptors (Friedman & Strickler, 1975); they may aid in collecting and ingesting food; or they may be functional in swimming, either in propulsion (natatory setae) or steering (furcal setae) (cf. Strickler, 1975a).

The discrete secondary structures on setae and spines, i.e., setules, spinules, and denticles, as well as the hairs and spinules with distinct insertion sites, apparently are all of similar structure. They are discrete formations, mainly (larger hairs?) or completely (cf. setules, Raymont et al., 1974; Friedman & Strickler, 1975), of the integument. Their connection with the supporting cuticle via a concave-convex plane of attachment (concave on the pedestal, convex on the structure proper) presents the only but presumably essential difference with the hairs and spinules that are not delimited at their base (see below). This consideration would justify their classification in a separate category. However, the type of attachment might also be secondary, due to functional causes only. The articulated type of insertion of setules might be functional in the hydrodynamics of swimming, while for all structures holds that this attachment might merely involve the presence of an extremely proximal breaking plane, restricting damage to the cuticle in case of injuries of the protruding parts. In the last case, an essential difference with other hairs and spinules would not be real.

The hairs and spinules with confluent connections to the surrounding integument also are essentially integumental formations. The presence of an independent lumen has not been observed, though their relatively large size may influence the shape of the internal lining of the supporting cuticle. In case the absence of a discrete insertion site would prove a basic difference, they would not be related to the hairs and spinules dealt with above. Of all larger structures, those here under consideration most closely resemble the small Integumental Structures, i.e., wrinkled and straight integumental hairs. Therefore, a possible origin as enlarged integumental structures does not seem to be improbable. In fact, it may well be that some of the present hairs really are integumental structures, as their distinctness relative to the smaller emergents is not always obvious. Moreover, Blades & Youngbluth (1979) demonstrated the epicuticular nature of relatively large 'spines' (c. 12 µm long) in *Labidocera aestiva* by transmission electron microscopy.

As regards the fringe of 'hairs' on the posterior dorso-lateral rim of urosomal somite 3, structures of this kind have been referred to as being sensory in nature by both Gharagozlou-van Ginneken & Bouligand (1973) and Strickler (1975a).

Serrations on setae or spines apparently represent original outgrowths of the cuticle, not referable to other secondary structures. The influence of the external protrusion on the shape of the internal lining of the cuticle should be considered a side-effect of the size of these structures, which otherwise have no independent lumen. Just like outgrowths on somites or segments, there seems to be hardly any homology with other structures.

Aesthetascs (cf. Giesbrecht, 1892) appear to be separately evolved organs, comparable to but not homologous with articulating setae or spines. They are inserted on pedestal-like structures and comparable in size to setae. However, since they are superimposed on the regular setal arrangement of the antennule, their non-homologous character relative to setae and spines seems obvious. Aesthetascs have been proven to represent chemosensory organs, and their fine structure is in accordance with this function (Ghiradella, Case & Cronshaw, 1968a, b, c; Griffiths & Frost, 1976).

COMPARISON WITH PREVIOUS DESCRIPTIONS AND SUMMARY DISCUSSION

The extensive description of the *Euchirella messinensis* female as presented herein, has been compared to existing descriptions of the species as summarized in the Restricted Synonymy. General characteristics of the genus have also been taken into account by involving major reviews of *Euchirella* and descriptions of other species in the comparison as well (i.e., Lubbock, 1856; Claus, 1866; Brady, 1883, 1918; Giesbrecht, 1892; Esterly, 1905, 1911; Sars, 1905, 1924-25; Wolfenden, 1905, 1911; With, 1915; Willey, 1919; Farran, 1929; Sewell, 1929; Rose, 1933; Vervoort, 1949, 1952, 1957, 1963; Brodskii, 1950; Wilson, 1950; Tanaka, 1957; Omori, 1965; Grice & Hulsemann, 1968; Tanaka & Omori, 1969a, b; Park, 1968, 1975, 1976a, b, 1978; Bradford & Jillett, 1980). The main conclusion to be drawn from this comparative survey is, that data published up till now are incomplete, and thereby often erroneous, rather than being essentially controversial to the present results. For instance, I have tried in vain to find a proper description, other than my own (cf. also Von Vaupel Klein, 1980 and in press b), of the following structures:

1. the C-Th1 boundary;
2. the anterior ridges on the free thoracic somites;
3. the pleuro-tergal boundaries of Th1 to Th4+5;
4. the Th4-Th5 boundary;
5. the Ur5-furca boundary;
6. the frontal organ's external structure;
7. the labral papillae;
8. the chaetotaxy of the oral field;
9. the detailed structure of the genital field;
10. the morphology of the asymmetrical outgrowth of the genital somite, in relation to the structure of the seminal receptacles;
11. the warted area on the genital somite;
12. the structure of A1 segment 2;
13. the presence of segment 26 of A1;
14. the special appearance of the distal seta of A1 segment 5;
15. ditto of A1 segment 12;
16. the typology of the other small setae of A1;
17. the special structure of the posterior large seta on A1 segment 22;
18. the Ba2-Re boundary of A2;
19. the partly fused condition of A2Re1+2 to 7;
20. the terminal sclerite of A2Re;
21. the terminal lobe of A2Ri2+3;
22. the subterminal spinules on A2Ri2+3;
23. the masticatory edge of the mandible;
24. the spinules on the Md gnathobasis;
25. the condition of the boundaries of the segments of MdRe;
26. the presence of MdRe6;
27. the vestigial seta on MdRi1;
28. the pedestal of the 8th seta on MdRi2;
29. the chaetotaxy of MxlBa1, 1st inner lobe, anterior and posterior face;
30. the exact condition of the spinulosity and type of insertion of the setae on MxlBa1, 1st inner lobe;
31. ditto, of the setae on MxlBa1, outer lobe;
32. the field of globular warts on MaxBa1;
33. the exact condition of the pectinations and spinulosity on the setae of the Max, in particular: the curved seta on E1; the spinulose seta on E1; the heavy setae on E4 and E5;
34. the hook-shaped outgrowth on MaxBa1, endite 1;
35. the compressed condition of MaxRi1;
36. the spinules on MaxBa2, E5;
37. the exact structure of the pair of adhesive pads on MxpBa1/Ba2;
38. the compressed distal part of MxpBa2;
39. the specialized, short seta, distally on MxpBa2;
40. the exact condition of the spinulosity on the setae of the Mxp;

41. the typology of the A and B natatory setae of the swimming legs;
42. the joints (modified sites) in the natatory setae, including the terminal spines of P2-4;
43. the specialized structures present on P1Ri, combined with the S-curved seta of P1Ba2 (cf. also VonVaupel Klein, 1972);
44. the secondary spinules on the legs' external articulating spines;
45. the descriptions of various integumental organs (cf. also Von Vaupel Klein, in press b);
46. the mapping of the integumental organs of the body (cf. this species only);
47. the mapping of integumental organs of the appendages (cf. all calanoids);
48. the urn-shaped pores in the oral cavity;
49. the wrinkled integumental hairs;
50. the integumental granular areas;
51. breaking planes of various kinds in a variety of setae and spines;
52. and many other fine details of more subtle nature.

From the above, it should be clear why existing descriptions of other *Euchirella* species are unfit for comparison with the present description of *E. messinensis* and why I am preparing redescriptions of all these species. These will be condensed descriptions, stating only differences with the type-species. It should, however, not be understood that all 50-odd items listed above present interspecific variation: but, if never described properly, the presence or absence of such variation may never be established. In conclusion, I would like to paraphrase a statement of Lang (1948b), as follows: To arrive at a natural system of the Copepoda surely is a long and difficult way, but much would be gained if everyone working taxonomically on copepods would present one scrutinous description of one species of the genus he or she is most familiar with, and try to interpret the specific structures found in terms of general copepod morphology, eventually from a phylogenetic point of view. It is evident that this may lead to mistakes, but the result will perhaps lead to a discussion among copepodologists, out of which an approximation of the truth, in the form of a tentative reconstruction of the group's natural system, will later crystallize.

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* = non vidi

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EXPLANATION OF THE PLATES

PLATE 1

Euchirella messinensis (Claus, 1863), ♀ ♀ from "Dana" Exped. sta. 4119^{x}, by S.E.M. a, anterior view of rostrum and frontal organ; b, frontal organ with both hairs in situ; c, frontal organ with hairs detached, note the concave distal faces of the tubercles and the unpaired midventral pore; d, left lateral view of anterior part of cephalon, showing hair-sensillum C-PT-b-l-2 (arrow); e, the same sensillum, enlarged; f, remnants of the former suture between cephalon and Th1, in the middorsal area; g, middorsal region of Th2 showing posteriorly directed hair-sensilla Th2-PT-b-l,r-1 and slit-shaped pores -b-m and -c-m. Scales (in μm): a,d,f = 100; b(=c),e = 10; g = 50.

PLATE 2

Euchirella messinensis (Claus, 1863), ♀ ♀ from "Dana" Exped. sta. 4119^{x}, by S.E.M. a, overall ventral view of the cephalic region, with all appendages removed; empty sockets of antennule (A1), antenna (A2), mandible (Md) and maxillule (Mxl) have been indicated; part of the same view is shown enlarged in pl. 3; b, map of the chaetotaxy of pl. 3, indicating code-nos. from table I; c, left lateral view of the cephalic region, slightly distorted as a result of drying; note the large, semi-dome-shaped upper lip and the curved lobes of the lower lip, together delimiting the channel (arrow), in situ occupied by the gnathobases of the mandibles; d-e, details of oral field chaetotaxy: d, row of spinules no. 1; e, spinules of group 3. Scale-bar of c equals (μm): for a = 400, c = 800, d = 40, e = 8.

PLATE 3

Euchirella messinensis (Claus, 1863), ♀ from "Dana" Exped. sta. 4119^{x}. Overall ventral view of the right-hand side of the oral field, shown by a composition of S.E.-micrographs. For explanation of the chaetotaxy see pl. 2b and table I. Top = anterior, bottom = posterior. Scale equals 100 μm.

PLATE 4

Euchirella messinensis (Claus, 1863), ♀ ♀ from "Dana" Exped. sta. 4119^{x}, by S.E.M. Details of oral field chaetotaxy: a, hairs of row 2; b, spinules of row 4 (background: group 3); c, groups 3, 4, and 5; d, spinules of row 7; e, group 6 (arrow); f, cascading rows 8, 9, 10, 11, and 12 (row 10 interrupted in this specimen); g, patches 13, 14, and 15. Scale-bar of a equals (μm): for a,c,d,e,f = 40, for b,g = 20.

PLATE 5

Euchirella messinensis (Claus, 1863), ♀ ♀ from "Dana" Exped. sta. 4119^{x}, by S.E.M. a, detail of oral field chaetotaxy: hairs and spinules of groups 17-25, as indicated; b, the pair of median papillae on the upper lip (see also fig. 3); c-e, urn-shaped pores on the inner face of the upper lip, details from pl. 6 (see also fig. 3): c, pore 1; d, pore 2-l; e, pore 2-m. Scales (in μm): a = 40; b = 10; c = d = e = 5.

PLATE 6

Euchirella messinensis (Claus, 1863), ♀ from "Dana" Exped. sta. 4119^{x}, by S.E.M. a, overall view of the ventral wall of the oral cavity, i.e., the inner face of the upper lip, showing chaetotaxy and urn-shaped pores; a′, map of same indicating code-nos. See also fig. 3 and table I. Scale equals 20 μm.

PLATE 7

Euchirella messinensis (Claus, 1863), ♀ from "Dana" Exped. sta. 4119ˣ, by S.E.M. a, overall view of the urosome from caudo-laterad, shown by a composition of S.E.-micrographs. Scale equals 100 µm.

PLATE 8

Euchirella messinensis (Claus, 1863), ♀♀ from "Dana" Exped. sta. 4119ˣ, by S.E.M. a, dorsal view of urosome; b, do., detail of the asymmetrical outgrowth of the genital somite; c, d, urosome in ventral respectively left-lateral view; e, large dorsal pore Ur1+2-PT-b-m, present in one specimen only. Scales (in µm): a,c,d = 300; b = 100; e = 10.

PLATE 9

Euchirella messinensis (Claus, 1863), ♀♀ from "Dana" Exped. sta. 4119ˣ, by S.E.M. a, vulva with genital operculum in ventral view; b, the same, of another specimen, note broken fertilization tubules (arrows); c, detail of (a): the two adjoining brushes of stiff setae, mid-caudally on the operculum; d, dorsal view of the attachment of cephalothorax and urosome, showing remnants of former suture between Th4 and Th5 and posterior limits of former Th5, as indicated; e, hairs of the dorso-lateral fringe, along the posterior edge of Ur3. Scales (in µm): a = 50; b = 100; c = 25; d = 200; e = 10.

PLATE 10

Euchirella messinensis (Claus, 1863), ♀♀ from "Dana" Exped. sta. 4119ˣ, by S.E.M. a, ventral view of anal somite, showing posterior mid-ventral indentation, anal operculum, and partly fused sutures with furcal rami (arrows); b, detail of this area in another specimen, showing tubular pores Ur5-S-a-l,r-1; c, postero-dorsal view of the same area as in (a); d, ventral view of left furcal ramus, showing attachment of curved median seta and tubular pores F-V-a-l-2 and -l-3; e, detail of warted area, antero-dorsally on the genital somite; f, the same, enlarged, to show the stellate shape of the warts. Scales (in µm); a,c = 100; b = 25; d,e = 50; f = 10.

PLATE 11

Euchirella messinensis (Claus, 1863), ♀♀ from "Dana" Exped. sta. 4119ˣ, by compound microscope with differential interference contrast. Structures of the antennula: a, proximal part of anterior large seta, left A1, segment 24, showing breaking region (BR) with central breaking plane (BP); b, do., large seta of segment 7; c, the same seta of segment 7 in right antennule, broken-off at breaking plane; d, left A1, the two small setae on segment 6, showing small type breaking plane in the proximal seta, which is in focus; e, A1 right, proximal portions of terminal large setae of segment 25+26, and of posterior large seta of segment 24, all without breaking planes; f, A1 left, posterior large seta of segment 23, broken-off irregularly at an arbitrary site; g, A1 left, segment 2, second seta from distad, previously broken at BP, now with regenerated distal part (Re); h, A1 left, overall view of caudal large seta of segment 22. Scale equals 100 µm for all figures.

PLATE 12

Euchirella messinensis (Claus, 1863), ♀♀ from "Dana" Exped. sta. 4119ˣ, by S.E.M. a, peg-sensillum A1-1-ae-1 in situ; b, A1, segment 1, brush of wrinkled integumental hairs along caudal edge; c, lateral view of segment 2, showing remnants of former intersegmental sutures (black arrows); note also the holes left by the peg-sensilla on segments 1, 2, and 3 (white arrows); d, remnants of former suture between segment 8 and 9, lateral face; e, elaborate structure of lateral part of suture between segments 17 and 18; f, terminal part of antennule, showing readily distinguishable remnants of sutures between segments 24 and 25, and 25/26 (arrows); g, detail of insertion of aesthetasc on segment 14 with adjoining slit-shaped pore A1-14-ae-1 (arrow); h, antero-lateral view of left A2, segments 3-6, to show shape and relative size; note also pore A2-Re4-lf-1 (arrow); i, lateral view of same antenna, showing remnants of suture between segments 1 and 2 (arrow); j, same antenna, attachment of exopodite to basipodite, showing presumed exopodal segment no. "0". Scale-bar of h equals (μm): for a,b = 10, c = 100, d,h-j = 40, e,f = 20, g = 4.

PLATE 13

Euchirella messinensis (Claus, 1863), ♀♀ from "Dana" Exped. sta. 4119^x, by S.E.M. a, anterior view of masticatory edge of right mandible, showing molariform and setiform teeth (see also text); b, gnathobasis of right mandible, showing situation of the two fields of spinules; c, do., detail, showing relative size and shape of both median (m) and lateral (l) patches; d, do., detail of spinules of the median patch; e, enlarged detail of spinules of this patch, other specimen, left Md; f-i, details of gnathobasis of left mandible: f, detail of spinulose setiform tooth; g, multi-serrate setiform tooth and multi-cuspidate molariform complex, showing digitiform projections; h, brushes of spinules on anterior face, at base of serrate setiform tooth; i, brush of spinules on posterior side of same. Scales (in μm): a = 50; scale-bar in g equals: for b = 100, c = 40, d,f-i = 10, e = 4.

PLATE 14

Euchirella messinensis (Claus, 1863), ♀♀ from "Dana" Exped. sta. 4119^x, by S.E.M. a, Ri of left mandible, detail of insertion of 5th-9th setae, showing 8th seta being inserted on pedestal (p); b, Re of left mandible, detail of terminal segments 4-6; c, detail of masticatory setae on first inner lobe of maxillula, showing alternating bipectinate setae (b) and bipectinate/spinulose ones (b/s); d, right maxillule, anterior view, terminal part of Ba2 and endopodite, the latter with three of its four setae in situ; e-h, details of 1st inner lobe chaetotaxy (see also figs. 8, 14 and pl. 15): e, group *a5*; f, groups *a3* and *a4*; g, groups *a1* and *a2*; h, detail of group *a1*. Scales (in μm): a = 10; scale-bar of e equals: for b-d,g = 20, e,f,h = 10.

PLATE 15

Euchirella messinensis (Claus, 1863), ♀ from "Dana" Exped. sta. 4119^x, by S.E.M. a, overall view of first inner lobe of right maxillule, partly showing anterior face chaetotaxy (see also figs. 8, 14 and pl. 14); a', map of same, indicating code-nos. to patches of spinules. Scale equals 30 μm.

PLATE 16

Euchirella messinensis (Claus, 1863), ♀ from "Dana" Exped. sta. 4119^x, by S.E.M. a, overall view of first inner lobe of right maxillule, showing posterior face chaetotaxy (see also figs. 8, 14 and pl. 17); a', map of same, indicating code-nos. to patches of spinules. Scale equals 30 μm.

PLATE 17

Euchirella messinensis (Claus, 1863), ♀♀ from "Dana" Exped. sta. 4119ˣ, by S.E.M. a-f, details of individual patches of spinules from pl. 16: a, group *p1*; b, group *p2*; c, group *p3*; d, group *p4*; e, groups *p5* and *p6*; f, group *p8*; g, detail of one of the large bipectinate/spinulose setae of the maxilla, showing proximal part of bipectinate row, starting with one or (here) two unpaired denticles. Scales (in μm): a = e = 10; b = 10; c = d = g = 10; f = 10.

PLATE 18

Euchirella messinensis (Claus, 1863), ♀♀ from "Dana" Exped. sta. 4119ˣ, by S.E.M. a, composite S.E.-micrograph showing combs of spinules on postero-medial face of endites 1-4 of left maxilla; b, left Max, detail of hook-shaped outgrowth on endite 1; c, right Max, detail of Ri; d, e, details of pectinations and spinulosity of the two largest setae of the maxilla: d, the heavy seta on the fourth endite (E4); e, the heavy seta on E5, showing rows a, b, and c (see fig. 7 g-i); f, detail of globular warts on postero-medial face of Ba1 of maxilla. Scales (in μm): scale-bar of b equals: for a,c,e = 20, b = 4, d = 10; scale f = 5.

PLATE 19

Euchirella messinensis (Claus, 1863), ♀♀ from "Dana" Exped. sta. 4119ˣ, by S.E.M. a-d, structures of right maxilliped, medial view: a, terminal patch of spinules on Ba1; b, do., detail; c, proximal comb of spinules on Ba2; d, do., detail of spinules; e, left maxilliped, lateral view of segments 2-5 of Ri, to show attachment of setae, note also slit-shaped pore Mxp-Ri4-lf-1 (arrow); f, right first leg, lateral view of Re3 showing hair-fringe; g, h, the same hair-fringe, enlarged. Scales (in μm): scale-bar of d equals: for a,g = 10, b,d,h = 4, c = 20, e,f = 40.

PLATE 20

Euchirella messinensis (Claus, 1863), ♀♀ from "Dana" Exped. sta. 4119ˣ, by S.E.M. a-f, structures of the endopodite of leg 1, anterior face: a, overall view of left Ri; b, detail of thin-walled distal hairs; c, detail of central hairs, showing four hairs (the fourth broken); d, e, combs of spinules of left, respectively right Ri in different specimens: d, 23 spinules; e, 17 spinules; f, detail of terminal part of tubercle of left Ri, showing complex tubular pore system (arrows). Scales (in μm): a = 40; b,c,d,e,f = 10.

PLATE 21

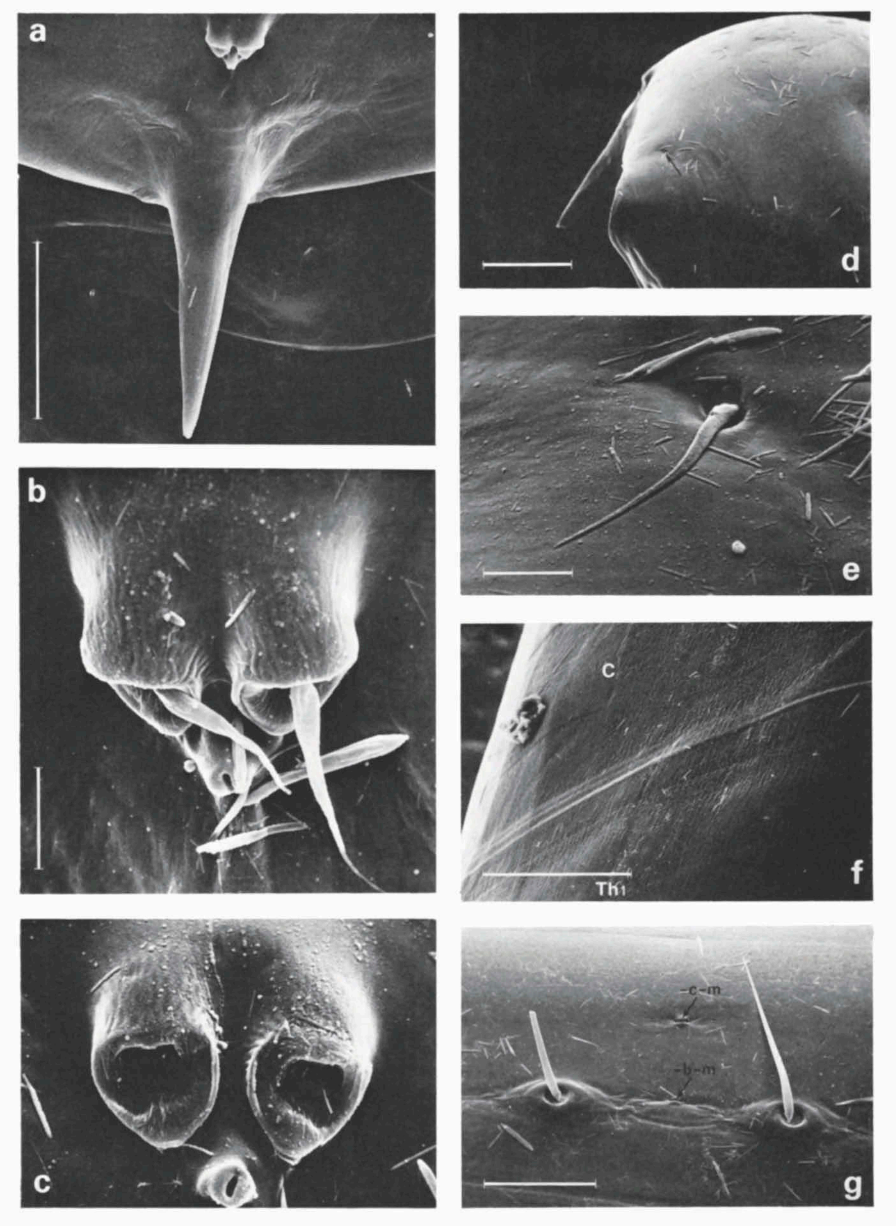
Euchirella messinensis (Claus, 1863), ♀♀ from "Dana" Exped. sta. 4119ˣ, by S.E.M. a-h, structures of the 2nd and 3rd pairs of swimming legs: a, lateral spine of P2Re2, showing adjoining acute outgrowth and contiguous row of secondary spinules; b, detail of this row of spinules; c, P2Ri, detail of proximo-lateral point in anterior view, note also hole left by concealed pore P2-Ri1+2+3-af-1; d, anterior aspect of terminal part of P2Ri, showing tubular pore P2-Ri1+2+3-af-2 in centre of distal hair-brush; e, detail of P2Ba2, showing granular area adjacent to partly concealed pore P2-Ba2-af-1; f, P3Ri1, detail of double lateral points, anterior view; g, P3Ri2, detail of disto-lateral point in anterior aspect; h, P3Re2, position of closing-flap pore P3-Re2-af-1 near base of lateral spine. Scales (in μm): scale-bar of a equals: for a,c,d,h = 20, b = 4, e,f,g = 10.

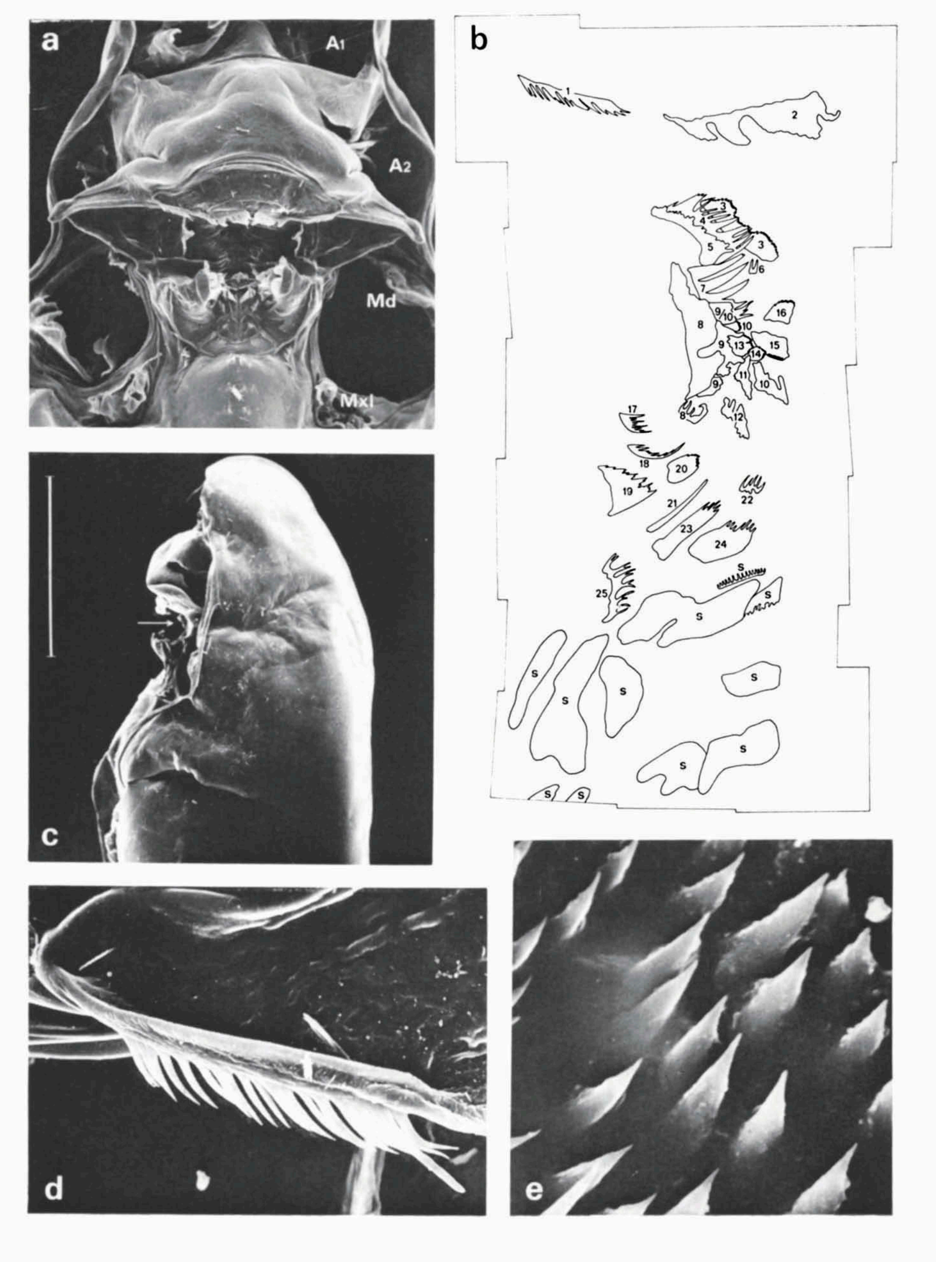
PLATE 22

Euchirella messinensis (Claus, 1863), ♀♀ from "Dana" Exped. sta. 4119ˣ, by S.E.M. a-i, structures of the fourth pair of swimming legs: a, b, the double spines on P4Ba1 in two different specimens, posterior view; c, detail of spiniform outgrowth in disto-lateral corner of Ba2, posterior face, note the underlying edge (of slit?) (arrow); d, left Ba2 and adjacent segments, posterior aspect, showing hair-sensilla(-hole) P4-Ba2-pf-1, 2, 3, P4-Ri1-pf-1, and spiniform outgrowth of Ba2; e, detail of serrate edge of terminal spine of Re3; f, extreme disto-lateral corner of Ba1, posterior face, showing patchy pattern of granular areas; g, detail of double lateral points of Ri1, note also adjacent granular area and slit-shaped pore P4-Ri1-af-1 (arrow); h, the disto-lateral point of Ri2; i, detail of lateral edge of Re3, showing lateral spines 1 and 2 with intermediately produced integument. Scales (in µm): a = 50; c = 10; scale-bar of b equals: for b,i = 40, d = 60, e,f = 20, g,h = 10.

PLATE 23

Euchirella messinensis (Claus, 1863), ♀♀ from "Dana" Exped. sta. 4119ˣ, by S.E.M. a-c, various types of thin integumental hairs on the sternum, posteriad to the oral area: a, wrinkled hairs; b, c, slender and somewhat stouter, straight hairs; d, e, details of granular areas on, respectively, P4Ba1 and P3Ri1; f, uncertain organ P3-Ri3-af-1; g, frontal organ, detail of distal face of left tubercle, showing elongate hole left by detached hair (arrow); h, i, integumental organs on sites Ur5-PT-a-l,r-1 and -2, showing aberrant asymmetrical development: on the left (h) the normal situation of peg-sensillum plus slit-shaped glandular pore occurs, on the right (i) two peg-sensilla are present. Scales (in µm): scale-bar of a equals: for a,b,c = 20, d,e = 4, f = 2; scale of g = 5; scale of h (= i) = 10.


a
b
c
d
e
c
Th1
f
-c-m
-b-m
g


a
A1
A2
Md
Mxl
b
1
2
3
4
5
6
7
8
9
10
11
12
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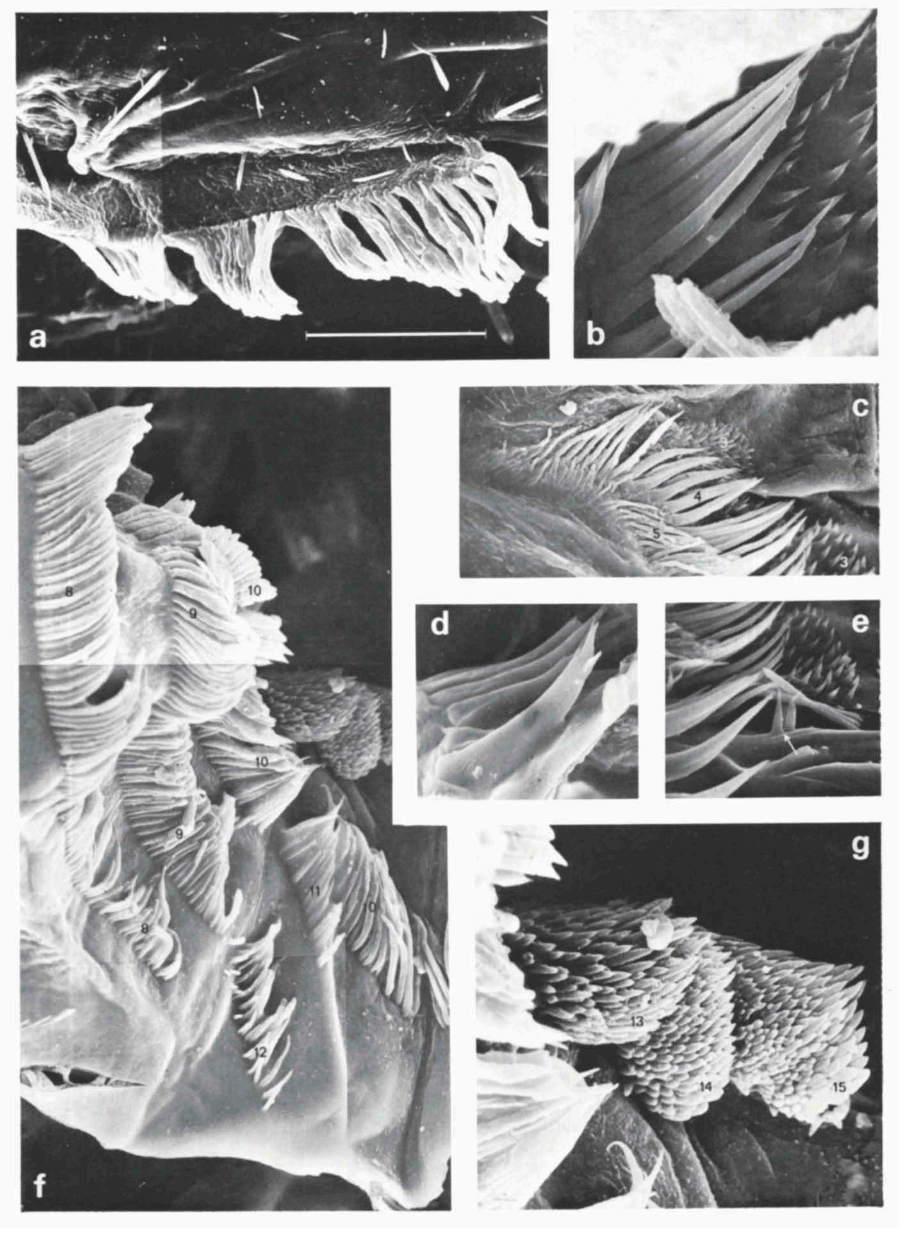
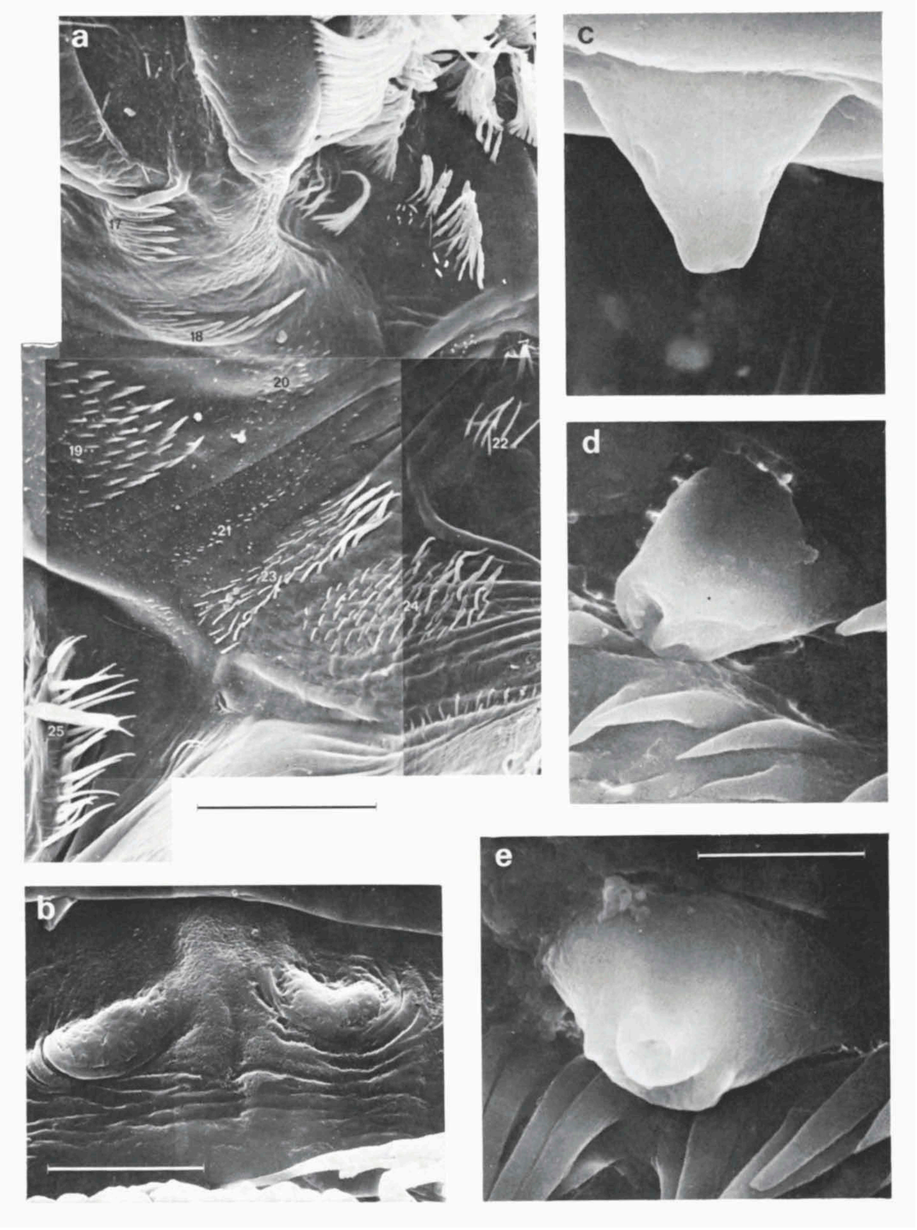
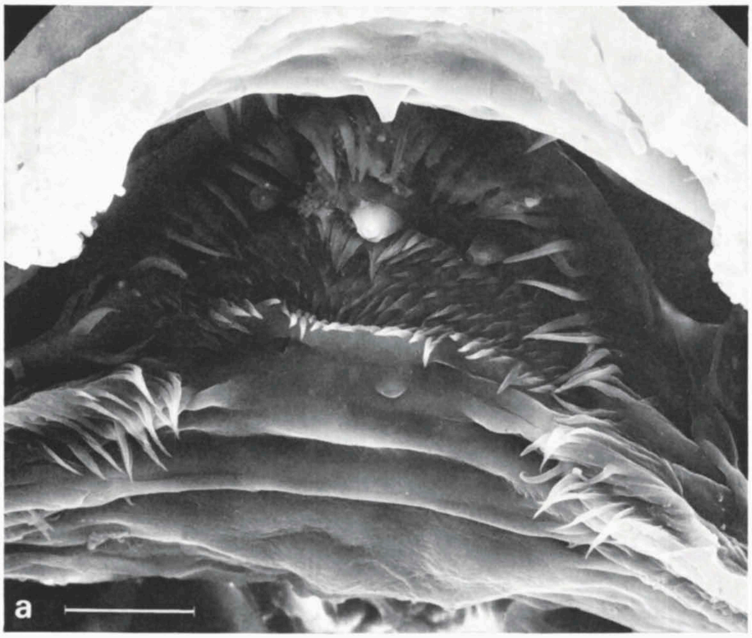
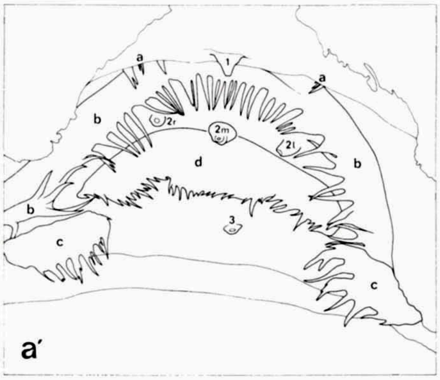
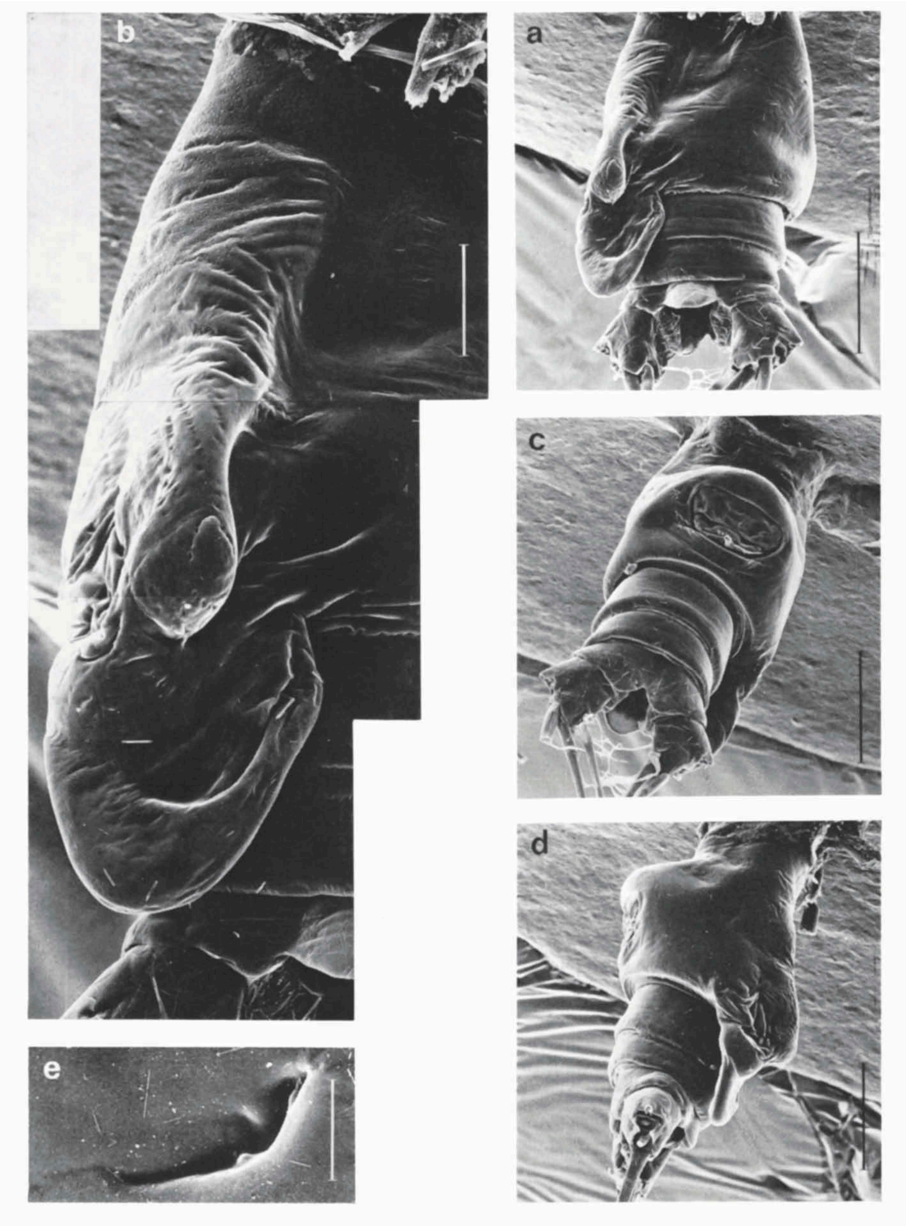
14
15
16
17
18
19
20
21
22
23
24
25
s
c
d
e

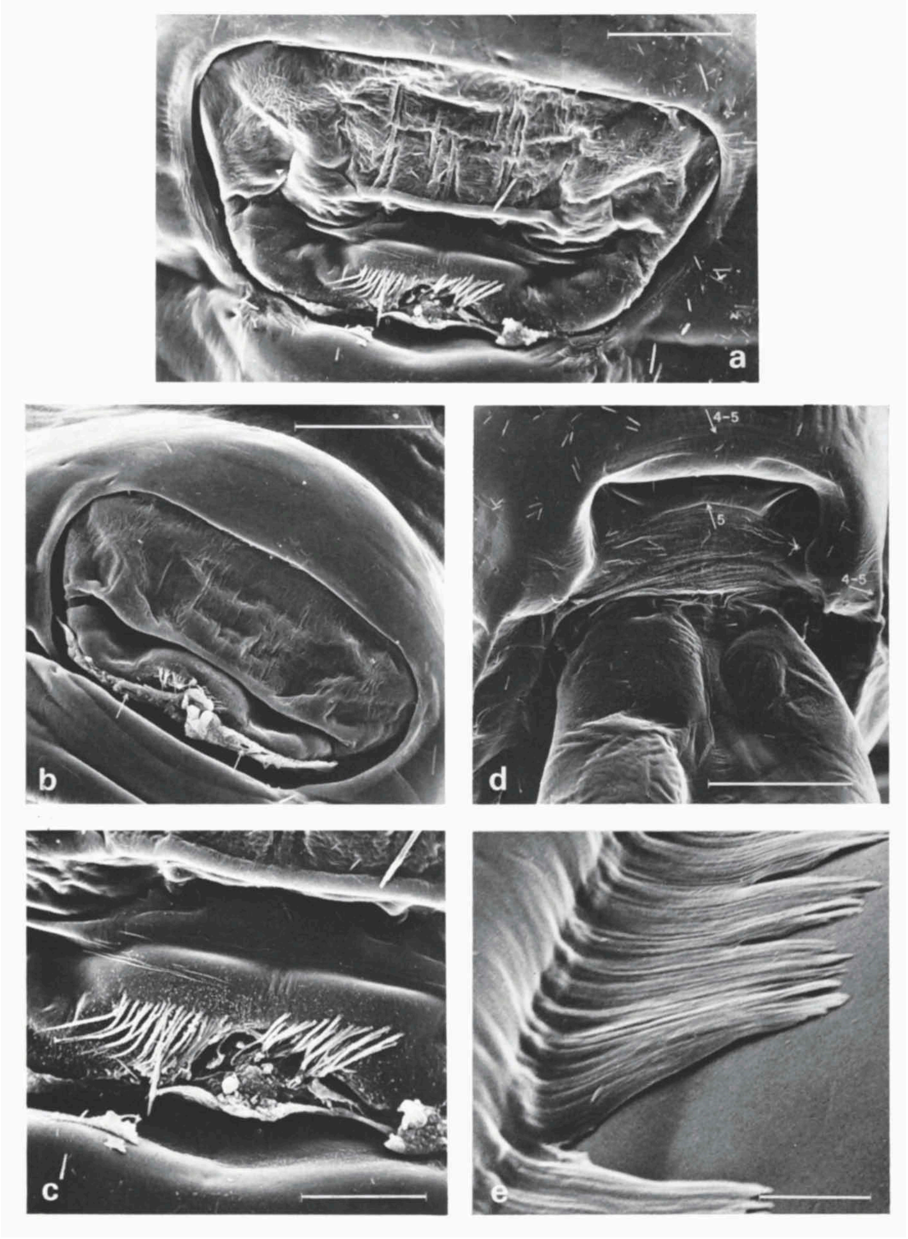

a
b
c
3
4
5
3
d
e
8
9
10
10
9
11
10
8
12
f
g
13
14
15

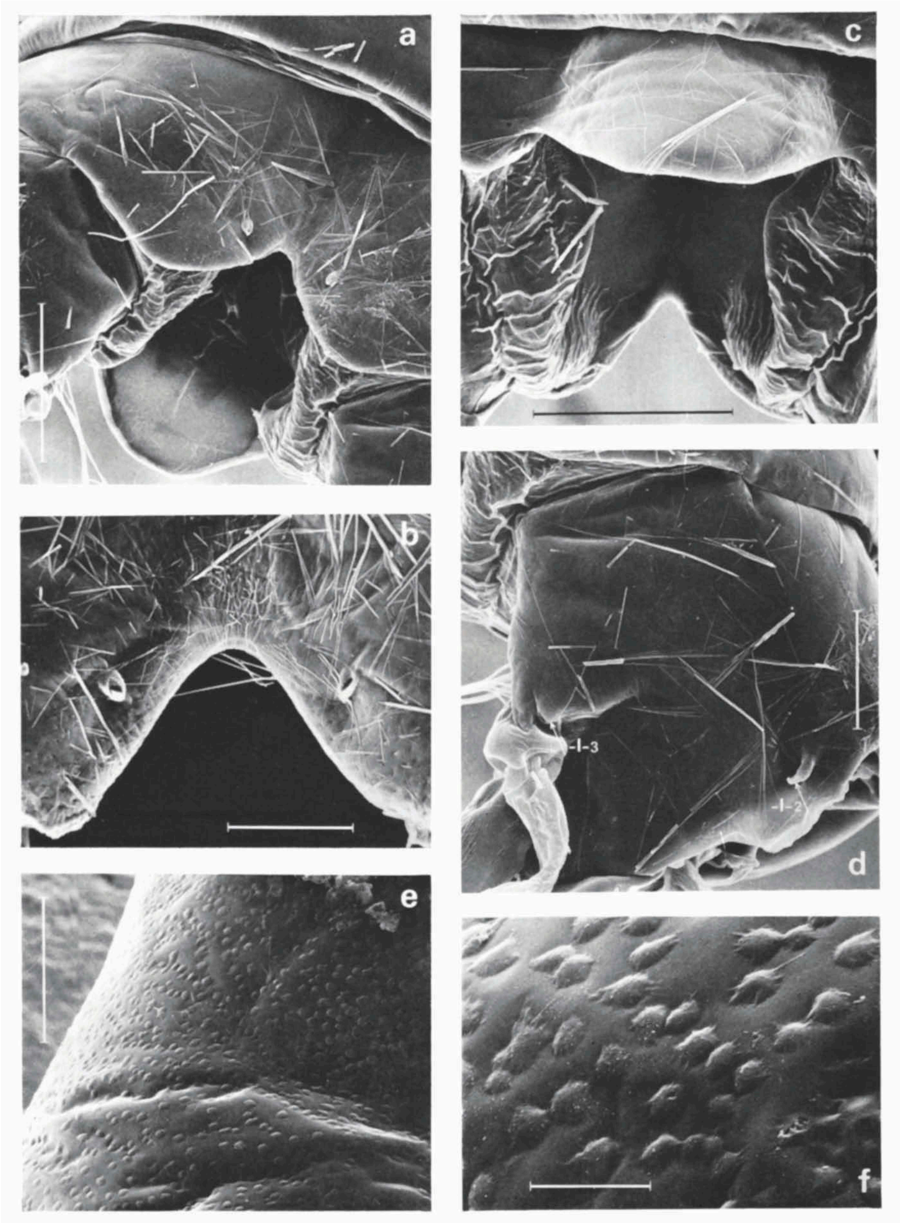

a
17
18
20
19
22
21
23
24
25
b
c
d
e

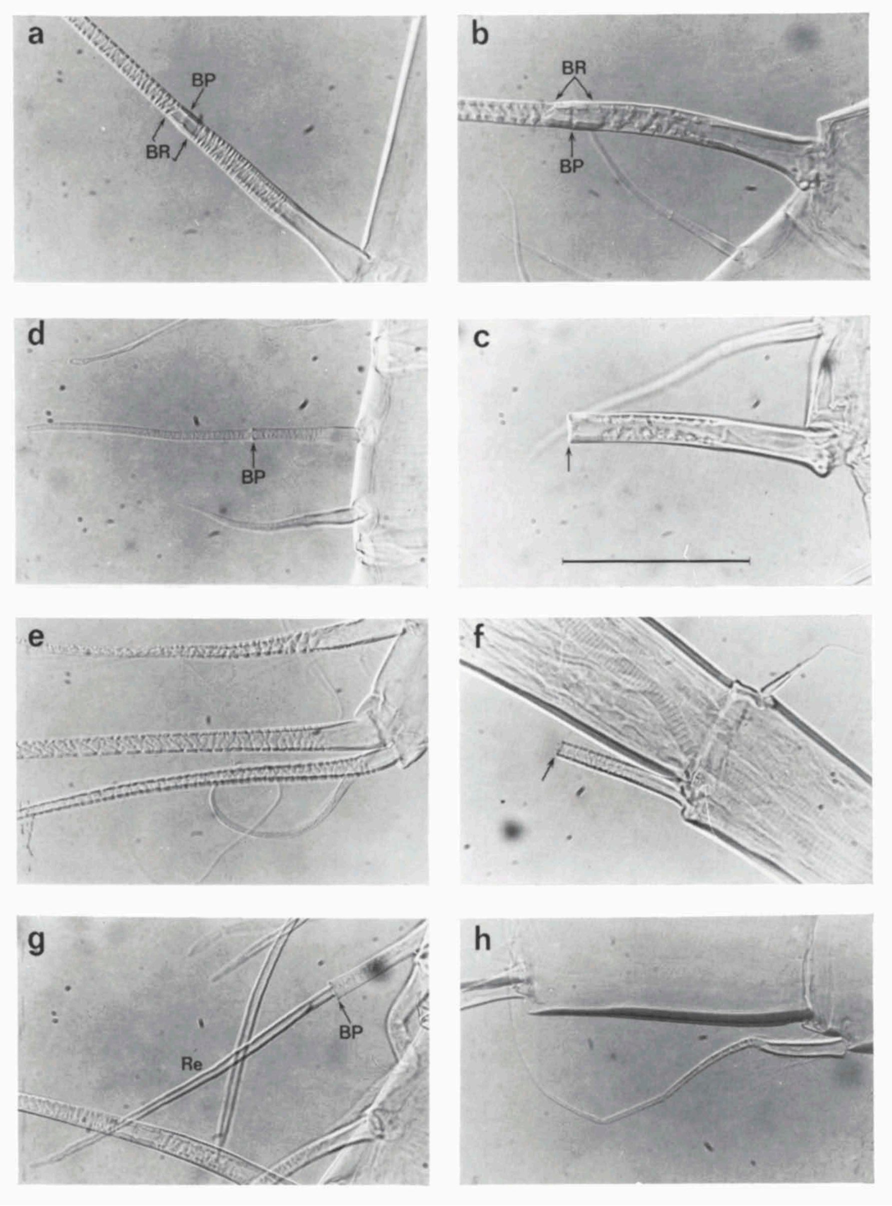

a

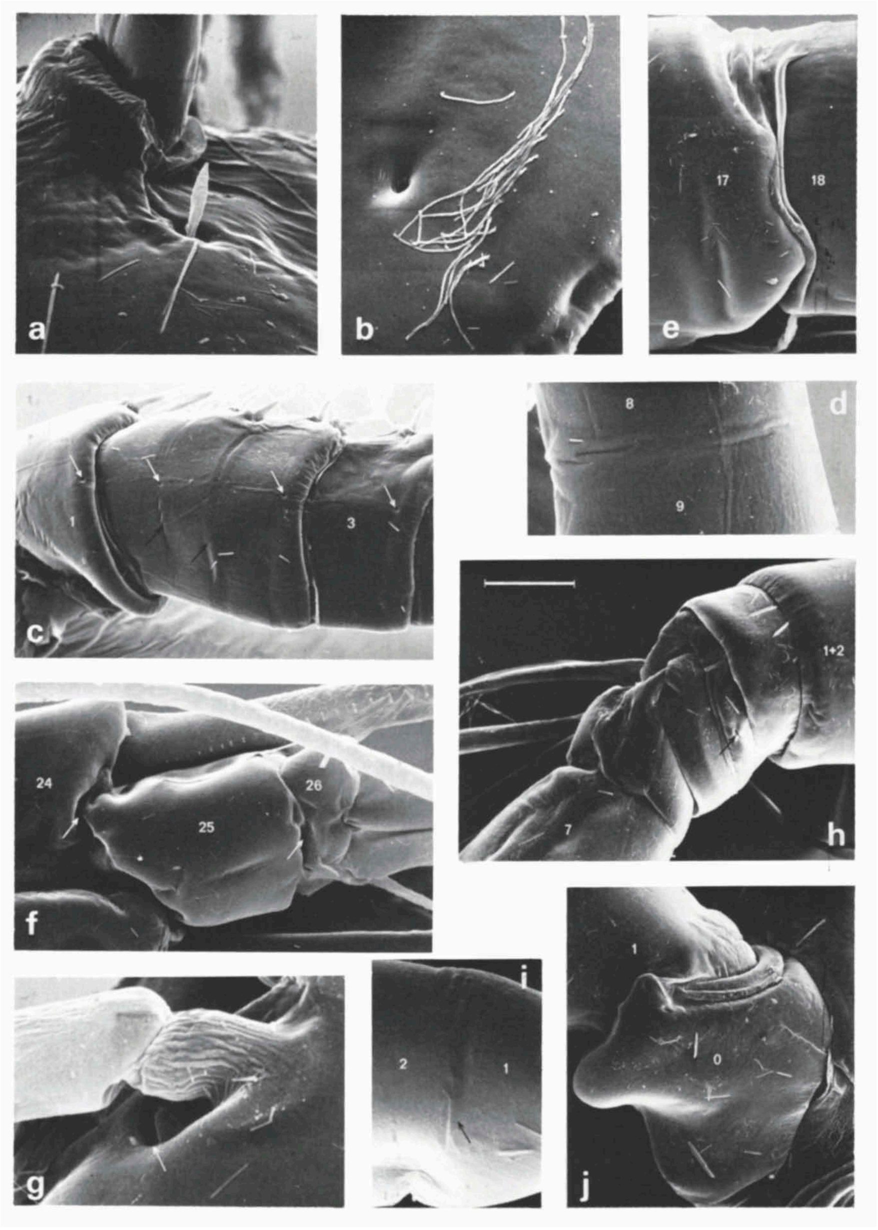

a
1
a
b
2r
2m
2l
b
d
b
3
c
c
a′


b
a
c
d
e

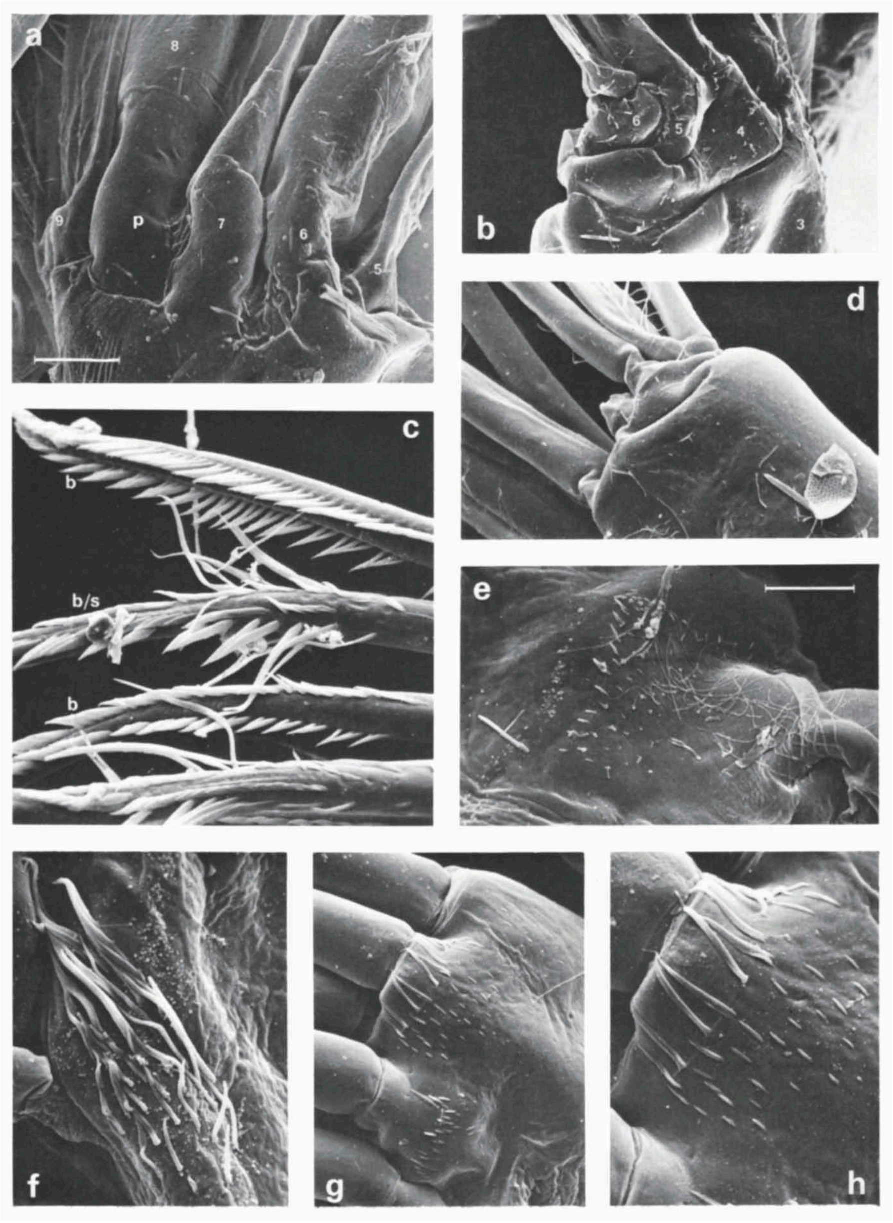

a
b
4-5
5
4-5
d
c
e

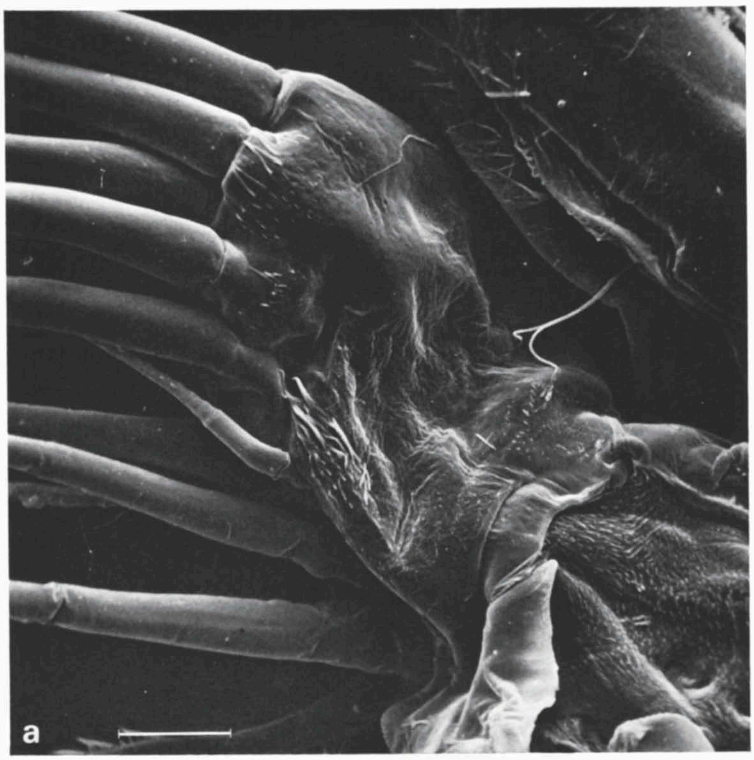

a
c
b
-I-3
-I-2
d
e
f


a
BP
BR
b
BR
BP
d
BP
c
e
f
g
BP
Re
h

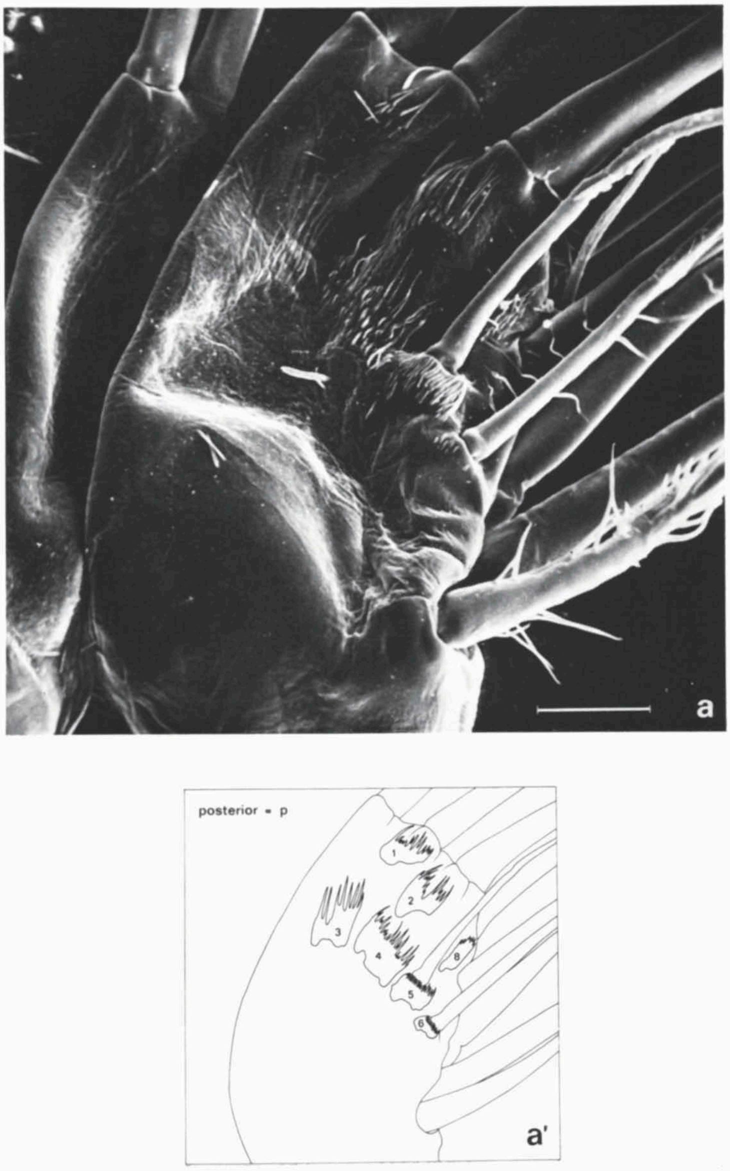

a
b
17
18
e
1
3
c
8
d
9
1+2
7
h
24
26
25
f
g
i
2
1
1
0
j

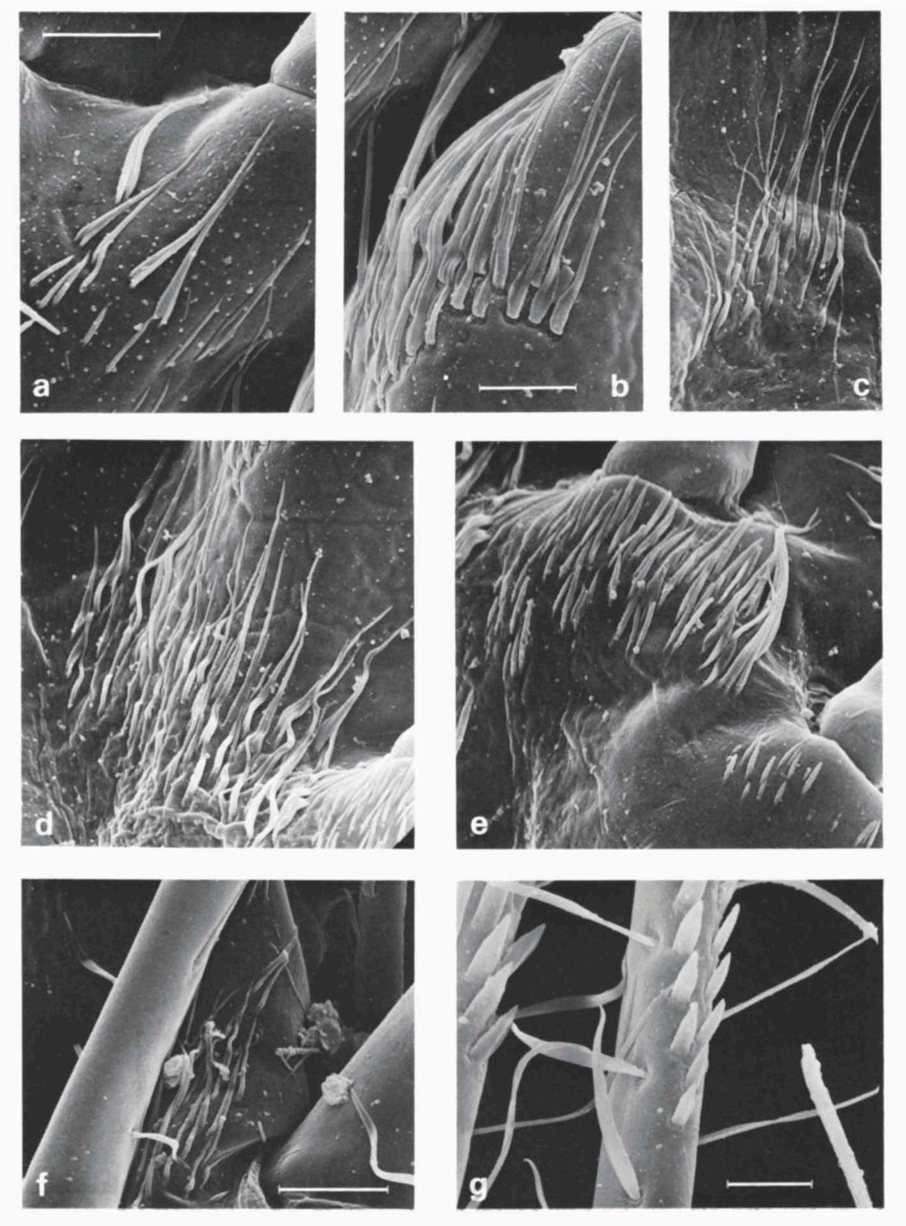

a
c
m
l
e
f
b
d
g
h
i

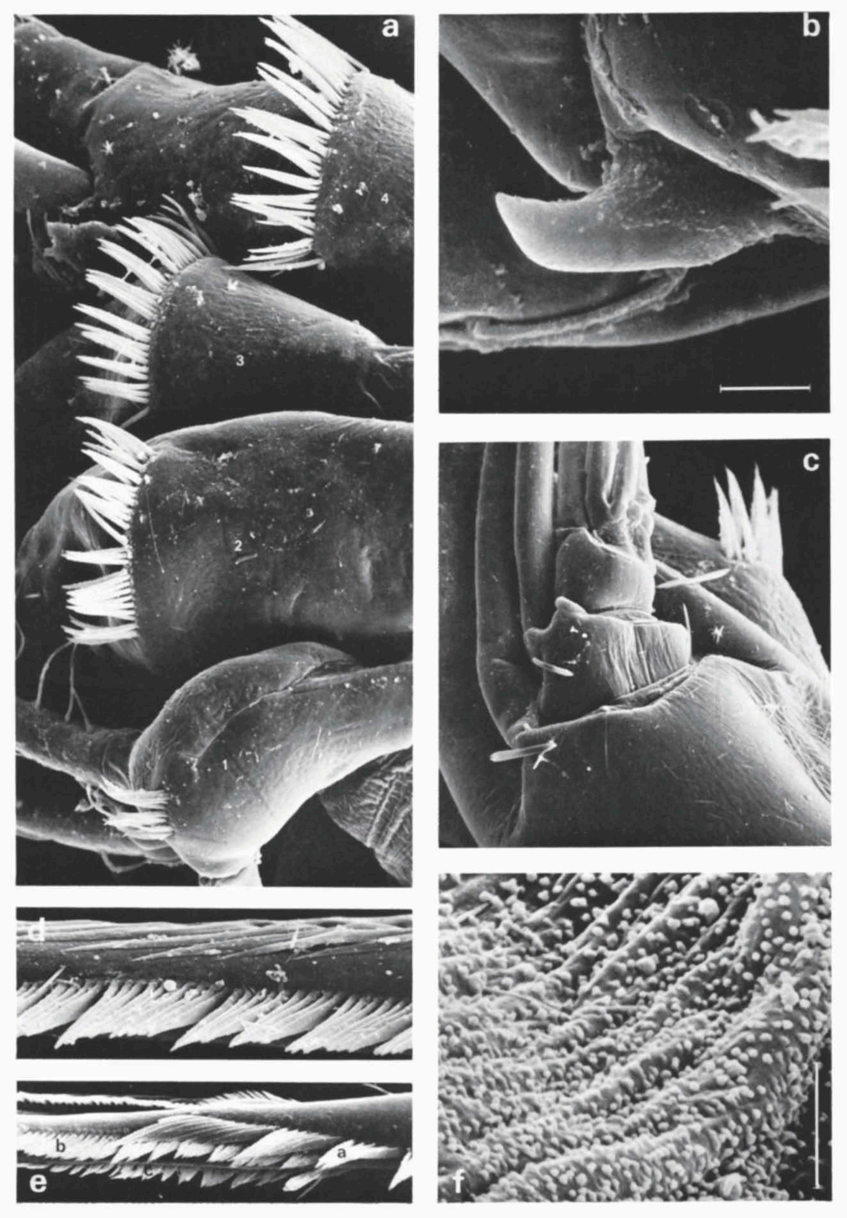

a
8
9
p
7
6
5
b
6
5
4
3
c
b
b/s
b
d
e
f
g
h

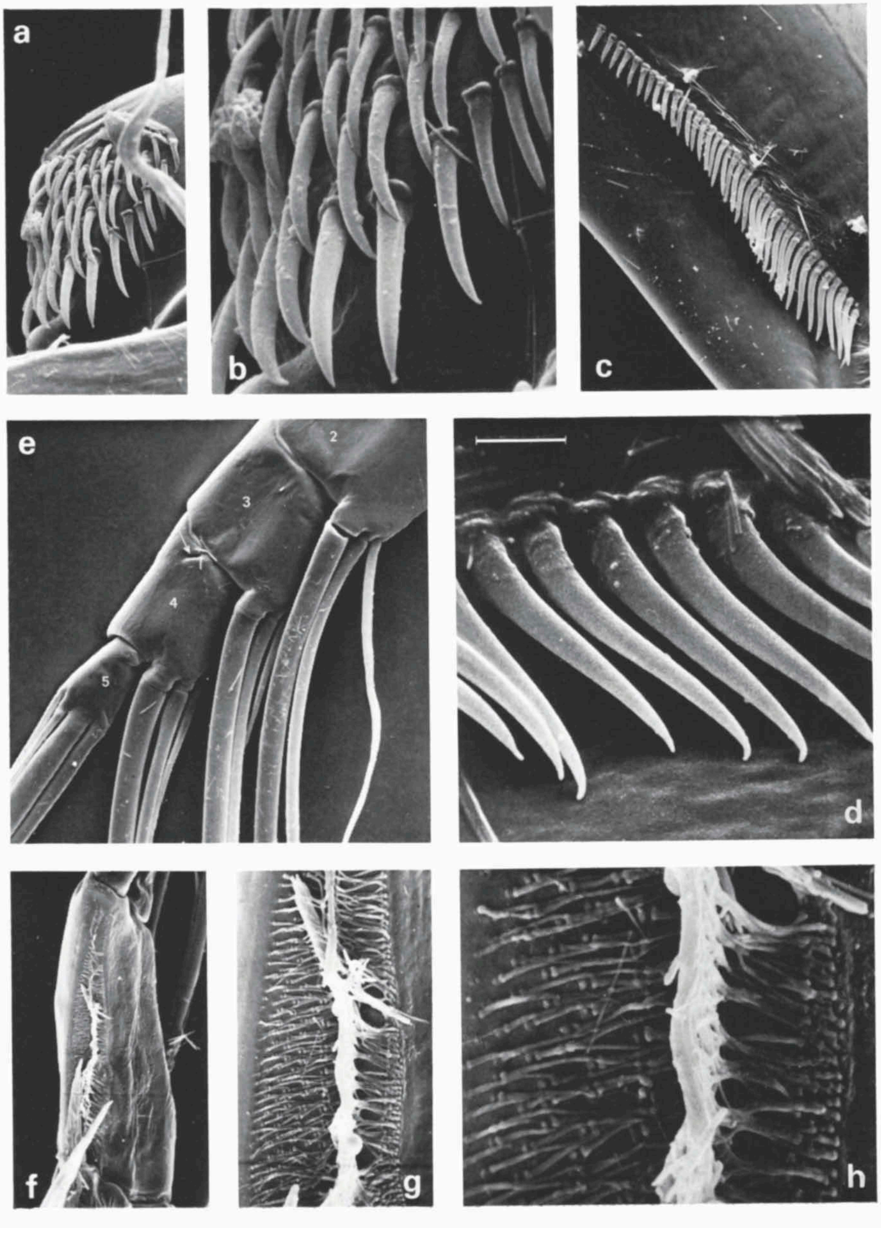

a

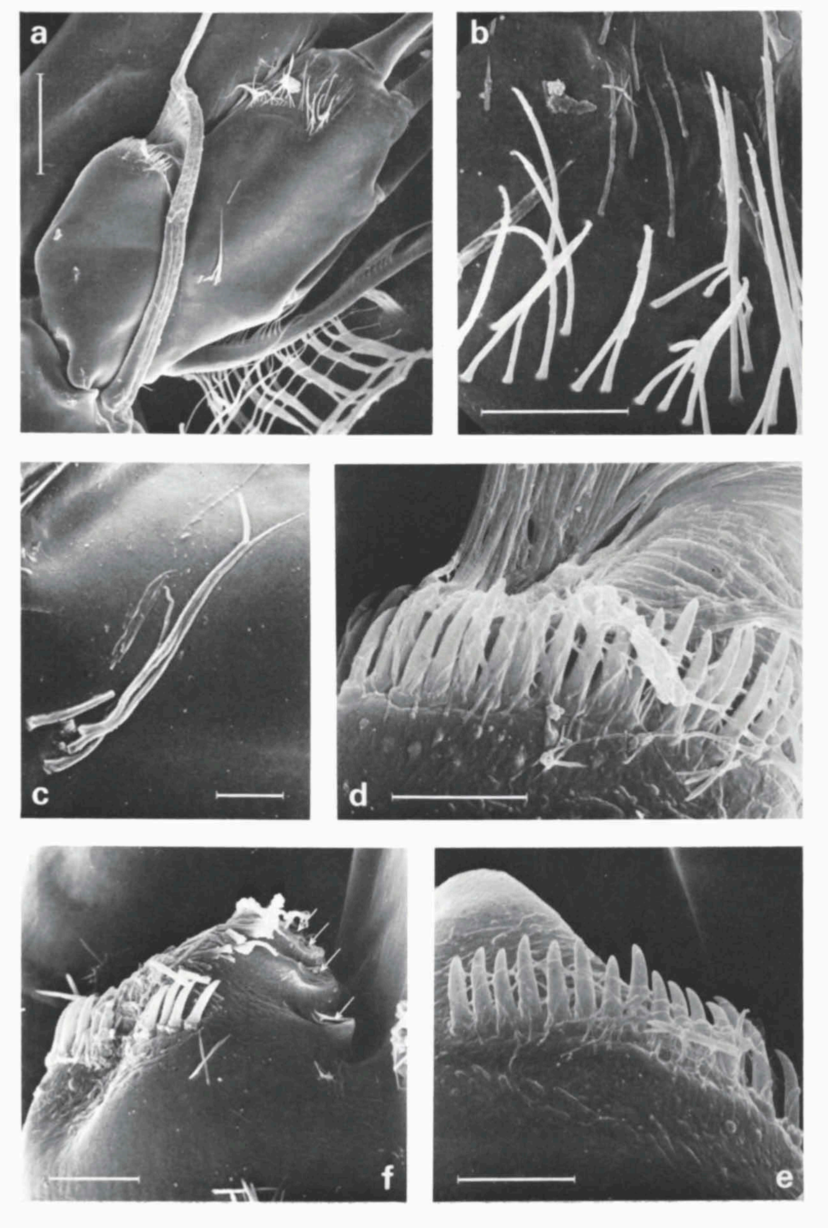

anterior = a
1
2
3
4
5
a′

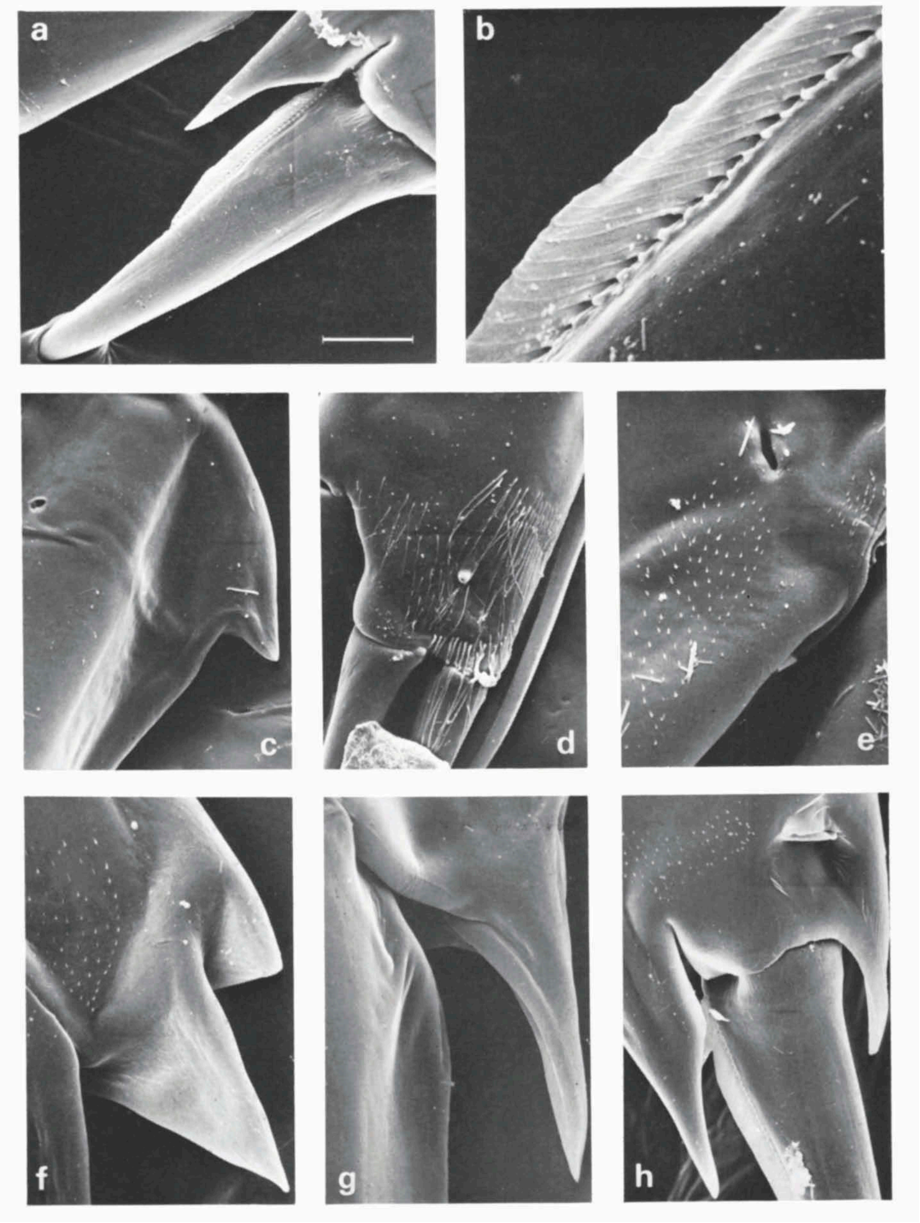

a
posterior = p
1
2
3
4
5
6
8
a'


a
b
c
d
e
f
g


a
4
3
2
1
b
c
d
e
b
a
f


a
b
c
e
2
3
4
5
d
f
g
h


a
b
c
d
f
e


a
b
c
d
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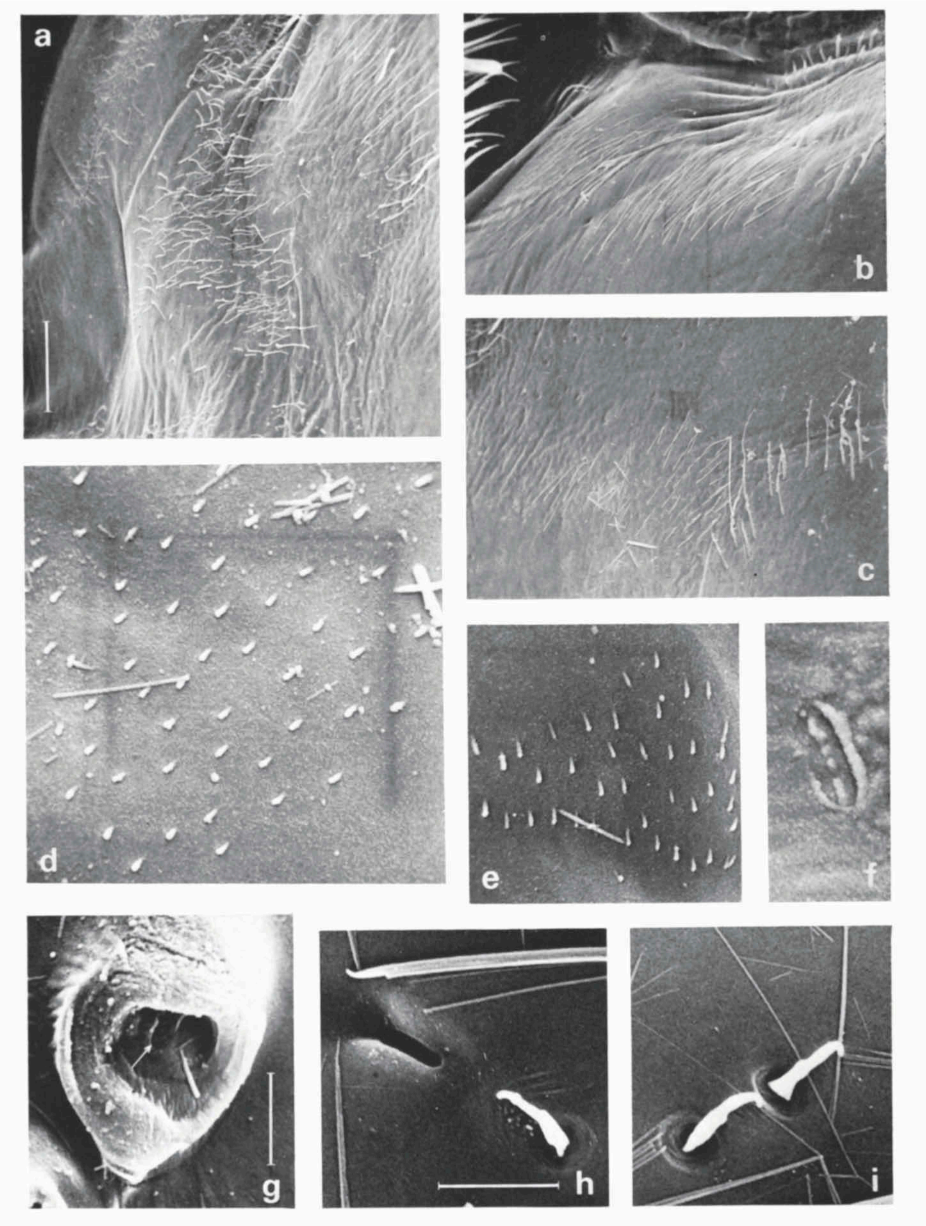
f
g
h


a
b
c
f
e
d
g
h
1
2
i


a
b
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g
h
i