Skaracarida, a new order of Crustacea from the Upper Cambrian of Västergötland, Sweden

Klaus J. Müller and Dieter Walossek

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Skaracarida, a new order of Crustacea from the Upper Cambrian of Västergötland, Sweden

KLAUS J. MÜLLER and DIETER WALOSSEK

Skara Müller 1983, has been re-examined on the basis of more than 120 specimens. The body has two tagmata: a cephalon with five pairs of appendages, and a trunk composed of one pedigerous, 10 apodous ring-shaped and conical segments, telson and furca. The head shield is small and does not overhang the body on any sidé. The forehead extends from the shield terminating in a tubular dorsofrontal process which may represent a sensory organ. Eye structures are absent. The labrum is prominent, nose-shaped and posteroventrally directed. The antennal gland exits at its sides, in front of the bases of the antennae. The antennulae are uniramous and tubular. Antennae and mandibulae assisted locomotion and trophic functions. The two pairs of maxilles and the pairs of maxillipeds are biramous and of the same design. All postantennular limbs participated in a short cephalic filter apparatus. The material proved to consist only of adults, but belonging to two almost equally represented size groups of a similar gross morphology. The large-sized group is represented by the holotype of *Skara anulata* Müller, 1983. Differences in size as well as various details led to the establishment of a new species, *Skara minuta* n.sp., for the smaller type. The two species most probably inhabited distinct ecological niches, feeding on particles of different size. *Skara* was a soft-integumented, marine filter-feeding crustacean. Its well developed setose antennal and mandibular exopods as well as the plumose, paddle-shaped exopods of the postmandibular limbs suggest that they were nectobenthic, most probably in a soft-bottom environment which was rich in detrital matter. *Skara* is a true crustacean showing affinities to Recent Maxillopoda, but differences between this genus, now with two species, and all known taxa motivates the erection of a new order.

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Since 1975 extensive research on Swedish *orsten* from the Upper Cambrian has yielded a large quantity of tiny phosphatized arthropods (cf. Müller 1982a; Walossek 1983). Studies on some of the more common phosphatocopid ostracodes have already been presented by Müller (1979, 1982b). Recently the same author (1983) described six hitherto unknown marine crustaceans, establishing the genus *Skara* with the type species *S. anulata,* a slender form of approximately 1.5 mm length. Since that study went to press, there has been a substantial increase of specimens from new samples as well as from a second sorting from the residues already on hand. This now permits a detailed and more definitive description of *Skara* than could be accomplished in the earlier paper.

Up to now the majority of taxonomic descriptions of fossilized arthropods are based mainly on details of hard parts, e.g. carapaces, or information obtained from totally flattened specimens preserved in slates. However, infraspecific variability of morphological characters as well as diagenetic artefacts may diminish the taxonomic value of recognizable structures. Thus even today a large number of taxa, especially of animals lacking a firm exoskeleton, have not been defined sufficiently. The extraordinary, three-dimensional preservation of *Skara* and other *orsten* forms permits a detailed reconstruction of these poorly sclerotized, chitinous fossils. For the first time it is possible to study a number of minute morphological details on Paleozoic material. This helps us not only to obtain more criteria for a taxonomic assignment but also to present more conclusive interpretations of the functional morphology and mode of life.

Furthermore, the documentation of all observable characters widens the basis for phylogenetic considerations. Together with information derived from the Arthropoda of the Burgess Shale (cf. Whittington 1979), these findings constitute not only the basic knowledge of the morphology of Early Paleozoic Crustacea but also present more evidence for discussions about the phylogeny of Arthropoda, and in particular of Crustacea.

This re-examination revealed two distinct size-groups within the material of *Skara*. Each group is homogeneous in itself, but there are numerous minute morphological differences between both of them, so that even fragments can easily be assigned to one or the other of the two groups. Thus they are separated herein at species level. The holotype of *S. anulata* Müller, 1983, (UB 646) and paratype (UB 648) are representatives of the large-sized type. The second paratype, UB 647, is identified as a member of the small-sized new species and is removed from *S. anulata.*

Differences from all hitherto defined crustacean groups led to the placing of *Skara* in a new taxon at order level.

In the text the terms 'frontal organ', 'maxilliped' and 'telson' are used for structures which reveal a great similarity to those of extant Crustacea. We prefer, however, to use the neutral term 'shaft' instead of 'precoxa' for the proximal portion of all postantennular limbs. The more distal portion named 'base' encloses the well sclerotized coxa and the basipod which carries the two rami.

Material and methods

The material was collected in 1977, 1979 and 1981 in Sweden. The productive rock is a dark limestone locally called *orsten* which occurs either in nodules or in beds. It is generally accepted that the enclosing sediment originally was a marine calcareous mud. The different zones of the Upper Cambrian were determined after Westergård (1922, 1947) by trilobite index species contained in the samples.

Up to now *Skara* has been found only in the region of Falbygden, Västergötland. The majority of new individuals is from Gum south of Blomberg on Kinnekulle, the same locality and bed in the *Agnostus pisiformis* Zone (= zone 1) as the holotype of *S. anulata* (UB 646). Additional specimens were recovered from the same zone at Backeborg, Kinnekulle, and at Stolan; and others are from Kestad, Kinnekulle, occurring together with *Olenus gibbosus* (Wahlenberg, 1821) (= zone 2a).

One hundred and twenty-three specimens, including the type-material, were sorted from the residues. Investigations by thin sections and translucent light proved not to be efficient. All specimens were glued to small metal stubs with double-sided adhesive tape, coated with carbon and/or gold, and photographed with a scanning electron microscope, S4 Cambridge, mainly at 10 kV.

For comparisons, the lengths of the cephalic shield, the trunk, the telson, the furca, the labrum, and the appendages were measured to the nearest 5 μm, taken from the SEM-photos. The magnification was calculated from the SEM-magnification factor. Although this method produces some systematic error (Lange & Blödorn 1981), it was preferred because of its obvious advantages such as avoidance of handling the extremely fragile fossils and easy access to the data. All values are listed in Tables 1 and 2.

As the majority of individuals were incompletely preserved, the total and trunk length, in particular, have been estimated. Missing values were taken from specimens of

Table 1. List of studied specimens of *Skara anulata* Müller, 1983; with locality, zonation, preservation, and sizes of: total length, cephalic shield (height, length, width), trunk segments, telson, furca, trunk with and without furca, and labrum; localities: Gum = 1, Stolan = 2, Kestad = 3, Backeborg = 4 (all sizes in μm; five specimens not measured).

UB/ST	loc	z	preserved	tl	cs(h/l/w)	T1	2	3	4	5	6	7	8	9	10	11	tel	f	Twt/Twot	l
646	1	1	t,wap,pf	1280	250/85/−	(55)	70	80	100	100	90	+	+	+	60	60	120	45/−/−	990/870	110
2125	1	1	cs,6ts,wap	1180	235/70/−	85	80	75	70	75	80	−	−	−	−	−	−	−	910/790	110
2178	1	1	cs,9ts,app	1200	220/−/−	80	80	80	80	80	80	90	70	70	+	−	−	−	950/830	−
2458	1	1	csp,5ts,app	−	+	70	65	70	70	65	+	−	−	−	−	−	−	−	−	−
2863	1	1	cs,9ts,wap	−	230/−/−	85	85	80	70	70	+	+	+	+	−	−	−	−	−	−
2698	1	1	cs,4ts,app	−	270/95/−	+	+	+	100	+	−	−	−	−	−	−	−	−	−	120
696	1	1	cs,6ts,wap	1250	270/−/−	80	80	90	90	80	80	+	−	−	−	−	−	−	950/830	130
695	1	1	cs,1s,app	−	230/65/−	70	+	−	−	−	−	−	−	−	−	−	−	−	−	130
722	1	1	cs,7ts,app	1140	230/70/−	75	80	75	75	70	70	65	−	−	−	−	−	−	875/755	120
697	1	1	cs,8ts,app	1200	260/75/−	85	80	80	80	80	80	70	65	−	−	−	−	−	910/790	120
3057	1	1	10ts,app	1170	−	80	80	80	80	80	75	70	65	60	55	−	−	−	895/775	−
718	1	1	cs,5ts,pa	−	235/75/−	70	75	75	80	+	−	−	−	−	−	−	−	−	−	125
3251	1	1	cs,8ts,pa	1160	235/75/−	80	80	80	75	75	70	70	+	−	−	−	−	−	895/775	120
719	1	1	cs,3ts,app	−	270/100/−	80	80	75	+	−	−	−	−	−	−	−	−	−	−	130
734	1	1	cs,6ts,wap	−	270/−/−	+	+	90	90	90	−	−	−	−	−	−	−	−	−	120
712	1	1	cs,6ts,wap	−	230/60/−	85	100	85	85	80	+	−	−	−	−	−	−	−	−	120
728	1	1	cs,5ts,wap	−	255/75/135	85	90	85	95	95	+	−	−	−	−	−	−	−	−	130
4075	1	1	cs,6ts,wap	−	245/−/−	(65)	85	80	65	70	65	+	−	−	−	−	−	−	−	125
4070	1	1	cs,5ts,wap	−	250/−/−	70	75	75	75	+	−	−	−	−	−	−	−	−	−	110
692	1	1	cs,3ts,app	−	280/−/−	80	75	80	+	−	−	−	−	−	−	−	−	−	−	130
2052	1	1	9ts,wap	1260	+	90	90	90	90	80	80	70	70	70	+	−	−	−	970/850	+
729	1	1	T,wap	1220	−	+	80	80	80	80	80	80	70	70	60	60	−	−	940/820	−
734	1	1	csp,T,app,pf	1180	+	75	80	80	80	80	80	70	60	60	60	55	125	40/75/−	910/780	−
693	1	1	csp,T,app,wf	1180	+	70	75	75	75	80	70	85	80	60	60	60	+	−	910/790	−
2488	1	1	ts4−11	−	−	−	−	−	90	90	85	85	70	70	70	+	−	−	−	−
2855	1	1	ts6−tel,wf	−	−	−	−	−	−	−	+	70	70	70	60	65	145	−	−	−
736	1	1	ts8−tel,pf	−	−	−	−	−	−	−	−	+	75	70	70	60	125	+	−	−
727	1	1	ts4−8	−	−	−	−	+	75	75	75	75	75	75	+	−	−	−	−	−
3059	1	1	ts2−8	1230	−	−	80	90	90	90	75	75	65	+	−	−	−	−	950/830	−
4087	1	1	ts4−11	1170	−	−	−	+	75	80	80	75	65	65	55	50	+	−	905/785	−
4032	1	1	11ts	1360	−	90	85	90	95	90	90	90	80	70	70	70	+	−	1060/920	−
745	1	1	csp,T,wap,pf	1130	−/80/−	70	70	70	70	80	80	75	65	60	50	50	130	40/−/−	870/740	−
723	1	1	cs,7ts,app	1190	275/−/−	85	85	80	85	85	75	70	+	+	−	−	−	−	915/795	−
4104	1	1	cs,7ts,app	−	250/−/150	70	70	70	65	60	60	+	+	−	−	−	−	−	−	120
737	1	1	t,app,f	1130	−/65/−	80	85	70	70	65	65	65	65	65	60	60	115	35/70/+	870/755	−
691	1	1	t,wap,wf	1190	230/−/−	75	80	80	80	80	80	75	65	65	60	60	125	−	925/800	120
4116	1	1	cs,8ts,pa	−	210/−/−	+	70	70	60	60	60	+	+	−	−	−	−	−	−	+
4126	1	1	csp,10ts,wap	1230	+	75	90	90	90	80	75	75	70	70	65	−	−	−	960/840	−
715	1	1	cs,9ts,pa	1220	230/60/170	75	80	80	80	80	75	75	70	70	+	−	−	−	960/840	120
4147	1	1	csp,wap,11ts	1160	+	90	85	80	80	80	75	70	65	60	55	50	(110)	−	900/780	+
4148	1	1	cs,pa,9ts	1080	210/−/−	70	75	75	75	75	70	65	+	+	−	−	−	−	840/730	−
740	1	1	csp,pa,6ts	−	+	70	80	75	80	80	85	−	−	−	−	−	−	−	−	−
4150	1	1	csp,10ts	1060	+	80	75	70	65	60	60	55	55	55	55	+	−	−	810/700	−
4152	1	1	csp,10ts,wap	−	−/70/−	60	70	70	80	80	80	75	70	60	60	−	−	−	−	−
721	1	1	csp,pa,10ts	1110	240/−/−	80	80	70	75	+	+	65	60	+	−	−	−	−	840/730	−
711	1	1	cs,11ts	1240	250/85/135	85	90	90	85	80	80	75	70	65	60	60	+	−	960/840	+
4156	1	1	cs,pa,11ts	1130	250/80/140	75	75	75	75	75	70	65	60	55	60	+	−	−	850/740	−
746	2	1	t,wap,wf	1290	260/75/−	80	85	85	85	85	80	80	75	70	60	60	150	−	995/845	150
713	2	1	cs,2ts,app	−	260/90/−	70	70	+	−	−	−	−	−	−	−	−	−	−	−	125
3028	2	1	cs,1ts,wap	−	260/85/−	95	+	−	−	−	−	−	−	−	−	−	−	−	−	−
648	2	1	csp,2ts,app	−	+	100	85	85	+	−	−	−	−	−	−	−	−	−	−	−
720	2	1	cs,1ts,app	−	250/70/−	90	+	−	−	−	−	−	−	−	−	−	−	−	−	−
2545	2	1	ts4−tel,wf	1240	−	−	−	+	80	95	85	75	65	65	65	65	(130)	−	980/850	−
2692	3	2a	ts4−9	−	−	−	−	+	60	60	70	70	60	60	−	−	−	−	−	−
3016	4	1	cs,app	−	260/80/−	+	+	+	−	−	−	−	−	−	−	−	−	−	−	+
694	4	1	cs,3ts,app	−	230/−/−	80	80	70	+	−	−	−	−	−	−	−	−	−	−	(130)
3083	4	1	csp,5ts,wap	−	−	90	85	80	85	95	+	−	−	−	−	−	−	−	−	−

similar size. Eleven specimens were too poorly preserved for measurements and are not listed in the tables. The length data presented under the heading 'Dimensions' at each species description are means which have been derived from the tables and graphically from the length-frequency diagrams of Fig. 9. UB 747 was added during the revision of this paper and is not included in Table 2 and Fig. 9.

The following abbreviations are used (main symbols shown in Fig. 1):

a	anterior
Abd	abdomen
agl	antennal gland
am	arthrodial membrane
an	anus

Table 2. List of studied specimens of *Skara minuta* n.sp.; data as in Table 1, but with presumed sexes (S) (six specimens not measured).

UB/ST	loc	z	S	preserved	tl	cs (l/h/w)	T1	2	3	4	5	6	7	8	9	10	11	tel	f	Twt/Twot	l
730	1	1		cs,11s,wap	—	140/—/—	+	+	+	+	35	40	40	35	+	+	+	—	—	—	80
724	1	1	♂	t,wf,app	680	140/60/—	45	35	45	40	40	45	40	30	30	30	30	90	—	510/420	+
2352	1	1	♂	cs,9ts,app	600	120/—/—	40	40	40	40	35	35	35	30	25	20	20	+	—	450/360	85
2443	1	1		t,wf,app	—	130/—/—	+	+	+	+	+	+	+	+	+	+	+	(100)	—	—	+
2861	1	1	♂	t,wf,wap	550	+	+	+	+	+	35	30	30	25	20	20	20	80	—	400/320	+
708	1	1	♂	cs,11s,app	590	130/60/90	50	40	40	40	40	40	35	30	30	30	20	>70	—	430/345	+
647	1	1	♀	cs,10ts,app	770	170/70/—	50	45	50	45	50	50	50	40	35	30	30	+	—	575/475	110
2854	1	1	♂	t,wf,app	590	120/65/—	40	40	45	40	35	(30)	(30)	+	+	+	+	+	—	440/350	—
2709	1	1	♂	t,wf,app	660	125/—/—	40	35	40	40	40	35	40	35	30	25	25	120	—	505/385	—
3567	1	1	♂	t,pf,pa	500	115/—/—	30	25	35	30	30	25	25	20	20	20	20	75	—	355/280	+
702	1	1	♂	t,pf,app	570	130/50/—	35	30	35	40	40	30	25	25	20	20	20	90	—	420/330	70
709	1	1	♂	t,pf,pa	610	135/60/—	30	30	40	40	35	35	35	30	30	30	25	90	—	450/360	80
699	1	1	♀	t,wf,wap	730	145/55/—	50	50	45	45	40	35	35	30	30	25	25	150	—	555/410	70
3226	1	1	♂	t,wf,pa	640	120/65/—	50	45	40	40	40	35	35	30	30	25	20	+	—	490/400	—
2923	1	1		t,pf,wap	—	150/—/—	+	40	40	40	+	+	+	+	+	+	+	90	—	—	+
3228	1	1	♂	cs,.s,wap	580	+	+	+	35	40	35	35	30	30	25	25	20	+	—	435/345	+
2998	1	1		t,wap,wf	—	+	+	+	+	+	+	40	35	+	+	30	30	+	—	—	—
700	1	1		t,app,wf	—	110/40/—	+	+	+	+	+	35	30	30	25	20	20	80	—	—	+
725	1	1	♂	t,app,wf	520	+	40	30	30	30	30	+	+	+	+	+	+	+	—	—	+
3581	1	1	♂	cs,9ts,wap	580	+	40	35	40	40	40	40	35	30	25	—	—	—	—	445/365	+
3410	1	1	♂	t,app,wf	550	+	+	+	+	+	+	+	+	+	+	+	+	—	—	410/—	—
4089	1	1	♂	t,app,pf,	540	110/—/—	+	+	+	+	+	+	+	+	+	+	+	80	—	400/—	70
701	1	1	♂	t,app,pf	630	130/60/90	40	35	40	35	35	30	30	30	25	20	20	(130)	—	470/340	+
4082	1	1	♂	t,wap,wf	540	+	35	(25)	35	30	30	30	30	25	25	20	20	85	—	400/310	+
4081	1	1	♂	t,app,pf	540	+	+	+	+	+	+	+	30	25	20	20	20	80	—	400/320	—
4054	1	1	♂	cs,9ts,app	590	120/60/—	30	40	40	40	40	35	30	25	25	+	—	—	—	440/350	+
714	1	1	♂	cs,11s,app	650	165/65/—	45	40	40	40	40	40	30	30	25	25	20	+	—	460/375	80
703	1	1	♂	ts,app,f	550	—	—	+	+	35	35	30	30	25	20	20	20	75	22/45/25	410/335	—
733	1	1		ts3-tel,f	—	—	—	—	+	+	30	30	30	25	20	20	20	105	—	—	—
3077	1	1		ts5-tel,pf	—	—	—	—	—	—	40	30	35	30	25	20	20	80	—	—	—
742	1	1	♂	11ts	560	—	40	40	35	35	35	35	30	25	20	20	20	—	—	420/335	—
2964	1	1	♂	csp–tel,pf	610	+	+	40	40	35	35	30	30	30	30	25	20	95	—	460/365	—
3104	1	1	♂	ts3–tel,pf	590	—	—	—	+	40	35	30	30	25	20	20	20	100	20/—/—	440/340	—
3593	1	1		ts5–tel,pf	—	—	—	—	—	—	+	35	30	25	25	20	20	90	20/—/—	—	80
741	1	1		ts1–tel	—	—	+	+	+	+	+	+	30	30	30	25	20	100	—	—	—
716	1	1	♂	t,wap	530	100/40/..	45	40	35	30	30	30	25	25	20	20	20	85	—	405/320	75
707	1	1	♂	t,app,pf	580	120/50/—	40	30	40	40	35	35	30	25	25	20	20	90	20/—/—	430/340	80
735	1	1	♂	t,pa,pf	580	115/45/—	30	30	40	40	40	30	30	30	25	20	20	80	—	435/355	—
710	1	1	♂	cs,11s,app	630	130/55/—	40	40	45	40	40	40	35	30	25	25	20	(85)	—	475/390	+
726	1	1	♂	t,pa,wf	520	—	—	—	—	—	35	35	30	25	20	20	20	80	—	400/320	80
2544	2	1		cs,8ts,wap	640	155/60/	50	50	50	50	50	45	45	30	30	+	—	—	—	440/350	(80)
3026	2	1	♂	cs,11s,app	650	140/—/—	40	35	45	35	40	40	40	30	30	25	25	+	—	485/395	—
744	2	1	♀	csp,T,wap,pf	970	—/85/—	+	50	55	60	60	60	60	55	40	40	35	220	—	780/560	—
732	3	2a	♂	cs,10ts,app	580	120/—/—	30	35	40	40	35	35	30	30	25	20	20	+	—	430/340	70
706	3	2a	♂	t,wf,app	490	120/45/90	30	20	25	25	25	25	25	20	20	20	15	90	—	340/250	—
2691	3	2a	♂	t,wap,wf	660	130/70/—	35	45	45	45	45	40	35	30	30	25	25	+	—	500/405	—
738	3	2a		cs,6ts,app	—	140/—/—	40	40	40	40	40	+	—	—	—	—	—	—	—	—	—
2483	3	2a	♂	t,wf,app	620	130/—/—	+	40	40	35	35	40	40	30	25	25	25	80	—	460/375	—
731	3	2a	♂	t,wap,wf	610	150/45/—	30	30	35	40	35	35	35	30	30	25	20	—	—	435/345	90
739	3	2a	♀	t,pa,pf	870	190/85/—	60	50	55	50	50	50	50	50	45	40	30	125	—	655/530	—
704	4	1	♀	t,wf,app	780	160/—/—	50	40	45	45	40	40	40	35	35	30	30	150	—	590/440	—
705	4	1	♀	cs,9ts,app	870	190/90/135	55	50	60	60	55	55	50	45	45	+	—	—	—	650/535	100
742	4	1	♂	t,wap,pf	540	+	25	30	35	35	35	35	30	25	20	20	20	80	—	390/310	—
717	4	1	♀	t,wap,wf	820	170/65/—	50	40	45	45	40	40	40	40	35	35	30	180	—	625/450	90
3934	4	1	♀	cs,8ts,app	—	170/—/—	60	50	60	60	60	50	45	45	—	—	—	—	—	—/520	—

ap	attachment point		ep	enditic process or endite
aI	antennula		ex	exopod
aII	antenna		f	furca
bas	basipod		fd	fold
br	bristle		fh	forehead
bu	bulge at the flanks of the labrum		fo	frontal process or organ
C	cephalic region or cephalon		fr	fringe
cox	coxa		gn	shovel-like endite of mandibular coxa
cry	crystal		l	labrum or upper lip
cs	cephalic shield		loc	locality
csp	cephalic shield partly preserved		m	mouth
en	endopod		md	mandibula
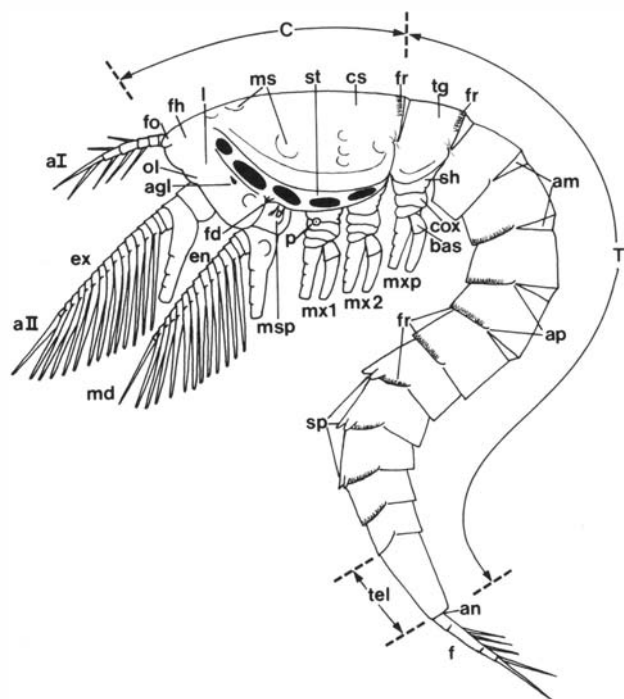
Fig. 1. Gross morphology of *Skara* Müller 1983.

mem	membrane or membraneous area
mfp	median furcal podomere
ms	muscle scar
msp	masticatory spine of coxal endite of mandibula
mx1	maxillula
mx2	maxilla
mxp	maxilliped = limb on 1st trunk segment
ol	origin of labrum
p	pore or pit
pa	partly preserved appendages
pf	partly preserved furca
pfp	proximal furcal podomere
pw	phosphatic wall
S	sex
s	seta
sc	scale
sec	secondary coating
sf	sickle-shaped furrow (part of antennal gland?)
sh	shaft of limbs and shaft of setae
sk	steinkern
sp	spine
spl	spinule
ST	specimen
st	sternum
stl	setula
T	trunk region
t	totally preserved body
tel	telson
tfp	terminal furcal podomere
tg	tergite of 1st trunk segment
Th	thorax
tl	total length
Twt	trunk with telson
Twot	trunk without telson
ts1-11	trunk segments 1–11
UB	repository number (*Universität Bonn*)
wa	walled area (part of antennal gland?)
wap	preserved without appendages
wf	preserved without furcal rami
wtel	preserved without telson
z	zone
+	structure present
−	structure absent
()	estimated value

Mode of preservation

Phosphatization. – The unique preservation of cuticular structures in certain *orsten* fossils is due to phosphatization, either because the cuticle primarily contained phosphatic matter, as is the case in the carapace of phosphatocopid Ostracoda, or by secondary phosphatization of the body wall, which most probably was chitinous as in all other Arthropoda. Secondary phosphatization occurred either by thin phosphatic coatings (mode 1; Fig. 2A, B), or by replacement of the cuticle by phosphatic substance (mode 2; Fig. 2 C, D). Both types can also occur together on the same specimen. Rough coatings may coarsen details (Fig. 2B), but also fine coatings may smoothen surface structures, e.g. folds or joints. Due to accretion of phosphatic matter, exposed structures such as setae may appear thicker than they were originally (Pl. 7:3; Pl. 16:6).

On the other hand, even when phosphatic coatings are quite uneven distally, surprisingly fine details, especially at protected areas, may still be observable, as on one individual where the proximal and medial parts of maxillulae and maxillae are preserved with all details while the distal portions of the limbs are coated with coarse phosphatic granules (Pl. 2:8, Pl. 10:6; Pl. 15:7; Pl. 16:3). Replacement or substitution (mode 2) in general led to better preservation. However, this mode also shows considerable variation in quality between different samples (e.g. Pl. 16:4 and 5).

On a specimen illustrated in Pl. 13:1 the trunk wall is covered by a very delicate phosphatic layer which has also overgrown the arthrodial membranes. This feature is well visible because the cover has been partly peeled off and can easily be recognized as secondary coating (mode 1). In other cases, however, it is not always clear whether observed wall layers were caused by secondary phosphatization or whether the substituted cuticle was originally multi-layered (Pl. 17:1).

Numerous individuals are coated with alien phosphatic grains which are attached to the phosphatic wall and mostly cannot be removed without breakage. Sometimes they even prevent recognition of details (limbs in Pl. 2:7; upper rim of Pl. 15:7; limbs in Pl. 16:6). Often the phosphatization is incomplete, and the wall of the specimen then contains numerous holes (Pl. 3:4; Pl. 6:3, upper left corner). Such partial phosphatization can be recognized mainly by its rounded deposition borders caused by polycentric growth of the crystallites (Pl. 16:2; Pl. 11:1; Fig. 2E). It can be easily distinguished from breakage which is often found at exposed structures, resulting in sharp-edged borders or surfaces of fracture (Pl. 17:1; Pl. 9:4; Fig. 2F).

On the surface of some specimens small phosphatic crests or walls were deposited. They delineate the limits of calcite crystallites which had formerly grown on the wall but were etched away during preparation (Pl. 16:1). Comparable structures have also been found on conodonts, e.g. from the Lower Ordovician of Iran (Müller 1973, Pl. 7:7). On the specimen illustrated on Pl. 16:4, even an alien phosphatic particle attached to the cuticle was overgrown by such a wall. This indicates that growth of the calcite had occurred after the process of phosphatization.

Commonly the body cavity was filled with calcite. After etching the specimens are more or less empty (Pl. 11:1; Pl.

6:1; Pl. 17:1). In some cases the cavities were filled with coarse and uneven phosphatic matter which resisted the etching process (Pl. 13:2; Pl. 17:1). Thin, cylindrical structures in the trunk region may represent steinkerns of the tube-like intestine (Pl. 11:1; Pl. 17:3). Some steinkerns are thicker and annulate. But their rings do not always correspond exactly to the annulation of the trunk. This may be caused by shrinkage during the crystallization of the originally collophane matrix (Pl. 17:4). Other phosphatic steinkerns occupy almost the entire cavity below the cuticle which in this case is not preserved and leaves a small space between the coating phosphatic layer and steinkern (Pl. 16:1). It is unclear whether the hollow space observed in setae has been caused by a loss of the seta (leaving the secondary coating) or whether the seta was substituted and thus was originally hollow (Pl. 15:1).

The primary phosphatic carapaces of phosphatocopid Ostracoda range up to 3.5 mm in length. However, as the length of complete or fragmented specimens in general does not exceed 2 mm, the secondary phosphatization in the *orsten* seems to have an upper size limit. Apart from this restricted fossilization potential by size selection, secondary phosphatization seems to require other conditions such as chitinous or similar substances as substrate for the precipitation of phosphatic matter. It is possible that chitin or chitinous matter may represent the only substances suitable for such substitution.

The peculiar mode of phosphatization yielded specimens fossilized as if preserved in their original life-positions (Pls. 1 and 2). This circumstance even permits interpretation in respect of functional morphology and mode of life. On the other hand, various details can be observed only on single individuals. This has made it necessary to base description and reconstruction on a large number of specimens.

Entombment. – Specimens may be wrinkled, especially at less sclerotized parts of the cephalon and limbs. The soft cuticle most probably had collapsed prior to embedding. Flattening or stretching could not be observed in the study material, and once deposited the individuals obviously have not altered their shape significantly. This is in contrast e.g. to the compressed soft-integumented fossils from the Middle Cambrian Burgess Shale (cf. Whittington 1980:131, Fig. 3). Because various individuals of *Skara* are preserved as if in original life-positions and because even finest details show no recognizable decay, it is suggested that the remains have been buried immediately after death. Again, the findings of specimens with widely extended limbs or entirely stretched bodies indicate that the material was not preserved within or after having passed through the intestine of a predator. The individual illustrated in Pl. 17:2 may be an exception, because it was possibly included in a coprolite. *Orsten* trilobites are regarded mainly as fossilized exuviae. Most probably this was not true for *Skara* as there are no recognizable signs of ecdysial sutures or comparable structures.

The unsorted and unoriented (*'uneingesteuert'* cf. A. H. Müller 1981: A32) embedding of agnostids in the various layers of the *orsten* demonstrates clearly that, as a rule, the Upper Cambrian sequences of Sweden were deposited under still water conditions. This observation is corroborated by findings of conodont assemblages in the same samples pre-
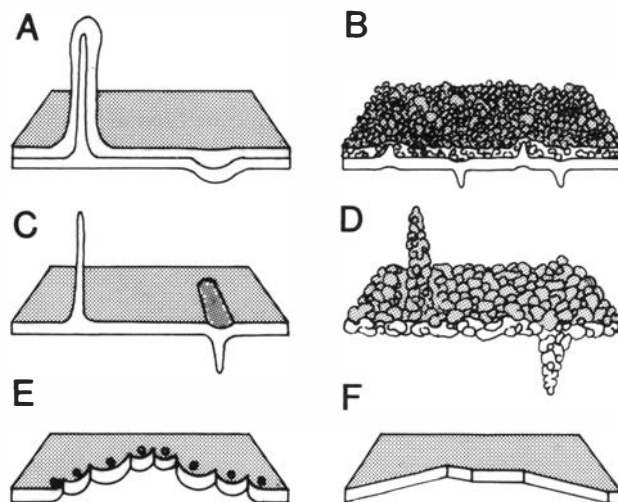
Fig. 2. Types of secondary phosphatization; explanations see p. 6.

served in their original context on the bedding surfaces of shales deposited immediately adjacent to the *orsten* (Andres 1981; Müller & Andres 1976).

Taxonomy

Skaracarida, new order of the class Crustacea

Diagnosis. – Small, soft-integumented, marine forms with slender, annulate body and six pairs of well developed limbs; two distinct tagmata; cephalon with five paris of limbs; small dorsal shield of about 1/4 to 1/5 of the total length; forehead with moveable, rod-shaped frontoterminal process; eyes absent; labrum large and ventrocaudally directed; uniramous antennulae, shorter than the succeeding limbs; biramous antennae and mandibulae, with one coxal endite and multisegmented exopods, each exopodal podomere with one rigid, long seta; maxilles and maxillipeds of the same shape, their exopods being paddle-shaped; all postantennular limbs join a short cephalic filter apparatus; trunk composed of 11 segments and a telson with segmented furcal rami; antennal gland present; no recognizable gonopores; anus terminal, dorsal to the furcal base.

Etymology and composition. – The name Skaracarida is based on the genus name *Skara* and *caris* = shrimp. The order is monotypic.

Skaraidae, new family

Type-genus. – *Skara* Müller 1983

Diagnosis. – With characters of the order.

Skara Müller 1983

Type-species. – *Skara anulata* Müller 1983

Diagnosis. – With characters of the order. Further characterization: shield smooth, suboval, dinghy-shaped, lateral rims
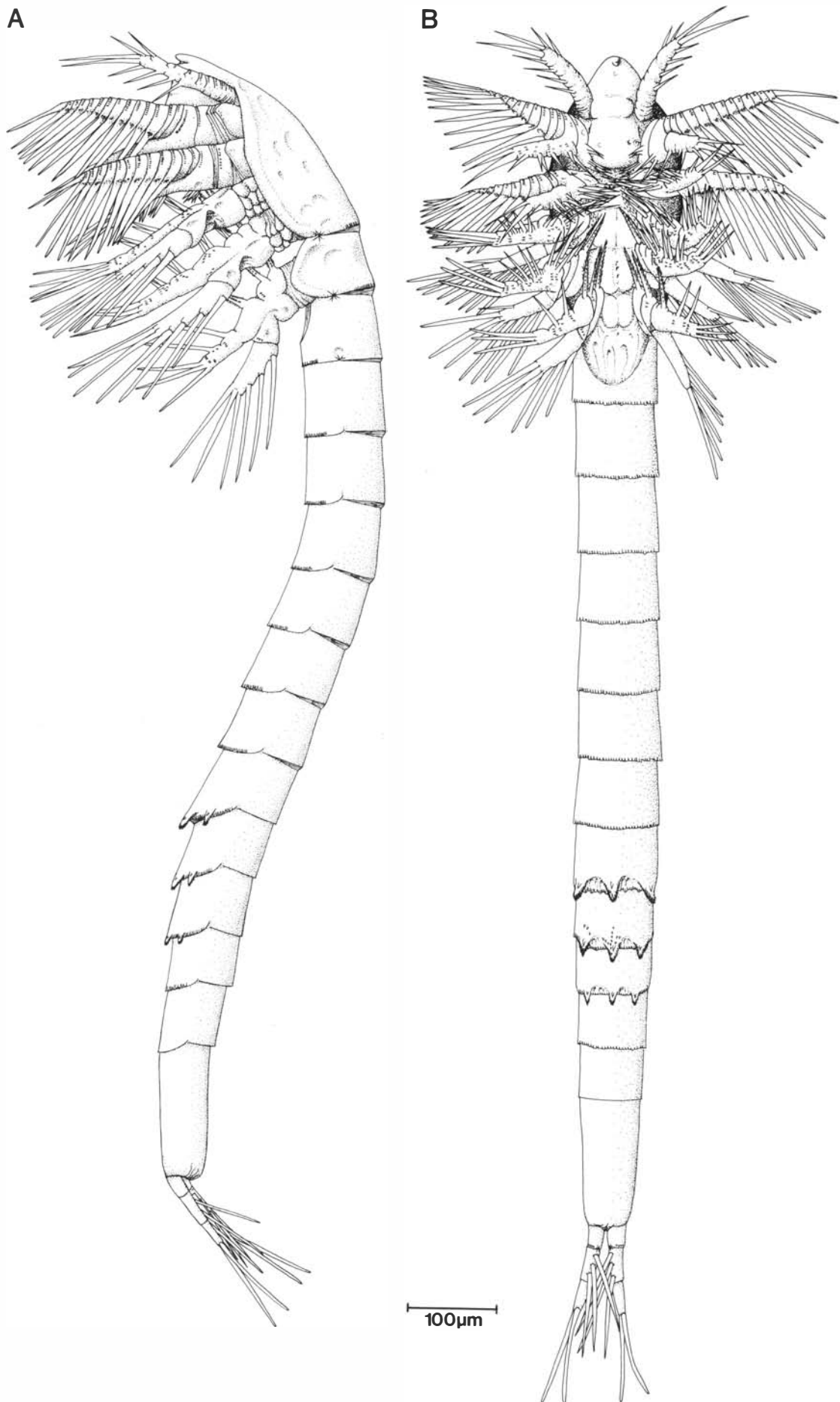
Fig. 3. Reconstruction of *Skara anulata* Müller 1983. □ A lateral, □ B ventral view.

not fusing anteriorly; forehead slender and protruding from the shield; labrum nose-shaped, narrow at its origin and widening to its rounded posterior end which overtops the mouth area; antennal coxal endite with two groups of setae; mandibular coxal endite either with denticulated grinding plate (gnathobase) or two masticatory spines; antennae and mandibulae with scale-like sclerotization at the lateral surface of their shafts, exopods composed of 12–14 segments, the distal 10–12 with one rigid, long seta; endopods of all limbs three-segmented; proximal portions of postmandibular limbs pliable and laterally folded (shaft); exopods of these limbs uniform, paddle-shaped and with plumose margins; first trunk segment with tergite, segments 2–11 ring-shaped and conical (anterior diameter smaller than posterior); most anterior trunk segments ventrally membranous and recessed to enable a wide ventral curvature of the trunk; ventrocaudal rims of almost all trunk segments fringed; additionally segments seven to nine with three posteriorly directed spines each at these rims; telson long and conical; furcal rami segmented and tube-shaped; life-habit: most probably nectobenthic filter-feeders.

Skara anulata Müller 1983

General views in Pl. 1, details on Pl. 3–17; Figs. 3–5, 10–16

Material. – 60 specimens, including the type-material (Table 1). The holotype (UB 646; Müller 1983, Fig. 9A; Pl. 14:1 and 2 herein) is from Gum, Kinnekulle, Upper Cambrian, *Agnostus pisiformis* Zone 1. The body is almost complete and comprises the cephalon, a strongly ventrally curved trunk, and the proximal podomeres of the furcal rami. The shield is slightly laterally compressed. Forehead and all appendages are broken off. Paratype UB 648 (Müller 1983, Fig. 9C; Pl. 7:3 herein) is a fragment which consists only of the posterior part of the cephalon and two trunk segments. However, the exopods of the right mandibula and maxillula are preserved with their thick, long setae. The second paratype (UB 647) is removed from *S. anulata*.

Dimensions. – Mean length in micrometers of different body portions and appendages: Total length 1200; cephalic shield (length/height/width) 250/80/145; trunk without telson 810; telson 130; furca 40/80/+; labrum 120; antennula 140; antenna 210; mandibula 200; maxillula 190; maxilla 180; maxilliped 170.

Description of the cephalon. – (a) Shield (Pl. 1:1, 2, 6, 7). The soft shield comprises about 1/5 of the body length and covers only the five limb-bearing cephalic segments (Fig. 3A). The cross-section approximates to an inverted U-shape. An anterior margin is absent; above the antennulae the ventral rims fade into the forehead (Pl. 4:4). Towards the posterior they curve down ventrally to the mandibulae and from there run straight to the widely rounded caudal corners (maximum length: height ratio 3:1; Pl. 3:1; Figs. 10A, 11A, 12). The rims are slightly bulging but overhang the body only little. In profile the shield is slightly arched in the anterior third. In dorsal view it widens from anterior to a maximum

width at about the level of the mandibulae (length: width ratio 3:2) and from there tapers to its rounded posterior end (Pl. 3:4; Fig. 12B). Below the caudal corners of the shield and the tergite of trunk segment one, the lateral cuticle turns directly into the shafts of the adjacent limbs (Pl. 3:5; Fig. 11A). The dorsocaudal rims of shield and tergite comprise a row of broad fringes which are composed of several sub-units (Pl. 3:6). A pliable arthrodial membrane connects shield and tergite. On the surface of the shield several shallow grooves can be seen. Most probably they represent scars of musculature which attached underneath and ran towards limbs and labrum (Pl. 3:1, 4, not emphasized).

(b) Forehead and labrum (Pl. 1:1, 2, 4–8). The forehead protrudes from the shield about 1/7 of the shield length and is not distinctly separated from the shield. The unpaired frontoterminal process is not completely preserved on any examined specimen. In most cases it is broken off or has collapsed (Pl. 4:1–3, 5, 6). It is assumed that this 'frontal organ' had a similar rod-shaped habit as in *S. minuta* n.sp. (see below). Just beneath the organ, a tiny pore is situated, probably representing the opening of a gland, as can be found in various extant Crustacea (G. Hartmann, personal communication).

Posteroventrally the forehead broadens to the nose-shaped labrum. The latter comprises about 1/3 of the head length and is almost straight in profile. Its base is laterally slightly bulged, being bordered by shallow transverse furrows (Pl. 4:1–3). Shallow depressions on the surface in front of the rounded posterior end of the labrum indicate the position of interior muscles which could move the labrum abaxially (Pl. 4:2, 3, 7). Laterally, at the antennal origins, a tripartite structure is developed. It consists of a 'walled area' composed of several slightly elevated walls arranged in a semicircle, a small triangular pore, and a sickle-shaped furrow or fold surrounding the walled area anteriorly (Pl. 4:7–9; Figs. 10A, 11A). The pore is identified as the exit of the 'antennal gland'. The walled area may be the expression of interior folds which enlarged the surface for the excretory organ, as can be found in extant Crustacea (Kästner 1967:900). Opposite the antennular origins the surface is covered with several tiny bristles. Their function, however, could not be clarified (Pl. 4:9).

(c) Sternum (Pl. 1:5, 8). The postoral sternites are fused to a single sternum. Only shallow transverse furrows still indicate the former segmentation (Pl. 6:1, 2). Anteriorly the sternum deepens to the funnel-shaped mouth opening. The area around the mouth and on the lower surface of the labrum is covered with setulae about 3–4 µm long. Here the innermost setulae are arranged in parallel rows (Pl. 6:1, 3, 4). More setulae arise from folds of the labrum posterolaterally (Pl. 4:7) and from the median surface of the mandibular shaft (Pl. 7:7). The sternum is anteriorly about as wide as the labrum. Behind the mandibulae, it tapers strongly towards the posterior. The mid-line is only slightly concave (Pl. 6:1–3). The small sternite of the maxillipedal segment is surrounded by a pliable membrane which extends caudally to the succeeding segment (Pl. 12:4, 5).

Description of the appendages. – *Skara anulata* has only six pairs of well developed appendages: five cephalic ones and one pair of maxillipeds. With the exception of the antennulae,
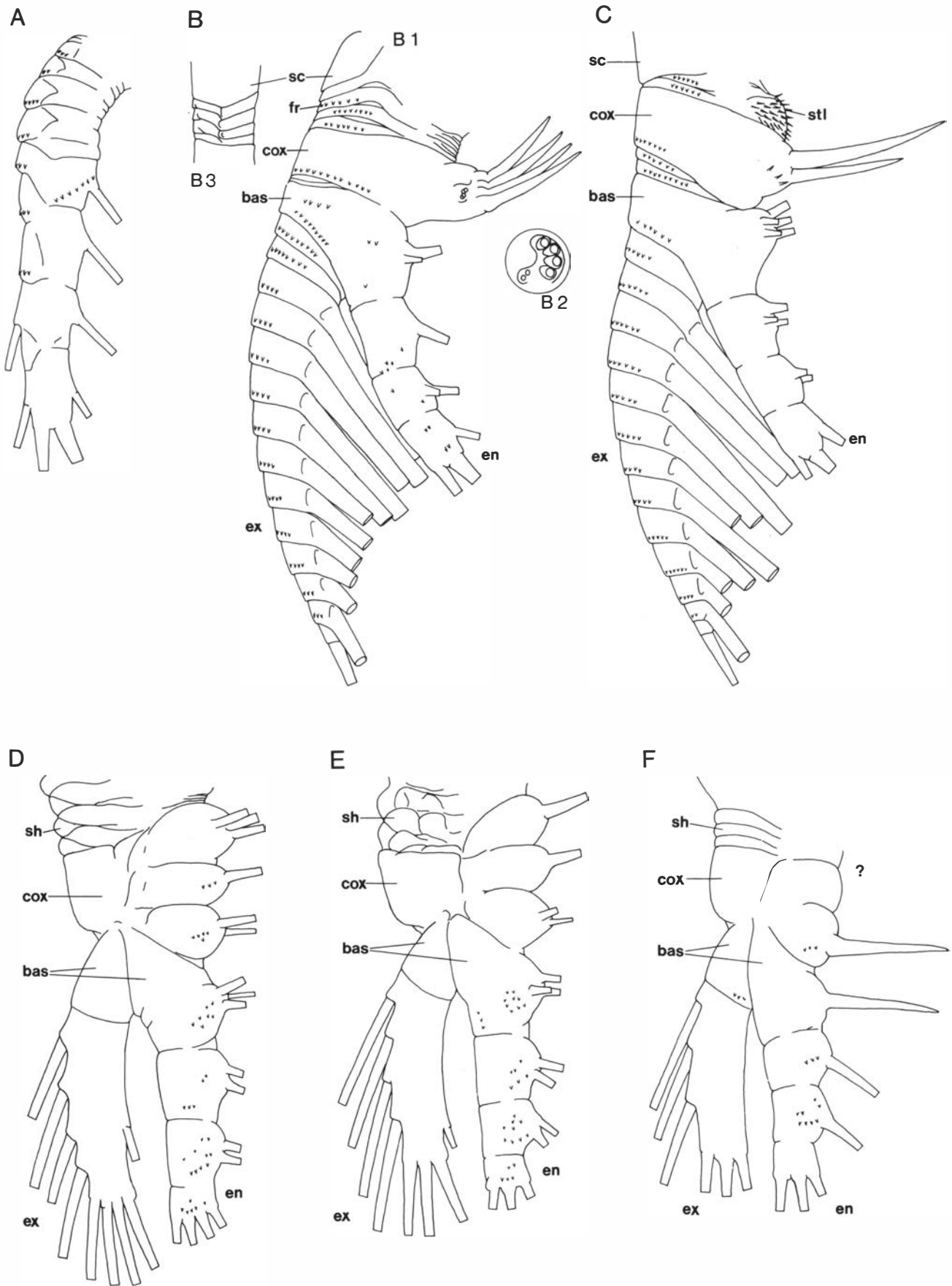
Fig. 4. Appendages of *Skara anulata*, frontal views: □ A. Antennula. □ B1. Antenna (aII). □ B2. Median view on the coxal endite with its two clusters of setae. □ B3. Lateral view on the shaft with scale and folds. □ C. Mandibula (md). □ D. Maxillula (mx1). □ E. Maxilla (mx2). □ F. Maxilliped (mxp).
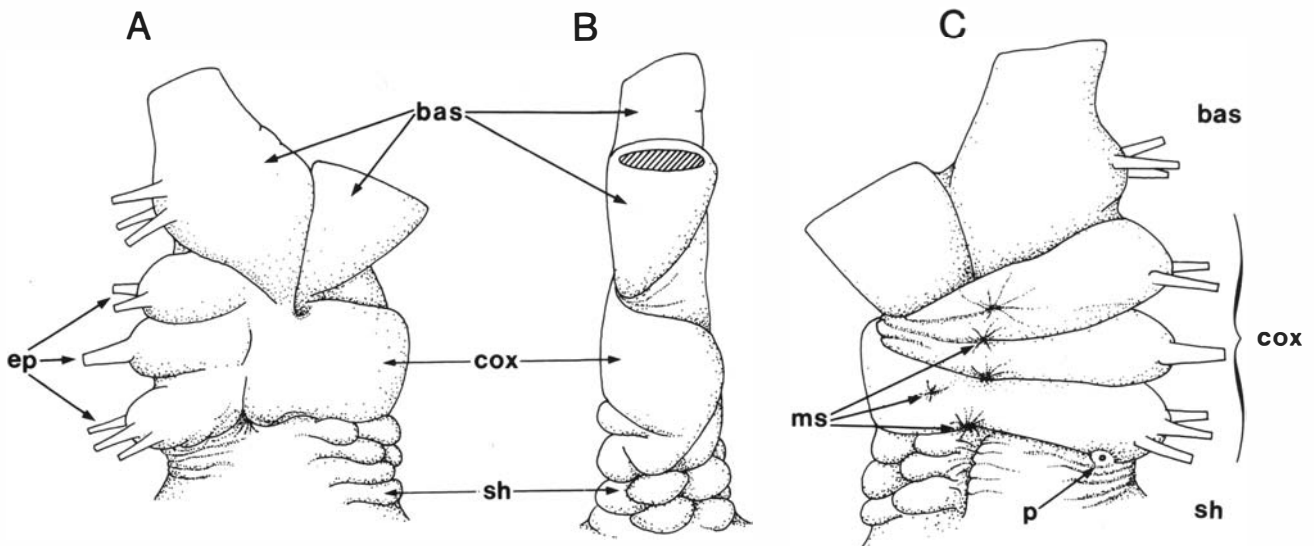
Fig. 5. Protopod of a postmandibular limb of *Skara anulata*. □ A. Anterior; □ B, lateral; □ C, posterior view.

the limbs are attached beneath the shield rims, with the protopods being more or less ventrally directed. Reconstructions are presented in Figs. 4 and 5. In most cases the distal portions of the setae have been omitted.

(a) Antennulae (Pl. 1:1, 5). The uniramous antennulae inserted below the starting point of the shield rims are the smallest appendages. They are almost cylindrical and composed of nine podomeres (Pl. 7:1; Fig. 4A). The outer surface of the proximal portion is well sclerotized and shows a division into five short ringlets. The median surface is unsegmented and simply finely folded. The distal portion is composed of four tubular podomeres. The surface of the antennulae is adorned with rows of tiny bristles about 1 µm long, most of them being situated on the distolateral rims of each podomere. Podomeres six, seven and eight bear one or two thin setae each on their median margins, and segment eight has another one on the outer surface. The ninth podomere carries medially and laterally a thin seta and terminally two strong ones. As these thick setae are broken off in all specimens, it could not be clarified whether these had sensory function (aesthetascs?).

(b) Antennae and mandibulae (Pl. 1:2, 4, 5; Fig. 1). These two pairs are the most prominent limbs (Pl. 7:2, 3; Figs. 3A, B, 4B, C). The bases of the antennae reach the posterolateral folds of the labrum. The position in relation to the mouth opening cannot be described exactly. It may be slightly preoral. The antennal shaft is very pliable medially. Its outer surface is more sclerotized, bearing a scale at its base and some knicked folds distally of it (Pl. 7:6 Pl. 15:6; Fig. 4 B1, B3). The coxa has an elongate masticatory endite which points posteromedially, flanking the rounded distal end of the labrum. The endite carries two groups of setae: a frontal one composed of two thin setae directed against the labrum, and a posterior group with four long, pilose setae (Fig. 4B 2). The latter reach almost to the mouth (Pl. 6:1–3; Pl. 7:5; Pl. 11:2, 3). The basipod is mediodistally elongated. Its little pronounced endite has two median setae. The endopod is tube-shaped and does not taper markedly to its distal end. It is composed of three podomeres which are longer than wide and from proximal to distal bear one, two,

and three setae (Pl. 7:2). The two terminal ones are much thicker than all the others. The exopod inserts on the sloping distolateral surface of the basipod which imports a slightly lateral orientation to the ramus. It is composed of 14 ring-shaped podomeres. While the proximal one or two podomeres lack a seta, the distal ones each bear one rigid, posteromedially directed seta which inserts in a thick, possibly movable shaft (Pl. 7:2, 3, 8; Pl. 15:1). As shown in Pl. 7:4, the segmentation is not always regularly developed: on the posterior side there are more joints than on the anterior one. As in the antennula, the antennal surface is furnished with tiny bristles: in rows on several parts of the protopod, probably on the distal rims of all exopodal podomeres, and in clusters on the anterior and posterior surfaces of the basipod and endopod (Fig. 4B).

The mandibulae are inserted behind the posterolateral folds of the labrum and look quite similar to the antennae (Fig. 4C). Shared details are: the scale at the outer surface of the base; the exopod composed of setose ringlets; the tri-segmented endopod, its apical podomere bearing one medial and two thick terminal setae; and the adornment with bristles (Pl. 7:2, 3, 4, 8; Pl. 15:6). Distinct features are: the protopodal shaft which lacks the folds between scale and coxa; the elongate coxal endite with two pilose masticatory spines, one thick proximal and a less strong distal one (Pl. 6:1, 2; Pl. 7:6, 7; Pl. 11:1–3). Furthermore, the median surface of the shaft is covered with numerous setulae as in the mouth area (Pl. 7:7). Coxa and basipod are laterally separated by one or two folds. The basipodal endite is protruding and bears five setae. The two proximal endopodal podomeres have three and two hairs medially. Again, the exopod is only 12-segmented (Pl. 7:3, 4, 8).

(c) Postmandibular appendages (Pl. 1:2–4; Fig. 1). Apart from a successive size decrease, and related to this some minor differences in shape and armature with setae, the maxilles and the pair of maxillipeds have the same design (Pl. 8; Figs. 3A, B. 4D–F, 11A, 16A). As in antennae and mandibulae, the protopods are oval-shaped in cross-section. In accordance with an oral orientation, they were successively more axially positioned (Pl. 6:1, 2; Pl. 11:1, 2; Fig.

Table 3. Major morphological differences between *Skara anulata* Müller 1983, and *S. minuta* n.sp.; abbreviations, see list on p. 00; measurements in μm.

	S. minuta	S. anulata
range of total length	490–970	1060–1360
shield (l/h/w) ♂♀	135/60/90–190/85/135	250/80/145
ratio males	1:0,44:0,67	1:0,32:0,58
females	1:0,45:0,71	
pore below frontal organ	no	yes
labrum: profile	concave	straight
origin	recessed	slightly bulged
lateral bulges	distinct, rounded	absent
agl with 'walled area'	no	yes
limbs: mandibular coxa	grinding plate	2 masticatory spines
endopodal podomeres	width>length, tapering	l.>w., little tapering
postmandibular exopods	rounded margins	concave median margin

	aII	md	mx1	mx2	mxp	aII	md	mx1	mx2	mxp
endites on coxa	1	1	3	4	2?	1	1	3	3	2?
setae on coxa (aII, md)	3 + 4	gn+1?	.	.	.	2 + 4	2	.	.	.
proximal endite (ml–mxp)	.	.	7	3+4	?	.	.	3	1	?
median endite (mxl–mxp)	.	.	6	3	?	.	.	1	1	?
distal endite (mxl–mxp)	.	.	5	6	?	.	.	2	2	1
setae on basipod	4	9	4	4	2	2	5	3	3	1
s on end: proximal podomere	2	4	3	3	2	1	3	2	2	1
median podomere	2	3	3	3	2	2	2	2	2	1
distal podomere	2 + 2	2 + 2	5	4	4	1 + 2	1 + 2	4	3	3
setae on exopods	14	12	9	8	8	14	12	8 + 1	7 + 1	6
relation en/ex	en<1/2ex		en>ex	en=ex	en<ex	en=1/2ex		——ex<en——		

	S. minuta	S. anulata
trunk:	spindle-shaped, compact	conical, slender
segments: length decrease	o 40–20 / o 60–30	80–60
width change of segments	increase and decrease	only decrease
range of membranous area	ts2 + anterior part of ts3	only half of ts2
fringes: number/thickness	80–100/0,3–0,5	40–50/1,0–3,5
ts7–ts9: distance betw. sp	50/40/40	40/30/20
fringes betw. the spines	50/40/35	25/15/?
telson: length (♂/♀)	90/175	130
furca: length of podomeres	20/40/20	40/80/?
proximal podomere	4, 1 spinule	>11 bristles, no spl

16A). The shafts are medially soft and finely wrinkled. Laterally they are provided with thick folds (Pl. 8:1, 4–7; Pl. 17:5). Due to their bulging endites, the coxae are medially enlarged and peg-like. The two maxilles bear three setose endites, the maxillipeds only one or two (Pl. 8:1–3). As illustrated in Fig. 5, the anterior and posterior sides of the protopods are differently designed. Anteriorly, the coxa is uniform. But its distal margin runs on the posterior side medially down to the proximal endite. This separates the well sclerotized proximal portion with one endite from the distal one with the remaining two endites, the latter portion being soft and wrinkled (Pl. 8: 1, 5, 7). Most probably this part of the coxa functioned as a joint for the whole distal limb portion. The basipod is slightly divided by a shallow furrow into two portions: a median one which is elongated towards the endopod (similar to the antennae and mandibulae), and an outer triangular portion which carries the exopod.

The two proximal podomeres of the tri-segmented endopod are longer than wide. Medioproximally they are armed with one or two stiff setae which arise from small elevations. The terminal podomere bears a cluster of three to four distally directed setae apically. As in the antennae and mandibulae, the endopod tapers only slightly. The exopods

are uniform, slender and paddle-shaped, and their median margins are concave. Only in the two maxilles is a seta developed, positioned subterminally (Pl. 8:6). From lateral to terminal the exopods bear 6–8 strong setae (Pl. 7:3; Pl. 8:1–4, 7, 8). Only the anterior and posterior surfaces on the endopods are adorned with tiny bristles, as on antennae and mandibulae (Pl. 7:2; Pl. 8:1, 2, 7).

In several specimens a small circular pore has been recognized on the maxillula posteromedially at the border between shaft and coxa (Pl. 8:5; Pl. 17:5). As on the shield and labrum, numerous muscle scars can be seen on the surfaces of shafts, coxae, basipods, and in some cases on the rami (Pl. 8:5–7; Pl. 11:1). For comparisons, the major features of all appendages are listed in Table 3.

Description of the trunk (Pl. 1). – The slender trunk is composed of one limb-bearing, 10 ring-shaped segments, and a long telson with furcal rami.

(a) Segments. Only the first trunk segment is pedigerous and carries a pliable tergite with rims similar to those of the head shield (Pl. 3:5, 6; Pl. 12:4–6). The following segments are ring-shaped and almost circular in cross-section (Pl. 17:6). The segments are jointed to one another by lateral attachment points, the articulations being covered by pliable

arthrodial membranes (Pl. 3:5; Pl. 4:5, 6; Pl. 12:1, 8). The anterior six segments are about 80 μm long whereas from segment seven to eleven the length decreases successively to 60 μm (Table 1). Again the diameter, which is 100 μm in the anterior three segments, decreases successively to 60 μm in segment 11. Because of this, the trunk is more or less conical. As the diameter of each segment is smaller anteriorly than posteriorly, all segments fit together telescopically (Fig. 3).

In segment one, the ventrocaudal corners of the tergite are widely rounded, reaching laterally to the depressions of the dicondylic attachment points (Pl. 3:1, 5, 6; Pl. 12:6). The membraneous area which surrounds the sternite between the maxillipeds extends posteriorly and covers also the deeply recessed anterior half of segment two. This recession may have provided space for the maxillipeds when the trunk was strongly curved ventrally (Pl. 1:1, 7; Pl. 12:4, 5; Figs. 3A, B; 10A, 11A). The trunk segments are not separated into tergites and sternites. The lateral attachment points divide the arthrodial membranes into distal and ventral portions. It is possible that this indicates a former boundary between the two sclerites. The cuticle close to the attachment points is very pliable, and in some cases muscle scars can be observed there (Pl. 3:6).

(b) Fringes and spines (Pl. 1:1, 3). The ventrocaudal rims of segments two to ten are adorned with a row of 40–50 tiny fringes. Each fringe is about 4 μm long. The thickness ranges from 1.0 to 3.5 μm because the fringes are composed of a varying number of subordinate fibres (Pl. 12:2, 3 7; Pl. 16:4; Fig. 13A). The ventrocaudal rims of segment seven to eleven extend further backwards than the more anterior ones (Pl. 12:1). Furthermore, the ventrocaudal rims of segments seven to nine bear three tooth-shaped, slightly lifted and posteriorly directed spines, the cuticle between them being less sclerotized (Pl. 12:1, 2, 7; Fig. 13A).

The spines of the same rim are of about the same size but become successively smaller from segments seven to nine. Whereas the diameter of these segments decreases successively, the distance between the lateral spines decreases first from 100 to 80 μm and remains at 80 μm in segment nine. The spines are not always symmetrically arranged. In several individuals the distances from the median to the two lateral spines differ markedly. One specimen bears only one spine on segment nine (ST 4156); another individual even lacks spines at the same segment (UB 711). Between lateral and median spine there are about 20–25 fringes in segment seven, and about 15 in segment eight. The spines themselves are covered with several rows of bristles around the tip. A small seta is positioned on the median surface of each spine (Pl. 12:2, 7; Fig. 13A). On the eighth segment of UB 727 there is a V-shaped row of setulae at the right side of the median spine, whereas the left side has only a few single bristles (Pl. 12:2, 7) This unique arrangement, however, may represent an individual variation rather than a specific character.

(c) Telson and furca (Pl. 14). The telson is more than twice as long as the preceding trunk segment. It is almost cylindrical or slightly tapering and terminates in a pair of tube-shaped, segmented furcal rami (Fig. 3A, B). The anal slit is positioned dorsally to their bases. Numerous delicate folds surround the anus suggesting that this region had been very pliable. This assumption is corroborated by the observation that, whenever preserved, this area is either collapsed or inflated (Pl. 14:1, 2, 4, 6, 7). In UB 734, a globular structure has been trapped between the furcal rami, possibly representing a faecal pellet (Pl. 14:4).

The proximal podomeres bear a row of more than 11 tiny bristles at their dorsodistal rim (Pl. 14:2). Due to their soft-jointed articulation, these podomeres could be bent far upward. The succeeding podomeres are about twice as long as the proximal ones being tightly attached to them. At their inner rim they bear three or more long setae. However, the distal part is not completely preserved on any specimen (Pl. 14:4, 8). It is possible that the furca of *S. anulata* is similar to that of *S. minuta*.

Remarks. – On the whole trunk there are no structures which can be interpreted as gonopores. Considering the extraordinary preservation of the material and the recognition of other pores, it is concluded that such structures would have been apparent, had they been present.

The infraspecific variation of morphological features proved to be small. A few minute differences could be found, but only on single individuals:

□ two instead of one seta at the median surface of the distal antennular podomeres

□ different number and arrangement of bristles on the endopods

□ one or two ringlets without a seta on the antennal exopod

□ one seta less or more on the postmandibular exopods.

Slight differences in the shapes of the soft shields may have been caused by postmortem events such as collapsing. Again, the frequency distributions for various morphological features in Fig. 9 demonstrate homogeneity within the study material of *S. anulata*.

Skara minuta n.sp.
General views. – Pl. 2.; Figs. 6–8, 10–13, 15, 16B

Synonymy. – * 1983 pars *Skara anulata* Müller, Fig. 9B (UB 647), cet. ex.

Derivatio nominis. – From *minutus* (Lat.) = minute (in comparison to *Skara anulata* Müller, 1983, which is twice as long).

Holotypus. – Specimen ST 4055, UB 707 (Pl. 2:10; Pl. 5:3, 4; Pl. 9:2; Pl. 13:7). The holotype is almost completely preserved. It comprises the cephalon and the trunk with telson and the proximal furcal podomeres. Due to lateral compression of the shields, the anterior limbs are stretched out far anteriorly. The maxillae and maxillipeds are broken off. The holotype is assumed to represent a male specimen (see below). For measurements see Table 2.

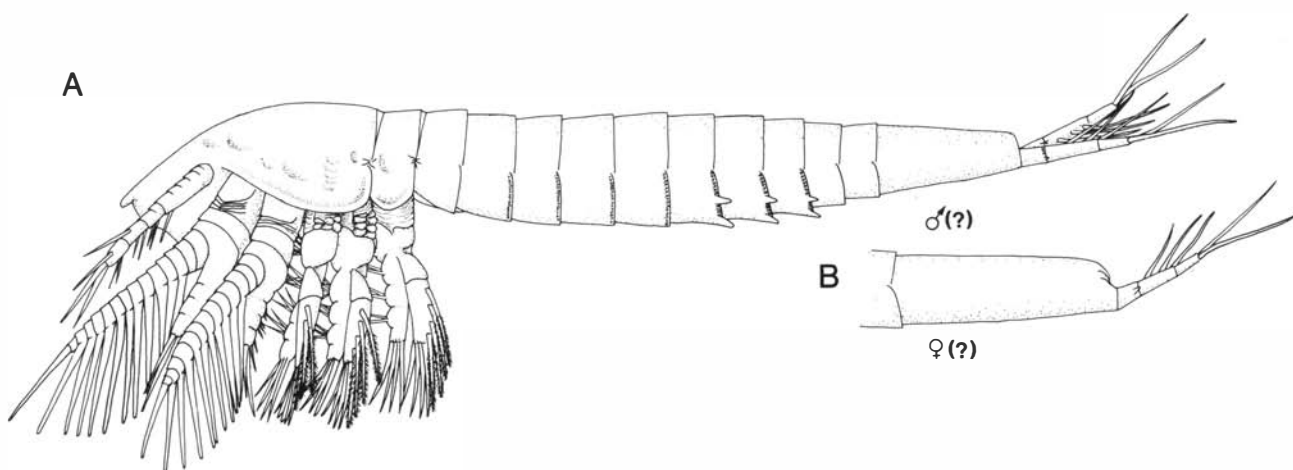*Locus typicus.* – Gum south of Blomberg, Kinnekulle, Västergötland, Sweden.

Fig. 6. Reconstruction of *Skara minuta* n.sp. □ A. Lateral view of a probable male. □ B. Posterior end of trunk with telson and furca of a probable female (explanations see text).

Stratum typicum. – Upper Cambrian, *Agnostus pisiformis* Zone (zone 1); sample 6409.

Paratypes. – 63 specimens (Pl. 2; measurements see Table 2)

Dimensions. – Mean length in micrometers of different body portions and appendages in the two size groups; values for the larger size group within brackets: total length 600 [850]; cephalic shield (length/height/width) 135/60/90 [190/85/135]; trunk without telson 360 [530]; telson 95 [140–220]; furca 20/40/20 [no data]; labrum 80 [80]; antennula 95 [no data]; antenna 150 [no data]; mandibula 130 [no data]; maxillula 120 [no data]; maxilla 110 [no data]; maxilliped 90 [no data].

Diagnosis. – In general appearance strongly resembling *S. anulata*, but shield, trunk somites and furcal podomeres about 1/2 as long, labrum 2/3; shield more arched; lateral rims not bulging, starting above the antennae, running down ventrally with sharp S-curvature and turning into the caudal rim almost at a right angle; caudal rim straight; no fringes posterodorsally on shield and tergite of the first trunk segment; labrum in profile with concave median line caused by the recessed origin; widely rounded tip; distinct lateral bulges between the origin of labrum and its posterolateral folds; opening of antennal gland present but 'walled area' absent; sternites separated, only little tapering towards the posterior end.

Appendages much as in *S. anulata* but about 2/3 as long; postantennular limbs more compact and with more setae on almost every portion; antennal coxal endite with three setae at the anterior group; mandibular coxa with pilose gnathobase; maxillar coxa with four endites; basipods not elongated towards the endopods; endopods tri-segmented as in *S. anulata* but podomeres strongly decreasing in size from proximal to distal being as wide as long or wider than long; exopods of postmandibular limbs uniform, leaf-like; median margins convex and without seta.

Fringes at the ventrocaudal rims of trunk segments three to ten 0.3–0.5 μm thick, 80–100 on each rim; spines at segments seven to nine with only one row of setulae at their flanks; median spine smaller than the lateral ones; distance between lateral spines successively decreasing; telson three times as long as the preceding trunk segment or even longer; furcal rami tri-segmented; proximal podomere with four bristles and one spinule at the distal rim; median podomere twice as long as the proximal and the distal one, with three setae and one small spinule at its inner rim; distal podomere with two long, soft setae terminally.

Description of the cephalon. – (a) Shield (Pl. 1:1–4, 7, 8, 10, 11). As in *S. anulata* the shield is soft and lacks any ornamentation and its lateral rims fade anteriorly into the forehead. But whereas in the former species the rims start above the antennulae, here they start above the antennae. Again they curve sharply ventrally to the maxillae. Because of the sharp ventrocaudal corners and the straight caudal rim the shield looks caudally truncated (Pl. 3:2, 3; Figs. 6A, 11B, 12). The shield is almost as high and as wide. In contrast to *S. anulata*, it is more arched and much shorter, causing the postantennular limbs to be nearer to each other. Similar to *S. anulata*, numerous muscle scars can be seen on the surface of the shield (Pl. 3:3), and the body wall beneath the ventrocaudal corners of shield and tergite turns directly into the shafts of the adjacent limbs (Pl. 3:2). Fringes at the dorsocaudal rims of shield and tergite, however, are not developed (Pl. 3:7).

(b) Forehead, labrum and sternum. The forehead extends from the shield by about 1/4 to 1/5 of the shield length. By this, the origins of the first two or three pairs of appendages appear more exposed than in *S. anulata* (Pl. 3:2, 3; Pl. 5:1, 2, 4, 5; Figs. 6A, 10B, 11B). The frontoterminal process or organ is completely preserved in UB 716 (Pl. 5:2, 7). It is assumed that the ventrally jointed, tubular organ could be moved up and down to some extent. In contrast to *S. anulata*, a pore beneath the organ is absent (Pl. 2:8; Pl. 5; 1, 3, 5). The distal end of the nose-shaped labrum is broadly rounded, slightly depressed at the tip and overhanging the mouth region (Pl. 2:1, 4, 6, 8, 10, 12; Pl. 5:1–3, 5). Behind the recessed origin which is bordered by shallow transverse furrows (Pl. 9:1, 4), the sides of the labrum are bulged. These bulges reach caudally to setulose folds which ran from the antennal and mandibular bases to the lateral end of the labrum (Pl. 5:1–3, 5, 6; Pl. 6:6). The pore of the antennal gland can be recognized anterior to the antennal base. The

'sickle-shaped furrow' is also present, situated in front of the bulges. But the 'walled area' of the latter species is absent. As the bulges are in the same position, it is assumed that they represent a comparable structure (i.e. containing the excretory organ) (Pl. 5:6). Bristles opposite of the antennular origins could not be found.

The sternum is well-divided into the three sternites corresponding to the postantennal segments. They are slightly elevated but medially recessed and have almost the same width. The lateral margins are rounded. The lower surface of the labrum and the lateral surface of the sternum are covered by numerous fine setulae which extend back almost to the level of the maxillae (Pl. 6:5, 6; Pl. 11:4; Fig. 16B).

Description of the appendages (Pl. 2:2–12; Fig. 6A). – All appendages look similar to those of *S. anulata* but are only 2/3 times as long. Reconstructions of them are shown in Fig. 7A–F. The setae are drawn either with their origins or with their proximal portions.

(a) Anterior three appendages (Pl. 2:2, 3, 6, 7, 9–11). As in *S. anulata*, the antennulae are the shortest appendages being composed of nine podomeres: five short and four longer ones. But the distal podomeres have pairs instead of single setae medially. The surface is also covered with tiny bristles (Pl. 5:4; Pl. 9:1, 2; Fig. 7A). The prominent antennae (Pl. 5:4; Pl. 9:3, 6; Fig. 7B) and the mandibulae (Pl. 9:5, 6; Fig. 7C) have the same basic design. Their long exopods served as the main locomotory organs (Pl. 10:7). In both limbs the proximal portions of the bases are almost identical to those of *S. anulata* and bear scales and folds too (Pl. 9:1, 3, 7; Figs. 7 B1, B3, C). But the distal portions are slightly different: the antennal coxal masticatory endite has three hairs on its anterior and four in the posterior group (Fig. 7B2) and the mandibular coxa bears, in contrast to the masticatory setae of *S. anulata*, a slightly oblique gnathobase with bristles on its surface and some denticles at its median rim (Pl. 5:1, 3; Pl. 6:5, 6; Pl. 9:5, 6; Pl. 11:4, 5; Fig. 16B). In both limbs the basipods have more setae than in *S. anulata* and are not elongated towards the endopods. The three endopodal podomeres decrease markedly in size successively. Likewise, the endopods reach less than half way up to the exopods. The two proximal podomeres are wider than long and medially elongated into a setose process (Pl. 9:3; Pl. 10:2, 7).

(b) Postmandibular limbs (Pl. 2:3–11; Fig. 6A). The maxilles and maxillipeds resemble those of *S. anulata*. All have the same general plan but decrease slightly in size successively (Pl. 9:3, 4; Pl. 10; Figs. 5, 6; Figs. 7D–F, 11B, 16B). As in *S. anulata*, the shafts are thickly folded at their outer surface and the coxa is also peg-like and enlarged medially due to the bulging endites. Again, the coxae are posteriorly divided into a more sclerotized proximal portion with one endite and a softer distal portion with two distally directed endites (see Fig. 5). But the number of enditic setae is much larger than in *S. anulata*, and all endites are posteromedially elongated into a pilose spine. In front of it, pilose setae are positioned which curve towards the mouth and form a sieve from proximal to distal.

Furthermore, the surfaces of all protopodal endites are covered by numerous projecting bristles (Pl. 10:2–4, 6; Pl. 11:4, 5; Pl. 15:7; Fig. 16B). The maxillar coxa bears four

instead of three endites on maxillula and maxilliped (Pl. 10:6). As in *S. anulata*, the basipod is divided into a median and an outer portion and arises from the sloping back of the coxa. Medially it has a setose enditic process similar to those of the coxa. In contrast to *S. anulata*, the basipod is not elongated distally towards the endopod (Pl. 10:4–7).

The two rami appear shorter and more compact than in the larger species. The endopods have the same shape as the antennae and mandibulae (Pl. 10:5, 7) but the short distal podomere bears a cluster of four to five setae. The exopods originate from the sloping surface of the triangular outer basipodal portion. They are more rounded than in *S. anulata* and leaf-like. The convex margins bear eight to nine thick, pilose setae from lateral to distal (Pl. 10:1, 5, 7; Pl. 15:2; Pl. 17:6). In contrast to *S. anulata*, the sides of all limbs are not adorned with tiny bristles. All major differences in shape and setation between the postmandibular limbs are listed in Table 3, in comparison with *S. anulata*.

Description of the trunk with telson and furca (Pl. 2:1–12; Fig. 6A, B). – The major features of the trunk are the same in both species such as: 11 segments, the first with a soft tergite and limbs; a long telson; jointed furcal rami; fringes at the ventrocaudal rims; three tooth-like spines each at segments seven to nine.

(a) Segments. All segments are about half as long as in *S. anulata* (compare Tables 1 and 2). Whereas the length decreases successively, the width first increases from segments one to six and then tapers towards the end. This results in a more spindle-shaped habit of the trunk (Figs. 6, 10B). On the ventral side of the most anterior segments the membranous area expands from the maxillipeds to a small anterior part of segment three; the entire ventral cuticle of segment two is pliable (Pl. 6:5; Pl. 13:7; Fig. 16B). It is possible that the shortness of the segments caused this enlargement of the pliable area in order to achieve a similar wide trunk curvature as in *S. anulata*.

All segments except the first are ring-shaped and connected by well developed arthrodial membranes (Pl. 3:3; Pl 13:1, 2), but the lateral attachment points at the caudal rims are faintly developed (Pl. 13:1). The ventrocaudal rims of segments seven to eleven are only slightly backwardly extended. In accordance with the successive size decrease of the segments, the spines become smaller too. The distance between lateral spines and the shorter median one decreases from about 80 to 60 and 40 μm (Pl. 2:1, 2, 6, 9, 12; Pl. 13:1, 4, 5; Pl. 17:6; Fig. 13B). The number of fringes at the ventrocaudal rims which may have had a length of about 1/4 of that of the following segment ranges from 80 to 100 (Pl. 13:6), but they are much thinner than in *S. anulata*. The fringes range from 0.3 to 0.5 μm, possibly being composed of only one or two fibres. The number of fringes between the spines decreases successively between segments seven to nine from about 50 to 40 and 35. A small hair is developed on the median surface of each spine, but in contrast to *S. anulata*, the flanks of the spine have only one row of bristles (Pl. 13:3–6; Fig. 13B).

(b) Telson and furca. The conical telson is about three times as long as the preceding trunk segment (Pl. 2:1–5, 7, 9, 10, 12; Figs. 6, 8, 10B). The anus is positioned at the truncate caudal end, just dorsal of the furcal origin and
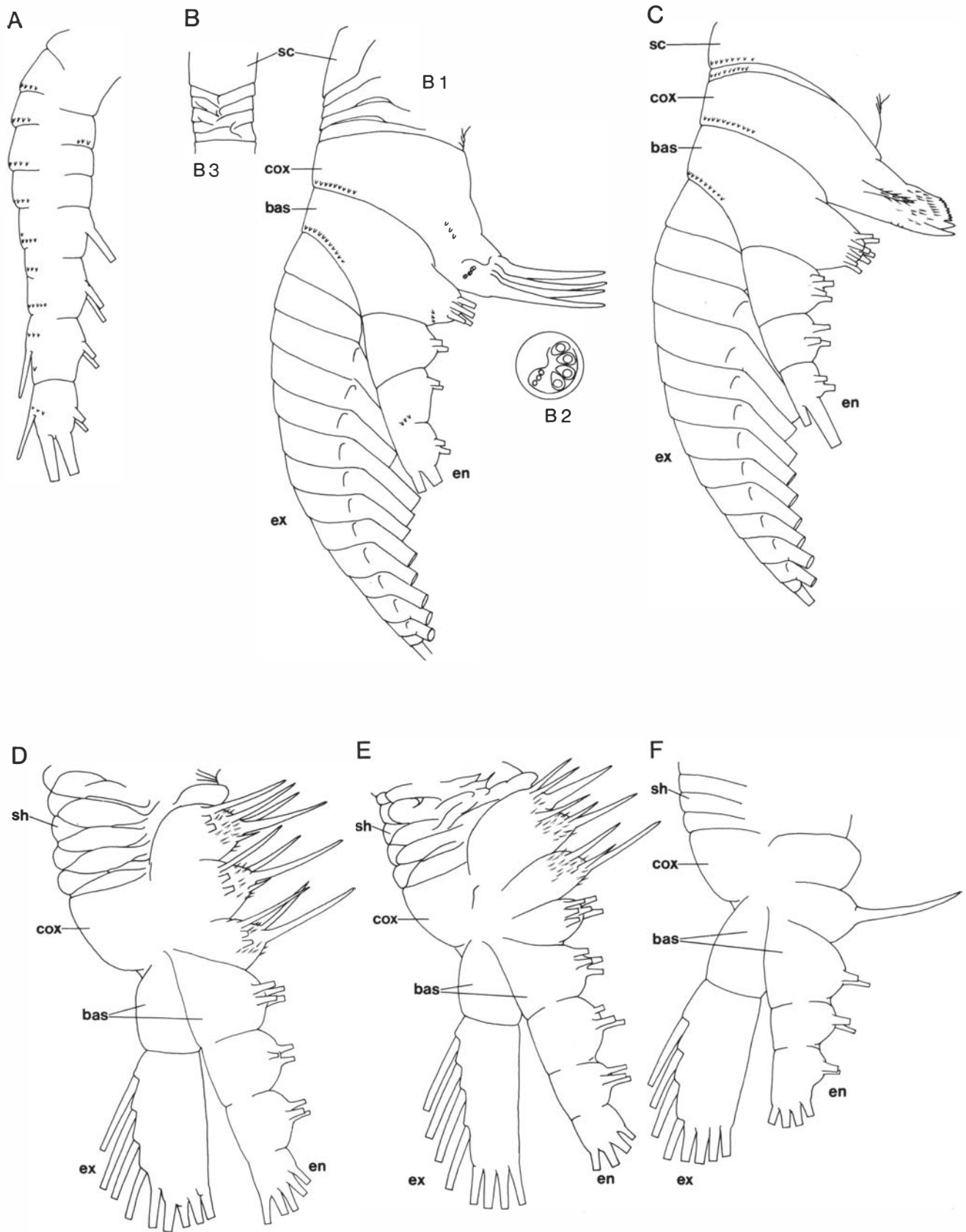
Fig. 7. Appendages of *Skara minuta*, frontal views. □A. Antennula. □B1. Antenna (aII). □B2. Median view on the coxal endite with its two clusters of setae. □B3. Lateral view on the shaft with scale and folds. □C. Mandibula (md). □D. Maxillula (mx1). □E. Maxilla (mx2). □F. Maxilliped (mxp).
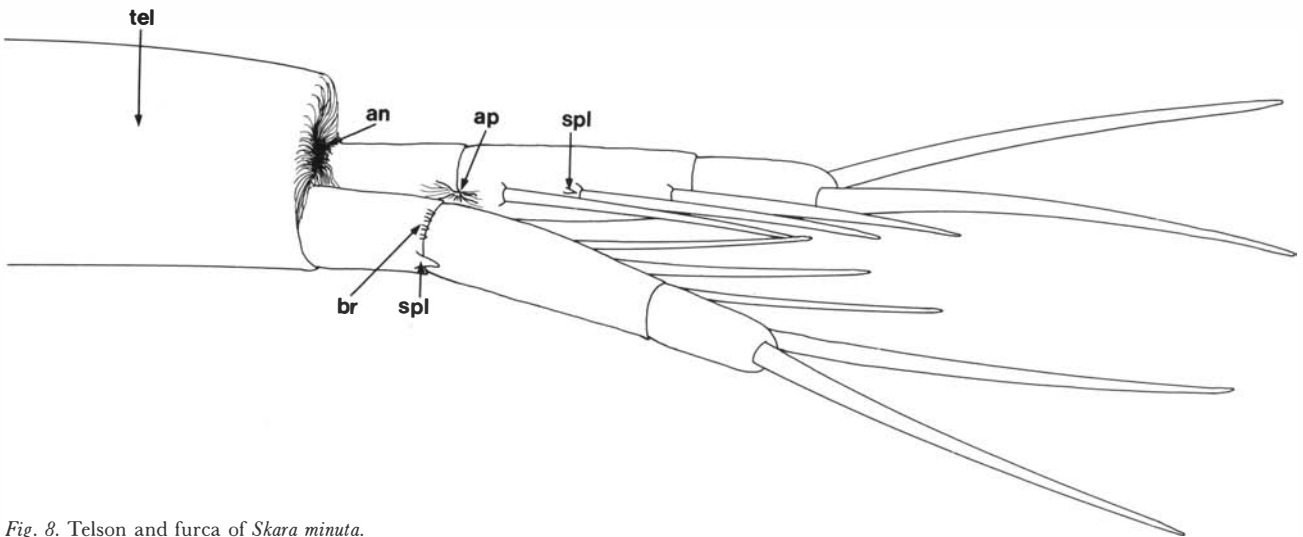
Fig. 8. Telson and furca of *Skara minuta.*

surrounded by numerous delicate folds (Pl. 14:5). The furca is entirely preserved only in one single specimen (UB 703, Pl. 2:5; Pl. 14:3). Each ramus is composed of three rod-shaped podomeres. The proximal podomere bears a spinule and a row of four bristles dorsodistally (Pl. 14:9). The second podomere is twice as long as the proximal and the terminal one and has three long setae on its median surface. Additionally, a tiny spinule is situated just in front of the most distal seta. The terminal podomere has two setae apically. These may have been pliable and even longer than 50 μm (Pl. 14:3).

Remarks and infraspecific variation. – As in *S. anulata,* no gonopores or structures referrable to this function have been detected on the whole trunk. In the length-frequency distributions of Fig. 9 the size range of various body portions is fairly large, all distributions except that of the labrum (Fig. 9E) being extended towards the larger values. This is obviously due to a small number of individuals which proved to have the same morphology (tagmosis, segments etc.), with two exceptions: (1) apart from the labrum they are larger in all measured details; (2) at least four specimens have a much longer telson, even longer than in *S. anulata* (Pl. 2:1, 7; Figs.
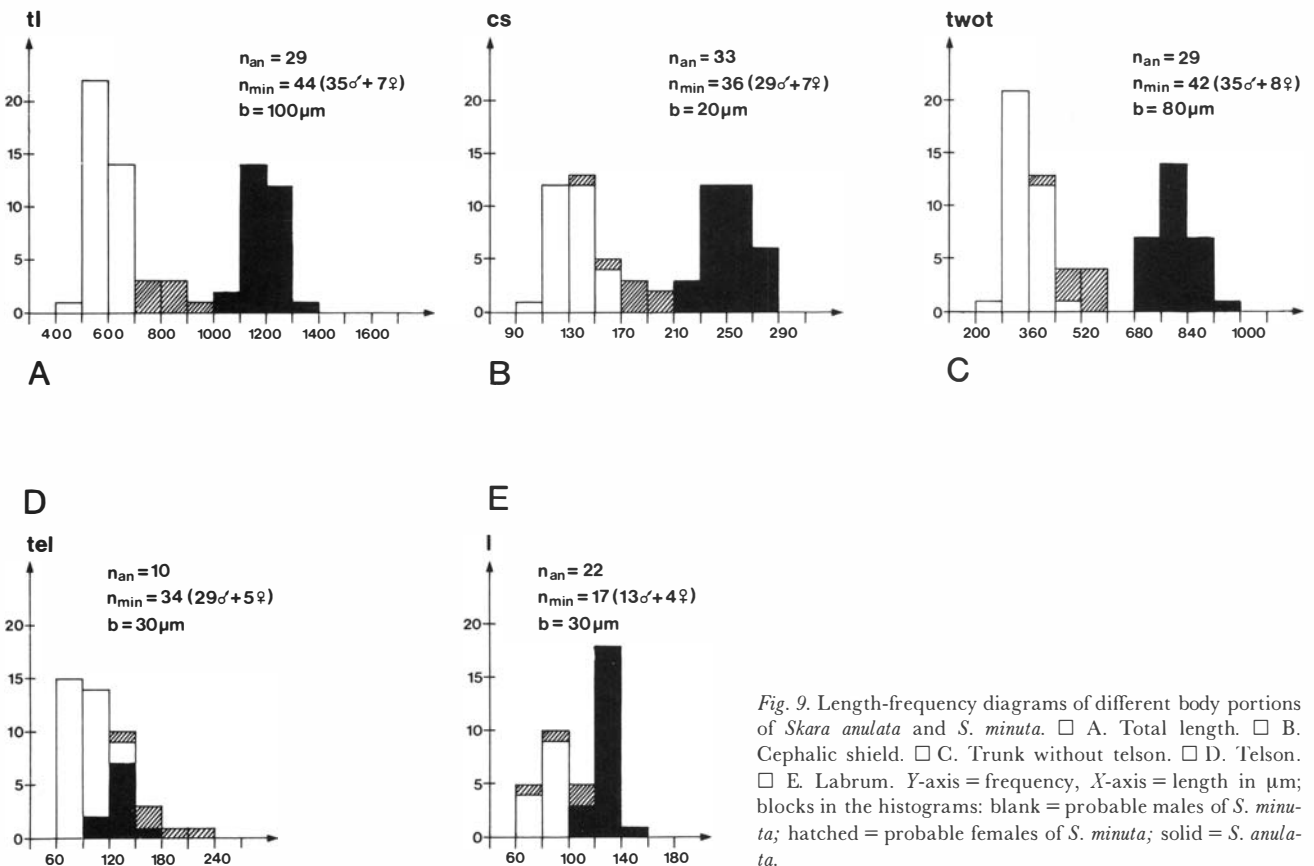
Fig. 9. Length-frequency diagrams of different body portions of *Skara anulata* and *S. minuta.* ☐ A. Total length. ☐ B. Cephalic shield. ☐ C. Trunk without telson. ☐ D. Telson. ☐ E. Labrum. *Y*-axis = frequency, *X*-axis = length in μm; blocks in the histograms: blank = probable males of *S. minuta;* hatched = probable females of *S. minuta;* solid = *S. anulata.*

2 – Müller/Walossek
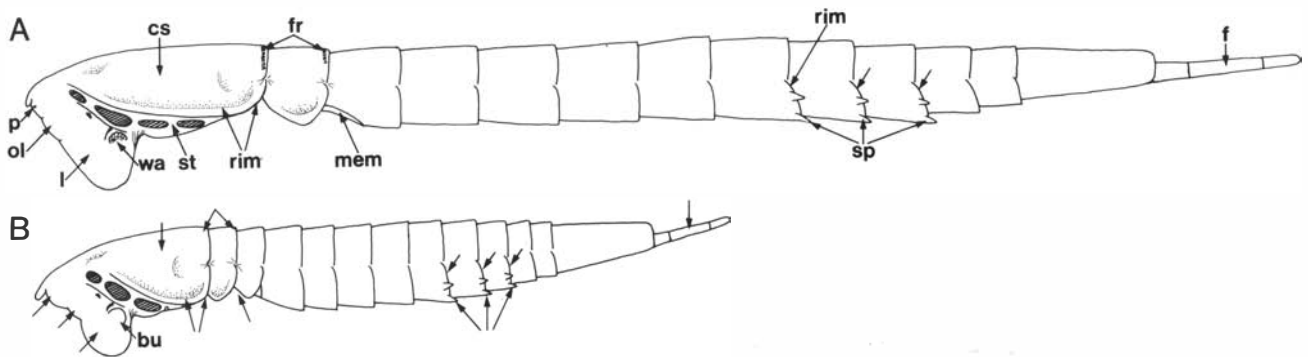
Fig. 10. Lateral views of (A) *Skara anulata* and (B) *S. minuta* (probable male); limbs omitted; arrows with symbols indicate major diagnostic differences (see text and Table 3).

6B, 9D) Due to incomplete preservation, however, it was difficult to recognize more than about eight of them in the material and to obtain measurements. For example, the limbs may also be longer, as one individual, UB 705, has distinctly longer maxillae and maxillipeds than the major group (Pl. 2:8). But these are the only data at present. The length–height- and the length–width-ratios of the cephalic shield differ only slightly between the two groups, but both are distinct from *S. anulata* (Fig. 12).

In our opinion the two size groups represent heteromorph sexes rather than two moulting stages. The large-sized group is assumed to represent the females (Pl. 2:1, 6, 7, 8; fig. 6B). The small-sized group, comprising the majority of specimens in the material, is assumed to represent the males (Pl. 2:2–5, 9–12; Fig. 6A).

Comparisons

Skara minuta and *S. anulata* differ strongly in size. Furthermore, they possess a large number of minute morphological differences which are regarded as distinct specific characters rather than simply expressing individual variability or even differences between moulting stages. All major diagnostic features which permit the assignation of even fragments to one or the other of the two species, are summarized in Table 3. Additionally, some of the main distinctive characters are presented in Figs. 10–13.

Size and proportions. – The large size differences between the two species becomes apparent when looking at the size-frequency distributions for several body parts in Fig. 9. The distributions of total length, head shield and 'trunk without telson' do not even overlap (figs. 9A, B, C). The mean length for the telson of *S. anulata* is 1.3 times larger than in the presumed males of *S. minuta*. The presumed females of the latter species, however, have a telson which is as long as or even much longer than in *S. anulata* (Fig. 9D). The labrum of *S. anulata* is 1.5 times larger than in *S. minuta*. The sexes could not be distinguished by this character (Fig. 9E).

The profiles of the two species are reconstructed in Fig. 10 and drawn in the same size. They emphasize the large size difference but also the differences in shape and proportions which are most apparent on the shield and trunk (the limbs are omitted to permit a view on labrum and sternum). The major distinctive features on cephalon and trunk (indicated by arrows with symbols) are:

☐ on the forehead: the degree of protrusion; the presence of a pore beneath the frontal organ
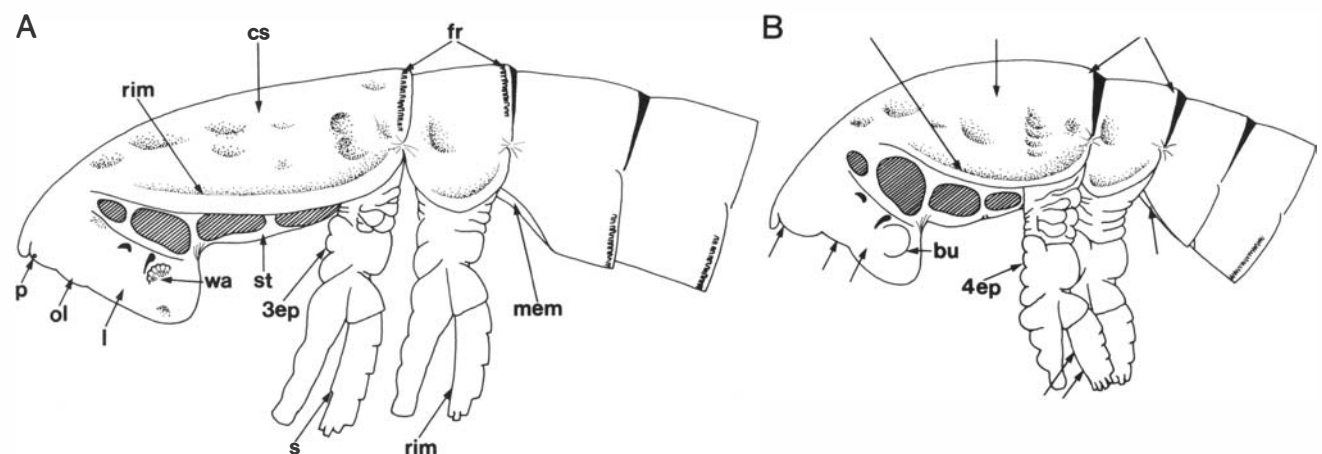
Fig. 11. Lateral view of the anterior portion of (A) *Skara anulata* and (B) *Skara minuta* (probable male); anterior four appendages omitted; arrows with symbols indicate distinctive features (see text and Table 3).
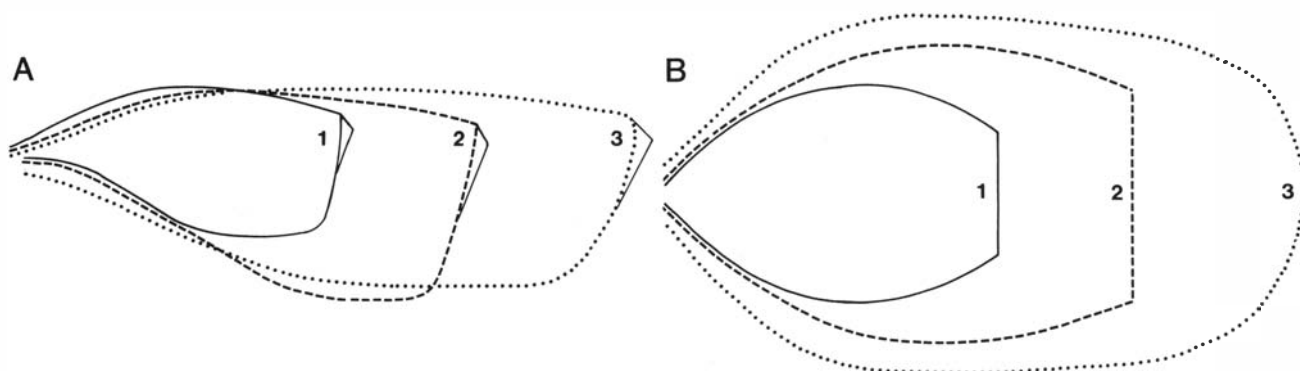
Fig. 12. Shield outlines of (1) probable males and (2) females of *Skara minuta,* and (3) of *S. anulata.* □ A. Lateral, □ B, dorsal view.

□ on the labrum: the shape; the degree of depression of the origin; the presence of either a walled area or a bulge at the side

□ on the sternum: the degree of sub-division; shape of the surface

□ on shield and tergite: the presence of fringes

□ on the trunk: the degree of extension of the ventrocaudal rims of segments seven to eleven; the size of the spines at segments seven to nine; their adornment with bristles and setulae; the lengths of telson and furcal podomeres

Because of the shorter trunk segments, the increase in width up to the mid-level and the decrease to the posterior end, *S. minuta* looks more compact and spindle-shaped than the slender and conical *S. anulata.*

   In addition to Fig. 10, in Fig. 11 the anterior portions are enlarged to emphasize the differences in this part: i.e. the relation between forehead and the rest of the cephalon and the height–length ratio of the shield. The maxillae and maxillipeds are drawn to demonstrate some major differences on these limbs, too, for example in the number of endites and in the shape of the endopod and exopod. As in Fig. 10, the distinctive features are indicated by arrows with symbols.

Shield. – Whereas the dorsal and lateral outlines of the head shields are different between the two species (Fig. 12), the shields of the two sexes of *S. minuta* differ only in size. The differences between the two species in profile can be seen in: proportions (ratios see Table 3); curvature of the lateral rims; caudal corners; and the posterior margin (Fig. 12A). In dorsal view the sides of the shield of *S. minuta* are widely rounded, expand quickly to their maximum width between mandibulae and maxillulae, and converge caudally to the sharp posterior corners (Fig. 12B1 males, Fig. 12B2 females). The posterior rim is straight. In *S. anulata* the width of the shield increases to the level of the mandibulae and tapers only slightly towards the rounded posterior corners (Fig. 12B3). Here the posterior rim is convex.

Trunk. – More differences between the two species can be seen on the ventral surface of trunk segments seven to nine,

reconstructed in Fig. 13 (compare also Pl. 12:1–3, 7 with Pl. 13:3–6). The ventrocaudal rims of these segments are further extended in *S. anulata* than in *S. minuta.* In the former species the width decreases successively between segments seven and nine whereas the distance between the lateral spines decreases only from segments seven to eight. In *S. minuta* both features decrease successively.

   Furthermore, the spines of *S. minuta* are much smaller than in *S. anulata,* especially the median one. The degree and arrangement of bristles on the spines is also different. In *S. anulata* numerous bristles are arranged in rows at the flanks of each spine, some more covered the ventral surface whereas in *S. minuta* only one row of bristles plus a few single ones are developed at the sides of the spines. Again, the two species have fringes of different size and density on the trunk segments and between the spines, as can be seen in Table 3.

Shared features and life habit. – Common structures of the two species are: the tagmosis; the head shield; the projecting forehead with frontoterminal process; the prominent labrum; the opening of the antennal gland; the general habit of all appendages; the trunk with one pedigerous, tergite-bearing and ten annular segments; fringes at the ventrocaudal rims of the trunk segments and three tooth-like spines at segments seven to nine; the long telson with terminal anus dorsally of the articulated furcal rami. Besides these gross similarities, *S. anulata* and *S. minuta* share also various, minute characters, for example: the number of antennular podomeres and the number of antennal and mandibular exopodal podomeres.

   These corresponding features show clearly that both forms were closely allied and cannot be separated higher than at species level. Both were sorted in almost the same quantities from the same samples which indicates that they do not represent species of different geological age. Most probably the two forms lived close together in the same area. But due to size and the habit of the filter apparatus (see below) they may have inhabited different ecological niches and fed on diets of different size.

Variation. – The infraspecific (individual) variation of morphological characters in the study material is fairly small. It can be recognized mainly in a slightly different degree and arrangement of setulae and bristles on limbs and sternum or the number of setae of the postmandibular exopods. Vari-

A

ts7

ts8

ts9

10 µm

B

ts7

ts8

ts9

10 µm
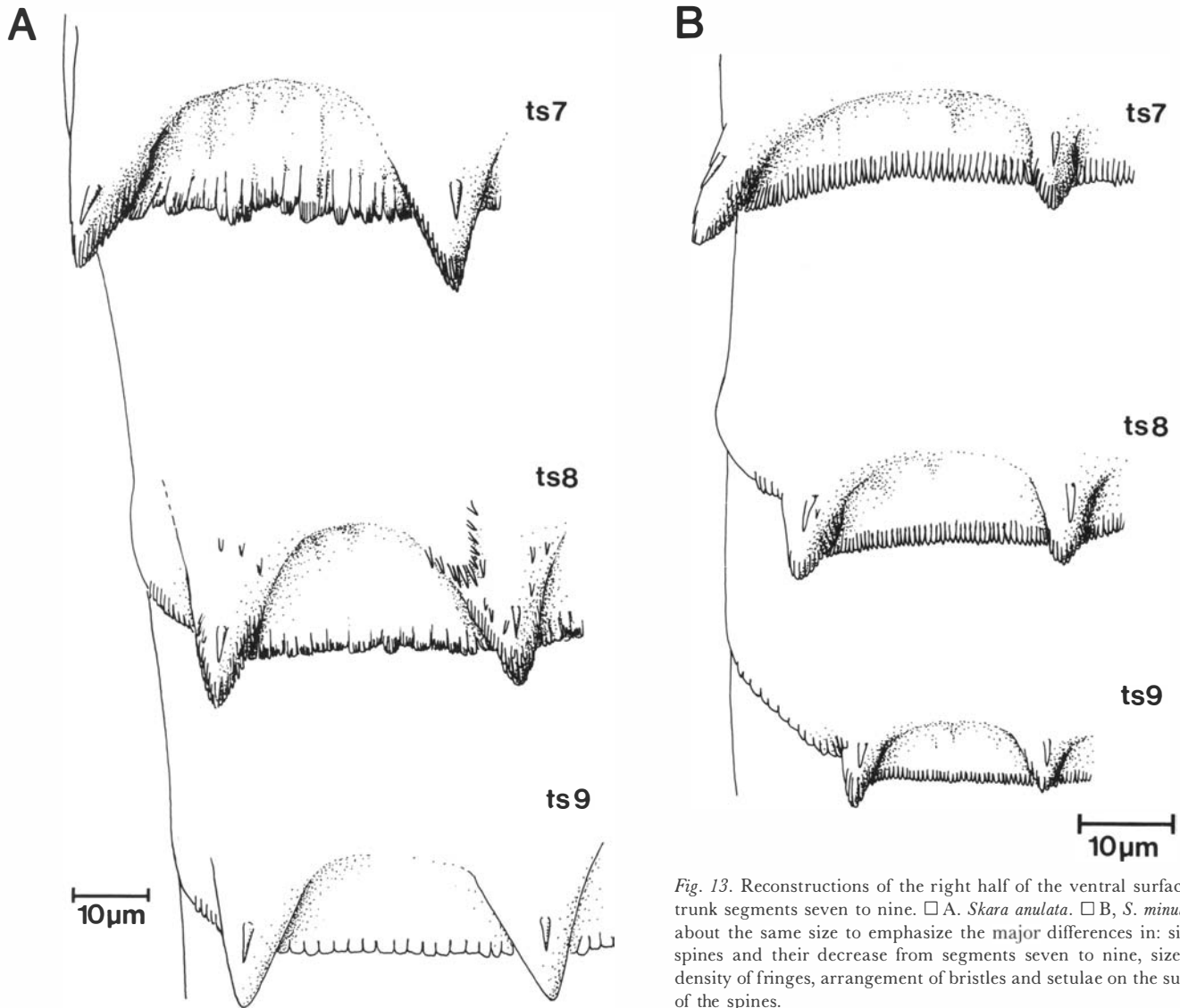
Fig. 13. Reconstructions of the right half of the ventral surfaces of trunk segments seven to nine. □ A. *Skara anulata.* □ B, *S. minuta,* in about the same size to emphasize the major differences in: size of spines and their decrease from segments seven to nine, size and density of fringes, arrangement of bristles and setulae on the surface of the spines.

ations which can be observed in the shapes of shield and labrum or in the degree of dorsoventral compression of trunk segments and telson are more likely to have been caused by collapsing.

Again, the interspecific range of variation proves to be rather limited. This demonstrates a conservatism in the development of morphological features which may be compared with those extant Crustacea having a very basic appearence, e.g. Cephalocarida or Mystacocarida. Lombardi & Ruppert (1982) stress that members of the latter group all have the same basic plan, and the interspecific range of variation appears to be minimal. Again, Hessler (1969) found that apart from the size difference *Derocheilocaris ingens* Hessler, 1969, and *D. typica* Pennak & Zinn, 1966, have almost the same morphology (the former species is about 1,5 times larger than the latter).

Hairs and similar cuticular structures (mainly Pl. 15). – Hairs as special developments of the crustacean cuticle take part in a large number of functions, e.g., locomotion, enlargement of the sinking drag, food gathering and mastication, cleaning, and protection. In *Skara* almost all parts are smooth. Pilose

structures are restricted to certain areas. The observed hairlike structures can be grouped into strong setae (which also may be spine-like), finer hairs, tiny setulae, bristles, and fringes. None of them, however, are distinctly articulated in the cuticle. The two species share the majority of types.

(a) Robust setae are attached to the ringlets of the antennal and mandibular exopods. They have been longer than 80 µm and insert in broad, pliable shafts suggesting that they were moveable to a certain extent. The setae are cylindrical over a long distance and taper only in their distal portion (Pl. 7:3). Most probably they had natatory function (Pl. 15:1). Other long setae which probably aided the same function, are developed on all terminal antennular and endopodal podomeres. The long furcal setae may have served mainly for steering (Pl. 14:3).

(b) Long, prominent setae are also developed on the paddle-shaped postmandibular exopods. At least in *S. minuta*, these setae are distally adorned with two opposing rows of 3–4 µm long setulae. This may have enlarged the efficiency for the exopod during its backstroke (Pl. 15:2; Pl. 7:3; Pl. 10:1).

(c) Other robust, pilose setae are restricted to the median

surface of limbs included in the filter apparatus. The major-
ity of them are inwards and mouthwards directed. One type
with a proximal portion having a corona of setulae and with
a distal end having rows of setulae, is represented in the
posterior group of setae on the antennal coxa; and the
endites of the postmandibular limbs of *S. anulata* (well pre-
served in the specimen illustrated in Pl. 15:3, 4). The proxi-
mal endopodal podomere of the maxilliped is armed with
one strong seta which has four rows of setulae (Pl. 15:5). In
S. minuta only the setae projecting from the posteromedian
elevations of the coxal endites may represent this type of
strong, pilose setae (Pl. 10:3; Pl. 15:7).

(d) Two thick and slightly flattened masticatory setae
arise from the mandibular coxal endite of *S. anulata*. Distally
they are furnished with some setulae (Pl. 7:7; Pl. 11:3).

(e) The other hairs arising from medial surfaces of endo-
pods and endites of the postantennular limbs of *S. minuta* are
markedly thinner than the types described above. The ante-
romedian setae of the coxal endites of the postmandibular
limbs are soft, mouthwards curved, and adorned with a row
of setulae posteriorly (Pl. 10:3, 4; Pl. 15:7).

(f) Thin hairs without setulae project from the antennular
podomeres, from the anterior process of the antennal coxal
endite (Pl. 9:6), and from the coxal endites in *S. minuta*, just
above the major seta (Pl. 10:3, 4).

The following types of bristles and fringes are not consid-
ered to be true hairs but to be simply small extensions of the
cuticle.

(g) In both species numerous densely spaced, 3–4 μm long
setulae cover the cuticle in the mouth area, below the la-
brum, on the posterolateral folds of the labrum, and on the
sternum (Pl. 5:1; Pl. 6:3, 4, 6). In *S. anulata* more of them are
developed on the mandibula beneath the coxal endite. In *S.
minuta* there are several setulae on the distal surface of the
mandibular gnathobase. Again in this species, the protopo-
dal endites of maxilles and maxillipeds are covered with
numerous projecting setulae (Pl. 15:7).

(h) The most anterior appendages are furnished with tiny
bristles of about 1 μm length, most of them arranged in rows
(Pl. 15:6; Pl. 7:4; Pl. 9:1). In both species similar tiny bristles
are developed on the distal rims of the proximal furcal
podomeres (in *S. minuta* together with a small spinule) (Pl.
14:2, 9). Only in *S. anulata* single bristles or clusters of them
can be seen on the lateral surfaces of all endopods (Pl. 7:2;
Pl. 8:1, 2, 7). In this species other tiny bristles are developed
immediately opposite the antennular origins (Pl. 4:9). Their
function is as yet unknown.

(i) Fringes at the dorsocaudal rims of the shield and the
tergite of the first trunk segment are present only in *S. anulata*
(Pl. 3:6). But in both species, similar fringes project from the
ventrocaudal rims of almost all trunk segments. In *S. anulata*
these fringes are similar to those of the shield and tergite,
being unequal in thickness and composed of a varying num-
ber of subordinate fibres (Pl. 12:2, 3; Pl. 16:4). In *S. minuta*
the fringes are, in general, much thinner and most probably
consist of only one or two fibres (Pl. 13:3, 4, 6). Only the
fringes dorsal to the lateral spines of segments seven to nine
are like those of *S. anulata* (Pl. 13:4, 5; Fig. 13A, B).

Functional morphology and ecology

Articulation

Numerous specimens look as if preserved in their original
life-positions. This aids in reconstructing the mode of artic-
ulation and degree of flexure, as presented in Fig. 14 (com-
pare with Pls. 1 and 2). Each figured position has been
redrawn from one or two actual individuals and completed
where necessary. The high flexibility of *Skara* may be com-
pared to small extant Crustacea with a worm-like trunk such
as Mystacocarida, harpacticoid Copepoda, Bathynellacea,
Thermosbaenacea or Cephalocarida where the long trunk
helps in locomotion within the interstitium, on or near to the
bottom.

Pliable arthrodial membranes connected the successive
trunk segments in *Skara* and facilitated a wide up and down
curvature of the trunk. However, dicondylic pivot joints
(term used by Manton 1977:41) between the segments limit-
ed sideways movement like wriggling, the type of locomo-
tion, e.g., of the Recent harpacticoid copepod *Evansula incerta*
Scott (cf. Kästner 1967:992) (Pl. 12:1; Pl. 13:1; Fig. 15). The
deeply recessed membranous ventral area of the anterior
trunk segments permitted a stronger ventral flexure of this
trunk portion than of the caudal one. Furthermore, it pro-
vided space for the posterior limbs (see also Pls. 1, 2; Fig.
11). On the other hand, the caudal trunk portion was re-
duced in its ventral flexure by the extended ventrocaudal
rims of segments seven to eleven.

Joints with only one medial attachment point were devel-
oped at the proximal podomeres of the furca. This limited
gaping but permitted wide bending in all other directions
(Pl. 14). The distal furcal podomeres and the segments of
the endopods had only faint joints in *S. anulata* and most
probably could not be moved separately. Hinge joints could
not be observed.

The presumed major movements of all postantennular
limbs are indicated by arrows in Fig. 15. The appendages
did not originate from distinct articulations and were almost
ventrally orientated (Pl. 3:5; Pl. 9:1). The proximal antennu-
lar joints were semicircles which alternated on median and
lateral surfaces (Pl. 7:1). Thus, the major direction of the
movement was forward-outward–backward-inward. Scales,
thick folds, and well sclerotized coxae and basipods prob-
ably limited the dorsolateral flexure of the antennal and
mandibular protopods. In order to attain more efficiency for
the propulsive backstroke, the exopods project somewhat
laterally from the sloping basipodal surface (Pl. 3:2; Pl. 7:2).
They taper to the distal end, being composed of ring-shaped
podomeres. Because the ringlets are connected by distinct
joints, the exopods could have been twisted to some extent
(Pl. 9:3).

The postmandibular protopods have flexible shafts with
thick folds laterally and numerous finer folds anteriorly and
posteriorly. Most probably they were able to rotate around
the axis to a certain extent. As the distal portion of the coxa
is pliable and may function as a joint, the entire distal
portion of the limb could be bent further posteriorly. The
exopod is slightly laterally orientated because of the sloping
lateral surface of the triangular outer portion of the basipod
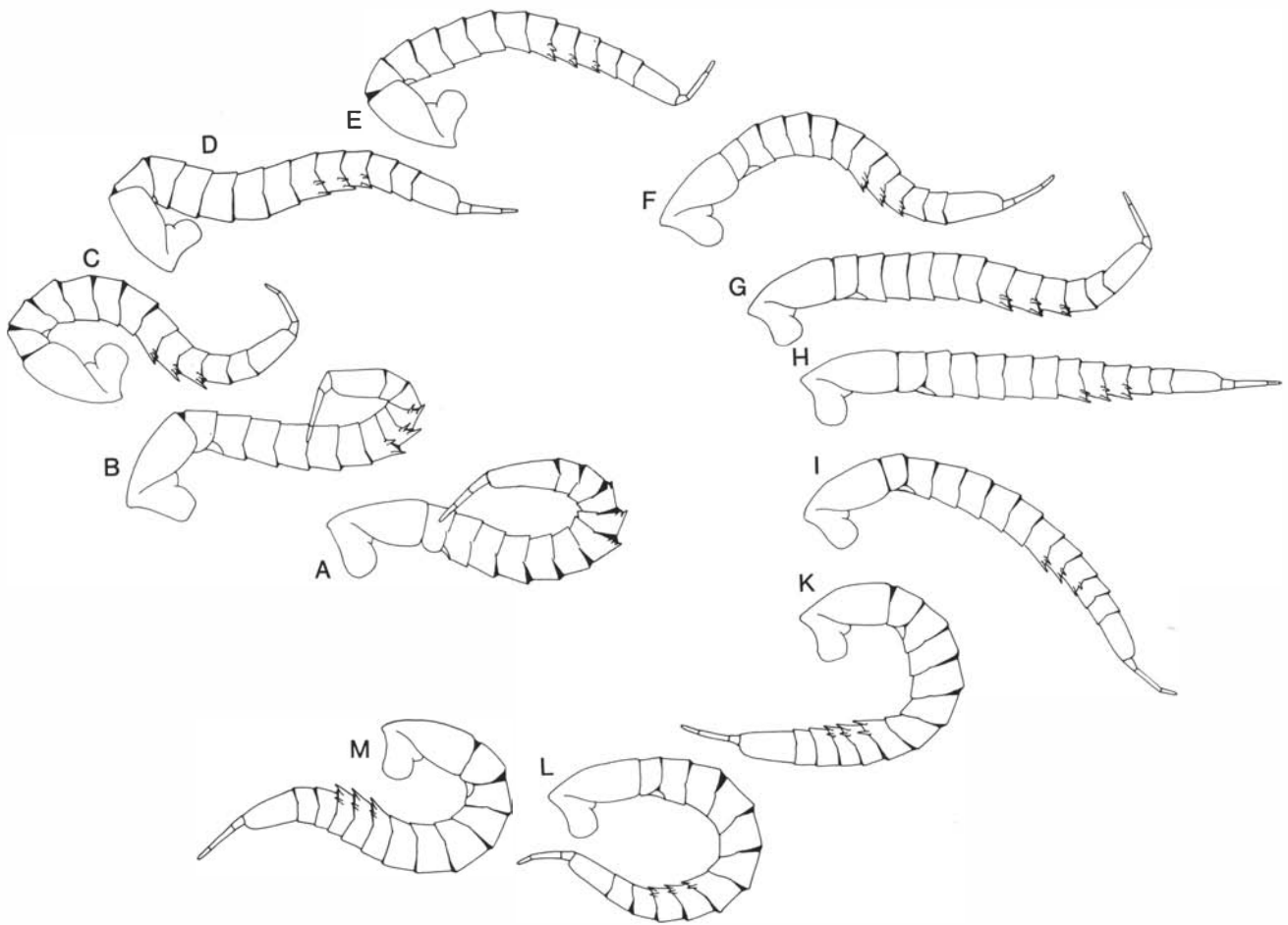on which it inserts (more pronounced in *S. anulata*) (Pl. 8; Pl.

Fig. 14. Reconstructions to show the flexibility of *Skara;* each figure based mainly on one or two specimens: □ A. UB 703. □ B. UB 716, 730. □ C. UB 734, 740. □ D. UB 737, 739. □ E. UB 691, 697. □ F. UB 744, □ G. UB 745. □ H. UB 693, 709. □ I. 715, 746. □ K. UB 704, 741. □ L. UB 646. □ M. UB 707.

10:5). The joint between basipod and exopod is well developed and permitted a slight to and fro bending of the ramus (Pl. 7:4). Separate movements of the endopodal podomeres were limited because of their faint joints. The enditic processes could only be moved together with the whole limb from which they arise.

Highly specialized joints (often with sensory bristles to recognize the actual position of each segment) as in modern Crustacea are not developed in *Skara*. This may be interpreted as a feature indicating the low evolutionary level of this Cambrian fossil. But it can also be related to the soft integument and minute size. In various small and soft-integumented Recent crustaceans, joints are only faintly developed and mainly turgor pressure keeps body and appendages inflated.

Much work has been done by various authors in respect to functional and evolutionary aspects of ex- and intrinsic musculature (e.g. Hessler 1964; Manton 1977). In *Skara*, numerous muscle scars can be observed on various body parts, indicating a large series of muscles. However, no internal structures are preserved in the material of *Skara*, and it would be but speculative to reconstruct or even interpret internal features merely on the basis of muscle scars.

Locomotion

The rather short antennulae may have had sensory function, but special structures for that purpose have not been recognized. All postantennular limbs lack specialized structures for crawling or walking. The strong setose exopods of the prominent antennae and mandibulae indicate that *Skara* most probably was able to swim, using these appendages as major force-generating elements. Also the postmandibular limbs with their flattened exopods may have supported swimming. The activity of all appendages may have resulted in a pulsating swimming mode, comparable to small extant Crustacea or their larvae.

The beating cycle of antennae and mandibulae may have started with a far anterior stretching of these limbs (Pl. 5:4). On the propulsive backstroke, all setae pointed posteriorly, almost perpendicularly spreading out from the exopods to provide resistance to the water (Pl. 1:5). On the relaxed forward stroke, the exopods were twisted towards the distal end and the setae were folded against the axis of the exopod to minimize the drag.

The postmandibular limbs may have undergone a similar beating cycle. But facilitated by their pliable shafts, the protopods may have enlarged the angle of swing by additional rotary movements. Again, the joint between basipod and exopod permitted a further backwards clapping of the

exopod at the end of each backward stroke. As on natatory setae of Recent Crustacea, the exopodal setae, at least in *S. minuta,* were distally adorned with rows of setulae which enlarged the surface of the exopod (Pl. 15:2). Swift, undulating up and down movements of the flexible tail possibly stabilized the body during swimming. This may have been supported by beats of the setose furca, especially when escaping, as is reported from Mystacocarida (Lombardi & Ruppert 1982).

Recent Crustacea are highly adapted to various swimming strategies and often have torpedo- or drop-like bodies. The appendages have undergone numerous specializations for that purpose. In respect of this, especially the long, rigid setae of the antennal and mandibular exopods of *Skara* suggest that this crustacean was not a very elegant swimmer.

Fig. 15. Scheme of the cephalo-maxillipedal filter apparatus of *Skara* (features of both species mixed); appendages drawn only with their coxae or protopods; dotted arrow = water current; short, thick arrows = food transport towards the mouth below the labrum; thin arrows above each limb = possible range of movement.

Cleaning and protective structures

Skara had comb-like fringes at the ventrocaudal rims of almost all trunk segments. These may have prevented the pliable arthrodial membranes from contamination with mud particles, especially when the trunk was flexed. The combs of segments seven to nine in addition with the groups of pilose spines may have also aided in cleaning the appendages, in particular their long distal setae. This assumption is based on the observation that several specimens are preserved with their trunk curved far ventrally while the limbs approach the trunk close to the spines (Pl. 17:6). The high flexibility of the trunk combined with only one pair of trunk limbs could have facilitated such a mechanism.

When *Skara* cleaned its limbs and hairs, it first may have bent its trunk ventrally to approach the cephalon. Next, the setae or the entire limbs were placed between the spines of segments seven to nine. By stretching the body, the setae and/or limbs were pulled through the combs and pilose spines. Extant Crustacea with an elongated, annular trunk such as Cephalocarida and Mystacocarida have developed comparable grooming structures. But, for example, the Cephalocarida have, in contrast to *Skara,* a series of thoracic appendages. Most probably due to this, their cleaning combs are developed at the posterior end of the trunk. The cleaning mechanism also differs from that supposed for *Skara* (Sanders 1963).

Filter apparatus (mainly Pl. 11)

Function. – As shown in the scheme of Fig. 15, the postantennular appendages including the maxillipeds, form a 'cephalo-maxillipedal filter apparatus'. All protopods, endites and medial setae are orally orientated (Pl. 11:1–5). Epipods, moveable endites and a filter groove are not developed. Again, a hydraulic system of alternate suction and expulsion of water by special interlimb-chambers was not present. All limbs may have aided in locomotion as well as the production of nutrient currents. These entered mainly from behind, guided by rotary and slightly outward–inward movements of the postmandibular limbs (thick, dotted arrow in Fig. 15). As the water was expelled through the inter-limb spaces, particles were trapped by the anteriorly directed setae at the filtratory endites of maxilles and maxillipeds. Subsequent water threw off particles from the setae and transported them towards the mouth (small, black arrows). The posteriorly directed labrum flanked by the setose antennal endites stopped the forward flow (Pl. 11:2, 4). From the sides, the mandibular coxal endites (grinding plates or spines) pushed the food into the mouth (Pl. 11:3). Setulae covered the surface around the mouth and guided the nutrients (Pl. 6; Fig. 15). Special aids for grasping or biting food are not developed, and it seems evident that *Skara* was mainly filter-feeding.
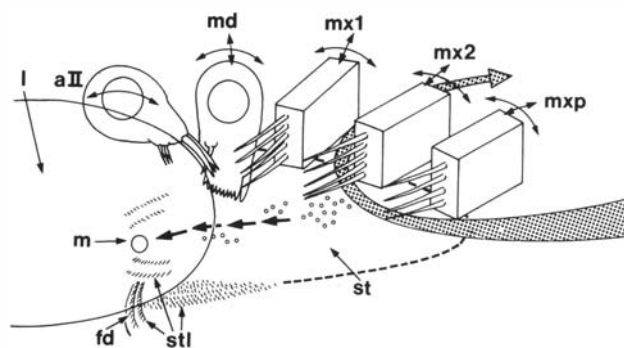
Comparisons. – The reconstructions of the filter apparatuses of *Skara anulata* and *S. minuta* (Figs. 16A and 16B) demonstrate the differences in size and detail. First, the mandibular coxa bears two thick, pilose masticatory spines in *S. anulata* (Pl. 7:7; Pl. 11:2, 3) whereas *S. minuta* has a plate-like gnathobase with setulae on its distal surface (Pl. 6:6; Pl. 11:4, 5). The shape of the sternum is different, too. In *S. anulata* it is deeply recessed towards the mouth, almost plain in the mid-line, almost undivided, and tapering markedly behind the mandibulae (Pl. 6:1–3). In *S. minuta* the sternum is only slightly recessed towards the mouth, the sternites are well separated, each being slightly elevated and medially depressed. The whole sternum tapers gently posteriorly (Pl. 6:5, 6).

In *S. minuta* there are many more setae on the endites and endopodal podomeres than in *S. anulata* (see also Table 3). On the postmandibular protopods, in *S. minuta* the anterior setae of all endites are soft and orally curved. Most probably all of them are adorned with a single row of setulae on their posterior surface. They form a close sieve by being stacked one above the other. The endopodal setae are also rather soft and are curved towards the sternum. Subordinate setulae are more or less randomly distributed on the setae (Pl. 10:2–4; Pl. 11:5; Fig. 16B). The coxal endites of the postmandibular limbs are, in contrast to *S. anulata,* covered by numerous projecting setulae. They are slightly flattened and postero-medially produced into a strong, major spine (Pl. 15:7).

On the other hand, only in *S. anulata* are the endopods furnished with tiny bristles at the anterior and posterior surfaces. In this species, the enditic setae are widely spaced and in most cases stronger and longer than in *S. minuta.* The endopodal setae are somewhat distally curved having rows
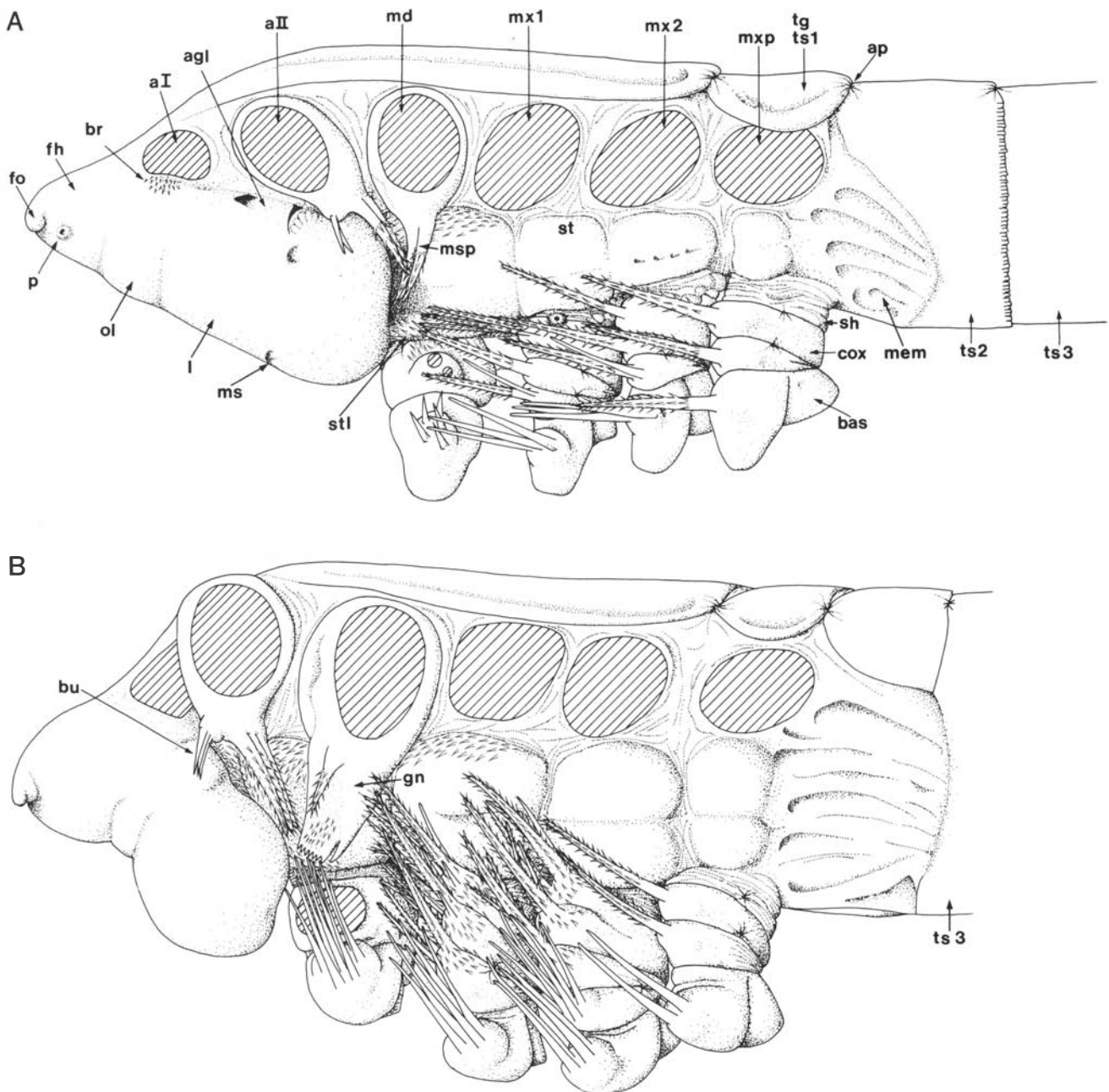
Fig. 16. Reconstruction of the filter apparatus of (A) *Skara anulata* and (B) *Skara minuta*; outlines redrawn from UB 709 (Pl. 2: 12); antennulae and left postantennular appendages except antennal and mandibular coxae omitted; right limbs drawn with their protopods; armature of right mandibular coxa omitted.

of setulae on their surface (Pl. 11:1, 2; Pl. 15:3–5; Fig. 16A; compare Figs. 4 and 7). The rigid setae may have functioned only as rather coarse sieves. Probably they could also push food towards the mouth. This leads to the conclusion that *S. anulata* selected much larger food particles than the smaller *S. minuta*.

Lithological aspects and associated faunal elements

Information for reconstructing the mode of life of a fossil organism can be obtained from functional interpretations of the grosser morphology, as described above, from the lithology, and from the associated fauna in the rock.

Lithology. – The Upper Cambrian alum shale is a very fine-grained mud with a considerable amount of organic matter. The *orsten* nodules and bands were formed by replacement of the pore water with calcium carbonate which was supplied from the adjacent shales and prevented the compaction of fossils almost entirely. The high degree of compaction found in the surrounding shales shows that the sediment must have been rather soft. Trilobite exuviae occur commonly unsorted, and also conodont clusters have been preserved in their original context in various localities (Müller & Andres 1976). This gives reason to assume stillwater conditions near the sea floor at the time of embedding, excluding the tidal zone as an environment for *Skara*.

Fossils. – The vast majority of fossils in the limestone luma-chelle are disjunctive exuviae of agnostid and/or olenid trilo-bites. Complete specimens are uncommon. These forms seem to be rarer in the dense, mostly fine-grained and more anthraconitic variety of the *orsten* which contains more bitu-men. However, the abundance may be biassed by preferring the lumachelle type of rock during sampling. Purer lime-stone yields less bulky residues after etching and sieving and therefore is easier to process. Besides trilobites, other major components are conodonts which in some cases are rather large and thickly phosphatic, and phosphatocopid Ostra-coda. In relation to these common forms, *Skara* is rare within the etched residues. On the other hand, it is still more abundant than other associated *orsten* arthropods (Müller 1983).

Several samples in which *Skara* occurs also contain various larval stages. The majority of them are nauplius larvae with three pairs of hook-like structures on their dorsal surface which seem to correspond to the limbs (K. J. Müller 1981; Walossek 1983). However, the assignment of early larvae to larger growth stages is difficult even in Recent material, and detailed studies have not yet been finished (Müller & Walos-sek, in preparation). To date no apparent infaunal elements have been etched from the euxinic, pyritic rock. Again, apart from a few lingulid brachiopods, no sessile organisms have been identified. No molluscs have been found. Some phos-phatic miscellaneous microfossils have still not been exam-ined in detail.

Size and maturity

The largest specimens of *S. anulata* are about 1.5 mm long, and *S. minuta* is even smaller (see Tables 1 and 2). On the other hand, Müller (1983) concluded that the material he used for the description of *Skara* consisted of adults only. This can be corroborated by the present study which is based on more than 120 specimens. Apart from the fact that numerous extant Crustacea are of a similar size (some exam-ples are listed in Table 4), evidence has been derived from several aspects:

☐ both species have the same gross morphology and the same level of development

☐ all recognizable morphological structures, especially all appendages including the maxillipeds, are well developed

☐ the cephalic filter apparatus includes well developed max-illipeds

☐ rudimentary organs have not been observed

☐ extant crustacean larval stages with a comparable number of segments all have vestigial appendages, at least the most caudal ones

☐ *Skara* has a tagmosis similar to adult Maxillopoda: a cephalon with five pairs of appendages, a trunk with 11 segments (the first one with maxillipeds), and a telson with segmented furca

Table 4. Examples of Recent crustacean groups with small-sized adults (approximate values in millimetres, from various authors).

Cephalocarida	2.4–3.5	Copepoda	0.3–17
Branchiura	0.5–30	Mystacocarida	0.5–1
Cladocera	0.2–18	Cirripedia	0.2–>50
Anaspidacea	2–50	Ostracoda	0.1–30
Bathynellacea	0.5–5.4	Thermosbaenacea	1.5–4
Cumacea	0.5–4		

☐ neither smaller nor larger elements have been found in the *orsten* which show any resemblance to *Skara*

☐ it seems unlikely that two forms with a length difference of about 50 % but the same basic design represent subsequent growth stages.

Phylogenetic significance and systematic position

Implications of the morphology

Head. – The soft and smooth head shield of *Skara* simply consists of the fused tergites of the limb-bearing cephalic segments. Its sides do not overlap the body ventrally. Anter-iorly, the projecting forehead is not separated from the shield by a distinct furrow. Again, posteriorly the shield neither overlaps the trunk nor is fused with any of the adjacent trunk segments. Thus it represents a simple head shield but not a carapace (definitions, cf. Kästner 1967:885–886). The Cephalocarida have a simple head shield too, but it pro-trudes markedly over the body (Sanders 1963). *Skara* has a true head which comprises only the five limb-bearing seg-ments (preantennal segments not counted). Within the ex-tant Crustacea, only some basic groups such as Mystacocar-ida, Cephalocarida, Notostraca, Anostraca, Phyllocarida, and Bathynellacea share this feature; all other groups in-clude at least one more trunk segment in a 'cephalothorax' (Kästner 1967:882–885).

Appendages. – One interesting and controversial feature can-not at present be clarified sufficiently, *viz* the segmentation of the limb base. All postantennular limbs provide a soft shaft which is distinct from the succeeding, well sclerotized distal portion. The basiopod is well defined by carrying the two rami. Consequently, the portion proximal to it must be regarded as the coxa having one or more endites medially. The outer surface of the shaft is covered by a scale and folds on antennae and mandibulae but thick folds on all postman-dibular limbs (Figs. 4, 5, 7). Thus, the shaft may represent a distinct portion, the precoxa. Several authors argue against the recognition of a precoxa. Some even refuse an original division of the protopod assuming that the cephalocaridean mixopodial limb and its undivided protopod represent the central focus from which all other forms have been derived (e.g., Hessler & Newman 1975; Kästner 1967:887; Lauter-bach 1973, 1974, 1980, 1983; Sanders 1963). Other authors,

however, argue in favour of a precoxa (e.g. Hartmann 1966; see also Figs. 661 and 672 in Kästner 1967). Schulz (1976), basing on his studies on platycopid Ostracoda, gives strong evidence for the recognition of this portion.

Trunk. – The tagmosis of the trunk may be interpreted in different ways:

□ the trunk is one unit, composed of 11 metameres plus telson

□ the trunk is subdivided into one thoracic segment having a pair of limbs, and an abdominal portion with 10 ring-shaped segments plus telson and furca

□ the trunk is subdivided behind segment six into a thorax with six segments (the most anterior with a pair of limbs), and an abdomen with five segments plus telson and furca

The facts that segments seven to eleven have slightly extended ventrocaudal rims and additionally segments seven to nine bear tooth-like spines at the same rims may corroborate a division into thorax and abdomen. However, as there are no other features to support this interpretation, we prefer herein to consider the trunk as simply one unit.

The exceptionally long caudal trunk segment terminates in segmented furcal rami and a dorsocaudal anus. Bowman (1971) regards a furca dorsal of the anus as not homologous to one on the ventral surface of the last body segment. This author proposes to term the former 'telson' and the latter 'uropods'. But as there are several inconsistencies in his examples and conclusions (see also Schminke 1976), we did not adopt his terms, in accordance with Kornicker (1975), Marcotte (1982) and McLaughlin (1980).

The telson is not a true somite (Kästner 1967:885); however, the major features for its recognition are internal structures, such as the presence of coelom and ganglia. These are not preserved in our material. If the telsonic segment is regarded as trunk segment, *Skara* would then comprise 12 instead of 11 trunk segments. At present, this important question cannot be definitely clarified for *Skara*. We prefer to regard the last body segment as a telson, although accepting that other interpretations may be possible.

Further observations. – Crustacea retained only two of the ancestral segmental excretory organs: the 'antennal gland' which opens at the antennal base, and the 'maxillary gland' at the maxilla. The shape varies among the different taxa. Often only one of the types is developed. Larvae may comprise another type distinct from the adults (Kästner 1967:900). In *Skara* only the antennal gland with its triangular exit at the antennal base could be identified. Pores at or close to the maxillae are absent, suggesting that the maxillary excretory pore has been reduced.

On the maxillula a small circular pore is positioned posteromedially at the border between shaft and coxa (Pl. 8:5; Pl. 17:5). In an earlier stage of the examination it was assumed that this pore represents the exit of the maxillary segmental organ which, according to this interpretation, must have shifted to the maxillula. However, and more reasonably, this pore may simply represent the opening of a salivary gland,

as is developed in various Crustacea (Hartmann, personal communication).

Gonopores or structures aiding in copulation have not been identified. Extant Crustacea, however, generally have well defined gonopores on the ventral trunk surface which are mostly paired. Although constant within systematic units, the position of the gonopores varies among Crustacea, and even sexual dimorphism occurs (cf. Kästner 1967:907). Furthermore, to date little or no information can be obtained from other fossil Crustacea, especially from Paleozoic ones. Thus it is difficult to reconstruct the primordial position and, based on it, to search successfully for such structures on new forms like *Skara*. As the examined specimens are adults, it is assumed that the lack of gonopores may be simply correlated with the minute size and soft cuticle. As supposed for Mystacocarida (Dahl, personal communication), sexual products might have been released in combination with an ecdysis at the stage of maturity.

Special respiratory organs are absent in *Skara*. But this may simply be due to its small size. Numerous small-sized extant Crustacea lack external respiratory structures, even when living in an environment with little oxygen such as in the interstitium. They mainly use the whole body wall for respiration.

Mode of life and feeding. – The shape of the appendages points to a swimming mode of life for *Skara* rather than crawling or burrowing. On the other hand, protective and cleaning fringes on the ventral trunk surface indicate that *Skara* lived in a zone near the bottom which was rich in suspended particles. Again, the lack of eye structures and the worm-like, slender trunk which is similar to various extant benthic, bottom-dwelling or infaunal Crustacea such as harpacticoid Copepoda (Kunz 1974; Swedmark 1964; Marcotte 1982), Thermosbaenacea (Moore & McCormick 1969), Amphipoda (Dahl 1977) or Mystacocarida (Dahl 1952), suggests that *Skara* lived near the bottom or on it rather than in the plankton (cf. also Kästner 1967:895).

The development of a 'cephalo-maxillipedal' filter apparatus and the lack of grasping or biting structures show clearly that *Skara* was a typical filter-feeder, with preference for small-sized food, e.g. detrital particles or bacterial films. From the lithology it is concluded that the environment was rich in organic matter (confirming the assumption above). This must have been very attractive to filter feeders, as various other *orsten* forms, including the phosphatocopid Ostracoda, were also provided with a well developed filter apparatus (McKenzie, Müller & Gramm 1983; Müller 1979, 1982, 1983).

Affinities to other ORSTEN Crustacea

Müller (1983) described five other monotypic genera with well defined morphological features distinct from *Skara*. *Rehbachiella kinnekullensis* Müller, 1983, and *Walossekia quinquespinosa* Müller, 1983, have a large head shield (carapace?), eyes, and a filter apparatus which includes a series of thoracic appendages. *Bredocaris admirabilis* Müller, 1983, also has a thoracic filter apparatus, a prominent shield and eyes. But this form, as well as *Dala peilertae* Müller, 1983, are from the

Upper Cambrian zones 5/6 and do not occur together with *Skara.*

The phosphatocopid Ostracoda can be easily distinguished from *Skara* by their large, bivalved carapace which covers the whole body. Additionally, the Hesslandonina Müller, 1982, have a median eye, tiny antennulae, a large, uniform mandibular protopod with a strong, protruding gnathobase, and a series of postmandibular limbs with flattened, plumose exopods (Müller 1979, 1982b; see also McKenzie, Müller & Gramm 1983). The Vestrogothiina Müller, 1982, were not associated with *Skara.*

Besides *Skara,* only the poorly preserved single specimen of *Oelandocaris oelandica* Müller, 1983, from the *Olenus* Zone (zone 2) has a true head tagma. But the shield which overtops the five limb-bearing head segments is frontally extended in a rostrum projecting from the shield. Furthermore, *Oelandocaris* bears eyes, a not-protruding labrum, and trunk tergites with spinose margins.

Characters so far found exclusively in *Skara* are: the projecting forehead with a frontal organ but absence of eyes; the small dorsal shield which lacks an anterior margin; only six pairs of limbs; two pairs of maxillae and one pair of maxillipeds of the same plan; the long, annulate trunk with lateral attachment points; the large telson and tri-segmented tubular furcal rami.

On the other hand, several morphological structures, mainly on the anterior cephalic portion are apparently similar between *Skara* and the other *orsten* Crustacea: the rod-shaped antennula with rather low number of podomeres; the prominent labrum; antennae and mandibulae of the same plan having large, annulate exopods which served as major force-generators during swimming. However, these features may simply represent shared plesiomorphies (the naupliar head). To sum up, it is reasonable to assume that the other described *Orsten* Crustacea can be ruled out from being closely allied to *Skara.*

Affinities to other fossil Arthropoda

To date, no fossil arthropods have been described which share any morphological details with *Skara* that might indicate closer relationships (cf. Bergström 1979, 1980; Briggs 1983; Rolfe 1969; Schram 1982; Ulrich & Bassler 1931; Whittington 1979). In particular those forms from the Middle Cambrian Burgess Shale which are described as Crustacea (mainly Phyllocarida) were much larger than all *orsten* crustaceans, lived in a different environment, and comprise a completely distinct gross morphology. Other arthropods, the probable Phyllocarida *Caryocaris stewarti* Jell, 1980, and *Corcorania trispinosa* Jell, 1980, from the Early Ordovician of Australia, have prominent head shields (carapaces?) and are much larger than *Skara.* The Middle Devonian *Lepidocaris rhyniensis* Scourfield, 1926, has proved to be closely related to Anostraca (Tasch 1969). It has compound eyes, three distinct tagmata, specialized cephalic and a series of thoracic limbs. These features are very dissimilar to those of *Skara.*

Affinities to Recent Crustacea and systematic position of SKARA

Position. – One barrier for finding relationships between *Skara* and extant Crustacea is the small amount of information about other well-preserved Paleozoic forms and the lack of fossil links. Another is the absence of a widely accepted theory of the phylogeny of Arthropoda which leads to a clear definition of the taxon Crustacea on the basis of true autapomorphies (cf. Weygoldt 1980 for discussion of this problem). It is not the scope of the present paper to enter this discussion, but recently affinities of *orsten* forms to Crustacea have been questioned (Lauterbach 1983).

Skara as a crustacean. – *Skara* without doubt proves to be a true crustacean. It has a distinct head tagma with a small dorsal shield and a large, moveable labrum. The five pairs of limbs are differentiated into the three pairs of naupliar limbs (uniramous antennulae, biramous antennae and mandibulae of the same plan) and two pairs of maxilles. The first segment of the 11-segmented trunk bears one pair of maxillipeds which has the same shape as the two maxilles. The long telson terminates in segmented furcal rami. From the two excretory organs, the 'antennal gland' is present with an opening at the base of the antenna. Some of these features are accepted by Lauterbach (1983) as typical characters of the Crustacea.

The unique structures mentioned above separate *Skara* from all Recent crustacean taxa too. As a unit, they preclude the placement of *Skara* into any hitherto described crustacean group. Taken alone, the lack of a carapace and eyes contributes little information for a systematic approach, as totally different forms such as Cephalocarida on one hand and Copepoda and Mystacocarida on the other also lack these structures. Furthermore, such characters may be easily lost during evolution (for 'regressive evolution' cf. Kosswig 1963). Conversely, lost features may be useful indicators for relationships at lower taxonomic levels when combined with other diagnostic characters. Paired or single frontoterminal processes or organs, though probably derived from different structures and with different functions, are widely distributed among Crustacea (Andersson 1977, 1979; Eberhardt 1981; Elofsson 1966; Kauri 1966). It is possible that the 'frontal organ' of *Skara* constitutes the primordial type of a frontal receptor organ postulated by Kästner (1967:895) and would give further evidence for the placement within the Crustacea.

The entire anterior cephalic portion of *Skara* seems to reveal striking similarities not only to Recent filter-feeding crustacean larvae of different taxonomic units, but also to those forms which retained these larval features into adulthood, such as Copepoda, Mystacocarida or Cephalocarida.

Cephalocarida. – Metanauplial stages of Cephalocarida having a similar size show striking similarities to *Skara,* especially in details of the anterior appendages, for example the antennal exopod with 14 ring-shaped podomeres. Even the maxillulae can be derived from the plan of *Skara:* the coxa has lost two endites; the remaining one has been elongated; and the basipod has lost its subdivision (compare Fig. 4D–F and Sanders 1963, Fig. 36). During ontogeny, however, the differences become obvious: in the Cephalocarida the shape

of limbs changes significantly: segments are added; rami become reduced; endites are elongated; the thoracopods gain epipods; and the trunk metameres develop tergitic pleurae. Again,the postcephalic protopod of the Cephalocarida is, in contrast to *Skara*, always uniform.

Furthermore, Cephalocarida have cleaning combs at the posterior end of the trunk from the first larval stage to adulthood, have more trunk segments, a large head shield, and an apodous abdomen with a telson terminating in unsegmented furcal rami (Hessler 1964; Hessler & Sanders 1971; Knox & Fenwick 1977; Sanders 1963; Sanders & Hessler 1964). Accordingly, the Cephalocarida cannot be regarded as closely related to *Skara*. The majority of similarities between the two forms prove to be superficial and are simple plesiomorphies.

Other crustacean groups. – Dahl (1956) stressed that the feeding mechanism may have been a promoting selective factor in the evolution of Crustacea. Taking this into account, there are no stronger affinities between *Skara* and all groups using a thoracic filter apparatus with a series of thoracic filter limbs as the only feeding mechanism. Furthermore, groups with epipods as well as those with abdominal appendages can be excluded. These are the Anostraca, Phyllopoda, and all Malacostraca. The latter group, in particular, comprises an entirely different design. The basic plan comprises a true carapace, compound eyes, thoracic and abdominal limbs, epipods, and a segmentation of the postcephalon with 8 + 5(6) metameres (Brooks *et al.* 1969).

Maxillopoda. – Affinities are more likely with those Crustacea that retained the cephalic filter apparatus, as among the Maxillopoda (sensu Dahl 1956). Again, the lack of epipods in all members of this super-group may be a useful indicator for relationships to *Skara*. The development of a pair of maxillipeds on a free trunk segment in *Skara* may also confirm affinities.

Skara has 11 trunk somites plus telson. The parasites *Basipodella* and *Deothertron* were originally assigned to Copepoda or Cirripedia (Becker 1975; Bradford & Hewitt 1980; Boxshall 1983), but recently Boxshall & Lincoln (1983) included both in a new separate class, the Tantulocarida, based on the recognition of one more abdominal segment (they regard the Crustacea as sub-phylum and not as class). Thus, now this group has the same number of trunk metameres as *Skara*, i.e. 11. If *Skara* and Tantulocarida prove to be (or remain) closely allied to Maxillopoda, 11 segments may represent the basic number for the maxillopodan ancestor rather than ten. Differences in one or two somites more or less can also be found in other groups of Crustacea such as Branchiopoda and Malacostraca.

The validity of the taxon Maxillopoda as a super-group including the Mystacocarida, Copepoda, Ascothoracida, Branchiura, and Cirripedia has been questioned, as synapomorphies could not be defined sufficiently as yet (e.g. Boxshall 1983; Boxshall & Lincoln 1983; Hessler *et al.* 1982). Other authors argue in favour of this term from different aspects (e.g. Bowman & Abele 1982; Grygier 1983; Hessler & Newman 1975; Newman 1983; Siewing 1960). One argument supporting the validity may be the 'organ of Bellonci'. This complex sensory head organ is similarly developed in

the Mystacocarida, Copepoda and Cirripedia but differently in the Malacostraca (Andersson 1977, 1979). Grygier (1983) tentatively includes the Ostracoda, as was already suggested by Dahl (1956). Andersson (1977, 1979), Elofsson (1966) and Siewing (1960) also give support for this assignment. Schulz (1976) recognized in the Platycopa (Podocopa, Ostracoda) ten postcephalic metameres plus telson and furca. He stresses that their endoskeleton shares more than superficial similarities to the Maxillopoda.

The Mystacocarida have been regarded as the most primitive group within the Maxillopoda (Dahl 1956) because they show great morphological conservatism (Hessler 1971; Hessler & Sanders 1966). The major features shared with *Skara* are: the small cephalic shield (apart from the anterior portion) which is not fused with thoracic segments; the absence of eyes; five pairs of rather unspecialized cephalic limbs and a single pair of maxillipeds on the free first trunk segment (even number of podomeres and setation); the cephalic filter apparatus in its general architecture. The trunk of the Mystacocarida is annular too, but has 6 + 4 metameres + telson, i.e. one segment less than in *Skara*. The anterior portion of *Derocheilocaris galvarini* Dahl, 1952, about 0.5 mm long in the adult, looks similar to *Skara*, especially when comparing the large labrum as well as antennae and mandibulae. However, this may be simply plesiomorphic due to its larval origin (naupliar head).

On the other hand, several structures of the Mystacocarida have undergone changes due to an adaptation to a crawling life within the interstitium. Thus they may appear more different to *Skara* than they actually are: the long antennulae with a strut at their base; the lack of exopods on the maxilles and maxillipeds (reduction of the natatory parts); the four pairs of lobate rudimentary thoracopods; and the claw-like furca (Dahl 1952, 1956).

The Copepoda are regarded as closely related to Mystacocarida. There are striking similarities between copepodite stages (Kästner 1967:930–931; Katona 1971) and *Skara*, but these may also be considered to be plesiomorphies. Most of the Copepoda have three distinct tagmata, but also wormlike forms can be found among the harpacticoid Copepoda (Kunz 1974; Swedmark 1964). The segmentation of the postcephalon is 6 + 4 + telson with furca. Adult filter-feeding Copepoda (Kästner 1967:994–995) have retained a cephalic filter apparatus with some similarity to *Skara* . They lack a carapace, but, in contrast to *Skara*, one or two thoracic metameres are fused with the head and form a cephalothorax which frontally terminates in a small rostrum-like protrusion or plate. Furthermore, the antennulae are very long and serve as the main locomotory organs. Again, Copepoda have a series of post-cephalothoracic limbs which are connected by intercoxal sclerites, mainly aiding in swimming (e.g. Palmer 1969).

Cirriped larvae also reveal superficial similarities to *Skara*. After metamorphosis, however, the Cirripedia change their morphology so much that it can hardly be compared to *Skara*. Cirripedia also have a series of thoracic limbs, and some forms have a carapace (Newman *et al.* 1969).

Results. – On the basis of common characters, *Skara* appears to be more closely allied to the Maxillopoda than to any other group within the Crustacea. These characters are

again: the true head with a simple head shield; the cephalic filter apparatus; the shape of the maxillipeds; the lack of epipods; and the tagmosis. Some other shared features, especially the nauplial-like anterior head region with a rather primitive design of antennae and mandibulae, may be simply plesiomorphies because they can be found in other Crustacea too (e.g. Cephalocarida).

On the other hand, the trunk of *Skara* with only one pair of maxillipeds can be easily derived from the maxillopodan plan by loss of the thoracic limbs in order to gain a long, cylindrical trunk. The maxilliped has been retained because of its function within the feeding apparatus. In conclusion, we prefer to regard the Skaracarida as a separate order within the Crustacea, but with affinities to Maxillopoda. There may be closer relationships to Mystacocarida and/or Copepoda than to any other members of the super-group. However, it seems not very likely that the Maxillopoda or representatives of the group have directly originated from the Skaracarida.

Remarks on the Remipedia. – Recently a remarkable class, the Remipedia, has been described from a cave environment. The remipedes are characterized by 31–32 serially developed trunk segments all having a pair of biramous limbs (Yager 1981). Affinities to other defined classes of Crustacea are denied, but the description and illustration still provide insufficient information for detailed comparative studies (see also Hessler *et al.* 1982; Schram 1983). In respect to the range of crustacean body plans, remipedes and skaracarids appear to represent the two opposing ends: remipedes have a large series of homonomous, pedigerous trunk segments, whereas skaracarids have only six pairs of limbs but a long, annular trunk with apodous segments.

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Plates

Plate 1

Skara anulata Müller 1983, general views. Measurements, localities, zones, and sample numbers, see Table 1.

☐ 1. ST 4115, UB 691: lateral view; cephalic shield, prominent labrum and trunk almost complete, but only the anterior three appendages with their proximal portions preserved; telson posteriorly broken off; note the tooth-like spines on ventrocaudal rims of trunk somites seven to nine (same specimen as in Pl. 4:3, 4; Pl. 14:6.)

☐ 2. ST 4068, UB 692: lateral view of the cephalic shield, large labrum and three trunk somites; laterally compressed; appendages of left side almost broken off; right antenna well preserved, its exopod with long, stiff setae; postantennal limbs of right side partly preserved (same specimen as in Pl. 4:1; Pl. 7:2, 8; Pl. 15:1.)

☐ 3. ST 2171, UB 693: ventral view of posterior end of cephalon and straight trunk; right maxilla and left maxilliped well preserved; spines on trunk somites seven to nine (trunk covered with grains of contamination; same specimen as in Pl. 8:3.)

☐ 4. ST 3023, UB 694: ventrolateral view of the right side of cephalon with partly preserved limbs and some trunk segments; coarse and partial phosphatization caused voids in the cuticle, especially on labrum and trunk where the steinkern is uncovered (same specimen as in Pl. 11:1, 2; Pl. 15:3, 4, 5; Pl. 16:2)

☐ 5. ST 3559, UB 695: ventral view of the cephalon with labrum, sternum and anterior trunk somites; right antennula entirely preserved, all other limbs only with their proximal portion; the endites point towards the mouth which is covered by the labrum (same specimen as in Pl. 6:2; Pl. 7:1, 4, 7; Pl. 11:3.)

☐ 6. ST 2853, UB 696: lateral view of the cephalic shield, labrum and six trunk somites; all appendages broken off; strong curvature of the trunk; by this, the arthrodial membranes between the trunk somites can be partly observed (same specimen as in Pl. 4:5, 7, 8.)

☐ 7. ST 3548, UB 697: lateral view of the cephalic shield, labrum and proximal parts of the anteriormost limbs; the trunk is distally poorly preserved and broken off at trunk somite nine (same specimen as in Pl. 3:1; Pl. 4:2; Pl. 15:6.)

☐ 8. ST 4005, UB 698: view of the rather incomplete and distorted specimen; cephalon posteriorly compressed; the labrum is posteriorly broken off; appendages preserved only with their proximal portions; here their cavities are, in some cases, filled with a steinkern; the trunk has lost its cuticle entirely, uncovering the steinkern (possibly of the gut; same specimen as in Pl. 6:1.)
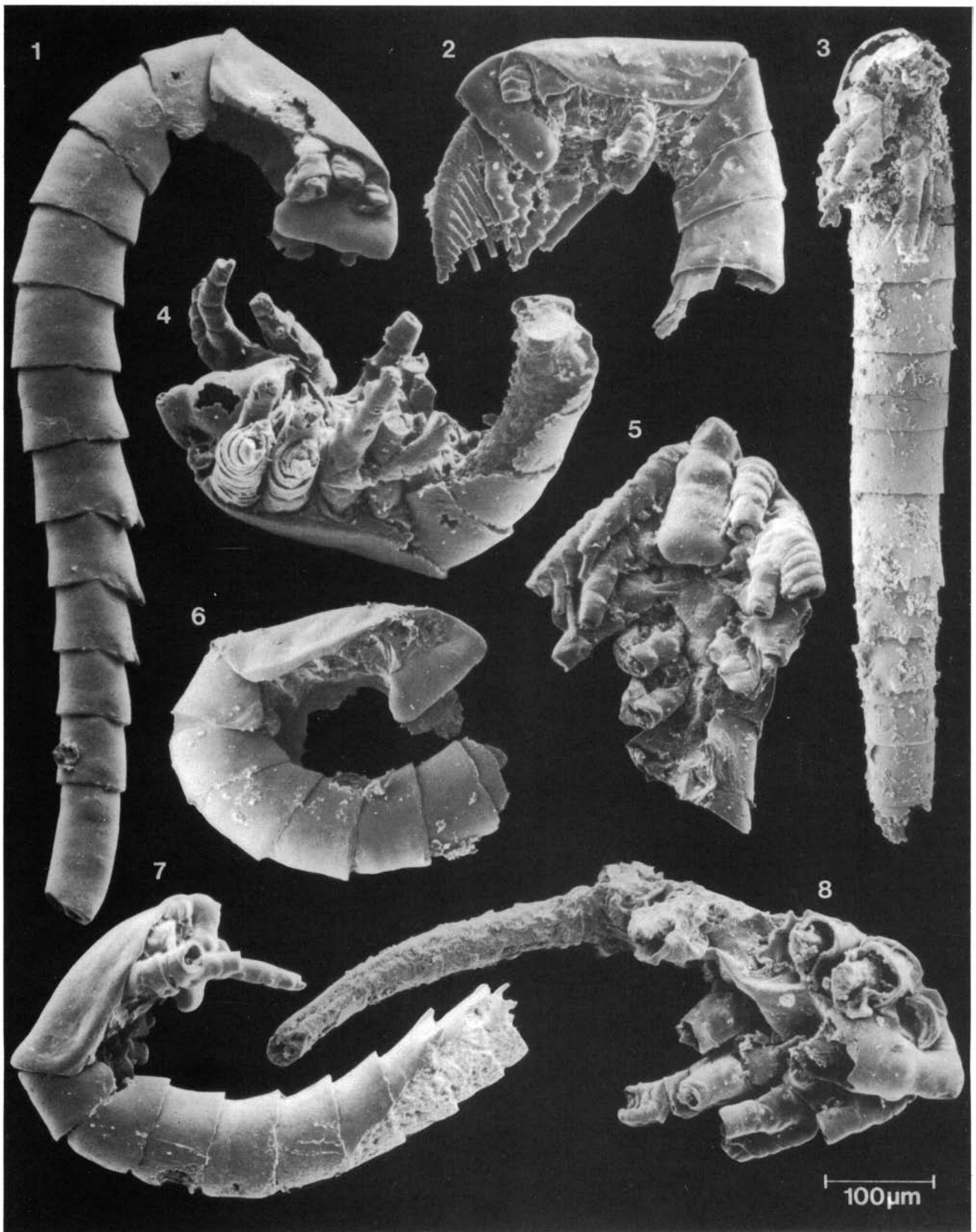
Plate 2

Skara minuta n.sp., general views. Measurements, localities, zones, and sample numbers, see Table 2.

☐ 1. T 3262, UB 699: lateral view of the cephalic shield, protruding forehead, labrum, and trunk with telson; appendages and furca absent (wrinkled areas at the side of labrum indicate their former positions); note the spines at the ventrocaudal rims of trunk somites seven to nine which are present, as in *S. anulata;* long telson (presumed female); for explanation see pp. 17–18.

☐ 2. ST 3227, UB 700: lateral view of the cephalic shield, labrum, post-antennular limbs, and trunk with telson; furca not preserved; right antenna twisted around the forehead; maxilliped disguised; trunk strongly S-curved, anterodistally poorly preserved; short telson (presumed male).

☐ 3. ST 4068, UB 701: lateral view of the almost complete specimen; anteriormost limbs are distally broken off, and the furca is not preserved; maxilliped disguised; spines on somites seven to nine distally broken off; short telson (presumed male).

☐ 4. ST 3411, UB 702: lateral view of the S-curved specimen; the distal parts of appendages and the furca are absent; right maxilliped completely preserved; short telson (presumed male; same specimen as in Pl. 9:4; Pl. 10:5.)

☐ 5. ST 3469, UB 703: lateral view of the posterior part of cephalon with some poorly preserved limbs and the strongly upward curved trunk; furca complete and touching the trunk with their long terminal setae at the level of the posterior limbs; short telson (presumed male; same specimen as in Pl. 14:3.)

☐ 6. ST 2856, UB 647: oblique-ventral view of the cephalon and most of the trunk; appendages of left side mostly distally broken and facilitating the view into the filter apparatus; telson not preserved; long form (presumed female; same specimen as in Pl. 9:1, 6; Pl. 10:4, 7; Pl. 11:4.)

☐ 7. ST 3021, UB 704: lateral view; specimen almost complete; only the posterior end of telson is broken off; cephalon slightly compressed; grains of contamination around limbs and on the trunk; anterior limbs frontally curved, postmandibular limbs backward directed, some of the distal setae preserved; sharp-edged hole in the trunk most probably caused by breakage; long telson (presumed female; same specimen as in Pl. 17:1.)

☐ 8. ST 3022, UB 705: lateral view of the cephalic shield, protruding forehead with 'frontal organ' (fo), prominent, rounded labrum with pronounced lateral bulges, and nine trunk somites; anterior limbs of left side absent; maxilla and maxilliped, however, entirely preserved with long exopodal setae as well as setulae on the enditic processes; coarse phosphatic matter coats the distal part of these appendages; limbs of the right side poorly preserved; body with L-shaped curvature; very large specimen (presumed female) cf. Table 2 (same specimen as in Pl. 3:3; Pl. 5:6; Pl. 10:6; Pl. 15:7; Pl. 16:3.)

☐ 9. ST 2482, UB 706: ventral view of the straight body slightly S-curved; anterior part of the cephalon pressed against the sternum; left antenna complete; all other appendages poorly preserved; deep furrow on trunk somites three and four caused by lateral compression; spines on somites seven to nine rather short; furca not preserved; short telson (presumed male; same specimen as in Pl. 9:3; Pl. 10:2.)

☐ 10. ST 4055, UB 707 (holotype): lateral view; specimen almost complete; cephalon and anterior part of trunk compressed; anterior four limbs partly to almost entirely preserved and far frontally directed, in this view disguising the well preserved antennulae; due to the sharp curvature of the trunk, several arthrodial membranes are visible between the trunk somites; furcal rami preserved with their proximal podomeres; short telson (presumed male; same specimen as in Pl. 5:3, 4; Pl. 9: 2; Pl. 13:7; Pl. 16:7.)

☐ 11. ST 2573, UB 708: lateral view of the enrolled specimen; all appendages visible except the antennula which is disguised behind the upward twisted antenna; antenna and mandibula wrinkled; telson posteriorly broken off; short form (presumed male; same specimen as in Pl. 13:6.)

☐ 12. ST 3074, UB 709: ventral view; body entirely stretched out; limbs except the proximal portions of antenna and mandibula poorly preserved, opening the view on the whole sternum behind the projecting labrum and the membranous area of trunk somites one and two; coxal gnathobase of the left mandibula points into the mouth; furcal rami preserved with their origins; short telson (presumed male; same specimen as in Pl. 6:5, 6; Pl. 9:5.)

Plate 3

Cephalic shield and trunk segment one.

☐ 1. *Skara anulata,* ST 3548, UB 697: dorsolateral view of the shield (cs) and anterior part of trunk (ts1–ts3); only the proximal portions of the three anterior limbs (aI, aII, md) are preserved disguising the labrum (l); shield only slightly arched; its caudal rims are widely rounded (arrow); shallow grooves on the anterior surface of the shield represent muscle scars (ms), (Same specimen as in Pl. 1:7; Pl. 4:2; Pl. 5:6.)

☐ 2. *S. minuta,* ST 4125, UB 710: similar view as in 1; the limbs are coarsely but almost entirely preserved, disguising the forehead (fh) and labrum; note that the S-curvature of the lateral rim of the shield above antennae and mandibulae as well as the caudal corner are much sharper that in *S. anulata* (arrows); tergite of trunk somite one (tg) with widely rounded posterior corner (arrow).

☐ 3. *S. minuta,* ST 3022, UB 705: dorsal view of the shield and tergite, slightly from posterior; caudal rim straight (white arrow); arthrodial membranes (am) between shield, tergite and succeeding trunk somite well visible; on the shield numerous muscle scars (ms) of limb musculature attached underneath. (Same specimen as in Pl. 2:8; Pl. 5:6; Pl. 10:6; Pl. 15:7; Pl. 16:3.)

☐ 4. *S. anulata,* ST 4155, UB 711: dorsal view of the shield; on the left side the forehead (fh) is flanked by the proximal parts of anteriormost limbs; numerous muscle scars can be seen on the shield; the shield has its maximum width at about the level of the mandibulae and tapers slightly posteriorly; caudal rim rounded (arrow). (Same specimen as in Pl. 7:6.)

☐ 5. *S. anulata,* ST 4073, UB 712: lateral view of the posterior end of shield and tergite of first trunk somite; the body wall below the posterior corners of the rims turns directly into the shafts of the adjacent appendages (arrows); the segments are laterally fixed to one another (ap).

☐ 6. *S. anulata,* ST 3027, UB 713: dorsal view of the caudal rims of shield and tergite; both with a row of fringes (fr) almost extending to the lateral attachment points. (Same specimen as in Pl. 8:2.)

☐ 7. *S. minuta,* ST 4090, UB 714: view of the shield and tergite, as in 6; in this species the rims lack fringes (arrows).
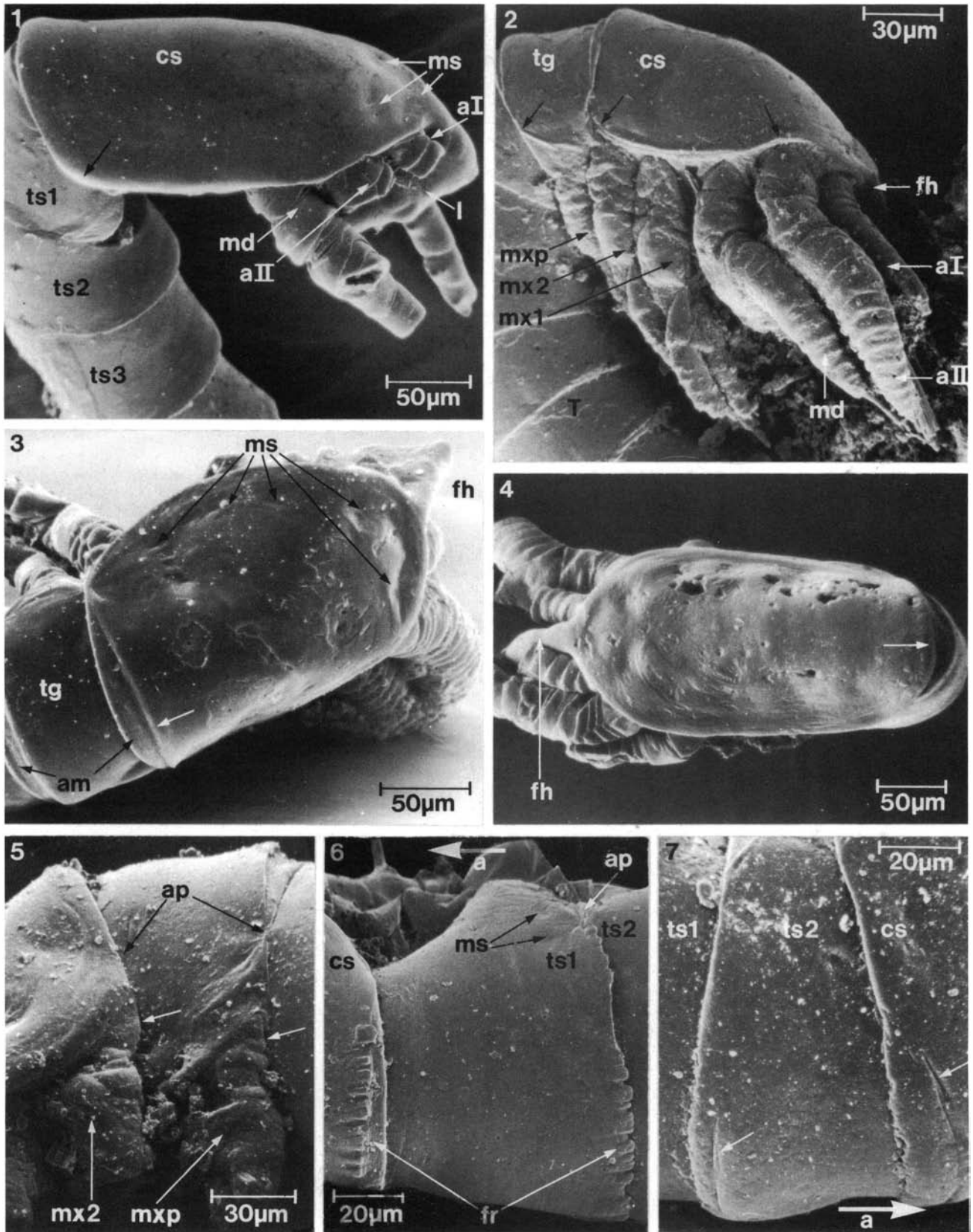
Plate 4

Forehead, labrum and antennal gland of *Skara anulata*.

☐ 1. ST 4068, UB 692: lateral view of the forehead, slightly from anterior; the original position of the frontal organ (fo) is visible as a groove at the tip of the forehead; the large, nose-shaped labrum (l) is straight and terminally rounded; its origin (ol) is slightly elevated, limited by shallow transverse furrows. (Same specimen as in Pl. 1:2; Pl. 7:2, 8; Pl. 15:1.)

☐ 2. ST 3548, UB 697: similar view as in 1, but opposite side; the frontal organ (fo) is broken off, indicated by the even, solid infilling at its original position; a small pit (p) just below the frontal organ probably represents a glandular exit; the origin of the labrum is laterally slightly bulging; a pair of muscle scars on the surface of the labrum indicates the musculature which moved the labrum. (Same specimen as in Pl. 1:7; Pl. 3:1; Pl. 15:6.)

☐ 3. ST 4115, UB 691: frontal view of the labrum which is flanked by the origins of the anteriormost appendages; the frontal organ (fo) in the upper middle is broken off; a small, artificial furrow leads to the pit below; the labrum becomes broader from its origin to the level of the muscle scars, its posterior end is broadly rounded. (Same specimen as in Pl. 4:4; Pl. 1:1; Pl. 14:6.)

☐ 4. ST 4115, UB 691: dorsal view of the anterior portion of the cephalon; the forehead (fh) is slender and protruding from the shield, being flanked by the origins of the anteriormost limbs; the rims of the shield are not fused anteriorly (arrow). (Same specimen as in Pl. 4:3; Pl. 1:1; Pl. 14:6.)

☐ 5. ST 2853, UB 696: enlarged view of the frontal organ and the pit below; in this case the organ had probably been collapsed rather than broken off. (Same specimen as in Pl. 4:7, 8; Pl. 1:6.)

☐ 6. ST 4127, UB 715: enlarged frontal view of the frontal organ and pit. (Same specimen as in 9.)

☐ 7. ST 2853, UB 696: lateral view of the labrum behind its origin (anterior direction indicated by arrow 'a'); the 'antennal gland' is positioned between folds (fd) which run anteriorly and posteriorly of the antennal origin towards the labrum (details in 8). (Same specimen as in Pl. 4:5, 8; Pl. 1:6.)

☐ 8. ST 2853, UB 696: enlarged view of 7; the triangular pore (p) of the antennal gland can be seen on the lower middle; from there, a fold reaches to the 'sickle-shaped' furrow in front of the slightly elevated region, the 'walled area' (wa) in the upper middle. (Same specimen as in Pl. 4:5, 7; Pl. 1:6.)

☐ 9. ST 4127, UB 715: similar view as in 8, but on the opposite side of the labrum; the walled area (wa) is visible in the upper middle, above the sickle-shaped furrow (deeper than in 8) the pore is disguised in a deep fold (p); the surface immediately opposite of the antennula is covered with numerous bristles of unknown function (absent in *S. minuta*). (Same specimen as in 6.)
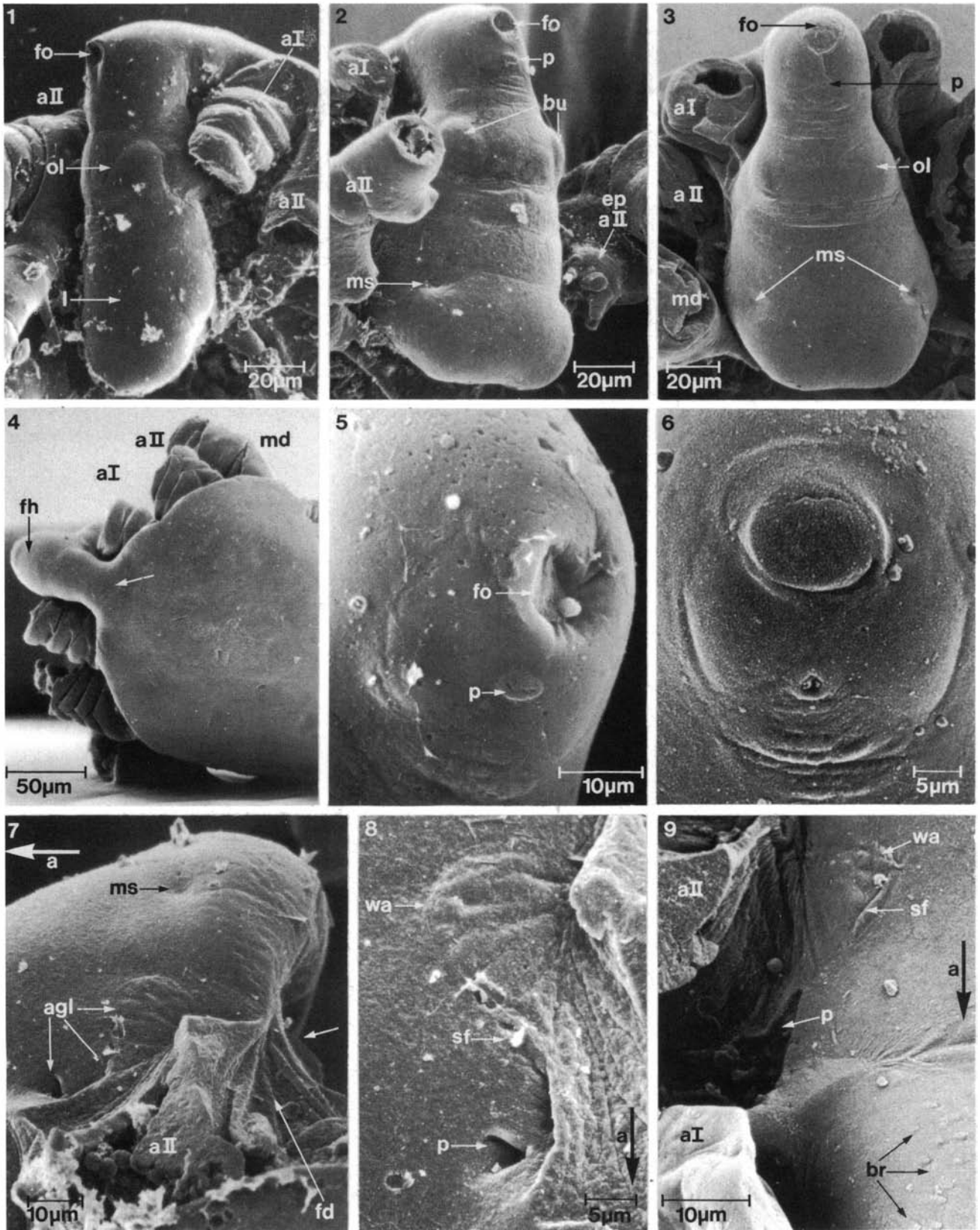
Plate 5

Forehead, labrum, and antennal gland of *Skara minuta* n.sp.

☐ 1. ST 4108, UB 716: oblique-lateral view of the forehead and labrum – a large hole indicates the original position of the frontal organ (fo); *S. minuta* lacks the pore below the organ; the origin of the labrum (ol) is deeply recessed and limited by shallow furrows (compare with Pl. 4:1–3); the labrum is projected; its posterior end is widely rounded and covers the mouth region; laterally pilose folds (fd) run towards the origins of antenna and mandibula; in front of them the labrum is bulging (bu); the coxal endite of the mandibula (gn) points under the labrum. (Same specimen as in 2, 7.)

☐ 2. ST 4108, UB 716: similar view as in 1; here the frontal organ (fo) is entirely preserved (enlarged view in Fig. 7). (Same specimen as in 1, 7.)

☐ 3. ST 4055, UB 707: almost ventral view of the anterior part of the cephalon, slightly from posterior; the frontal organ is distally broken off and is visible as a hollow tube; the labrum is projecting from the body; its tip is slightly depressed; the left coxal endite of the antenna (ep aII) still bears its two clusters of setae: three short hairs anteriorly and four long ones posteriorly; the shovel-like mandibular gnathobase (gn) is directed abaxially, as if to push particles on the sternum (st) into the recessed mouth (detailed view in Pl. 16:7). (Same specimen as in Pl. 4:4; Pl. 2:10; Pl. 9:2; Pl. 13:7.)

☐ 4. ST 4055, UB 707: dorsal view of the anterior portion of the cephalon (compare with Pl. 4:4); the slender forehead is flanked by the well-preserved antennulae and antennae which are extended far anteriorly; antenna with a scale (sc) at its base. (Same specimen as in 3.)

☐ 5. ST 3935, UB 717: view of the forehead; the specimen is roughly phosphatized, a hole at the forehead indicates the former position of the frontal organ; note the straight dorsal line of the slender forehead.

☐ 6. ST 3022, UB 705: lateral view of the labrum at the level of the antenna; the pore (p) of the antennal gland and the sickle-shaped furrow (sf) are situated in front of the lateral bulge (bu) which may represent a similar structure as the walled area in *S. anulata;* the pilose folds can be seen on the lower left running towards the posterolateral end of the labrum (compare with Pl. 4:7–9). (Same specimen as in Pl. 2:8; Pl. 3:3; Pl. 10:6; Pl. 15:7; Pl. 16:3.)

☐ 7. ST 4108, UB 716: enlarged view of the tube-shaped frontal organ. (Same specimen as in 1, 2.)
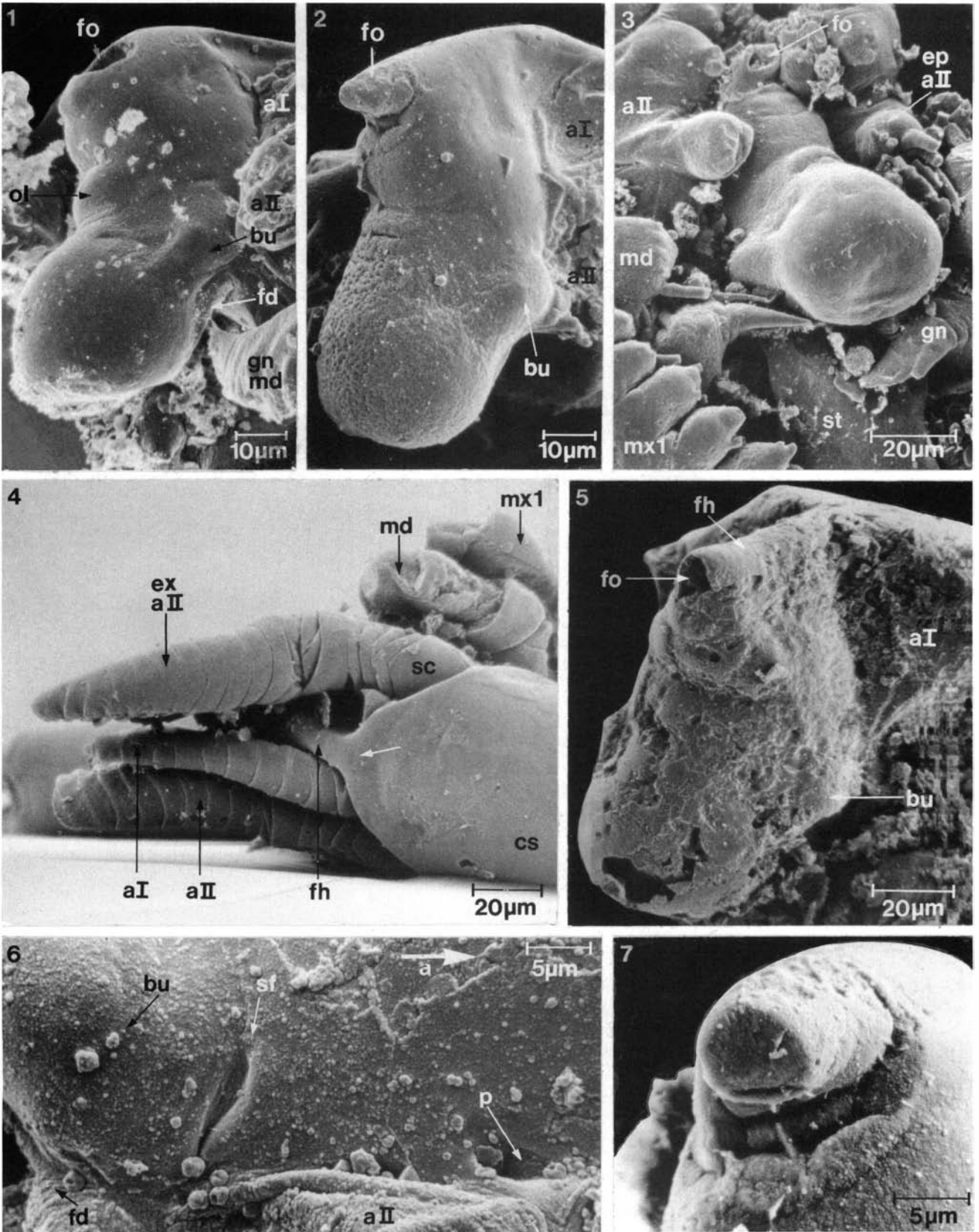
Plate 6

Mouth area and sternum of both species.

☐ 1. *S. anulata,* ST 4005, UB 698: posterior view of the anterior part; the labrum is caudally broken off; its cavity is partly filled with coarse-grained phosphatic matter; the appendages are poorly preserved, the endites (ep) of left antenna, mandibula and maxillula point toward the mouth (m); the sternum (st) is anteriorly broad and recessed, behind the mandibulae, however, tapering markedly. (Same specimen as in Pl. 1:8.)

☐ 2. *S. anulata,* ST 3559, UB 695: view of the sternum; the long setae of the antennal coxal endite (ep aII) and the masticatory spines of the mandibular coxal endites (msp) point under the labrum; corresponding to the posteriorly tapering sternum, the distance between the right and left limbs becomes successively smaller. (Same specimen as in Pl. 1:5; Pl. 7:1, 4, 7; Pl. 11:3.)

☐ 3. *S. anulata,* ST 3250, UB 718: view of the mouth area and sternum; numerous fine setulae (stl) stand around the mouth; the phosphatization is coarse and incomplete; white arrows emphasize the rounded margins of the polycentric phosphatization on labrum and sternum (see p. 00, and Pl. 16:2.)

☐ 4. *S. anulata,* ST 3095, UB 719: enlarged view into the recessed mouth opening; fine setulae cover the sternum, the folds at the posterolateral corners of the labrum and the lower surface of the latter (the innermost setulae in rows [arrows]); on the left side, one of the setae (s) of the antennal coxa points under the labrum. (Same specimen as in Pl. 8:5, 7; Pl. 12:6, 8.)

☐ 5. *S. minuta,* ST 3074, UB 709: ventral view of the cephalon and anterior portion of trunk; the appendages are poorly preserved; only the strong mandibular coxa is preserved, its gnathobase (gn) pointing to the mouth (see also Pl. 5:1, 3); the cuticle around the origins of the limbs and around the more sclerotized sternites is pliable; the ventral surface of trunk somite two is entirely membranous (mem), the surface of somite three in its anterior portion. (Same specimen see Pl. 6:6; Pl. 2:12; Pl. 9:5.)

☐ 6. *S. minuta,* ST 3074, UB 709: detailed view of Fig. 5, but slightly lateral view of the sternum; the mandibular gnathobase points under the labrum; as in *S. anulata,* the folds posterolateral of the labrum and the sternum are covered with numerous fine setulae; one of the shallow transverse furrows which indicate the division of the sternum (st) is emphasized by a white arrow; each sternite is slightly elevated, but medially depressed; the lateral margins are rounded. (Same specimen as in Pl. 6:5; Pl. 2:12; Pl. 9:5.)
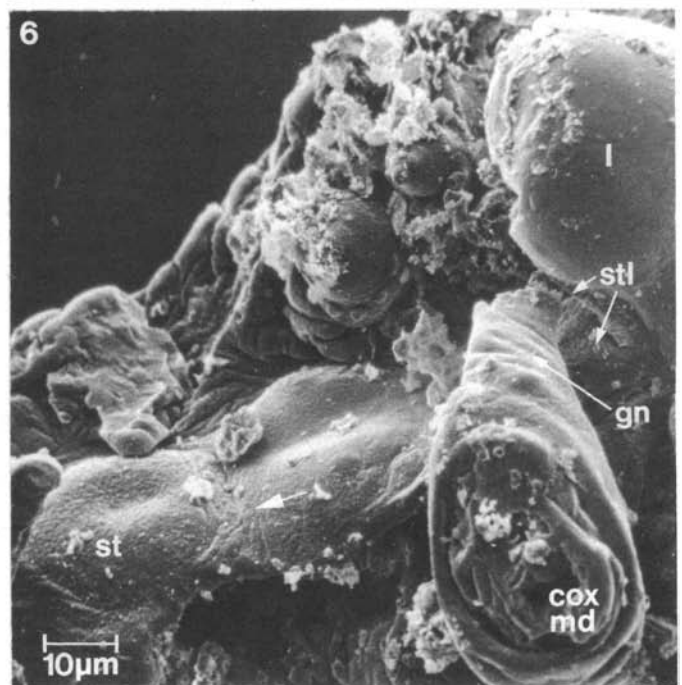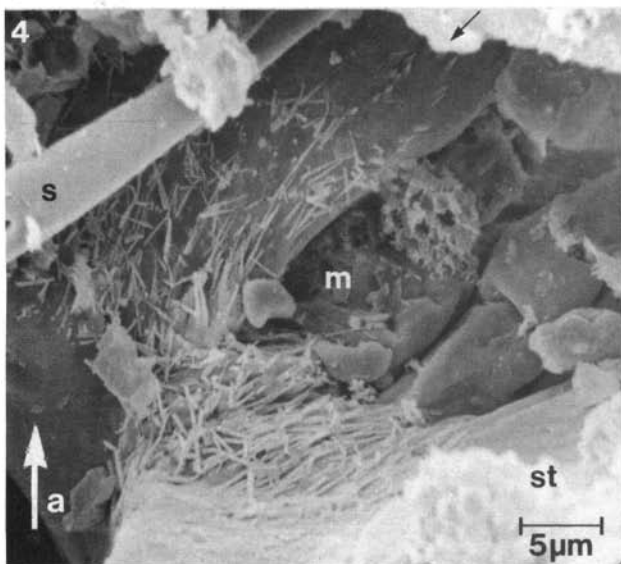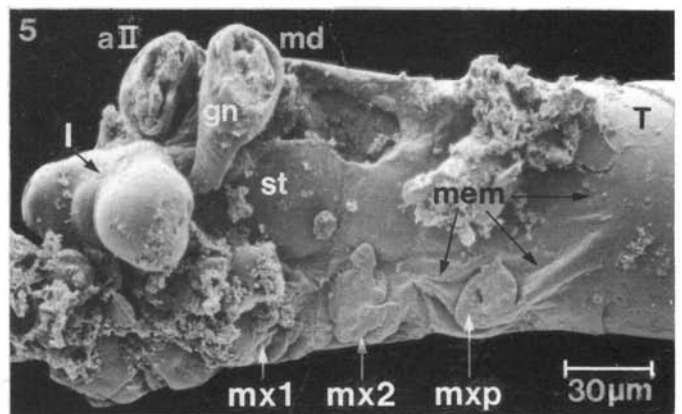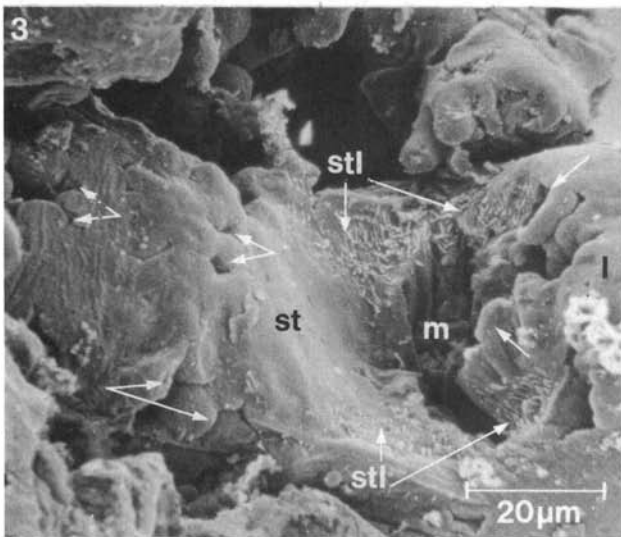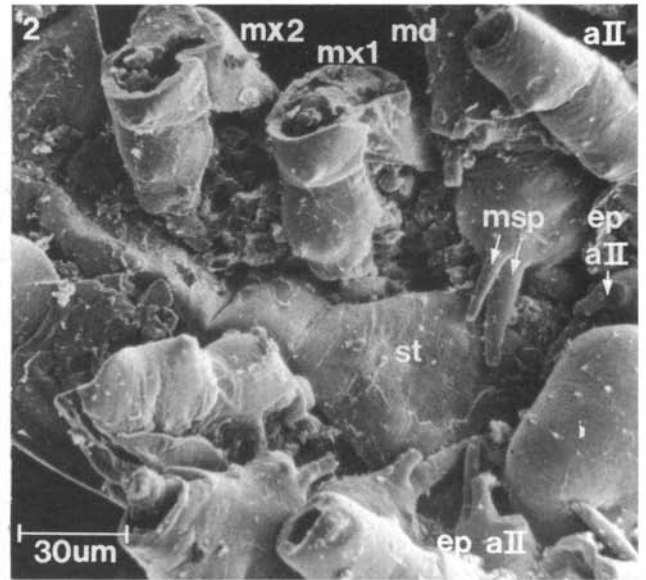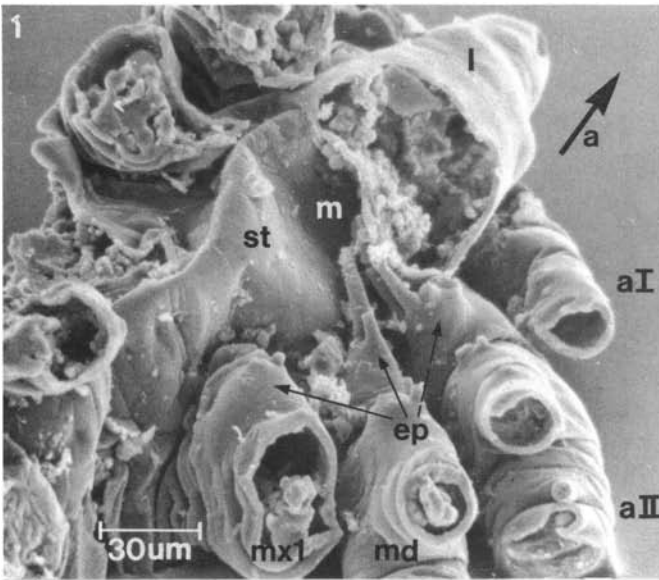
Plate 7

Appendages of *Skara anulata*. All figures except 2 and 7 presented upside down.

□ 1. ST 3559, UB 695: frontal view of the right antennula; the proximal segments are ring-like, the distal ones cylindrical; the most distal podomere bears four setae, the terminal two may have been very robust; the origins of the finer setae on the median surface are indicated by arrows. (Same specimen as in Pl. 7:4, 7; Pl. 1:5; Pl. 6:2; Pl. 11:3.)

□ 2. ST 4068, UB 692: view of the anterior surface of the right antenna, with its endopod (en) and exopod (ex); the tube-shaped endopod is three-segmented and arises from the medioterminally elongated basipod (bas); the joints between the endopodal segments and between endopod and basipod are only faint; the lateral surface of the endopods are covered by widely spaced single, or clusters of bristles (br); the exopod is composed of numerous ringlets each bearing one long, rigid seta which is directed posteriorly. (Same specimen as in Pl. 7:8; Pl. 1:2; Pl. 4:1; Pl. 15:1.)

□ 3. ST 2547, UB 648: view of the proximal part of the antenna, the entire mandibula, with the long exopodal setae preserved, and the maxillula; its robust, exopodal setae, however, appear to be thickened by secondary coating (see p. 6, and Pl. 16:6.)

□ 4. ST 3559, UB 695: view of the most distal part of antennal and mandibular exopods (detail of 8 below); the white arrows point to intercalated segments; the distal rim of each segment provides laterally a row of tiny bristles (br); the small apical podomere of the mandibular exopod terminates in a strong seta (s) which is broken off. (Same specimen as in Pl. 7:1, 7; Pl. 1:5; Pl. 6:2; Pl. 11:3.)

□ 5. ST 3562, UB 720: medial view of the elongated antennal coxal endite with its two groups of setae; the anterior cluster (a) is composed of two thin setae which point towards the labrum, the posterior group (b) comprises four strong pilose setae which are curved around the posterior end of the labrum and point to the mouth (m); numerous setulae (stl) cover the anterolateral surface of the sternum.

□ 6. ST 4155, UB 711: lateral view of the proximal portions of the three anteriormost appendages; antennae and mandibulae are provided with a scale-like sclerotization at their origins (sc); between scale and coxa several folds (fd) are developed to gain more flexibility. (Same specimen as in Pl. 3:4.)

□ 7. ST 3559, UB 695: medial view of the coxal endite of the right mandibula; two strong, setose masticatory spines (msp) arise from the median surface; just below the spines, the cuticle is covered by numerous fine setulae (stl), as on the sternum. (Same specimen as in Pl. 7:1, 4; Pl. 1:5; Pl. 6: 2; Pl. 11:3.)

□ 8. ST 4068, UB 692: frontolateral view of the forehead with origins of the antennulae, exopods of right antenna and mandibula. (Same specimen as in Pl. 7:2; Pl. 1:2; Pl. 4:1; Pl. 15:1.)
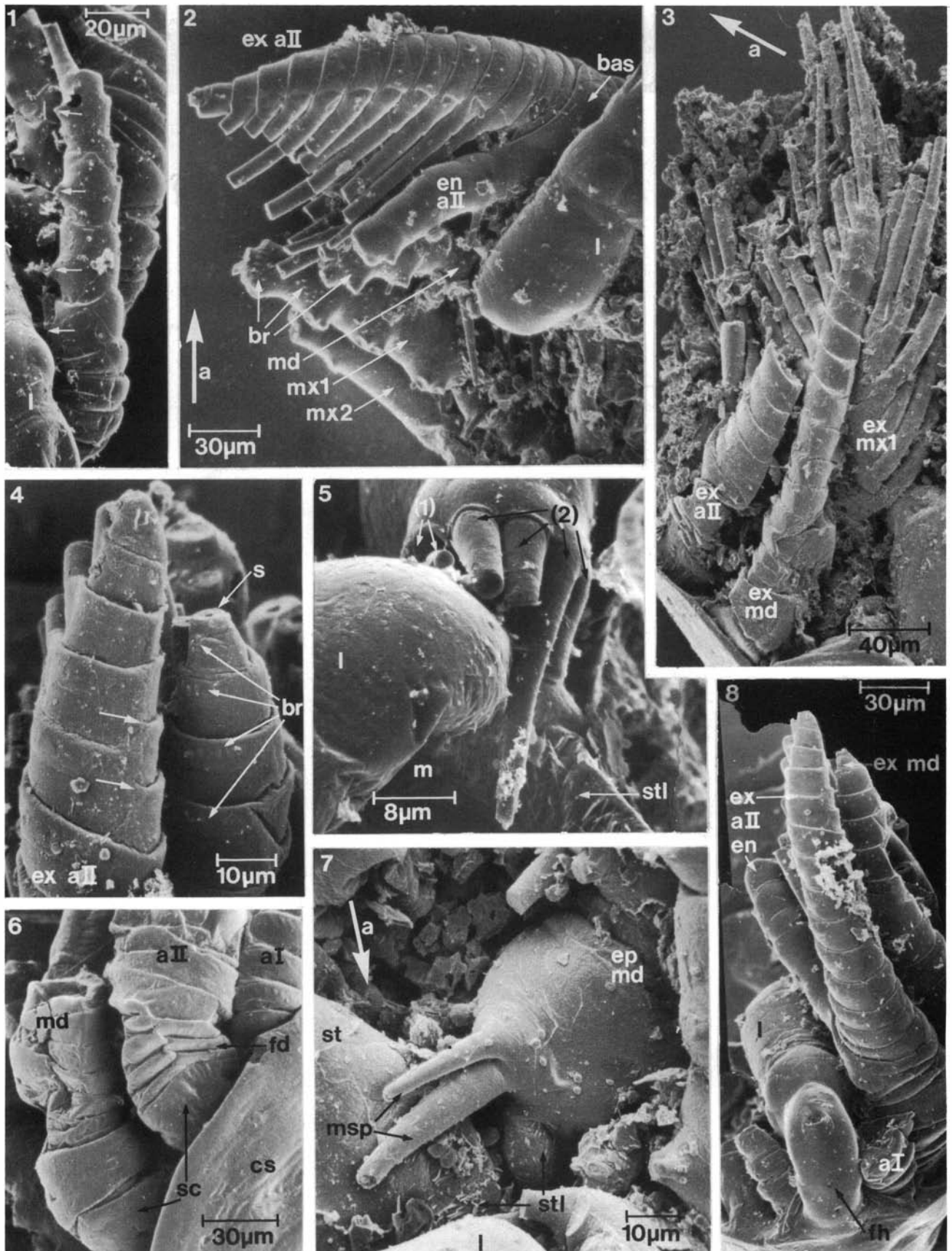
Plate 8

Appendages of *S. anulata*. All figures upside down.

☐ 1. ST 4153, UB 721: view of the anterior surfaces of right maxillula and maxilla; the soft cuticle of the shaft (sh) is anteriorly collapsed; the coxa (cox) is medially enlarged and provides three endites (ep); the basipod (bas) is elongated towards the three-segmented endopod; the triangular lateral portion of the basipod is separated from the anterior part by an axial furrow (white arrow); the strong marginal setae (s) of the exopod are broken off above their origins (compare with Pl. 7:3); the exopod of the maxillula is broken off. (Same specimen as in Pl. 17:3.)

☐ 2. ST 3027, UB 713: view of the median surfaces of the left maxillula and maxilla, with the origins of the strong setae (s) on endites (ep) and endopodal podomeres; the maxillula and the maxillar exopod are distally broken off, the maxilliped (mxp) is preserved only with its origins; widely spaced bristles cover the anterior surfaces of maxillula and maxilla (br). (Same specimen as in Pl. 3:6.)

☐ 3. ST 2172, UB 693: view of the right maxilla and left maxilliped; the furrow between endites and coxa (arrow) is caused by twisting of the limbs; some of the strong setae are preserved with their proximal portions (s). (Same specimen as in Pl. 1:3.)

☐ 4. ST 3560, UB 722: view of the right postmandibular limbs; the exopod of the maxillula is broken off; the thick origins of the marginal setae of the maxillar and maxillipedal exopods are well visible; arrows emphasize the joints between basipods and exopods.

☐ 5. ST 3095, UB 719: enlarged detail of 7, posterior view of the soft shaft and coxa of the maxillula; here the coxa is two-divided: the proximal portion with one endite medially is more sclerotized than the distal part which has two endites (compare with 1, where the coxa is uniform anteriorly) posteromedially, just below the proximal rim of the coxa, a pore (p) of unknown function is situated; muscle scars (ms) can be observed at different places. (Same specimen as in Pl. 8:7; Pl. 6:4; Pl. 12:6, 8.)

☐ 6. ST 4103, UB 723: view of the left postmandibular limbs; the soft shafts are thickly folded on the outer surface; the lateral portions of the basipods are bent backwards; the maxillular exopod is broken off; the subterminal seta on the medial rim of the maxillar exopod is indicated by a white arrow.

☐ 7. ST 3095, UB 719: posterior view of the right maxillula with origins of all median setae; the exopod is broken off; the joint between basipod and endopod is only weak; several widely spaced bristles (br) cover the posterior surface of the endopod (see also Pl. 7:1). (Same specimen as in Pl. 8:5; Pl. 6:4; Pl. 12:6, 8.)
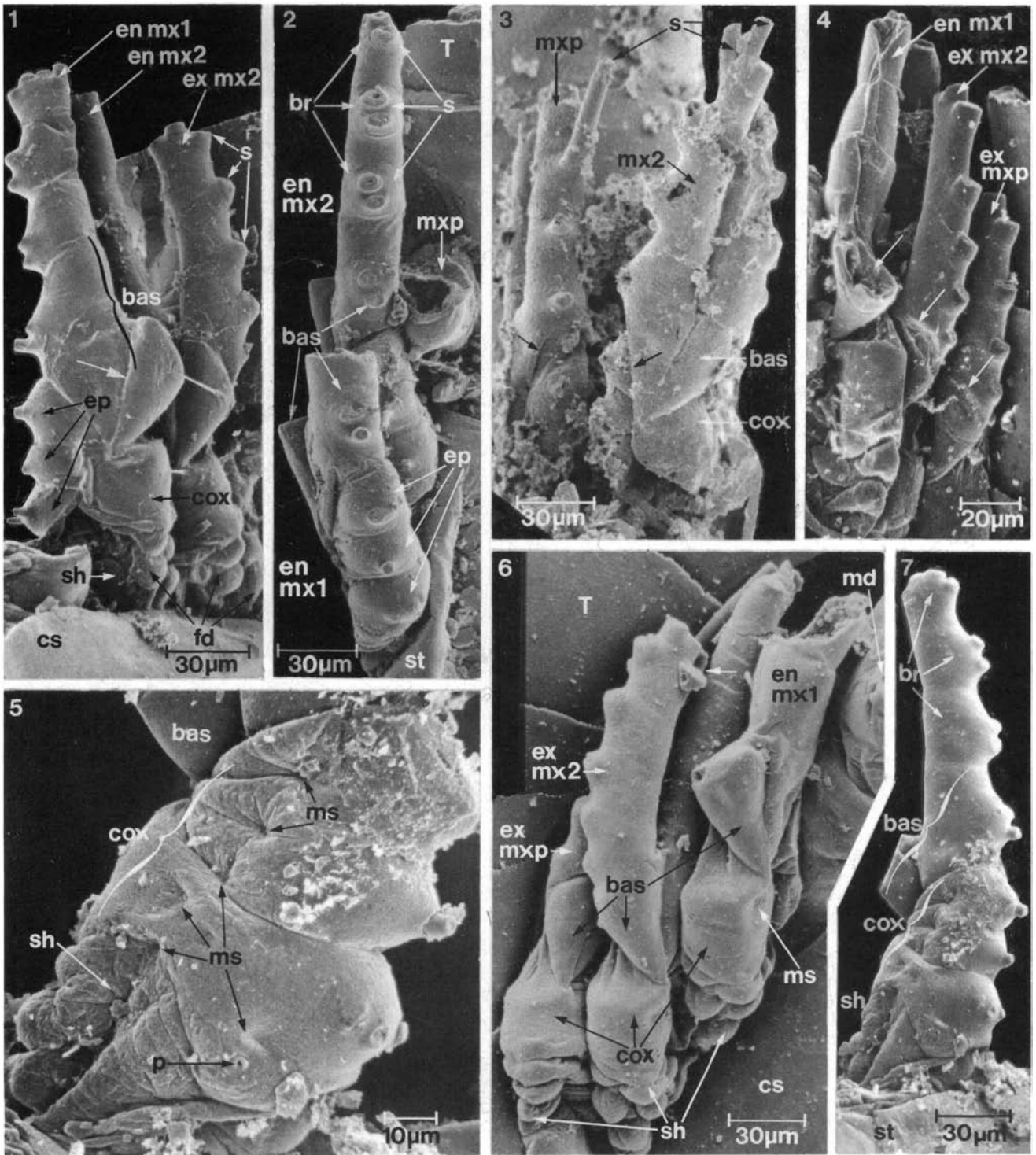
Plate 9

Appendages of *Skara minuta*. All figures except 4 presented upside down.

☐1. ST 2856, UB 647: anteriormost part of the cephalon with forehead (fh), distally broken antennula, and antenna. As in *S. anulata,* the antennal shaft has a scale (sc) on its outer surface: rows of tiny bristles (br) are developed on an antennular podomeres, as well as on the antenna; one of the muscle scars (ms) on the cephalic shield (cs) can be seen in the lower left. (Same specimen as in Pl. 9:6; Pl. 2:6; Pl. 10:4, 7; Pl. 11:4.)

☐2. ST 4055, UB 707: view of the left antennula, with the origin of one of the thick terminal setae, and antenna (aII). (Same specimen as in Pl. 2:10; Pl. 5.:3, 4; Pl. 13:7; Pl. 16:7.)

☐3. ST 2482, UB 706: anterior view of the left antenna; in contrast to *S. anulata* the basipod is not elongated mediodistally; thus, the inner ramus appears to be much shorter; the endopod terminates in two thick setae; the setae of the exopodal ringlets are preserved only with their broad shafts which are successively directed more anteriorly from proximal to distal. (Same specimen as in Pl. 2:9; Pl. 10:2.)

☐4. ST 3411, UB 702: ventral view of the insertions of all right appendages; the maxilliped (mxp) is entirely preserved; the sternum (st) is divided into sternites which have almost the same width each, are slightly elevated and have rounded lateral margins. (Same specimen as in Pl. 2:4; Pl. 10:5.)

☐5. ST 3074, UB 709: medial view of the mandibular coxa which is elevated into a flattened gnathobase (gn) terminating in one stronger and a row of tiny denticles (arrow). Note that, in contrast to this, two masticatory spines arise from the same endite in *S. anulata* (compare with Pl. 7:7). (Same specimen as in Pl. 2:12; Pl. 6:5, 6.)

☐6. ST 2856, UB 647: medial view of the antennal, mandibular, and proximal maxillular coxal endites; the antennal endite bears medially two clusters of setae: the anterior group (1) consists of three thin, the posterior group (2) of strong setae; probably a pilose hair (s?) was situated anterodistally at the base of the coxal endite of the mandibula; the sternum (st) is covered with fine setulae. (Same specimen as in Pl. 9:1; Pl. 2:6; Pl. 10:4, 7; Pl. 11:4.)

☐7. ST 2455, UB 724: lateral view of the antennal base with scale and several folds between scale and coxa. (Same specimen as in Pl. 10:3.)
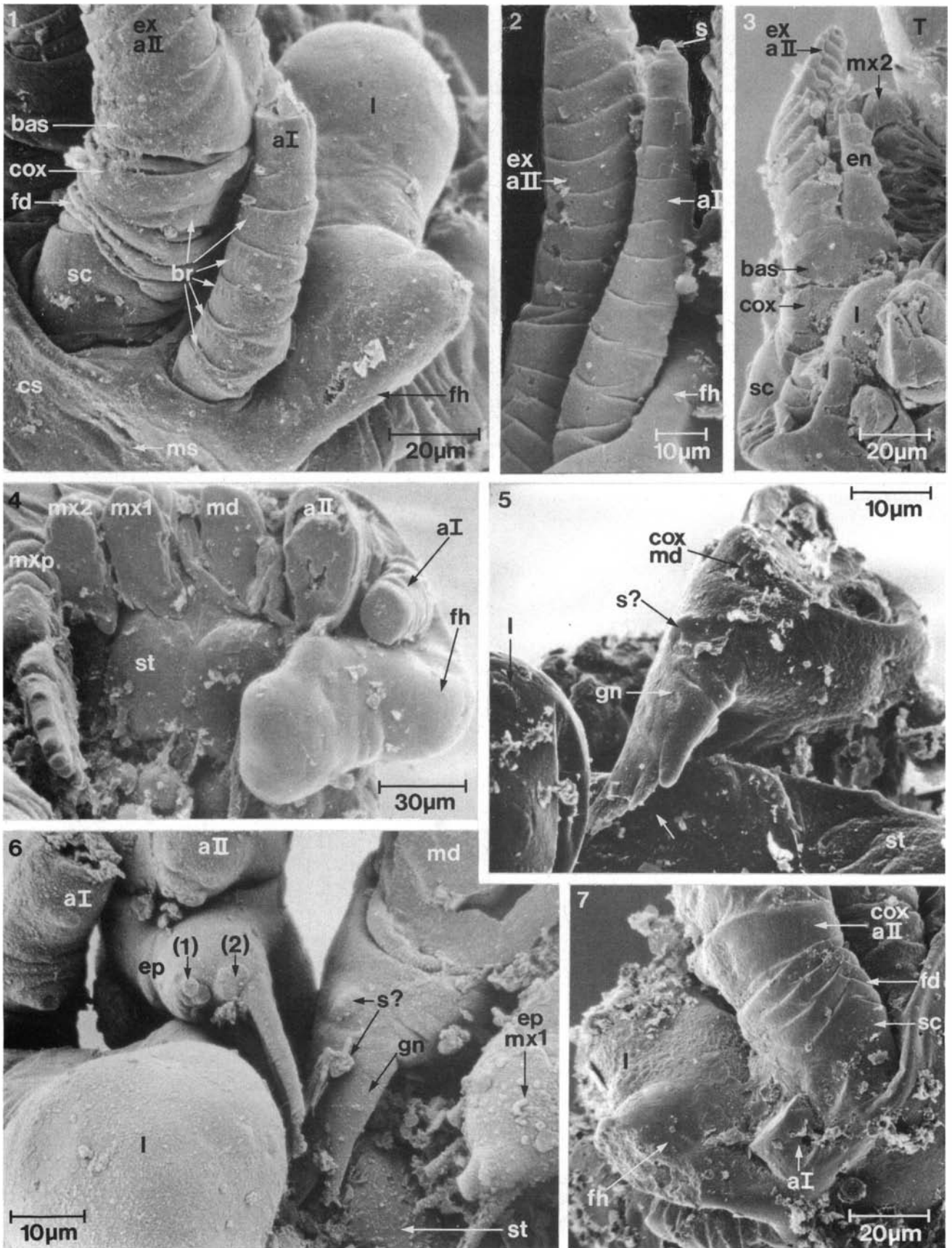
Plate 10

Appendages of *Skara minuta*.

☐ 1. ST 3412, UB 725: anterior view of the right maxilla which is coarsely phosphatized and covered with alien grains; the distal portion is still bearing some of the long marginal setae, even a few subordinate setulae (stl) are preserved.

☐ 2. ST 2482, UB 706: median view of the almost completely preserved enditic setae of the left maxilliped; the endites and proximal portions of the setae are covered with numerous setulae (stl); endopod and exopod of this limb are broken off. (Same specimen as in Pl. 2:9; Pl. 9:3.)

☐ 3. ST 2455, UB 724: ventral view of the right maxilla with setulae arising from its coxal endite; posteriorly, the enditic setae are adorned with at least one row of setulae; two globules of unknown origin are lying between the limbs (arrows) (see also Pl. 5:3; and Pl. 16:7). (Same specimen as in Pl. 9:7.)

☐ 4. ST 2856, UB 647: Median view of the right mandibula and maxillula, showing the arrangement of setae on endites and endopodal segments (detailed view of 7); posteromedially, the endites are elongated, tapering into a spine-like, pilose seta (s); anteriorly three or four pilose, mouthward curved setae are developed (one of them emphasized by a white arrow); these setae form a narrow sieve from proximal to distal. (Same specimen as in Pl. 10:7; Pl. 2:6; Pl. 9:1, 6; Pl. 11:4.)

☐ 5. ST 3411, UB 702: view of the anterior surface of the right maxilliped; the outer surface of the shaft (sh) bears thick folds; as in *S. anulata* the basipod is divided into two portions, however, mediodistally not elongated towards the three-segmented endopod; the triangular lateral portion bears the leaf-like exopod; its strong setae are preserved only with their origins. (Same specimen as in Pl. 2:4; Pl. 9:4.)

☐ 6. ST 3022, UB 705: frontal view of the maxillar protopod; the shaft is thickly folded; the coxa bears four endites (ep), in contrast to three on the maxillula. (Same specimen as in Pl. 2:8; Pl. 3:3; Pl. 5:6; Pl. 15:7; Pl. 16:3.)

☐ 7. ST 2856, UB 647: anterior view of all right postantennular limbs; the distal exopodal podomeres of antenna and mandibula are directed anteriomedially, whereas the proximal ones point posteriorly; some of the exites are broken off (smooth surface of fracture with sharp-edged borders); several enditic setae are preserved and point mouthward; several muscle scars (ms) can be seen on the antennal coxa. (Same specimen as in Pl. 10:4; Pl. 2:6; Pl. 9:1, 6; Pl. 11:4.)
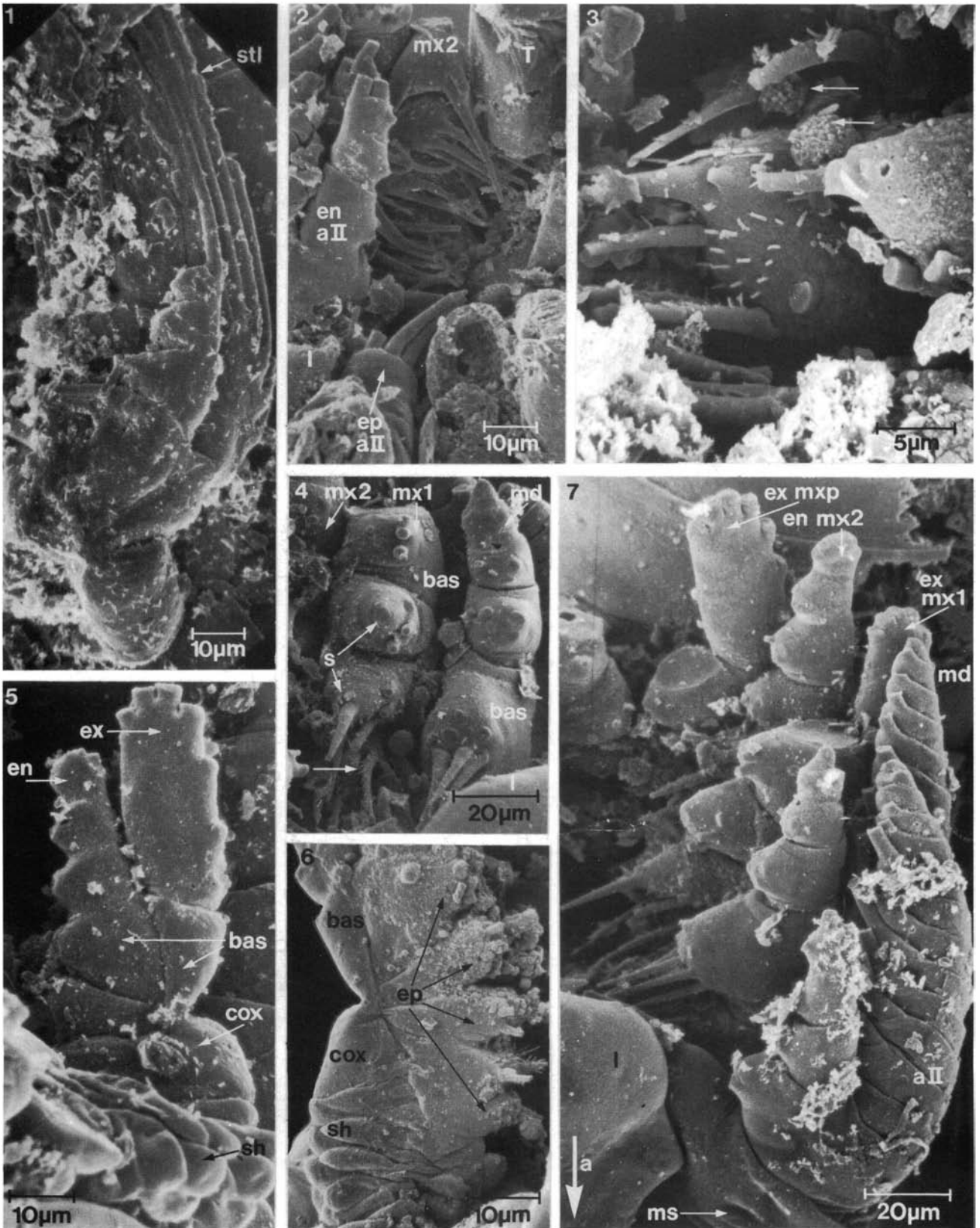
Plate 11

Filter apparatus of *Skara*.

☐ 1. *S. anulata*, ST 3023, UB 694: ventral view of the whole filter apparatus; the distal parts of the limbs are broken off (see also Pl. 1:4); all limbs enclose a narrow space which is anteriorly terminated by the labrum and the antennae, posteriorly by the maxillipeds; the latter limbs are almost axially positioned; the enditic setae point toward the mouth under the labrum; because the ventral cuticle of the trunk is not preserved, the steinkern (of the whole body cavity?) is uncovered. (Same specimen as in Pl. 11:2; Pl. 1:4; Pl. 15:3, 4, 5; Pl. 16:2.)

☐ 2. *S. anulata*, ST 3023, UB 694: enlarged detail of 1; posteriorly the labrum (1) is wrinkled; the long setae of the antennal coxal endite and the masticatory spines (msp) of the mandibulae reach to the middle of the sternum; setulae (stl) are preserved on the setae and on the sternum (st). (Same specimen as in Pl. 11:1; Pl. 1:4; Pl. 15:3, 4, 5; Pl. 16:2.)

☐ 3. *S. anulata*, ST 3559, UB 695: enlarged view of the mouth area; the mandibular masticatory spines are adorned with setulae; they collected the food from the sternum and stuffed it into the recessed, funnel-shaped mouth opening under the labrum. (Same specimen as in Pl. 1:5; Pl. 6:2; Pl. 7:1, 4, 7.)

☐ 4. *S. minuta*, ST 2856, UB 647: ventral view of the filter apparatus; as in *S. anulata,* all protopods are arranged around the sternum and enclosing a small space between the limbs; the setae of both antennal endites fit into the recess between lateral bulge and posterior end of the labrum, the setae are curved towards the mouth; setulae (stl) cover sternum, endites and setae. (Same specimen as in Pl. 2:6; Pl. 9:1, 6; Pl. 10:4, 7.)

☐ 5. *S. minuta*, ST 4159, UB 726: ventral view of the anterior body portion, comparable to 1; the forehead and the anteriormost limbs are distorted; right maxilliped except the distal parts of all limbs broken off; the origins of the enditic setae are, however, well visible; note the fine setulae (stl) on the coxal endites of the postmandibular limbs.
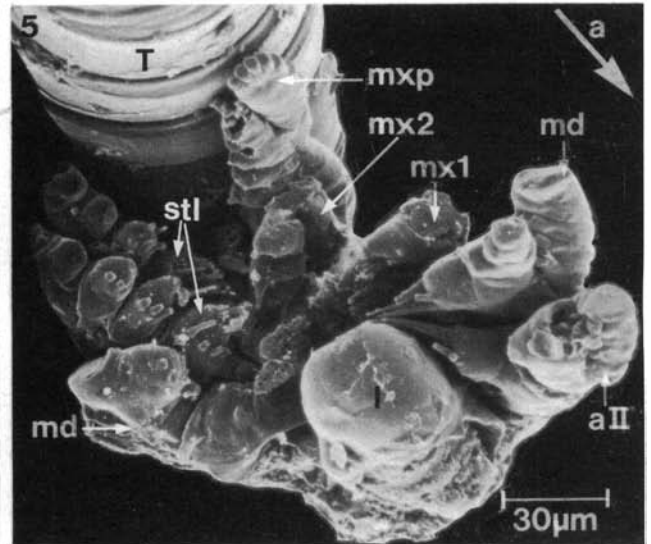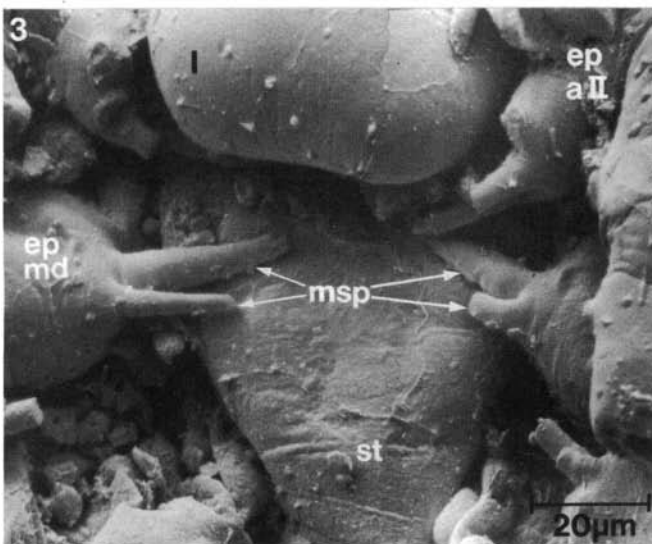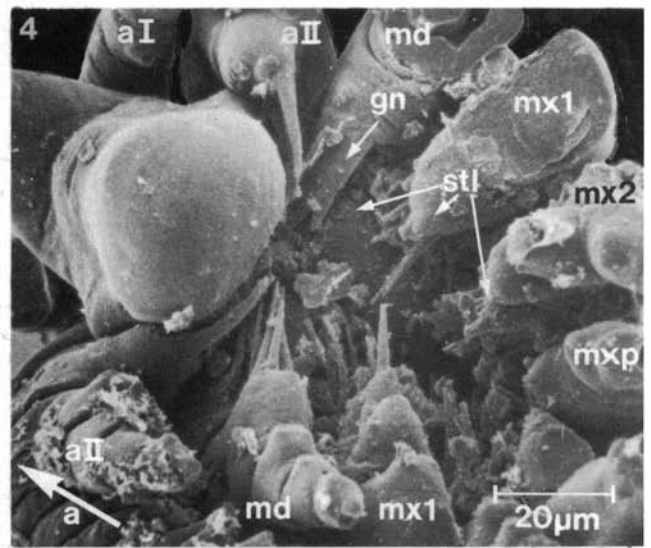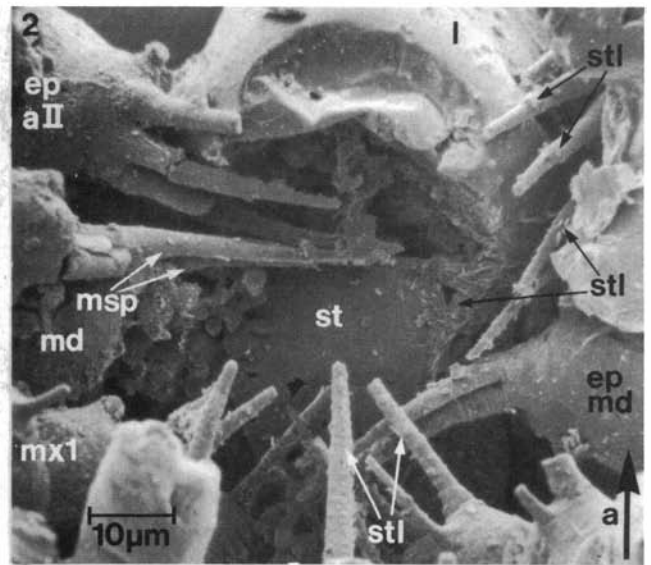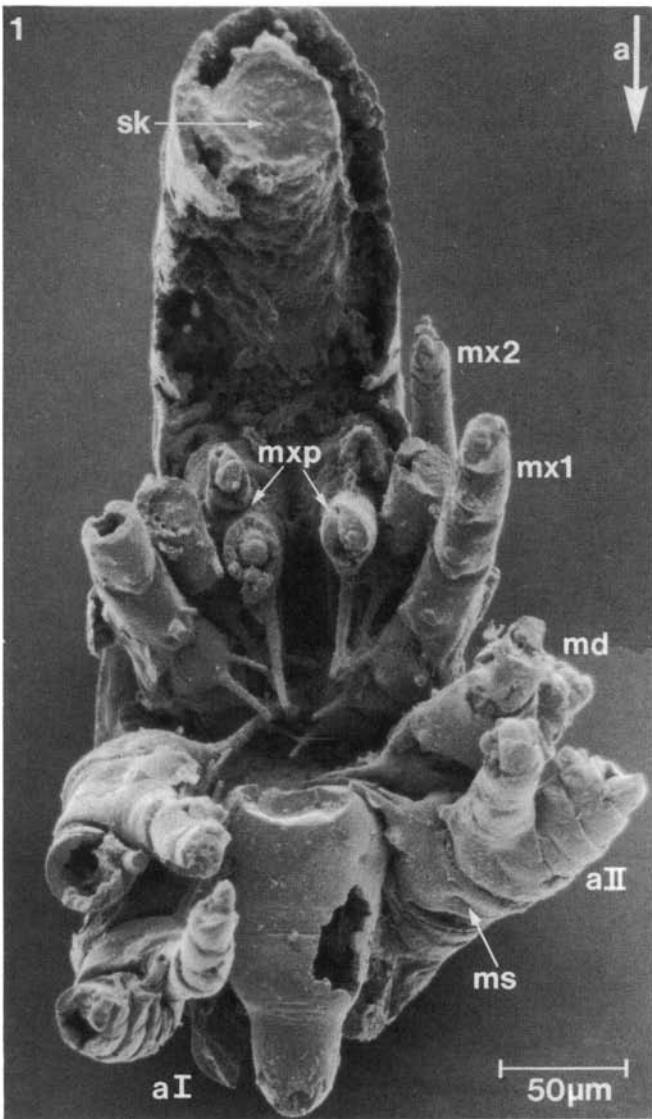
Plate 12

Skara anulata – details of the trunk.

□ 1. ST 2122, UB 646 (holotype): ventral view of somites seven to nine (ts7–ts9); ventrally of the lateral attachments points (ap) the caudal rims are backward extended and provided with three medial tooth-like spines; the fringes at these rims are only poorly preserved. (Same specimen as in Pl. 14:1, 2.)

□ 2. ST 4006, UB 727: ventral view of somites seven and eight with entirely preserved fringes (fr); the cuticle between the spines is softer and slightly collapsed. (Same specimen as in Pl. 12:3, 7; Pl. 16:4.)

□ 3. ST 4006, UB 727: enlarged view of fringes seen in 2; these are composed of a varying number of subordinate fibres resulting in different thicknesses. (Same specimen as in Pl. 12:2, 7; Pl. 16:4.)

□ 4. ST 4074, UB 728: oblique-ventral view of trunk somite one; both maxillipeds are broken off; the sternite between their insertions is rather small and surrounded by a pliable membrane which expanded backward to the concave anterior rim of somite two (here the recession at the front of somite two is filled with grains of contamination); the tergite (tg) of somite one is laterally attached to the succeeding trunk somite (ap); its ventrocaudal corner is soft and wrinkled (white arrow).

□ 5. ST 2035, UB 729: ventral view of somite one and two; here the recessed membranous anterior part of somite two (mem) is well preserved; both maxillipeds are broken off, and the lateral sides of the tergite are pressed against the sternite.

□ 6. ST 3095, UB 719: view of the attachment point between the tergites of somites one and two in high magnification. (Same specimen as in Pl. 12:8; Pl. 6:4; Pl. 8:5, 7.)

□ 7. ST 4006, UB 727: enlarged view of the median spine of somite eight; an inverted V-shaped row of setulae (stl) at the base of the spine is developed only on the right side; on the left side there are only some single bristles; the tip of the spine is adorned with numerous bristles (br); in the mid-line, below the tip, a thin seta (s) was positioned. (Same specimen as in Pl. 12:2, 3; Pl. 16:4.)

□ 8. ST 3095, UB 719: posterior view of the pliable and delicately folded arthrodial membrane between two succeeding trunk somites. (Same specimen as in Pl. 12:6; Pl. 6:4; Pl. 8:5, 7.)
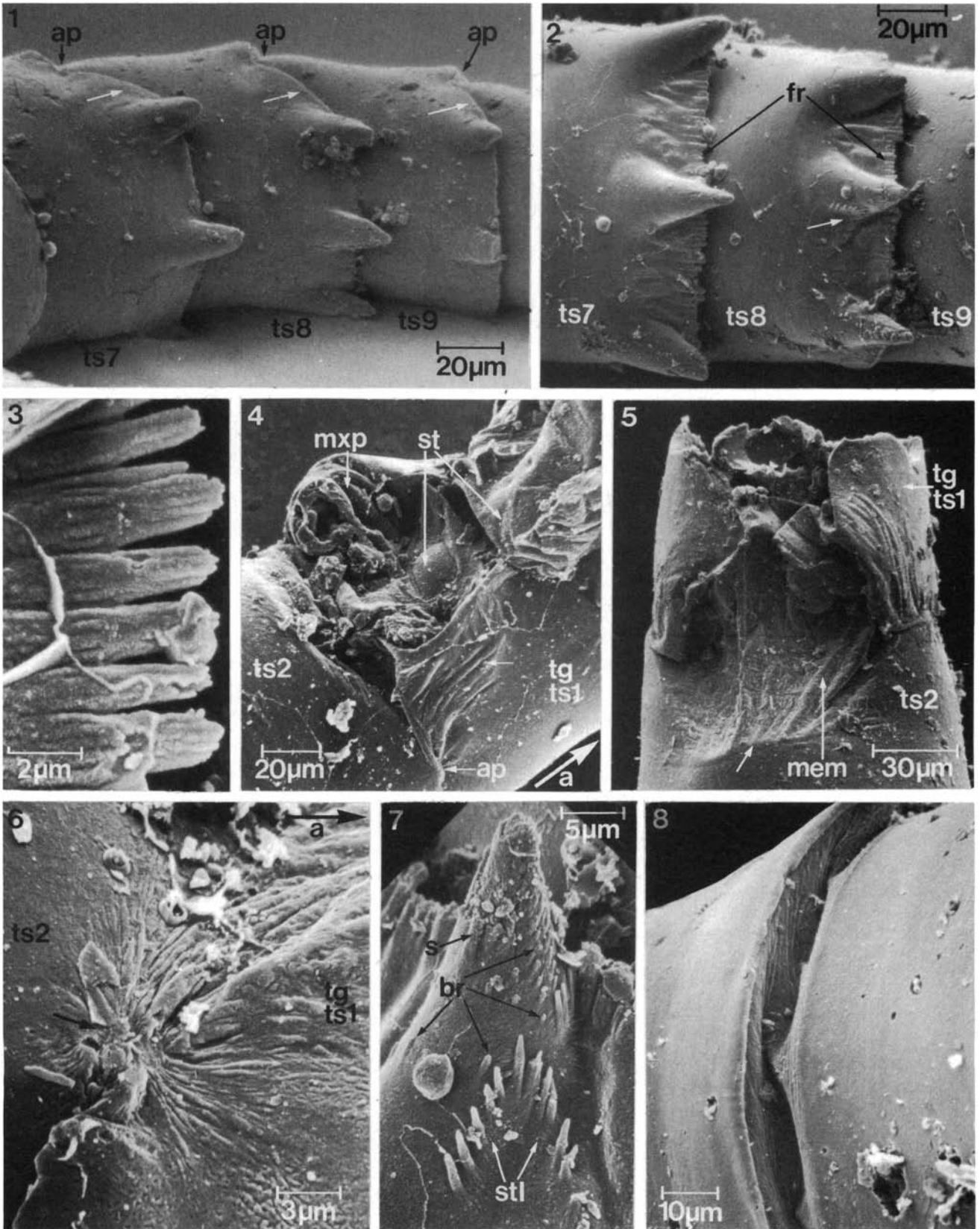
Plate 13

Skara minuta, details of the trunk.

☐ 1. ST 1956, UB 730: view of the strongly upward curved trunk between somites seven to ten (illustrated upside down); the ventral parts of the pliable arthrodial membranes (am) between the segments are widely expanded, laterally reaching to the attachment points (ap); a delicate layer of phosphatic matter covers the surface, visible only where partly broken off (white arrows); this layer also covered the arthrodial membranes and thus can be clearly identified as secondary coating, though scarcely diminishing details (see also Pl. 16:1, 2, 7); the posteriorly pointing spines are less strong than in *S. anulata*.

☐ 2. ST 2969, UB 731: view of the trunk from posterior (upside down) showing that telson and somites are almost circular in cross-section; as the diameter of the somites decreases successively, the segments fit together telescopically.

☐ 3. ST 2351, UB 732: enlarged view of the lateral spine of somite seven (see also 4); the row of fringes ends close to the spine which bears one or two rows of tiny bristles on its lateral surface. (Same specimen as in Pl. 13:4; Pl. 15:2; Pl. 17:6.)

☐ 4. ST 2351, UB 732: ventral view of somites seven to nine with spines at their ventrocaudal rims; in contrast to *S. anulata*, the median spine of each rim is less strong than the lateral ones; the fringes between the spines (arrow 1) are much finer than those distally of the lateral spines (arrow 2); a thin median hair (s) was developed on each spine, as in *S. anulata*. The spine, which is shown also in 3, is indicted by a white arrow. (Same specimen as in Pl. 13:3; Pl. 15:2; Pl. 17:1.)

☐ 5. ST 3076, UB 733: ventrolateral view of somites seven to nine; the space between the lateral spines and also the size of the spines decreases successively; due to rough phosphatization, only the thicker lateral fringes are presented (arrow). (Same specimen as in Pl. 14:9.)

☐ 6. ST 2573, UB 708: enlarged view of the fringes at the ventrocaudal rims of one of the more anterior trunk somites; the fringes have a length of more than 1/4 of the length of the following somite. (Same specimen as in Pl. 2:11.)

☐ 7. ST 4281, UB 747: ventral view of the posterior part of the cephalon and some trunk somites; all posterior limbs roughly but entirely preserved; the membranous area which extends backwards to the concave anterior rim of trunk somite three is deeply recessed (compare with Pl. 12:4, 5.)
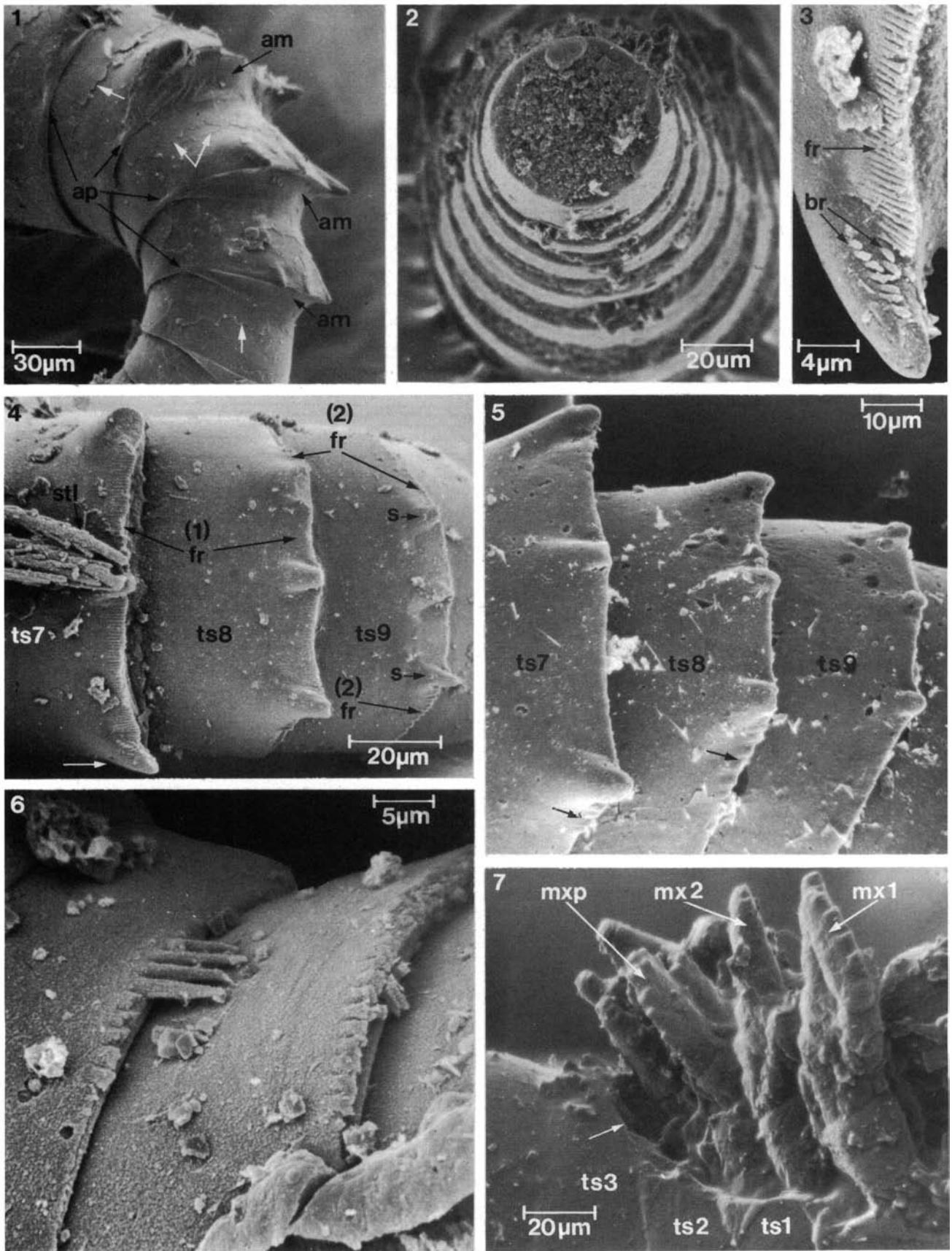
Plate 14

Telson, anus and furca.

□ 1. *Skara anulata*, ST 2122, UB 646 (holotype): posteroventral view of the telson (tel); only the cylindrical proximal furcal podomeres (pfp) are preserved; the cuticle between their origins is soft (arrow). (Same specimen as in Pl. 14:2; Pl. 12:1.)

□ 2. *S. anulata*, ST 2122, UB 646: dorsal view of the posterior end of the telson; the protruded anus (an) is surrounded by numerous fine folds; the distal rim of the proximal podomere bears a row of tiny bristles (br). (Same specimen as in Pl. 14:1; Pl. 12:1.)

□ 3. *S. minuta*, ST 3469, UB 703: view of the ventral surface of the completely preserved furca; on the right the spinule (spl) of the proximal podomere can be seen; the median podomere (mfp) is more than twice as long as the other two and has three long setae (s) medially; a tiny spinule is positioned between them. The apical podomere (tfp) terminates in two long, probably soft setae (s) which are attached to the body above roughly phosphatized appendages (app) in the lower right. (Same specimen as in Pl. 2:5.)

□ 4. *S. anulata*, ST 2373, UB 734: lateral view of the posterior end of telson and the proximal two upward pointing furcal podomeres; between the rami a spherical structure is trapped which probably constitutes a piece of faeces (a); the hole on the telson (b) is due to incomplete, polycentric phosphatization (indicated by its rounded margins).

□ 5. *S. minuta*, ST 4117, UB 735: view of the slightly collapsed posterior end of telson; the proximal podomeres of the furca are strongly upward bent, their surface is contaminated by alien crystals (cry); the spinules at the distal rims of the proximal furcal podomeres (pfp) are well visible; as in *S. anulata* the anus (an) is surrounded by delicate folds.

□ 6. *S. anulata*, ST 4115, UB 691: view of the posterior end of the telson; holes indicate the former position of the furcal rami; the folded area around the anus (an) has collapsed. (Same specimen as in Pl. 1:1; Pl. 4:3, 4.)

□ 7. *S. anulata*, ST 3103, UB 736: similar detail as in 6, but slightly more laterally; the anus (an) can be seen as a slit surrounded by numerous folds; only the proximal portion (pfp) of the right furcal ramus is present and strongly bent upwards.

□ 8. *S. anulata*, ST 4105, UB 737: ventral view of the incompletely phosphatized furcal rami; the second podomere (mfp) bears three setae (s) at its median surface.

□ 9. *S. minuta*, ST 3076, UB 733: enlarged view of the proximal podomere; at the sides of the spinule (spl), a group of about four bristles (br) is situated at the distal rim (in contrast, *S. anulata* has many more bristles but lacks the spinule; see also 2). (Same specimen as in Pl. 13:5.)
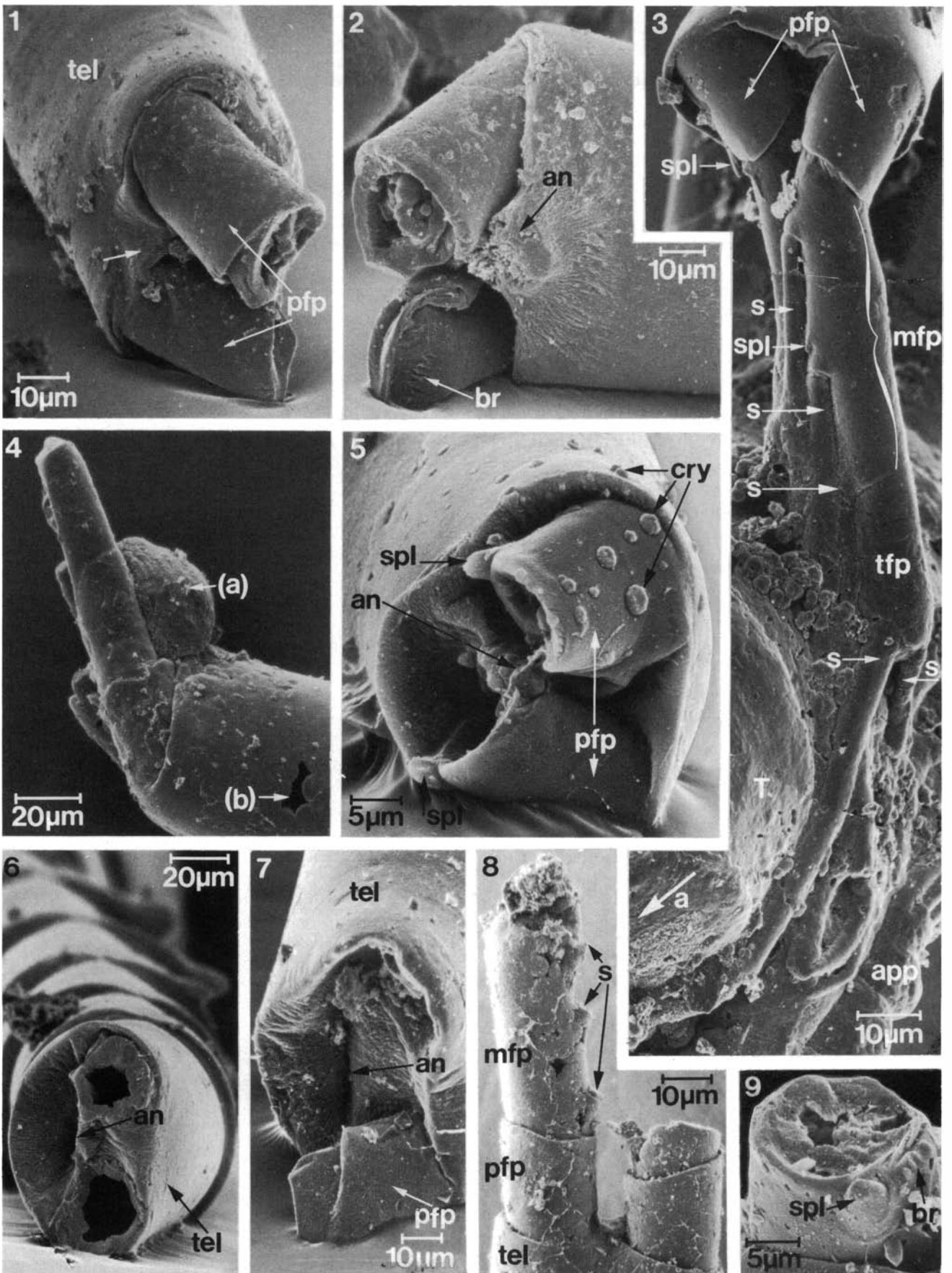
Plate 15

Setae, setulae, bristles and fringes.

☐ 1. *Skara anulata*, ST 4068, UB 692: view of the strong setae of the antennal exopod inserting in broad and pliable shafts (sh); the setae are distally broken off; the hollow spaces either may indicate the original position of the setae which are not preserved leaving a tube of secondary coating, or the setae were originally hollow; the surfaces of the endopods are adorned with a few bristles (br). (Same specimen as in Pl. 1:2; Pl. 4:1; Pl. 7:2, 8.)

☐ 2. *S. minuta*, ST 2351, UB 732: view of some of the marginal setae of the maxillipedal exopod which bear opposite rows of subordinate setulae (stl) in their distal portion; the setae reach backwards to the fringes (fr) of trunk segment seven. (Same specimen as in Pl. 13:3, 4; Pl. 17:1.)

☐ 3. *S. anulata*, ST 3023, UB 694: enlarged view of two of the pilose enditic setae of the antennal coxa; some setulae are arranged in a corona (white arrow), to the distal side of it the setulae (stl) are standing in two opposite rows; in the lower left, the setulae on the lateral folds behind the labrum can be observed. (Same specimen as in Pl. 15:4, 5; Pl. 1:4; Pl. 11:1, 2; Pl. 16:2.)

☐ 4. *S. anulata*, ST 3023, UB 694: enlarged view into the filter apparatus with its strong, pilose enditic setae (arrows) of the post-mandibular limbs. (Same specimen as in Pl. 15:3, 5; Pl. 1:4; Pl. 11:1, 2; Pl. 16:2.)

☐ 5. *S.anulata*, ST 3023, UB 694: view of one strong seta arising from the basipodal endite of the maxilliped in high magnification; this seta is adorned with four rows of distally pointing setulae. (Same specimen as in Pl. 15:3, 4; Pl. 1:4; Pl. 11:1, 2; Pl. 16:2.)

☐ 6. *S. anulata*, ST 3548, UB 697: enlarged view of the folded outer surface of the mandibula, between coxa and basipod; arrows point at rows of tiny bristles positioned just below each distal rim. (Same specimen see Pl. 1:7; Pl. 3:1; Pl. 4:2.)

☐ 7. *S. minuta*, ST 3022, UB 705: median view of the maxillar coxal endites; projecting setulae arise not only from the median surfaces but also from the posteromedian protrusions which taper towards their spine-like setae (arrows), the anteriorly situated, mouthward curved setae (s) are adorned with setulae on their posterior surface. (Same speicmen see Pl. 2:8; Pl. 3:3; Pl. 5:6; Pl. 10:6; Pl. 16:3.)
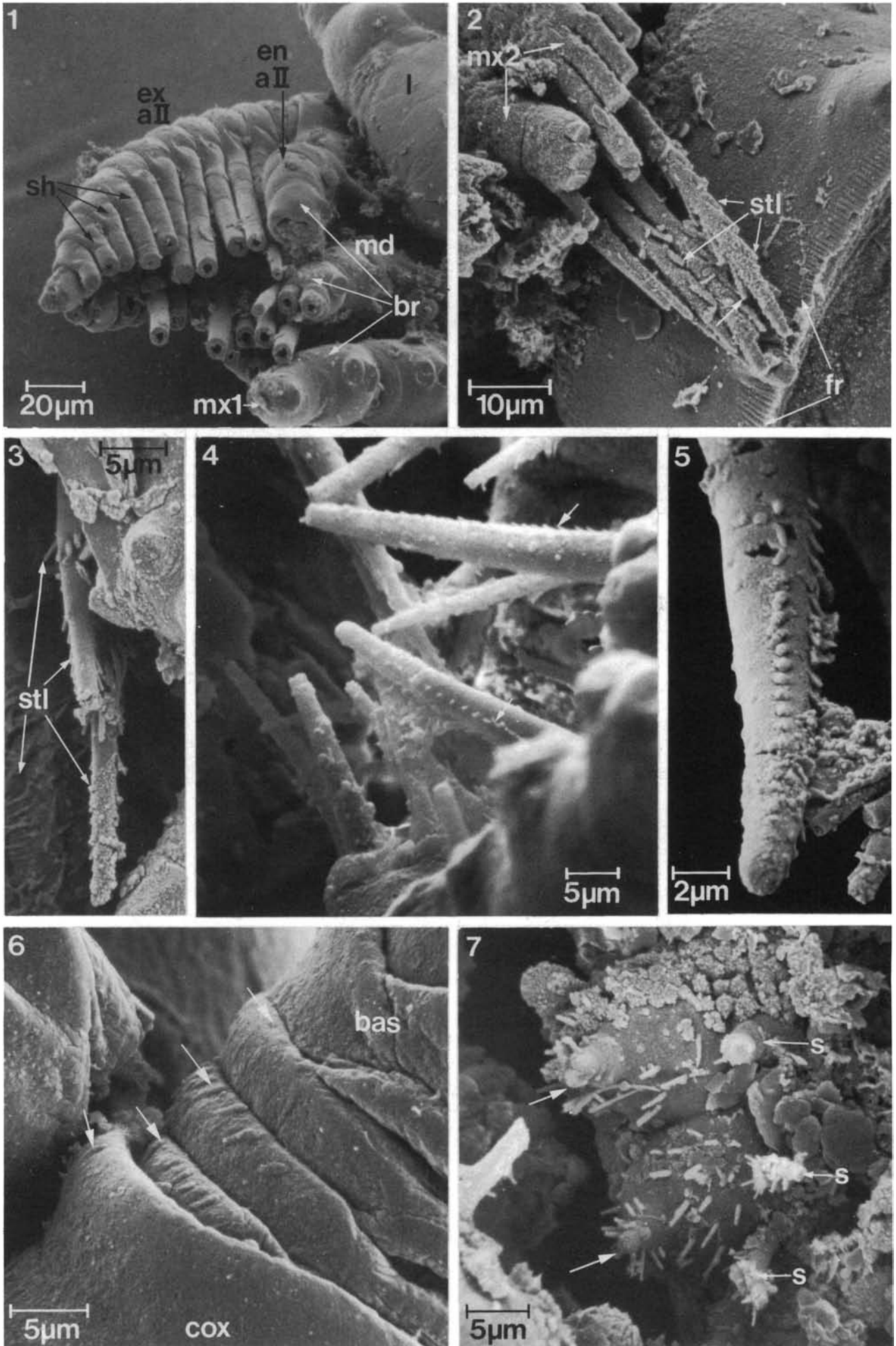
Plate 16

Phosphatization.

☐ 1. *Skara minuta*, ST 2852, UB 738: view of the anterior surface of mandibula and maxillula; the hollow spaces between secondary coatings (sec) and steinkerns (sk) of the limb cavities may represent the original cuticle which is not preserved (arrows); small phosphatic walls cover the surface which originated from phosphatic edges of calcite crystals (see p. 6 and Fig. 4).

☐ 2. *S. anulata*, ST 3023, UB 694: view of an aperture in the labrum which is caused by incomplete phosphatization; polycentric growth of the crystals results in margins around the holes having numerous small curves (arrows). (Same specimen as in Pl. 1:4; Pl. 11:1, 2: Pl. 15:3, 4, 5.)

☐ 3. *S. minuta*, ST 3022, UB 705: view of the distal part of the left maxilla, whereas the protopod is well preserved (see Pl. 10:6), the exopod is distally coated with rough phosphatic matter (sec) which blurs all details. (Same specimen as in Pl. 2:8; Pl. 3:3; Pl. 5:6; Pl. 10:6; Pl. 15:7.)

☐ 4. *S. anulata*, ST 4006, UB 727: enlarged view of the ventral surface of trunk somites eight and nine; small phosphatic walls (pw) depict the former position of calcite crystallites which have been etched away; the overgrowing of alien phosphatic particles (cry) by the walls has occurred after phosphatization of the fossil (see also 1). (Same specimen as in Pl. 12:2, 3, 7.)

☐ 5. *S. minuta*, ST 4027, UB 739: view of the trunk wall in high magnification; the crystal skeletons result from recrystallization of the deposited collophane.

☐ 6. *S. anulata*, ST 4149, UB 740: view of parts of the postmandibular limbs; the limb in the upper middle is well preserved, and its setae (s) have retained their original thickness; the limb below the former is covered with a thick secondary coating (sec) which has smoothened the segment borders and thickened the setae; their original thickness can still be observed at the surface of fracture (arrows).

☐ 7. *S. minuta*, ST 4055, UB 707: enlarged view of the mandibular gnathobase; the terminal denticles are smoothened by coarse phosphatization (arrows); the tiny setulae (stl), however, which arise from the distal surface of the shovel-like process can still be seen; the phosphatic globule (cry) in the upper middle most probably represents aggregated crystallites rather than a food particle (see also Pl. 10:3). (Same specimen see Pl. 2:10; Pl. 5:3, 4; Pl. 9:2; Pl. 13:7.)
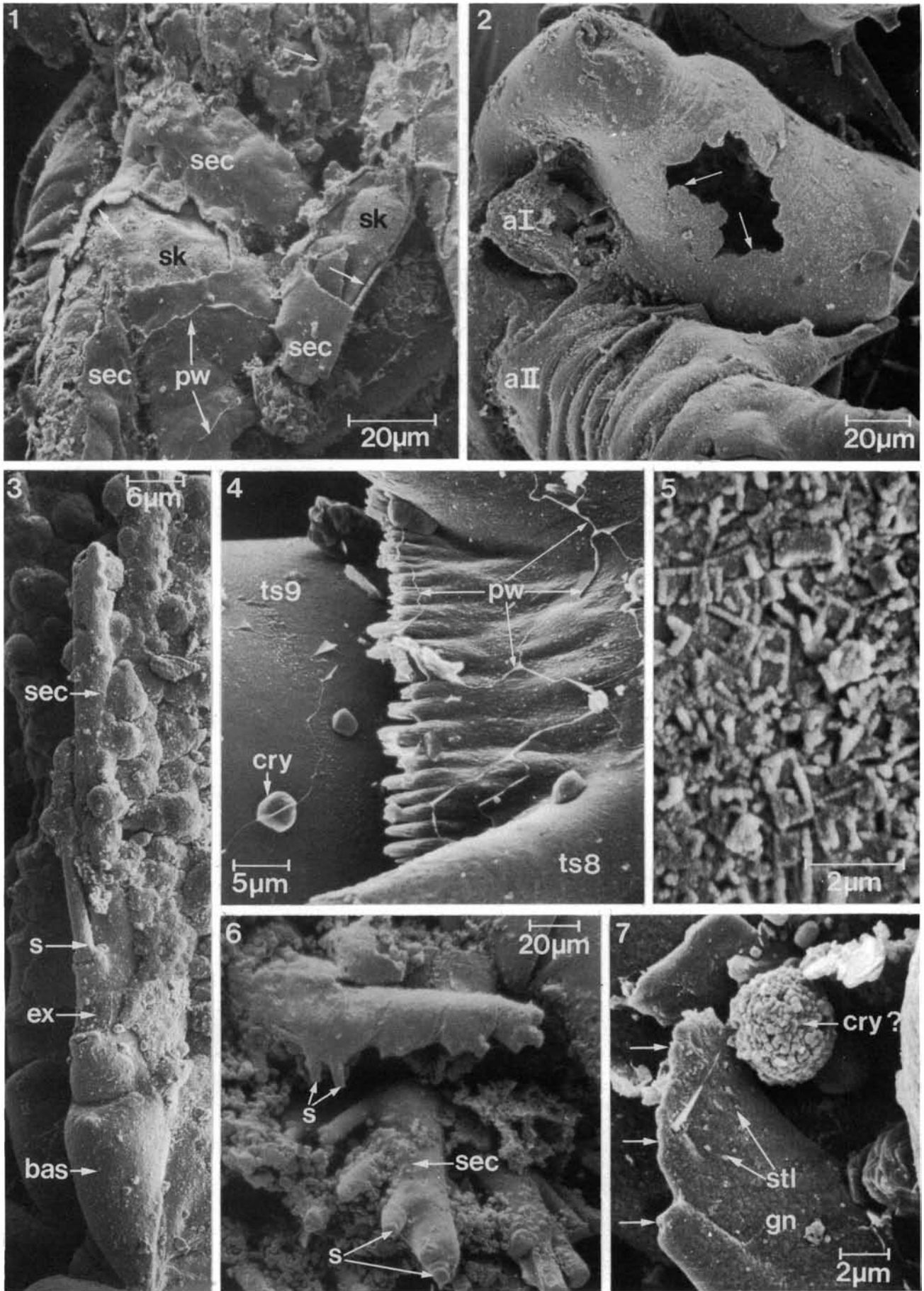
Plate 17

Phosphatization and supplement.

☐ 1. *S. minuta*, ST 3021, UB 704: view of a hole in the trunk which is caused by breakage, indicated by the sharp-edged margin; the wall is composed of at least three layers: a thin outer (1), a thick median (2), and a thin innermost layer (3); the cavity is filled with coarse phosphatic matter. (Same specimen as in Pl. 2:7.)

☐ 2. *S. minuta*, ST 2939, UB 741: view of a specimen which probably is enclosed in a coprolith, together with fragments of other unidentified arthropods (arrows).

☐ 3. *S. anulata*, ST 4153, UB 721: ventral view of the trunk with partly removed phosphatized cuticle; the uncovered cylindrical steinkern (sk) within the cavity probably represents the gut. (Same specimen as in Pl. 8:1.)

☐ 4. *S. minuta*, ST 3078, UB 742: view of a hole in the trunk which is caused by breakage; the steinkern fills the cavity almost entirely, and the space between wall and the annulate steinkern is only small; however, the annulations (black arrows) do not correspond with the segmentation of the trunk (white arrows); it is probable that the annulations on the steinkern result from shrinking of the original collophane during the process of crystallization.

☐ 5. *S. anulata*, ST 3544, UB 743: view of the posterior surface of the maxillular protopod; a pore (p) can be seen posteromedially between shaft and coxa (compare with Pl. 8:5).

☐ 6. *S. minuta*, ST 2351, UB 732: lateral view; the posterior appendages and distal setae are preserved, lying close to the spines of somite seven to nine (ts7–9); the anterior limbs are distally broken off. (Same specimen as in Pl. 13:3, 4; Pl. 15:2.)
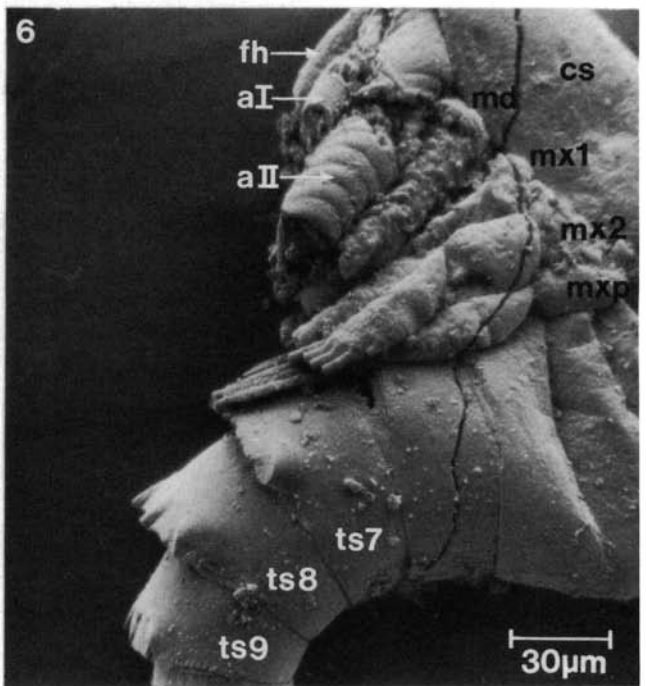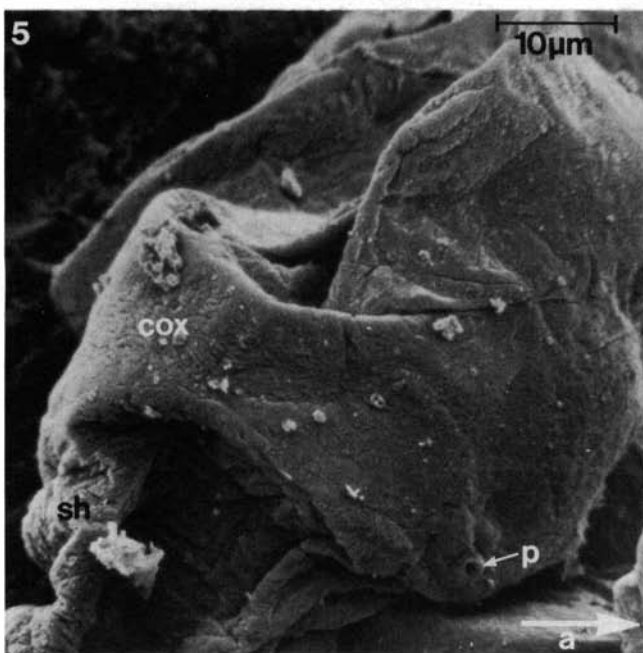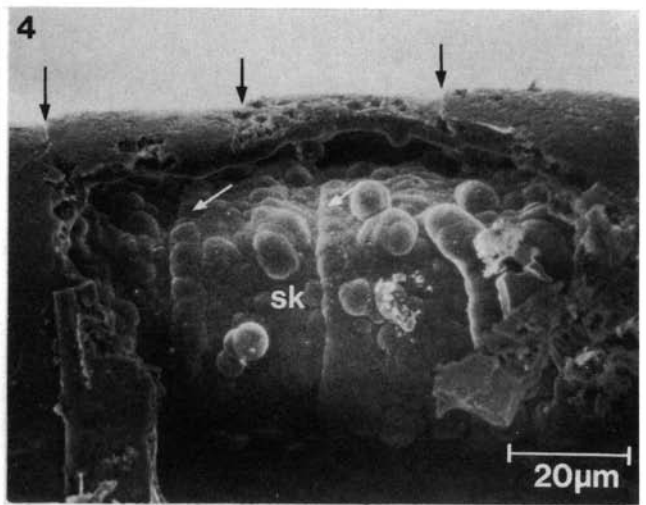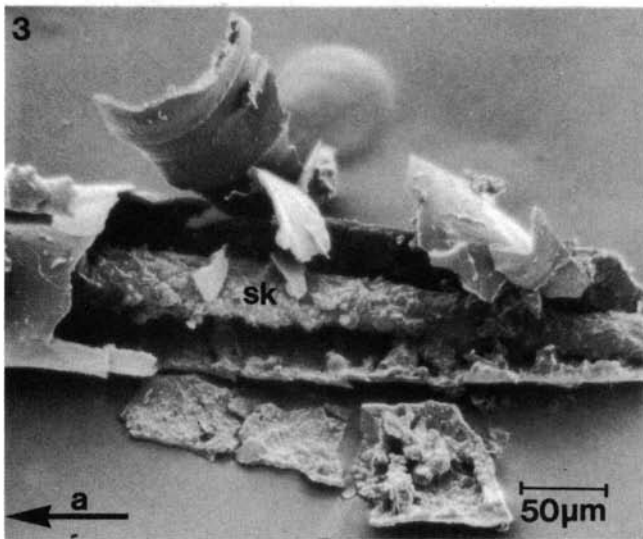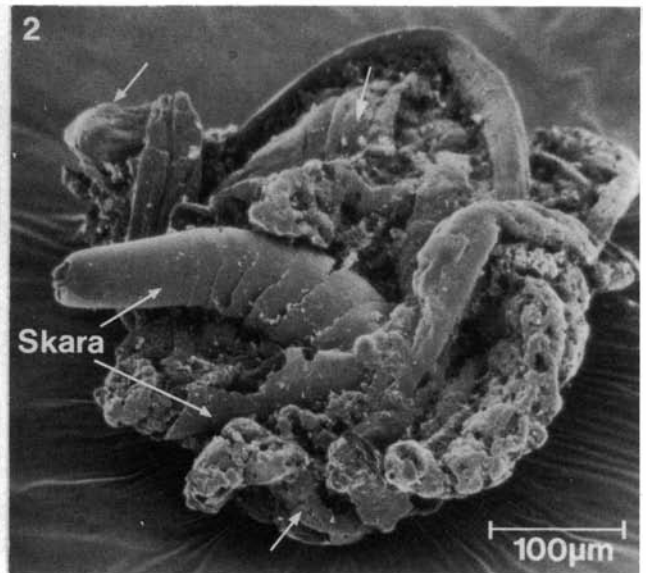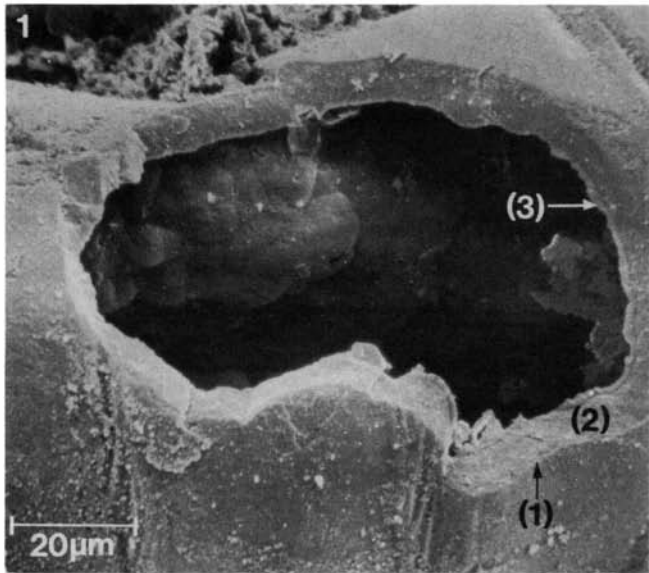
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Lindström, M. 1971: Lower Ordovician conodonts of Europe. *In* Sweet, W. C. & Bergström, S. M. (eds.): Symposium on conodont biostratigraphy. *Geological Society of America, Memoir 127,* 21–61.

Popov, L. E. (Попов, Л. Е.) 1975: Беззамковые брахиоподы из среднего ордовика хребта Чингиз. [Inarticulate brachiopods from the Middle Ordovician of the Chingiz Range.] *Палеонтологический журнал 1975:4,* 32–41.

Rudwick, M. J. S. 1970: *Living and Fossil Brachiopods.* 199 pp. Hutchinson, London.

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FOSSILS AND STRATA